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A new review of the Western Indian Ocean genus *Danais* (Rubiaceae: Danaideae), with seven new species from Madagascar

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Abstract

TAYLOR, C.M., S. RAZAFIMANDIMBISON, M.W. CALLMANDER & H.H. SCHMIDT (2024). A new review of the Western Indian Ocean genus *Danais* (Rubiaceae: Danaideae), with seven new species from Madagascar. *Candollea* 79: 235–276. In English, English abstract. DOI: <http://dx.doi.org/10.15553/c2020v792a3>

Danais Comm. ex Vent. (Rubiaceae) comprises about 49 species in Madagascar, the Mascarenes, and East Africa. A new species taxonomy is presented here, with an updated description and key to all *Danais* species, details of taxonomic changes, and lectotypifications. Four previously described species that were excluded from *Danais* are reinstated here: *D. aptera* Wedd. ex Homolle, *D. baccata* Homolle, *D. coerulea* Homolle ex Cavaco, and *Sabicea verticillata* Wernham under the replacement name *Danais confusa* C.M. Taylor. Identities and circumscriptions of some previously described *Danais* species are revised. The taxonomic circumscription of *D. aurantiaca* Baker is narrowed by the separation of a new species, *D. reticulata* C.M. Taylor; *D. cernua* Baker is diagnosed here by some different characters; *D. fragrans* (Lam.) Pers. in the Mascarenes is separated from plants of Madagascar formerly included in this species, now named *D. lyallii* Baker; *D. longipedunculata* Homolle and *D. masoalana* C.M. Taylor are no longer distinguishable and are synonymized; *D. nigra* Homolle is narrowed by the separation of the new species *D. puffiana* Razafim. & C.M. Taylor; *D. perrieri* Homolle is distinct from *D. nigra* Homolle; and *D. terminalis* Boivin ex Drake is still poorly known, but its circumscription is clarified and narrowed. Seven new species of *Danais* are described: *D. coriacea* C.M. Taylor, *D. gracilis* C.M. Taylor, *D. ovata* C.M. Taylor, *D. puffiana* Razafim. & C.M. Taylor, *D. reticulata*, *D. sambiranensis* C.M. Taylor, and *D. schatzii* C.M. Taylor. All the new species are threatened using the IUCN Red List Criteria: two are preliminarily assessed as “Critically Endangered” and five as “Endangered”.

Keywords

RUBIACEAE – Danaidae – *Danais* – Western Indian Ocean – East Africa – New species – Taxonomy – Typification

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Introduction

The genus *Danais* Comm. ex Vent. (Rubiaceae) includes 49 species found in the Western Indian Ocean [WIO] region (except the Seychelles). The new taxonomy of *Danais* here is outlined in Table 1, and a morphological overview of the genus is shown in Figures 1–3. Only one species is found outside the WIO, in a limited area in Tanzania in East Africa (*D. xanthorrhoea* (K. Schum.) Bremek.). The rest are restricted to the WIO islands: one species is endemic to the Comores (*D. comorensis* Drake), three are restricted to the Mascarenes (*D. corymbosa* Balf. f., *D. fragrans* (Lam.) Pers., *D. sulcata* Pers.), one is shared between the Comores and Madagascar (*D. humblotii* Homolle), and the rest are only found on Madagascar, where some species are widespread. *Danais* has a notable range of flower color and size (Fig. 1A–D), and presumably of pollination mode (BUCHNER & PUFF, 1993; PUFF & BUCHNER, 1994). Species of *Danais* are found in humid or wet vegetation from low to montane elevations, and in both well-preserved and disturbed habitats. The genus was revised by PUFF & BUCHNER (1994) but treated in other regions only in local floras (VERDCOURT, 1976; VERDCOURT et al., 1989). *Danais lyallii* Baker and *D. rhamnifolia* Baker are the most commonly collected and ecologically wide-ranging species of this genus on Madagascar and are both endemic.

Danais as delimited by PUFF & BUCHNER (1994) is characterized morphologically by its twining or lianescent, climbing habit; opposite or sometimes verticillate leaves; triangular to 2-lobed or multifid, generally interpetiolar and persistent stipules; terminal and/or axillary, bracteate, cymose inflorescences; distylous flowers with basically five calyx lobes, corolla lobes, and stamens (Fig. 2A, B); funnellform to salverform corollas with the lobes valvate-reduplicate in bud (Fig. 1B); bilobed stigmas (Fig. 1D, 3A); bilocular ovary with numerous ovules in each locule; capsular, subglobose, loculicidal, papery to woody fruits; and characteristically flattened, circular to elliptic or rhombic seeds. *Danais* was additionally characterized by them, in practice, by having consistently winged seeds. They did not cite that as a diagnostic feature, but their emphasis on this feature as a part of the morphology of *Danais* in their treatment and their exclusion of species based on their unwinged seeds made it clear they considered it diagnostic. However, as detailed below, our review of new specimens and molecular analyses found more variation than they saw in seed form in *Danais*, from winged to unwinged, and that feature is neither diagnostic nor characteristic of this genus.

Danais is similar to *Payera* Baill. and *Schismatoclada* Baker, which are both endemic to Madagascar; these three genera constitute the tribe *Danaideae* that belongs to the *Spermacoceae* alliance in the subfamily *Rubioideae* (KRÜGER et al., 2012; RAZAFIMANDIMBISON et al., 2022). BUCHNER & PUFF (1993) distinguished *Danais* within its tribe by its climbing habit, inflorescences that may sometimes be axillary, and loculicidal

capsules that are not prominently beaked; in contrast to an erect tree and shrub habit, consistently terminal inflorescences, and fruits that are prominently beaked and variously loculicidal or septicidal in *Payera* and *Schismatoclada*. Accordingly, they excluded four species from this genus, which they transferred to *Payera*: *Danais bakeriana* Homolle, *D. decaryi* Homolle, *D. madagascariensis* Cavaco, and *D. mandrarensis* Homolle ex Cavaco (Table 1; see also TAYLOR & COLLABORATORS, 2024). However, the fruits of some species of *Danais* can be considered shortly beaked (i.e. with the top part of the fruit, inside the persistent calyx limb, prolonged above the insertion point of the calyx limb), so this character is not completely diagnostic for *Danais* or at least subjective. In the other two *Danaideae* genera, the capsules are shortly beaked to semi-inferior and generally split open from the top, through the beak portion, to near or below the middle of the capsule body. In these, the pyramidal or tubular beak portion then splits again, and the seeds are released mainly through that beak portion. A few species of these other genera are similar to *Danais* in having relatively short beaks and similar loculicidal dehiscence, however. RAZAFIMANDIMBISON et al. (2022) studied these genera with molecular data and found *Danais* well supported as a monophyletic lineage sister to a poorly supported clade comprising *Payera* and *Schismatoclada*. They reviewed the morphology of these genera in light of the phylogenetic results and concluded that only the climbing habit is morphologically diagnostic for *Danais*.

Previous studies of *Danais*

Prior to the work of PUFF & BUCHNER (1994), *Danais* was only treated morphologically through descriptions of individual new species (Homolle, 1936) and in some regional floristic works (e.g. CAVACO, 1966; VERDCOURT, 1976; VERDCOURT et al., 1989). CAVACO (1966) presented a key to all the then-accepted species (Table 2). An unfortunate number of *Danais* species were described only from fruiting specimens (e.g. HOMOLLE, 1936), which are not fully informative as to the identity of the plant. PUFF (1991) first addressed the genus limits of *Danais*, BUCHNER & PUFF (1993) first detailed the overall morphology and anatomy of *Danais*, and PUFF & BUCHNER (1994) presented a taxonomic revision of the Madagascar and Comores species that forms the basis for the treatment here.

PUFF & BUCHNER (1994) recognized 26 species of *Danais* on Madagascar, including three new ones they described. They treated several of their species as notably variable morphologically and not clearly characterized (e.g. *D. cernua* Baker, *D. fragrans*), and their descriptions and comments indicated the difficulty of separating some of these. Overall, Puff & Buchner's taxonomic treatment was well analyzed but complicated to use, in large part because a number of *Danais* species were incompletely known and subtle to separate so

their key was not fully developed. This key was minimally detailed; relied heavily on vegetative features that are not fully diagnostic; did not include the full morphological ranges given in the descriptions for some species; omitted several species they reported from Madagascar; and keyed none of the *Danais* species from elsewhere. Puff & Buchner's species concepts and circumscriptions relied heavily on vegetative characters, notably the number of leaves per node, stipule form, details of stem and leaf pubescence, and arrangement of the leaf venation, even though they noted that these features were sometimes variable. They also detailed the flowers and fruits but did not analyze inflorescence arrangement as an informative character. Also problematic for Puff & Buchner's study was the description of a number of *Danais* species by earlier authors (e.g. HOMOLLE, 1936; CAVACO, 1966) based only on fruiting specimens that lacked any unique vegetative features. The fruits and seeds of most *Danais* species are generally similar and the seeds overlap among them in size, so those earlier-described species were difficult for them to fully characterize. Puff & Buchner excluded several previously described species from *Danais* (*Sabicea verticillata* Wernham, *Danais aptera* Homolle, *D. baccata* Homolle) based on their conclusion that these lacked winged seeds. They did not provide any satisfactory new generic placements for these species, however, which has created some confusion. They also separated three species (*D. baronii* Homolle, *D. coerulea* Homolle ex Cavaco, *D. comorensis* Drake) they considered "imperfectly known" (PUFF & BUCHNER, 1994: 62) and did not either exclude or accept them. They knew most of the Malagasy *Danais* species from very limited material and a number of types were incomplete, and these last three species could not then be matched with any additional specimens to understand them better.

PUFF & BUCHNER (1994) arranged the Madagascar species of *Danais* into several informal species groups, which were described or diagnosed only in the commentaries accompanying some of their species so the groups are not easily used for identification. Some of the species they considered related are quite similar (e.g. *D. microcarpa* Baker, *D. ligustrifolia* Baker, *D. rhamniflora* Baker (Fig. 1C), and *D. breviflora* Baker) especially in their flower form and color. However, some of the species they grouped have differing inflorescence arrangements, and they did not detail the fruits even when they seem to have considered those for their groupings. Puff & Buchner were not able to elucidate any larger patterns of relationships or morphological and ecological radiation in Malagasy *Danais*, though the presentation of their results suggests that may not have been a main objective of their study.

TAYLOR & ROGERS (2013) later published a short taxonomic study of *Danais* that mainly described six new species from Madagascar. These new species showed some morphological features that were newly reported, but they did not analyze the overall genus further.

The molecular studies of *Danaideae* by KRÜGER et al. (2012) and RAZAFIMANDIMBISON et al. (2022) sampled broadly from *Danais* and *Danaideae* and found *Danais* to be monophyletic; they did not analyze dating the origins of the group's genera and clades. Within their *Danais* phylogenies (KRÜGER et al., 2012; RAZAFIMANDIMBISON et al., 2022), *D. nigra* Homolle from the Sambirano Region (KOECHLIN et al., 1974) in north-western Madagascar was shown to be sister to a large clade containing the rest of the genus. This large clade encompassed three major lineages: the Malagasy-African-Comorian *Danais* clade; the Mascarene *Danais* clade; and the Malagasy *Danais* clade. These first two clades formed a monophyletic group that was sister to the last clade.

Studies by KRÜGER et al. (2012) and RAZAFIMANDIMBISON et al. (2022) shed significant light on the systematics of this genus and highlighted some problems. In particular, they found conflicting taxonomic characterizations for species recognized by PUFF & BUCHNER (1994), and that some of the individual species they studied included more than one lineage. Puff & Buchner suggested there may be ongoing hybridization in *Danais*, but the confused morphological characterizations of some of their species circumscriptions were so fundamental that this needs to be evaluated again after the limits and characters of these species are revised. Notably, KRÜGER et al. (2012) concluded that PUFF & BUCHNER's (1994) circumscription of *D. fragrans* included two distinct lineages: one on Mauritius, where the type of that name was collected, and the other on Madagascar. They treated these in their analysis as "*Danais fragrans* 1", for the plants from Mauritius, and "*Danais fragrans* 2" and "*Danais fragrans* 3", with these last both from Madagascar and sister to each other. They concluded that the Malagasy plants of *D. fragrans* should probably be separated from *D. fragrans* and named *D. lyallii* Baker but did not publish a formal taxonomic statement for this. They did later adopt the name *D. lyallii* for the Malagasy plants of this group (RAZAFIMANDIMBISON et al., 2022; Fig. 3C), with reference to the previous study but no taxonomic details. The plants of PUFF & BUCHNER's (1994) *D. fragrans* are reviewed here morphologically and in the context of their results, and the separation of the two species they treated is formalized.

RAZAFIMANDIMBISON et al. (2022) also found some of the apparently conspecific *Danais* specimens they analyzed were not retrieved as monophyletic or, in some cases, not even as closely related, and accordingly noted problems in some taxa of Madagascar with species monophyly. These results seem to be due variously to real, incompletely separated (or perhaps hybridizing) lineages, and to taxonomic limitations for identification of the samples. RAZAFIMANDIMBISON et al. (2022) were not able to include the rare and poorly documented species that PUFF & BUCHNER (1994) excluded from *Danais*, so that work remains for the future along with further taxonomic study of some samples they did analyze.

Two species described by previous authors that have been considered possibly related to *Danais* but have been unclear as to identity are studied here, *Sabicea verticillata* and *Danais chassallia* Poir. *Sabicea verticillata* is confirmed as a species of *Danais* and transferred to this genus, as detailed below under *D. confusa* C.M. Taylor. *Danais chassallia* was described from Mauritius but not mentioned again by later authors, including VERDCOURT et al. (1989) in their flora of that island. This name was based on a Philibert Commerson (1727–1773) collection that is a species of *Chassalia* Comm. ex Poir., not *Danais*, and may be the same collection on which that genus was based. Further study will be needed to clarify the identity of *D. chassallia* and is beyond the scope of this study of *Danais*.

This contribution updates the taxonomy and morphological characters of the almost exclusively WIO genus *Danais*, based on a new review of this group that incorporates recently collected specimens, molecular systematic data (KRÜGER et al., 2012; RAZAFIMANDIMBISON et al., 2022), and the study of type material recently curated in online images. This update significantly enlarges the size of the genus and clarifies its characteristics. This new taxonomic review of *Danais* (Table 1) benefits greatly from the extensive botanical exploration of Madagascar that has taken place in the last three decades. This contributes to our knowledge of the floristics and biodiversity of Madagascar and develops a basis for evolutionary studies in this group. Most of PUFF & BUCHNER's (1994) taxonomic conclusions are incorporated in this treatment, but details of that are updated and a few species they recognized are treated differently. In this article, we present a key to all the species of *Danais*, some new synonymies, clarification of the identities and circumscriptions of several taxa, and seven new species from Madagascar. Several species are again circumscribed partly by vegetative characters, similarly to the concepts of PUFF & BUCHNER (1994), and some *Danais* species recognized in this new taxonomy are still markedly variable morphologically, ecologically, and in molecular characters. Several species excluded by Puff & Buchner from *Danais* are included again based on our better knowledge of these species and all the *Danaideae* genera (KRÜGER et al., 2012; RAZAFIMANDIMBISON et al., 2022), and the current view of the *Rubiaceae* as having frequent homoplasious character reversals. And, several names of unclear identity can now be matched to modern collections for fuller documentation. Extensive field work will still be needed to develop our understanding of this genus further.

Morphological, ecological, and taxonomic notes on *Danais*

The main morphological characters of *Danais* are presented in the formal genus description, below. Some additional features are of ecological and other significance or sometimes have inaccurately been noted, as discussed here.

General plant characteristics

Dried specimens of *Danais*, especially those collected in the 19th and early 20th centuries, often have a characteristic yellow-green drying color, perhaps due to drying conditions or plant age. Such color has sometimes been suggested to characterize the genus or individual species, but it appears to be correlated with drying method and variable within all the species. Plants of several *Danais* species have a foetid odor, but this is not well enough documented to correlate this chemistry with individual species or species groups.

The species of *Danais* are all climbers of various forms. Most of these appear to climb by twining, but the manner of attachment is not clear for all the species. The habit of the plant is not well detailed on many specimen labels, and when it is, a variety of terms are used by different collectors and authors for the same plant, and this has generated some confusion. *Danais* plants are variously documented as climbers, vines, lianas, twiners and scrambling shrubs. The habit of the species treated here is cited only with the generalized term “climbing plants” to reduce confusion, even when more detailed descriptions are found on a few labels. Overall, label data and photographs suggest that a range of morphological climbing forms is found across the genus, as in some other climbing genera (e.g. *Schradera* Vahl), and also within some individual species. In any case, when the label data of some *Danais* specimens describe the plants as shrubs or scrambling shrubs, those species all seem to be climbers that sometimes spread with weakly ascending stems across an open substrate. This habit confusion is seen frequently in collections of other *Rubiaceae* climbers that are growing in dense vegetation or on rocks (TAYLOR et al., 2019).

Leaves and stipules

Arrangement of the leaf venation, from secondary through higher-order levels, is not usually detailed or discriminated in *Rubiaceae* taxonomic work, because this usually does not vary significantly within a genus or only differs in a distinctive way for one or two species (e.g. TAYLOR, 1994). However, the arrangement and form of the tertiary and higher-order venation in *Danais* does differ markedly among the species and is unusual for *Rubiaceae* in several of them. These details were considered diagnostic (in combination with some other features) for some *Danais* species by PUFF & BUCHNER (1994), and additional collections support their conclusions. Such leaf details were not widely used by classical taxonomists but are now being found diagnostic in various plant groups (e.g. SWENSON et al., 2023). PUFF & BUCHNER (1994) noted distinctive venation for a few *Danais* species, describing the overall leaf venation variously as reticulate and raised or prominent. These venation arrangements are studied and described in more detail here, as to the order of the venation

being described, the shape and size of the areoles, and whether the venation is thickened or raised on one or both leaf surfaces.

The stipules are remarkably variable in *Danais*, from interpetiolar to shortly fused around the stem; from triangular to ovate, bilobed, multifid, and lacinate; and from marginally entire and glabrous to serrate, glandular-dentate, and/or densely ciliate. Stipule form was considered diagnostic for a number of *Danais* species by PUFF & BUCHNER (1994) and is still supported as such in many cases. However, the stipules not infrequently fragment and fall with age, and the partial remains are easily misinterpreted. And, a number of *Danais* species have similar interpetiolar, triangular stipules 0.5–2 mm long that are not informative of the species identity. Stipules of this last form are found on the most commonly collected species and also on some of the most problematic ones for identification (e.g. *D. aurantiaca* Baker, *D. cernua*, *D. lyallii*, *D. fragrans*, *D. distinctinervia* Homolle, *D. microcarpa*, *D. breviflora*).

Inflorescences

The inflorescences of *Danais* are basically cymose but vary widely in form and also position. The variation in inflorescence arrangement within the genus was synthesized as a reduction or depauperization from an extensively branched thyrses or pleiothyrses by BUCHNER & PUFF (1993: 33–35, fig. 3A–D), with the individual conditions characterized by them only generally as to the degree of reduction. Inflorescences in *Danais* are variously terminal (Fig. 1B) and sometimes also borne in the uppermost stem axils, or all axillary (i.e. borne in both axils of a node) along the lower stems (Figs. 1A, C, 2A, 3C). Many of the species have elongated, climbing stems with the axillary inflorescences borne along them, but also may produce inflorescences in a terminal position along short lateral stems or at the apex of an elongated stem (Fig. 3B). This variability in position is not unexpected in a climbing plant, but it complicates identification of many of the species when they are characterized by one inflorescence position. The inflorescences in some *Danais* species seem to be consistently deflexed to pendulous (Fig. 3B, D), though further field studies will be needed to fully document this. Several species that are known from only one collection (e.g. *D. baronii*, *D. terminalis* Boivin ex Drake) are documented as producing both axillary and terminal inflorescences, and some other poorly known species (e.g. *D. rubra* Puff & R. Buchner) that were characterized as having only terminal inflorescence may be found to include similar variation.

Flowers

The flowers of *Danais* vary from four- to six-merous, sometimes on the same stem, but are usually five-merous. The showy parts of the flowers (corolla, stamens, stigma) are variously pale to dark green, yellowish green, golden-green, white,

yellow, orange, red, violet, blue, bright purple, dark purple, or nearly black, and usually have a cluster of bright white trichomes in the corolla throat. Flower color apparently may vary markedly within a species, and characteristically the corolla tube and the lobes are differently colored. In particular, the corolla tube is frequently dull green, white, or purple while the exposed adaxial surfaces of the lobes are bright orange or red. The corollas of *Danais* often have nearly cylindrical tubes, which are often remarkably slender (Fig. 3B), and characteristically are swollen at the top in the long-styled form to accommodate the included anthers. PUFF & BUCHNER (1994: 20, fig. 3) presented a summary graph of corolla tube length for each of the Malagasy species, which shows widely varying sizes within some species and quite consistent sizes in others. Whether a species is common or uncommon does not seem to be correlated with the amount of variation in corolla size. The corolla tube is fenestrate in a number of *Danais* species, with short (1–2 mm long) slits at its base that are obscured internally by dense hirtellous pubescence. These form in the bud (BUCHNER & PUFF, 1993), and their function is not yet known. The development of corolla slits does not seem to be correlated with flower form, and varies within some species (e.g. *D. cernua*, Fig. 1A).

BUCHNER & PUFF (1993: 53–54) surveyed the diversification in flower form, color, presumed pollination mode, and scent in *Danais*, and postulated that the species are variously adapted for hawkmoths, other kinds of moths, and a range of diurnal insects. They noted that the flowers of some species are sweetly fragrant, while others appear to have no odor. Their survey was not comprehensive nor based on field studies, and did not consider inflorescence position as an element in pollination mode. The flowers of *Danais* have notably well exerted stamens and stigmas, which are reciprocally positioned in the long-styled and short-styled morphs of the distylous species seen.

