
A REVISION OF MALAGASY
GNIDIA (THYMELAEACEAE,
THYMELAEODEAE)¹

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ABSTRACT

A systematic revision of *Gnidia* L. is presented based on an analysis of morphological data. The circumscription of the genus adopted here includes *Lasiosiphon* Fresen. and excludes *Atemnosiphon* Leandri and *Dais* L. Six new combinations are made for species previously recognized as *Lasiosiphon*: *G. ambondrombensis* (Boiteau) Z. S. Rogers, *G. hibbertioides* (S. Moore) Z. S. Rogers, *G. humbertii* (Leandri) Z. S. Rogers, *G. linearis* (Leandri) Z. S. Rogers, *G. occidentalis* (Leandri) Z. S. Rogers, and *G. perrieri* (Leandri) Z. S. Rogers. Two names, *G. daphnifolia* L. f. and *G. linearis*, are resurrected from synonymy with *L. madagascariensis* (Lam.) Decne. and *L. decaryi* Leandri, respectively, and now pertain to more broadly circumscribed species. One new species, *G. neglecta* Z. S. Rogers, is described. These changes result in the recognition of 14 species, all endemic, making *Gnidia* the largest genus of Malagasy Thymelaeaceae. Lectotypifications are provided for 15 names: *Dais gnidioides* Baker, *G. danguyana* Leandri, *L. bojerianus* Decne., *L. decaryi*, *L. decaryi* var. *erectus* Leandri, *L. decaryi* var. *littoralis* Leandri, *L. decaryi* var. *tenerifolia* Leandri, *L. dumetorum* Leandri, *L. hildebrandtii* Scott-Elliot, *L. humbertii* Leandri, *L. madagascariensis* var. *angustifolius* Leandri, *L. madagascariensis* var. *mandrarensis* Leandri, *L. occidentalis* Leandri, *L. perrieri* Leandri, and *L. pubescens* (Lam.) Decne. var. *multifolius* Leandri. Each species is illustrated, mapped, and assigned a preliminary IUCN conservation status.

RÉSUMÉ

Le genre *Gnidia* L. est révisé sur la base d'une analyse de données morphologiques. Le genre est traité ici en incluant *Lasiosiphon* Fresen. mais en excluant *Atemnosiphon* Leandri et *Dais* L. Six nouvelles combinaisons sont effectuées pour des espèces déjà reconnues comme *Lasiosiphon*: *Gnidia ambondrombensis* (Boiteau) Z. S. Rogers, *G. hibbertioides* (S. Moore) Z. S. Rogers, *G. humbertii* (Leandri) Z. S. Rogers, *G. linearis* (Leandri) Z. S. Rogers, *G. occidentalis* (Leandri) Z. S. Rogers, et *G. perrieri* (Leandri) Z. S. Rogers. Deux noms, *G. daphnifolia* L. f. et *G. linearis*, sont retirés de la synonymie sous *L. madagascariensis* (Lam.) Decne. et *L. decaryi* Leandri, respectivement, et ils concernent désormais deux espèces plus largement circonscrites. Une espèce nouvelle, *G. neglecta* Z. S. Rogers, est décrite. De ces changements résulte la reconnaissance de 14 espèces, toutes endémiques, rendant *Gnidia* le plus grand genre de Thymelaeaceae à Madagascar. Des lectotypifications sont données pour 15 noms: *Dais gnidioides* Baker, *G. danguyana* Leandri, *L. bojerianus* Decne., *L. decaryi*, *L. decaryi* var. *erectus* Leandri, *L. decaryi* var. *littoralis* Leandri, *L. decaryi* var. *tenerifolia* Leandri, *L. dumetorum* Leandri, *L. hildebrandtii* Scott-Elliot, *L. humbertii* Leandri, *L. madagascariensis* var. *angustifolius* Leandri, *L. madagascariensis* var. *mandrarensis* Leandri, *L. occidentalis* Leandri, *L. perrieri* Leandri, et *L. pubescens* (Lam.) Decne. var. *multifolius* Leandri. Chaque espèce est illustrée, cartographiée et assignée à un statut de conservation provisoire de l'IUCN.

Key words: Africa, *Atemnosiphon*, *Gnidia*, IUCN Red List, *Lasiosiphon*, Madagascar, Thymelaeaceae, Thymelaeoideae.

Gnidia L. (ca. 140–160 species; Herber, 2003; Peterson, 2006) is the largest genus in the Thymelaeaceae, belongs to the largest subfamily Thymelaeoideae, and is almost completely restricted to Africa and Madagascar. More than 100 species occur in South Africa's Western Cape Province alone (Beaumont et al., 2001a; Bredenkamp & Beyers, 2003), and a single widespread species, *G. glauca*

(Fresen.) Gilg, reaches as far east as Arabia, India, and Sri Lanka (Townsend, 1981; Herber, 2003; Peterson, 2006). *Gnidia* was last revised in its entirety by Meisner (1857), but several significant regional treatments have been published in the important African floras of the last century (Pearson, 1910; Wright, 1915; Staner, 1935; Aymonin, 1966a, b; Gastaldo, 1969; Robyns, 1975; Peterson, 1978). The

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genus was last treated for Madagascar by Leandri (1950) in the *Flore du Madagascar et des Comores*. Generic delimitation of *Gnidia* and putative relatives has proven to be particularly problematic due to the considerable morphological variation in the characters that define the groups (see also Peterson, 1959; Aymonin, 1965; Rogers, 2006). A preliminary molecular study (Van der Bank et al., 2002) based on *rbcl* and *trnL-F* data suggests that the genus is paraphyletic, but additional genes and much broader sampling are needed before the taxonomic circumscription of *Gnidia* can be adequately addressed using molecular data.

Domke (1934), in the most comprehensive morphological classification of Thymelaeaceae to date, placed *Gnidia* in subtribe Gnidinae of tribe Gnidieae, along with six other African genera: *Craspedostoma* Domke, *Cryptadenia* Meisn., *Dais* L., *Lachnaea* L., *Lasiosiphon* Fresen., and *Struthiola* L. Tribal and generic limits have been defined traditionally by unique combinations of floral characters and, in some groups, supplemented by secondary leaf, bract, inflorescence, and fruit features (Meisner, 1857; Baillon, 1875; Gilg, 1894; Domke, 1934). Herber (2003), the first author to exhaustively update Domke's generic classification, recognized four informally ranked groups, i.e., the Daphne, *Gnidia*, *Linostoma*, and *Phaleria* groups, each one corresponding roughly to one of the four tribes of Thymelaeoideae recognized by Domke (1934). The *Gnidia* group is defined by an articulated hypanthium, a lateral style, and a seed with endosperm and relatively thin cotyledons. Several exceptions in these diagnostic character states are known to exist for some of the genera in the group, e.g., the hypanthium is reportedly rarely unarticulated in *Dais* (Peterson, 2006) and lacking in *Kelleria* Endl. (Heads, 1990), *Atemnosiphon* Leandri, and two species of *Gnidia* (Rogers, pers. obs.), and the style is terminal in *Drapetes* Banks ex Lam. (Heads, 1990). *Gnidia* is distinguished from other members within the *Gnidia* group by its eight or 10 included or only slightly exerted stamens, the sepals noticeably shorter than the tube, sessile or subsessile anthers, the petaloid scales (when present) borne near the mouth of the articulated hypanthium, and by the relatively small or absent disk surrounding the base of the ovary (Herber, 2003).

Historically, the overlapping and inconsistent variation in the diagnostic characters of *Gnidia* led to the description of several segregate genera, namely *Lasiosiphon* (1838), *Arthrosolen* C. A. Mey. (1843), *Gnidiopsis* Tiegh. (1893), *Rhytidosolen* Tiegh. (1893), *Englerodaphne* Gilg (1894), *Craspedostoma* (1934), *Basutica* E. Phillips (1944), *Pseudognidia* E. Phillips (1944), *Struthiolopsis* E. Phillips (1944), and *Atemno-*

siphon (1947). Most segregates were reduced to synonymy with *Gnidia* shortly after their publication without much controversy except for two genera, *Lasiosiphon* and *Atemnosiphon*. *Lasiosiphon*, originally segregated because of its 5- rather than 4-merous flowers, was maintained through the first half of the 20th century in African floras (e.g., Pearson, 1910; Wright, 1915) and in the most important morphological classification (Domke, 1934). Leandri (1950) in the *Flore des Madagascar des Comores* was probably the last author to uphold *Lasiosiphon* as a distinct genus, recognizing 15 species of *Lasiosiphon* and four species of *Gnidia* from Madagascar (neither genus recorded for the Comoro Islands). Peterson (1959) argued strongly to synonymize *Lasiosiphon* with *Gnidia*, a position based mainly on his observations of the morphological inconsistencies in the floral merosity of several African species, and his view has been followed by subsequent authors (for a review, see also Rogers, 2006). *Atemnosiphon*, the newest published segregate (Leandri, 1947), includes a single endemic Malagasy species (originally described in *Lasiosiphon* as *L. coriaceus* Leandri) and was only recently placed into synonymy with *Gnidia* by Herber (2003). *Atemnosiphon* does not fit very well within Herber's circumscription of *Gnidia* because of its distinctly exerted filaments and overall uncharacteristic appearance, e.g., leaves with a marginal vein, unarticulated hypanthium with a relatively large subgynoecial disk, and fruit that splits laterally through the side of the hypanthium during development. Aymonin (1965) noted similarities between *Atemnosiphon* and the widespread *G. glauca*, and the two do indeed share a similar inflorescence structure and lack an articulated hypanthium. Unfortunately, *Atemnosiphon* and *G. glauca* were not sampled in the molecular phylogeny of Van der Bank et al. (2002).

One other genus of Herber's *Gnidia* group occurs in Madagascar (*Dais*, one African and one Malagasy species). Unlike *Lasiosiphon* and *Atemnosiphon*, however, *Dais* has always been retained as a distinct genus. The African species, *D. cotinifolia* L., was included in the molecular phylogeny of Van der Bank et al. (2002) and formed a clade with *Phaleria capitata* Jack (99% bootstrap support), but the position of the clade was unresolved within a larger clade consisting of nearly all of the other sampled species of Thymelaeoideae. *Phaleria* Jack (25–30 species, Sri Lanka to Polynesia, Australia, and the Samoan Islands; Rye, 1990) was placed in subtribe Phalerieae (sensu Domke, 1934) and later in the *Phaleria* group (sensu Herber, 2003) because of the substantial morphological differences with *Dais*. Specifically, *Phaleria* differs from *Dais* by having a 2- versus 1-locular gynoecium, a terminal versus

lateral style, and a fibrous versus membranous or fleshy pericarp. Morphology suggests that *Dais* is more closely allied with *Gnidia* than *Phaleria*, but *Dais* can still be separated easily from *Gnidia* by the same androecial characters that separate *Atemnosiphon* from *Gnidia*. Given the unresolved phylogeny of the *Gnidia* group (Van der Bank et al., 2002; Rautenbach & Van der Bank, unpubl. data), the circumscription of *Gnidia* adopted for this revision includes *Lasiosiphon* and provisionally excludes *Atemnosiphon* and *Dais*.

Since the publication of the *Flore de Madagascar et des Comores* (Leandri, 1950), many new herbarium collections of *Gnidia* are now accessible, which, along with recent field observations, permit a reevaluation of the taxonomy of the Malagasy members of the genus. All taxa previously recognized by Leandri (1950) as *Lasiosiphon* are treated here as species of *Gnidia*, thus six new combination names are required. Aymonin (1962, 1965) previously indicated that several Malagasy names of *Lasiosiphon* should be treated as *Gnidia*, but his statements cannot be regarded as valid transfers according to Article 33.4 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006) because he did not provide full and direct references to the basionyms. A broader circumscription is adopted below for two geographically widespread and morphologically variable species, *G. daphnifolia* L. f. and *G. linearis* (Leandri) Z. S. Rogers, which Leandri (1950) previously recognized by the names *L. madagascariensis* (Lam.) Decne. and *L. decaryi* Leandri, respectively. One new species, *G. neglecta* Z. S. Rogers, is described. These changes result in the recognition of 14 species (Appendix 1), all endemic, making *Gnidia* the largest Malagasy genus of Thymelaeaceae.

Besides *Gnidia*, *Atemnosiphon*, and *Dais*, there are four additional genera and 15 species of Thymelaeaceae occurring on Madagascar and in the adjacent Comoro Island archipelago: *Peddia* Harv. ex Hook. (ca. 11 species: one Malagasy and ca. 10 African), *Octolepis* Oliv. (six species: five Malagasy and one African; Rogers, 2005), *Stephanodaphne* Baill. (nine species: eight Malagasy and one Comorian; Rogers, 2004), and *Synaptolepis* Oliv. (six species: one Malagasy and about five African).

MATERIALS AND METHODS

Herbarium specimens of ca. 530 collections (Appendix 2) were examined from the following institutions: A, B, BM, BR, F, G, GH, K, LINN, MA, MO, NY, P, TAN, TEF, US, and WAG. Specimens and pickled material were collected by the author for eight of the 14 species recognized here during four collecting trips to Madagascar (January–

March 2003, March–July 2004, January–February 2006, and November 2006). Field trips were planned so that plants from as many populations as possible could be observed and sampled. Populations of *Gnidia* occurring in the northwestern and far western regions of the island were unable to be reached due to logistical constraints.

The species concept and criteria follow those discussed in Rogers (2004). No infraspecific taxa are recognized. All examined specimens were databased and are available on the Missouri Botanical Garden's Tropicos website (<<http://www.tropicos.org/>>) along with images of types and representative herbarium vouchers. Geographic coordinates and elevations were assigned, whenever possible, using the *Gazetteer to Malagasy Botanical Collecting Localities* (Schatz & Lescot, 2009). Full specimen data including post-facto coordinates and elevations are available from the author by request. Species distributions are mapped over the outlines of the five simplified bioclimatic zones of Madagascar as discussed in Schatz (2000; following Cornet, 1974). Maps were created using ArcGIS 9 software (ESRI, Redlands, California, U.S.A.).

A summary of all names treated in the taxonomic section is provided in Appendix 3.

MORPHOLOGICAL CHARACTERS AND VARIATION IN MALAGASY *GNIDIA*

HABIT

The majority of species are erect, weakly to densely branched, shrubs or treelets from 1–2 m tall. The habit of a few species (e.g., *Gnidia daphnifolia*, *G. linearis*) can vary greatly, some individuals being small weakly branched shrubs, while others becoming trees up to 6 m tall with a diameter of 25 cm at breast height. *Gnidia humbertii* (Leandri) Z. S. Rogers differs from other Malagasy species by its rounded, densely branched habit, which rarely reaches 60 cm in height, and also has a well-developed underground root system that probably links nearby plants (presumably clones). Some species (e.g., *G. danguyana* Leandri, *G. linearis*) are reported to resprout from a common rootstock, allowing them to survive local harvesting and the periodic burning (M. Madeleine & R. Ramiandrisoa, pers. comm.). It is quite evident that some populations of *G. daphnifolia* remain small and shrubby only because of frequent burning. Specimens from one particularly stunted individual served as the basis for the name *Lasiosiphon suffrutescens* Leandri (1947). Most species, at 1 m tall, have a single primary root with several smaller secondary roots, each one possessing a few to many thin, fibrous roots.

Malagasy species generally exhibit some form of sympodial growth. Many species have obvious equal or subequal dichotomous branching. *Gnidia gnidioides* (Baker) Domke (Fig. 7A) is the only species known to possess a distinctive branching pattern composed of trichotomous orthotropic shoots that was discussed by Hallé et al. (1978) and referred to in that work by the illegitimate name "*Gnidia bakeri* Gilg." The same branching pattern occurs in two closely related African species, *G. bambutana* Gilg & Ledermann ex Engl. and *G. mollis* C. H. Wright, and the architecture of all three was carefully studied and described in detail in Aymonin (1966c).

Most species have spiral phyllotaxy. *Gnidia decaryana* Leandri (Fig. 5A) and *G. neglecta* (Fig. 11A) differ markedly by their opposite to decussate leaves, but leaves on vigorous shoots may sometimes be subopposite or more rarely alternate. Internode length, while quite variable in most species, is so short in *G. ambondrombensis* (Boiteau) Z. S. Rogers (Fig. 1A) and *G. humbertii* (Fig. 9A) that adjacent leaf bases slightly overlap along most of the stem. In both species, as well as *G. razakamalalana* Z. S. Rogers (Fig. 14), branches are covered by conspicuous leaf scars.

As in all Thymelaeaceae, the bark of *Gnidia* is strong and fibrous, and in Malagasy *Gnidia*, it is usually longitudinally striate on younger branches. Bark on older branches of *G. ambondrombensis* and often *G. humbertii* frequently exfoliates. Most species have gray, brown, or black bark. *Gnidia neglecta* and *G. razakamalalana* have dark red bark. In *G. perrieri* (Leandri) Z. S. Rogers, bark on the young branches dries a characteristic red-purple or orange-red. Lenticels are densely arranged on the bark of *G. danguyana*, *G. decaryana*, *G. bojeriana* (Decne.) Gilg, and *G. perrieri*, whereas the lenticels are more sparsely spaced (when present) on the bark of *G. daphnifolia*, *G. linearis*, and *G. occidentalis* (Leandri) Z. S. Rogers.

INDUMENT

Trichomes are unicellular, unbranched, short, silver-colored, and generally appressed. Indument presence or absence, density, type, position, and length are taxonomically important characters. Specific patterns of variation present on particular organs are discussed in subsequent sections.

LEAVES

Leaf shape is most often obovate or elliptic. *Gnidia gnidioides* (Fig. 7A) and some populations of *G. linearis* (Fig. 10B) have small needle-shaped leaves,

which are also prevalent in continental African species of the genus (e.g., *G. mollis*, *G. pinifolia* L.). The blades of some species with larger obovate leaves are often asymmetrical (e.g., *G. daphnifolia*, *G. gilbertae* Drake, and *G. occidentalis*).

For a few species, the size and, to a lesser degree, the shape, of leaves may vary substantially between individuals growing in the same population, and even between leaves on the same branch (e.g., *Gnidia daphnifolia*). Beaumont et al. (2001a) conducted a morphometric investigation of 18 *Gnidia* species exhibiting a wide range of variation in leaves (and bracts), including two Malagasy species, *G. danguyana* and *G. daphnifolia* (as "*G. madagascariensis* var. *baronii*," sic), and found that the length to width (l:w) ratio of leaves and bracts are taxonomically important characters, and that the l:w ratios of the leaves compared to the bracts are not correlated. Their results (Beaumont et al., 2001a, b) can be extended to include all of the other bracteate Malagasy species. Leaf l:w ratios are more consistent and taxonomically useful than linear size measurements in some species, e.g., *G. daphnifolia* (Fig. 4A–C) versus *G. occidentalis* (Fig. 12A, B). The largest leaf l:w ratios reach 14–15:1 in *G. gnidioides* (Fig. 7A) and *G. linearis* (Fig. 10A).

In live plants and sometimes on dry material of *Gnidia decaryana*, the leaves are appressed adaxially against the stems, thereby concealing most, if not all, of the sessile or subsessile few-flowered inflorescences (Fig. 5A). For most species, leaves are generally persistent along most of the branch on a typical herbarium specimen, but only the leaves located ca. 1–2(–3) cm from the branch tips remain persistent in *G. ambondrombensis* (Fig. 1A) and usually in *G. gilbertae* (Fig. 6A) and *G. humbertii* (Fig. 9A). Leaf texture is generally chartaceous to coriaceous. Leaves, when dry or fresh, are usually darker in color adaxially. The abaxial blade surfaces of *G. neglecta* and *G. perrieri* are often glaucous, at least after drying. Leaves are shortly petiolate or sessile, but this distinction becomes blurred in species with long-attenuate leaf bases.

Most species have at least some trichomes on their leaves, at least initially. Leaves (and stems) are completely glabrous in four species: *Gnidia danguyana*, *G. decaryana*, *G. neglecta*, and *G. perrieri*. Trichomes on leaves are generally appressed. The subappressed trichomes of *G. hibbertioides* (S. Moore) Z. S. Rogers (Fig. 8A) may simply be a drying artifact present on the only known specimen of the species. Leaves of some species, e.g., *G. bojeriana* (Fig. 2A), *G. gilbertae* (Fig. 6A), and sometimes *G. daphnifolia* (Fig. 4D), may have many persistent trichomes remaining on both surfaces of the blade. In these

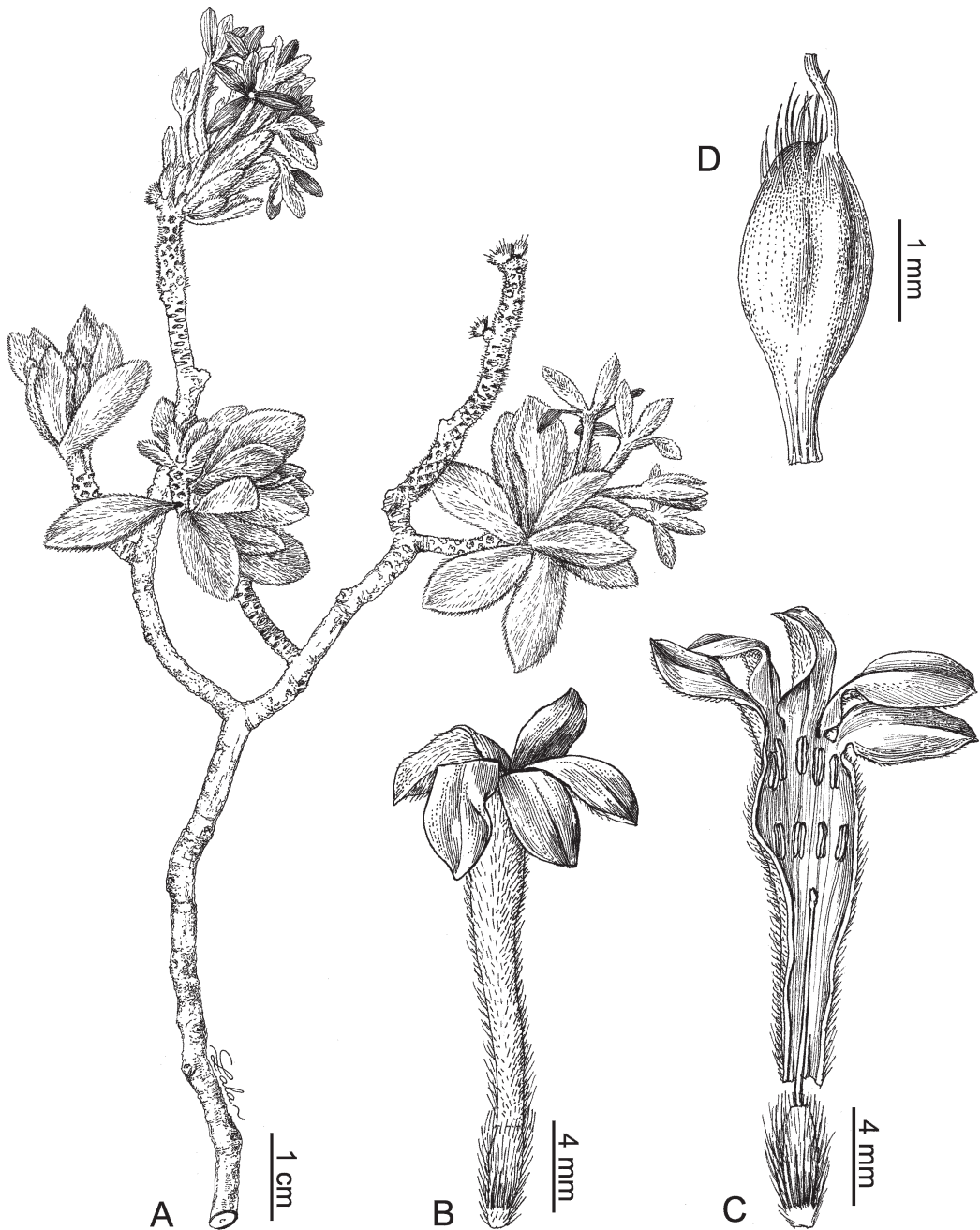


Figure 1. *Gnidia ambondrombensis* (Boiteau) Z. S. Rogers. —A. Habit. —B, C. Flower. —D. Gynoecium. Habit and gynoecium drawn from isotype, Boiteau (*Hb. Jard. Bot. Tananarive*) 4643 (TAN). Flower drawn from Rogers & Rakotonasolo 706 (MO).

cases, however, the trichomes are faint and imperceptible by the unaided eye, and the indument does not generally obscure the leaf surface and venation pattern, at least not adaxially. Alternatively, the sericeous indument remains so dense on both leaf surfaces in *G. ambondrombensis* (Fig. 1A) and *G.*

humbertii (Fig. 9A), and on the abaxial leaf surface of *G. razakamalalana* (Fig. 14B) and rarely *G. daphniifolia* (Fig. 4D), that the surface and venation pattern remain completely hidden. Leaf trichomes of *G. humbertii* are generally matted and ca. 0.3 mm long, whereas those of *G. ambondrombensis*, *G. razakama-*

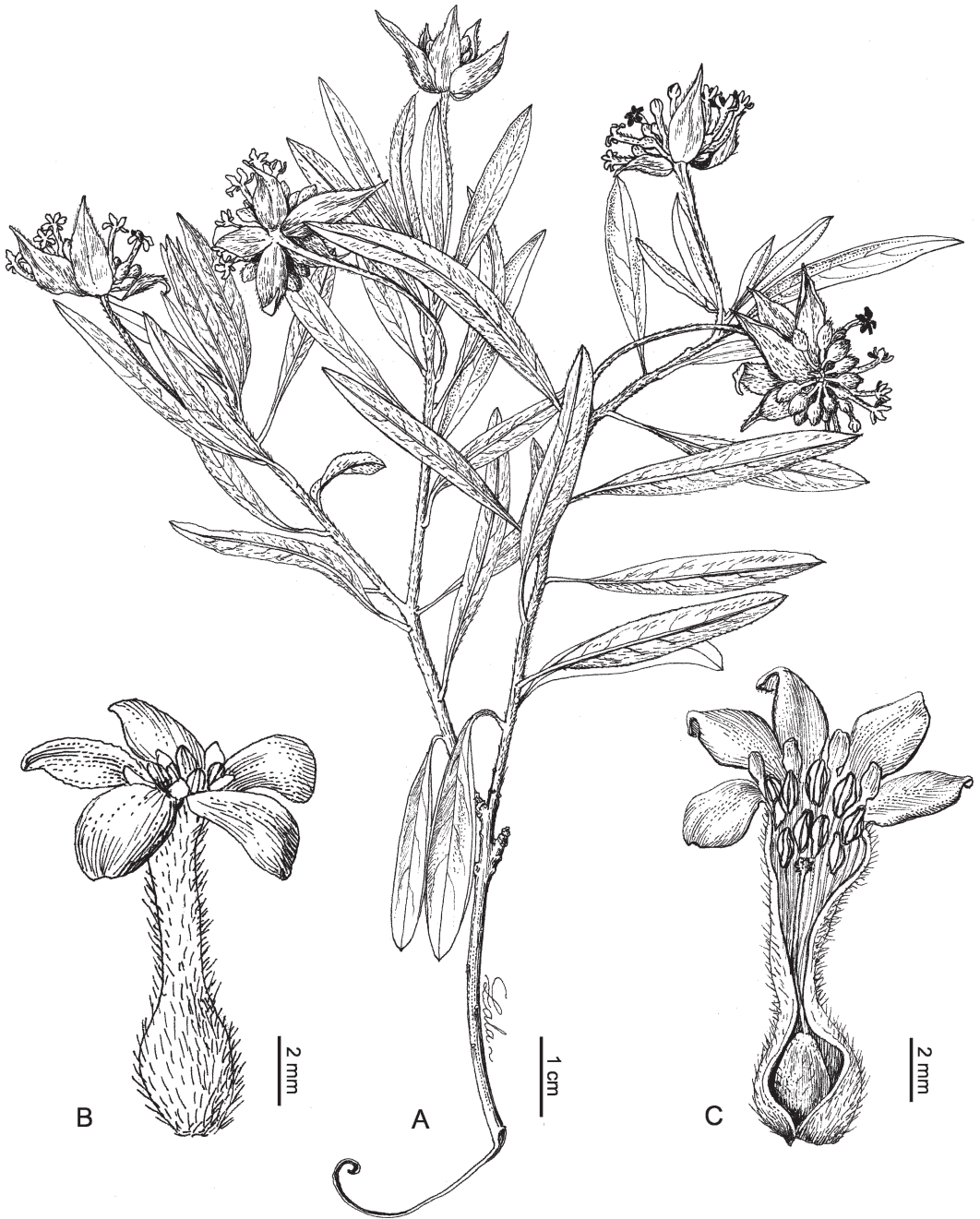


Figure 2. *Gnidia bojeriana* (Decne.) Gilg. —A. Habit. —B, C. Flower. Habit drawn from Rogers & Randrianaivo 175 (MO). Flower drawn from Rogers & Randrianaivo 183 (MO).

lalana, and *G. daphnifolia* are straight and exceed 1 mm in length.

Leaf bases are usually cuneate to attenuate and decurrent along the petiole, but the bases of *Gnidia danguyana* (Fig. 3A) and *G. neglecta* (Fig. 11B) are at least slightly cordate. Within a species, leaf apices vary from obtuse to acute and the tips are usually

rounded or mucronate. Leaf margins are entire, a family characteristic, but may vary between flat to somewhat revolute, the latter character state occurring more frequently on wider leaves and especially near the base of the blade.

Most Malagasy species of *Gnidia* exhibit some form of brochidodromous venation. The venation pattern



Figure 3. *Gnidia danguyana* Leandri. —A. Habit. —B, C. Flower. Drawn from Rogers *et al.* 76 (MO).

consists of one, or sometimes two, submarginal loops interconnected with an anastomosing network near the margin (e.g., *G. danguyana*, Fig. 3A), or of strongly arcuate secondaries meeting the margin in the upper 1/4 to 1/2 of the blade (e.g., *G. daphnifolia*, Fig. 4B), or by a pattern only represented on the abaxial surface by a midrib and two or four longitudinal plicate veins (*G. gnidioides*, Fig. 7A). Most species have concolorous venation compared to the blade. Fine venation anastomoses in an irregular pattern when visible. Generally, venation is slightly raised and more prominently so abaxially.

