



Notes on Isoglossinae (Acanthaceae) in Madagascar, with four new species of *Isoglossa*

Iain Darbyshire^{1,2} , Guy E. Onjalalaina^{3,4} , Martin W. Callmander⁵ , Peter B. Phillipson^{6,7} & Carrie A. Kiel⁸

Summary. Current generic delimitation in subtribe Isoglossinae of Acanthaceae is discussed using available morphological and molecular data. Particular consideration is given to the small genera endemic to Madagascar — *Celerina* Benoist, *Melittacanthus* S.Moore, *Sphacanthus* Benoist and the illegitimate *Conocalyx* Benoist — and how these relate to the current circumscription of *Isoglossa* Oerst. The relative merits and challenges of recognising a broadly circumscribed *Isoglossa* are considered. *Isoglossa* s.l. is readily recognisable by combining a bilabiate corolla, with an androecium comprising two bitheous stamens and lacking staminodes, and with the presence of gürtelpollen (i.e. biporate pollen, circular in apertural view and with a pronounced interapertural “girdle” of tectate exine), whilst the segregate genera as currently defined are not separable morphologically. However, the limited molecular phylogenetic data available to date indicate that *Isoglossa* s.l. is paraphyletic. Pending further molecular studies of this group to clarify generic delimitation, it is proposed that all new taxa in bitheous Isoglossinae should be described in *Isoglossa* as an interim solution. Four new species of *Isoglossa* are described: *I. eburnea* Onjalal. & I.Darbysh., *I. pterocalyx* I.Darbysh. & Phillipson, *I. pseudoanisotes* I.Darbysh. and *I. conocalyx* I.Darbysh. & Callm., the lattermost of which is based on *Conocalyx laxus* Benoist nom. illegit. In addition, *Justicia onilahensis* Benoist (including *Ritonia poissonii* Benoist) and *Anisotes perplexus* T.F.Daniel, Letsara & Martín-Bravo are transferred to *Isoglossa*, and three names within *Justicia* L. are synonymised within existing taxa in Isoglossinae. Lectotypes are selected for *Sphacanthus brillantaisia* Benoist, *S. humbertii* Benoist and *Justicia subpaniculata* Benoist (= *Celerina seyrigii* Benoist var. *egena* Benoist).

Key Words. Diversity, generic delimitation, IUCN Red List assessment, pollen, taxonomy.

Introduction

The recent reclassification of Acanthaceae (Manzitto-Tripp *et al.* 2021), based on the accumulated molecular phylogenetic and morphological data from the past 20 years and beyond, provides a robust taxonomic framework at the subfamilial, tribal and subtribal ranks. These authors noted, however, that there remain significant challenges regarding generic circumscription across a range of lineages in the family. Previous generic circumscriptions that rely heavily on floral morphology have sometimes proven to be unrepresentative of phylogenetic relationships due to widespread homoplasy (Manzitto-

Tripp *et al.* 2021; McDade *et al.* 2021). Problems with generic delimitation have also been linked to specific geographic Regions. Madagascar, in particular, has been noted as problematic because of apparently excessive segregation of endemic genera without satisfactory morphological diagnoses (Onjalalaina & Darbyshire 2016; Manzitto-Tripp *et al.* 2021; Phillipson *et al.* in press). Whilst the solution to these problems is sure to lie in densely sampled phylogenetic studies using Next Generation Sequencing (NGS) techniques (e.g., RADseq, Hybseq), such studies require significant resources (funding, suitable material for sampling and scientists with relevant

Accepted for publication 18 August 2022. Published online 7 January 2023

¹ Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK. e-mail: i.darbyshire@kew.org

² Honorary Senior Researcher, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050, South Africa.

³ CAS Key Laboratory of Plant Germplasm Enhancement and Specialty Agriculture, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, 430074, China.

⁴ Formerly of Kew Madagascar Conservation Centre, Antananarivo, Madagascar.

⁵ Conservatoire et Jardin botaniques de Genève, ch. de l'Impératrice 1, C.P. 71, 1292, Chambésy, Switzerland.

⁶ Missouri Botanical Garden, 4344 Shaw Blvd, St. Louis, Missouri, 63110, USA.