Fruits and seeds

As noted above, the capsules of *Danais* are not always useful to identify species because they are similar in form among species and also vary in size and texture within a number of species. Both capsules and seeds show a range of size within *Danais*. PUFF & BUCHNER (1994: 21, fig. 4) presented summary graphs of capsule and seed sizes for each of the Malagasy species, and found no clear pattern of variation except that species with relatively larger capsules often also have larger seeds, and capsules that reach a larger size are more variable in their mature size range. The seeds of *Danais* are generally flattened with a thickened, lenticular to ellipsoid seed portion and marginal wings. The wings are variable in outline and irregularly developed around the circumference, and generally similar in form among the species. PUFF & BUCHNER (1994) did find some differences in overall seed size, at least as to the general range

(e.g. c. 0.5–2 mm diam. vs. c. 2.5–5 mm), among some *Danais* species. They also found some variation in the development of the seed wing in correlation with the overall seed size, from quite small (e.g. c. 0.1–0.3 mm in width) to well-developed (e.g. c. 1 mm in width), and that the wings of elongated, elliptic-rhombic seeds are developed on the ends but reduced to narrow margins along the sides (e.g. BUCHNER & PUFF, 1993: 48, fig. 11B, *D. ligustrifolia*).

Two species, *Danais aptera* and *D. baccata*, have ellipsoid to cylindrical seeds that are sometimes angled and lack clearly developed wings, but otherwise these plants match *Danais*. These two species were excluded from *Danais* by PUFF & BUCHNER (1994) due to their lack of developed seed wings, even though this feature was not explicitly cited by them as a diagnostic feature of the genus (BUCHNER & PUFF, 1993). Some seeds of these two species do have thinly developed marginal flanges that are not dissimilar to the narrow wings of more strongly flattened seeds of other species (e.g. *D. ligustrifolia*), so they do not seem morphologically distinct from those of accepted *Danais* species. PUFF & BUCHNER (1993) documented wide variation in seed form and wing development in the related genera *Payera* and *Schismatoclada*, including irregularly developed, narrow marginal seed wings or reduced wings, and the analysis of RAZAFIMANDIMBISON et al. (2022) suggests that reduction of these seed wings in those genera is homoplasious. Thus, there seems no basis to assume that *Danais* does not have similar morphological radiations, and these species are reinstated in this genus here. The new species *D. sambiranensis* C.M. Taylor sp. nov. also has lenticular to angled seeds that may be unwinged or have only a thin wing along one side, and this species also otherwise matches *Danais* and is included here. These three species have not been studied yet with molecular data.

Materials and methods

This work is based on standard taxonomic techniques. Additional information, including detailed specimen data and high-resolution scans of representative specimens, is available on-line in TROPICOS (2024), and the MADAGASCAR CATALOGUE (2024) and Rubiaceae Project there (TAYLOR & COLLABORATORS, 2024). The species treated here are arranged in alphabetical order. Specimen accession numbers in brackets are barcode numbers, and citation of permanently printed accession numbers is used preferentially here when these are available. Morphological terminology follows LAWRENCE (1951), PUFF & BUCHNER (1994), and TAYLOR & ROGERS (2013) unless explained here. All of the species of *Danais* recognized in this study (Tables 1, 2) are keyed, but only selected species are discussed here. The species treated here are denoted in the key with a number corresponding to their sequence in the text. Full descriptions are presented for

new species and some previously described species that were poorly known or have significantly revised circumscriptions here. Morphological measurements are based on dried specimens. The order of the structure in the descriptions follows traditional sequence for *Rubiaceae* to facilitate comparisons (e.g. TAYLOR, 2020; TAYLOR & ROGERS, 2013; PUFF & BUCHNER, 1994). Comparative descriptions of the sizes of morphological structures refer only to species of *Danais*. Habitat and distribution are summarized for all the taxa treated, with the vegetation classification generally following the outline of GAUTIER et al. (2018). Lectotypifications are by CMT unless otherwise noted. Some of the changes in classification of *Danais* species have been noted anecdotally in herbarium annotations and molecular studies but are formally published for the first time.

The conservation assessment analyses here are preliminary, pending submission to the regional Red Listing Authority, and are authored by HHS. The preliminary conservation assessments are based on geo-referenced, specimen collection records from TROPICOS (2024). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were estimated using GeoCAT (BACHMAN & MOAT, 2012). The AOO is based on a defined cell width of 2 km. Number of locations for each new species is based on the IUCN Guidelines for Using the IUCN Red List Categories and Criteria Version 15.1 (IUCN, 2022), and the designation of Red List Categories and Criteria is based on the IUCN Red List Categories and Criteria (IUCN, 2012).

Taxonomy

Danais Comm. ex Vent., Tabl. Règn. Vég. 2: 584. 1799.

Typus: *Danais fragrans* (Lam.) Pers.

= *Alleizettea* Dubard & Dop in J. Bot. (Morot) 3: 6. 1910.

Typus: *Alleizettea bracteata* Dubard & Dop [= *Danais volubilis* Baker].

Scrambling, low to high-climbing, suffrutescent to woody climbing plants, climbing as high as 25 m, terrestrial, unarmed, with raphides, glabrous or variously pubescent, regularly branched, apparently not deciduous, sometimes with foetid odor. *Leaves* opposite, ternate, or 4-verticillate, decussate, subsessile to petiolate, sometimes with pubescent domatia in abaxial axils of secondary veins, with higher-order venation not lineolate, sometimes with higher-order venation laxly to closely reticulated and prominulous; stipules interpetiolar or infrequently fused around the stem (*Danais coriacea* C.M. Taylor sp. nov., *D. longipedunculata* Homolle), generally persistent or fragmenting with age, with interpetiolar portion triangular to broadly so, truncate, elliptic, or ovate, in its upper part variously acute to obtuse, rounded, subtruncate, serrate, bilobed, bidenticulate, laciniate, or multifid, erect or infrequently reflexed. *Inflorescences* terminal and/or axillary, 1- to

many-flowered, fasciculate, cymose, thyrsiform, or racemiform, subsessile to pedunculate, bracts reduced to developed. *Flowers* subsessile to pedicellate, distylous, diurnal or perhaps sometimes nocturnal; calyx limb shortly to deeply (4–)5(–6)-lobed, lobes equal to unequal on an individual flower, without calycophylls; corolla salverform to funnelform, white to pale green, olive green, lavender, dull to dark purple, purple-black, yellow, orange, or dull to bright red with colors often differing on tube and lobes, externally generally glabrous, tube 2–22 mm long, usually slender with the distalmost portion swollen to accommodate anthers in long-styled form, internally usually puberulous to pilosulous, in throat usually pilose with pubescence often denser in long-styled form, sometimes at base of tube fenestrate with short preformed slits, these alternate to corolla lobes, 1–2 mm long, and with opening blocked internally by interlocking trichomes, lobes (4–)5(–6), valvate-reduplicate in bud, lanceolate to triangular or ligulate, acute to obtuse, at tip without appendages; stamens (4–)5(–6), inserted in upper part of corolla tube, anthers dorsifixed, ellipsoid to narrowly oblong, dehiscent by longitudinal slits, without connective appendages, in long-styled form included, subsessile, and positioned in corolla throat, in short-styled form exerted on well-developed filaments, pollen characterized by BUCHNER & PUFF (1993) as spheroidal to subspheroidal, 10–26 µm, 3- to 5-colporate, and dimorphic, with supratectal verrucae present in grains of short-styled flowers but absent in grains of long-styled flowers; ovary 2-locular, with numerous seeds on peltate axile placentas, with papillate disk surrounding style at top, stigmas 2, linear, exerted in long-styled flowers, included and positioned in upper part of tube in short-styled flowers. *Infructescences* similar to inflorescences. *Fruits* capsular, deeply loculicidal from top, subglobose to ellipsoid or oblate, papery to chartaceous, coriaceous, or woody, 2–12 mm in diam., sometimes partially fused together, with calyx limb persistent or tardily deciduous, without beak or with weakly broadly angled beak portion up to 1 mm high; seeds numerous, 0.5–6 mm long, reticulated, flattened and circular to elliptic with circumferential wing, or infrequently angled to cylindrical and unwinged (*D. aptera*, *D. baccata*, *D. sambiranensis*), margin of wing when present entire to irregular or lacerate.

Notes. – At least 49 species distributed widely in humid to wet vegetation in the WIO region and eastern Africa, mainly on Madagascar but three species in the Mascarenes (Mauritius, Réunion, Rodrigues), two species in the Comores (one shared with Madagascar), and one species in East Africa (Tanzania).

Key to the species of *Danais*

1. Leaves 3 or 4 per node 2
- 1a. Leaves opposite 7

2. Stipules laciniate; leaves subsessile 3
- 2a. Stipules entire, triangular or reduced to a line; leaves with developed petioles 2–50 mm long 5
3. Inflorescences axillary; calyx lobes 8–9 mm long 6. *D. confusa*
- 3a. Inflorescences terminal or axillary at uppermost stem nodes; calyx lobes 1–10 mm long 4
4. Calyx lobes 4–10 mm long; fruits 8–12 mm in diam. *D. laciniata*
- 4a. Calyx lobes c. 1 mm long; fruits c. 3.5 mm in diam. *D. verticillata*
5. Inflorescences terminal; fruits 2.5–4 mm in diam.; Rodrigues *D. corymbosa*
- 5a. Inflorescences axillary; fruits 8–15 mm in diam.; Madagascar 6
6. Calyx lobes 0.5–1.5 mm long *D. coronata*
- 6a. Calyx lobes 2.5–9 mm long *D. volubilis*
7. At least some stipules laciniate, serrate, multifid, bilobed, denticulate, or with dense ciliate pubescence obscuring the margins 8
- 7a. Stipules entire or cuspidate, apex triangular to broadly so, rounded, or truncate 19
8. Stipules unlobed but with margins densely ciliate 10. *D. hispida*
- 8a. Stipules variously laciniate, serrate, lobed, or bidenticulate 9
9. Stipules laciniate, serrate, or multifid 10
- 9a. Stipules bilobed or bidenticulate on each interpetiolar side 14
10. Plants densely hirsute; leaves subsessile or some of them with petioles to 10 mm long, blades truncate to cordulate at base *D. vestita*
- 10a. Plants glabrous to pilosulous; leaves with regularly developed petioles 5–20 mm long, blades obtuse to acute at base 11
11. Stipules 1–2 mm long, triangular to elliptic in outline 17. *D. reticulata*
- 11a. Stipules 3–15 mm long, triangular to ovate in outline ... 12
12. Leaves robust, blades 12–24 × 6–9.5 cm; inflorescences terminal, generally exceeding the leaves *D. antilabimenae*
- 12a. Leaves medium-sized, blades 3.8–17.5 × 2–5.5 cm; inflorescences axillary, generally shorter than the leaves ... 13
13. Calyx lobes 1–2.5 mm long, narrowly triangular; bracts 1–2 mm long, narrowly triangular; stipules deeply laciniate *D. brickavillensis*
- 13a. Calyx lobes 2–4 mm long, triangular; bracts 0.8–5 mm long, narrowly elliptic to ligulate; stipules serrate *D. rakotovaoui*

14. Leaves subsessile or with petioles 2–10 mm long, blades subtruncate to cordulate at base *D. andribensis*
- 14a. Leaves with regularly developed petioles 2–35 mm long, blades sometimes subtruncate on some leaves, but obtuse or acute on at least some leaves 15
15. Leaf blades broadly elliptic, 9–18.5 × 4–13 cm; petioles 12–35 mm long; corolla lobes 7–7.5 mm long *D. randrianaivoi*
- 15a. Leaf blades elliptic to narrowly elliptic, 6–11 × 2.5–4.5 cm; petioles 5–10 mm long; corolla lobes c. 1.5 mm long ... 16
16. Inflorescences terminal, or terminal and in axils of uppermost leaves 17
- 16a. Inflorescences all axillary 18
17. Pedicels 0.5–1 mm long; corolla tubes 2–3 mm long *D. breviflora*
- 17a. Pedicels 3–15 mm long; corolla tubes 13–19 mm long 15. *D. perrieri*
18. Calyx limbs 0.8–3 mm long, lobed nearly to base, with lobes narrowly triangular to linear, often markedly unequal on an individual flower, often becoming reflexed 4. *D. cernua*
- 18a. Calyx limbs 0.5–1.2 mm long, lobed shallowly or for up to $\frac{3}{4}$ of its length, with lobes deltate to triangular, generally equal on an individual flower, generally erect 12. *D. lyallii*
19. Leaves all relatively small, blades up to 1 × 0.3 cm *D. disticha*
- 19a. Fully developed stem leaves larger than this, blades 1.5–22 × 0.5–9 cm 20
20. Inflorescences with 1–9 flowers borne on developed pedicels, variously fasciculate or in cymes branched to 1–2 orders 21
- 20a. Inflorescences with generally 10 or more subsessile to pedicellate flowers, branched to 1–3 orders, if flowers fewer than 10 then these subsessile 28
21. Leaves subsessile; inflorescences axillary; seeds angled and unwinged 1. *D. aptera*
- 21a. Leaves with developed petioles 2–20 mm long; inflorescences terminal and/or axillary; seeds winged or unwinged 22
22. Flowers 1–3, regularly borne at apices of short lateral stems and in leaf axils along developed stems; corolla tubes c. 13 mm long; seeds unwinged 2. *D. baccata*
- 22a. Flowers 1–9, terminal and/or axillary on regularly developed stems; corolla tubes 8–18 mm long; seeds winged (unknown in *D. sulcata*) 23
23. Calyx lobes 5–6 mm long; Mauritius *D. sulcata*
- 23a. Calyx lobes 0.5–3 mm long; Madagascar 24
24. Calyx lobes 0.5–3 mm long, often unequal on an individual flower and at least some lobes 1.5 mm or longer 13. *D. nigra*
- 24a. Calyx limb 0.5–1 mm long, generally equal on an individual flower and 1 mm long or shorter 25
25. Leaf blades regularly ovate, base rounded to truncate or cordulate; corolla lobes 10–12 mm long 14. *D. ovata*
- 25a. Leaf blades ovate to elliptic, base obtuse to acute; corolla lobes 4–6 mm long (unknown in *D. terminalis*) 26
26. Leaf blades 1–2.8 cm wide; fruits 8–12 mm in diam. 20. *D. terminalis*
- 26a. Leaf blades 1–5 cm wide, with at least some 2.9–5 cm wide; fruits 4.5–7 mm in diam. (unknown in *D. gracilis*) 27
27. Inflorescences terminal and sometimes also in uppermost leaf axils, peduncles 1–3 cm long *D. dauphinensis*
- 27a. Inflorescences all axillary, peduncles 0.2–0.5 cm long 9. *D. gracilis*
28. Stipules shortly (0.5–1 mm) united around stem, broadly triangular to subtruncate 29
- 28a. Stipules interpetiolar, triangular to broadly triangular, ovate, ligulate, subtruncate, or reduced to a line 30
29. Calyx limbs 1–1.5 mm long; corolla white to yellow, tube c. 3 mm long 7. *D. coriacea*
- 29a. Calyx limbs 0.3–0.5 mm long; corolla green to pink, orange, or red, tube 5.5–6 mm long 11. *D. longipedunculata*
30. Plants hirsute; stipules ovate to ligulate or triangular, 2–15 mm long; flowers subsessile in 1–5 heads; calyx lobes 1.5–5.5 mm long 31
- 30a. Plants glabrous to velutinous, tomentulose, villosulous, hirtellous or hirsute; stipules triangular to subtruncate or reduced to a line, 0.5–5 mm long; flowers subsessile to pedicellate in congested to lax cymes; calyx lobes 0.2–2.5 mm long [Note: if some characters similar to the previous lead, then not in the same combination] 32
31. Stipules ligulate to triangular, erect; calyx lobes ligulate to narrowly triangular, 1.5–3.5 mm long; corolla tubes c. 12 mm long *D. capituliformis*
- 31a. Stipules ovate, usually becoming reflexed; calyx lobes linear, 4–5.5 mm long; corolla tubes 18–20 mm long 5. *D. coerulea*
32. [Supposedly] high-climbing lianas; stems and leaves moderately to densely, regularly velutinous to tomentulose, at least on abaxial surface of blades; flowers and fruits subsessile to shortly pedicellate; fruits sometimes partially fused to each other *D. magna*
- 32a. Scrambling to high-climbing weak shrubs, vines, and lianas; stems and leaves glabrous to puberulous, pilosulous, villosulous, hirtellous, or hirsute; flowers and fruits

- subsessile or pedicellate; fruits free or sometimes partially fused in *D. aurantiaca* 33
33. Inflorescences axillary 34
- 33a. Inflorescences terminal, or terminal and in axils of uppermost leaves 45
34. Inflorescences with peduncle and/or basalmost secondary axes 3–15 cm long and half or more as long as the entire inflorescence, flowers all pedicellate and separated 35
- 34a. Inflorescences with peduncle 0.1–3 cm long, longer than basalmost secondary axes and less than half of the total length of the inflorescence, flowers separated or clustered in glomerulate groups 39
35. Leaf blades with secondary and tertiary venation lax, sparsely reticulated, areoles 2–5 mm long 36
- 35a. Leaf blades with secondary and tertiary venation closely and regularly reticulated, areoles 0.2–1 mm long 37
36. Leaf blades 1–4.5 cm wide; stipules 1–1.5 mm long; calyx lobes 0.5–1 mm long *D. dauphinensis*
- 36a. Leaf blades 5–9 cm wide; stipules 3–4 mm long; calyx lobes 1–2 mm long 18. *D. sambiranensis*
37. Peduncles 0.5–2 cm long; calyx limbs c. 1.5 mm long; N Madagascar 3. *D. baronii*
- 37a. Peduncles 1.5–10.7 cm long; calyx limbs 0.5–1 mm long; E-C and S Madagascar 38
38. Petioles 10–22 mm long; peduncles 1.5–6 cm long; fruits 5–10 mm in diam.; S Madagascar 17. *D. reticulata*
- 38a. Petioles 18–40 mm long, with at least some of them 23 mm long or longer; peduncles 4.5–10.7 cm long; fruits c. 4 mm in diam.; E-C Madagascar 19. *D. schatzii*
39. Stems and leaves densely villosulous, hirtellous, or hispid throughout, pubescence generally persistent 10. *D. hispida*
- 39a. Stems and leaves glabrous or sparsely to moderately hirtellous, pilosulous, or puberulous throughout or only on lower leaf surfaces, pubescence tardily deciduous at least on stems 40
40. Leaf blades with secondary and higher-order venation closely and regularly reticulated and prominulous (sometimes subtle to see adaxially) 41
- 40a. Leaf blades with secondary and tertiary venation lax, often irregularly reticulated and plane or weakly prominulous [Note: these species are not well differentiated morphologically yet, but widely separated geographically and separated in molecular analyses] 43
41. Leaf blades elliptic to narrowly elliptic, apex acuminate; calyx limbs 0.3–0.5 mm long; seeds 1–1.4 mm in diam. *D. distinctinervia*
- 41a. Leaf blades elliptic to broadly elliptic, oblanceolate, or obovate, apex shortly acuminate to obtuse or rounded; calyx limbs 0.5–1 mm long; seeds 1.6–2 mm in diam. 42
42. Leaf blades oblanceolate or obovate; flowers subsessile in glomerules or congested cymes of 3–5; fruits free or sometimes partially fused *D. aurantiaca*
- 42a. Leaf blades elliptic to broadly so; flowers subsessile in glomerules or cymes of 3–9; fruits free, separated on tardily developing stipes *D. pubescens*
43. Leaf blades drying chartaceous to subcoriaceous or coriaceous; corollas salverform to funnellform, tubes 2–6 mm long; fruits 5–8 mm in diam., chartaceous to woody; Madagascar 12. *D. lyallii*
- 43a. Leaf blades drying papery to chartaceous; corollas salverform, tubes 2.5–10 mm long; fruits 2.5–5 mm in diam., chartaceous; continental Africa and Mascarenes 44
44. Corolla tubes 5–10 mm long, lobes 2–5 mm long; Mauritius & Réunion 8. *D. fragrans*
- 44a. Corolla tubes 2.5–6 mm long, lobes 2.5–4 mm long; East Africa *D. xanthorrhoea*
45. Leaf blades on both surfaces with venation smooth or weakly and irregularly evident to raised 46
- 45a. Leaf blades on one or both surfaces with secondary veins and some higher-order venation regularly prominulous and laxly to closely reticulated 48
46. Leaf blades lanceolate to narrowly elliptic, 0.9–2 cm wide; corolla tubes 3–4 mm long; Rodrigues *D. corymbosa*
- 46a. Leaf blades elliptic to ovate, 1–3.5 cm wide; corolla tubes 17–19 mm long; Madagascar 47
47. Pedicels 1–5 mm long; corollas brown to orange or red, lobes 3–4 mm long; fruits 6–13 mm long; 665–1250 m *D. pauciflora*
- 47a. Pedicels 3–15 mm long, with at least some more than 7 mm long; corollas yellow, lobes 4–8 mm long; fruits c. 4 mm in diam.; 70–640 m 15. *D. perrieri*
48. Leaf blades drying coriaceous, adaxially with higher-order venation prominulous to prominent and closely reticulated, areoles regular in size and 0.1–0.3 mm wide [Note: some of these species are incompletely known, see the notes for *D. baronii* for discussion on their separation] 49
- 48a. Leaf blades drying papyraceous to coriaceous, adaxially with higher-order venation prominulous and laxly to regularly reticulated, areoles irregular in size and shape, 0.5–3 mm wide 51
49. Petioles 5–20 mm long, with at least some less than 20 mm long; fruits 4–5 mm in diam. *D. rubra*
- 49a. Petioles 18–40 mm long; fruits 4–6 mm in diam. 50
50. Petioles 20–25 mm long; peduncles 0.5–2 cm long; calyx limbs c. 1.5 mm long; N Madagascar 3. *D. baronii*