INFLORESCENCES

Species with opposite or decussate phyllotaxy (e.g., *Gnidia decaryana*) consistently have terminal inflorescences, whereas species with spiral phyllotaxy have axillary or pseudoterminal inflorescences, the latter condition being the most pronounced when branch internodes are short. In a few pedunculate species (e.g., *G. danguyana*, sometimes *G. daphnifolia*), the inflorescence can be extra-axillary with the peduncle being carried several millimeters above its axil as the stem develops.

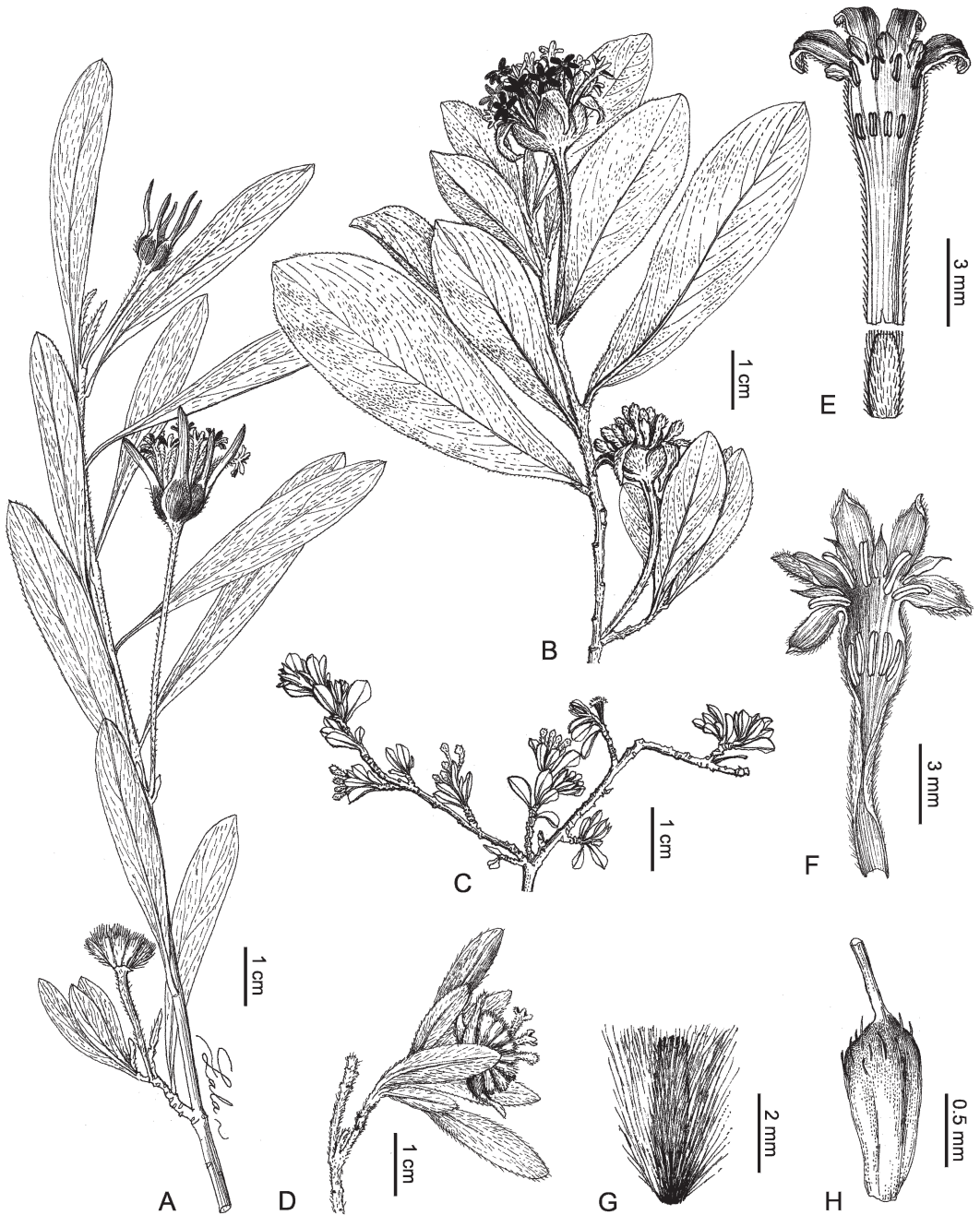


Figure 4. *Gnidia daphnifolia* L. f. —A–D. Habits. Note large amount of variation in leaves, length of peduncles, and the apex of bracts. —E, F. Flowers, with dissections of caducous portion of hypanthium. One sepal, one petaloid scale, and two anthers removed from part E. Note size and shape variation in the petaloid scales and anthers. —G. Persistent portion of hypanthium. —H. Gynoecium. Habits drawn from Rogers & Rakotonasolo 133 (part A, MO), Service Forestier (*Rabevohitra*) 34923 (part B, TEF), Humbert 12844 (part C, type of *Lasiosiphon suffrutescens*, TAN), and Humbert 18836 (part D, TAN). Floral parts drawn from Service Forestier (*Rabevohitra*) 34923 (part E, TEF), Rogers & Rakotonasolo 133 (part F, MO), Humbert 18836 (part G, TAN), and Humbert 12844 (part H, TAN).

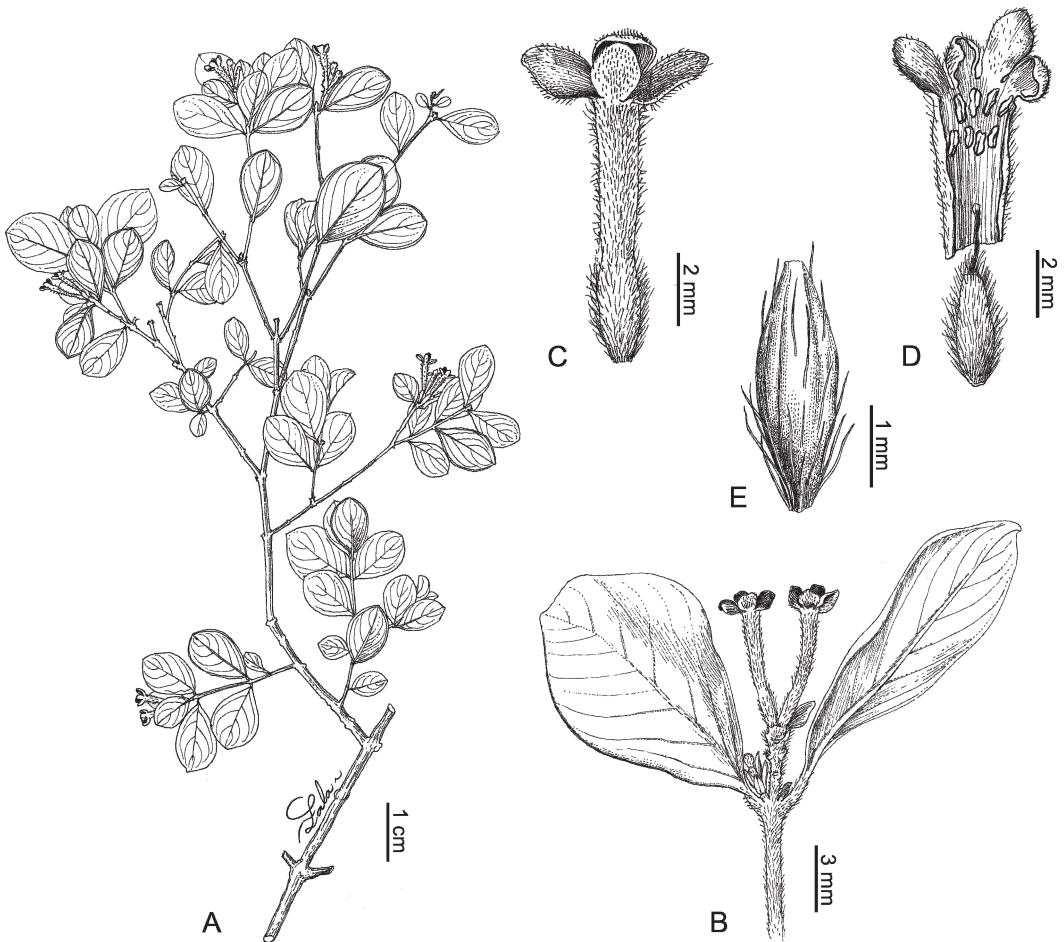


Figure 5. *Gnidia decaryana* Leandri. —A. Habit. —B. Inflorescence. Note small bracteole subtending flower. —C. Flower. —D. Dissection of caducous portion of hypanthium (above), and the persistent portion surrounding the gynoecium (below). —E. Fruit. Habit drawn from *Service Forestier (Capuron) 28650 (P)*. Inflorescence and flower drawn from *Rogers & Rakotonasolo 108 (MO)*. Fruit drawn from *Decary 4332 (TAN)*.

There is substantial variation in the inflorescence structure of Malagasy *Gnidia*. Nine of the 14 species have many-flowered, long-pedunculate, involucrate inflorescences (e.g., *G. linearis*, Fig. 10A, C). The remaining species possess one of the following kinds of inflorescences: (1) 1-flowered, ebracteate, terminal, and sessile (*G. razakamalana*, Fig. 14A); (2) few-flowered, ebracteate, and long-pedunculate (*G. neglecta*, Fig. 11C); (3) few-flowered, bracteate, and sessile or subsessile (*G. decaryana*, Fig. 5B); (4) many-flowered, bracteate, and long-pedunculate with flowers racemously arranged along a short fertile portion at the tip of an otherwise sterile peduncle (*G. danguyana*, Fig. 3A); (5) many-flowered, bracteate, composite-like heads (*G. gnidioides*, Fig. 7A).

Peduncles are usually erect and sparsely pubescent with the same kind and density of indument as that

found on the leaves. Leandri (1931a, b, 1947, 1950) considered peduncle length to be an important taxonomic character to distinguish between species possessing involucrate inflorescences. His observations were based, in most cases, on one or two collections and the length distinctions he used to distinguish species collapse immediately when additional specimens are examined. In actuality, the majority of the species have highly variable peduncle length. For example, on a single specimen of *G. daphnifolia* the flowering peduncles can be 3–5 cm long, while others even in the fruiting stage might only reach 1.5 cm long. Nonetheless, species can generally be classified according to the length of their peduncles as follows: (1) completely absent (e.g., *G. ambondrombensis*), or nearly so (e.g., *G. gnidioides*); (2) short, no more than 8 mm long (e.g., *G. hibber-*

tioides, *G. perrieri*); (3) long, reaching 5 cm or more in length (e.g., *G. bojeriana*, *G. danguyana*, *G. daphnifolia*).

Involucrate inflorescences are always many flowered and usually consist of five, or rarely six, imbricate bracts, but the involucre of *Gnidia gilbertae* are composed of only four, or rarely five, bracts. Involucral bracts may or may not be strongly differentiated from the leaves; however, in many species the bracts are noticeably different from the leaves in shape and size and sometimes in texture and indument. In general, involucral bracts are substantially smaller than the leaves. The bracts of most species are 2 to 3.5 times longer than wide. Bracts of *G. linearis* are typically almost orbicular (ca. 1–1.5:1), whereas those of *G. occidentalis* are more lanceolate (ca. 3–7:1). The bracts within an involucre may differ noticeably, as in *G. daphnifolia* and *G. perrieri*, where usually one or two of the innermost bracts will be narrower, shorter, and not as strongly acuminate as the rest.

Involucral bracts are usually broadly rounded at the base and acuminate or rostrate at the apex. Bracts rarely have conspicuous nervation, and the midrib is faint on both surfaces or only perceptible abaxially. Generally, bracts are appressed to the flowers and fruits, at least in their lower half, and remain persistent until all of the fruits have fallen off. The bracts usually fall off earlier in *Gnidia linearis* and sometimes *G. daphnifolia*, exposing relatively long trichomes on the pedicel and lower portion of the hypanthium that resemble bristles on a brush (e.g., Fig. 4A).

Generally, involucral bracts are coriaceous and indument typically remains densest on the abaxial surface and also on the upper half of the adaxial surface. Even after drying, bracts of *Gnidia perrieri* remain semi-succulent and become glaucous, as do the leaves. Trichome densities on the leaves and bracts are almost always positively correlated, but the indument on the bracts in *G. bojeriana* is much denser compared to the leaves. *Gnidia decaryana* (Fig. 5B) is the only Malagasy species with bracteoles.

FLOWERS

The flowers in *Gnidia* are hermaphroditic, diplostemonous, tubular, and either 4- (e.g., *G. danguyana*, Fig. 3C) or 5-merous (*G. razakamalalana*, Fig. 14C). Based on herbarium labels and personal observations, flower color is most often yellow. The character is usually always consistent within a single population; however, the feature appears to be more variable between populations of *G. daphnifolia* and *G. linearis* (yellow, orange, or red), *G. decaryana* (red-green,

yellow, or greenish white), and *G. gnidioides* (pink, red, white, or yellow). Flowers within a single inflorescence of *G. bojeriana* change from yellow or orange to red in late anthesis. Similar color changes may be occurring in other species (e.g., *G. daphnifolia*) given the variation reported on specimen labels. Conspicuous yellow blisters usually develop on the flowers (and fruits) of *G. danguyana* after drying, similar to those found in other distantly related Thymelaeoideae (e.g., *Aquilaria* Lam., *Phaleria*).

Flowers are sessile to short pedicellate. The pedicels of species without involucre inflorescences are glabrous to moderately pubescent with short trichomes, and similar to those borne on the leaves and peduncles. Pedicels of species with involucre inflorescences are almost always 0–1.5 mm long and hidden by long, silver, pedicel trichomes. The flowers of *Gnidia bojeriana* are borne on conspicuous 1.5–3.1 mm long pedicels (Fig. 2A) that are not always obvious in early anthesis without dissection. The pedicel trichomes may be similar in length to those borne on the persistent portion of the hypanthium (e.g., *G. bojeriana*, *G. perrieri*), or much longer (e.g., *G. gnidioides*, *G. linearis*). In the latter case, the trichomes reach up to 4 mm long and resemble a dense, silver-colored brush (Fig. 7D).

The floral tube is treated here as a hypanthium following Gilg (1894) and Herber (2003). For a thorough review concerning the various interpretations of the structure, see Heinig (1951). In Malagasy *Gnidia*, the hypanthium is cylindrical or nearly so and the tube is almost always articulated slightly above the ovary. The portion of the hypanthium above the articulation line falls away, while the portion below the line persists and surrounds the developing fruit. In the remainder of this paper, the part of the tube above the line will be referred to as the caducous portion, while the part below the line will be described as the persistent portion. Only two species of the entire genus are known to completely lack the articulated hypanthium, the continental African *G. glauca* and the Malagasy *G. gilbertae* (Fig. 6B). In *G. gilbertae*, the lower one third of the tube tears irregularly across as the fruit develops. In species with both articulated and unarticulated flowers, the fruit remains inside the persistent portion through dispersal.

Leandri (1931a, b, 1947, 1950) considered the length of the hypanthium to be an important taxonomic character, and certainly there is some taxonomically distinctive variation in several species. *Gnidia razakamalalana*, with its 5 cm long hypanthium, has the longest flowers in the genus and perhaps even in the family (Rogers, 2006). Tubes of the remaining Malagasy species approach but never reach 2 cm in length. In a few species, such as *G.*



Figure 6. *Gnidia gilbertae* Drake. —A. Habit. —B. Flower. —C. Gynoecium. Drawn from *Hb. Inst. Sci. Madag.* 432 (TAN).

daphnifolia, the hypanthium may vary greatly (6.5–15 mm long) among populations and even between individuals within the same population. This observation cannot always be explained by differences in the developmental stage of the inflorescences or flowers. The persistent portion of the hypanthium is usually 2–4(–5) mm long, except in *G. hibbertioides*, where it is 5–7 mm long.

The density and length of trichomes on the hypanthium of Malagasy *Gnidia* are taxonomically

important characters. *Gnidia neglecta* is the only species with a completely glabrous hypanthium, inside and out (Fig. 11C). For species with internally pubescent tubes, the indument is generally most prevalent just above the articulation. The inner surface of the hypanthia in *G. ambondrombensis* and *G. danguyana* is the most obviously pubescent of any species in Madagascar, but the indument itself usually remains only faintly visible with magnification (these trichomes are sometimes impossible to see when

flowers are wet). In most species, however, the outer surface of the hypanthium, above and below the articulation, is covered with a conspicuous dense, appressed or subappressed indument (e.g., *G. humbertii*, Fig. 9B). The trichomes on the outer surface of the hypanthium are either of uniform length (e.g., *G. decaryana*, Fig. 5C) or noticeably (i.e., ca. 2–5 times) longer on the persistent portion (e.g., *G. linearis*, Fig. 10D, E). In these cases, the trichomes borne on the persistent portion of the hypanthium are generally longer in the lower half and become shorter approaching the articulation. The ratio of trichome length on the upper versus lower portion of the hypanthium varies substantially between populations of *G. daphnifolia*, where northern populations have flowers with trichome ratios of 3.5–5:1 (above:below the articulation) and southeastern populations fall into the 1.5–2.5:1 range.

A unique condition exists in *Gnidia gnidioides* where the hypanthium on the abaxial surface is densely pubescent above the articulation and completely glabrous below (Fig. 7B, note the long brush of trichomes belongs to the pedicel). The long trichomes on the persistent portion of *G. daphnifolia* aid in fruit dispersal, allowing the fruit enclosed in the lower part of the hypanthium to be carried farther by the wind (Rogers, pers. obs.). Beaumont et al. (2001a) speculated that long trichomes on the persistent portion of *G. polycephala* (E. Mey. ex Meisn.) Gilg, a mainland African species, aid in wind dispersal. Many other African species possess long trichomes on the persistent portion of the hypanthium and those probably serve a similar function.

The number of calyx lobes in Malagasy *Gnidia* is consistently either four or five, with twice the number of stamens, respectively. Five species have flowers with four lobes (and eight stamens): *G. danguyana*, *G. decaryana*, *G. gilbertae*, *G. gnidioides*, *G. neglecta*. Aestivation of the calyx lobes is always imbricate. During anthesis, lobes spread and normally become adaxially convex. For most species, the apex of the lobe is usually rounded (*G. decaryana*, Fig. 5C) or emarginate (*G. linearis*, Fig. 10D, E). Lobes are generally obovate or oblong, ca. 1.5–3 × 1.5–3 mm, and ca. 2 to 3 times larger than the petaloid scales (when those are present; discussed in next paragraph). Sometimes one lobe (when 5-merous) or two lobes (when 4-merous) are ca. 1/2 to 3/4 the size of the others. Generally, calyx lobes are glabrous adaxially and densely pubescent abaxially with an indument similar to, or slightly longer than, that present on the outer surface of the hypanthium.

More than half of the Malagasy species have small scale-like structures located in the sinuses of adjacent

calyx lobes (e.g., Fig. 14C, F). There has been much controversy regarding the interpretation of these organs, which are regarded here as petaloid scales (see review in Heinig, 1951). Petaloid scales are membranous, glabrous, free, and equal in number to the calyx lobes. Six species lack these petaloid scales: *Gnidia ambondrombensis*, *G. danguyana*, *G. decaryana*, *G. gnidioides*, *G. neglecta*, and usually *G. humbertii*. Scales generally fall into the 0.5–2 × 0.5–1 mm range. Some species have a large amount of size and shape variation within a species (e.g., *G. daphnifolia*, *G. linearis*). Most Malagasy species have scales that are usually apically rounded, emarginate, acute, or only rarely possess up to a few rounded lobes. Petaloid scales are generally the same color or slightly lighter than the calyx lobes. No scale vascularization was obvious with a dissecting scope for any species. When fresh, the scales of some populations of *G. linearis* are weakly carinate and this ridge becomes darker after drying.

The androecium of *Gnidia* consists of two equal whorls of four or five stamens per cycle with each whorl positioned at different heights within the tube. No rudimentary or aborted stamens were observed, as is known to occur in a few continental African species of *Gnidia* (e.g., *G. aberrans* C. H. Wright, *G. anomala* Meisn.). In a few Malagasy species, the anthers of the lower whorl were rarely observed as being about half the size of those in the upper whorl, but these smaller anthers still produced pollen. Stamens are glabrous and introrse. Filaments are narrow, membranous, and usually almost completely adnate to the inner wall of the hypanthium (sometimes only weakly fused), which results in sessile or subsessile anthers. The upper whorl of stamens is opposite the sepals and generally borne near the mouth or partially exerted. Rarely, the entire length of the anthers is exerted. The lower whorl alternates with the sepals and is borne ca. 0–2(–4) mm below the upper whorl. Anthers are basifixed, bithecal, and longitudinally dehiscent.

A small annular or cupuliform disk surrounds the base of the ovary in most Malagasy species and is referred to as the subgynoecial disk in the taxonomic treatment. The disk is glabrous, fleshy, and usually ca. 0.1–0.3 mm tall, but reaches 0.7 mm tall in *Gnidia ambondrombensis* (Fig. 1D). Disks are completely absent or inconspicuous (i.e., less than 0.1 mm tall) in the flowers of *G. danguyana* and *G. decaryana*. The apex of the disk is most often smooth or shallowly lobed. Lobing is often irregular, and individual lobes rarely attain one third of the total height of the disk.

The gynoecium is composed of a pseudomonocarpous ovary (only one of the two uniovulate carpels

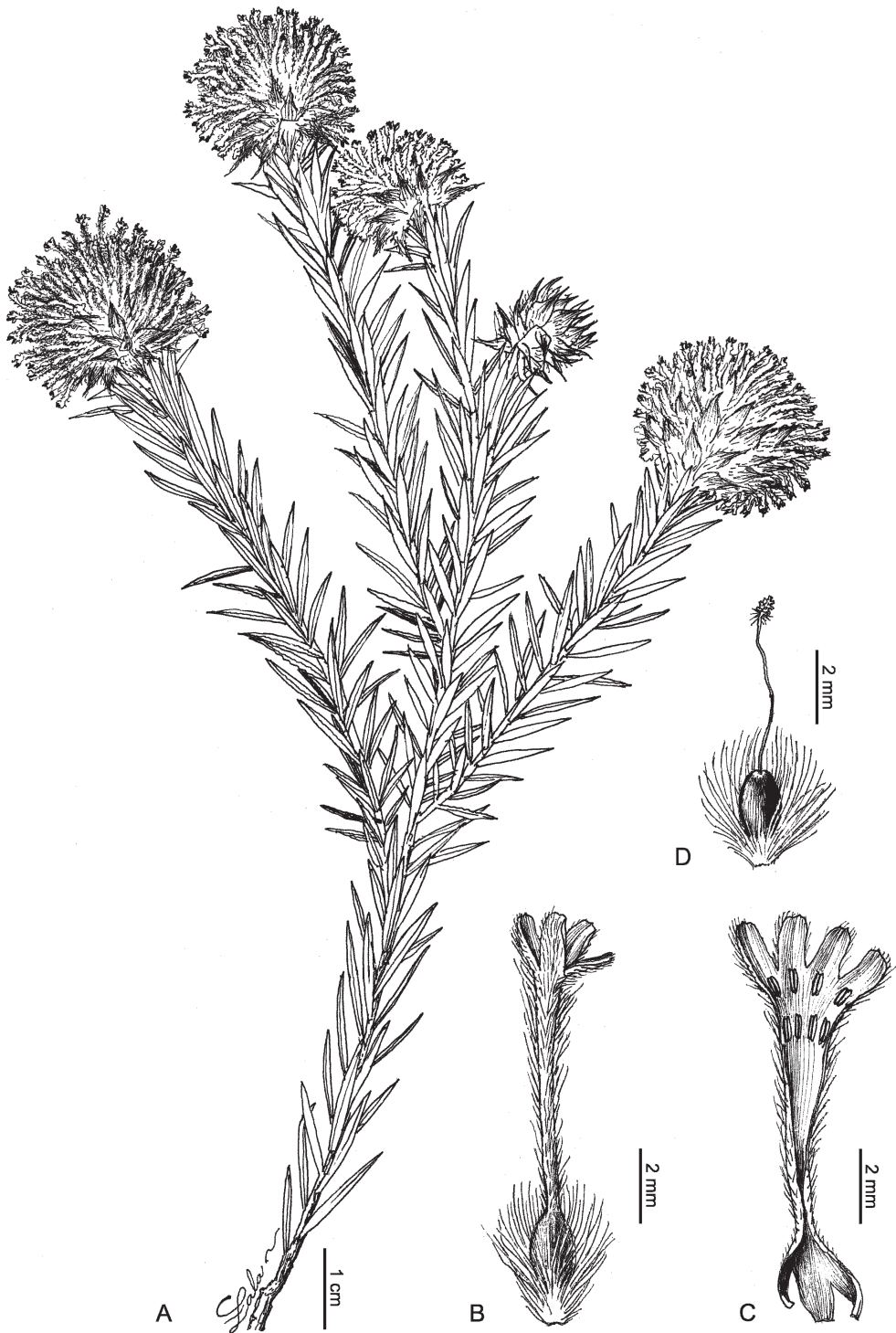


Figure 7. *Gnidia gnidioides* (Baker) Domke. —A. Habit. —B, C. Flower. Note long brush of pedicel trichomes in B. —D. Gynoecium. Drawn from Rogers *et al.* 126 (MO).

develops), a lateral style, and a capitate stigma. Ovules are anatropous and suspended. The superior ovary is completely free from the hypanthium and shortly stipitate at the base in most species. Most variation of the ovary is related to the density, position, and length of trichomes on the surface. Typically, the entire ovary is either sparsely pubescent or glabrescent. When pubescent, the indument on most of the surface is caducous with only a few trichomes remaining at the apex in mature fruit. In a few species, the apex of the ovary is covered by a conspicuous brush of relatively long, silver trichomes (e.g., *Gnidia danguyana*, Fig. 3C) that persists through fruit.

The style is filiform, straight, and persistent in fruit. Styles are glabrous, but rarely a few trichomes are irregularly found along its length. Style length may vary significantly between populations and sometimes individuals, but this variation is not associated with differences in the position of anthers within the tube, and thus the flowers are probably not truly heterostylous.

Stigmas are always papillate and usually globose (Fig. 2C). At anthesis, in a single population or species, the stigma can be at the height of either whorl of anthers, several millimeters below the lowest whorl, or slightly above the articulation. Stigmas never surpass the upper whorl in any Malagasy species.

FRUITS

Fruits are small single-seeded achenes that remain completely surrounded by the lower portion of the hypanthium when mature (Fig. 5D, E). Most species have ellipsoid fruits from 2–4 mm long. Two species have distinctly ovoid fruits, *Gnidia bojeriana* and *G. danguyana*. In fruit, the persistent styles in species with articulated hypanthia will protrude through the apical circular aperture of the persistent portion (Fig. 1C). The pericarp is dry, thin, and usually membranous, except in *G. bojeriana* where it is commonly more fleshy and opaque. Most of the indument on the ovary is lost as the fruit develops, but the fruits of two species, *G. danguyana* and *G. decaryana*, retain the distinctive brush of apical trichomes from the ovary.

SEEDS

Seeds show minor variation with the shape and size essentially matching that of the fruit. The seed coat is crustaceous, thin, and can be either black or dark brown. The embryo is fleshy and the endosperm is absent from mature seeds. Cotyledons are slightly flattened in cross-section, and the radicle and plumule are minute.

DISTRIBUTION AND ECOLOGY

All 14 species are Malagasy endemics and their distributions are provided in Figures 15–17. Given the wide distribution of some species of *Gnidia* in Madagascar, it is rather surprising that the genus has not been found in the nearby Comoro Archipelago. The genus occurs in all five provinces (Antananarivo, Fianarantsoa, Mahajanga, Toamasina, Toliara) and in each of five simplified bioclimatic zones (humid, subhumid, montane, dry, subarid) as discussed in Schatz (2000). The general bioclimate transitions from wet to dry from east to west across the island, but the far north is particularly arid.

Clearly, some species are restricted to higher elevations (ca. 1000–2550 m) along the central plateau in the subhumid and montane bioclimatic zones, e.g., *Gnidia ambondrombensis*, *G. gnidioides*, *G. perrieri*. *Gnidia bojeriana* is basically limited to mid-elevations in the subhumid zone. *Gnidia danguyana* and *G. neglecta* are endemic to fragments of coastal littoral forest near sea level in the island's humid bioclimate. *Gnidia gilbertae* and *G. occidentalis* occur on the drier western side of the central plateau in northwestern Madagascar (dry bioclimatic zone). *Gnidia humbertii* is restricted to the subarid zone. *Gnidia linearis* is almost completely confined to the subarid zone in southern and southwestern Madagascar. Five species appear to be narrow endemics: *G. ambondrombensis* (Mt. Ambondrombe), *G. hibernioides* (exact locality unknown), *G. neglecta* (Andevoranto), *G. perrieri* (Andringitra), *G. razakamalalana* (Ivohibe Forest). Two species, *G. neglecta* and *G. hibernioides*, are only known from their type collection.

Ecologically, Malagasy *Gnidia* are associated with open sunlit areas and found in habitats periodically disturbed by fire. *Gnidia gnidioides* grows in marshes and other moist places. Numerous recently revised Malagasy genera in other families, e.g., *Buxus* L. (Schatz & Lowry, 2002), *Ehretia* P. Browne (Miller, 2002), and *Leptolaena* Thouars (Schatz et al., 2001), are reportedly associated with, and restricted to, particular soil and rock types. This does not appear to be the case for most species of *Gnidia* on the island. *Gnidia daphnifolia* has been recorded on a number of diverse substrates including sand, laterite, limestone, granite and gneiss, and perhaps marble, whereas *G. linearis*, mostly confined to the southern and southwestern part of the island, occurs on sand, sandstone, and calcareous limestone. Based on label data and personal observations, four species apparently show substrate-specific distributions: *G. danguyana* and *G. neglecta* only occur on sand; *G. ambondrombensis* and *G. razakamalalana* grow on black soil on granite rock.