⁷ Institut de Systématique, Evolution et Biodiversité (ISYEB), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Ecole Pratique des Hautes Etudes, Université des Antilles, C.P. 39, 57 rue Cuvier, 75005, Paris, France.

⁸ California Botanic Garden, 1500 North College Avenue, Claremont, California, 91711, USA.

skillsets) that are not always readily available, and there are still major gaps in the available data for Acanthaceae. In the meantime, many species of Acanthaceae — including a significant proportion that are highly range-restricted, scarce and potentially threatened — remain undescribed. Until a species has been formally described, it is essentially invisible to science and conservation, yet species that remain to be discovered are often those most likely to be at risk of extinction (Cheek *et al.* 2020). Given the biodiversity crisis and the significant threats faced by rare and range-restricted species, there is a real risk that, if we wait for generic delimitations to be fully resolved, such species may become extinct before they are even described.

Genera of subtribe Isoglossinae (Acanthaceae: Acanthoideae: Justicieae), such as palaeotropical *Isoglossa* Oerst. and *Brachystephanus* Nees and neotropical *Stenostephanus* Nees, are noted to contain a high number of narrowly range-restricted species, with many confined to forest habitats (see, e.g., Daniel 1999; Champluvier & Darbyshire 2009; Darbyshire 2009; Darbyshire *et al.* 2011; Balkwill *et al.* 2017; Wood 2019a, 2019b; Champluvier & Fischer 2020). As a result, many of these species are of high conservation concern, and it is important that the alpha diversity within Isoglossinae is documented and that local-endemic species are described in a timely manner in order to help guide conservation planning. In Madagascar, several new species to science of Isoglossinae with highly restricted ranges have been identified for some time and are in urgent need of description given their narrow distributions and potential threats to their future survival. However, uncertainty over generic placement has hindered their recognition to date.

Current generic delimitation in Isoglossinae

Subtribe Isoglossinae currently comprises seven genera and has a pantropical distribution (Manzitto-Tripp *et al.* 2021). Isoglossinae are marked by the presence of “gürtelpollen” — i.e., biporate (more rarely tri- or tetraporate) pollen, circular in apertural view and with a pronounced interapertural “girdle” of tectate exine — which has been hypothesised as a synapomorphy for the subtribe (Kiel *et al.* 2006). A similar pollen type is recorded in Whitfieldieae: Whitfieldiinae (Manktelow *et al.* 2001; Grall & Darbyshire 2021; Manzitto-Tripp *et al.* 2021), but molecular phylogenetic evidence confirms that these two lineages are not closely related, and the similarity in pollen type is homoplastic (McDade *et al.* 2008).

Based on current taxonomy, Madagascar is the centre of generic diversity for Isoglossinae, with five genera represented: *Brachystephanus* (3 spp.), *Celerina* Benoist (1 sp., 2 vars.), *Isoglossa* (9 spp.), *Melittacanthus* S.Moore (1 sp., 2 vars.) and *Sphacanthus* Benoist (2 spp.) (taxon numbers modified from Madagascar Catalogue 2022, and not including undescribed

species). Of these, *Celerina*, *Melittacanthus* and *Sphacanthus* are all endemic to Madagascar. A fourth endemic genus, *Conocalyx* Benoist, has been described, but the name is illegitimate because Benoist (1967) did not designate a type specimen in the protologue, and it was not upheld in the recent reclassification of Acanthaceae (Manzitto-Tripp *et al.* 2021). None of these genera has been subject to a recent taxonomic treatment, with the exception of *Brachystephanus* (Champluvier & Darbyshire 2009). *Brachystephanus* is unique among palaeotropical Isoglossinae in having monothealous anthers, a trait shared with Neotropical *Stenostephanus* and *Sebastiano-schaueria* Nees, the only Neotropical representatives of Isoglossinae. The other genera of Isoglossinae have bitheous anthers, with the thecae of each anther ranging from parallel and held at an equal height to being highly oblique and/or being held at a markedly unequal height. For Madagascar, a distinction appears to have been made by previous taxonomists between these differing anther states within the Justicieae with gürtelpollen, and taxa with offset and/or oblique thecae have been treated in *Isoglossa* whilst taxa with thecae $\pm$ parallel and held at an equal height have been treated in the segregate endemic genera *Celerina*, *Conocalyx*, *Melittacanthus* and *Sphacanthus*. However, the protologues for these genera do not clearly differentiate them from one another or from *Isoglossa* (Manzitto-Tripp *et al.* 2021; McDade *et al.* 2021; Phillipson *et al.* in press). Furthermore, the circumscription of *Isoglossa* in continental Africa is broader and encompasses all these anther configurations and a range of intermediate states. Other morphological traits observed in the segregate genera in Madagascar are also readily encompassed by the range of variation observed in *Isoglossa* s.l. in continental Africa (McDade *et al.* 2021). Hence, morphological evidence could support the recognition of a single, variable genus, delimited by having the combination of a bilabiate corolla with ascending-cochlear aestivation, two bitheous stamens that lack appendages on the thecae, 4-seeded stipitate capsules and (usually¹) gürtelpollen.