- 50a. Petioles 18–40 mm long; peduncles 4–10.7 cm long; calyx limbs c. 0.5 mm long; E-C Madagascar ... 19. *D. schatzii*
51. Leaf blades drying coriaceous, 4–7 × 1–3.5 cm, regularly ovate, concolorous, shiny abaxially *D. tsaratananensis*
- 51a. Leaf blades drying subcoriaceous to papery, 5–12 × 1.5–5.5 cm, ovate to elliptic, obovate, or oblanceolate, concolorous to discolorous, abaxially shiny to matte, if ovate then drying chartaceous, discolorous, and abaxially matte 52
52. Flowers and fruits borne on pedicels 0.5–30 mm long; corolla tubes 8–17 mm long (unknown in *D. terminalis*); fruits 4.5–12 mm in diam. 53
- 52a. Flowers and fruits subsessile or borne on pedicels to 3.5 mm long; corolla tubes 2–8 mm long; fruits 2.5–4.5 mm in diam. 55
53. Leaf blades matte abaxially, adaxially with higher-order venation regularly prominulous; corollas yellow to pale purple externally 16. *D. puffiana*
- 53a. Leaf blades matte or shiny abaxially, adaxially with higher-order venation plane to weakly thickened; corollas pale green to white or olive green externally (unknown in *D. terminalis*) 54
54. Leaf blades shiny abaxially; fruits 4.5–7 mm in diam. *D. dauphinensis*
- 54a. Leaf blades matte abaxially; fruits 8–12 mm in diam. 20. *D. terminalis*
55. Leaf blades obovate, when dry the older ones becoming weakly bullulate and often irregularly discolorous in patches *D. rhamnifolia*
- 55a. Leaf blades obovate to oblanceolate or elliptic, when dry and/or older smooth and not discolored in patches ... 56
56. Flowers borne in lax cymes, all on pedicels 0.5–4 mm long, well separated from each other *D. humblotii*
- 56a. Flowers borne in weakly to markedly congested cymes, subsessile or on pedicels to 3 mm long, with at least some of them closely set in glomerulate groups 57
57. Leaf blades adaxially smooth or with secondary and some tertiary venation irregularly prominulous; flowers subsessile or pedicels to 1 mm long; corollas with tube 2–3 mm long *D. breviflora*
- 57a. Leaf blades adaxially with secondary and tertiary venation regularly prominulous; flowers subsessile or on pedicels to 3 mm long; corollas with tube 2–5 mm long 58
58. Flowers borne in congested groups of 2–5; corolla tubes c. 5 mm long; fruit c. 5 mm in diam.; Comores *D. comorensis*
- 58a. Flowers borne in congested to lax groups of 3–9; corolla tubes 2–4.5 mm long; fruits 2–5.5 mm in diam.; Madagascar [Note: if some characters similar to the previous lead, then not in the same combination] 59
59. Inflorescences with flowers borne at the ends of axes and/or along spiciform axes; corolla tubes 3–4.5 mm long; fruits 2–5.5 mm in diam.; 0–1400 m *D. ligustrifolia*
- 59a. Inflorescences with flowers borne at the ends of branching axes; corolla tubes 2–4 mm long; fruits 2–3 mm in diam.; 600–2000 m *D. microcarpa*
1. *Danais aptera* Wedd. ex Homolle in Notul. Syst. (Paris) 5: 279. 1936.
- Lectotypus** (designated here): **MADAGASCAR:** Domaine oriental, sur la côte, s.d., *Chapelier s.n.* (P [P00057135] image!; isolecto-: P [P00057136, P00057137] images!).
- Distribution and ecology.* – This species was collected once on the east coast of Madagascar, and nothing more is known of its ecology.
- Notes.* – *Danais aptera* is poorly known. It was described from one incomplete, fruiting collection and its type has not been matched to modern collections. This species is characterized by opposite, elliptic, subsessile leaves, narrowly triangular stipules, axillary flowers that are solitary or few and fascicled on slender peduncles or pedicels c. 2 cm long, narrowly triangular calyx lobes c. 1 mm long, subglobose loculicidal capsules c. 8 mm in diam., and cylindrical seeds that are apparently about 1 mm long (if the seeds on the type are mature).
- HOMOLLE (1936) classified this species in *Danais* apparently because it has the habit, fruit form, and general aspect of *Danais*. The original label on the lectotype describes the plant as a “liane grimpant”, so it has the diagnostic character of this genus. BUCHER & PUFF (1993: 73–74) excluded this species from *Danais*, however, based on its seeds that lack wings. As discussed above, other genera in *Danaideae* vary extensively in seed form and wing development (BUCHNER & PUFF, 1993; RAZAFIMANDIMBISON et al., 2022), and a seed wing is not here considered diagnostic for *Danais*. Accordingly, this species is here reinstated in *Danais*.
- The authorship of *Danais aptera* has been sometimes attributed solely to Homolle, but in the protologue she credited the coining of this name for the Chapelier type collection to “*D. aptera* Wedd. mss. in Herb. Mus. Par.”, which satisfies the criteria of ICN Art. 46.5 (TURLAND et al., 2018) for crediting Weddell for this epithet. Homolle provided the morphological description and taxon circumscription and thus remains the actual author of this name. Puff annotated two specimens of Chapelier’s at P as the holotype and isotype of *D. aptera*, respectively, and BUCHNER & PUFF (1993: 73) cited these two specimens as such without further detail to identify the corresponding specimens. Three duplicates of this collection are now curated at P, with the newly discovered one annotated by C.V. Naudin (1815–1899) but not Puff. None of these specimens were annotated or otherwise directly indicated as a

holotype by Homolle. Buchner & Puff's incomplete published citation does not fulfill the requirements for an inadvertent lectotypification because it does not conclusively identify their intended holotype, so this name is typified here. The specimen annotated by Puff as the holotype was apparently originally chosen for having the most ample material including seeds, and that specimen has been consulted as such by later authors and is chosen as the lectotype.

2. *Danais baccata* Homolle in Notul. Syst. (Paris) 5: 280. 1936.

Lectotypus (designated here): **MADAGASCAR. Reg. Ihorombe [Prov. Fianarantsoa]:** alluvions des bords de l'Itomampy, VI.1919, *Perrier de la Bâthie* 12663 (P [P00057140] image!; isolecto-: MO-04613606!, P [P00057141, P00539961] images!).

Distribution and ecology. – This species is found in lowland moist evergreen forest, sometimes on sandy substrates, from sea level to 600 m along the eastern escarpment of Madagascar (Reg. Anosy [Prov. Toliara], Reg. Analanjirofo [Prov. Toamasina], Reg. Ihorombe [Prov. Fianarantsoa]).

Notes. – *Danais baccata* is not well known. It was described based on one incomplete collection, and its type has now been matched to two modern collections. This species is characterized by a branching pattern with the leaves and flowers borne on short lateral stems arising along an elongated, weakly flexuous main stem; opposite, elliptic, shortly petiolate leaves; triangular, deltate to sometimes acuminate, small stipules; axillary flowers that are solitary or few and fascicled on slender peduncles or pedicels 5–15 mm long; narrowly triangular calyx lobes c. 1 mm long; a slenderly salverform, brown-flushed corolla with the tube c. 13 mm long and fenestrate at the base; subglobose, loculicidal capsules 8–12 mm in diam.; and angled to ellipsoid, unwinged seeds about 1 mm long. The two modern specimens of *D. baccata* are from widely separated localities, but the distinctive branching pattern and wingless seeds indicate that these belong to the same species or represent closely related species that cannot currently be distinguished. The habit of this species appears to be variable, or at least difficult to characterize.

The branching arrangement of *Danais baccata* is uncommon in this genus, with the leaves and fruits borne on short lateral stems from elongated main stems. The type collection has regular, rather stiff branching with some of the long stems weakly curving, while the two modern specimens (*Ludovic* 1614, *Manjato et al.* 264, MO) have a similar growth form but markedly flexuous main stems. The labels of the type and one of the modern collections describe the plant as a shrub, while the label data of the other modern collection describe it as a liana. As PUFF & BUCHNER (1994) noted, the habit of *Danais* is basically climbing but sometimes described by collectors as

shrubby when the young plants develop a clumped form, or when the plants spread and clamber over a substrate such as rock. Thus, the conflicting label descriptions do not seem to confirm this species has an erect rather than supported habit.

Danais baccata is similar to *D. aptera* in its unwinged seeds, and it has a similar classification history. Homolle described this species as “*Danais*?”, apparently because it has the general aspect and fruit form of *Danais* but a supposed shrub habit and wingless seeds. BUCHNER & PUFF (1993: 74) excluded this species from *Danais* based on these last two features. The seeds of *D. baccata* are ellipsoid, angled, and not clearly winged, although many of them have a weakly flattened margin that is often to flange-like along one side. As discussed above, winged seeds are not a diagnostic feature for *Danais*, and the habit of this species is at least sometimes climbing so it is here reinstated in *Danais*.

BUCHNER & PUFF (1993: 74) cited the holotype specimen of *Danais baccata* as the single specimen they saw at P, without details to identify the individual sheet, and Puff annotated one specimen of the type collection there as the holotype [P00057140]. However, neither the protologue nor annotations by Homolle denote a single specimen that can be considered the holotype. Three duplicates of the type collection are deposited at P, and so must be considered syntypes. Two of these were annotated with this name and “n. sp.” by Homolle [P00057140, P00057141], and the third lacks any annotation by her [P00539961]. P00057140 has more and better plant material, a label with original collection data, an analysis in Homolle's hand, and Puff's annotation as holotype, and is therefore designated here as the lectotype. These last two specimens belonging to the same gathering are here considered isolectotypes.

3. *Danais baronii* Homolle in Notul. Syst. (Paris) 5: 281. 1936.

Holotypus: **MADAGASCAR:** “North Madagascar”, s.d., *Baron* 6607 (P [P00057143] image!; iso-: K [K000046178] image!).

Distribution and ecology. – This species is known from one collection from northern Madagascar, which lacks collection data.

Notes. – *Danais baronii* was incompletely treated by PUFF & BUCHNER (1994: 62–63), and it is still incompletely known and problematic as to its identity. It was described based on one collection with immature fruits from an unspecified locality somewhere in northern Madagascar. *Danais baronii* is characterized by puberulous vegetative organs; opposite, petiolate leaves with the higher-order venation closely, densely reticulated and prominulous on both surfaces of the blade; interpetiolar, triangular stipules; cymose, pedunculate inflorescences borne in both axillary and terminal position on

peduncles 0.5–2 cm long; flowers and fruits borne in regularly umbelliform groups on pedicels 1–2 mm long; and ellipsoid to subglobose fruits 4–5 mm in diam. The leaf blades in the type images are shiny on both surfaces and have dried with a coriaceous texture. The type of *D. baronii* has not yet been matched to any other collections, so is characterized here based on its few known features. The identity of this species is not only problematic in general, it is problematic for the taxonomy of *Danais*: some other species share its few known features but cannot be conclusively separated or synonymized with it because *D. baronii* is incompletely known. These similar species are separated and treated here because they can be characterized and analyzed, but one of these names may eventually be found to apply to the plants described as *D. baronii*.

Danais baronii is similar to *D. rubra*, which is also known from northern Madagascar. *Danais rubra* is also incompletely known, from only one flowering collection. *Danais rubra* differs from *D. baronii* in its longer petioles (20–25 mm long vs. 5–20 mm long in *D. baronii*); shorter calyx lobes (0.5–0.8 mm long vs. c. 1.5 mm long in *D. baronii*); and a different general aspect. *Danais schatzii* C.M. Taylor sp. nov. (described below) is also similar to *D. baronii* and is found in a different floristic region in east-central Madagascar. *Danais schatzii* differs from *D. baronii* in its glabrous stems and leaves; peduncles 4.5–10.7 cm long; pedicels 0.5–4 mm long and varying in length within a cyme so the flowers are less regularly arranged; and a shorter calyx limb, c. 0.5 mm long.

4. *Danais cernua* Baker in J. Bot. 20: 137. 1882 (Fig. 1A).

Holotypus: MADAGASCAR: “forests of the Tanala country, chiefly in Betsileo-Land”, s.d., *Baron 189 ex parte* (K [K000046142] image!; iso-: P [P00057148 fragm.] image!).

Distribution and ecology. – This species is found widely in lowland and medium altitude moist evergreen forests from sea level to 1800 m, from northern to southern Madagascar (Reg. DIANA and SAVA [Prov. Antsiranana], Reg. Alaotra-Mangoro and Analanjirofo [Prov. Toamasina], Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa], Reg. Anosy and Atsimo-Andrefana [Prov. Toliara]).

Notes. – *Danais cernua* is circumscribed more narrowly here than by PUFF & BUCHNER (1994) and diagnosed in part by different characteristics. This species is widespread and commonly collected, and characterized here by an extensively branched habit with elongated, flexuous stems; glabrous to puberulous or hirtellous stems and abaxial leaf surfaces; opposite or rarely ternate, petiolate, elliptic to obovate or oblanceolate leaf blades 3–9 × 1.5–4.5 cm that dry with a papyraceous to chartaceous texture; interpetiolar stipules that are triangular in outline and bilobed; axillary cymose inflorescences about half as long

as the leaves, with the flowers all pedicellate; a calyx limb divided nearly to the base into narrowly triangular to linear lobes 0.8–3 mm long that are often unequal in length on an individual flower; slenderly funnelform corollas with the lobes 2–4 mm long and generally orange to red; and subglobose fruits 4–9 mm in diameter. The calyx lobes characteristically become reflexed with age, which is unusual in *Danais* and distinctive for *D. cernua* when present. The corolla tubes are 5–9 mm long, and they apparently lack slits at the base but occasionally have corresponding lines of thinned tissue here. The corolla tubes expand regularly and notably (for *Danais*) in diameter from the base to the top and are wide enough at the top to accommodate the included anthers of the long-styled form without an abrupt swelling. *Danais cernua* is frequently collected in secondary vegetation.

PUFF & BUCHNER (1994: 57–59) circumscribed *Danais cernua* more broadly than done here, to include wider variation in both vegetative and flowering characters, and they effectively broadened its circumscription even more in their specimen annotations. In particular, they included in *D. cernua* plants with leaf blades that dry variously membranaceous to papery, subcoriaceous, or coriaceous; stipules ranging from obtuse to acute and bilobed; and calyx limbs varying from deeply divided to tubular and only shallowly lobed, even though they characterized this structure in their commentary as “typically... the calyx lacks a basal tubular part” (PUFF & BUCHNER, 1994: 58). PUFF & BUCHNER (1994: 58, as *D. fragrans*) noted accurately that *D. cernua* is similar to and easily confused with *D. lyallii*, but review of specimens identified by them finds no consistent use of their own diagnostic features and no evident morphological differences between their working concepts of these two species. Review here of specimens that correspond to Puff & Buchner’s *D. cernua* and *D. lyallii* does find two morphologically distinguishable groups of plants, however, which generally correspond to their stated species concepts. One group of plants consistently has a papery or chartaceous leaf drying texture, distinctly bilobed stipules, and a calyx limb divided to the base into narrow, usually spreading to reflexed lobes; this group agrees with the type of *D. cernua*, and the circumscription of this species here. The other group of plants consistently has leaves with a chartaceous to coriaceous drying texture, stipules that are acute or infrequently denticulate, and a calyx limb divided for $\frac{1}{3}$ – $\frac{2}{3}$ of its length into triangular, erect lobes; this second group agrees with the type of *D. lyallii*, and this second species is diagnosed here by these features. Puff & Buchner also contrasted these two species as to flower size, with *D. cernua* characterized as having longer corolla tubes, but the measurements they gave for these two species were overlapping: “(4–)5–9 mm” (PUFF & BUCHNER, 1994: 57) for *D. cernua*, vs. 2–4.5 mm long in *D. lyallii* (PUFF & BUCHNER, 1994: 54, as *D. fragrans*). Review here with numerous additional collections finds no significant difference in corolla



Fig. 1. – *Danais* Comm. ex Vent. on Madagascar. **A.** *Danais cernua* Baker; **B.** *Danais volubilis* Baker; **C.** *Danais rhamnifolia* Baker; **D.** *Danais schatzii* C.M. Taylor.
[**A:** Randrianarivony 886; **B:** Rakotovao 3998; **C:** Antilahimena 8315; **D:** Schatz 4430] [Photos: **A:** F. Rakotoarivony; **B:** C. Rakotovao; **C:** P. Antilahimena; **D:** G. Schatz]

size between these two species, however: corollas of *D. cernua* have a tube 4–9 mm long, and those of *D. lyallii* have a tube 2.5–6 mm long. The corollas of *D. cernua* are indeed often longer than those of *D. lyallii*, as noted by them, but definitely not always; the corollas of *D. cernua* are often also relatively more slender and can appear longer in comparison due to this difference in form. In the taxonomy here, most of the plants Puff & Buchner included in *D. fragrans* and many of those they included in *D. cernua* are placed in *D. lyallii*. Several hundred collections corresponding to these two species were studied in this review, and only one specimen (De Block *et al.* 2335, MO) appears to be intermediate between the two species, with the tubular, shortly lobed calyx limb of *D. lyallii*, the bidentate stipules of *D. cernua*, and a corolla tube c. 5 mm long that agrees with both species. Given the frequency and sympatry in secondary vegetation of these two species and the hundreds of specimens that clearly correspond to one species or the other, this one collection is regarded as having a putative hybrid origin rather than as an intermediate plant that indicates that these species are not distinct.

PUFF & BUCHNER (1994: 57) synonymized several other names under *Danais cernua*, which all agree with this species in the circumscription here and are cited again only in Tables 1 and 2.

5. *Danais coerulea* Homolle ex Cavaco in Bull. Mus. Natl. Hist. Nat., sér. 2, 37: 718. 1966.

Lectotypus (designated here): **MADAGASCAR. Reg. DIANA [Prov. Antsiranana]:** Domaine du Centre, massif de Manongarivo, montagne du Sambirano, IV.1909, Perrier de la Bâthie 3823 (P [P00057145] image!; isolecto: P [P00057146] image!).

Distribution and ecology. – This species is found in medium altitude moist evergreen forest at c. 850 m in northwestern Madagascar (Reg. DIANA [Prov. Antsiranana]).

Notes. – *Danais coerulea* is characterized by its combination of hirsute pubescence on stems, leaves, stipules, and inflorescences; opposite, petiolate leaves with the blade drying papery; well-developed, ovate to lanceolate stipules 5–15 mm long that are often reflexed in their upper parts; axillary, pedunculate, subcapitate inflorescences; well-developed, linear calyx lobes 4–5.5 mm long; and purple or bluish black corollas with the tube 18–21 mm long. This species was described based on one flowering specimen, and its identity has not been clear until recently when a modern collection was matched to the type (Gautier 2988, G, MO, P).

Danais coerulea was treated as doubtfully placed in this genus by PUFF & BUCHNER (1994: 39–40), and not keyed or given a full description by them so it has been overlooked. They excluded this from *Danais* based on its label data

describing it as a shrub and because they could not confirm it has winged seeds. As discussed above, specimens of *Danais* can be described as shrubs or “scrambling shrubs” due to a habit confusion with lianas growing in dense vegetation or on rocks or young plants. The fruits of *D. coerulea* have apparently still not been documented, but this new collection confirms this plant is a climber and it is here reinstated in *Danais*.

Danais coerulea has been confused in herbarium identifications with *D. sambiranensis*, described and separated below, and *D. capituliformis* Homolle. *Danais capituliformis* can be recognized by its ligulate to narrowly triangular stipules 2–10 mm long that are erect and often prolonged at the tip, narrowly ligulate to triangular calyx lobes 1.5–3.5 mm long, and a corolla tube c. 12 mm long. *Danais capituliformis* was known to PUFF & BUCHNER (1994: 39–40) from only three collections, and they noted that these three specimens showed notable variation in leaf size, inflorescence branching, and calyx lobe shape so further morphological variation was expected. However, the characters of *D. coerulea* are quite different and these two species are clearly distinct.

Two duplicates of the type collection of *Danais coerulea* are curated at P, and both were annotated with this name by Cavaco. There is no indication in the protologue or specimen annotations that one of these was to be considered the holotype, so they must be regarded as syntypes. Puff annotated one of these as the holotype and did not annotate the other. PUFF & BUCHNER (1994: 63) cited the holotype as deposited at P but gave no more identifying information so this cannot be considered as an inadvertent lectotypification. A lectotype is designated here, and the specimen annotated as the holotype by Puff is chosen.

6. *Danais confusa* C.M. Taylor, **nom. nov.**

= *Sabicea verticillata* Wernham, Monogr. Sabicea: 74. 1914 [not *Danais verticillata* Baker, 1883].

Holotypus: **MADAGASCAR:** “North Madagascar”, s.d., Humblot 213 (P [P00150784] image!).

Etymology. – The species epithet refers to the confused classification history of this species and competing informal names that have been used for it.

Distribution and ecology. – This species is known only from the type, which is from Madagascar but otherwise lacks collection data.

Notes. – *Danais confusa* is characterized by its densely hirsute stems, calyces, and hypanthia; ternate, subsessile, medium-sized, elliptic to obovate leaves; shallowly to deeply pectinate or lacinate stipules c. 8 mm long; flowers that are axillary at lower stem nodes, solitary, and subsessile or with a peduncle up to 5 mm long; notably well-developed calyx limbs,

c. 9 mm long, that are divided nearly to the base into narrowly elliptic lobes; and slenderly salverform, externally hirsute corollas with the tube 17–20 mm long and the narrow lobes c. 9 mm long. This species is only known from one collection, which is in flower, but no color was noted.