In regards to phenology, many Malagasy species, especially widespread ones, may flower and fruit year round, at least within some part of their geographic range.

VERNACULAR NAMES AND USES

According to dozens of herbarium specimen labels and several literature sources (e.g., Randriatavy, 1998), the most common vernacular name for *Gnidia* in Madagascar is havoah (also written as “avoha” and “havoha”), a Malagasy word for fiber. Fibrous bark of some *Gnidia* species (e.g., *G. linearis*, and probably *G. danguyana* and *G. daphnifolia*) is harvested as the raw material used in the fabrication of papier Antaimora, a coarse paper that was originally gathered and used locally (Estragon, 1933), but now is used as part of a much larger handicraft trade and sold to tourists (M. Madeleine & R. Ramiandrisoa, pers. comm.; Rogers, pers. obs.). Randriatavy (1998) reported that the bark of *Dais glaucescens* Decne. in C. A. Mey., which superficially resembles some other species of *Gnidia*, is also known as havoah and used to make papier Antaimora. Several other species of Thymelaeaceae are known by havoah or one of its orthographic variants in Madagascar, such as *Octolepis dioica* Capuron (Rogers, 2005), three species of *Stephanodaphne* (Rogers, 2004), and *Peddica involucreata* Baker.

In addition to paper, local artisans have reported that the bark of *Gnidia* is used to make ceremonial clothing (M. Madeleine & R. Ramiandrisoa, pers. comm.), and bark of *G. daphnifolia* is used for cordage (*Luckow* 4226). The leaves of *G. gilbertae* are ingested to induce vomiting (*Randrianaivo et al.* 614).

CONSERVATION STATUS

At least some Malagasy species of *Gnidia* survive annual burning regimes and grazing by livestock through resprouting from underground rootstocks (Rogers, pers. obs.). A few species commonly harvested for the papier Antaimora trade are reported to regenerate from a xylopodium after the above ground growth is cut (M. Madeleine & R. Ramiandrisoa, pers. comm.). Vigorous populations of *G. bojeriana*, *G. daphnifolia*, *G. gnidioides*, and *G. linearis* were observed in highly disturbed unprotected areas, including cow pastures, cultivated fields, *Pinus* L. stands, and along the edges of towns. Altogether, these factors suggest that most Malagasy *Gnidia* are not particularly threatened, and thus seven of the 14 species are considered species of Least Concern (LC)

by IUCN (2001) criteria. *Gnidia neglecta* and *G. hibbertioides* are the only two species assigned a preliminary status of Critically Endangered (CE), while *G. razakamalalana* and *G. ambondrombensis* are Endangered (EN). *Gnidia danguyana* and *G. perrieri* are considered Vulnerable (VU) to extinction.

TAXONOMIC TREATMENT

Gnidia L., Sp. Pl. 1: 358. 1753. TYPE: *Gnidia pinifolia* L.

Dessenia Adans., Fam. Pl. 2: 285. 1763, nom. superfl.

Lasiosiphon Fresen., Flora 21: 602. 1838. TYPE: *Lasiosiphon glaucus* Fresen. [= *Gnidia glauca* (Fresen.) Gilg].

Arthrosolen C. A. Mey., Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg, sér. 2, 1: 356, 359. 1843. TYPE: *Arthrosolen spicatus* (L. f.) C. A. Mey. [= *Passerina spicata* L. f.].

Shrubs or small trees. **Leaves** alternate to opposite, sometimes decussate; venation generally brochidodromous, often inconspicuous in needle-shaped leaves. **Inflorescences** terminal or axillary, usually composed of many-flowered heads borne on elongating peduncles; bracts usually involucreal, less often foliose, poorly differentiated, or absent. **Flowers** hermaphroditic, tubular, 4- or 5-merous, actinomorphic; hypanthium \pm cylindrical (in Madagascar) to funnel-shaped, articulated above the ovary (unarticulated in *Gnidia glauca* in Africa, *G. gilbertae* in Madagascar, and also possibly *G. razakamalalana*); upper portion of hypanthium caducous in late anthesis; lower portion of hypanthium persistent; calyx lobes 4 or 5, imbricate, spreading; petaloid scales usually small or absent, alternisepalous (adnate to the sinus between adjacent calyx lobes), free, thin, membranous; androecium diplostemonous; stamens 8 or 10, arranged in 2 alternating whorls at different heights, introrse, included or rarely only the upper whorl slightly exerted; filaments fused to the inner wall of the hypanthium for most of their length; anthers basifixed, bithecal, longitudinally dehiscent, sessile or subsessile; subgynoecial disk small or absent, annular or cupuliform when present; gynoecium pseudomonomerous; ovary sessile to shortly stipitate at base; ovule 1, apical, anatropous; style lateral, filiform, persistent; stigma usually capitate and globose, rarely fusiform or club-shaped, papillate, included or nearly so. **Fruits** small, single-seeded achenes, enclosed by the persistent lower portion of the hypanthium; pericarp thin, dry, membranous, rarely coriaceous or semi-fleshy. **Seeds** with a thin, crustaceous coat; endosperm absent.

KEY TO THE MALAGASY SPECIES OF *GNIDIA*

- 1a. Calyx lobes 4; stamens 8.
 - 2a. Phyllotaxy opposite to decussate, sometimes subopposite or less often alternate on vigorous shoots; inflorescence bracts 0 to 4, not imbricate.
 - 3a. Leaf blades 1–8.3 × 0.6–5 cm; petioles 1–4 mm long; inflorescences 6- to 23-flowered, flowers racemously arranged along a short, fertile portion of a much longer, mostly sterile peduncle 3. *G. danguyana*
 - 3b. Leaf blades 0.4–1.8 × 0.2–1.2 cm; petioles to 1 mm long; inflorescences 2- to 4-flowered, flowers arranged in a sessile, subsessile, or long-pedunculate cluster.
 - 4a. Leaves broadly ovate, leaf base cordate; fine venation clearly visible and uniformly reticulate, densely congested and darker than the blade; inflorescences with peduncles to 2.5 cm long; hypanthium glabrous externally 11. *G. neglecta*
 - 4b. Leaves obovate to suborbicular, leaf base cuneate to attenuate; fine venation usually inconspicuous, when visible weakly anastomosing and concolorous with the blade; inflorescences sessile or subsessile; hypanthium densely pubescent externally 5. *G. decaryana*
 - 2b. Phyllotaxy alternate, rarely subopposite; inflorescence bracts 4 to many, imbricate.
 - 5a. Leaf blades needle-shaped, rarely very narrowly obovate or ovate; inflorescences 50- to 100-flowered; flowers arranged in composite-like heads 7. *G. gnidioides*
 - 5b. Leaf blades broadly obovate to nearly elliptic; inflorescences to 28-flowered; flowers arranged in a capitulum and surrounded by 4 or 5 involucre bracts 6. *G. gilbertae*
- 1b. Calyx lobes 5; stamens 10.
 - 6a. Inflorescences 1-flowered; hypanthium ca. 5 cm long 14. *G. razakamalalana*
 - 6b. Inflorescences 6- to 40-flowered; hypanthium to 1.9 cm long.
 - 7a. Calyx lobes 7–8.3 × 3.5–4.2 mm 1. *G. ambondrombensis*
 - 7b. Calyx lobes rarely to 5.2 × 2.5 mm.
 - 8a. Petaloid scales 4.6–6 × 3.8–4.7 mm, upper half irregularly lacerate or sinuate; persistent portion of hypanthium 5–7 mm long 8. *G. hibernioides*
 - 8b. Petaloid scales rarely to 3.7 × 2 mm, upper half acute to rounded, emarginate, or rarely with a few rounded lobes; persistent portion of hypanthium rarely to 5 mm long.
 - 9a. Rounded, compact, densely ramified shrubs; both leaf surfaces hidden by a dense sericeous indument 9. *G. humbertii*
 - 9b. Laxly branched shrubs to small trees; both leaf surfaces usually visible, or only the abaxial leaf surface rarely obscured by dense strigose or tomentose indument.
 - 10a. Inflorescences drooping on living plants; involucre bracts strongly recurved (most obvious on fresh material), the largest (6–)8–16 mm wide; pedicels 1.5–3.1 mm long; persistent portion of hypanthium at least twice the diameter of the caducous portion . . . 2. *G. bojeriana*
 - 10b. Inflorescences erect on living plants; involucre bracts erect or spreading, and planar or reflexed near the midpoint (but never recurved), the largest rarely to 8 mm wide; pedicels 0–1.5 mm long; persistent and caducous portion of the hypanthium roughly the same diameter.
 - 11a. Broadest leaf blades 7–21 mm wide; bracts usually long-acuminate or rostrate, often with a reflexed upper half, less often short-acuminate or acute and ± erect.
 - 12a. Involucre bracts generally broadly ovate (l:w ratios 2–4:1), usually drying black or brown in the lower half; hypanthium 6.5–12(–15) mm long; widespread throughout Madagascar 4. *G. daphnifolia*
 - 12b. Involucre bracts narrowly lanceolate or elliptic-ovate (l:w ratios 3–7:1), drying light green, green-red, or yellow-brown throughout; hypanthium 12.5–16 mm long; restricted to northwestern Madagascar 12. *G. occidentalis*
 - 11b. Broadest leaf blades 2–5(–9) mm wide; bracts with a 1–2 mm long, strongly decurved apicule (usually *G. linearis*), short-acuminate and spreading, or less often acute and ± erect.
 - 13a. Plants with completely glabrous stems and leaves; young stems red-purple or orange-red when dry; longest peduncles 2–5(–8) mm long; involucre bracts with l:w ratios of 2–3.5:1; subhumid region, endemic to Andringitra, 2000–2550 m elevation 13. *G. perrieri*
 - 13b. Plants usually at least sparsely pubescent initially; young stems green, brown, or black when dry; longest peduncles (5–)10–50 mm long; involucre bracts with l:w ratios of 1–1.5(–2):1; dry and subarid regions in southern and western Madagascar, 0–1400 m elevation 10. *G. linearis*

1. *Gnidia ambondrombensis* (Boiteau) Z. S. Rogers, comb. nov. Basionym: *Lastiosiphon ambondrombensis* Boiteau, Bull. Trimestriel Acad. Malgache, n.s., 24: 83. 1941 [1942], as “*ambondrombense*.”
 TYPE: Madagascar. Fianarantsoa: Mt. Ambon-

drombe, rocky summit, 1900 m, 11 Apr. 1941, P. Boiteau (Hb. Jard. Bot. Tananarive) 4643 (holotype, P!; isotypes, MO!, TAN!). Figure 1.
 Sparsely branched shrubs to 60 cm tall; internodes inconspicuous; young branches densely seri-

ceous to tomentose, covered with prominent leaf scars; bark of mature branches often exfoliating. **Leaves** alternate, spirally arranged, sessile, very closely spaced (adjacent leaf bases overlapping), persistent only at tips of branches; blades broadly obovate or elliptic, 1.5–2.3 × 0.5–1.1 cm, l:w ratios ca. 2–3:1, silver-green, both surfaces completely obscured with a dense sericeous indument (trichomes 1–1.5 mm), apex apiculate or obtuse, base long-attenuate; midrib and venation obscured by indument. **Inflorescences** terminal, erect, capitate, 8- to 15-flowered, sessile, surrounded by a rosette of leaves; involucre bracts 5, similar to leaves (ca. 3/4 the size and less obovate compared to adjacent leaves), 8.3–9 × 3.3–3.8 mm, l:w ratios 2.3–2.7:1, densely pubescent in upper half adaxially, sparsely pubescent to glabrescent in lower half abaxially; midrib strongly raised adaxially, inconspicuous abaxially; nervation inconspicuous on both surfaces, or very faint in lower half adaxially. **Flowers** 5-merous, yellow; pedicels 0.7–1 mm, covered by 0.3–0.8 mm trichomes; hypanthium 14–16 mm, articulate (line sometimes faint), coriaceous; caducous portion covered by dense indument externally, trichomes ca. 1 mm, sparsely to moderately pubescent internally; persistent portion 3–4 mm, covered with dense indument externally, trichomes 1–2 mm, moderately pubescent internally; calyx lobes 5, spreading or reflexed, broadly elliptic to obovate, 7–8.3 × 3.5–4.2 mm, more membranous than hypanthium, glabrous adaxially, densely to moderately pubescent abaxially, apex emarginate; petaloid scales absent; stamens 10, upper whorl of anthers ca. half-exserted, lower whorl 1.5–2 mm below upper whorl; anthers oblong, 1.2–1.5 × 0.4–0.6 mm, subsessile; subgynoecial disk cupuliform, 0.4–0.6 mm tall, glabrous, fleshy, apex irregularly lobed, sinuses shallow to deep; ovary ellipsoid, ca. 1.6 × 1 mm, stipitate (stipe 0.3–0.4 mm), lower half glabrescent or sparsely pubescent, upper half moderately pubescent, apex densely pubescent, trichomes 1–1.5 mm; style 3–7.1 mm, glabrous; stigma inserted, ca. 2 mm below lower whorl of anthers. **Fruits** not seen.

Distribution and habitat. *Gnidia ambondrombensis* is endemic to the windswept summit of Mount Ambondrombe from 1800–1900 m elevation (Fig. 15). The site is situated along the boundary separating the subhumid and humid bioclimatic zones. The only known population grows on scattered patches of soil on a large outcrop of weathered granite that caps the peak.

Phenology. The species has been collected in flower in April, May, and October.

Vernacular name. Borona (Boiteau [*Hb. Jard. Bot. Tananarive*] 4643).

IUCN Red List category. More than 100 individuals of *Gnidia ambondrombensis* were observed on the summit of Ambondrombe Mountain in 2004 (Rogers, pers. obs.). While the site is not formally protected, the remaining forest on the mountain, located between 1400 and 1900 m elevation, are considered sacred by the local people. As a result, woodcutting and burning inside the forest are regarded as taboo and are not permitted by leaders living in the villages below the forest. In fact, this local ban probably grants the Ambondrombe forest more protection than most government-protected lands. Nevertheless, agricultural fields border the edge of the forest and some trees are still selectively cut down for local use. This species is assigned a conservation status of Endangered (EN) according to IUCN (2001) criteria because the species is known from a single unprotected population with an estimated area of occurrence (AOO) of 1 km² (B1ab + 2ab; D1). Our attempt to bring this attractive species into cultivation in 2004 proved unsuccessful, but additional efforts should be made to ensure the longevity of the species.

Discussion. *Gnidia ambondrombensis* is recognized by its sparsely branched habit, closely spaced leaves that are covered on both surfaces by a dense sericeous indument (trichomes 1–1.5 mm long), its sessile inflorescences, and by its large (7–8.3 × 3.5–4.2 mm) calyx lobes. *Gnidia humbertii*, another species with very dense vegetative indument and closely arranged leaves, differs by its distinctive rounded, compact, densely ramified habit, narrower leaves (1.9–3 vs. 5–11 mm wide) with shorter sericeous indument (trichomes 0.2–0.5 mm long), and its much smaller (2–4.5 × 1.7–2.5 mm) calyx lobes.

Selected specimen examined. MADAGASCAR. **Fianarantsoa:** Mt. Ambondrombe, summit, Rogers & Rakotonasolo 706 (K, MO [2], P, TAN).

2. *Gnidia bojeriana* (Decne.) Gilg, Nat. Pflanzenfam. 3(6a): 228. 1894. Basionym: *Lasiosiphon bojerianus* Decne., Voy. Inde 4: 149. 1844. TYPE: Madagascar. Antananarivo: Emirnae, mtns., s.d., *W. Bojer s.n.* (lectotype, designated here, P 00370315!; isotypes, BM!, K!, P [2]!). Figure 2.

Gnidia bojeriana Baill., Hist. Phys. Madagascar, 35(5) [Atlas 3], pl. 312. 1895, nom. illeg. TYPE: "Madagascar" (type, pl. 312!, Baillon in Grandidier, 1895).

Shrubs to 1.5 m tall; bark dark gray-brown, usually lenticellate, densely pubescent on young branches. **Leaves** alternate, persistent on older branchlets, subsessile or petiolate; petioles to 4 mm, densely

pubescent; blades narrowly elliptic or obovate, 1.6–7(–8.4) × 0.3–1.1(–1.5) cm, l:w ratios ca. 4–7:1, both surfaces densely to moderately strigose (trichomes ca. 1–1.5 mm), apex apiculate, base long-attenuate; midrib plane or slightly depressed adaxially, raised and lighter than blade abaxially; venation raised on both surfaces, more pronounced abaxially. **Inflorescences** axillary, pedunculate, drooping when living, involucre, (22- to)30- to 40-flowered; peduncles (0.4–)1–5 cm, densely pubescent; involucre bracts 5, broadly ovate, (9–)13–25 × (6–)8–16 mm, l:w ratios 2–3:1, persistent, green-yellow, becoming strongly recurved (often only obvious on fresh material), both surfaces obscured by dense pubescence, apex apiculate or acute, base rounded to truncate; midrib plane or inconspicuous adaxially, raised abaxially; nervation usually conspicuous. **Flowers** 5-merous, yellow, becoming orange-red in late anthesis, pedicellate; pedicels 1.5–3.1 mm, light green, densely puberulent, trichomes 0.2–0.4 mm, slightly longer near flower; hypanthium 9–11 mm, articulate, coriaceous, densely pubescent externally, trichomes ca. 0.2–0.5 mm, sometimes slightly longer and denser below articulation, glabrescent to moderately puberulent between anthers and ovary internally; caducous portion ca. 0.5 mm wide, becoming light brown after anthesis; persistent portion 3–4 mm, ca. 2 mm diam. (i.e., at least twice the diam. of the caducous portion); calyx lobes 5, spreading, broadly elliptic or obovate, 1.9–2.8 × 1–2.1 mm, glabrous adaxially, densely pubescent abaxially, apex emarginate or rarely rounded; petaloid scales 5, ovate-oblong, 0.5–0.9 × 0.2–0.3 mm, membranous, glabrous, lighter yellow than the calyx lobes when fresh, apex emarginate or rounded; stamens 10, upper whorl of anthers ca. 1/2 to 3/4 exerted, lower whorl 0.2–0.5 mm below upper whorl; anthers oblong, 0.8–1.2 × 0.2–0.4 mm, sessile or subsessile; subgynoecial disk cupuliform, to 0.4 mm tall, glabrous, fleshy, apex smooth or irregularly lobed; ovary ovoid to ellipsoid, 1.5–1.7 × 0.6–0.7 mm, stipitate (stipe to 0.3 mm), moderately to sparsely pubescent, denser in upper half, trichomes 0.4–0.7 mm; style 2.7–5.6 mm, glabrous; stigma near mouth or at height of lower whorl of anthers. **Fruits** ovoid, 3.2–3.5 × 1.5–1.7 mm, sparsely to moderately pubescent, denser in upper half; pericarp membranous or fleshy.

Distribution and habitat. *Gnidia bojeriana* occurs along the central plateau of Madagascar from Antananarivo to the Mahafaly Plateau and Isalo from 800–1700 m elevations (Fig. 15). The species is commonly found in open sunlit areas and notably present in Madagascar's tapia forests, woodlands dominated by species of *Uapaca bojeri* Baill. (Eu-

porbiaceae). *Gnidia bojeriana* grows on gneiss, quartzite, and sandstone rock types in the subhumid and subarid bioclimatic zones.

Phenology. The species flowers and fruits from January through June.

Vernacular name. Kelimafana (Boiteau [Hb. Jard. Bot. Tananarive] 5051).

IUCN Red List category. *Gnidia bojeriana* is widespread and has been recorded in one protected area (Isalo). Populations dating back to 1928 at Isalo and 1959 near Arivonimamo were found again in 2006 and 2003, respectively, and more than 75 healthy individuals were seen in the latter population (Rogers, pers. obs.). The habitat in both areas is burned periodically, and the species obviously tolerates frequent disturbances over time. *Gnidia bojeriana* should be considered a species of Least Concern (LC) by IUCN (2001) criteria.

Discussion. *Gnidia bojeriana* is easy to recognize by its broad, strongly recurved involucre bracts measuring (6–)8–16 mm wide, its distinctly pedicellate flowers (pedicels 1.5–3.1 mm long), and its hypanthium with a persistent portion at least two times the diameter of the caducous portion. It is also worth noting that the recurved appearance of the bracts is usually lost on dried material, and that the peduncles on live plants droop distinctively.

Nomenclature and typification. The provenance in the protologue (Decaisne, 1844: 149) was cited as “Hab. Madagascar in montibus provinciae Emirnae (herb. Mus. Paris.)” without mention of a specific collector or collection number. However, judging from the epithet it seems likely that the name was based on material that was either collected or provided by Wenceslas Bojer (1795–1856). Three unnumbered sheets attributed to Bojer were found at P bearing labels with the typewritten script Herb. Mus. Paris. Decaisne's handwriting does not appear to be present on any of the specimens, but one sheet (P 00370315) has the exact locality information cited in the protologue (except for the final “e” missing from the old provincial name Emirnae). Specimens on all sheets match the original description, and sheet P 00370315 is designated as the lectotype. Two other Bojer sheets of *Gnidia bojeriana* at BM and K are regarded as isolectotypes.

Original material of the later validly published homonym *Gnidia bojeriana* Baill. (1895), non *G. bojeriana* (Decne.) Gilg (1894), is represented in the protologue by a nice diagnostic illustration bearing the inscriptions “Madagascar” and the name of the species, the latter of which did not include any authorship or other attribution to an earlier basionym

name published by Decaisne or Gilg. The plate without doubt corresponds taxonomically to *G. bojeriana* (Decne.) Gilg and must be regarded as the type of Baillon's name.

Selected specimens examined. MADAGASCAR. **Antananarivo:** Imerintsiasosika, Km 22 along Natl. Rte. #1 (Antananarivo–Imerintsiasosika), *Rogers & Randrianaivo 175* (BR, G, K, MO, P, TAN); Mahevelona, rte. Majunga, Km 47, *Rauh 1677* (TAN); Mt. Antongona, W of Antananarivo, *Perrier de la Bâthie 18459* (G, P [2], TAN). **Fianarantsoa:** Isalo Natl. Park, Tsimanabaro Tapia forest, *Rogers et al. 821* (K, MO, P, TAN, US); Itremo, *Perrier de la Bâthie 12472* (P).

3. *Gnidia danguyana* Leandri, Bull. Soc. Bot. France 77: 35. 1930. TYPE: Madagascar. Toamasina: Tampina forest, Dec. 1923, *M. Louvel 118* (lectotype, designated here, P!). Figure 3.

Shrubs or small trees to 6 m tall; young branches light green, densely to moderately pubescent; mature branches light brown-red to dark black-brown; bark often lenticellate. **Leaves** opposite to decussate, pairs sometimes suboppositely or alternately arranged on vigorous shoots, distinctly petiolate; petioles 1–4 mm, glabrous; blades broadly ovate or ovate-elliptic, 1–8.3 × 0.6–4.5(–5) cm, l:w ratios ca. 1.5–2.5:1, lighter in color abaxially, glabrous on both surfaces, apex acuminate, apiculate, or acute, rarely emarginate, margin with a distinct vein, base cordate or slightly cordate; midrib depressed adaxially, raised abaxially, glabrous, lighter green than blade on both surfaces; venation raised on both surfaces, more pronounced abaxially. **Inflorescences** terminal, drooping, 6- to 23-flowered, those racemously arranged at the tip of a long and otherwise sterile peduncle; peduncles to 7 cm; sterile portion to 6.5 cm, glabrous; fertile portion to 1.3 cm, sparsely to moderately strigose or tomentose; inflorescence bracts 2 or 4, foliaceous, much smaller than leaves, 4–15 × 1–6 mm, l:w ratios 3–6:1, ± membranous, glabrous on both surfaces, apex acute or acuminate, base attenuate or cordate, often persistent in fruit; bract stalk 0.5–1 mm; midrib and nervation usually visible. **Flowers** 4-merous, yellow, often covered with yellowish blisters when dry, distinctly pedicellate; pedicels 3–4 mm, moderately to sparsely pubescent; hypanthium 7.5–9 mm, articulate, ± membranous, sparsely to moderately strigose externally (surface still clearly visible), trichomes 0.2–0.5 mm, glabrous internally; persistent portion 3–3.2 mm; calyx lobes 4, spreading, broadly elliptic or orbicular, 2–3.9 × 1.4–3 mm, glabrous adaxially, moderately to densely pubescent abaxially, smaller pair of lobes less pubescent, apex rounded; petaloid scales absent; stamens 8, upper whorl of anthers slightly below mouth or up to 1/4 exerted, lower whorl ca. 0.5–1 mm below

upper whorl; anthers elliptic, 0.6–0.8 × 0.2–0.3 mm; subgynoecial disk absent or cupuliform, composed of several irregularly fused segments when present, each segment to 0.2 mm tall, glabrous, apex irregularly lobed, sinuses shallow to deep; ovary ovoid to ellipsoid, 0.7–1 × 0.4–0.6 mm, stipitate (stipe ca. 0.1 mm), glabrous or sparsely strigose on lower half, becoming densely strigose at apex, trichomes 1–1.5 mm; style 2.5–3.6 mm, glabrous; stigma at height of lower whorl of anthers or just above articulation. **Fruits** ovoid, 2.9–3.2 × 1.8–2 mm, lower half glabrous, upper half glabrescent to sparsely strigose, apex densely pubescent; pericarp membranous.

Distribution and habitat. *Gnidia danguyana* is distributed along most of Madagascar's east coast littoral forest from the Masoala peninsula to around Fort Dauphin from 0–15 m elevation (Fig. 16). The species grows on sandy substrates in open, often disturbed, sunlit areas in the humid bioclimatic zone.

Phenology. The species flowers and fruits year round.

Vernacular names. Avoha (*Réserves Naturelles [Pierre] 8874, Plantes de Madagascar 5871*); havoa (*Service Forestier [Rakotomanana] 5100*); havoa hafotra (*Louvel 118, 197*).

IUCN Red List category. *Gnidia danguyana* has not yet been recorded within Madagascar's protected area network. The extent of occurrence (EOO) of the species is 18,200 km² and the AOO is 1600 km² given a 10 × 10 km grid cell size. Nine subpopulations occur in small patches of highly fragmented and severely threatened littoral forest (Consiglio et al., 2006). The species is assigned a preliminary IUCN (2001) conservation assessment of Vulnerable (VU) to extinction (B1ab + 2ab).

Discussion. *Gnidia danguyana* is easily recognized by its large (1–8.3 × 0.6–5 cm), ovate or ovate-elliptic leaf blades with cordate or slightly cordate bases and by its distinctive 6- to 23-flowered inflorescences. *Gnidia neglecta* can be separated by its 2- to 4-flowered inflorescences and smaller leaves (8–17 × 4–12 mm) with conspicuous densely congested fine venation.

Typification. The original material for *Gnidia danguyana* was cited incorrectly in the protologue as “*M. Humbert 118, 197*” (Leandri, 1930a: 35). Both syntypes were actually collected by Louvel, rather than Humbert, a mistake that Leandri corrected years later in the *Flore de Madagascar et des Comores* (Leandri, 1950). One sheet of each syntype is deposited at P. Both are annotated by Leandri, closely match the description, and bear the same handwritten

locality on the label. *Louwel 118* (P) is chosen as the lectotype because it is fertile and in better physical condition than *Louwel 197* (P).

Selected specimens examined. MADAGASCAR. **Antsir-anana:** Masoala Natl. Park, near Cap Est, *Schmidt et al. 4402* (BR, G, K, MO, P, TAN, US, WAG). **Fianarantsoa:** Ampasimaneva, Ambahy, N of Nosy Varika, Ambolo Forest, *Razakamalala et al. 1445* (MO, P, TEF); Mahabo forest, ca. 4 km NE of Mahabo village, *Rogers et al. 76* (B, BOL, K, L, LE, MO [2], NY, P, PE, PRE, TAN, WAG); Manampano, Ambodivoanato, Mananjary, *Service Forestier (Rakotomanana) 5100* (TEF); Vohipeno, *Hb. Jard. Bot. Tananarive 6513* (TAN). **Toamasina:** Ile Sainte Marie, Lonkinty, Sahasifotra, Ambohidenana Forest, *Razakamalala et al. 447* (B, BM, GH, MO, P, TEF); Tampina forest, *Louwel 197* (P); Vohibola Forest, *Rabehevitra et al. 409* (CAS, F, MO, P, TEF). **Toliara:** Mandena Forestry Station, *Rogers et al. 891* (BM, G, MO, P, TAN, US); Mandromondromotra, N of Fort-Dauphin, *Service Forestier (Capuron) 28646* (P, TEF); Sainte Luce, near Fort-Dauphin, *Falinianina et al. 29* (BM, BR, MO, P, TEF).

4. *Gnidia daphnifolia* L. f., *Suppl. Pl.* 225. 1782, as “*daphnaefolia*.” *Gnidia daphnifolia* L. f. var. *glabra* L. f., *Suppl. Pl.* 225. 1782. *Dessenia daphnifolia* (L. f.) Raf., *Fl. Tellur.* 4: 106. 1838, as “*daphnefolia*.” TYPE: Madagascar. *Hb. Smith No. 688.5* (lectotype, designated by Rogers in Rogers & Spencer, 2006: 486, LINN-SM!). Figure 4.

Dais madagascariensis Lam., *Encycl.* 2: 254. 1786. Syn. nov. *Lasiosiphon madagascariensis* (Lam.) Decne., *Voy. Inde* 4: 148. 1844. *Gnidia madagascariensis* (Lam.) Gilg, *Nat. Pflanzenfam.* 3(6a): 228. 1894. TYPE: Madagascar, s.d., *P. Commerson s.n.* (holotype, P-LA!; isotype, P!).