This species was described in *Sabicea* Aubl., and it agrees with several species of that genus on Madagascar (WERNHAM, 1914) in its lacinate stipules, presumably climbing habit (no label data document this, but no author has questioned it), solitary axillary flowers with a well-developed calyx limb, and general corolla form. This plant is also similar to *Danais* in these same features, and was studied by Homolle, who provided a hand-written analysis of the type specimen that is mounted on it. She did not finally publish a name for this collection in *Danais*, similarly to others that she studied and annotated as new species for this genus but never finally described (CAVACO, 1965). Cavaco later regarded this plant as a species of *Danais* and annotated it as such, but did not formally transfer it taxonomically to this genus. In contrast, PUFF & BUCHNER (1994: 64) regarded this as a species of *Sabicea*, based on the apparent lack of winged seeds. Some *Sabicea* species on Madagascar are similar to some species of *Danais*, but these genera differ in corolla aestivation, fruit type, and seed shape. In *Sabicea*, the corolla aestivation is valvate, the fruits are baccate and fleshy or juicy, and the seeds are angled and unwinged; in *Danais* the corollas are reduplicate-valvate, the fruit is capsular, and the seeds are angled to flattened and winged or not. The corolla lobes on the type specimen of *S. verticillata* are poorly preserved and their aestivation not entirely clear in the online image available, but these appear to be thinly valvate-reduplicate. The fruits are immature but not notably fleshy. Homolle's hand-written analysis on the type noted the details of a dissected ovary and the presence of wings already present on the developing seeds, but neither an ovary that has been dissected nor any seeds seem to be preserved on this specimen today (seen only as an image). Puff & Buchner concluded that the observation of winged seeds was inaccurate or at least not confirmable, and as discussed above, they regarded winged seeds as diagnostic for *Danais*. However, Homolle's drawing and statement that she found the developing seeds to be winged is considered credible here, and indicates this species is better classified in *Danais*. Additionally, some other features of *S. verticillata* are more similar to *Danais* than *Sabicea*. Wernham noted in the protologue that verticillate leaves were not otherwise known in *Sabicea*, and this apparently is still the case, but these are found in *Danais*. Also, the corollas of the type specimen are anomalous in *Sabicea* but agree with *Danais* in their very slender tubes that are abruptly enlarged at the top to accommodate the included anthers, and the short fenestrate slits at their bases are common in *Danais* but not known in *Sabicea*. Accordingly, this species is here transferred to *Danais*.

PUFF & BUCHNER (1994) noted that Cavaco actually had regarded this species anecdotally as *Danais* twice, separately, once in a print citation and once in a herbarium annotation. He used two different names for it, proposed as replacement names in *Danais*, and these have been used by others and in curation, but neither is validly published. One of his unpublished names honored Herbert Fuller Wernham (1879–1941) and was cited in as a nomen nudum in a publication, while the other name honored Prof. Anne-Marie Homolle (1905–1988) and was only used in specimen annotations. The replacement name published here is newly coined in part to avoid confusion with those previous invalid names.

Danais confusa is similar to *D. laciniata* C.M. Taylor, which differs in its opposite leaves, branched inflorescences that are terminal and sometimes also produced in the uppermost leaf axils, and longer pedicels 15–26 mm long. *Danais confusa* is also similar to *D. vestita* Baker, which differs in its opposite leaves and pedunculate cymose inflorescences.

7. *Danais coriacea* C.M. Taylor, **sp. nov.** (Fig. 2B, 4).

Holotypus: MADAGASCAR. **Reg. Atsinanana [Prov. Toamasina]:** Distr. Brickaville, comm. Maroseranana, Fkt. Ambodilendemy, Ankerana, 18°25'40"S 48°47'17"E, 990 m, 24.III.2011, *Antilahimena* 7781 (MO-6407815!; iso-: P, TAN).

Danais coriacea C.M. Taylor is distinguished from *D. longipedunculata* Homolle by its shorter, white to yellow corollas.

Climbing plants, climbing to 16 m high, fleshy; stems glabrous, flattened to weakly quadrangular becoming terete. *Leaves* opposite; blade elliptic to elliptic-oblong or obovate, 7–14.5 × 3–6 cm, at base cuneate to acute, at apex obtuse to rounded or subtruncate and sometimes with acuminate tip 1–3 mm long, drying chartaceous to coriaceous, adaxially and abaxially glabrous; secondary veins 6–9 pairs, extending to near margins, without domatia, with 1–2 well-developed intersecondary veins present between pairs of secondary veins, with costa and secondary veins thickened to prominulous adaxially and prominent abaxially, with tertiary and quaternary venation laxly reticulated and prominulous adaxially and sometimes abaxially; petiole 1.2–3 cm long, glabrous; stipules shortly united around stem, persistent or caducous, glabrous, with interpetiolar portion triangular and sometimes becoming broadly triangular to subtruncate with age (as stipule is stretched due to stem diameter increase), 3–4 mm long, obtuse to acute or acuminate, abaxially glabrous and sometimes costate, with intrapetiolar portion 0.5–2 mm long and sometimes becoming narrower with age (as tissue is stretched around stem). *Inflorescences* axillary or sometimes terminal on short paired axillary stems, cymose to paniculiform, pedunculate, densely puberulous or strigillose to glabrescent; peduncle



Fig. 2. – *Danais* Comm. ex Vent. on Madagascar. A. *Danais magna* Puff & R. Buchner; B. *Danais coriacea* C.M. Taylor [A: Antilahimena 7730; B: Antilahimena 7781] [Photos: A, B: P. Antilahimena]

1–5 cm long; branched portion $4.5\text{--}15 \times 4\text{--}15$ cm, branched to 3 orders, with 3–5 pairs of secondary axes, with flowers borne in subcapitate groups of 3–5, these groups borne at apices of axes; bracts deltate to ligulate, 0.5–1 mm long, strigillose to puberulous or glabrous. *Flowers* subsessile, distylous; hypanthium obconic, c. 1 mm long, densely puberulous to strigillose; calyx limb densely puberulous to strigillose, 1–1.2 mm long, 5-lobed for about half its length, lobes deltate; corolla funnelform, white or sometimes with yellow lobes, externally glabrous, tube 3–3.5 mm long, 1.2–1.8 mm in diam. near middle, without slits at base, internally glabrous in basal half and densely pilose or hirsute in upper half and throat, lobes 5, ligulate, 2–2.5 mm long, acute, plane at tip; anthers narrowly ellipsoid, in short-styled form 1–1.2 mm long and exserted on well-developed filaments, in long-styled form c. 1.5 mm long, exserted, and positioned just above top of corolla tube; stigmas linear, 1.2–1.5 mm long, in short-styled form exserted and positioned just above top of corolla tube, in long-styled form well exserted. *Fruits* ellipsoid, $3\text{--}3.5 \times 2.5\text{--}3.5$ mm, weakly laterally flattened, glabrous but with surface granular, woody, with smooth rounded beak portion c. 1 mm high; seeds rhombic to irregularly angled in outline, flattened, 0.5–1 mm long, central seed portion elliptic and smooth, marginally with irregular lacerate wing.

Etymology. – The species epithet refers to the relatively thick texture of the leaves that is an uncommon character in *Danais*.

Distribution and ecology. – This new species is found in lowland and medium altitude moist evergreen forests between 606–990 m in central eastern Madagascar (Reg. Atsinanana [Prov. Toamasina]).

Conservation status. – *Danais coriacea* is known from only three recent collections dating from 2006 to 2011. These collections represent three unique occurrences, two populations, and two locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 23 km², within the limits for “Critically Endangered” under IUCN Red List Criterion B1; and the AOO is estimated at 8 km², also within the limits for “Critically Endangered” under Criterion B2 (IUCN, 2012). Of the three known collections, two are from the area near the summit of Ankerana massif and are considered a single location (sensu IUCN, 2022) with regard to the most likely serious threat. Ankerana Massif is part of the Ankeniheny Zahamena Corridor (IUCN category VI, natural resources reserve), a large, protected area in eastern Madagascar. This site is threatened by slash-and-burn agriculture, illegal mining (quartz, pink beryl, gold), and illegal logging (for *Dalbergia* L. f. species, *Fabaceae*). The protected site was designated in 2015, but a loss of 6.6% in forest cover has been reported from 1996–2016 (GOODMAN et al., 2018). The remaining collection is from the area of Ambinanindrano II, which is not a formally protected area and thus is considered a separate locality; it is one of the main areas of sugar cane plantations in the region. Only two documented locations for this species meet the IUCN criterion for “Endangered”; however, one locality is in an unprotected area subject

to threat from plantation and shifting agriculture practices as well as human settlement, potentially decreasing suitable habitat. The species has not been collected at this locality since 2006 and may no longer be extant there. A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, and the number of locations and *D. coriacea* is assessed as “Critically Endangered” [CR B1ab(i,ii,iii,iv)+2ab(i,ii,iii,iv)].

Notes. – *Danais coriacea* is characterized by opposite, petiolate, stiff-textured leaves; triangular to subtruncate stipules that are shortly fused around the stem; axillary, pedunculate, cymose inflorescences with the flowers subsessile in congested groups; a relatively small, funnelform, white to yellow corolla; and relatively small, subglobose capsules with relatively small seeds. This species is unusual in *Danais* in its relatively thick-textured leaves and white flowers. The woody capsules are closely clustered on the infructescence, but do not appear to become fused as in some *Danais* species.

Danais coriacea is similar to *D. longipedunculata* (Fig. 3B), which is the only other species of the genus with stipules fused around the stem. *Danais longipedunculata* can be separated by its corollas with the tube dull purple to brown or blackened and 5–6 mm long, and the lobes usually bright yellow to red. *Danais coriacea* is also similar to *D. aurantiaca* (Fig. 3A) which can be separated by its interpetiolar stipules, leaves with the higher-order venation closely densely reticulated and prominent adaxially, and bright orange to red corollas with the tube 4–9 mm long.

Additional specimens examined. – MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Distr. Brickaville, Comm. Maroseranana, Fkt. Ambodilendemy, vers le sommet d’Ankerana, 18°25’42”S 48°46’57”E, 816 m, 19.III.2011, Ravelonarivo et al. 3715 (MO, P, TAN); Distr. Vatmandry, Ambalabe, Ambinanindrano II, à l’W de Toby Foara, 19°09’53”S 48°34’33”E, 606 m, 19.IX.2006, Razanatsima 167 (MO, P, TAN).

8. *Danais fragrans* (Lam.) Pers., Syn. Pl. 1: 198. 1805.

= *Paederia fragrans* Lam., Encycl. 2: 260. 1786.

– *Danais denudata* Pers., Syn. Pl. 1: 198. 1805 [nom. illeg. superfl.].

Lectotypus (first-step designated by PUFF & BUCHER, 1994: 54; second-step designated here): MAURITIUS: “Isle de France, dans les bois de Palma”, s.d., Commerson s.n. (P-LA [2-part specimen: P [P00308616, P00308619] microfiche 294/17-18!; isolecto-: B [B -W 05104 -01 0] image!, LINN [LINN-HS432-2, LINN-HS432-3] images!, MPU [MPU023584, MPU023587, MPU023588] images!, P [P00539954, P00539953, P00057156] images!).

Distribution and ecology. – This species is found in dry to humid lowland to highland forests on Mauritius and Réunion

Islands (VERDCOURT et al., 1989), and frequently today in or on the edge of forest remnants.

Notes. – *Danais fragrans* is circumscribed markedly more narrowly here than done by VERDCOURT et al. (1989) and PUFF & BUCHNER (1994: 53–56), who both included also in this species many *Danais* plants from Madagascar that we here ascribe to another taxon. In particular, the circumscription of Puff & Buchner included a notably wide range of variation, especially morphologically in inflorescence, flower, and fruit characters, and in ecological range. The morphological description presented by Puff & Buchner for *D. fragrans* was apparently based only on plants from Madagascar, where they studied this genus. Their treatment cited also names from the Mascarenes but did not apparently incorporate morphological features from those plants, except they noted (PUFF & BUCHNER, 1994: 55) in commentary that the plants from these two regions generally differ in flower and fruit size. The plants from Madagascar and the Mascarenes that were said to belong to the same species do not seem to have been directly studied together taxonomically until recently, when they were analyzed with molecular data by KRÜGER et al. (2012) and RAZAFIMANDIMBISON et al. (2022). Those studies found them separated into two lineages, with one lineage in each region. Morphological review here finds the plants of these two regions to be generally morphologically separable, although some individual features of some plants in each region are similar to those of some plants of the other region so the full descriptions of these two groups have some overlapping characteristics. The plants of these two regions are formally separated taxonomically here as *D. fragrans*, found in the Mascarenes, and *D. lyallii*, found on Madagascar (RAZAFIMANDIMBISON et al., 2022; Fig. 3C). A description and nomenclatural synonymy of *D. fragrans* corresponding to its circumscription here were presented by VERDCOURT et al. (1989: 41).

Danais lyallii differs from *D. fragrans* by its leaf blades that dry with a chartaceous to subcoriaceous texture, salverform to broadly funnelform corolla tubes 2–6 mm long, and stiffly chartaceous to woody fruits, vs. leaf blades drying papyraceous to chartaceous, salverform corolla tubes 5–10 mm long, and chartaceous to papery fruits in *D. fragrans*. *Danais fragrans* is also similar to *D. xanthorrhoea* of Tanzania, in continental East Africa, which has a corolla tube 2.5–6 mm long. All three of these species are rather weakly distinguishable morphologically, in spite of their clear molecular separation (RAZAFIMANDIMBISON et al., 2022). *Danais fragrans* and *D. xanthorrhoea* are the most widely separated species geographically in the genus, and by far the most similar species pair in *Danais*. Their close but apparently homoplasious morphological similarity may be informative, when the genus is



Fig. 3. – *Danais* Comm. ex Vent. on Madagascar. **A.** *Danais aurantiaca* Homolle; **B.** *Danais longipedunculata* Homolle; **C.** *Danais lyallii* Baker; **D.** *Danais antilahimena* C.M. Taylor.

[**A:** Razafimandimbison et al. 1035; **B:** Ravelonarivo 4278; **C:** Kainulainen et al. 123; **D:** Schatz 3386]

[Photos: **A:** S. Razafimandimbison; **B:** D. Ravelonarivo; **C:** K. Kainulainen; **D:** G. Schatz]



Fig. 4. – Holotype of *Danais coriacea* C.M. Taylor.
[Antilahimena 7781, MO-6407815; © Missouri Botanical Garden, St. Louis]

better understood, about diversification and adaptive potential in *Danais*.

The original material corresponding to this name comprises several specimens. The protologue treated this species under both a common name, “Danaïde odorante”, and the formal binomial *Paederia fragrans*, with only the common name attributed to Commerson. The name *P. fragrans* has been attributed to “Comm. ex Lam.” in various treatments based on this citation, but this does not meet the criteria for ascribing the published name in *Paederia* to Commerson (ICN Art. 46.4). The type collection is represented by a number of specimens, especially in the historical collections of MPU and P, but no individual specimen was denoted as the type in the protologue nor annotations by Lamarck so these must be considered syntypes. PUFF & BUCHNER (1994: 54) cited the “holotype” of this name as deposited in P-LA along with isotype material in P, which constitutes a first-step lectotypification. There are six specimens from Mauritius in Lamarck’s herbarium (P-LA), which are imaged online and also photographed in the microfiche of that herbarium (BURNS-BALOGH, 1987). One of these is attributed to Joseph Martin (1760?–1826) as “Jos. Mart.”, and three lack any collector information although one has the number “499”. Two other flowering specimens there are curated with one label, and so comprise a two-part specimen. This label has the locality information “Isle de Fr.” for Isle de France, now Mauritius, and “Com.^{on}” for Commerson in Lamarck’s hand. It is the only one in either Lamarck’s herbarium or other general collections that is also annotated with “danaïde odorante”. This P-LA specimen agrees with the protologue and is therefore designated here as the lectotype. Two specimens at MPU originating from Cambessèdes’s herbarium [MPU023588, MPU023584] and another in the general collection there [MPU023587], one in LINN [LINN-HS432-2], and one in the P general collection [P00057156] also correspond to this gathering, and have flowers, original label data with the locality information as given in the protologue, Commerson as the collector, and no conflicting dates so these are apparently isoelectotypes. Additional specimens of this species are attributed to Commerson in various collections, and some of these were also cited as isotypes by PUFF & BUCHNER. Most of those are labelled only with information copied from the protologue of *P. fragrans*. Several of these match the lectotype and isoelectotypes in condition and leaf size and lack conflicting information, and also seem to be isoelectotypes. Some other specimens are curated as possible types of this name but are not here confirmed as isoelectotypes. One at B-W [B-W 05104 -01 0] lacks any collector information and is in fruit while the confirmed Commerson collection comprises only flowering stems. One specimen at MPU [MPU023586] is curated as a type but lacks confirming label data. Two other specimens curated as possible types seem to have instead been collected after *P. fragrans* was described,

one at BM [BM001024823] that is labelled as collected in 1810 and one at K [K000395000] that corresponds to Sieber’s collecting trip to Mauritius in the 1820’s.

9. *Danais gracilis* C.M. Taylor, **sp. nov.** (Fig. 5).

Holotypus: MADAGASCAR. **Reg. Analanjirifo [Prov. Toamasina]:** Distr. Maroantsetra, 5 km E of Sabavary village, 15°19'11"S 49°50'40"E, 180 m, 30.VIII.2009, *Ralimanana, Andrianainvoravelona, Mananjandry & Jaovita 1231* (MO-6593981!; iso-: BR, G [G00415957]!, K, TAN).

Danais gracilis C.M. Taylor is distinguished from *D. terminalis* Boivin ex Drake by its leaf blades with the higher-order venation closely regularly reticulated and prominulous adaxially, and regularly axillary inflorescences with shorter peduncles and pedicels.

Climbing plants, to 3 m high; stems glabrous, weakly flattened becoming terete. *Leaves* opposite; blade ovate to elliptic, 4.2–10 × 2.2–5 cm, at base acute to usually obtuse, at apex acute to acuminate with tip 5–23 mm long, drying stiffly chartaceous, on both surfaces glabrous, abaxially with epidermis comprising relatively large cells; secondary veins 4–6 pairs, looping to interconnect, without domatia, with 1–2 weakly developed intersecondary veins present between pairs of secondary veins, with costa and secondary veins adaxially thinly sulcate, abaxially costa, secondary, and sometimes intersecondary veins prominent and remaining venation closely regularly reticulated and prominulous on both surfaces; petiole 0.6–1.4 cm long, glabrous; stipules interpetiolar, persistent, glabrous, broadly triangular, 1–1.5 mm long, obtuse and shortly apiculate. *Inflorescences* axillary, cymose or fasciculate, 3- or 5-flowered, pedunculate, glabrous; peduncle 0.2–0.5 cm long, articulated near middle, with 1–2 peduncles arising from an apparently persistent inflorescence base; branched portion umbelliform or branched to 1 order with 1 pair of secondary axes; bracts narrowly triangular, 0.3–0.5 mm long, glabrous; pedicels 3–7 mm long, sometimes articulated. *Flowers* pedicellate, whether distylous unknown; hypanthium ellipsoid, c. 1 mm long, glabrous; calyx limb glabrous, c. 0.5 mm long, deeply 5-lobed, lobes narrowly triangular; corolla salverform, pink to white, pale green, or orange, externally glabrous, tube 16–18 mm long, c. 0.5 mm in diam. near middle, with slits at base, internally glabrous except pilosulous in upper ¼, lobes 5, narrowly ligulate, 5–5.5 mm long, obtuse to acute, fleshy, plane at tip; anthers in long-styled form narrowly oblong, c. 1.8 mm long, positioned at top of corolla tube; stigmas linear, in long-styled form 4–5 mm long and well exerted. *Fruits* not seen.

Etymology. – The species epithet refers to the relatively very slender corolla tubes.

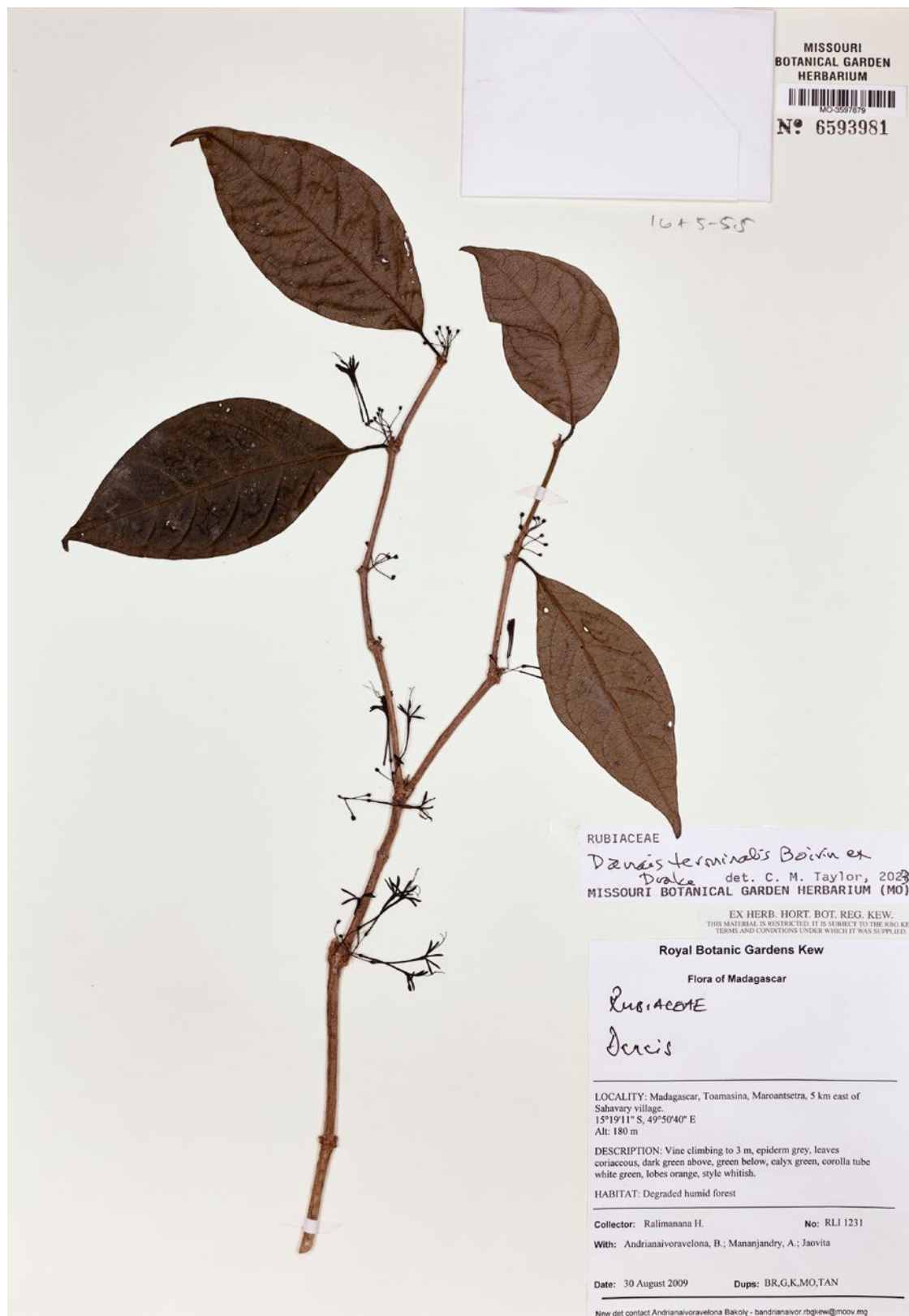


Fig. 5. – Holotype of *Danais gracilis* C.M. Taylor.
[*Ralimanana* 1231, MO-6593981; © Missouri Botanical Garden, St. Louis]

Distribution and ecology. – This new species is found in lowland moist evergreen forest at c. 180 m in east central Madagascar (Reg. Analanjirofo [Prov. Toamasina]).

Conservation status. – *Danais gracilis* is known from only two recent collections dating from 2003 and 2009. These collections represent two unique occurrences, one population, and one location (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 0 km²; however, if EOO is less than AOO, EOO should be changed to make it equal to AOO to ensure consistency with the definition of AOO as an area within EOO (IUCN, 2012). Thus, the EOO is adjusted here to equal 8 km², the estimated area of occupancy (AOO). Both the EOO and AOO are within the limits for “Critically Endangered” under IUCN Red List Criterion B1 and B2 (IUCN, 2012). Both of the known collections are in the Farankaraina Forest area, a community-managed forest without formal protection status. Forests without formal protection on the Masoala Peninsula are subject to degradation by small-scale slash-and-burn agriculture (tavy) and resource exploitation, including logging, hunting and mining (GOODMAN et al., 2018). A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations and the number of mature individuals, and *D. gracilis* is assessed as “Critically Endangered” [CR B1a b(i,ii,iii,iv,v)+B2ab(i,ii,iii,iv,v)].

Notes. – *Danais gracilis* is characterized by opposite, petiolate, medium-sized leaves, with the higher-order leaf venation closely regularly reticulated and prominulous on both surfaces and the secondary veins sulcate adaxially; axillary, umbelliform inflorescences borne on short articulated peduncles and with three to five pedicellate flowers; and medium-sized, notably slender corollas that are variously pale green or pink to white and/or orange. This species is known only from two collections, but these match each other and were made some years apart at different localities in the same region, which is not well explored botanically. *Danais gracilis* has very slender corolla tubes even for this genus that are distinctive. The label data on both specimens of this new species describe differing colors on the buds, tube, and lobes, as in most species of *Danais*, but vary in the colors noted. Such variation in corolla color has been reported in several *Danais* species with corollas of similar shape and size (PUFF & BUCHNER, 1994), none of which have been studied in the field for this. The fruits of *D. gracilis* are not yet documented, but the flowers and inflorescences distinguish this new species within *Danais*.

Danais gracilis is similar to *D. terminalis*, which is found in the same general region and, in contrast, only known in fruit. *Danais terminalis* can be separated from *D. gracilis* by its narrower leaf blades, 1–2.8 cm wide, with the venation weakly and

laxly reticulated and plane or only irregularly thickened, along with its usually terminal inflorescences with longer peduncles, 2–3.8 cm long.

Additional specimen examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Distr. Maroantsetra, comm. Anjahana, Fkt. Andranofotsy, Farankaraina forest, 15°26'30"S 49°51'00"E, 11.VI.2003, *Antilabimena* 1985 (MO, P, TAN).

10. *Danais hispida* Baker in J. Linn. Soc., Bot. 20: 161. 1883.

Lectotypus (designated here): MADAGASCAR: “Central Madagascar, in forests of the province of Imerina”, s.d., *Baron 1304* (K [K000046174] image!; isolecto: K [K000046175] image!).

Distribution and ecology. – This species is found in medium altitude moist evergreen forest in the Central Plateau of Madagascar.

Notes. – *Danais hispida* is characterized by its combination of paired leaves, triangular stipules that are densely ciliate marginally, cymose inflorescences that range from shorter than to about as long as the leaves, a corolla tube 3.5–6 mm long, and fruits 5–6 mm in diameter with papery walls. PUFF & BUCHNER (1994: 61) included in this species plants with the leaves and stems variously “covered with long multicellular hairs” and “hairy to more or less glabrous”, but the pubescence is characterized in more detail here as villosulous, hirtellous, or hispid and generally persistent. PUFF & BUCHNER (1994: 62) reported that *D. hispida* was poorly documented and no modern material had been seen by them, and suggested it may be extinct due to the extensive habitat destruction of the Central Plateau of Madagascar. No modern specimens of *D. hispida* have been seen in this study. Puff & Buchner also noted that this species is similar to *D. cernua*, so it may be confused with that common species in some herbaria although the pubescence and stipules clearly separate it.

Puff & Buchner annotated two specimens of *Baron 1304* at K as the “holotype” [K000046175] and “isotype” [K000046174] of *Danais hispida*, and cited these two specimens (PUFF & BUCHNER, 1994: 61) as such. No individual specimen was identified as the type of *D. hispida* in the protologue or annotations by Baker, so these must be considered syntypes. No conclusive identifying information for the individual type specimens was cited by Puff & Buchner in their published treatment either, so that citation cannot be considered as an inadvertent lectotypification. Accordingly, *D. hispida* is typified here. The specimen annotated by Puff & Buchner as the isotype bears an original label of Baron’s with the number 1304 with an annotation with this species name, apparently by Baker, and a note that the specimen was sent to K in 1882; two stems with well-developed infructescences and fruits; and an annotation that this specimen is the type of this name with

the protologue reference in an unidentified hand that may be Sandwith's. This specimen seems to effectively represent the holotype, because it was apparently available at K to Baker before *D. hispida* was described in 1883. The other specimen at K was annotated by Puff & Buchner as the holotype, but this may be problematic. This second specimen has one stem in good condition; a hand-written and hand-drawn morphological analysis of the plant; and a similar label to the other specimen identifying this as *D. hispida* and as *Baron 1304* from Central Madagascar but noting that this was purchased by K in June 1889. This second specimen seems to be a duplicate of the other and part of the type gathering, but perhaps not available to Baker before this species was described. These two specimens seem to logically represent the holotype and an isotype of *D. hispida*, but this is reverse of the interpretation of Puff & Buchner, so this name is lectotypified here for clarity.

11. *Danais longipedunculata* Homolle in Notul. Syst. (Paris) 5: 285. 1936 (Fig. 3B).

Lectotypus (designated here): **MADAGASCAR. Reg. Alaotra-Mangoro [Prov. Toamasina]:** forêt d'Anamalazaotra, 800 m, s.d., *Perrier de la Bâthie 6930* (P [P00057171] image!; isolecto-: P [P00057172] image!).

= *Danais masoalana* C.M. Taylor in Candollea 68: 175. 2013, **syn. nov. Holotypus: MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]:** Masoala Peninsula, S of Ambanizana, Andranobe, Piste A, 15°41'S 49°58'E, 50 m, 12.II.1999, *Hoffmann, Robinson, McPherson & Harimalala 36* (MO-5938276!; iso-: G [G00369979]!, K, TAN).

Distribution and ecology. – This species is found in lowland and medium altitude moist forest from sea level to 1200 m, from northeastern to southeastern Madagascar (Reg. SAVA [Prov. Antsiranana], Reg. Analamanga [Prov. Antananarivo], Reg. Analanjirofo and Alaotra-Mangoro [Prov. Toamasina], Reg. Atsimo-Atsinanana [Prov. Fianarantsoa], Reg. Anosy [Prov. Toliara]).

Notes. – *Danais longipedunculata* is characterized by opposite, petiolate, elliptic to usually obovate leaves; distinctive tubular stipules; lax, axillary, pedunculate, cymose inflorescences; and slender corollas with the tube dull- or dark-colored and 5–6 mm long and the lobes generally yellow to red. The stipules are subtruncate to triangular and 2–5 mm long, and are initially fused around the stem in a tubular sheath 0.5–1 mm long. With age the upper, interpetiolar portion of the stipule usually is deciduous, and the intrapetiolar portion of the sheath tardily splits as the stem enlarges so the stipule form can be mistaken if only older nodes are studied. This tubular stipule form is unusual in *Danais* and was considered

unique in the genus by PUFF & BUCHNER (1994) but is now also known in *D. coriacea*; see that species for their distinctions.

Danais longipedunculata was known to PUFF & BUCHNER (1994: 31–32) from nine specimens that all have average-sized leaves for *Danais*, and it was characterized by them by its short stipules, 2–2.5 mm long, that are fused around the stem; peduncles they characterized as “long” and “up to 100 mm long” (p. 31); and habitat at 150–1200 m along the eastern escarpment. *Danais masoalana* originally appeared to differ from this in its triangular stipules 4–5 mm long, shorter peduncles 1.5–3.5 cm long, and range in the Masoala Peninsula at 0–400 m, and it was known from only three specimens with relatively large leaves. Additional and more recent specimens now show wide morphological variation in various features, including leaf size, stipule form and size, and peduncle length, and this variation is now documented as continuous, with the extreme forms of the variation sometimes both found on the same collection. Therefore, these species can no longer be separated. *Danais longipedunculata* is now documented across a relatively wide geographic range by more than 25 collections.

Two duplicates of the type collection of *Danais longipedunculata* are curated at P, and both were annotated with this name by Homolle. There is no indication in the protologue or by annotation that one of these was a holotype, so these must be considered syntypes. Puff annotated one of these as the holotype and did not annotate the other. PUFF & BUCHNER (1994: 31) cited the “holotype” as deposited at P, but gave no more identifying information to distinguish which specimen that was so this cannot be considered as an inadvertent lectotypification. A lectotype is designated here, and the specimen annotated as the holotype by Puff is chosen.

12. *Danais lyallii* Baker in J. Linn. Soc., Bot. 22: 481. 1887 (Fig. 3C).

Lectotypus (designated by PUFF & BUCHNER, 1994: 54): **MADAGASCAR:** “Central Madagascar”, s.d., *Baron 3895* (K [K000046124] image!).

= *Danais obovata* Drake in Bull. Soc. Bot. France 45: 348. 1899. **Lectotypus** (designated by PUFF & BUCHNER, 1994: 54): **MADAGASCAR:** sine loco, s.d., *Boivin s.n.* (P [P00057182] image!).

Distribution and ecology. – This species is found widely and frequently on Madagascar, in lowland and medium altitude moist evergreen forest and associated secondary vegetation from sea level to 2000 m, (Reg. Analamanga, Bongolava, Itasy, and Vakinankaratra [Prov. Antananarivo], Reg. DIANA and SAVA [Prov. Antsiranana], Reg. Amoron'i Mania, Atsimo-Atsinanana, Ihorombe, Matsiatra Ambony, and Vatovavy-Fitovinany [Prov. Fianarantsoa], Reg. Sofia [prov. Mahajanga], Reg. Alaotra-Mangoro, Analanjirofo, and Atsinanana [Prov. Toamasina], Reg. Anosy [Prov. Toliara]).

Notes. – *Danais lyallii* is circumscribed markedly differently here from the treatment of PUFF & BUCHNER (1994). This species is characterized by glabrous to puberulous or pilosulous stems and leaves; opposite, petiolate, elliptic to oblanceolate or obovate leaves with the blades drying chartaceous to coriaceous; interpetiolar, triangular stipules that are apically acute to broadly rounded or infrequently bidenticulate; axillary, pedunculate, cymose inflorescences that are shorter than the leaves and often less than half as long as them; a calyx limb 0.3–1 mm long that is lobed for about $\frac{1}{3}$ – $\frac{2}{3}$ of its length; funnelform to salverform, relatively small, orange to red corollas; and stiffly chartaceous to woody capsules 5–8 mm in diameter. The leaf blades are 3–9 × 1.5–6 cm and vary in shape markedly from narrowly elliptic to broadly obovate, and apically in shape from acute to acuminate, obtuse, or sometimes rounded to subtruncate with a short (3–5 mm long), abruptly narrowed tip. The venation is laxly reticulated and prominulous adaxially, and the blade is usually shiny on both surfaces. The corollas also vary in size and form, as detailed below, but overall have a tube 2.5–6 mm long and lobes 1.5–4 mm long, with basal slits sometimes present on the tube.

As noted in the discussion above of *Danais fragrans*, the plants here treated as *D. lyallii* were included previously within the circumscription of that other species (VERDCOURT et al., 1989; PUFF & BUCHNER, 1994); see the discussion there for their distinctions. And, as noted in the discussion of *D. cernua*, PUFF & BUCHNER (1994: 53–56) also included in *D. fragrans* some plants but here separated into *D. cernua*; see the discussion of *D. cernua* for the separation of that other species from *D. lyallii*. Even with these taxonomic changes, *D. lyallii* is still the most morphologically variable, commonly collected, and widely distributed species of *Danais* on Madagascar.

Three groups of plants can be generally characterized within *Danais lyallii* and may represent diversifying forms although they are not fully distinguishable morphologically. These are noted here for further study:

- Most of the plants included here in *Danais lyallii* agree with the circumscription of PUFF & BUCHNER (1994, as *D. fragrans*), and have leaf blades that are generally obovate to broadly elliptic, obtuse to subtruncate at the apex sometimes with a short acuminate tip, stiff-textured to coriaceous when dry, and relatively larger compared to the full size range of the species; stipule margins that are entire or more often densely ciliolate; and a funnelform corolla with the tube 2.5–5 mm long and the lobes usually half or more as long as the tube, 1.5–3 mm long. These corollas are rather slenderly funnelform, with the throat at most twice as wide as the base. These plants are found at 0–1770 m widely from northern to southern Madagascar and match the types of *D. lyallii* and *D. obovata*.
- Another group of plants included here in *Danais lyallii* has leaf blades that are obovate to oblanceolate, acute to

rounded and acuminate at the apex, chartaceous when dry, and relatively smaller compared to the full size range of the species; stipule margins that are densely ciliolate; and a salverform corolla with the tube 4–6 mm long and the lobes 1.5–4 mm long. These corolla tubes are cylindrical, but wide enough in diameter to accommodate the included anthers without an abrupt distal swelling. These plants are found at 700–2000 m from northern to central-southern Madagascar (e.g. *Anderberg et al.* 18, *Leeuwenberg* 14209, *Razanatsoa* 26). These correspond to some of the plants that were included in *D. cernua* by PUFF & BUCHNER (1994) that are here treated as *D. lyallii* (e.g. *Croat* 29469, *Dorr et al.* 4566).

- A last group of plants included here in *Danais lyallii* is similar to the preceding group in its leaves and stipules but has corollas with a stout funnelform tube 2.5–3.5 mm long and more than twice as wide at the throat as at the base, and corolla lobes that are always more than half as long as the tube and often almost as long. These plants are also found widely from northern to southern Madagascar and from 60–1600 m. This group includes plants that can easily be keyed incorrectly as *D. cernua* in PUFF & BUCHNER's (1994) treatment (e.g. *Antilabimena* ♂ *Félix* 3160, *Antilabimena et al.* 3245, *Leeuwenberg et al.* 14480), and these are the plants that have contributed significantly in practice to the confusion over the identity and circumscription of *D. lyallii*.

13. *Danais nigra* Homolle in Notul. Syst. (Paris) 5: 286. 1936.

Lectotypus (first-step designated by PUFF & BUCHNER 1994: 45; second-step designated here): **MADAGASCAR.** **Reg. DIANA [Prov. Antsiranana]:** Bas Sambirano, IV.1924, *Perrier de la Bâthie* 16277 (P [P00057178] image!; islecto-: P [P00057179, P00057180] images!).

Climbing plants, climbing to 8 m high; stems glabrous or puberulous, weakly flattened becoming terete. *Leaves* opposite; *blade* ovate, 5–8 × 1.8–4 cm, at base obtuse to rounded, at apex acute to acuminate with tip 6–10 mm long, drying stiffly chartaceous to subcoriaceous, adaxially glabrous, abaxially glabrous to puberulous; secondary veins 5–10 pairs, weakly to well differentiated from higher-order venation, weakly looping to interconnect near margins, without domatia, sometimes with 1 weakly developed intersecondary vein present between pairs of secondary veins, adaxially with costa sulcate and secondary and tertiary venation laxly, sparsely, regularly reticulated and plane to thickened, abaxially costa and sometimes secondary veins prominent and remaining venation plane to thickened; petiole 0.3–0.7 cm, glabrous to puberulous; stipules interpetiolar, persistent or tardily deciduous, glabrous, broadly triangular, 1–2 mm long, acute or apiculate, sometimes becoming indurated with age. *Inflorescences* terminal and also axillary

along lower parts of stems, laxly cymose, pedunculate, puberulous; peduncle 0.8–3.5 cm long, flexuous, often articulated in lower half, axillary peduncles sometimes borne from apparently persistent inflorescence bases; branched portion 2–4 × 2–5 cm, umbelliform or branched to 1 order with 1 pair of secondary axes, with 3–9 flowers in cymes of 3–5; bracts narrowly triangular to linear, 1–3.5 mm long, puberulous; pedicels 6–15 mm long. *Flowers* pedicellate, whether distylous unknown; hypanthium ellipsoid, c. 1.2 mm long, puberulous; calyx limb puberulous, 5-lobed to base, lobes narrowly triangular to linear, 0.5–3 mm long and unequal on an individual flower, at least some lobes 1.5 mm long or longer; corolla salverform, dull to dark red or dark purple, externally glabrous, tube 16–18 mm long, c. 0.8 mm in diam. near middle, with slits at base, internally glabrous except densely pilosulous in uppermost 2.5 mm, lobes 5, narrowly triangular, 7–8 mm long, acute, fleshy, plane at tip; anthers narrowly oblong, in long-styled form c. 3 mm long, included, positioned at top of corolla tube; stigmas linear, in long-styled form c. 3 mm long and well exerted on slender style. *Fruits* oblate to ellipsoid, c. 6 mm in diam., chartaceous, glabrous, with truncate top; seeds not seen.

Distribution and ecology. – This species is found in lowland moist evergreen forest from 40 to 310 m in northern Madagascar (Reg. DIANA [Prov. Antsiranana]).

Notes. – *Danais nigra* is characterized by a slender, laxly twining habit; opposite, petiolate leaves with ovate, stiff-textured blades with the higher-order venation adaxially plane to thickened; short interpetiolar stipules that are triangular and acute or sometimes apiculate; pedunculate, lax, terminal and axillary inflorescences with well-developed axes and flexuous pedicels; relatively well-developed, narrow calyx lobes; and slenderly salverform, dark purple to dark red corollas with a well-developed tube. The stems are notably flexuous and laxly branched. The few flowering specimens all agree with the long-styled form of *Danais* species, but whether this species is distylous cannot yet be confirmed.

Danais nigra is circumscribed differently here than done by PUFF & BUCHNER (1994), and in particular, more narrowly. They included in this species plants from east-central to northwestern Madagascar and reported it from a wide range of habitats with a wide range of corolla colors. The type of *D. nigra* is from northwestern Madagascar, and this species is circumscribed here to include only plants from that region, which are morphologically consistent and distinct from those of the east-central region. This second, east-central group of plants does not match any other named species of *Danais* and is newly described here as *D. puffiana* Razafim. & C.M. Taylor (see below). That new species differs from *D. nigra* in its leaf blades adaxially with the costa prominulous and the higher-order venation prominulous and regularly reticulated; larger

inflorescences, with 12 to 36 flowers, and shorter pedicels, half or less as long as those of *D. nigra*; and a yellow to pale purple, internally glabrous corolla tube. PUFF & BUCHNER (1994: 46) tentatively also included *D. perrieri* Homolle in their circumscription of *D. nigra*, but this species is also distinct as outlined in its treatment below.

Danais nigra is also similar to *D. rubra*, which is known only in flower and can be separated by its leaf blades with the higher-order venation densely closely reticulated and prominulous on both surfaces, shorter calyx lobes 0.5–0.8 mm long, and shorter corollas, with the tube 7.5–8.5 mm long. *Danais nigra* is also similar to *D. terminalis*, which is only known in fruit; *D. terminalis* can be separated by its elliptic to elliptic-ovate leaves, calyx limb with deltate lobes 0.5–1 mm long, and allopatric range in central eastern Madagascar.

Two syntype collections were cited in the protologue of *Danais nigra*: Perrier de la Bâthie 3830 and 16277. PUFF & BUCHNER (1994: 45) cited the latter as the lectotype. Three duplicates of the latter collection are deposited at P. Thus, a second step lectotypification is necessary and P00057178 annotated by Puff & Buchner as lectotype is here designated as such.

14. *Danais ovata* C.M. Taylor, **sp. nov.** (Fig. 6).

Holotypus: MADAGASCAR. Reg. Alaotra-Mangoro [Prov. Toamasina]: Distr. Moramanga, Andasibe, Menalamba, Ambatovy forest, 18°49'38"S 48°18'48"E, 1205 m, III.2005, *Antilabimena*, *Andriantiana* & *Félix* 3725 (MO-6406412!; iso-: G [G00415958]!, P [P04541056] image!, TAN).

Danais ovata C.M. Taylor is distinguished from *D. tsaratananensis* Homolle by its regularly axillary as well as sometimes terminal inflorescences, longer pedicels, larger corollas, and flowers with the stamens and stigmas all partially or fully included.