Dais pubescens Lam., *Encycl.* 2: 255. 1786. Syn. nov. *Lasiosiphon pubescens* (Lam.) Decne., *Voy. Inde* 4: 148. 1844. TYPE: Madagascar, s.d., *P. Commerson s.n.* (holotype, P-LA!; isotypes, G [2]!, MA!, P [3]!).

Gnidia rostrata Drake, *Hist. Phys. Madagascar* 35(5) [Atlas 3], pl. 315. 1896. Syn. nov. TYPE: “Madagascar” (type, pl. 315!, Drake in Grandidier, 1896).

Lasiosiphon rostratus Meisn., *Prodr.* 14: 597. 1857. Syn. nov. *Lasiosiphon madagascariensis* (Lam.) Decne. var. *rostratus* (Meisn.) Leandri, *Bull. Mus. Natl. Hist. Nat. (Paris)*, sér. 2, 3: 151. 1931. TYPE: Madagascar. Antsirananana: Port Leven, Mar.–Apr. 1849, *L.-H. Boivin 2384* (holotype, G-DC!; isotype, P!).

Lasiosiphon baronii Baker, *J. Linn. Soc., Bot.* 25: 342. 1890. Syn. nov. *Lasiosiphon madagascariensis* (Lam.) Decne. var. *baronii* (Baker) Leandri, *Bull. Mus. Natl. Hist. Nat., sér.* 2, 3: 151. 1931. TYPE: Madagascar. NW Madagascar, s.d., *R. Baron 5770* (holotype, K!; isotype, P!).

Lasiosiphon hildebrandtii Scott-Elliott, *J. Linn. Soc., Bot.* 29: 47. 1891. Syn. nov., non *Lasiosiphon hildebrandtii* Vatke ex Engl., *Abh. Konigl. Akad. Wiss. Berlin* 2: 310. 1891 [1892], nom. nud. *Gnidia hildebrandtii* (Scott-Elliott) Gilg, *Nat. Pflanzenfam.* 3(6a): 228. 1894. *Lasiosiphon madagascariensis* var. *hildebrandtii* (Scott-Elliott) Leandri, *Bull. Mus. Natl. Hist. Nat., sér.* 2, 3: 151. 1931. TYPE: Madagascar. Antsirananana: Montagne

d’Ambre, May 1880, *J. Hildebrandt 3369* (lectotype, designated here, BM!; isotypes, G [3]!, K!, P!, US!).

Lasiosiphon saxatilis Scott-Elliott, *J. Linn. Soc., Bot.* 29: 46. 1891. Syn. nov. TYPE: Madagascar. Toliara: Sainte Luce, rocky places near Fort-Dauphin, s.d., *G. Scott-Elliott 3030* (holotype, K!; isotype, P!).

Gnidia pubescens Baill., *Hist. Phys. Madagascar* 35(5) [Atlas 3], pl. 314. 1895, nom. illeg., non *Gnidia pubescens* P. J. Bergius, *Descr. Pl. Cap.* 124. 1767. TYPE: “Madagascar” (type, pl. 314!, Baillon in Grandidier, 1895).

Lasiosiphon pubescens (Lam.) Decne. var. *multifolius* Leandri, *Bull. Soc. Bot. France* 76: 1042. 1929 [1930]. Syn. nov. *Lasiosiphon multifolius* (Leandri) Leandri, *Notul. Syst. (Paris)* 13: 51. 1947. TYPE: Madagascar. Toliara: S Madagascar, Sep. 1900, *C. Alluud 85* (lectotype, designated here, P!).

Lasiosiphon madagascariensis (Lam.) Decne. var. *parvifolius* Leandri, *Bull. Mus. Natl. Hist. Nat., sér.* 2, 1: 436. 1929 [1930]. Syn. nov. TYPE: Madagascar. Toliara: Ambovombe (Androy), 27 Apr. 1924, *R. Decary 2605* (holotype, P 00380375!; isotype, P!).

Lasiosiphon pubescens (Lam.) Decne. var. *carinatus* Leandri, *Bull. Mus. Natl. Hist. Nat. (Paris)*, sér. 2, 1: 436. 1929 [1930]. Syn. nov. *Lasiosiphon carinatus* (Leandri) Leandri, *Notul. Syst. (Paris)* 13: 50. 1947. TYPE: Madagascar. Toliara: Ambovombe, along ocean, calcareous limestone and sand, 8 May 1924, *R. Decary 2694* (holotype, P!; isotypes, P!, TAN!).

Lasiosiphon madagascariensis (Lam.) Decne. var. *angustifolius* Leandri, *Bull. Mus. Natl. Hist. Nat., sér.* 2, 3: 151. 1931. Syn. nov. TYPE: Madagascar. Antsirananana: Vohémar, 1840, *J. Richard 580* (lectotype, designated here, P!).

Lasiosiphon waterlotii Leandri, *Bull. Mus. Natl. Hist. Nat., sér.* 2, 3: 153. 1931. Syn. nov. TYPE: Madagascar. Antsirananana: Ambilobe, s.d., *E. Waterlot 331* (holotype, P!).

Lasiosiphon dumetorum Leandri, *Notul. Syst. (Paris)* 13: 52. 1947. Syn. nov. TYPE: Madagascar. Toliara: Manambolo Valley, Mandrare basin, near the Isomono (confluence of the Sakamali), Mt. Morahariva, 1000–1400 m, Dec. 1933, *H. Humbert 13242* (lectotype, designated here, P!; isotypes, BM!, G!, K!, TAN!, US!).

Lasiosiphon madagascariensis (Lam.) Decne. var. *mandrariensis* Leandri, *Notul. Syst. (Paris)* 13: 47. 1947. Syn. nov. TYPE: Madagascar. Toliara: Manambolo Valley, Mandrare basin, near the Isomono (confluence of the Sakamali), Mt. Morahariva, 1000–1400 m, Dec. 1933, *H. Humbert 13154* (lectotype, designated here, P 00380344!; isotypes, BM!, G!, K!, P [2]!, TAN!, US!).

Lasiosiphon suffrutescens Leandri, *Notul. Syst. (Paris)* 13: 45. 1947. Syn. nov. TYPE: Madagascar. Toliara: Manambolo Valley, Mandrare basin, near the Isomono (confluence of the Sakamali), Mtns. Kotriha & Isomonobe, 400–600 m, Dec. 1933–Jan. 1934, *H. Humbert 12844* (holotype, P 00370336!; isotypes, BM!, G [2]!, K!, MO!, P!, TAN!, US!).

Shrubs or trees to 6 m tall; young branches densely to moderately pubescent; mature branches sometimes lenticellate. **Leaves** alternate, rarely subopposite, petiolate; petioles 1–2(–3) mm, densely to moderately pubescent; blades broadly obovate or obovate-elliptic, rarely narrowly elliptic, 7–61 × 4–21 mm, l/w ratios

ca. 3–5(–7):1, often slightly inequilateral, both surfaces usually strigose or tomentose initially before becoming glabrescent, sometimes densely pubescent (but indument never dense enough to hide the adaxial surface), apex acute, rounded, or obtuse, tip usually apiculate, base attenuate, less often cuneate; midrib depressed or rarely plane adaxially, raised and pubescent abaxially; venation often discolorous, usually raised on both surfaces, more pronounced abaxially. **Inflorescences** terminal or axillary, sometimes extra-axillary, erect, involucrate, (8– to) 11– to 35-flowered; peduncles 3–50 mm, densely to sparsely pubescent, rarely glabrescent; involucre bracts 5, generally broadly ovate (often 1 or 2 bracts within inflorescence with a broader base and shorter acumen or rostra), (3–)5–19 × (2–)5–6 mm, l:w ratios ca. 2–4:1, persistent, lower half of bracts appressed to flowers, glabrous to densely pubescent on both surfaces, apex usually rostrate or long-acuminate, less often short-acuminate, acumen or rostra to 1.1 cm when present, upper half often reflexed when longer (but never apically decurved), base rounded-truncate; nervation conspicuous near margin. **Flowers** 5-merous, yellow, orange, or red; pedicels (0.2–)0.5–1.5 mm, covered with 1.5–3 mm trichomes; hypanthium 6.5–12(–15) mm, articulate, densely pubescent externally, usually glabrescent internally; caducous portion densely covered externally with ca. 0.5 mm trichomes; persistent portion (2.5–)3–4 mm, densely covered externally with (1.5–)2.5–4 mm trichomes that obscure the surface in fruit; calyx lobes 5, broadly elliptic, obovate, or ovate, 1.2–3.5 × 1–2.3 mm, glabrous adaxially, densely pubescent abaxially, apex emarginate or rounded; petaloid scales 5, narrowly ovate-elliptic or obovate, sometimes approaching linear or orbicular, 0.8–1.4 × 0.2–1.3 mm, membranous, glabrous, apex acute to rounded, emarginate, or with a few rounded lobes, sometimes with a conspicuous dark midvein; stamens 10, upper whorl of anthers located just below mouth or to 3/4 exerted, lower whorl 1–1.5 mm below upper whorl; anthers elliptic, 0.6–1.1 × 0.2–0.3 mm, subsessile; subgynoecial disk cupuliform, 0.1–0.4 mm tall, glabrous, fleshy, apex smooth or irregularly lobed; ovary ellipsoid, ca. 1.3 × 0.6 mm, sessile or shortly stipitate (stipe to 0.2 mm), mostly glabrescent, apex sometimes moderately pubescent; style to 12 mm, glabrous; stigma ca. 2 mm below or at height of lower whorl of anthers. **Fruits** ellipsoid, 2.3–4 × 1–1.5 mm, usually glabrous, sometimes with a few sparse trichomes near apex.

Distribution and habitat. *Gnidia daphnifolia* is widespread in Madagascar from 0–1400 m elevations, with most populations occurring either in the drier areas of the far north, or in the humid regions of the

southeast (Fig. 15). Several disjunct populations (e.g., at Ankara Plateau, Tampoketsa d'Ankazobe, Tsiribihina Valley, Fanjahira) scattered along the central and occidental side of the high plateau link the disjunct northern and southern populations. The species occurs in degraded open savannas on sandy or lateritic soils, and is less frequently found on rocky slopes of granite, gneiss, limestone, and possibly marble.

Phenology. The species flowers and fruits year round.

Vernacular names. Avoha (*Decary 4030; Humbert 20403*); avoha madinika (*Cloisel 135*); havoa (*Randriatafika 349*); havoha (*Réserves Naturelles 13004*); mandrakieka (*Service Forestier [Serrado] 1282*); mandreankaine (*Bernier 157*); mandriankiaka (*Guittou et al. 4; Luckow 4226*); tsifoladriotra (*Rogers & Rakotonasolo 147*).

IUCN Red List category. *Gnidia daphnifolia* is widespread and common throughout Madagascar and has been recorded in at least several protected areas (e.g., Andohahela, Ankarana, Tsaratanana). The species is assigned a provisional IUCN (2001) conservation status of Least Concern (LC).

Discussion. *Gnidia daphnifolia* is the most geographically widespread and morphologically variable species of *Gnidia* in Madagascar. The substantial morphological variation in this taxon is probably due to the wide array of biophysical parameters (e.g., elevation, substrate, bioclimate, habitat) affecting the various populations that occur throughout a broad geographic distribution (Fig. 15, ▲). Plants, even within a single population, are capable of exhibiting a large amount of morphological variation, especially in those features (e.g., leaf and bract size and pubescence, peduncle length, hypanthium length) that were previously considered taxonomically important in various treatments of the group (Leandri, 1931a, b, 1947, 1950). Furthermore, most of Leandri's taxa were based on the examination of relatively few specimens made from disjunct localities that did not show the morphological overlap and continuous variation in the characters he deemed diagnostic. As a result, 13 of Leandri's names (five at the specific and eight at the varietal rank) are now placed into synonymy with *G. daphnifolia*.

Gnidia daphnifolia can be distinguished from similar Malagasy species (e.g., *G. gilbertae*, *G. hibbertioides*, *G. linearis*, *G. occidentalis*) by a combination of features, including its relatively wide leaves (reaching 21 mm wide) that are generally broader above the midpoint, the involucre inflorescences usually borne on long peduncles (to 5 cm

long), the involucre bracts typically with a long rostrate or acuminate apex, the articulated hypanthium with five calyx lobes, and the petaloid scales measuring 0.8–1.4 × 0.2–1.3 mm.

Outside of Madagascar, *Gnidia daphnifolia* differs from the widespread *G. glauca*, a species distributed roughly from central Africa to southern India (Peterson, 2006), by its inflorescences with five (vs. six to 12) involucre bracts, the articulated (vs. unarticulated) hypanthium, and the leaves with fewer secondary and intersecondary veins.

Nomenclature and typification. The validly published name, *Gnidia daphnifolia* (Linnaeus, 1782), has usually been treated in the literature as a synonym of either *Lasiosiphon madagascariensis* or *L. pubescens*, combinations both based on *Dais* basionyms originally published by Lamarck (1786) that were later transferred to *Lasiosiphon* by Decaisne (1844). Meisner (1857: 597) was probably the first author to formally treat *G. daphnifolia* as pro parte synonyms of *L. madagascariensis* and *L. pubescens*, respectively, but Gilg (1894: 228) appears to have been the first person to resurrect the Linnaean *G. daphnifolia*. Leandri (1931b: 149), in his first revision of the Malagasy *Gnidia*, incorrectly placed *G. daphnifolia* L. f. into synonymy with *G. bojeriana*. These two taxa are difficult to confuse and thus he might have actually been referring to “*G. daphnaefolia*,” a manuscript name of Bojer’s that appeared as a synonym in the protologue of *L. bojerianus* (Decaisne, 1844: 149). Strangely, Leandri did not mention *G. daphnifolia* L. f. in his second revision of the group (1947) nor in his *Flore de Madagascar et des Comores* treatment (1950). Whatever the case, Leandri certainly did not consult the original Linnaean material used to describe *G. daphnifolia* that is still extant in the Smith Herbarium at LINN and was recently designated as the lectotype of the name in Rogers and Spencer (2006).

Two collections were cited in the protologue of *Lasiosiphon hildebrandtii* (Scott Elliot, 1891): *Hildebrandt 3369* (BM, G [3], K, P, US) from far northern Madagascar and *Scott-Elliot 2368* (BM, K, P) from extreme southern Madagascar. The Hildebrandt collection more closely matches the protologue description and the BM sheet is chosen as the lectotype.

Two collections, *Alluaud 85* and *Alluaud 106*, were cited in the protologue of *Lasiosiphon pubescens* var. *multifolius*, both of which are deposited at P and match the original description (Leandri, 1930a). *Alluaud 85* (P) is selected as the lectotype because the original label bears Leandri’s handwritten annotation of the name. The other syntype is in equally good condition and instead bears Leandri’s annotation on a typewritten Paris herbarium label.

Two collections are cited in the protologue of *Lasiosiphon madagascariensis* var. *angustifolius* (Leandri, 1931b): *Perrier de la Bâthie 1276* and *Richard 580*. Later, Leandri (1947) went on to use *Perrier de la Bâthie 1276* as one of five syntypes for *L. occidentalis* (= *Gnidia occidentalis*). In the *Flore*, Leandri (1950) did not recognize his variety *angustifolius* and instead cited *Richard 580* under the species *L. madagascariensis*. Thus, *Richard 580* more closely matched Leandri’s concept of *L. madagascariensis* var. *angustifolius*, and the sheet deposited at P is chosen as the lectotype.

Five collections of *Lasiosiphon dumetorum* were cited in the protologue (Leandri, 1947): *Humbert 6742* (G [2], P), *12812bis* (P), *13010* (P), *13242* (BM, G, K, P, TAN, US), *13800* (P). All examined specimens match the description, but *Humbert 13242* is the most widely distributed collection and the P sheet is selected as the lectotype.

Three collections were cited in the protologue of *Lasiosiphon madagascariensis* var. *mandranensis* (Leandri, 1947): *Humbert 13154* (BM, G, P [3], TAN, US), *13860* (P), *14053* (P). All three closely match the description. *Humbert 13154* is the most widely distributed collection and P 00380344 is selected as the lectotype.

Selected specimens examined. MADAGASCAR. **Antananarivo:** Angavo massif, near Ankazobe, *Decary 7353* (P); Antananarivo–Majunga rd., Km 184, *Descoings 3283* (MO, TAN); Vohimbohitra massif, near Manakana, *Cours (Hb. St. Agric. Alaotra) 1518* (MO, P, TAN). **Antsiranana:** Ambilobe, SW of Ambilobe, *Humbert & Capuron 25579* (P); Analabe forest, near village of Analabe & Lac Sahaka, Fivondronana Vohémar, *Razakamalala et al. 538* (BR, MO, P, TEF); Analamazava, part of Binara Range, SW of Daraina (Vohémar), *Meyers 17* (MO, P, TAN); Analamera, calcareous hills & plateau, *Humbert 19145* (P); Anivorano Avaratra, Lac Sacré, near Anivorano-Nord, *Humbert 32321* (MO, P); Ankarana Special Reserve, *Rogers & Rakotonasolo 155* (MO, P, TAN); Babaomby Forest, Firaiana Ramena, *Rabenantoandro & Razantsoa 598* (MO, P, TAN); Irodo forest, *Seigler 12881* (MO, TAN); Ivovona, Diego Suarez–Orangea rd., *Rogers & Rakotonasolo 149* (G, MO, P, TAN); Joffreville, 2 km SE of Joffreville on rd. from Diego Suarez to Montagne d’Ambre Natl. Park, *Rogers & Rakotonasolo 147* (MO [3]); Montagne d’Ambre, Les Roussettes at Ankazobe, *Homolle 167* (P); Montagne des Français, 6–8 km N of Diego Suarez, *Rogers & Rakotonasolo 133* (MO, TAN); Port Leven, *Boivin 2384* (G, P); Vovo Village Distr., *Harder 1665* (MO, TAN). **Mahajanga:** Ankarana massif, *Decary 14524* (BM, K, P, US); Ikopa valley, W of Ankazobe, *Decary 7676* (G, P); Masokoamena, Tampoketsa Masokoamena, *Perrier de la Bâthie 8552* (P [2]); Masokoamena, Bemarivo, *Perrier de la Bâthie 8548* (P). **Toliara:** Amboasary, 1 km E of town, *Rogers et al. 914* (G, K, MO, P, TAN, US); Ambovombe, *Decary 8391* (MO, P); Andohahela Natl. Park (Parcel #1), 200 m N of Mahamavo village, *Rogers & Rakotonasolo 110* (MO, TAN); Andriamanga, Lac Mananivo, *Dumetz et al. 614* (K, MO, TAN, TEF, WAG); Andriambe, above Belavenoky River, *Rogers et al. 954* (B, G, K, MO, P, TAN, US); Ebakika, N of Fort-Dauphin, *Decary 10102* (MO, P, US); Emena

village (Andohahela Natl. Park [Parcel #1]), *Réserves Naturelles (Randriamiera) 13004* (TEF); Fanjahira, plateau & valley of Isalo, *Humbert 2755* (P); Fort-Dauphin, *Decary 4030* (P, TAN); Fort-Dauphin, rocky places in open country, *Scott-Elliott 2368* (BM, K, P); Kotriha, Mandrare basin, Mtns. Kotriha & Isomonobe, *Humbert 12812bis* (P); Imonty, Mananara basin, betw. the Andohahela & Elakelaka, *Humbert 14053* (P); Imonty, Canton Behara, Distr. Androy, *Réserves Naturelles (Ramarokoto) 2312* (P [2], TAN); Mahamavo, Mananara basin, *Humbert 13800* (P); Mahatalaky, 3–4 km S of Mahatalaky village, *Randrianasolo 571* (BM, G, MO, P, TAN); Manambolo Valley, Mandrare basin, *Humbert 6742* (G [2], P); Manantenina, N of Fort-Dauphin, *Decary 3897* (P, TAN); Morahariva, Manambolo Valley, Mandrare basin, *Humbert 13154* (BM, G [3], TAN, US), *13242* (BM, G, K, P, TAN, US), *13860* (P); Nosibe, ca. 5 km E of Manambaro, *Rogers et al. 906* (G, K, MO, P, TAN); Pic Saint Louis, near Fort-Dauphin, *Rogers & Rakotonasolo 106* (K, MO [2], P); Ranopiso, 6 km W of Ranopiso village, *Croat 31930* (MO, TAN); Sakamalia, Manambolo Valley, Mandrare basin, Isomono, *Humbert 13010* (P); S Madagascar, *Alluaud 106* (P); Tsiribihina, betw. Soahanina & Tsiribihina, *Perrier de la Bâthie 8551* (P).

5. *Gnidia decaryana* Leandri, Bull. Mus. Natl. Hist. Nat., sér. 2, 1: 436. 1929 [1930]. TYPE: Madagascar. Toliara: Fort-Dauphin, 3 July 1926, *R. Decary 4332* (holotype, P 00373426; isotypes, P!, TAN!). Figure 5.

Shrubs to 2 m tall; young branches reddish when fresh, flattened (more pronounced near internodes), densely to moderately pubescent, covered with prominent leaf scars; mature branches lenticellate. **Leaves** opposite to decussate, pairs rarely alternate on vigorous shoots, appressed adaxially against stems, caducous on older branchlets; petioles 0.4–0.8 mm, glabrescent to moderately pubescent; blades obovate to suborbicular, (4.1–)8–15(–18) × (2–)5–11 mm, l:w ratios ca. 1–2.5:1, both surfaces glabrous, lighter green or brown abaxially, apex apiculate, obtuse or rounded, margin with a distinct vein that appears red on young leaves when fresh, base cuneate to attenuate; midrib slightly depressed adaxially, glabrous or sparsely pubescent, raised and glabrescent abaxially, or with a few sparse strigose trichomes, lighter green than blade abaxially; secondary venation glabrous, raised or inconspicuous adaxially, usually conspicuous and more pronounced abaxially. **Inflorescences** terminal or axillary, erect, capitate, 2- to 4-flowered, sessile or subsessile, subtended by 2 pairs of closely spaced decussate bracts, the upper pair smaller and caducous. **Flowers** 4-merous, red-green, green-white, or yellow?, subsessile; pedicels 0.4–0.8 mm, densely pubescent; hypanthium 6.1–9 mm, articulate, ± membranous, densely pubescent externally, trichomes to 0.3 mm, trichomes of similar length on both portions or slightly longer on the persistent portion, glabrescent or sparsely pubescent

in lower half near articulation internally; caducous portion becoming light brown in fruit when fresh; persistent portion 2.5–3 mm; calyx lobes 4, spreading, broadly elliptic or orbicular, 1.4–1.9 × 1.4–1.9 mm, one opposing pair smaller, glabrescent or sparsely puberulent adaxially, tomentose on lower half abaxially, otherwise glabrous, apex rounded or obtuse; petaloid scales absent; stamens 8, upper whorl of anthers ca. 1/4 exerted, lower whorl 0.2–0.5 mm below upper whorl; anthers elliptic, 0.6–0.8 × 0.2 (–0.3) mm, subsessile; subgynoecial disk cupuliform or absent, to 0.1 mm tall, glabrous, apex irregularly lobed to nearly entire; ovary ovoid to ellipsoid, 0.9–1.1 × 0.4–0.5 mm, sessile or very shortly stipitate (stipe to 0.1 mm), lower half densely to sparsely pubescent, rarely glabrescent, upper half densely to sparsely pubescent, apex always densely pubescent with 1–1.5(–2) mm trichomes; style 2.2–6 mm, sparsely to moderately strigose, rarely glabrescent; stigma ca. 1.5 mm below lower whorl of anthers. **Fruits** ovoid-ellipsoid or ellipsoid, 3.1–3.4 × 1.3–1.5 mm, sparsely to moderately pubescent, apex usually densely pubescent.

Distribution and habitat. *Gnidia decaryana* occurs in southeastern Madagascar near Fort Dauphin (Toliara Province) from sea level to 950 m elevation (Fig. 17). The species grows in open sunlit areas and has been recorded on sand and gneiss in the humid bioclimatic zone.

Phenology. The species has been found in flower and fruit in January, March, July, October, and December.

IUCN Red List category. *Gnidia decaryana* occurs within the boundaries of one protected area (Andohahela). In 2003, a small, unprotected population of *G. decaryana* was located growing on the outskirts of Fort Dauphin along the base of the Pic St. Louis, bordering agricultural fields and no more than 25 m away from the edge of the town (Rogers, pers. obs.). The species is assigned a provisional IUCN (2001) conservation status of Near Threatened (NT).

Discussion. *Gnidia decaryana* is distinguished from *G. neglecta*, the most morphologically similar Malagasy species, by its obovate to suborbicular blades with cuneate to attenuate bases (vs. broadly ovate blades with cordate bases), a different venation pattern, its sessile or subsessile (vs. pedunculate) inflorescences, and by the dense (vs. completely absent) pubescence on the outer surface of the hypanthium. In addition, populations of *G. decaryana* occur more than 600 km to the south of *G. neglecta*.

Gnidia subcordata Meisn., an African species in the closely related segregate genus *Englerodaphne* (as *E. subcordata* (Meisn.) Gilg), differs from *G. decaryana* by

its pedunculate (vs. sessile or subsessile) inflorescences, longer flowers (11–15 mm vs. 6.1–9 mm long), and sparsely pubescent (vs. densely pubescent), \pm funnel-shaped (vs. cylindrical) hypanthium.

The inflorescence structure of *Gnidia decaryana* (Fig. 5B) is unique within the Malagasy species, with its two pairs of decussately arranged foliose bracts, located directly below two to four sessile or subsessile flowers. The bracts closest to the flowers are usually about half the size of the lower pair and fall off earlier. A clear distinction between leaf and bract, if one can be made, is definitely blurred in this species. One small membranous bracteole subtends each flower and lacks obvious nervation and will rarely persist until anthesis.

Typification. Two sheets of *Decary 4332* are deposited at P. Both sheets closely match the description in the protologue (Leandri, 1930b: 436) and were annotated by Leandri. The sheet bearing the accession number P 00373426 has the locality and date cited in the protologue and is regarded as the holotype.

Selected specimens examined. MADAGASCAR. **Toliara:** Andohahela, Mananara basin, mtns. betw. Andohahela & Elakelaka, Mahamavo, *Humbert 13384* (G, P [2], TAN); Imonty, Mananara basin, mtns. betw. Andohahela & Elakelaka, S of Imonty, *Humbert 14084* (P); betw. Mandromdromotra & Lokaro, N of Fort-Dauphin, *Service Forestier (Capuron) 28650* (MO, P, TEF); Pic Saint Louis, *Rogers & Rakotonasolo 108* (BM, G, MO, P, TAN, WAG).

6. *Gnidia gilbertae* Drake, Bull. Mens. Soc. Linn. Paris 2: 1218. 1896. TYPE: Madagascar. Mahajanga: betw. “Madounga et Antsalahanki,” 1876, *A. Grandidier s.n.* (holotype, P!). Figure 6.

Shrubs or trees to 4 m tall; young branches pubescent; mature branches not lenticellate. **Leaves** alternate, rarely subopposite, leaves crowded near branch tips, rarely persistent on older branchlets; petioles 0–2(–3) mm, densely pubescent or glabrescent; blades broadly obovate to nearly elliptic, 1.4–5.5 \times 0.4–1.7 cm, l:w ratios 2.3–3.6:1, both surfaces moderately to sparsely pubescent, rarely densely pubescent, apex rounded or emarginate, tip usually apiculate, base attenuate or less often cuneate; midrib depressed or rarely plane adaxially, raised and densely pubescent abaxially; venation often discolorous, usually raised on both surfaces, more pronounced abaxially. **Inflorescences** terminal or rarely axillary, erect, involucre, 16- to 28-flowered; peduncles 0.5–5(–9) mm, densely pubescent; involucre bracts 4(5), broadly ovate or orbicular, 7–12 \times 4–7 mm, l:w ratios 1.1–2.6:1, chartaceous, erect, persistent, usually glabrescent adaxially, rarely sparsely or densely strigose in upper half abaxially, apex short-acuminate or acute, acumen to 3 mm, spreading (i.e., not

reflexed), base rounded-truncate; midrib inconspicuous or visible on both surfaces, more pronounced abaxially; nervation often conspicuous on both surfaces and represented by 2 or 4 veins, those more obvious near the margin. **Flowers** 4-merous, yellow or orange; pedicels 0.5–1(–1.5) mm, densely covered with 0.5–1 mm trichomes; hypanthium (10–)12.5–17 mm, unarticulated, coriaceous, densely pubescent externally, trichomes (0.5–)1–1.5 mm, usually glabrescent internally; caducous portion torn irregularly in the lower 1/3 by the developing fruit; calyx lobes 4, broadly elliptic-oblong or obovate, 2.1–2.7 \times 1.2–1.4 mm, glabrescent or sparsely puberulous adaxially, densely pubescent abaxially, apex emarginate or rounded; petaloid scales 4, narrowly ovate-elliptic, 0.9–1.2 \times 0.2–0.3(–0.5) mm, membranous, glabrous, apex acute or with 1 to several irregular rounded lobes, often with a conspicuous midnerve when dry; stamens 8, upper whorl of anthers just below mouth, lower whorl ca. 1–1.5 mm below upper whorl; anthers elliptic-oblong, 0.8–0.9 \times ca. 0.2 mm, subsessile; subgynoecial disk cupuliform, 0.2–0.4 mm tall, glabrous, fleshy, apex smooth or slightly lobed; ovary ellipsoid, 1.2–1.6 \times 0.4–0.7 mm, stipitate (stipe ca. 0.2 mm), glabrous; style 3.4–5.7 mm, glabrous; stigma 0–7 mm below lower whorl of anthers. **Fruits** ellipsoid, 2.9–3.1 \times 1.1–1.2 mm, glabrous or rarely with a few sparsely spaced trichomes at the apex.

Distribution and habitat. *Gnidia gilbertae* is endemic to semi-deciduous gallery forests in north-western Madagascar (Mahajanga Province) from ca. 100–250 m elevation (Fig. 16). The species occurs in open sunlit areas on sandy substrates in Madagascar’s dry bioclimatic zone.