Climbing plants, extensively twining, climbing to 7 m high; stems glabrous, weakly flattened becoming terete. *Leaves* opposite; blade ovate, 2.5–9 × 1–4 cm, at base rounded to usually truncate or cordulate, at apex acute to acuminate with tip 5–12 mm long, drying stiffly chartaceous to subcoriaceous, on both surfaces glabrous and shiny; secondary veins 5–6 pairs, weakly differentiated from higher-order venation, weakly looping to interconnect near margins, without domatia, with 1–2 weakly developed intersecondary veins present between pairs of secondary veins, with costa thinly prominulous adaxially and prominent abaxially, with remaining venation regularly, laxly reticulated and prominulous on both surfaces; petiole 0.4–1.5 cm long, glabrous; stipules interpetiolar, persistent, glabrous, broadly triangular to truncate, 0.2–1 mm long, obtuse and apiculate or reduced to a thickened line, perhaps glandular. *Inflorescences* axillary and sometimes terminal, cymose to paniculiform, pedunculate, glabrous;

peduncle 0.5–2.5 cm long, flexuous, articulated at base and sometimes also near middle, axillary peduncles borne from an apparently persistent inflorescence bases; branched portion 1–5 × 1–3 cm, branched to 1 order, with 1–2 pairs of secondary axes, with flowers solitary on a peduncle or in lax cymes of 3 (or sometimes 5); bracts narrowly triangular, 0.5–1.5 mm long, glabrous; pedicels 6–25 mm long. *Flowers* pedicellate, distylous; hypanthium ellipsoid, c. 0.8 mm long, glabrous; calyx limb glabrous, 0.8–1 mm long, 5-lobed shallowly or for up to half its length, lobes deltate to narrowly triangular; corolla salverform, yellowish green to yellowish pink or yellow, externally glabrous, tube c. 18 mm long, c. 0.8 mm in diam. near middle, with slits at base, internally glabrous in basal $\frac{1}{3}$ and pilosulous in upper $\frac{1}{3}$, lobes 5, narrowly triangular, 10–12 mm long, acute, fleshy, plane at tip; anthers narrowly oblong, in short-styled form c. 3 mm long and partially exserted, in long-styled form c. 3 mm long, included, positioned at top of corolla tube; stigmas linear, in long-styled form c. 4 mm long and partially exserted, in short-styled form 1–2 mm long, included, and positioned near middle of corolla tube. *Fruits* ellipsoid to subglobose, 5–10 × 5–10 mm, glabrous, chartaceous to subcoriaceous, with smooth rounded beak portion 2 mm high, with pedicel becoming markedly thickened at top; seeds elliptic to circular, flattened, 2.5–3 mm in diam., central seed portion elliptic and smooth, marginally with narrow lacerate wing 0.2–0.8 mm wide.

Etymology. – The species epithet refers to the ovate shape of the leaf blades.

Distribution and ecology. – This species is found in lowland and medium altitude moist evergreen forest between 200 and 1200 m in eastern Madagascar (Reg. Alaotra-Mangoro, Analanjirofo, Atsinanana [Prov. Toamasina]).

Conservation status. – *Danais ovata* is known from only six recent collections dating from 2002 to 2012. These collections represent six unique occurrences, four populations, and three locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 1,325 km² and the AOO at 12 km². Both the EOO and AOO are within the limits for “Endangered” under IUCN Red List Criterion B1 and B2 (IUCN, 2012). Three of the six occurrences are within the mine footprint of the Ambatovy (Reg. Alaotra-Mangoro) nickel-mining project and have been removed from the dataset for the calculation of assessment parameters due to planned or actual destruction of this habitat. Of the remaining three occurrences, one is from Ankerana forest (Reg. Atsinanana), which has no known formal protection; one is from Miarinarivo Ifasina, along the Onibe River (Reg. Atsinanana), also with no known formal protection; and the northern-most occurrence is from

Maroantsetra, within the Farankaraina Forest (Reg. Analanjirofo), a community-managed forest also without formal protection status. Forests without formal protection on the Masoala Peninsula are subject to degradation by small-scale slash-and-burn agriculture (tavy) and resource exploitation, including logging, hunting and mining (GOODMAN et al., 2018). Each of these three collection sites is considered an individual location, and this low number of locations is within the limits of “Endangered” under the subcriterion ‘a’ of criterion B2 (IUCN, 2012). A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations, and the number of mature individuals, and *D. ovata* is assessed as “Endangered” [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Notes. – *Danais ovata* is characterized by an extensively twining habit; opposite, petiolate leaves with stiff-textured, ovate blades; interpetiolar, broadly triangular stipules that are relatively quite small; axillary and sometimes also terminal (*Antilabimena et al. 1216*), few- to several-flowered, pedunculate, cymose inflorescences with well-developed pedicels; slender, medium-sized, yellowish green to yellow or yellowish pink corollas; and fruiting pedicels that become strongly thickened at the top. The ovate shape of the leaf blades is distinctive and unusually consistent among the specimens of this species, and this feature aids identification of *D. ovata*. The leaf blades are also distinctive in being shiny on both surfaces, with the laxly reticulated tertiary venation usually thickened on both sides. Notably, *D. ovata* differs in its distylous morphology from most species of this genus: in most species the stigma or stamens are fully exserted and held well above the top of the corolla in the corresponding long-styled or short-styled form, with well-developed slender filaments or styles, and these structures are reciprocally positioned but only partially exserted in the corresponding flower forms in this new species.

Danais ovata is similar to *D. tsaratananensis*, which can be separated by its inflorescences that are all terminal and sometimes also produced in the uppermost leaf axils, shorter pedicels 2–3 mm long, smaller corollas, with the tube 8–10 mm long and the lobes 3–4 mm long, and flowers with either the stigmas or the stamens fully exserted and held well above the top of the corolla. These two species are both notable in *Danais* in their distinctive, consistently ovate leaf blades. *Danais ovata* is also similar to *D. terminalis*, detailed below, which is known only in fruit but can be separated by its elliptic to elliptic-ovate leaf blades; mostly shorter petioles, 4–7 mm long; triangular to acuminate stipules 1–1.5 mm long; fruiting pedicels that do not become strongly thickened at the top; and seeds with a broader marginal wing.

Additional specimens examined. – MADAGASCAR. Reg. Alaotra-Mangoro [Prov. Toamasina]: Distr. Moramanga, Antsangimaso, Fkt. Ampitambe, comm. Ambohibary, Ambatovy, 18°51'32"S 48°19'29"E, 1115 m, 24.II.2005,

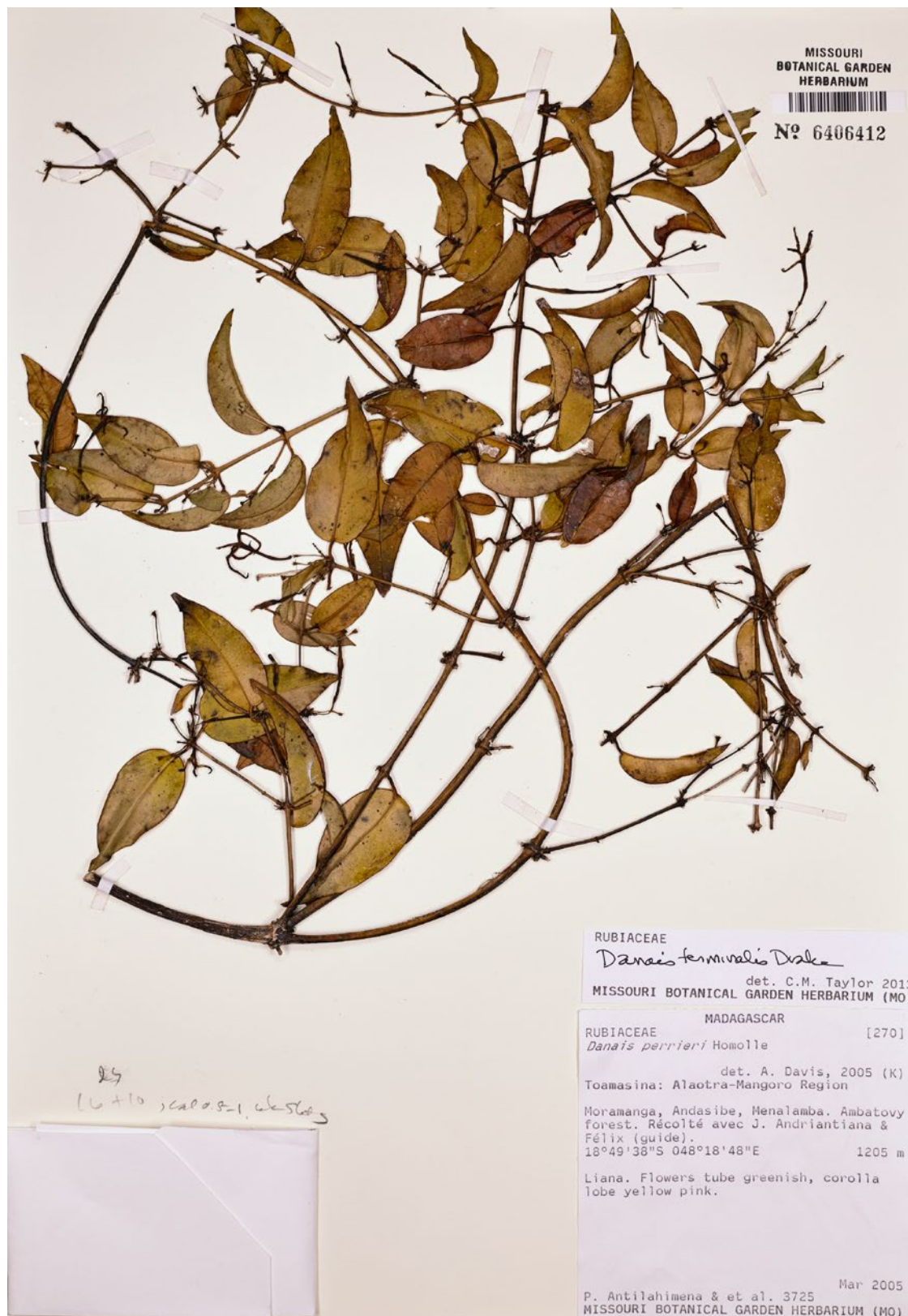


Fig. 6. – Holotype of *Danais ovata* C.M. Taylor.

[Antilahimena et al. 3725, MO-6406412; © Missouri Botanical Garden, St. Louis]

Razanatsoa 293 (MO, P, TAN), 344 (MO, P, TAN); *ibid.*, 18°50'43"S 48°17'22"E, 1044 m, 26.II.2005, *Razanatsoa* 344 (MO, P, TAN). **Reg. Analanjirofo [Prov. Toamasina]:** Distr. Maroantsetra, comm. Anjahana, Fkt. Ambodivangy, 15°25'47"S 49°50'07"E, 200 m, 19.VII.2002, *Antilabimena* et al. 1216 (MO, P, TAN); Distr. Vavatenina, comm. Miarinarivo Ifasina, à 4 km au NO d'Ampasimaventy, le long de la rivière Onibe, 17°44'42"S 48°58'42"E, 300–350 m, 10.VII.2003, *S. Randrianasolo* et al. 392 (MO, P, TEF). **Reg. Atsinanana [Prov. Toamasina]:** Distr. Brickaville, Anjahamamy, Anivoranokely, Ankerana forest, 18°24'50"S 48°49'26"E, 768 m, 28.I.2012, *Antilabimena* 8103 (MO, P, TAN).

15. *Danais perrieri* Homolle in Notul. Syst. (Paris) 5: 286. 1936.

Lectotypus (designated here): **MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]:** Mont Andriantan-tely au Nord d'Anivorano, VI.1922, *Perrier de la Bâthie* 14752 (P [P00057185] image!; isolecto-: P [P00057184, P00057186] images!).

Distribution and ecology. – This species is found in lowland moist evergreen forest between 60 and 70 m in eastern Madagascar (Reg. Atsinanana [Prov. Toamasina], Reg. Vatovavy [Prov. Fianarantsoa]).

Notes. – The identity of *Danais perrieri* has not been entirely clear to recent authors (e.g. PUFF & BUCHNER, 1994), and its seeds are still not known but the type collection can now be matched to another collection that significantly clarifies its identity (*Capuron* 28053-SF, MO). *Danais perrieri* is characterized by opposite leaves with relatively short petioles, 2–5 mm long; ovate to lanceolate leaf blades that dry papery and have tertiary venation that is laxly reticulated and weakly thickened on both surfaces; interpetiolar, variably triangular to bilobed stipules c. 1 mm long that become subtruncate, indurated, and fragmented with age; terminal, pedunculate, cymose, lax inflorescences with 12–30 flowers borne on well-developed pedicels, 3–15 mm long; a calyx limb 0.8–1 mm long that is deeply divided into triangular lobes; slenderly salverform yellow corollas with the tube 13–19 mm long; and thin-textured fruits c. 4 mm in diameter. This newly identified second collection agrees with the first specimen of *D. perrieri*, except perhaps for its stipule morphology. The protologue described the stipules of *D. perrieri* as small and membranaceous, without detailing the size or shape. The stipules on the type collection are not well preserved and not entirely visible in the online scans but seem to vary from triangular to subtruncate and possibly are also bilobed. The stipules on the second specimen are well preserved, and those on younger nodes are variously triangular, bilobed, and subtruncate with well-developed colleters inserted adaxially, while those on older nodes are thickened and subtruncate with, apparently, their upper portion tardily deciduous. Puff & Buchner noted variation within several *Danais* species in stipule form, from acute to bilobed, and this is found in some species studied here

(e.g. *D. lyallii*), so the apparent variation on this specimen does not disagree with the characterization of this species.

PUFF & BUCHNER (1994: 46–47) included *Danais perrieri* in their circumscription of *D. nigra*, and noted some morphological differences between them but commented that the differences did not seem diagnostic. However, the circumscription here of *D. nigra* is substantially changed, and these are no longer similar. *Danais nigra* can now be separated from *D. perrieri* by its chartaceous to subcoriaceous leaf blades, inflorescences with 3 to 9 flowers, dark to dull red or purple corollas, and distribution in northeastern Madagascar. The plants that Puff & Buchner actually confused with *D. perrieri* and used to characterize it are those separated here from *D. nigra* into the new species *D. puffiana*. *Danais puffiana* can be separated by its chartaceous leaf blades with the higher-order venation regularly areolate and prominulous on the adaxial surface, shorter pedicels 0.5–3 mm long, linear calyx lobes, and a distribution centered further north, around the Masoala Peninsula and the escarpment near there.

PUFF & BUCHNER (1994: 46) cited the holotype of *Danais perrieri* as deposited at P, without further specification. Three duplicates of the type collection are curated there, with one of them annotated by Puff as the “holotype”. However all of these are similarly annotated by Homolle as types of this name, and no indication was made on the specimens or in the protologue that one of them was the primary specimen so they must be considered syntypes. Two of these specimens have ample and complete material and full label data, while the third has a small stem and few flowers. The specimen with the most and best material is designated here as the lectotype. This is not the specimen that Puff annotated as the holotype, but it seems preferable as the reference specimen for this name.

16. *Danais puffiana* Razafim. & C.M. Taylor, **sp. nov.** (Fig. 7).

Holotypus: **MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]:** Distr. Maroantsetra, NW coast of Masoala Peninsula, trail along Ampanga River, c. 5 km S of village of Hiaraka, ESE of Maroantsetra, 300 m, 13.X.1986, *Lowry, Rakotozafy & Nicoll* 4100 (MO-3436425!; iso-: K, P [P04004803] image!).

Danais puffiana Razafim. & C.M. Taylor is distinguished from *D. nigra* Homolle by its leaf blades adaxially with the costa prominulous and the higher-order venation prominulous and regularly reticulated, larger inflorescences with 12–36 flowers and shorter pedicels half or less as long as those of *D. nigra*, and an internally glabrous corolla tube.

Climbing plants, climbing to 2 m high; stems glabrous, weakly flattened becoming terete. *Leaves* opposite; blade ovate, 6–13 × 3.5–7.5 cm, at base obtuse to subtruncate, at apex acute to acuminate with tip 5–10 mm long, drying stiffly chartaceous, glabrous on both surfaces, abaxially matte and perhaps pale;

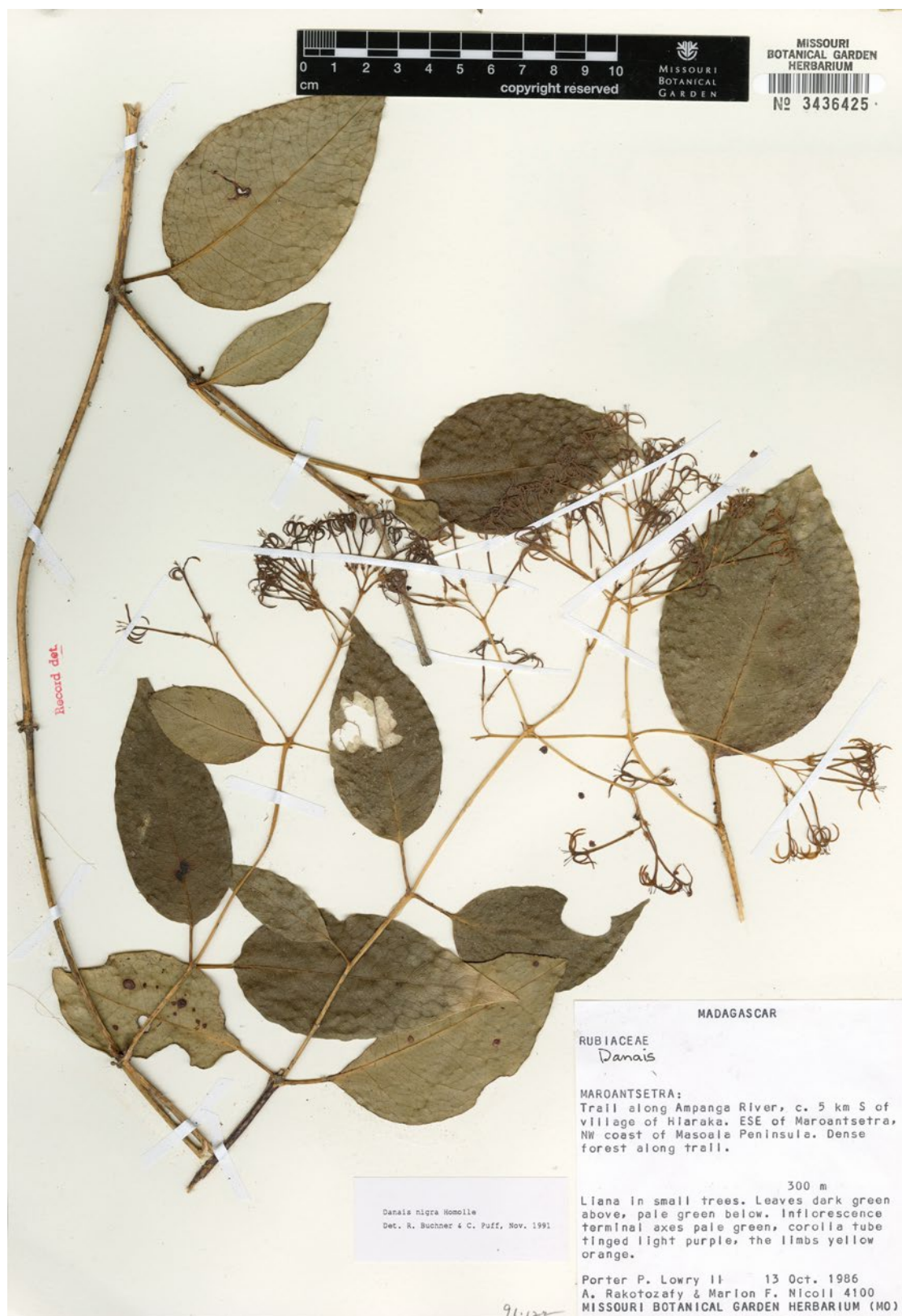


Fig. 7. – Holotype of *Danais puffiana* Razafim. & C.M. Taylor.

[Lowry et al. 4100, MO-3436425; © Missouri Botanical Garden, St. Louis]

secondary veins 5–7 pairs, weakly to well differentiated from higher-order venation, weakly looping to interconnect near margins, without domatia, sometimes with 1 weakly developed intersecondary vein present between pairs of secondary veins, adaxially with costa and secondary veins prominulous and higher-order venation prominulous and reticulated, with areoles irregular in size and shape, 1–3 mm wide, abaxially costa prominent, secondary veins prominulous, and remaining venation thickened to prominulous; petiole 0.8–2.5 cm long, glabrous; stipules interpetiolar, glabrous, basal portion truncate, 0.1–0.2 mm long, persistent, upper portion narrowly triangular, 1–2 mm long, acute, deciduous. *Inflorescences* terminal, laxly cymose, subsessile to pedunculate, glabrous; peduncle 0.1–8.5 cm long, flexuous, not articulated; branched portion 2–8 × 2–16 cm (not including corollas), pyramidal, branched to 2–3 orders with 1–3 pairs of secondary axes, with 12–36 flowers in cymes of 3–5; bracts narrowly triangular to linear, 1–4 mm long, glabrous; pedicels 0.5–3 mm. *Flowers* pedicellate, whether distylous unknown; hypanthium ellipsoid, c. 1 mm long, glabrous; calyx limb glabrous, 5-lobed to base, lobes narrowly triangular to linear, 1–1.5 mm long, subequal on an individual flower; corolla salverform, externally pale purple and glabrous, tube 16–18 mm long, c. 0.8 mm in diam. near middle, with slits at base, internally glabrous, lobes 5, narrowly ligulate, 7–8 mm long, acute, orange-yellow, fleshy, plane at tip; anthers narrowly oblong, in short-styled form c. 1.5 mm long, well exerted; stigmas linear, in short-styled form c. 6 mm long and positioned in uppermost part of corolla tube. *Fruits* subglobose, c. 5 mm in diam., glabrous, weakly pustulose, subcoriaceous, with truncate top, with pedicel becoming thickened and up to 5 mm long; seeds elliptic, flattened, c. 1 mm in diam., central seed portion elliptic and smooth, marginally with narrow lacerate wing 0.2–0.5 mm wide.

Etymology. – The species epithet honors the first author of the previous treatment of Malagasy *Danais*, Prof. Dr. Christian Puff (1949–2013), for his valiant detailing of this genus with a limited specimen representation.

Distribution and ecology. – This new species is found in lowland moist evergreen forest between 205 and 550 m in eastern Madagascar (Reg. Analanjirofo [Prov. Toamasina]).