Phenology. The species flowers and fruits from April through November.

Vernacular names. Famoty (*Réserves Naturelles [Harizo] 1022*); sisitry (*Réserves Naturelles [Rakotovo] 4234*); tzoangamena (*Randrianaivo et al. 614*).

IUCN Red List category. *Gnidia gilbertae* has been recorded in two formally protected areas (Ankarafantsika, Namoroka). The species has also been collected, both frequently and recently, at Ampijoroa and Ankarafantsika. The species is assigned a provisional IUCN (2001) conservation status of Least Concern (LC).

Discussion. *Gnidia gilbertae* is distinguished from *G. daphnifolia* by the 4- (vs. 5-)merous flowers, the hypanthium that lacks an articulation and is instead torn irregularly in the lower 1/3 by the developing fruit, the leaves that usually only remain persistent near the tips of the branches (vs. leaves persistent

along most of the stem), the four or rarely five (vs. five) involucre bracts, and the generally shorter peduncles 0.5–5(–9) mm vs. 3–50 mm long.

Selected specimens examined. MADAGASCAR. **Mahajanga:** Ampijoroa Forest Station, *Phillipson 1936* (K, MO, P, TAN, WAG); Anjiafitatra [Tsitontroina], *Réserves Naturelles (Randrianasolo) 2180* (P, TAN); Anjamamgirana, near village of Analanambe, *Ranaivojaona et al. 314* (BM, G, MO, P, TAN); Ankarafantsika Plateau, June 1928, *Lavauden s.n.* (P); Ankirihitra, near Mt. Tsitondroina at Ankirihitra, *Perrier de la Bâthie 998* (P); Bongalava, *Bisset M3* (K); Namoroka, *Réserves Naturelles 9701* (P, TEF); Port Berge, Bongalava, dry forest of Marosely, *Razakamalala et al. 1742* (G, MO, P, TEF, US); Tsitampiky [Sitampiky], *Decary 8181* (P, TAN).

7. *Gnidia gnidioides* (Baker) Domke, *Biblioth. Bot.* 27 (111): 46. 1934. Basionym: *Dais gnidioides* Baker, *J. Linn. Soc., Bot.* 20: 244. 1883. *Gnidia bakeri* Gilg, *Nat. Pflanzenfam.* 3(6a): 227. 1894, nom. superfl. *Arthrosolen gnidioides* (Baker) Leandri, *Bull. Soc. Bot. France* 76: 1043. 1929 [1930]. TYPE: Madagascar. Antananarivo: “grassy hills of the province of Imerina,” s.d., *R. Baron 2061* (lectotype, designated here, K!; isotype, P!). Figure 7.

Shrubs to 80 cm tall, branching subequally (di-)trichotomously, sometimes one shoot in trichotomy does not elongate; branches not lenticellate, orange-red when fresh, usually dark red after drying, densely to sparsely strigose or strigose-tomentose, indument denser near branch tips. **Leaves** alternate, rarely subopposite, usually persistent on older branchlets, erect, drying subappressed or appressed to stems adaxially, subsessile; petioles to 0.8 mm, densely to sparsely strigose; blades needle-shaped, rarely very narrowly obovate or ovate, 7–19 × 0.75–2(–3) mm, l:w ratios (4.5–)6–15:1, involute, ± coriaceous, both surfaces sparsely strigose to glabrescent (indument more obvious near base and along midrib), apex acute or short-acuminate, tip rounded or rarely apiculate, base cuneate or attenuate; midrib inconspicuous or slightly raised adaxially, plane or slightly raised abaxially; venation inconspicuous adaxially, abaxially represented by 2 or 4 longitudinal plicate veins when dry. **Inflorescences** terminal, erect, subsessile, globose, resembling composite-like heads (composed of many closely arranged clusters of bracteate flowers), ca. 50- to 100-flowered, to 2.8 cm diam.; peduncles 0.5–3 mm, densely to moderately pubescent; bracts surrounding the base of the head 5 to 7, imbricate, spreading, persistent, broadly ovate or less often narrowly elliptic-ovate, 5–10.2 × 1.5–4.6 mm (various dimensions within the inflorescence), ± coriaceous or membranous, densely pubescent to

glabrescent, apex acuminate to aristate, acumen or arista to 4 mm, margin densely ciliate, base cuneate or attenuate-truncate; midrib and nervation conspicuous; bracts within the head 50 or more, subtending floral clusters, imbricate, persistent, broadly elliptic-obovate to linear-elliptic, 3.2–5.2 × 0.5–2 mm (various dimensions within the inflorescence), chartaceous-membranous, scabrous, densely to sparsely pubescent adaxially, glabrous to densely pubescent abaxially, apex acute or slightly acuminate, margin densely ciliate, base cuneate or attenuate; midrib and nervation conspicuous. **Flowers** 4-merous, pink, red, white?, or yellow?; pedicels 0.4–0.7 mm, covered by a dense brush of 3–4 mm trichomes; hypanthium 6.5–10 mm, articulate; caducous portion ± membranous, densely covered with erect indument externally, trichomes 1–1.5 mm, glabrous internally; persistent portion ca. 2 mm, membranous, glabrous externally and internally; calyx lobes 4, erect, white-pink, red, or yellow, broadly oblong or elliptic, 1–2.2 × 0.5–1.3 mm, glabrous adaxially, densely to moderately pubescent abaxially, apex rounded, truncate, or emarginate; petaloid scales absent; stamens 8, upper whorl of anthers just below mouth, lower whorl 0.1–0.5 mm below upper whorl; anthers elliptic, 0.4–0.6 × 0.15–0.2 mm, subsessile; subgynoecial disk cupuliform or absent, less than 0.1 mm tall when present, glabrous, fleshy, apex smooth or irregularly lobed; ovary ellipsoid, 0.7–1.1 × 0.3–0.5 mm, sessile, glabrous; style 3–4.7 mm, glabrous; stigma 0–2.5 mm below the lower whorl of anthers. **Fruits** ellipsoid, 1.6–1.9 × 0.9–1 mm, glabrous. *n* = 9 (Rabakonandrianina & Carr, 1987).

Distribution and habitat. *Gnidia gnidioides* occurs on the central plateau of Madagascar from 1000–2500 m elevation (Fig. 17). Populations occur from the Tampoketsa of Ankazobe (a region located to the north of Antananarivo) to the Andringitra massif. *Gnidia gnidioides* is associated with marshy areas and other moist places, and grows in open sunlit areas, including prairies and *Tapia* woodlands, in the subhumid bioclimatic zone. Some specimen labels mention that the species occurs on gneiss or quartzitic rocks.

Phenology. The species flowers and fruits year round.

Vernacular name. Bambola (*Réserves Naturelles [Razafindrakoto] 3055*, *Réserves Naturelles [Rabevazaha] 10387*; *Service Forestier [Marlange] 1950*).

IUCN Red List category. *Gnidia gnidioides* is common in both protected (Ambohitantely, Andringitra, Analamazoatra) and unprotected areas, at least some of which are periodically disturbed by fire

(Rogers, pers. obs.). The species is assigned a provisional IUCN (2001) status of Least Concern (LC).

Discussion. *Gnidia gnidioides* is easily distinguished by its needle-shaped leaves and 50- to 100-flowered, terminal, subsessile inflorescences that superficially resemble composite-like heads. The species is most morphologically similar to two continental African species, *G. bambutana* (Cameroun, Nigeria) and *G. mollis* (Congo-Kinshasa, Malawi, Mozambique, Tanzania, Zambia). Based on a study of the inflorescence architecture of all three species, Aymonin (1966c) found that *G. gnidioides* differs from *G. bambutana* by its fewer-flowered floral clusters within the head and its more coriaceous and thicker leaves. Examined specimens of *G. mollis* are similar to *G. gnidioides*, but tend to have broader leaves, larger inflorescences, and flowers with petaloid scales. Robyns (1975) in the *Flore d'Afrique Centrale* and Peterson (1978) in the *Flora of Tropical East Africa* noted that the three species are closely related, but considered each one to belong to a distinct species. It should be noted that the basionym of *G. gnidioides* (*Dais gnidioides* Baker, 1883) would have priority over *G. mollis* (Wright, 1906) and *G. bambutana* (Engler, 1921) if future studies indicate that these three taxa are conspecific.

Nomenclature and typification. The superfluous name *Gnidia bakeri* Gilg has been used incorrectly to refer to *G. gnidioides* as recently as the *Flore de Madagascar et des Comores* (Leandri, 1950). Baker (1883) originally described the species as *Dais gnidioides*, but Gilg (1894) chose not to retain the epithet when transferring the species to *Gnidia*. Leandri (1930a) transferred the species using the correct epithet (*gnidioides*) into *Arthrosolen*, a genus now widely considered to be synonymous with *Gnidia*. Later Domke (1934) created a combination for the species in *Gnidia* also using Baker's original epithet. In the *Flore*, Leandri (1950) placed both *A. gnidioides* and *D. gnidioides* into synonymy under the illegitimate name *G. bakeri* Gilg.

Two collections (*Baron 665*, *Baron 2061*) were cited in the protologue of *Dais gnidioides* (Baker, 1883). The K sheet of *Baron 2061* is selected as the lectotype to avoid any potential ambiguity caused by the fact that the only material of *Baron 665* at K was mounted on the same sheet as *Baron 1894*, and consequently might represent a mixed gathering.

Selected specimens examined. MADAGASCAR. **Antananarivo:** Ambohitantly Special Reserve, *Rogers et al. 126* (G, K, MO, P, WAG); Analabe swamp, *Cours (Hb. St. Agric. Alaotra) 1797* (MO, P, TAN); Betafo, *Perrier de la Bâthie 8541* (P); betw. Ambatolampy & Tsinjoarivo, *Vigüier 1800* (P

[2]); Central Madagascar, *Baron 665* (K); Km 30 on rd. betw. Antananarivo & Ambatolampy, *Keraudren & Aymonin 25160* (P); Mandraka forests, *D'Alleizette 1110* (P). **Fianarantsoa:** Andringitra massif, *Réserves Naturelles (Razafindrakoto) 2271* (GH, K, MO, P [2]); Ankarabe, *Rauh 79* (TAN); Fenoarivo, *Bosser 413* (TAN); Ibity massif, *Fosberg 52380* (US); Itremo massif, *van der Werff & McPherson 13577* (G [2], MO, TAN, WAG). **Toamasina:** Antsahapandrano (Ankara-aha), *Decary 17646* (K, P).

8. *Gnidia hibbertioides* (S. Moore) Z. S. Rogers, comb. nov. Basionym: *Lasiosiphon hibbertioides* S. Moore, J. Bot. 58: 189. 1920. TYPE: Madagascar, s.d., *J. Thompson & J. Forbes s.n.* (holotype, BM!). Figure 8.

Shrub?; young branches densely pubescent. **Leaves** alternate, closely arranged, caducous on older branchlets; petioles 1–2 mm, densely pubescent; blades narrowly elliptic or slightly obovate, 1.5–2.2 cm × 3–4 mm, l:w ratios ca. 4–6:1, involute, both surfaces covered with a dense uniform indument of ca. 0.5 mm, erect to subappressed, trichomes, apex apiculate, base long-attenuate; midrib inconspicuous adaxially, raised abaxially, densely to moderately pubescent on both surfaces; venation ± inconspicuous. **Inflorescences** terminal, erect, involucrate, ca. 7-flowered; peduncles to 3 mm, densely pubescent; involucre bracts 5, broadly ovate-elliptic, 1–1.2 cm × 3–4 mm, l:w ratios ca. 3:1, similar in texture to leaves, erect, glabrous adaxially, densely pubescent abaxially, apex acute or apiculate, base obtuse-rounded; midrib and nervation inconspicuous on both surfaces. **Flowers** 5-merous, sessile or subsessile; pedicels to 0.5 mm, densely covered with ca. 2 mm trichomes; hypanthium 1.7–1.9 cm, articulate; caducous portion densely pubescent externally, trichomes ca. 0.5–1 mm, glabrous or with a few appressed trichomes near articulation internally; persistent portion 5–7 mm, externally covered by 1.5–2 mm trichomes, those erect and nearly perpendicular to the surface of the tube, glabrous internally; calyx lobes 5, narrowly ovate-subtriangular, 4–5.2 × 1.5–1.6 mm, glabrous adaxially, densely pubescent abaxially, apex acute; petaloid scales 5, suborbicular or very broadly ovate, 4.6–6 × 3.8–4.7 mm, membranous, glabrous, upper half with an irregularly lacerate or sinuate margin; stamens 10, upper whorl of anthers located just below mouth, lower whorl ca. 3.5 mm below upper whorl; anthers oblong, 1.2–1.4 × ca. 0.25 mm, subsessile; subgynoecial disk cupuliform, ca. 0.5 mm tall, glabrous, apex smooth or irregularly lobed; ovary ellipsoid, ca. 1.2 × 0.5 mm, stipitate (stipe ca. 0.4 mm), mostly glabrous, apex with a few trichomes; style and stigma not seen in good condition. **Fruits** not seen.



Figure 8. *Gnidia hibbertioides* (S. Moore) Z. S. Rogers. —A. Habit. Note the large petaloid scales. —B. Persistent portion of hypanthium surrounding the gynoecium. Drawn from holotype, *Thompson & Forbes s.n.* (BM).

Distribution and habitat. *Gnidia hibbertioides* is endemic to Madagascar and known only from a poorly labeled type. More specific distribution or habitat information is not available.

Phenology. The type collection is in flower, but no collection date is recorded on the specimen label or in the protologue (Moore, 1920).

IUCN Red List category. *Gnidia hibbertioides* was collected in Madagascar on one occasion in the early 1800s and is represented by a single herbarium specimen with an unspecified locality. The species is assigned a provisional IUCN (2001) conservation status of Critically Endangered (CR) (B1ab + 2ab). At the present time, the species cannot be assigned to an Extinct category (EX or EW) because exhaustive surveys searching for additional individuals have not been conducted.

Discussion. *Gnidia hibbertioides* is distinguished from *G. daphnifolia* by its 1.7–1.9 cm long hypanthium (vs. rarely to 1.5 cm long) with a 5–7 mm long persistent portion (vs. to 4 mm long) and by its large (4.6–6 × 3.8–4.7 mm) petaloid scales, which surpass the calyx lobes. The petaloid scales of *G. hibbertioides* (Fig. 8A) are generally three to four times larger than the scales of most other species of Malagasy *Gnidia*, and may prove to be the largest in the genus. Another distinctive feature of the scales is the irregularly lacerate or sinuate apical margin. Other Malagasy species have petaloid scales with entire margins that are rounded, emarginate, or lobed at the apex.

Typification. *Gnidia hibbertioides* was based on a scantily labeled sheet deposited at BM. “Madagascar” is the only locality information mentioned on the original material and cited in the protologue (Moore, 1920: 189). In unidentified handwriting on the herbarium sheet, the names of the collectors were written as “Vaughn, Thompson & Forbes.” This information is possibly a distortion of the names of two men known to have collected in Madagascar, John Vaughn Thompson and John Forbes (Dorr, 1997: 485). However, it is impossible for both men to have collected the original material jointly, because Thompson visited the island in 1814 and Forbes did not arrive until 1822 (Dorr, 1997). Nevertheless, as the only extant material of the name, this particular sheet must be considered the holotype.

9. *Gnidia humbertii* (Leandri) Z. S. Rogers, comb. nov. Basionym: *Lasiosiphon humbertii* Leandri, Bull. Soc. Bot. France 76: 1039. 1929 [1930]. TYPE: Madagascar. Fianarantsoa: Isalo, mouth of Sakamarekely & Sambalinieto rivers, 500–1000 m, 19 Oct. 1924, *H. Humbert 2844*

(lectotype, designated here, P!; isotype, G!). Figure 9.

Rounded, compact, densely ramified subshrubs to 60 cm tall; young branches densely pubescent, covered with prominent leaf scars; mature branches densely pubescent, ± exfoliating. **Leaves** alternate, spirally arranged, closely spaced, rarely with internodes to 1.5 mm, persistent only at the tips of branches; young leaves adaxially appressed against stems; petioles 0–0.3 mm, densely pubescent; blades elliptic, slightly obovate, or linear, 7–17.1 × 1.9–3 mm, l:w ratios ca. 4–8:1, silver-green, both surfaces obscured by a dense sericeous-tomentose indument of 0.2–0.3(–0.5) mm trichomes, apex acute or short-acuminate, base cuneate or attenuate; midrib obscured by indument adaxially, obscured or nearly so abaxially; venation obscured on both surfaces. **Inflorescences** terminal, erect, involucrate, (6–)8- to 15-flowered, sessile or subsessile; peduncles to 1.5 mm, densely pubescent; involucre bracts 5, broadly ovate, 6–9 × 2–4 mm, l:w ratios ca. 2:1, erect, persistent, densely pubescent adaxially, densely pubescent on upper half abaxially, lower half sparsely pubescent or glabrescent, apex obtuse or rounded, base rounded-truncate; midrib inconspicuous adaxially, inconspicuous or slightly raised abaxially; nervation inconspicuous on both surfaces. **Flowers** 5-merous, yellow, sessile or subsessile; pedicels to 0.2 mm, densely covered with ca. 0.5(–1) mm trichomes; hypanthium 10–15 mm, articulate, coriaceous; caducous portion densely pubescent externally, trichomes 0.5–1 mm, glabrous internally; persistent portion 2–3 mm, obscured by 3–4.5 mm trichomes, glabrous internally; calyx lobes 5, spreading, broadly obovate or elliptic, 2–4.5 × 1.7–2.5 mm, glabrous adaxially, densely pubescent abaxially, apex emarginate or rounded; petaloid scales absent or 5; scales when present narrowly to broadly ovate or elliptic-linear, to 1.2 × 0.4 mm, membranous, glabrous, apex rounded; stamens 10, upper whorl of anthers ca. 1/2 exerted, lower whorl 1–4 mm below upper whorl; anthers oblong, 1–1.5 × 0.2–0.4 mm, subsessile; subgynoeical disk cupuliform, 0.3–0.5 mm tall, glabrous, membranous, apex smooth or irregularly lobed; ovary ovoid-ellipsoid, ca. 1.4 × 0.5 mm, stipitate (stipe 0.2–0.3 mm), lower half glabrous or sparsely pubescent, apex usually densely pubescent, trichomes to 1 mm; style 3.8–7 mm, glabrous or with a few trichomes on lower half; stigma near mouth or at height of lower whorl of anthers. **Fruits** ellipsoid, 2.8–3.2 × 1–1.2 mm, mostly glabrous, glabrescent or only densely pubescent near the apex.

Distribution and habitat. *Gnidia humbertii* is restricted to the subarid bioclimatic zone in southern

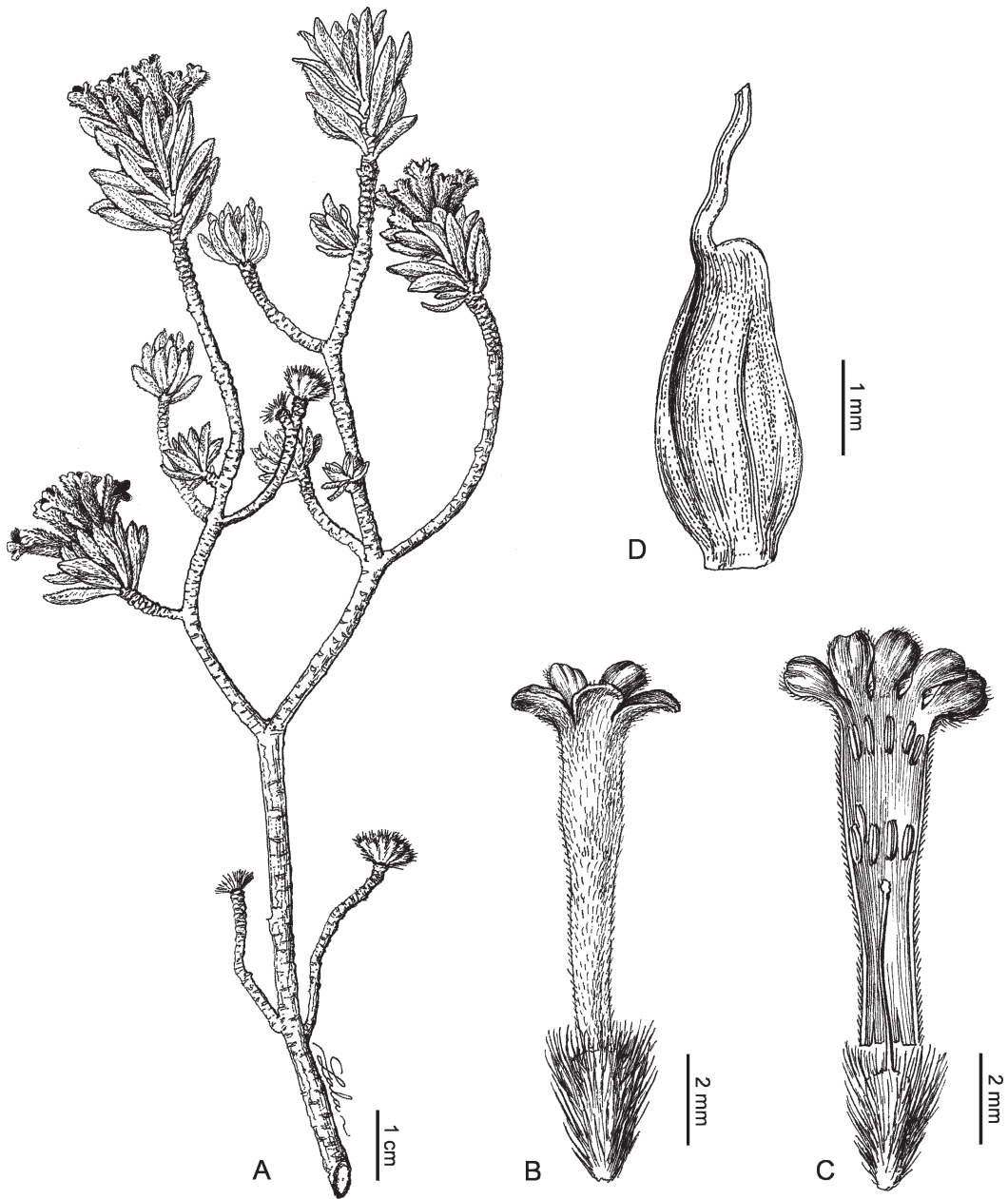


Figure 9. *Gnidia humbertii* (Leandri) Z. S. Rogers. —A. Habit. —B, C. Flower. —D. Fruit. Habit and fruit drawn from Peltier & Peltier 2469 (TAN). Flower drawn from Rogers & Rakotonasolo 399 (MO).

and southwestern Madagascar (Fig. 17). Populations occur from the Mahafaly Plateau and Isalo to Cap Sainte Marie and as far west as La Table (a mesa-like mountain on the west coast near Toliara). The species grows in open sunlit areas on sand, sandstone, and calcareous limestone (Rogers, pers. obs.).

Phenology. The species flowers and fruits year round.

IUCN Red List category. *Gnidia humbertii* has been recorded in two formally protected areas (Cap Sainte Marie, Isalo). Several large populations, obviously resistant to periodic burning, were observed at Isalo in 2004 and again in 2006. The species is assigned a preliminary IUCN (2001) status of Least Concern (LC).

Discussion. *Gnidia humbertii* is the only Malagasy species with a rounded, compact, densely ramified,

subshrub habit. The leaves of *G. humbertii* and *G. ambondrombensis* are covered on both surfaces by a dense sericeous indument, but the pubescence of the former is composed of much shorter trichomes (trichomes 0.2–0.5 mm vs. 1–1.5 mm long).

Typification. Two collections were cited in the protologue of *Lasiosiphon humbertii* (Leandri, 1930a): *Douillot [Douliot] s.n.* and *Humbert 2844*. Both collections are annotated by Leandri and match the protologue description. The P sheet of *Humbert 2844* is in better physical condition and is thus selected as the lectotype.

Selected specimens examined. MADAGASCAR. **Fianarantsoa:** Isalo Natl. Park, 2–3 km N of Natl. Rte. #7, *Rogers & Rakotonasolo 399* (BM, BR, G, K, MO [2], P, TAN, TEF, US). **Toliara:** La Table, near Tuléar, 15 Feb. 1913, *Afzelius s.n.* (P); Mahafaly Plateau, Menarandra basin, *Perrier de la Bâthie 8555* (K, P); Mangorovato, 1892, *Douillot [Douliot] s.n.* (P).

10. *Gnidia linearis* (Leandri) Z. S. Rogers, comb. nov.
Basionym: *Lasiosiphon linearis* Leandri, Bull. Soc. Bot. France 76: 1040. 1929 [1930]. *Lasiosiphon decaryi* Leandri var. *linearis* (Leandri) Leandri, Bull. Mus. Natl. Hist. Nat., sér. 2, 3: 154. 1931. TYPE: Madagascar. Toliara/Fianarantsoa: savanna betw. Bemketa [Bereketa] & Malio, 15 June 1923, *H. Poisson 692* (holotype, P!). Figure 10.

Lasiosiphon decaryi Leandri, Bull. Soc. Bot. France 76: 1041. 1929 [1930]. Syn. nov. TYPE: Madagascar. Toliara: Ambovombe (Amboasary), dunes, 21 May 1924, *R. Decary 2785* (lectotype, designated here, P!; isotypes, G!, TAN!).

Lasiosiphon decaryi Leandri var. *erectus* Leandri, Bull. Soc. Bot. France 76: 1041. 1929 [1930]. Syn. nov. *Lasiosiphon erectus* (Leandri) Leandri, Notul. Syst. (Paris) 13: 50. 1947. TYPE: Madagascar. Antananarivo: Tananarive, May 1916, *E. Waterlot s.n.* (lectotype, designated here, P 00373449!).

Lasiosiphon decaryi Leandri var. *littoralis* Leandri, Notul. Syst. (Paris) 13: 49. 1947. Syn. nov. TYPE: Madagascar. Toliara: betw. Tuléar & Manombo, May 1910, *Perrier de la Bâthie 8553* (lectotype, designated here, P 00373453!).

Lasiosiphon decaryi Leandri var. *tenerifolia* Leandri, Notul. Syst. (Paris) 13: 48. 1947. Syn. nov. TYPE: Madagascar. Toliara: Ambovombe distr., Antanimora, 6 Aug. 1924, *R. Decary 2971* (lectotype, designated here, P 00373439!; isotypes, BM!, K!, TAN!).

Shrubs to 3 m tall; young branches glabrescent to pubescent; mature branches usually lacking lenticels. **Leaves** alternate, subsessile or short petiolate; petioles to 2 mm, glabrescent to pubescent; blades linear, narrowly elliptic-oblong or obovate, 6–50 × 1.5–9 mm, l:w ratios ca. 3–14:1, both surfaces glabrescent to densely tomentose-strigose (indument gradually becoming denser moving from SE to SW populations), apex cuspidate or apiculate, base long-attenuate or cuneate; midrib inconspicuous or raised

on both surfaces, glabrescent; venation visible in larger leaves, otherwise usually inconspicuous. **Inflorescences** axillary or terminal, erect, involucrate, (9- to)12- to 18-flowered, pedunculate; peduncles 5–50 mm, glabrescent to sparsely pubescent, rarely moderately pubescent; involucre bracts 5, suborbicular or broadly ovate, 5–8 × 3.8–5.1 mm, l:w ratios 1–1.5(–2):1, often caducous, chartaceous or coriaceous, both surfaces glabrescent to moderately pubescent (southwestern coastal populations), apex apiculate (apicule 1–2 mm) with a strongly decurved tip, short-acuminate, or acute, base rounded-truncate; midrib nearly inconspicuous on both surfaces, more pronounced near apex abaxially; nervation absent or represented by 1 to 5 longitudinal veins. **Flowers** 5-merous, yellow or orange, rarely red; pedicels ca. 0.5 mm, densely pubescent, trichomes 3–4 mm; hypanthium 7.1–15 mm, articulate, semimembranous to ± coriaceous, densely pubescent externally, glabrous internally; caducous portion externally covered with ca. 0.5 mm trichomes; persistent portion 3–4.5 mm, externally covered with (1–)3–5 mm trichomes; calyx lobes 5, broadly oblong-elliptic, 2–2.5 × 0.9–1.5 mm, membranous, spreading, glabrous adaxially, densely pubescent abaxially, apex emarginate or rounded; petaloid scales 5, yellow, suborbicular or obovate, 0.9–3.7 × 0.5–1.5 mm, membranous, glabrous, spreading, apex most often emarginate, sometimes rounded, truncate, or with 3 to 5 irregularly rounded lobes; stamens 10, upper whorl of anthers ca. 1/2 to 3/4 exerted, lower whorl 0.5–1 mm below upper whorl; anthers elliptic, 0.8–1 × ca. 0.3 mm, subsessile; subgynoecial disk cupuliform, 0.1–0.3 mm tall, glabrous, fleshy, apex smooth or irregularly lobed; ovary ellipsoid, 1.2–1.4 × 0.6–0.7 mm, stipitate (stipe to 0.3 mm), glabrous; style 5.2–9 mm, glabrous; stigma 0–2 mm below lower whorl of anthers, or rarely exerted by 1 mm. **Fruits** ellipsoid, 3.1–3.4 × 1.1–1.4 mm, glabrous.

Distribution and habitat. *Gnidia linearis* is almost entirely restricted to the subarid bioclimatic zone of southwest Madagascar (Toliara Province) from 0–1000 m elevation (Fig. 16). The disjunct population at Bemaraha extends the distribution by ca. 200 km to the north of other populations, and into the island's dry bioclimatic zone. Several other collections along the central plateau in the humid bioclimatic zone (1200–1400 m elevation) may have been made from cultivated plants or plants that escaped cultivation, and are denoted using a different marker in the distribution map.

Phenology. The species flowers and fruits year round.