Conservation status. – *Danais puffiana* is known from only six collections dating from 1986 to 2013. These collections represent six unique occurrences, six populations, and four locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 522 km² and the AOO at 24 km². Both the EOO and AOO are within the limits for “Endangered” under IUCN Red List Criterion B1 and B2 (IUCN, 2012). The northwestern-most location is in the Makira Natural

Park (Reg. Analanjirofo) (IUCN category II, natural park). Though a formally protected area since 2012, Makira is subject to threat from slash-and-burn agriculture (tavy), illegal mining (gold, quartz), and illegal logging for charcoal (GOODMAN et al., 2018). The remaining five collections are along the northwest coast of the Masoala Peninsula. The next two most northern occurrences constitute two locations, are not in Masoala National Park, and do not have protected status. The remaining three occurrences constitute a single location within the Masoala National Park (IUCN category II, national park); however, two of the occurrences are very close to human settlements and occupation (Benjana, Antalavia) near the boundary of the Park, and most likely are subject to threat from subsistence agriculture as well as uncontrolled fires and resource exploitation that includes logging, hunting, and mining (GOODMAN et al., 2018). The low number of locations corresponds to “Endangered” under the subcriterion ‘a’ of criterion B2 (sensu IUCN, 2022). A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations, and the number of mature individuals, and *D. puffiana* is assessed as “Endangered” [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Notes. – *Danais puffiana* is characterized by opposite, ovate leaves with the higher-order venation regularly prominulous and reticulated on the upper surface; interpetiolar stipules with a short sheath portion and the small, triangular upper portion deciduous; terminal, cymose inflorescences with pedicellate flowers; medium-sized, yellow to purple or yellow-orange corollas; and medium-sized capsules. Only one specimen with mature flowers has been seen. Another specimen has buds, and both of these agree with the long-styled form of *Danais* flowers. Only one specimen with developing fruits has been seen, and its fruits are not fused together. Most of the seeds seen are clearly immature but one more mature one matches the elliptic, lacerate-winged seeds of most other *Danais* species. These plants were included within the circumscription of *D. nigra* by PUFF & BUCHNER (1994), but they are separated here as discussed above under *D. nigra*.

Danais puffiana is similar to *D. dauphinensis* Cavaco, which is found in southeastern Madagascar and can be separated by its leaf blades with the higher-order venation plane or only irregularly thickened adaxially and the abaxial surface shiny; shorter calyx lobes, up to 1 mm long but mostly shorter; and white to olive green corollas with shorter lobes, 4–6 mm long. *Danais puffiana* is also similar to *D. terminalis*, which is also found in southeastern Madagascar and can be recognized by its leaves with the higher-order venation abaxially plane or only irregularly thickened; flexuous pedicels 5–20 mm long; and relatively large fruits and seeds, 8–12 mm in diameter and 2.5–4 mm in diameter, respectively. *Danais puffiana* is also similar to *D. perrieri*, see that last species for their distinctions.

Additional specimens examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Distr. Maroantsetra, Masoala Peninsula, S of Ambanizana, Andranobe, 15°41'S 49°58'E, 205 m, 16.II.1999, Hoffmann *et al.* 55 (K, MO); *ibid.*, E of village of Hiaraka, 550 m, 10.X.1986, Lowry *et al.* 4061 (MO); *ibid.*, Ambanizana, 15°37'51"S 49°58'36"E, 233 m, 16.I.2013, Razafimandimbison *et al.* 1245 (MO, S); *ibid.*, c. 3 km N of Antalavia, along Antalavia river, 15°47'S 50°02'E, 200–380 m, 13–16.XI.1989, Schatz *et al.* 2823 (K, P); Makira Protected Area, near Ankirindro, c. 9 km NW of Ambinanitelo, 15°17'44"S 49°33'12"E, 500 m, 22.V.2007, Briggs 183 (K, MO, P).

17. *Danais reticulata* C.M. Taylor, **sp. nov.** (Fig. 8).

Holotypus: MADAGASCAR. Reg. Anosy [Prov. Toliara]: Distr. Taolagnaro [Fort-Dauphin], Antsotso Avaratra, forêt Tsitongambarika, 24°34'16"S 47°12'05"E, 271 m, 1.IV.2008, Razakamalala, Rabenantoandro, Randriatafika, Roger & Mara 4132 (MO-6308607; iso-: P, TAN).

Danais reticulata C.M. Taylor is distinguished from *D. aurantiaca* Homolle by its leaf blades that are not bullulate and have closely densely reticulated higher-order venation that is regularly prominulous on both surfaces, longer stigmas, capsules that do not become fused to each other, and narrowly rhombic seeds.

Climbing plants, climbing to 4 m high; stems glabrous or sometimes densely strigillose, flattened becoming terete. Leaves opposite; blade elliptic to oblanceolate-elliptic, 3–10 × 1.5–4.5 cm, at base cuneate to rounded, at apex obtuse then weakly acuminate to rounded, drying chartaceous to subcoriaceous, adaxially glabrous, abaxially glabrous or moderately to sparsely strigillose; secondary veins 6–8 pairs, weakly differentiated from higher-order venation, usually weakly looping to interconnect near margins, without domatia, sometimes with 1–2 weakly developed intersecondary veins present between pairs of secondary veins, with costa and secondary veins thickened adaxially and prominent abaxially, with tertiary and quaternary venation closely, regularly reticulated and prominulous on both surfaces; petiole 1–2.2 cm long, glabrous or densely strigillose; stipules interpetiolar, persistent, glabrous or densely strigillose, triangular to broadly triangular or subtruncate, 1–2 mm long, broadly obtuse, marginally erose and/or densely ciliate, abaxially glabrous or densely strigillose. Inflorescences axillary, cymose, pedunculate, glabrous; peduncle 1.5–6 cm long; branched portion 1.5–2 × 1.5–3 cm, branched to 2 orders, with 1–2 pairs of secondary axes, with flowers borne in subcapitate groups of 3–5, the groups borne at ends of axes; bracts narrowly triangular to narrowly lanceolate, 1–3 mm long, glabrous. Flowers subsessile, distylous; hypanthium obconic to ellipsoid, c. 1 mm long, glabrous; calyx limb glabrous, 0.5–1 mm long, 5-lobed shallowly or for up to half its length, lobes deltate; corolla salverform, orange, externally glabrous, tube c. 6 mm long, c. 1 mm in diam. near middle, with slits at base, internally glabrous in basal half and pilosulous in upper half, lobes 5, narrowly triangular, 4–5 mm long, acute, plane

at tip; anthers narrowly oblong, in short-styled form c. 2 mm long and exerted on well-developed filaments, in long-styled form included, positioned just above top of corolla tube, and c. 1.8 mm long; stigmas linear, in short-styled form c. 5 mm long and partially exerted, in long-styled form 3.5–4 mm long and well exerted. Fruits subglobose to ovoid, 5–10 × 5–10 mm, glabrous, woody, with smooth rounded beak portion 1–2 mm high; seeds narrowly rhombic, flattened, 2–3 × 1 mm, central seed portion elliptic and smooth, marginally with lacerate wing prolonged on each end.

Etymology. – The species epithet refers to the closely reticulated leaf venation.

Distribution and ecology. – This new species is found in lowland moist evergreen forest, sometimes on basalt, between 116 and 662 m in southern Madagascar (Reg. Atsimo-Atsinanana [Prov. Fianarantsoa], Reg. Anosy [Prov. Toliara]).

Conservation status. – *Danais reticulata* is known from only six recent collections dating from 2007 to 2010. These collections represent six unique occurrences, three populations, and three locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 2,455 km² and the AOO at 16 km². Both the EOO and AOO are within the limits for “Endangered” under IUCN Red List Criterion B1 and B2 (IUCN, 2012). Four of the six occurrences are in the area of Tsitongambarika forest (Reg. Anosy) (IUCN category VI, natural resources reserve), which has protected status since 2015. However, the forest is subject to threats from illegal logging, slash-and-burn agriculture (tavy), hunting, and illegal mining (mica) (GOODMAN *et al.*, 2018). These four occurrences are considered a single location (sensu IUCN, 2022). The fifth, western-most occurrence is within Andohahela National Park (Reg. Anosy) (IUCN category II, national park), a formally protected area. The lowland evergreen forest of Andohahela is subject to threat from slash-and-burn agriculture (tavy), uncontrolled fires, illegal logging and mining for mica (GOODMAN *et al.*, 2018). The last remaining occurrence is to the north of these and located in Ankatriky forest (Reg. Atsimo-Atsinanana), which is part of Ankarabolava Natural Resources Reserve (IUCN category VI, natural resources reserve), a small area protected since 2015. There are threats to this reserve from illegal logging, slash-and-burn agriculture (tavy), clove plantations, and uncontrolled fires (GOODMAN *et al.*, 2018). These last two occurrences constitute two locations, and along with the third location at Tsitongambarika place this species within the limits of “Endangered” under the subcriterion ‘a’ of criterion B2 (IUCN, 2012). A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations, and the

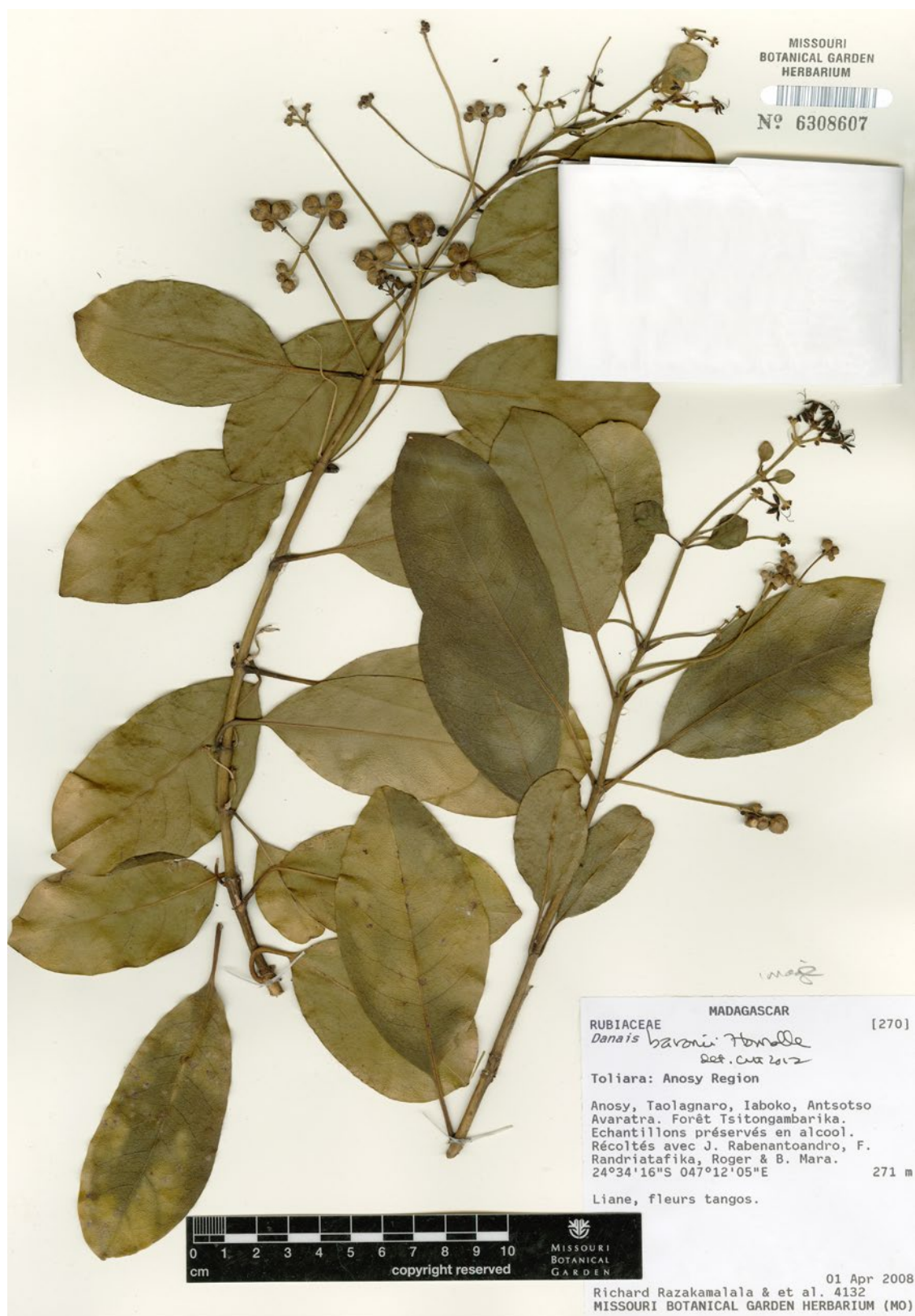


Fig. 8. – Holotype of *Danais reticulata* C.M. Taylor.

[Razakamalala et al. 4132, MO-6308607; © Missouri Botanical Garden, St. Louis]

number of mature individuals, and *D. reticulata* is assessed as “Endangered” [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Notes. – *Danais reticulata* is characterized by its opposite, shiny, elliptic leaves with the higher-order venation closely densely reticulated and prominulous on both surfaces; interpetiolar, triangular to subtruncate stipules; axillary, pedunculate, cymose inflorescences with subsessile flowers; medium-sized orange corollas; woody, free capsules; and narrowly rhombic seeds. Similarly reticulated leaf venation is found in several Malagasy species of *Danais* and aids their identification. Unusually for *Danais*, the inflorescences of *D. reticulata* are glabrous even when the vegetative structures are pubescent (e.g. *Birkinshaw et al.* 1723, MO); in most species these are pubescent even when the vegetative structures are glabrous. The corollas are densely pubescent inside the throat and the upper part of the tube, but the pubescence does not protrude out of the tube in a “beard” as in many species of this genus.

Danais reticulata is similar to *D. aurantiaca* (Fig. 3A) which can be separated by its leaf blades that become at least weakly bullulate between the secondary veins with age; higher-order leaf venation that is regularly and moderately to densely reticulated and prominulous adaxially but only irregularly so abaxially; generally shorter inflorescences, 1–6 cm long, that are half or less as long as the leaves; shorter stigmas, c. 2 mm long; capsules that become partially fused as they mature; and seeds that are mostly elliptic to circular and 1.7–2 mm in diameter. *Danais reticulata* is also similar to *D. baronii* and *D. schatzii*, the latter newly described below. Both of these differ in their larger leaf blades, 9–15 × 4.5–8.8 cm, and larger inflorescences, with the branched portion 6–8.5 cm wide; and, both are allopatric, in northern and east-central Madagascar, respectively.

Additional specimens examined. – **MADAGASCAR. Reg. Atsimo-Atsinanana [Prov. Fianarantsoa]:** Distr. Farafangana, Matanga, Mandritsara, Andranofasika forest, Ankatriky forest, 23°27'24"S 47°30'17"E, 116 m, 2.VI.2007, *Birkinshaw et al.* 1723 (MO, P, TAN). **Reg. Anosy [Prov. Toliara]:** Distr. Fort-Dauphin [Taolagnaro], Andohahela National Park, 8.IV.2010, *Krüger & Razafimandimbison* 89 (MO, S); Antsotso Avaratra, 24°34'11"S 47°12'17"E, 160 m, 11.XII.2007, *Razakamalala et al.* 3913 (MO, P, TAN); *ibid.*, 24°33'42"S 47°12'02"E, 662 m, 11.XII.2007, *Razakamalala et al.* 4003 (MO, P, S, TAN); *ibid.*, forêt Tsitongambarika, 24°34'16"S 47°12'05"E, 271 m, 1.IV.2008, *Razakamalala et al.* 4076 (MO, P, TAN).

18. *Danais sambiranensis* C.M. Taylor, **sp. nov.** (Fig. 9).

Holotypus: MADAGASCAR. **Reg. DIANA [Prov. Antsiranana]:** Distr. Ambanja, forêt classée d'Ambato, village de Bevoay, 40 km au N d'Ambanja, 13°27'30"S 48°33'01"E, 80–100 m, 17.V.1998, *Randrianaivo, Birkinshaw, Antilahimena, Ranaivojaona, Randrianasolo, Rakotomamonjy & Rasolomanana* 244 (MO-5206218!; iso-: P [P03794019] image!, TAN).

Danais sambiranensis C.M. Taylor is distinguished from *D. longipedunculata* Homolle by its leaves with more numerous secondary veins and the higher order venation laxly reticulated, interpetiolar stipules, longer calyx lobes, and longer corollas.

Climbing plants, height not noted; stems densely puberulous-strigillose, weakly flattened becoming terete. *Leaves* opposite; blade elliptic to obovate, 8–22 × 5–9 cm, at base acute to obtuse, at apex obtuse to acute and sometimes acuminate with tip 1–6 mm long, drying stiffly chartaceous, adaxially glabrous, abaxially densely puberulous-strigillose; secondary veins 14–16 pairs, looping to interconnect near margins, without domatia, with 1–2 weakly developed inter-secondary veins present between pairs of secondary veins, with costa and secondary veins plane to thickened adaxially and prominent abaxially, with remaining venation laxly reticulated and plane on both surfaces or sometimes thickened adaxially; petiole 1.5–2 cm long, puberulous; stipules interpetiolar, persistent or tardily fragmenting, adaxially puberulous, triangular, 3–5 mm long, acute to obtuse, sometimes apparently resinous. *Inflorescences* axillary, paniculiform, pedunculate, densely puberulous; peduncle 8.5–12.5 cm long, flexuous; branched portion 5.5–10 × 8–18 cm, branched to 3 orders, with 2–3 pairs of secondary axes, with flowers closely set in umbelliform cymes of 5–15; bracts narrowly triangular, 0.5–4 mm long, puberulous; pedicels 0.5–5 mm long. *Flowers* pedicellate, distylous; hypanthium ellipsoid to ovoid, 1–1.2 mm long, densely puberulous; calyx limb densely puberulous, 1.2–1.5 mm long, 5-lobed nearly to base, lobes linear, margins sometimes involute; corolla salverform, pale green to orange on tube and orange to red on lobes, externally sparsely puberulous, tube c. 19 mm long, c. 0.3 mm in diam. near middle, with slits at base, internally glabrous except pilosulous at throat, lobes 5, narrowly ligulate, c. 3.5 mm long, acute, fleshy, plane at tip; anthers narrowly oblong, c. 2 mm long, in short-styled form well exerted, in long-styled form included and positioned in upper part of corolla tube; stigmas linear, in short-styled form c. 4 mm long, included, and positioned in upper part of corolla tube, in long-styled form c. 4 mm long and well exerted. *Fruits* ellipsoid, c. 4 mm in diam., puberulous, woody, with smooth rounded beak portion c. 0.3 mm high; seeds lenticular, c. 1 mm in diam., flattened to angled, sometimes with a very narrow ridge or wing on one side.

Etymology. – The species epithet refers to Sambirano biogeographic domain in northwestern Madagascar (Koechlin et al., 1974), where this species is found.

Distribution and ecology. – This new species is found in lowland moist evergreen forest between 80 and 425 m in northwestern Madagascar (Reg. DIANA [Prov. Antsiranana]).



Fig. 9. – Holotype of *Danais sambiranensis* C.M. Taylor.

[Randrianaivo et al. 244, MO-5206218; © Missouri Botanical Garden, St. Louis]

Conservation status. – *Danais sambiranensis* is known from only three recent collections dating from 1998 to 2013. These collections represent three unique occurrences, two populations, and two locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 6 km² and the AOO at 12 km². The EOO is within the limits for “Critically Endangered” under IUCN Red List Criterion B1 and the AOO is within the limits for “Endangered” under IUCN Red List Criterion B2 (IUCN, 2012). Two of the occurrences are adjacent to the north of Tsaratanàna Strict Nature Reserve (Réserve Naturelle Intégrale de Tsaratanàna; Reg. DIANA) and constitute a single location. The remaining occurrence is to the northeast of the first location, in the Ambato Classified Forest (Reg. DIANA) and is near the town of Ambanja and other human settlements. Neither of these two locations are under formal protected status and the areas are subject to threat by slash-and-burn agriculture (tavy), uncontrolled fires, and resource exploitation, including logging, hunting and mining (GOODMAN et al., 2018). The restriction of this species to two locations falls within the limits of “Endangered” under the subcriterion ‘a’ of criterion B2 (IUCN, 2012). A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations, and the number of mature individuals, and *D. sambiranensis* is assessed as “Endangered” [EN B1ab(i, ii, iii, iv, v)+2ab(i, ii, iii, iv, v)].

Notes. – *Danais sambiranensis* is characterized by opposite, petiolate, well-developed leaves with relatively numerous secondary veins (for *Danais*); interpetiolar, triangular stipules; lax, well-developed, paniculiform inflorescences with elongated flexuous peduncles and pedicellate flowers; relatively well-developed calyx lobes; slender corollas with red lobes; and relatively small fruits and seeds. Also distinctive is the arrangement of the higher-order leaf venation, which is laxly reticulated and adaxially plane or sometimes weakly, sparsely thickened. The inflorescences are relatively large for *Danais* and appear to be pendulous. Few mature seeds are preserved on the fruiting paratype, and these appear to be to be variously unwinged or narrowly winged along one side. As discussed above, winged seeds were considered a characteristic feature for *Danais* by PUFF & BUCHNER (1994) but are not diagnostic for this genus, and several species with unwinged seeds are included here in *Danais*. *Danais sambiranensis* is known only from the Sambirano biogeographic domain in northwestern Madagascar, which has a distinctive flora (KOECHLIN et al., 1974).

Danais sambiranensis is similar to *D. longipedunculata* (Fig. 3B), which can be separated by its leaf blades with fewer secondary veins, 5 to 11 pairs, and the higher-order venation regularly reticulated and prominulous adaxially; stipules that

are at least shortly united around the stem; shorter calyx lobes 0.3–0.8 mm long; and shorter corollas, with the tube 5.5–6 mm long.

Additional specimens examined. – MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: Distr. Ambanja, lower slopes of Kalabenono, 13°38'11"S 48°39'56"E, 215 m, 20.III.2009, Briggs et al. 250 (K, MO, TAN); Distr. Ambilobe, Beramanja, Anketrahe Belinta, forêt de Manongarivo-Kalobinono, 13°38'16"S 48°40'21"E, 425 m, 29.IX.2013, Razakamalala et al. 7612 (MO, G, P, TAN).