Vernacular names. Hafodramena (*Boiteau 3097*; *Decary s.n.* [30 Aug. 1917]; *Humbert 20259*);

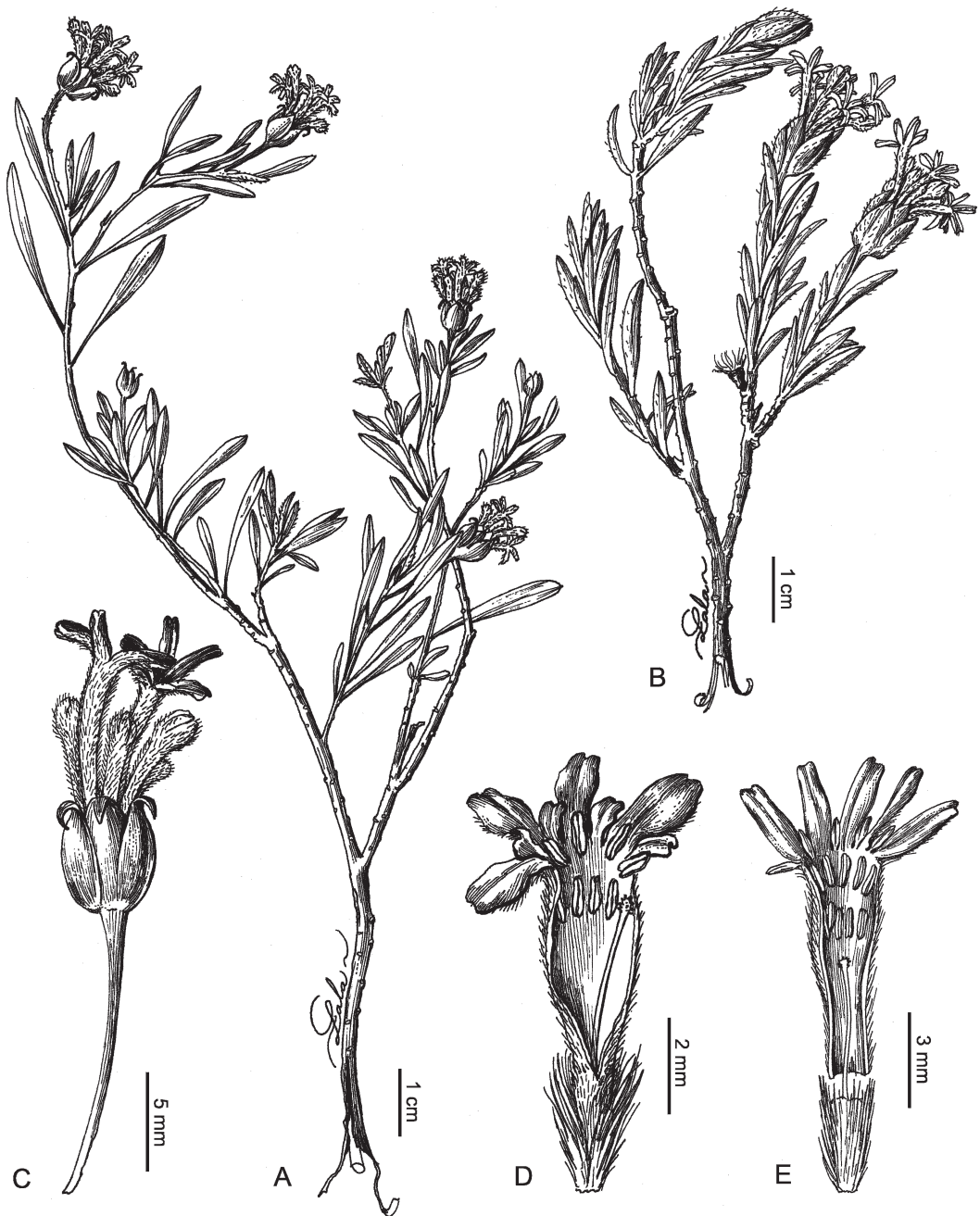


Figure 10. *Gnidia linearis* (Leandri) Z. S. Rogers. —A, B. Habits. Note variation in indument, peduncle length, and apex of involucre bract. —C. Inflorescence. —D, E. Flower dissections. One sepal, one petaloid scale, and one anther removed from part D. Habits drawn from *Rogers & Rakotonasolo 523* (part A, MO) and *Rogers & Rakotonasolo 419* (part B, MO). Inflorescence drawn from *Rogers & Rakotonasolo 523* (part C, MO). Flowers drawn from *Rogers & Rakotonasolo 523* (part D, MO) and *Rogers & Rakotonasolo 419* (part E, MO).

hafotra mena (*Cours 5275*); roinisa (*Réserves Naturelles [Rakotoniania] 2777*; *Réserves Naturelles [Ravelonahary] 4285*; *Rogers & Rakotonasolo 524*).

IUCN Red List category. Naturally occurring populations of *Gnidia linearis* are widespread in southwest Madagascar and have been recorded inside several protected areas (Andohahela, Isalo, Lac

Tsimanampetsotsa). The species is also cultivated in central Madagascar (Rogers, pers. obs.). *Gnidia linearis* is assigned to the conservation category of Least Concern (LC) according to IUCN (2001) criteria.

Discussion. Leandri (1930a) used two collections (*Waterlot s.n.* [June 1915] and *Waterlot s.n.* [May 1916]), both noted to be from Antananarivo, Madagascar's capital, in the description of *Lasiosiphon decaryi* var. *erectus*. Later, Leandri (1947, 1950) decided to treat the taxon at the species rank as *L. erectus*, distinguishing it from what he considered to be related species (*L. dumetorum* and *L. multifolia*, both treated here as synonyms of *Gnidia daphnifolia*) by having inflorescences of ca. 15, rather than seven to 10 flowers. Flower number can be extremely variable in many species of *Gnidia* with involucre inflorescences, and Leandri's distinction breaks down once additional material is consulted. Nevertheless, the two *Waterlot* collections, along with several other collections from Madagascar's central plateau, differ somewhat from other populations of *G. linearis* by having more fleshy leaves and glaucous bracts when dry. The differences observed in the high plateau populations are possibly caused by their substantial geographic disjunction and from variation due to diverse biophysical parameters, e.g., 1200–1400 m elevations in the subhumid bioclimatic zone versus up to 1000 m elevation in the dry and subarid bioclimatic zone. It is also plausible that the high plateau specimens could represent cultivated plants of *G. linearis* that hybridized with another high plateau species, such as *G. perrieri*. Plants of *G. linearis* continue to be brought from southwest Madagascar to paper factories operating in several cities on the central plateau (e.g., Antananarivo, Ambositra, Fianarantsoa, Ambalavao), and cultivated plants of *G. linearis* (e.g., Rogers *et al.* 734, not mapped) were found growing at a factory in the town of Ambalavao as recently as 2008 (Rogers, pers. obs.). Despite several attempts, the naturally occurring populations on the high plateau have not been located, and additional collections and information from the area are needed to better understand the observed variation.

In the *Flore de Madagascar et des Comores*, Leandri (1950) recognized *Gnidia linearis* as a variety of the name *L. decaryi*, along with two other varieties (*L. decaryi* var. *littoralis* and *L. decaryi* var. *tenerifolia*). His varieties were distinguished by differences in leaf size and shape (e.g., leaves broader and larger in variety *littoralis*; leaves longer, but not broader in variety *tenerifolia*), flower length (10–12 mm in variety *decaryi* vs. 8–10 mm in the other two), bract morphology (e.g., apex strongly decurved in variety *littoralis*), and petaloid scales (narrower in variety

linearis). With additional material, Leandri's distinguishing characters exhibit continuous, overlapping variation. No other differences have been found to justify the recognition of Leandri's varieties.

Lasiosiphon linearis and *L. decaryi* were validly published simultaneously (Leandri, 1930a: 1040–1041), the former name being most recently recognized by Leandri (1950) in the *Flore de Madagascar et des Comores* as a variety of *L. decaryi*. Both names are considered synonymous here, and if the *decaryi* epithet were transferred into *Gnidia* the resulting combination would cause unnecessary confusion with the nomenclaturally similar, but taxonomically different, *G. decaryana*. Therefore, Leandri's less familiar *linearis* epithet is adopted to form the new combination.

The more broadly circumscribed *Gnidia linearis* is distinguished from *G. perrieri* by the young stems drying green, brown, or black (vs. red-purple or orange-red), the less fleshy and membranous leaves, the bracts that are usually apiculate and strongly decurved at the tips (vs. usually long-acuminate or acute and with erect tips), narrower leaves, longer peduncles, and the longer hypanthium trichomes ([1–] 3–5 mm vs. 0.3–0.5[–0.7] mm long).

Typification. Five collections were cited in the protologue of *Lasiosiphon decaryi* (Leandri, 1930a: *Decary s.n.* (P), *Decary 2759* (P), *2785* (G, P, TAN), *3183* (MO, P, TAN, US), *3741* (P [2])). All examined syntypes are annotated in Leandri's handwriting and correspond closely to the description. The P sheet of *Decary 2785* is in particularly good condition and is chosen as the lectotype.

Two collections were cited in the protologue of *Lasiosiphon decaryi* var. *erectus* (Leandri, 1930a: *Waterlot s.n.* (June 1915) and *Waterlot s.n.* (May 1916)). One sheet of each collection has been located at P. The sheet dated May 1916 (P 00373449) is in better physical condition and is chosen as the lectotype.

Nine collections were cited in the protologue of *Lasiosiphon decaryi* var. *littoralis* (Leandri, 1947): *A. Grandidier s.n.* (Nov. 1868–Jan. 1869) (P), *Humbert 2489* (G, P, TAN), *Humbert & Swingle 5170* (P), *5294* (G, GH [2], MO, P, US, WAG), *5294bis* (P), *5414bis* (P), *Lam & Meeuse 5439* (P, WAG), *Perrier de la Bâthie 8553* (P), *12807* (K, P [2]). The Paris sheets of all nine syntypes bear Leandri's own handwritten annotations. *Perrier de la Bâthie 8553* (P) has bracts and leaves most closely matching the description and is designated as the lectotype.

Five collections were cited in the protologue of *Lasiosiphon decaryi* var. *tenerifolia* (Leandri, 1947): *Decary 2971* (BM, P, TAN), *3183* (MO, P, TAN, US),

8341 (P), 8966 (MO, P), Geay 6328 (P). *Decary 2971* closely matches the protologue and P 00373439 is chosen as the lectotype.

Selected specimens examined. MADAGASCAR. **Antananarivo:** Antananarivo [possibly cultivated], June 1915, *Waterlot s.n.* (P); Antsahady [possibly cultivated], *D'Alleizette 769M* (P). **Fianarantsoa:** Anjoma [possibly cultivated], Ambositra distr., Tapia forest, *Peltier 2181* (P); Horombe Plateau, *Jacquemin 1129* (P); Isalo Natl. Park, 2–3 km N of Natl. Rte. #7, *Rogers & Rakotonasolo 419* (K, MO, P, TAN); Itremo [possibly cultivated], *Perrier de la Bâthie 12471* (P). **Mahajanga:** Bemaraha Plateau, *Hb. Jard. Bot. Tananarive 6151* (P). **Toliara:** Amboasary, *Decary 3183* (MO, P, TAN, US); Ambondro-Tsihombe rd., *Croat 31647* (MO, P, TAN, WAG [2]); Ambovombe, *Decary 8966* (MO, P), 8341 (P); Ampanihy, *Humbert & Swingle 5527* (P [2]); Ampanihy to Androka rte., 16 km SW of Ampanihy, *Labat et al. 2073* (K, MO); Andohahela (Parcel #2), path from Tsimelahy W to Vohimainty, *Birkinshaw et al. 435* (GRA, MO, P, TAN); Andohahela (Parcel #3), *Eboroke 940* (GRA, MO, P, TAN); Androvo, 35 km N of Toliara along coast rd., *Schatz et al. 1744* (K, MO, P, TAN); Androka, Ampanihy on the Linta, on Etrobeke, *Allorge 2298* (P); Androka, 38 km SW of Ampanihy, on rd. to Androka, *Phillipson et al. 3447* (G, K, MO, TAN, WAG); Ankalityny, 95 W of Fort-Dauphin on Natl. Rte. #13, *Miller & Randrianasolo 6180* (K, MO, P, PRE, TAN); Ankarobato (Tuléar), *Peltier & Montagnac 3194* (P, TAN); Ankilizato, Morondava basin, *Perrier de la Bâthie 8539* (P [2]); Antanimora, forest station near Antanimora, *Service Forestier (Capuron) 341* (P, TEF); Antanimora–Ambovombe rd., 54 km NW of Ambovombe, *Dorr et al. 3964* (K, MO, TAN, US, WAG); Antreaky, 15 km ENE of Beloha, *Fosberg 52485* (MO); Beheloka village, near beach, *Rogers & Rakotonasolo 523* (BM, G, K, MO [2], P, TAN); Beloha, on rd. S to Tranovaho, near Barabay, *Phillipson & Milijaona 3625* (G, K, MO, TAN, WAG); Berenty, *O'Connor 112* (K); Beza-Esiva, middle Mandrare basin, *Descoings 2744* (MO, TAN); Fiherenana Valley, *Humbert & Swingle 5097* (P); Ifotaka, *Lam & Meeuse 5439* (P, WAG); Ifaty, 5 km N of town, *Rogers et al. 872* (B, MO, P, TAN); Imanombo, around Antanimora (Androy), 30–35 km N of Ambia, *Humbert & Capuron 28846* (MO, P); Italy, 30 km SW of Fort-Dauphin, *Randrianasolo et al. 143* (MO, P, TAN); Itampolo, *Phillipson et al. 3742* (G [2], K, MO, TAN, WAG); Kotriha, Manambolo Valley, Mandrare basin, around Isomono, Mtns. Kotriha & Isomonobe, *Humbert 12812* (G, MO, P); La Table, *Dequaire (Hb. St. Agric. Alaotra) 27333* (MO, P, TAN); Lac Tsimanampetsotsa, *Rogers & Rakotonasolo 544* (MO, P, TAN, TEF); Mangoky, on Malio River, *Perrier de la Bâthie 8543* (P); Ranopiso, 1 km E of the town, *Rogers et al. 911* (BM, BR, CAS, G, GH, K, MO, P, TAN, US, WAG); Tsimanampetsotsa, Lac Manampetsotsa, delta of Linta, sand near Beheloka, *Humbert & Swingle 5294* (G, GH [2], MO, P, US, WAG), *5294bis* (P), near Itampolo, *Humbert & Swingle 5414bis* (P); Tsvionoakely, 18–30 km N of Tuléar, *Miller & Randrianasolo 6104* (K [2], MO, P, PRE, TAN); Tuléar, Nov. 1868–Jan. 1869, *A. Grandidier s.n.* (P); same locality, *Humbert & Perrier de la Bâthie 2489* (G, P, TAN); Tuléar, near ocean, *Perrier de la Bâthie 12807* (K, P [2]); Tuléar, delta of Fiherenaha, *Humbert & Swingle 5170* (P); Tuléar–Manombo, *Perrier de la Bâthie 8553* (P).

11. *Gnidia neglecta* Z. S. Rogers, sp. nov. TYPE: Madagascar. Toamasina: Andevorante [Andevor-

anto], Moramanga, sandy plain, 3 Oct. 1912, K. *Afzelius s.n.* (holotype, P!). Figure 11.

Species nova quae a *Gnidia decaryana* Leandri lamina foliari late ovata basi cordata (haud obovata vel suborbiculari basi cuneata usque attentuata) reti venularum dense discolori fuscato (haud plus minusve inconspicuo concolori), inflorescentiis pedunculatis (haud sessilibus vel subsessilibus) et hypanthio glabro (haud extus dense pubescenti) differt.

Shrub; young branches glabrous, flattened (especially near internodes); branches not lenticellate, covered with prominent leaf scars. **Leaves** opposite, presumably decussate, pairs rarely subopposite; petioles 0.6–1 mm, glabrescent; blades broadly ovate, 8–17 × 4–12 mm, l:w ratios ca. 1.3–2:1, glabrous, abaxial surface slightly glaucous, apex rounded or obtuse, tip apiculate or rarely emarginate, margin with a distinct vein, base cordate; midrib depressed adaxially, raised abaxially, glabrescent and darker than blade on both surfaces; venation darker than blade, glabrous, raised on both surfaces, more pronounced abaxially; secondary veins forming a brochidodromous loop near the margin; fine venation uniformly reticulate, densely congested, more pronounced abaxially, smallest areolae ca. 0.2 × 0.2 mm. **Inflorescences** terminal, capitate, 2- to 4-flowered; peduncles to 2.5 cm, flattened, glabrous, subtended at base by leaves ca. 1/2 the size of next lower leaf pair (i.e., modified inflorescence bracts absent). **Flowers** 4-merous, sessile; hypanthium 7.8–8.2 mm, articulate, ± membranous, glabrous; persistent portion 2.8–3.4 mm; calyx lobes 4, broadly elliptic or orbicular, 2.1–2.5 × 1.5–2 mm, glabrous, apex rounded, obtuse, or less often emarginate; petaloid scales absent; stamens 8, upper whorl of anthers 1/4 to 1/2 exerted, lower whorl 0.7–1 mm below upper whorl; anthers elliptic, 0.7–0.8 × ca. 0.25 mm, subsessile; subgynoecial disk cupuliform, to 0.2 mm tall, glabrous, membranous, apex irregularly lobed; ovary ellipsoid, 1.1–1.2 × ca. 0.6 mm, not obviously stipitate, mostly glabrous, apex with a few 0.5(–0.8) mm trichomes; style ca. 2.7 mm, glabrous; stigma ca. 2.7 mm below lower whorl of anthers. **Fruits** not seen.

Distribution and habitat. *Gnidia neglecta* is an eastern littoral species known from a single specimen, which was collected on a sandy plain near Andevoranto and Ambila–Lemaitso in Madagascar's humid bioclimatic zone near sea level (Fig. 17).

Phenology. The species flowers in October.

IUCN Red List category. *Gnidia neglecta* was collected on one occasion in 1912. No populations were located at the type locality in February 2006. Due to the apparent rarity of the species, the period of

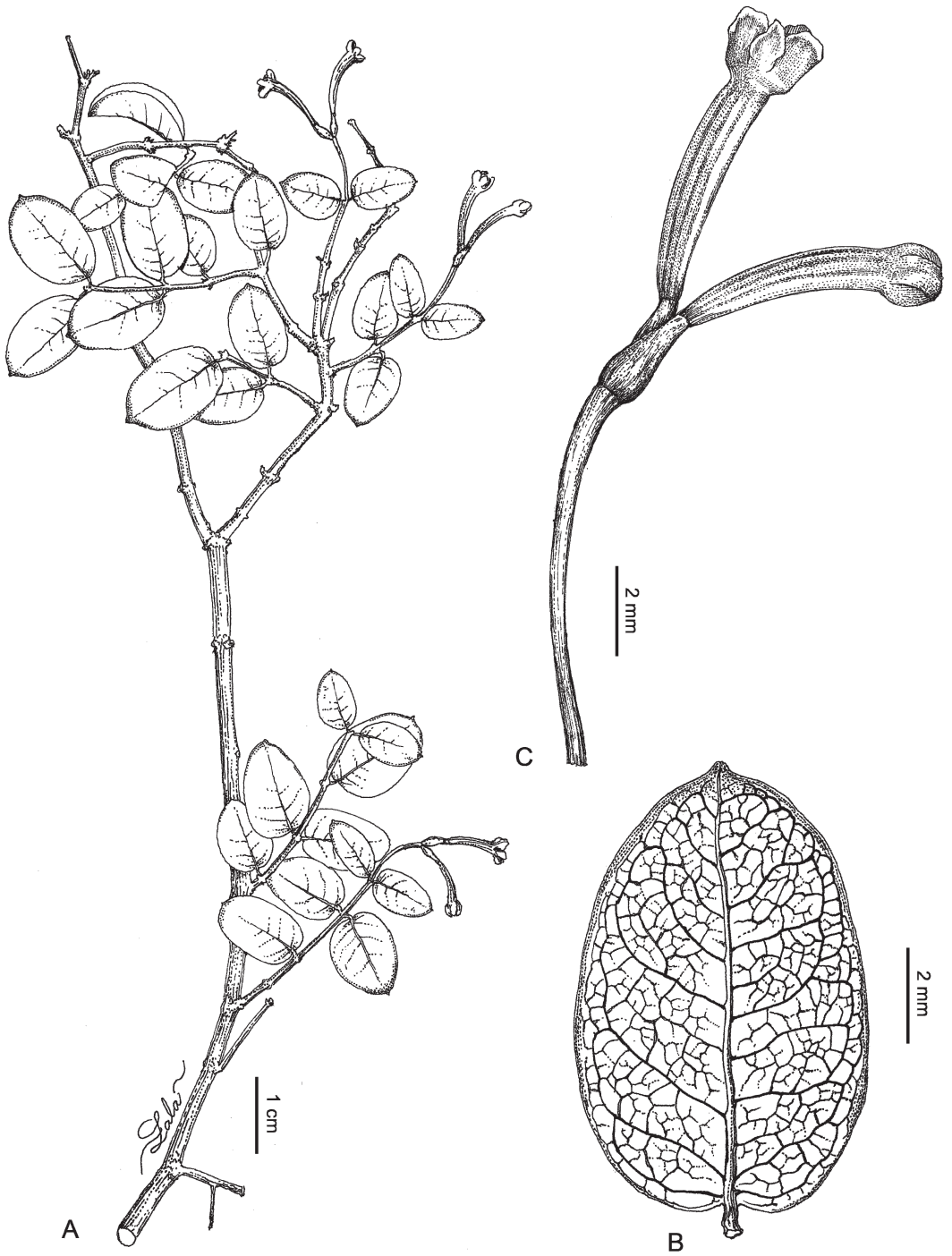


Figure 11. *Gnidia neglecta* Z. S. Rogers. —A. Habit. —B. Leaf, abaxial surface. —C. Inflorescence. Drawn from holotype, Afzelius s.n. (P).

time since it was last collected, an AAO estimated to be less than 10 km², and the highly threatened littoral forest habitat, it is prudent to assign *G. neglecta* a preliminary IUCN (2001) conservation status of Critically Endangered (CR) (B1ab + 2ab).

Discussion. Vegetatively, this new taxon might be mistaken as a species of the large genus *Wikstroemia* Endl. (distinguished from *Gnidia* by the unarticulated hypanthium and a relatively well-developed subgynoecial disk), or even confused with the small, usually lianescent, genus *Synaptolepis* (tube also unarticulated). The flowers on the type of *G. neglecta* are obviously articulated and lack or possess only a minute disk up to 0.2 mm tall, features which suggest that this new taxon best fits morphologically within *Gnidia*. No species of *Wikstroemia* (nor the closely related *Daphne* L.) have been collected on Madagascar, and the island's sole species of *Synaptolepis* (*S. perrieri* Leandri) in no way resembles the new species.

Gnidia neglecta differs from *G. decaryana* by its broadly ovate leaves with cordate bases (vs. obovate to suborbicular leaves with cuneate to attenuate bases), its more numerous, subparallel or more weakly arcuate secondary veins that form a discrete brochidodromous loop (vs. fewer, concolorous, strongly arcuate secondaries lacking a distinct loop), its conspicuous, dense, dark, fine venation (vs. inconspicuous or faint, irregular fine venation), its pedunculate (vs. sessile or subsessile) inflorescences, and its completely glabrous (vs. externally densely pubescent) hypanthium.

Gnidia neglecta superficially resembles the south-east African species *G. subcordata* (sometimes treated as *Englerodaphne subcordata*), but can be distinguished by the same venation patterns that separate it from *G. decaryana*, in addition to the shorter (7.8–8.2 mm vs. 11–15 mm long), completely glabrous (vs. sparsely pubescent), cylindrical (vs. ± funnel-shaped) hypanthium.

Etymology. The epithet *neglecta* draws attention to the fact that this distinctive new species was overlooked by botanists for almost 100 years, having been originally misidentified anonymously as *Gnidia decaryana*.

12. *Gnidia occidentalis* (Leandri) Z. S. Rogers, comb. nov. Basionym: *Lasiosiphon occidentalis* Leandri, Notul. Syst. (Paris) 13: 47. 1947. TYPE: Madagascar. Mahajanga: Kamakama forest, Ankara plateau, 14 July 1901, *H. Perrier de la Bâthie* 1276 (lectotype, designated here, P!). Figure 12.

Shrubs to 1 m tall, weakly branched; young branches densely to moderately pubescent; mature branches lacking lenticels or only sparsely lenticel-

late. **Leaves** alternate, persistent on older branchlets; petioles ca. 1(–2) mm, sparsely pubescent or glabrescent; blades narrowly elliptic or slightly obovate, 2.1–4.5(–6.2) × 0.5–1.6 cm, l:w ratios ca. 3.5–6:1, light green when dry, both surfaces sparsely to moderately pubescent, trichomes ca. 0.5–1 mm, apex apiculate or acute, base cuneate to long-attenuate; midrib depressed adaxially, raised abaxially, lighter green than blade abaxially when dry, glabrescent to moderately pubescent on both surfaces; venation usually raised on both surfaces, more pronounced abaxially. **Inflorescences** axillary or terminal, involucrate, 7- to 14-flowered; peduncles 2–20(–32) mm, densely to moderately pubescent; involucre bracts 5(6), narrowly lanceolate or elliptic-ovate, 8–15 × 1.8–4 mm, l:w ratios 3–7:1, spreading, persistent, apex acute, base rounded-truncate, moderately to sparsely pubescent on both surfaces; midrib conspicuous adaxially, usually conspicuous in upper half abaxially; nervation faint or inconspicuous on both surfaces. **Flowers** 5-merous, red; pedicels 0.4–1.5 mm, densely covered with (1.5–)2.5–3.5 mm trichomes; hypanthium 12.5–16 mm, articulate, coriaceous; caducous portion densely pubescent externally with 0.5–1(–1.5) mm trichomes, glabrous or sparsely pubescent near articulation internally; persistent portion 3–3.5 mm, densely pubescent externally with 1–2.5 mm trichomes, glabrous internally; calyx lobes 5, broadly elliptic-oblong or obovate, 1.7–2.9 × 1.2–1.7 mm, glabrous adaxially, densely pubescent abaxially, apex emarginate or rarely rounded; petaloid scales 5, linear or narrowly elliptic, 0.5–1 × 0.1–0.3 mm, membranous, glabrous, apex rounded or emarginate; stamens 10, upper whorl of anthers located just below mouth, lower whorl 1–1.5 mm below upper whorl; anthers oblong, 1–1.5 × ca. 0.3 mm, subsessile; subgynoecial disk cupuliform, 0.1–0.3 mm tall, glabrous, fleshy, apex smooth or irregularly lobed; ovary ovoid-oblong, 1.2–1.5 × ca. 0.6 mm, sessile or shortly stipitate (stipe to ca. 0.2 mm), glabrous; style 4–7.6 mm, glabrous; stigma 0–4 mm below lower whorl of anthers. **Fruits** ovoid, 3–3.4 × 1.3–1.6 mm, glabrous.

Distribution and habitat. *Gnidia occidentalis* is known from several collections from northwest Madagascar (Mahajanga Province) in the dry bioclimatic zone (Fig. 17). No elevation data are available on specimen labels, but the estimated range for the species is 150–400 m based on an ArcGIS digital elevation model (DEM). The species is noted on labels as occurring in forested habitats on calcareous limestone, basalt, and granite. Given what is known about the ecological preferences of other species of Malagasy *Gnidia*, it seems likely that *G. occidentalis* grows along forest edges or in open sunlit patches within scrub forest.

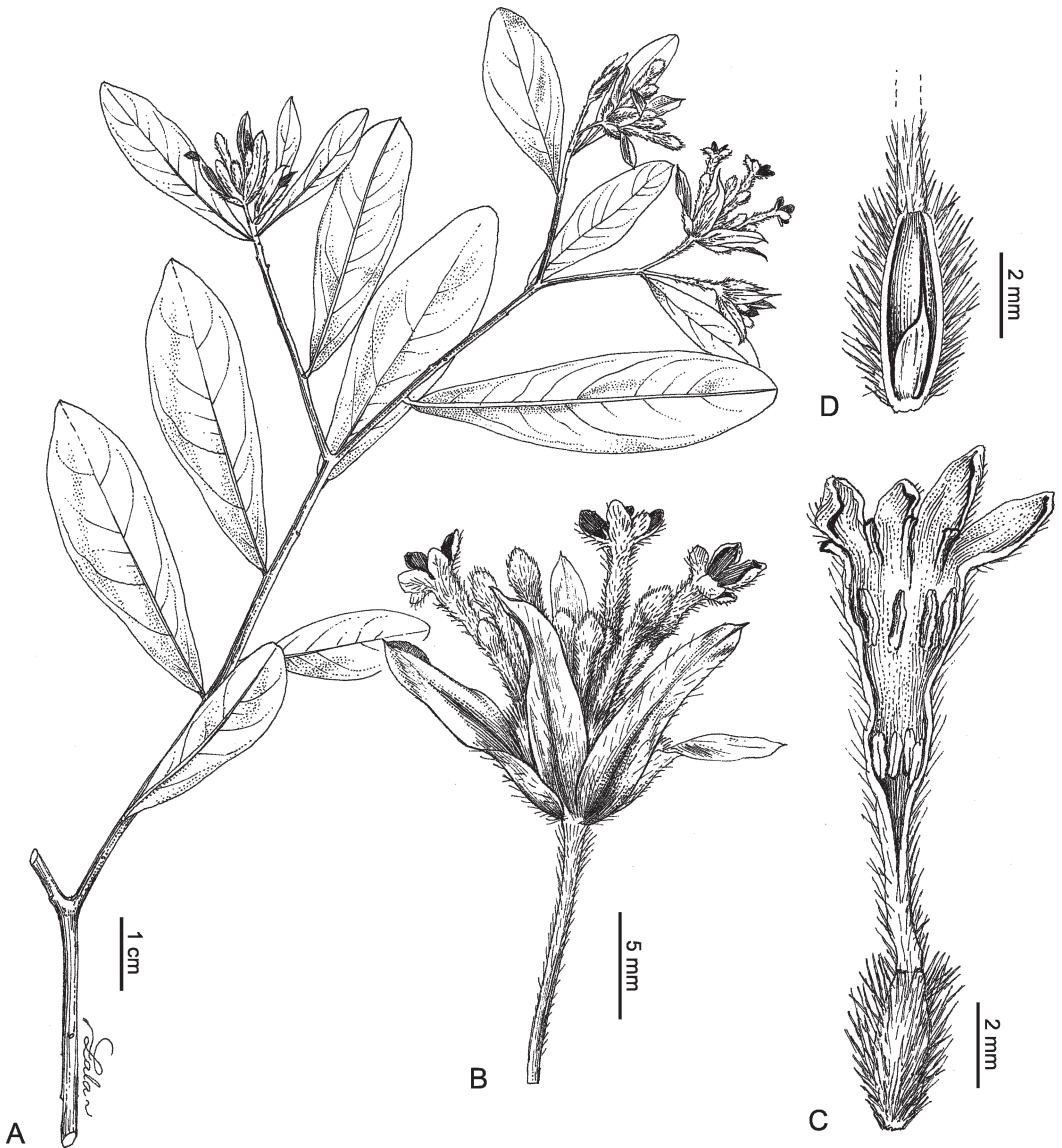


Figure 12. *Gnidia occidentalis* (Leandri) Z. S. Rogers. —A. Habit. —B. Inflorescence. —C. Flower, longitudinal section through caducous portion of hypanthium. —D. Longitudinal section through persistent portion of hypanthium. Drawn from Morat 4550 (TAN).