19. *Danais schatzii* C.M. Taylor, **sp. nov.** (Fig. 1D, 10).

Holotypus: MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Sahafina forest, W of Brickaville, 18°47'04"S 48°58'02"E, 200 m, 9.I.2017, Schatz, Lowry, Razakamalala & Randrianaivo 4430 (MO-6991769!; iso-: MO-6917297!, P, TAN).

Danais schatzii C.M. Taylor is distinguished from *D. longipedunculata* Homolle by its interpetiolar stipules and longer corollas.

Climbing plants to 10 m high; stems glabrous, weakly flattened becoming terete. *Leaves* opposite; blade lanceolate to ovate or elliptic-ovate, 8–15 × 3.5–8.8 cm, at base rounded to truncate or cordulate, at apex acute to acuminate with tip 1–6 mm long, drying stiffly chartaceous to subcoriaceous, on both surfaces glabrous and shiny; secondary veins 6–9 pairs, weakly differentiated from higher-order venation, weakly looping to interconnect near margins, without domatia, with 1–2 weakly developed intersecondary veins present between pairs of secondary veins, with costa thinly prominulous adaxially and prominent abaxially, secondary veins prominulous on both surfaces, and remaining venation regularly, closely, densely reticulated and prominulous on both surfaces; petiole 1.8–4 cm long, glabrous; stipules interpetiolar, persistent, glabrous, triangular, 1–2 mm long, acute. *Inflorescences* axillary and/or terminal, cymose to paniculiform, pedunculate, glabrous or sparsely puberulous; peduncle 4.5–10.7 cm long, flexuous; branched portion 6–8.5 × 10–12 cm, branched to 3 orders, with 1–3 pairs of secondary axes, with flowers in umbelliform cymes of 3 or 5; bracts narrowly triangular, 0.1–4 mm, glabrous; pedicels 0.5–4 mm long. *Flowers* pedicellate, whether distylous unknown; hypanthium ellipsoid to subglobose, c. 1.2 mm long, glabrous; calyx limb glabrous, c. 0.5 mm long, 5-lobed for ½–¾ its length, lobes deltate; corolla salverform, green on tube, white in throat, and orange on lobes, externally glabrous, tube c. 8 mm long, c. 0.8 mm in diam. near middle, with slits at base, internally glabrous except densely pilosulous in upper ¼ and on bases of lobes, lobes 5, narrowly ligulate, 3.5–4 mm long, acute, fleshy, plane at tip; anthers narrowly oblong, in long-styled form c. 1.8 mm long, included, and positioned at top of corolla tube; stigmas linear, in long-styled form c. 3.5 mm long and well exerted. *Fruits*

subglobose, c. 4 mm in diam., glabrous, woody, with smooth rounded beak portion c. 0.5 mm high; seeds not seen.

Etymology. – The species epithet honors Dr. George E. Schatz, who studied the Madagascar flora in depth for several decades and made the type collection.

Distribution and ecology. – This new species is found in lowland moist evergreen forest between 200 and 250 m in eastern Madagascar (Reg. Analanjirofo and Atsinanana [Prov. Toamasina]).

Conservation status. – *Danais schatzii* is known from only two collections dating from 1989 and 2017. These collections represent two unique occurrences, two populations, and two locations (sensu IUCN, 2022) based on the most likely serious threat of small-scale, shifting agriculture. The EOO is estimated at 0 km²; however, if EOO is less than AOO, then procedurally EOO is changed to make it equal to AOO to ensure consistency with the definition of AOO as an area within EOO (IUCN, 2012). The AOO is estimated at 8 km², and the EOO is adjusted to equal 8 km². Both the EOO and AOO are within the limits for “Critically Endangered” under IUCN Red List Criterion B1 and B2 (IUCN, 2012). One of the occurrences is adjacent to Mananara-Nord National Park (Reg. Analanjirofo) but in an unprotected area of human settlements and agriculture and is considered a single location. This collection was made in 1989, and no new collections have been reported from this area; the population at this location may no longer be extant. The other occurrence is in the Harmonious Protected Landscape of Sahafina (Reg. Atsinanana) (IUCN category V, protected harmonious landscape), which is subject to threat from illegal logging of hardwoods and from invasive species (GOODMAN et al., 2018). Each of these collection sites is considered a location, and their small number is within the limits of “Endangered” under the subcriterion ‘a’ of criterion B2 (IUCN, 2012). However, one of these localities is in an unprotected area subject to threat from shifting agriculture practices as well as human settlement, potentially decreasing suitable habitat. A continuing decline is inferred for the extent of occurrence, the area of occupancy, the area, extent, and/or quality of habitat, the number of locations, and the number of mature individuals, and *D. schatzii* is assessed as “Critically Endangered” [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Notes. – *Danais schatzii* is characterized by opposite, petiolate, well-developed leaves with the venation closely reticulated; interpetiolar triangular stipules; axillary and terminal, cymose, pedunculate, well-developed inflorescences with shortly pedicellate flowers; medium-sized, salverform corollas with a green tube and orange lobes; and rather small capsules. The color scheme of the corollas is the common one in *Danais*

flowers. Several immature capsules and a few mature ones that are fully dehiscent are preserved on the paratype specimen, but no fully developed seeds remain.

Danais schatzii is similar to *D. longipedunculata* (Fig. 3B), which is found in the same general region and can be separated by its stipules that are shortly united around the stem and its shorter corollas, with the tube 5.5–6 mm long. *Danais schatzii* is also similar to *D. baronii*; see the discussion of that species above for their distinctions.

Additional specimen examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Distr. Mananara-Nord, Ivontaka-Sud, fort à 100 m de la mer, 16°20'S 49°48'E, 250 m, 10–11.XI.1989, Dumetz 866 (MO, P, TAN).

20. *Danais terminalis* Boivin ex Drake in Bull. Soc. Bot. France 45: 350. 1899.

Lectotypus (designated here): MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Distr. Sainte-Marie [Nosy Boraha], 1848, Boivin 1773 (P [P00057196] image!; isolecto-: P [P00057198] image!, W [W 1889-0147599] image!). **Syntypus:** ibid., 1849, Boivin 1773 (G [G00014460]!, TCD [TCD0017832] image!).

Distribution and ecology. – This species is found in lowland moist evergreen forest from sea level to 245 m in eastern Madagascar (Reg. Analanjirofo [Prov. Toamasina], Reg. Vato-vavy [Prov. Fianarantsoa]), on Nosy Boraha and the coastal mainland.

Notes. – *Danais terminalis* was described from incomplete, fruiting material, and is not clearly diagnosed within the genus although it does not seem to match any other species. *Danais terminalis* is characterized by a combination of common characters in *Danais*: opposite, shortly petiolate leaves with rather small elliptic to oblanceolate blades, 4–6.5 × 1–2.8 cm, and laxly reticulated venation that is plane or only irregularly thickened; triangular interpetiolar stipules c. 1 mm long; few- to several-flowered, terminal and axillary inflorescences with lax peduncles 20–38 mm long and flexuous pedicels 5–20 mm long; and relatively large fruits and seeds, 8–12 mm in diam. and 2.5–4 mm in diam., respectively. Beyond this, the identity of *D. terminalis* is somewhat problematic, and was not fully clarified by PUFF & BUCHNER (1994: 48). They distinguished *D. terminalis* by the combination of its relatively larger fruits and “characteristic inflorescence”, which they described as terminal but occasionally also axillary, 1- to 7-flowered, lax, and with a form they considered reduced for the genus (BUCHNER & PUFF, 1993) but did not detail further. BUCHNER & PUFF (1993: 33–36) interpreted the inflorescences of both *D. terminalis* and *D. nigra* as reduced thyrses (here interpreted as cymes) with partial inflorescence sections comprising 1 or 3 flowers and articulations where axes have been reduced, vs.



Fig. 10. – Holotype of *Danais schatzii* C.M. Taylor.

[Schatz et al. 4420, MO-6991769; © Missouri Botanical Garden, St. Louis]

5 to 15 or more flowers in the unarticulated inflorescences they considered fully developed. Their “reduced” inflorescence form is found in *D. terminalis*, but also now documented in a number of other, similar *Danais* species, including some treated by Puff & Buchner without mention of the inflorescence arrangement (e.g. *D. dauphinensis*, *D. coronata* (Pers.) Steud.). *Danais terminalis* is indeed characterized in part by its lax and apparently reduced inflorescence structure, but this is not diagnostic alone for any *Danais* species. And, the relatively large fruits and seeds of *D. terminalis* seem to help identify it, but several of the similar species are known only in flower. Thus, as in the case of *D. baronii*, the identity of *D. terminalis* is problematic for the taxonomy of *Danais* because some other species share its few known features but are also poorly known and cannot be conclusively separated or synonymized with it. *Danais terminalis* is treated here based on the available information, so it eventually can be matched with additional specimens and its identity clarified. The four specimens included in this species by Puff & Buchner are from separated sites across a rather wide range, so it is possible that they represent more than one species.

Danais terminalis is similar in particular to *D. gracilis*, described above; see that species for their distinctions.

The holotype of *Danais terminalis* was cited by PUFF & BUCHNER (1994: 48) as deposited at P, where Boivin and Drake worked, with no additional information to identify a particular specimen. There are two duplicates of the type collection curated there, both of them complete specimens and none labelled as part of a set. No primary specimen was designated in the protologue or denoted in annotations by Drake, so these must be considered syntypes. One of the specimens has a hand-written label with collection data and the name “*Danais* ? *terminalis* Boiv”, mature fruits and seeds, and the date 1848. This was annotated by Puff as the “holotype”, and it is the only duplicate with mature fruits and is here chosen as the lectotype. Another sheet at P has a date range, 1847–1852, that includes the collection date on the lectotype and is here considered a duplicate of the type collection. Other specimens at G, P, and TCD labelled as *Boivin 1773* have a collection date of 1849. They belong to a different gathering and are here regarded as syntypes.

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Table 1. – Alphabetical list of accepted species and synonymy of *Danais* Comm. ex Vent. names in the new treatment here. Names in bold are accepted and cited with their geographic range; synonymous names are cited in italics with their accepted names; names newly published in this article are denoted with an asterisk.

Danais andribensis Homolle, Madagascar	<i>Danais littoralis</i> Homolle = Danais coronata (Pers.) Steud.
Danais antilahimenae C.M. Taylor, Madagascar	<i>Danais longiflora</i> Homolle = Danais volubilis Baker
Danais aptera Wedd. ex Homolle, Madagascar	Danais longipedunculata Homolle, Madagascar
<i>Danais argentea</i> Cavaco = Danais pubescens Baker	Danais lyallii Baker, Madagascar
Danais aurantiaca Homolle, Madagascar	<i>Danais madagascariensis</i> Cavaco = Payera madagascariensis (Cavaco) R. Buchner & Puff
Danais baccata Homolle, Madagascar	Danais magna Puff & R. Buchner
<i>Danais bakeriana</i> Homolle = Payera bakeriana (Homolle) R. Buchner & Puff	<i>Danais mandrarensis</i> Homolle ex Cavaco = Payera mandrarensis (Homolle ex Cavaco) R. Buchner & Puff
Danais baronii Homolle, Madagascar	<i>Danais masoalana</i> C.M. Taylor = Danais longipedunculata Homolle
Danais breviflora Baker, Madagascar	Danais microcarpa Baker, Madagascar
Danais brickavillensis J.-F. Leroy ex Puff & R. Buchner, Madagascar	Danais nigra Homolle, Madagascar
Danais capituliformis Homolle, Madagascar	<i>Danais nodulosa</i> Drake = Danais fragrans (Lam.) Pers.
Danais cernua Baker, Madagascar	<i>Danais nummularifolia</i> Baker = Danais pubescens Baker
<i>Danais chapelieri</i> Drake = Danais rhamnifolia Baker	<i>Danais obovata</i> Drake = Danais lyallii Baker
<i>Danais chassallia</i> Poir. = Chassalia Comm. ex Poir.	*Danais ovata C.M. Taylor, Madagascar
<i>Danais clematidea</i> Drake = Danais volubilis Baker	Danais pauciflora Baker, Madagascar
Danais coerulea Homolle ex Cavaco, Madagascar	Danais perrieri Homolle, Madagascar
Danais comorensis Drake, Comores	Danais pubescens Baker, Madagascar
*Danais confusa C.M. Taylor, Madagascar	*Danais puffiana Razafim. & C.M. Taylor, Madagascar
*Danais coriacea C.M. Taylor, Madagascar	<i>Danais purpurea</i> Homolle = Danais coronata (Pers.) Steud.
Danais coronata (Pers.) Steud., Madagascar	<i>Danais pyrifolia</i> J. St.-Hil. = Danais fragrans (Lam.) Pers.
Danais corymbosa Balf. f., Rodrigues	Danais rakotovaoui C.M. Taylor, Madagascar
Danais dauphinensis Cavaco, Madagascar	Danais randrianaivoi C.M. Taylor, Madagascar
<i>Danais decaryi</i> Homolle = Payera decaryi (Homolle) R. Buchner & Puff	*Danais reticulata C.M. Taylor, Madagascar
<i>Danais denudata</i> Pers. = Danais fragrans (Lam.) Pers.	Danais rhamnifolia Baker, Madagascar
Danais disticha C.M. Taylor, Madagascar	<i>Danais rotundifolia</i> Poir. = Danais fragrans (Lam.) Pers.
Danais distinctinervia Homolle, Madagascar	Danais rubra Puff & R. Buchner, Madagascar
Danais fragrans (Lam.) Pers., Mauritius and Réunion	*Danais sambiranensis C.M. Taylor, Madagascar
<i>Danais fragrans</i> var. <i>coronata</i> Pers. = Danais coronata (Pers.) Steud.	*Danais schatzii C.M. Taylor, Madagascar
<i>Danais gerrardii</i> Baker = Danais cernua Baker	Danais sulcata Pers., Mauritius
*Danais gracilis C.M. Taylor, Madagascar	Danais terminalis Boivin ex Drake, Madagascar
Danais hispida Baker, Madagascar	<i>Danais ternata</i> Baker = Danais cernua Baker
<i>Danais humbertii</i> Cavaco = Danais tsaratananensis Homolle	<i>Danais thouarsii</i> Drake = Danais sulcata Pers.
Danais humblotii Homolle, Madagascar and Comores	Danais tsaratananensis Homolle, Madagascar
Danais laciniata C.M. Taylor, Madagascar	Danais verticillata Baker, Madagascar
<i>Danais latisepala</i> Homolle = Danais volubilis Baker	Danais vestita Baker, Madagascar
<i>Danais laxiflora</i> DC. = Danais fragrans (Lam.) Pers.	Danais volubilis Baker, Madagascar
Danais ligustrifolia Baker, Madagascar	Danais xanthorrhoea (K. Schum.) Bremek., East Africa (Tanzania)

Table 2. – List of accepted species of *Danais* Comm. ex Vent. according to the main published treatments of this genus, exemplifying the rapid recent increase in our knowledge of the flora of this region. Name authors are detailed in Table 1. Note that PUFF & BUCHNER (1994) treated only the *Danais* species found on Madagascar.

CAVACO (1966, 1968)	BUCHNER & PUFF (1993), PUFF & BUCHNER (1994)	Current treatment (2024)	Distribution
47 species of <i>Danais</i> , 39 currently accepted, 35 in Madagascar	26 species of <i>Danais</i> in Madagascar, 3 newly described, 7 previously recognized species newly synonymized	49 species in <i>Danais</i> , 45 in Madagascar, 12 newly described or added, 2 previously recognized species newly synonymized	
<i>Danais andribensis</i>	<i>Danais andribensis</i>	<i>Danais andribensis</i>	Madagascar
—	—	<i>Danais antilahimenae</i> [publ. 2013]	Madagascar
<i>Danais aptera</i>	excluded from <i>Danais</i>	<i>Danais aptera</i>	Madagascar
<i>Danais argentea</i>	= <i>Danais pubescens</i>	= <i>Danais pubescens</i>	Madagascar
<i>Danais aurantiaca</i>	<i>Danais aurantiaca</i>	<i>Danais aurantiaca</i> [new circum.]	Madagascar
<i>Danais baccata</i>	excluded from <i>Danais</i>	<i>Danais baccata</i>	Madagascar
<i>Danais baronii</i>	not treated	<i>Danais baronii</i>	Madagascar
<i>Danais breviflora</i>	<i>Danais breviflora</i>	<i>Danais breviflora</i>	Madagascar
	<i>Danais brickavillensis</i> [publ. 1994]	<i>Danais brickavillensis</i>	Madagascar
<i>Danais capituliformis</i>	<i>Danais capituliformis</i>	<i>Danais capituliformis</i>	Madagascar
<i>Danais cernua</i>	<i>Danais cernua</i>	<i>Danais cernua</i> [new circum.]	Madagascar
<i>Danais clematidea</i>	= <i>Danais volubilis</i>	= <i>Danais volubilis</i>	Madagascar
<i>Danais coerulea</i>	generic position unclear	<i>Danais coerulea</i>	Madagascar
<i>Danais comorensis</i>	not treated	<i>Danais comorensis</i>	Comores
—	—	<i>Danais confusa</i> [nom. nov. for <i>Sabicea verticillata</i>]	Madagascar
—	—	<i>Danais coriacea</i> [sp. nov.]	Madagascar
<i>Danais coronata</i> [?]	<i>Danais coronata</i>	<i>Danais coronata</i>	Madagascar
<i>Danais corymbosa</i>	not treated	<i>Danais corymbosa</i>	Rodrigues
<i>Danais dauphinensis</i>	<i>Danais dauphinensis</i>	<i>Danais dauphinensis</i>	Madagascar
—	—	<i>Danais disticha</i> [publ. 2013]	Madagascar
<i>Danais distinctinervia</i>	<i>Danais distinctinervia</i>	<i>Danais distinctinervia</i>	Madagascar
<i>Danais fragrans</i>	<i>Danais fragrans</i>	<i>Danais fragrans</i> [new circum.]	Mauritius and Reunion
—	—	<i>Danais gracilis</i> [sp. nov.]	Madagascar
<i>Danais hispida</i>	<i>Danais hispida</i>	<i>Danais hispida</i>	Madagascar
<i>Danais humbertii</i>	= <i>Danais tsaratananensis</i>	= <i>Danais tsaratananensis</i>	Madagascar
<i>Danais humblotii</i>	<i>Danais humblotii</i>	<i>Danais humblotii</i>	Madagascar and Comores
—	—	<i>Danais laciniata</i> [publ. 2013]	Madagascar
<i>Danais latisejala</i>	= <i>Danais volubilis</i>	= <i>Danais volubilis</i>	Madagascar
<i>Danais ligustrifolia</i>	<i>Danais ligustrifolia</i>	<i>Danais ligustrifolia</i>	Madagascar
<i>Danais littoralis</i>	not treated	= <i>Danais coronata</i>	Madagascar

CAVACO (1966, 1968)	BUCHNER & PUFF (1993), PUFF & BUCHNER (1994)	Current treatment (2024)	Distribution
<i>Danais longiflora</i>	= <i>Danais volubilis</i>	= <i>Danais volubilis</i>	Madagascar
<i>Danais longipedunculata</i>	<i>Danais longipedunculata</i>	<i>Danais longipedunculata</i>	Madagascar
[<i>Danais lyallii</i> not treated]	= <i>Danais fragrans</i>	<i>Danais lyallii</i> [new circum.]	Madagascar
—	<i>Danais magna</i> [publ. 1994]	<i>Danais magna</i>	Madagascar
—	—	<i>Danais masoalana</i> [publ. 2013] = <i>D. longipedunculata</i> [syn. nov.]	Madagascar
<i>Danais microcarpa</i>	<i>Danais microcarpa</i>	<i>Danais microcarpa</i>	Madagascar
<i>Danais nigra</i>	<i>Danais nigra</i>	<i>Danais nigra</i> [new circum.]	Madagascar
<i>Danais nummularifolia</i>	= <i>Danais pubescens</i>	= <i>Danais pubescens</i>	Madagascar
—	—	<i>Danais ovata</i> [sp. nov.]	Madagascar
<i>Danais pauciflora</i>	<i>Danais pauciflora</i>	<i>Danais pauciflora</i>	Madagascar
<i>Danais perrieri</i>	<i>Danais perrieri</i>	<i>Danais perrieri</i>	Madagascar
<i>Danais pubescens</i>	<i>Danais pubescens</i>	<i>Danais pubescens</i>	Madagascar
—	—	<i>Danais puffiana</i> [sp. nov.]	Madagascar
<i>Danais purpurea</i>	= <i>Danais coronata</i>	= <i>Danais coronata</i>	Madagascar
—	—	<i>Danais rakotovaoui</i> [publ. 2013]	Madagascar
—	—	<i>Danais randrianaivoi</i> [publ. 2013]	Madagascar
—	—	<i>Danais reticulata</i> [sp. nov.]	Madagascar
<i>Danais rhamnifolia</i>	<i>Danais rhamnifolia</i>	<i>Danais rhamnifolia</i>	Madagascar
—	<i>Danais rubra</i> [publ. 1994]	<i>Danais rubra</i> [publ. 1994]	Madagascar
—	—	<i>Danais sambiranensis</i> [sp. nov.]	Madagascar
—	—	<i>Danais schatzii</i> [sp. nov.]	Madagascar
<i>Danais sulcata</i>	not treated	<i>Danais sulcata</i>	Mauritius
<i>Danais terminalis</i>	<i>Danais terminalis</i>	<i>Danais terminalis</i>	Madagascar
<i>Danais tsaratananensis</i>	<i>Danais tsaratananensis</i>	<i>Danais tsaratananensis</i>	Madagascar
<i>Danais verticillata</i>	<i>Danais verticillata</i>	<i>Danais verticillata</i>	Madagascar
<i>Danais vestita</i>	<i>Danais vestita</i>	<i>Danais vestita</i>	Madagascar
<i>Danais volubilis</i>	<i>Danais volubilis</i>	<i>Danais volubilis</i>	Madagascar
<i>Danais xanthorrhoea</i>	<i>Danais xanthorrhoea</i>	<i>Danais xanthorrhoea</i>	Tanzania