Phenology. The species flowers and fruits in May, October, and November.

Vernacular name. Fafitao (*Réserves Naturelles* [Rakotovo] 5393).

IUCN Red List category. *Gnidia occidentalis* has been recorded from one protected area (Namoroka). This species is provisionally assigned a conservation status of Least Concern (LC) based on IUCN (2001) criteria.

Discussion. At the time of the original description, Leandri (1947: 47–48) cited five collections of *Gnidia occidentalis*, which were informally categorized as either belonging to the normal form (*Perrier de la Bâthie* 1276), or “probablement des formes de la même espèce” (*Decary* 8181, *Perrier de la Bâthie* 998, 8549, 16324). The flowers of the species were described in the protologue as 5-merous. Strangely, Leandri (1947, 1950) failed to notice that two of his syntypes (*Decary* 8181 and *Perrier de la Bâthie* 998)

consistently have 4-merous flowers and that the leaves and bracts closely matched those of the similarly distributed species, *G. gilbertae*. Both collections without a doubt represent that species. Leandri (1947, 1950) mentioned that another one of the syntypes, *Perrier de la Bâthie 16324*, possessed certain characters of *G. daphnifolia*, and the collection is identified here as that species. The two remaining syntypes, *Perrier de la Bâthie 1276* and *Perrier de la Bâthie 8549*, differ consistently from *G. daphnifolia* and *G. gilbertae* by several characters, and thus are treated here as belonging to the recircumscribed *G. occidentalis*.

Gnidia occidentalis is distinguished from *G. daphnifolia* by its bracts drying light green, green-red, or yellow-brown with 3–7:1 l:w ratios (vs. drying black or brown at least in the lower half and with 2–4:1 l:w ratios), and its 12.5–16 mm (vs. 6.5–12[–15] mm) long hypanthia.

Compared to *Gnidia gilbertae*, *G. occidentalis* differs by its 5- (vs. 4-)merous flowers, its articulate (vs. unarticulate) hypanthium, and its narrower bracts measuring 1.8–4 mm (vs. 4–7 mm) wide.

When sterile, *Gnidia occidentalis* may be difficult to distinguish from *G. bojeriana*, but it can be recognized by its narrower spreading (vs. recurved) bracts with sparser indument.

Nomenclature and typification. The earlier invalid homonym *Gnidia occidentalis* Regel (1860) was originally published as a nomen nudum and presumably based on an Asian species of *Diarthron* Turcz. or *Stellera* L. *Gnidia occidentalis* Regel was never validated later by a description or diagnosis, making the epithet available for use in the new combination proposed here.

As mentioned above, Leandri (1947, 1950) considered *Perrier de la Bâthie 1276* to represent the most common form of *Gnidia occidentalis*, and now only two of the five collections cited in the protologue (Leandri, 1947) belong to the recircumscribed *G. occidentalis*: *Perrier de la Bâthie 1276* (P) and *8549* (P). The sheet of *Perrier de la Bâthie 1276* (P 00373473) is designated as the lectotype.

Selected specimens examined. MADAGASCAR. **Maha-janga:** Manasamody, betw. Port Bergé & Antsohihy, *Morat 4550* (P, TAN); Mt. Ambohibenga, Milanja, near Cap d'Andre, *Perrier de la Bâthie 8549* (P); Namoroka (Natural Reserve #8), Soalala, *Réserves Naturelles (Rakotovao) 5393* (P).

13. *Gnidia perrieri* (Leandri) Z. S. Rogers, comb. nov. Basionym: *Lasiosiphon perrieri* Leandri, Notul. Syst. (Paris) 13: 49. 1947. TYPE: Madagascar. Fianarantsoa: Andringitra Massif (Iratsy), valley of Riambava & Antsifotra, 2000–2500 m, 27 Nov. 1924, *H. Humbert 3827*

(lectotype, designated here, P!; isotypes, BM!, G [2]!, K!, MO!, TAN!, US!). Figure 13.

Shrubs to 1.5 m tall, weakly branched; young branches glabrous, red-purple or orange-red when dry; mature branches usually lenticellate. **Leaves** alternate, rarely subopposite, usually persistent on older branchlets, sessile or subsessile; petioles to 0.5 mm, glabrous; blades broadly elliptic or slightly obovate, 9–35 × 4–8 mm, l:w ratios ca. 2–5:1, usually drying dark green, sometimes glaucous, membranous and somewhat fleshy, both surfaces glabrous, apex apiculate, base long-attenuate or cuneate; midrib raised or plane on both surfaces, glabrous; venation discolorous, usually inconspicuous adaxially, inconspicuous or raised abaxially.

Inflorescences axillary or terminal, involucre, 6- to 19-flowered, subsessile to short-pedunculate; peduncles 2–5(–8) mm, glabrous, drying dark; involucre bracts 5, persistent through fruiting phase, ovate, 4.9–10.8 × 2–5.4 mm (of various sizes in the same inflorescence), l:w ratios 2–3.5:1, usually dark red-purple when dry, somewhat fleshy, erect, glabrous adaxially, densely to moderately pubescent abaxially, apex acuminate, acute, less often apiculate, base rounded or rounded-truncate; midrib raised or inconspicuous on both surfaces; nervation inconspicuous or with 2(4) veins diverging longitudinally from midvein near base. **Flowers** 5-merous, yellow or orange, short-pedicellate; pedicels 0.3–0.9 mm, densely puberulent, trichomes to 0.3 mm (i.e., not reaching base of ovary); hypanthium 6–8(–9) mm, articulate, ± coriaceous, densely pubescent externally, glabrescent or pubescent in lower half internally between anthers and above articulation; caducous portion with trichomes to 0.3 mm; persistent portion 2.5–3.5 mm, trichomes 0.3–0.5(–0.7) mm; calyx lobes 5, broadly elliptic or obovate, 1.4–2.9 × (0.8–) 1.2–2.1 mm, semi-membranous, glabrous and papillate adaxially, densely pubescent abaxially, apex emarginate or rounded; petaloid scales 5, oblong-elliptic or obovate to suborbicular, 0.3–0.6 × 0.2–0.5 mm, membranous, glabrous, apex emarginate or rounded; stamens 10, upper whorl of anthers ca. 1/4 to 3/4 exerted, lower whorl 0.1–0.5 mm below upper whorl; anthers elliptic or elliptic-oblong, 0.6–0.9 × 0.2–0.3 mm, sessile; subgynoecial disk cupuliform, 0.1–0.2 mm tall, glabrous, fleshy, apex smooth or with a few irregular lobes; ovary ellipsoid, 1.1–1.5 × 0.5–0.6 mm, sessile, glabrous, sometimes with a few trichomes to 0.3 mm near apex; style 3.2–7.8 mm, portion below articulation persistent, glabrous; stigma located just below or at height of upper whorl of anthers. **Fruits** ellipsoid, 3.3–4.1 × 1.4–1.5 mm, glabrous.

Distribution and habitat. *Gnidia perrieri* is endemic to the Andringitra massif from 2000–2550 m elevations (Fig. 16). The species occurs in sunlit,

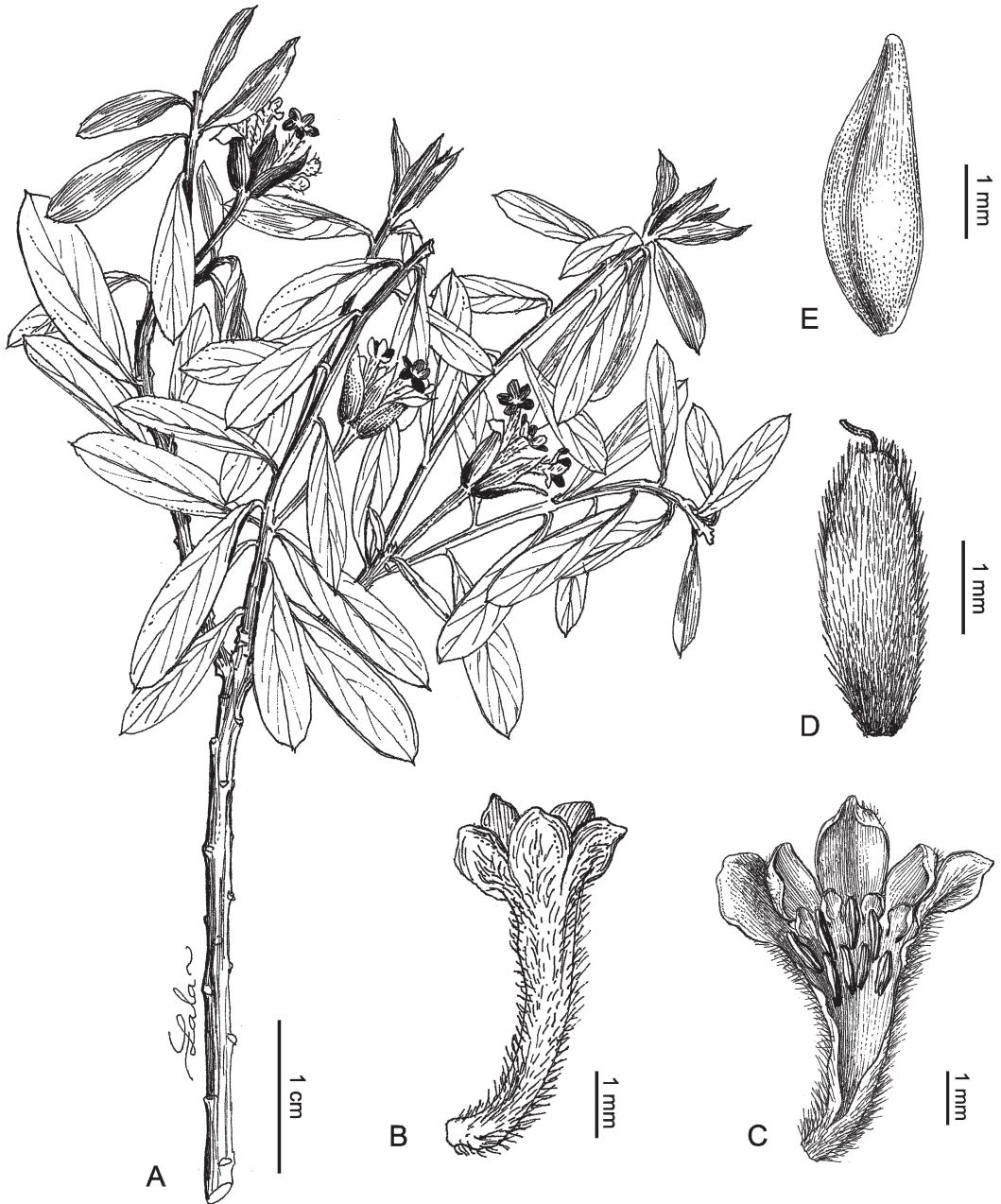


Figure 13. *Gnidia perrieri* (Leandri) Z. S. Rogers. —A. Habit. —B, C. Caducous portion of the hypanthium. —D. Persistent portion of the hypanthium surrounding the gynoecium. —E. Seed. Habit and floral parts drawn from isotype, Humbert 3827 (P). Seed drawn from Guillaumet 3550 (TAN).

ericoid scrubland and on rocky slopes in the subhumid bioclimatic zone.

Phenology. The species has been collected in flower and fruit in May, October, and November.

IUCN Red List category. *Gnidia perrieri* is endemic to one formally protected area (Andringitra). The species must be somewhat resistant to fire as it

grows in ericoid scrub along a few of the higher plateaus and peaks in the area. The species is assigned a provisional IUCN (2001) conservation assessment of Vulnerable (VU) to extinction (B1ab + 2ab).

Discussion. *Gnidia perrieri* is distinguished from *G. linearis* and *G. daphnifolia*, the two most

morphologically similar Malagasy species, by its red-purple or orange-red (vs. green, brown, or black) young stems after drying, its membranous, semi-fleshy (vs. coriaceous, chartaceous, or rarely slightly fleshy) blades and bracts, its 2–5(–8) mm (vs. up to 50 mm) long peduncles, and its 0.3–0.5(–0.7) mm (vs. [1–]3–5 mm) long trichomes on the persistent portion of the hypanthium. In the dried state, collections of *G. perrieri* usually have slightly glaucous leaves, bracts, and peduncles.

Compared to continental African *Gnidia*, *G. perrieri* is most similar to *G. macropetala* Meisn. *Gnidia perrieri* differs by its completely glabrous (vs. densely pubescent) stems and leaves, its more fleshy leaves and bracts, its five (vs. eight) involucre bracts, and its shorter hypanthia (6–9 mm vs. 12–18 mm).

Typification. Four collections were cited in the protologue: *Humbert 3827* (BM, G [2], K, MO, P, TAN, US), *Perrier de la Bâthie 8554* (P), *13700* (P), *14488* (P). Each one of these was annotated in Leandri's hand, and the morphology of all four closely correspond to the description. The P sheet of *Humbert 3827* is selected as the lectotype as it is in the best physical condition and its duplicates are the most widely distributed.

Selected specimens examined. MADAGASCAR. **Fianarantsoa:** Andringitra massif, *Perrier de la Bâthie 8554* (P), *13700* (P), *14488* (P); Andringitra, Pic Bory [Boby], *Guillaumet 3550* (MO, P, TAN).

14. *Gnidia razakamalalana* Z. S. Rogers, *Adansoniana*, sér. 3, 28: 156. 2006. TYPE: Madagascar. Toliara: Fivondronona Fort-Dauphin, Ivohibe Forest, 112 m, 29 Nov. 2005, R. Razakamalala, E. Ramisy & B. Mara 2670 (holotype, MO!; isotypes, K!, P!, TAN!). Figure 14.

Treelets 2 m tall, with dichotomous branching; internodes very short (ca. 1 mm long near branch tips); branches glabrous, covered by prominent leaf scars. **Leaves** alternate, spirally arranged, sessile or subsessile, persistent only at branch tips; blades ovate-lanceolate or elliptic, 4.5–8.4 × 1–1.2 cm, l:w ratios 4–7:1, adaxially glabrous, abaxially densely sericeous, apex acute, base obtuse–shortly decurrent or truncate; midrib depressed adaxially, raised abaxially; venation brochidodromous, inconspicuous or only faintly visible, more obvious abaxially; petioles 0–0.3 mm, densely sericeous. **Inflorescences** terminal, erect, 1-flowered, leaving prominent scars on older branches. **Flowers** 5-merous, reddish white, sessile or subsessile, surrounded by several

involute leaves (each at least partly appressed to the lower portion of the floral tube, the distal ones becoming smaller in size and lighter in color); hypanthium ca. 5 cm, ca. 1 mm diam. near base, ca. 3 mm diam. at mouth, articulation not seen, externally covered by dense sericeous-tomentose trichomes intermixed with longer straight trichomes, indument ± uniform along the length of the tube, glabrous internally; calyx lobes 5, spreading, lanceolate-elliptic, 1.7–2.2 cm × 3.5–5 mm, more membranous than hypanthium, papillate and sparsely tomentose-sericeous adaxially, trichomes shorter than those on the abaxial surface, indument not as dense as that on the tube abaxially, apex acute or apiculate, with a dense tuft of straight trichomes; petaloid scales 5, oblong, ovate, or subtriangular, 1.8–2.2 × 0.7–1 mm, membranous, glabrous, apex irregularly 1- to 5-lobed, with each lobe of varying length; stamens 10, upper whorl of anthers positioned just below mouth, lower whorl 2–4 mm below upper whorl; anthers oblong, ca. 3 × 0.5 mm; subgynoecial disk cupuliform, to 0.7 mm tall, glabrous, membranous, apex irregularly lobed, sinuses mostly shallow; ovary ellipsoid, ca. 2.2 × 1 mm, shortly stipitate, apex covered with a tuft of 1.5–2.3 mm trichomes, otherwise glabrous; style 1.5–1.8 cm, ± flattened, ca. 0.3 mm wide, glabrous; stigma ca. 1.5 mm below lower whorl of anthers (i.e., located near middle of tube), fusiform, ca. 4 mm long, ca. 0.5 mm wide, densely papillate. **Fruits** not seen.

Distribution and habitat. *Gnidia razakamalalana* is apparently a narrow endemic, with only one known population occurring in a subcoastal forest in southeastern Madagascar at ca. 100 m elevation (Fig. 17). The species grows on a slope among exposed granite boulders on black sandy soil (R. Razakamalala, pers. comm.).

Phenology. The species has been collected in flower in February and November.

IUCN Red List category. *Gnidia razakamalalana* is known from a single unprotected population. The AOO is estimated to be no more than 10 km² given a grid cell of the same size. Considering the restricted range of the species and unprotected habitat, the species is assigned an IUCN (2001) preliminary conservation status of Endangered (EN) (B1ab + B2ab).

Discussion. *Gnidia razakamalalana* is easily distinguished from all other Malagasy species by the ca. 5 cm long flowers arranged in 1-flowered terminal inflorescences, and the 1.7–2.2 cm × 3.5–5 mm

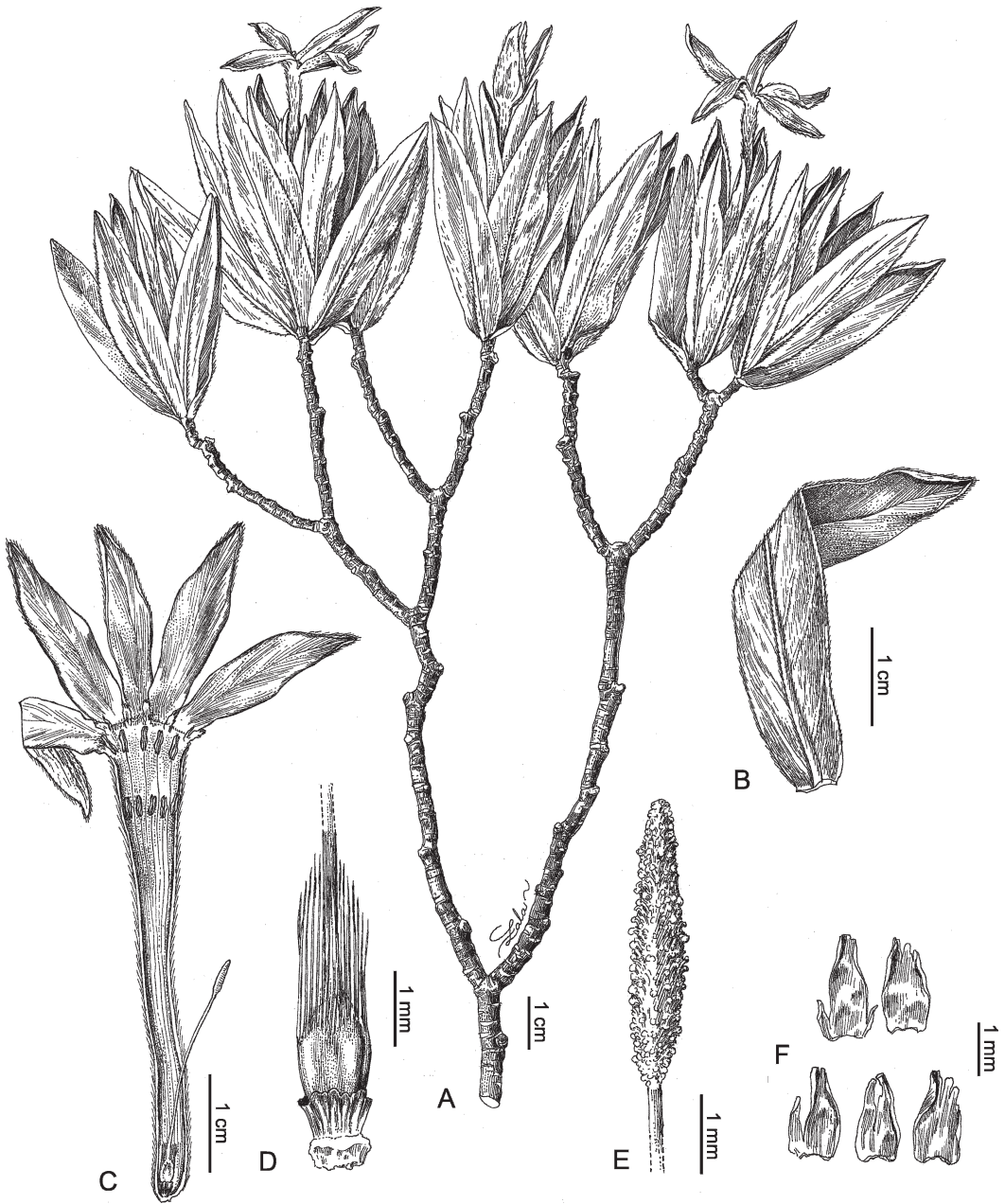


Figure 14. *Gnidia razakamalalana* Z. S. Rogers. —A. Habit. —B. Leaf. —C. Flower. —D. Gynoecium and subgynoecial disk. —E. Stigma. —F. Petaloid scales. Drawn from holotype, *Razakamalala et al.* 2670 (MO).

calyx lobes. Sterile specimens are also easy to identify because the leaves are densely sericeous abaxially and completely glabrous adaxially.

The large fusiform stigma (Fig. 14C) is unique within the Malagasy members of the genus. At present, this species is only known from flowering material and the hypanthium does not show any signs

of articulation. Presumably, the articulation develops in late anthesis, but additional collections are needed to confirm this hypothesis.

Selected specimen examined. MADAGASCAR. **Toliara:** Anosy region, Fort Dauphin, Commune Iabakoho, Quartier Antsofo, Ivohibe-Bemangidy, *Rabantoandro et al.* 1725 (MO, P, TAN).

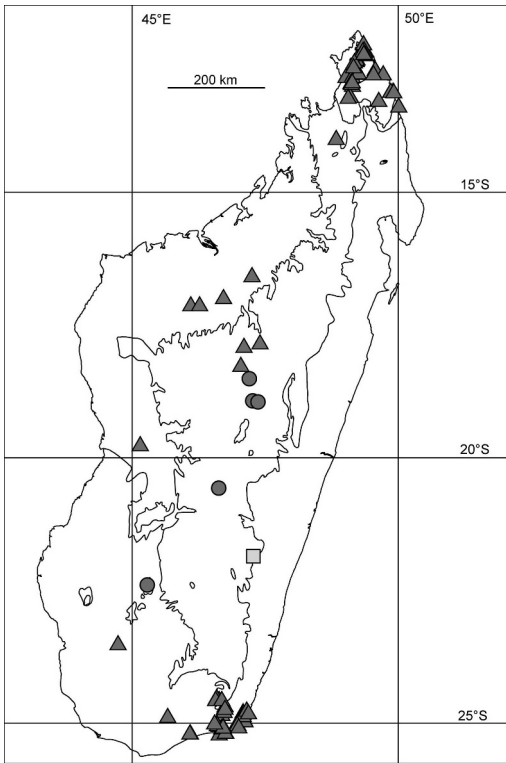


Figure 15. Geographic distribution of *Gnidia ambon-drombensis* (Boiteau) Z. S. Rogers (■), *G. bojeriana* (Decne.) Gilg (●), and *G. daphnifolia* L. f. (▲).

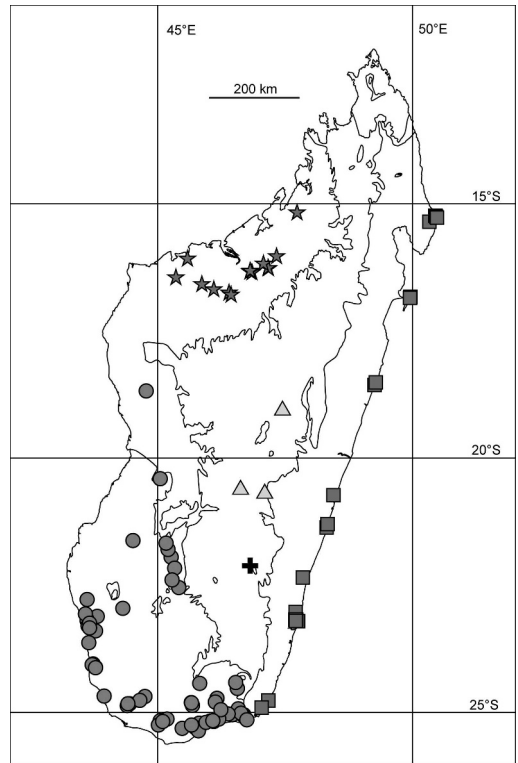


Figure 16. Geographic distribution of *Gnidia danguyana* Leandri (■), *G. gilbertae* Drake (★), *G. linearis* (Leandri) Z. S. Rogers (●), plants of *G. linearis* that were possibly cultivated or escaped from cultivation (▲), and *G. perrieri* (Leandri) Z. S. Rogers (⊕).

EXCLUDED NAMES

Arthrosolen madagascariensis Endl., Gen. Pl. Suppl. 4(2): 63. 1848, nom. illeg. [= *Phaleria octandra* (L.) Baill., *Adansonia* 11: 321. 1875].

Endlicher published *Arthrosolen madagascariensis* with reference to Lamarck's (1786: 254) description of *Dais octandra* L., a name that has been recognized by Rye (1990) as a synonym of the widespread Pacific species *Phaleria octandra* (L.) Baill.

Dais rhamnifolia Baill., Hist. Phys. Madagascar 35(5) [Atlas 3], pl. 318. 1895. TYPE: "Madagascar" (type, pl. 318!, Baillon in Grandidier, 1895) [= *Dais glaucescens* Decne. in C. A. Mey., Ann. Sci. Nat. Bot., sér. 2, 20: 51. 1843].

The protologue of *Dais rhamnifolia* Baill. consisted of a beautifully illustrated diagnostic plate engraved with "Madagascar" and the species name without authorship. *Dais rhamnifolia* taxonomically belongs to the earlier named species *D. glaucescens*.

Gnidia daphnifolia L. f. var. *hirsuta* L. f., Suppl. Pl. 225. 1782. *Dessenia hirsuta* (L. f.) Raf., Fl.

Tellur. 4: 106. 1838. TYPE: *Hb. Smith No. 688.1* (lectotype, designated by Rogers in Rogers & Spencer, 2006: 486, LINN-SM!) [= *Gnidia capitata* L. f., Suppl. Pl. 224. 1782].

Gnidia daphnifolia var. *hirsuta*, and most likely the material on which it was based, was mistakenly attributed to Madagascar by Linnaeus (1782: 225) and was apparently used as the original material in the description of *G. capitata* L. f., an African species described on the previous page (Linnaeus, 1782: 224). The name was therefore designated as the lectotype of *G. capitata* in Rogers and Spencer (2006). *Gnidia daphnifolia* var. *glabra* pertains to a Malagasy species and is based on the same original material as the binomial, *G. daphnifolia* (Rogers & Spencer, 2006; see above under that species).

Lasiosiphon cuneatus Decne., Voy. Inde 4: 149. 1844. [= *Gnidia* sp.?].

Decaisne (1844: 149) published a scant description in the protologue with reference to "*Dais cuneata*

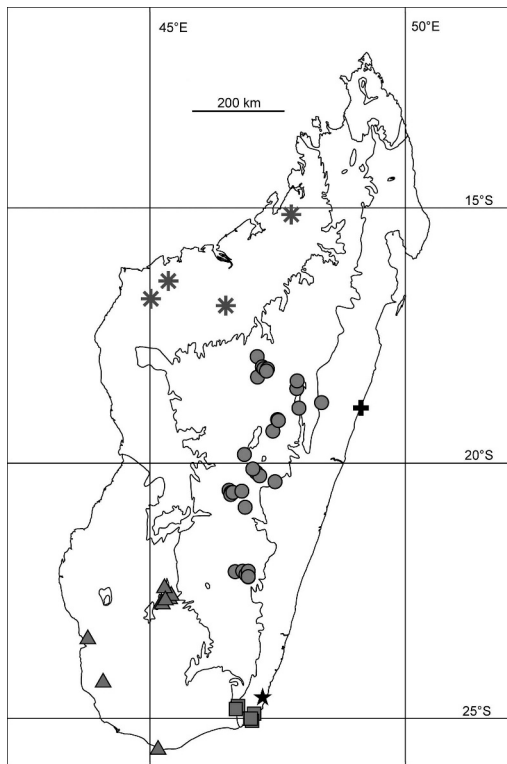


Figure 17. Geographic distribution of *Gnidia decaryana* Leandri (■), *G. gnidioides* (Baker) Domke (●), *G. humbertii* (Leandri) Z. S. Rogers (▲), *G. neglecta* Z. S. Rogers (✚), *G. occidentalis* (Leandri) Z. S. Rogers (*), and *G. razakamalalana* Z. S. Rogers (★).

Lamck., l.c.," which supposedly referred to a name given on page 255 of the second volume of Lamarck's *Encyclopédie Méthodique* (1786). Apparently, Lamarck never actually published the *Dais* name, and Decaisne might have instead been trying to cite a Lamarckian manuscript name. *Lasiosiphon cuneatus* Decne. was treated as an insufficiently known species by Meisner (1857: 599) and Leandri (1930a: 1042; 1931a: 676), and I have not been able to find any relevant original material for the name. The protologue description lacks sufficient diagnostic characters to determine the affinity of this taxon within the Thymelaeaceae.

Lasiosiphon rhamnifolius Baker, J. Linn. Soc., Bot. 25: 343. 1890, as "*Lasiosiphon? rhamnifolius*." TYPE: Madagascar. Vonizongo distr., s.d., *Baron 5115* (holotype, K!; isotypes, P [2!]) [= *Dais glaucescens* Decne. in C. A. Mey., Ann. Sci. Nat. Bot., sér. 2, 20: 51. 1843].

The original material of *Lasiosiphon rhamnifolius* belongs taxonomically to *Dais glaucescens*.

Literature Cited

Aymonin, G. G. 1962. Quelques Thymélacées de rocaillies montagnardes, III.—*Wikstroemia* et *Gnidia*. Pl. Mont. 3: 180–185.

———. 1965. Diversification, répartition et endémisme chez quelques groupes de Thymélacées de la flore africano-malgache. Compt. Rend. Sommaire Séances Soc. Biogéogr., no. 365: 6–21.

———. 1966a. Thymélacées. Pp. 35–95 in A. Aubréville (editor), Flore du Gabon, Vol. 11. Muséum National d'Histoire Naturelle, Paris.

———. 1966b. Thymélacées. Pp. 3–86 in A. Aubréville (editor), Flore du Cameroun, Vol. 5. Muséum National d'Histoire Naturelle, Paris.

———. 1966c. Sur un *Gnidia* (Thymélacées) à inflorescence complexe du Cameroun. Bull. Soc. Bot. France 112: 321–325.

Baillon, H. 1875. Histoire des Plantes, Vol. 6. L. Librairie Hachette et Cie, Paris.

Baker, J. G. 1883. Contributions to the flora of Madagascar, part III. J. Linn. Soc., Bot. 20: 237–303.

Beaumont, A. J., T. J. Edwards & F. R. Smith. 2001a. Leaf and bract diversity in *Gnidia* (Thymelaeaceae): Patterns and taxonomic value. Syst. Geogr. Pl. 71: 399–418.

———, ——— & ———. 2001b. Patterns of diversity among involucre bracts, inflorescences and flowers in *Gnidia* (Thymelaeaceae). Syst. Geogr. Pl. 71: 419–431.

Bredenkamp, C. L. & J. B. P. Beyers. 2003. Thymelaeaceae. Pp. 928–935 in G. Germishuizen & N. L. Meyer (editors), Plants of Southern Africa: An Annotated Checklist. Strelitzia 14, National Botanical Institute, Pretoria.

Consiglio, T., G. E. Schatz, G. McPherson, P. P. Lowry II, J. Rabenantoandro, Z. S. Rogers, R. Rabevohitra & D. Rabehevitra. 2006. Deforestation and plant diversity of Madagascar's littoral forests. Conservation Biol. 20: 1799–1803.

Cornet, A. 1974. Essai de cartographie bioclimatique à Madagascar. Not. Explic. ORSTOM No. 55.

Decaisne, J. 1844. Plantae Rariores, quas in India orientali. Pp. 57–183 in V. Jacquemont (editor), Voyage dans l'Inde, Vol. 4. Firmin-Didot, Paris.

Domke, W. 1934. Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen. Biblioth. Bot. 27(111): 1–151.

Dorr, L. J. 1997. Plant Collectors in Madagascar and the Comoro Islands. Royal Botanic Gardens, Kew.

Engler, H. G. A. 1921. Thymelaeaceae. Pp. 625–642 in H. G. Engler & C. G. Prance (editors), Die Vegetation der Erde, Vol. 9, Die Pflanzenwelt Afrikas, band 3, heft 2. Leipzig.

Estragon, M. 1933. Les industries locales, la fabrication du papier Antaimoro. Rev. Madagasc. 4: 59–62.

Gastaldo, P. 1969. Adumbratio Florae Aethiopicae, 19. Thymelaeaceae. Webbia 24: 337–389.

Gilg, E. 1894. Thymelaeaceae. Pp. 216–245 in A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, Vol. 3, 6a. W. Engelmann, Leipzig.

Grandidier, A. 1895. Histoire Physique, Naturelle et Politique de Madagascar, Histoire Naturelle des Plantes, Vol. 35, Tome 5 (Atlas 3), part 3, fasc. 38. Imprimerie nationale, Paris.

———. 1896. Histoire Physique, Naturelle et Politique de Madagascar, Histoire Naturelle des Plantes, Vol. 35, Tome 5 (Atlas 3), part 3, fasc. 40. Imprimerie nationale, Paris.

- Hallé, F., R. A. A. Oldeman & P. B. Tomlinson. 1978. *Tropical Trees and Forests: An Architectural Analysis*. Springer-Verlag, Berlin.
- Heads, M. J. 1990. A revision of the genera *Kelleria* and *Drapetes* (Thymelaeaceae). *Austral. Syst. Bot.* 3: 595–652.
- Heinig, K. H. 1951. Studies in the floral morphology of the Thymelaeaceae. *Amer. J. Bot.* 38: 113–132.
- Herber, B. E. 2003. Thymelaeaceae. Pp. 373–396 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants, Vol. 5: Flowering Plants, Dicotyledons. Malvales, Capparales and Non-betain Caryophyllales*. Springer, Berlin.
- IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- Lamarck, J. B. 1786. *Encyclopédie Méthodique, Botanique, Vol. 2*. Paris.
- Leandri, J. 1930a. Descriptions de Thyméléacées de Madagascar (*Lasiosiphon*, *Arthrosolen*). *Bull. Soc. Bot. France* 76: 1039–1043.
- . 1930b. Thyméléacées nouvelles de Madagascar. *Bull. Mus. Natl. Hist. Nat., sér. 2, 1*: 435–437.
- . 1931a. Révision des Thyméléacées de Madagascar. *Bull. Mus. Natl. Hist. Nat., sér. 2, 2*: 668–676.
- . 1931b. Révision des Thyméléacées de Madagascar. *Bull. Mus. Natl. Hist. Nat., sér. 2, 3*: 148–160.
- . 1947. Nouvelles observations sur les Thyméléacées de Madagascar. *Notul. Syst. (Paris)* 13: 38–55.
- . 1950. Thyméléacées (family 146). Pp. 1–40 in H. Humbert (editor), *Flore de Madagascar et des Comores (Plantes Vasculaires)*. Firmin-Didot, Paris.
- Linnaeus, C. (filius). 1782. *Supplementum Plantarum, Impensis Orphanotropei, Brunswick*.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersma & N. J. Turland (editors). 2006. *International Code of Botanical Nomenclature (Vienna Code)*. *Regnum Veg.* 146.
- Meisner, C. F. 1857. *Ordo CLXVII. Thymelaeaceae*. Pp. 493–605 in A. P. de Candolle, *Prodromus Systematis Naturalis Regni Vegetabilis, Vol. 14. Victoris Masson, Paris*.
- Miller, J. S. 2002. A revision of *Ehretia* (Boraginaceae) for Madagascar and the Comoro Islands. *Adansonia, sér. 3, 24*: 137–157.
- Moore, S. L. M. 1920. *Plantarum Mascarensium Pugillus*. *J. Bot.* 58: 187–190.
- Pearson, H. H. W. 1910. *Order CXVIII. Thymelaeaceae*. Pp. 212–255 in W. T. Thiselton-Dyer, *Flora of Tropical Africa, Vol. 6*. L. Reeve & Co., London.
- Peterson, B. 1959. Some interesting species of *Gnidia*. *Bot. Not.* 112: 465–480.
- . 1978. Thymelaeaceae. Pp. 1–35 in R. M. Polhill (editor), *Flora of Tropical East Africa*. Whitefriars Press, London.
- . 2006. Thymelaeaceae. Pp. 85–117 in G. W. Pope, R. M. Polhill & E. S. Martins (editors), *Flora Zambesiaca, Vol. 9, Part 3*. Royal Botanic Gardens, Kew.
- Rabakonandrianina, E. & G. D. Carr. 1987. Chromosome numbers of Madagascar plants. *Ann. Missouri Bot. Gard.* 74: 123–125.
- Randriatavy, L. D. 1998. Utilisation de la Plante *Dais glaucescens* (Thymelaeaceae). M.S. Thesis, University of Antananarivo, Antananarivo.
- Regel, E. 1860. *Catalogus Plantarum quae in Horto Aksakoviano Coluntur*. Typography of State Ministers, St. Petersburg.
- Robyns, A. 1975. Thymelaeaceae. Pp. 1–68 in P. Bamps (editor), *Flore d'Afrique Centrale (Zaire-Rwanda-Burundi)*. Jardin Botanique National de Belgique, Brussels.
- Rogers, Z. S. 2004. A revision of *Stephanodaphne* Baill. (Thymelaeaceae). *Adansonia, sér. 3, 26*: 7–35.
- . 2005. A revision of *Octolepis* Oliv. (Thymelaeaceae, Octolepidoideae). *Adansonia, sér. 3, 27*: 89–111.
- . 2006. A new species of Malagasy *Gnidia* and the lectotypification of *Octolepis decalapis* (Thymelaeaceae). *Adansonia, sér. 3, 28*: 155–160.
- & M. A. Spencer. 2006. Typification of Linnaean and Linnaeus filius plant names in Thymelaeaceae. *Taxon* 55: 483–488.
- Rye, B. L. 1990. Thymelaeaceae (excluding *Kelleria*). Pp. 122–215 in A. S. George (editor), *Flora of Australia, Vol. 18*. Australian Government Publishing Service, Canberra.
- Schatz, G. E. 2000. Endemism in the Malagasy tree flora. Pp. 1–9 in W. R. Lourenço & S. M. Goodman (editors), *Diversity and Endemism in Madagascar*. *Mém. Soc. Biogéogr., Paris*.
- & P. P. Lowry II. 2002. A synoptic revision of the genus *Buxus* L. (Buxaceae) in Madagascar and the Comoro Islands. *Adansonia, sér. 3, 24*: 179–196.
- & M. Lescot. 2009. Gazetteer to Malagasy Botanical Collecting Localities. Missouri Botanical Garden website, <<http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/>>, accessed 13 April 2009.
- , P. P. Lowry II & A.-E. Wolf. 2001. Endemic families of Madagascar. VII. A synoptic revision of *Leptolaena* Thouars sensu stricto (Sarco-laenaceae). *Adansonia, sér. 3, 23*: 171–189.
- Scott Elliot, G. F. 1891. *Lasiosiphon hildebrandtii*. *J. Linn. Soc., Bot.* 29: 47.
- Staner, P. 1935. Les Thyméléacées de la Flore du Congo Belge. *Bull. Jard. Bot. État* 13: 321–372.
- Townsend, C. C. 1981. Thymelaeaceae. Pp. 501–511 in M. D. Dassanayake (editor), *A Revised Handbook to the Flora of Ceylon, Vol. 2*. Amerind Publishing Co., New Delhi.
- Van der Bank, M., M. F. Fay & M. W. Chase. 2002. Molecular phylogenetics of Thymelaeaceae with particular reference to African and Australian genera. *Taxon* 51: 329–339.
- Wright, C. H. 1906. *Gnidia mollis*. *Bull. Misc. Inform.* 1906: 23.
- . 1915. *Order CXVIII. Thymelaeaceae*. Pp. 1–81 in W. T. Thiselton-Dyer (editor), *Flora Capensis, Vol. 5, Sect. 2, Pt. 1*. L. Reeve & Co., London.

APPENDIX 1. List of recognized species of Malagasy *Gnidia*.

1. *Gnidia ambondrombensis* (Boiteau) Z. S. Rogers
2. *Gnidia bojeriana* (Decne.) Gilg
3. *Gnidia danguyana* Leandri
4. *Gnidia daphnifolia* L. f.
5. *Gnidia decaryana* Leandri
6. *Gnidia gilbertae* Drake
7. *Gnidia gnidioides* (Baker) Domke
8. *Gnidia hibbertioides* (S. Moore) Z. S. Rogers
9. *Gnidia humbertii* (Leandri) Z. S. Rogers
10. *Gnidia linearis* (Leandri) Z. S. Rogers
11. *Gnidia neglecta* Z. S. Rogers
12. *Gnidia occidentalis* (Leandri) Z. S. Rogers
13. *Gnidia perrieri* (Leandri) Z. S. Rogers

14. *Gnidia razakamalalana* Z. S. Rogers

APPENDIX 2. Index to Exsiccatae.

Collections are listed alphabetically by the first collector's name, followed by collection number or date of collection in square brackets, if available, for unnumbered collections. Numbers in parentheses correspond to species numbers in the taxonomic treatment. Original material, including types and syntypes, are indicated in **boldface** for all names.

Afzelius **s.n.** [3 Oct. 1912] (**11**); s.n. [15 Feb. 1913] (9). Allorge 2298 (10); 2308 (10). Alluaud 36 (4); **85 (4)**; **106 (4)**. Andrianantoanina 186 (4).

Baron **665 (7)**; 1894 (7); **2061 (7)**; 3309 (7); 3489 (7); 4281 (2); 5254 (7); **5770 (4)**; 6191 (4). Basse s.n. [18 May–12 June 1931] (10); s.n. [23 May 1931] (9); s.n. [28 May 1931] (9); s.n. [9 July 1931] (10); s.n. [11 June 1931] (10); s.n. [11 June 1931] (10). Bernier 157 (4). Birkinshaw 435 (10). Bisset M3 (6). Boiteau 3097 (10); **4643 [= Hb. Jard. Bot. Tananarive 4643] (1)**. Boivin **2384 (4)**; s.n. [1853] (4). Bojer **s.n. (2)**; s.n. (7). Bosser 250 (10); 3701 (10); 4066 (10); 413 (7); 4313 (4); 4320 (10); 5929 (4); 6065 (7); 7269 (7); 8525 (7); 9936 (10); 10000 (7); 10229 (10); 10275 (10); 13002 (2); 14048 (10); 14315 (4); 14328 (4); 14329 (5); 19176 (10); 19457 (7).

Camponen s.n. (7). Catat 4327 (4). Cloisel 27 (10); 29 (10); 135 (4); 218 (4). Commerson **s.n. (4)**; **s.n. (4)**; s.n. (4); s.n. (4). Cours 1518 [= Hb. St. Agric. Alaotra 1518] (4); 1797 (7); 3143 (10); 4564 (10); 5108 (2); 5176 (7); 5275 (10); 5479 (4). Cremers 1632 (7). Croat 30900 (10); 31514 (10); 31647 (10); 31654 (10); 31660 (10); 31661 (10); 31681 (10); 31731 (10); 31930 (10); 31945 (4); 32018 (10).

D'Alleizette 394M (7); 769M (10); 1110 (7). D'Arcy 15430 (10). Debray 1373 (4); 1733 (4). Decary **2605 (4)**; **2694 (4)**; **2759 (10)**; **2785 (10)**; **2971 (10)**; **3183 (10)**; **3741 (10)**; 3897 (4); 4030 (4); **4332 (5)**; 4336 (4); 7353 (4); 7399 (7); 7676 (4); **8181 (6)**; 8340 (10); **8341 (10)**; 8391 (4); 8437 (4); **8966 (10)**; 9186 (10); 9831 (4); 9971 (5); 9972 (4); 10038 (4); 10049 (5); 10102 (4); 10111 (4); 14524 (4); 14559 (4); 16078 (10); 17197 (7); 17646 (7); **s.n. [30 Aug. 1917] (10)**; s.n. [3 July 1932] (5). Dequaire 24110 (10); 27333 (10); 27547 (10). Descoings 283 (4); 431 (4); 641 (4); 653 (4); 941 (7); 1251 (10); 1373 (10); 1395 (10); 1526 (10); 1701 (4); 2480 (10); 2616 (4); 2744 (10); 2845 (7); 2990 (2); 3283 (4). Dorr 2949 (6); 3964 (10); 4055 (10). Douliot s.n. [19 Oct. 1891] (10); **s.n. [1892] (9)**. Dumetz 614 (4); 615 (4). Dupuy, B. MB197 (4).

Eboroko 940 (10). Edmondson 95-36 (9); 95-51 (10); 95-56 (4).

Falinianina 29 (3). Fosberg 52380 (7); 52485 (10); 52495 (10).

Geay **6328 (10)**; 7538 (3); 7539 (3); 7540 (3); 7541 (3); 7542 (3). Gentry 11909 (4); 62151 (6). Gereau 3242 (4). Goudot s.n. [1834] (4); s.n. [1837–1838] (7); s.n. [1840] (10). Grandidier, A. **s.n. [Nov. 1868–Jan. 1869] (10)**; **s.n. [1876] (6)**. Guillaumet 3543 (7); 3550 (13). Guittou 4 (4).

Harder 1607 (4); 1665 (4). Heim s.n. [2 Oct. 1934] (1). Hb. Inst. Sci. Madag. 482 (6). Hb. Jard. Bot. Tananarive 2639 (4); **4643 [= Boiteau 4643] (1)**; 5051 (2); 5142 (7); 6151 (10); 6513 (3); 6615 (4). Hb. Smith No. 688.2 (4); 688.3 (4); 688.4 (4); **688.5 (4)**; 688.6 (4). Hb. Mus. Paris 4297 (4); s.n. (7); s.n. (4). Hb. St. Agric. Alaotra 1518 [= Cours 1518] (4); E.37 (7). Hildebrandt **3369 (4)**; 3883 (7). Homolle 167 (4); 1467 (10); s.n. [24 Feb. 1945] (7). Hong Wa 130 (3); 143 (7); 204 (4); 358 (7); 414 (6). Humbert **2489 (10)**; 2744 (4); 2755 (4); **2844 (9)**; 2936 (10); **3772 (7)**; **3827 (13)**; 4661 (7);

4962 (10); 5039 (9); 5097 (10); **5170 (10)**; **5294 (10)**; **5294bis (10)**; **5414bis (10)**; 5527 (10); 5593 (10); 5720 (4); 5720bis (10); 5890 (4); 5916 (5); 6742 (4); 12812 (10); 12812bis (4); **12844 (4)**; 13010 (4); **13154 (4)**; **13242 (4)**; 13800 (4); **13860 (4)**; 13884 (5); **14053 (4)**; 14084 (5); 18836 (4); 19104 (4); 19145 (4); 19337 (10); 19493 (10); 20259 (10); 20401 (5); 20403 (4); 25579 (4); 28058 (7); 28640 (2); 28846 (10); 29125 (4); 29140 (4); 29290 (9); 29681 (9); 29941 (7); 29967 (2); 32321 (4); s.n. [June 1928] (6); s.n. [3 Feb. 1960] (4).

Jacquemin 1129 (10).

Keraudren 928 (10); 987 (10); 1064 (5); 1214 (6); 24575 (7); 25160 (7); 25280 (7).

Labat 2073 (10). Lam **5439 (10)**; 6075 (4). Lavauden s.n. [June 1928] (6). Leandri 3623 (10). Lorence 2055 (10). Louvel **118 (3)**; **197 (3)**. Luckow 4105 (4); 4226 (4). Ludovic 261 (3); 413 (3); 699 (3); 722 (3).

Mabberley 967 (10). Manjakahery 171 (10). McPherson 14954 (10); 14959 (10). McWhirter 130 (10). Meyers 17 (4). Miede 142 (10); 159 (10). Miller 6097 (9); 6104 (10); 6180 (10); 10687 (4); 10701 (4). Morat 1288 (7); 1442 (4); 2920 (10); 2933 (10); 3422 (9); 4550 (4).

O'Connor 112 (10).

Paulian 1 (10); 63 (10). Peltier 1892 (7); 2181 (10); 2469 (9); 2802 (10); 3194 (10); 4350 (7); 4477 (2). Pernet 33 (10); 34 (10). Perrier de la Bâthie 666 (4); 666bis (4); **998 (6)**; **1276 (12)**; 8539 (10); 8541 (7); 8541bis (10); 8542 (7); 8543 (10); 8544 (4); 8545 (10); 8547 (4); 8548 (4); **8549 (4)**; 8550 (9); 8551 (4); 8552 (4); **8553 (10)**; **8554 (13)**; 8555 (9); 12471 (10); 12472 (2); **12807 (10)**; **13700 (13)**; **14488 (13)**; **16324 (4)**; 16581 (10); 16690 (9); 18459 (2). Phillipson 1772 (10); 1936 (6); 1948 (4); 2676 (10); 3447 (10); 3625 (10); 3742 (10); 4048 (7); 5929 (10). Plantes Madag. 5871 (3). Poisson 147 (4); **692 (10)**; 3455 (2); s.n. (4).

Rabehevitra 409 (3); 994 (4); 994A (4); 1186 (3). Rabenantoandro 598 (4); 735 (3); 987 (3); 1602 (3); **1725 (14)**. Rabevohitra 4119 (3); 4455 (4); 5071 (3). Rakotomalaza 357 (6). Rakotondrajaona 322 (4). Rakotonandrasana 1113 (4). Rakotozafy 1447 (4). Raliarison 1025 (7). Ranaivojoana 314 (6); 561 (3). Randriamampionona 293 (10). Randriambololona 34 (4). Randrianaivo 614 (6); 894 (10); 894A (4); 1043 (10). Randrianasolo, A. 143 (10); 529 (6); 571 (4). Randriatafika 349 (4). Rasoja 1191 (7). Rauh 79 (7); 1203 (10); 1229 (9); 1677 (2); 10524 (10). Razakamalala 446 (3); 447 (3); 538 (4); 800 (3); 1445 (3); 1742 (6); 1805 (6); 2670 (14). Réserves Naturelles 1022 (6); 1130 (10); 1421 (7); 1429 (9); 1437 (3); 1437b (10); 1899 (6); 2180 (6); 2271 (7); 2312 (4); 2777 (10); 3055 (7); 3818 (4); 3930 (10); 4028 (7); 4234 (6); 4285 (10); 5183 (10); 5393 (4); 5742 (4); 6357 (10); 8456 (13); 8874 [= Service Forestier 17671] (3); 9701 (6); 10361 (9); 10387 (7); 11484 (7); 11557 (7); 11571 (13); 13004 (4). Richard 65 (4); **580 (4)**. Rogers 76 (3); 77 (3); 106 (4); 107 (5); 108 (5); 109 (4); 110 (4); 126 (7); 133 (4); 134 (4); 135 (4); 136 (4); 136A (4); 147 (4); 148 (4); 149 (4); 155 (4); 175 (2); 176 (2); 177 (2); 178 (2); 179 (2); 180 (2); 181 (2); 182 (2); 183 (2); 389 (9); 392 (9); 393 (9); 394 (9); 395 (9); 396 (9); 397 (9); 398 (9); 399 (9); 409 (10); 410 (10); 411 (10); 412 (10); 413 (9); 414 (9); 419 (10); 523 (10); 524 (10); 525 (10); 526 (10); 543 (10); 544 (10); 545 (10); 705 (1); 706 (1); 707 (1); 734 (10); 821 (2); 872 (10); 891 (3); 906 (4); 911 (4); 914 (4); 928 (10); 929 (10); 930 (10); 931 (10); 934 (10); 949 (4); 954 (4); 978 (5); 979 (4); 1105 (4).

Saboureaux 49 (6). Schatz 1744 (10). Schmidt 4402 (3). Scott-Elliot 1962 (7); 2368 (4); **3030 (4)**. Seigler 12872 (4). Seligson 638 (4). Service Forestier 17 (6); 36 (6); 341 (10); 356 (10); 1282 (4); 1950 (7); 2271 (7); 4015 (6); 5100 (3);

9900 (3); 17671 [= Réserves Naturelles 8874] (3); 18572 (2); 18622 (10); 25234 (10); 26490 (4); 28646 (3); 28650 (5); 34923 [= Rabevoitra 3191] (4). Straka s.n. [18 Sep. 1957] (6); s.n. (10). Swingle 7746 (4).

Thompson s.n. (4); **s.n. (8)**. Thouars s.n. (3).

van Nek 1942 (4). van der Werff 13577 (7). Vesco s.n. [1850] (4). Viguier 1800 (7).

Waterlot **331 (4)**; **s.n. [June 1915] (10)**; **s.n. [May 1916] (10)**. White s.n. [15 Sep. 1929] (10).

Zarucchi 7572 (10).

APPENDIX 3. List of names and synonyms (including excluded names). Accepted names are presented in **boldface** and synonyms are *italicized*.

Arthrosolen C. A. Mey. = **Gnidia** L.

gnidioides (Baker) Leandri ≡ **Gnidia gnidioides** (Baker)

Domke

madagascariensis Endl. [= *Phaleria octandra* (L.) Baill., excluded name]

Dais gnidioides Baker ≡ **Gnidia gnidioides** (Baker) Domke

madagascariensis Lam. = **Gnidia daphnifolia** L. f.

pubescens Lam. = **Gnidia daphnifolia** L. f.

rhannifolia Baill. [= *Dais glaucescens* Decne. in C. A. Mey., excluded name]

Dessentia Adans. = **Gnidia** L.

daphnifolia (L. f.) Raf. = **Gnidia daphnifolia** L. f.

hirsuta (L. f.) Raf. [= **Gnidia capitata** L. f., African taxon]

Gnidia L.

ambondrombense (Boiteau) Z. S. Rogers

bakeri Gilg ≡ **Gnidia gnidioides** (Baker) Domke

bojeriana Baill. = **Gnidia bojeriana** (Decne.) Gilg

bojeriana (Decne.) Gilg

danguyana Leandri

daphnifolia L. f.

var. *glabra* L. f. ≡ **Gnidia daphnifolia** L. f.

var. *hirsuta* L. f. [= **Gnidia capitata** L. f., African taxon]

decaryana Leandri

gilbertae Drake

gnidioides (Baker) Domke

hibbertioides (S. Moore) Z. S. Rogers

hildebrandtii (Scott-Elliot) Gilg = **Gnidia daphnifolia** L. f.

humbertii (Leandri) Z. S. Rogers

linearis (Leandri) Z. S. Rogers

madagascariensis (Lam.) Gilg = **Gnidia daphnifolia** L. f.

neglecta Z. S. Rogers

occidentalis (Leandri) Z. S. Rogers

perrieri (Leandri) Z. S. Rogers

pubescens Baill. = **Gnidia daphnifolia** L. f.

razakamalalana Z. S. Rogers

rostrata (Meisn.) Drake = **Gnidia daphnifolia** L. f.

Lasiosiphon Fresen. = **Gnidia** L.

ambondrombense Boiteau ≡ **Gnidia ambondrombense**

(Boiteau) Z. S. Rogers

baronii Baker = **Gnidia daphnifolia** L. f.

bojerianus Decne. ≡ **Gnidia bojeriana** (Decne.) Gilg

carinatus (Leandri) Leandri = **Gnidia daphnifolia** L. f.

cuneatus Decne. [excluded name] = **Gnidia** sp.?

decaryi Leandri = **Gnidia linearis** (Leandri) Z. S. Rogers

var. *erectus* Leandri = **Gnidia linearis** (Leandri) Z. S. Rogers

var. *linearis* Leandri ≡ **Gnidia linearis** (Leandri) Z. S. Rogers

var. *littoralis* Leandri = **Gnidia linearis** (Leandri) Z. S. Rogers

var. *tenerifolia* Leandri = **Gnidia linearis** (Leandri) Z. S. Rogers

dumetorum Leandri = **Gnidia daphnifolia** L. f.

erectus (Leandri) Leandri = **Gnidia linearis** (Leandri) Z. S. Rogers

hibbertioides S. Moore ≡ **Gnidia hibbertioides** (S. Moore) Z. S. Rogers

hildebrandtii Scott-Elliot = **Gnidia daphnifolia** L. f.

humbertii Leandri ≡ **Gnidia humbertii** (Leandri) Z. S. Rogers

linearis Leandri ≡ **Gnidia linearis** (Leandri) Z. S. Rogers

madagascariensis (Lam.) Decne. = **Gnidia daphnifolia** L. f.

var. *angustifolius* Leandri = **Gnidia daphnifolia** L. f.

var. *baronii* (Baker) Leandri = **Gnidia daphnifolia** L. f.

var. *hildebrandtii* (Scott-Elliot) Leandri = **Gnidia daphnifolia** L. f.

var. *mandrarensis* Leandri = **Gnidia daphnifolia** L. f.

var. *parvifolius* Leandri = **Gnidia daphnifolia** L. f.

var. *rostratus* (Meisn.) Leandri = **Gnidia daphnifolia** L. f.

multifolius (Leandri) Leandri = **Gnidia daphnifolia** L. f.

occidentalis (Leandri) Leandri ≡ **Gnidia occidentalis** (Leandri) Z. S. Rogers

perrieri Leandri ≡ **Gnidia perrieri** (Leandri) Z. S. Rogers

pubescens (Lam.) Decne. = **Gnidia daphnifolia** L. f.

var. *carinatus* Leandri = **Gnidia daphnifolia** L. f.

var. *multifolius* Leandri = **Gnidia daphnifolia** L. f.

rhannifolius Baker [= *Dais glaucescens* Decne. in C. A. Mey., excluded name]

rostratus Meisn. = **Gnidia daphnifolia** L. f.

saxatilis Scott-Elliot = **Gnidia daphnifolia** L. f.

suffrutescens Leandri = **Gnidia daphnifolia** L. f.

waterlotii Leandri = **Gnidia daphnifolia** L. f.