A molecular phylogenetic study of Isoglossinae and allies based on three loci (nrITS, *trnT-L* and *trnS-G*) by Kiel *et al.* (2006) included five species of *Isoglossa* (one from Madagascar, four from tropical Africa) and

¹ Two species of *Isoglossa* with prolate, tricolporate hexapseudocolpate pollen — or “spangenpollen” — have been described from Africa (Darbyshire 2009), namely *I. faulknerae* I.Darbysh. and *I. variegata* I.Darbysh. However, the latter species was included in the molecular phylogenetic study of McDade *et al.* (2021) and was resolved within Tetrameriinae. McDade *et al.* (2021) hypothesised that species of *Isoglossa* with spangenpollen will be placed either in the Tetrameriinae (their *Tetramerium* Lineage) or Monotheceinae (their *Ptyssiglottis* Lineage) in future molecular phylogenetic studies.

Conocalyx laxis Benoist, and found that *Isoglossa* plus *Conocalyx* formed a well-supported clade. In an expanded molecular phylogenetic study of the Justicieae using additional loci (*trnL-F* and *rps16* intron), McDade *et al.* (2021) included a number of additional taxa of Isoglossinae from Madagascar and continental Africa, with 14 taxa that combine bitheous stamens and gürtepollen being represented (Fig. 1). These included representatives of *Conocalyx*, *Isoglossa*, *Melittacanthus* and *Sphacanthus*, alongside four potential new species to science. Also included was the enigmatic species *Anisotes perplexus* T.F.Daniel, Letsara & Martín-Bravo, which an earlier phylogenetic study had placed in Isoglossinae (Kiel *et al.* 2017). Contrary to the findings of Kiel *et al.* (2006), McDade *et al.* (2021) found that bitheous Isoglossinae — or *Isoglossa* s.l. — are paraphyletic, with the monothecous clade (*Brachystephanus*, *Stenostephanus* and *Sebastianoschaueria*) embedded within it (Fig. 1). In that study, *Isoglossa* Clade 1 was resolved as sister to the clade of monothecous taxa and contained two species of *Isoglossa* from Madagascar: *I. vestita* Benoist and *I. aff. justicioides* Baker. *Isoglossa* Clade 2 contained all other

sampld bitheous taxa, including the endemic Madagascar genera and all sampled continental African *Isoglossa* (Fig. 1). Amongst these was South African *I. ovata* (Nees) Lindau, which is morphologically similar to the type species of *Isoglossa*, *I. organoides* (Nees) S.Moore, also from South Africa (see Balkwill *et al.* 2017). Hence, it is possible that Clade 2 represents *Isoglossa* s.s. but this requires testing with further molecular phylogenetic data. However, it is perplexing as to why *I. vestita* and *I. aff. justicioides* did not fall within this clade given that they share a similar suite of characters to several of the sampled species in Clade 2. Relationships within *Isoglossa* Clade 2 were not well resolved in the phylogeny of McDade *et al.* (2021), although the sampled taxa from Madagascar (with the exception of the two species in Clade 1) were resolved with reasonable support in a separate subclade from the sampled continental Africa species. Of note, however, is the fact that this Madagascar subclade includes at least one species with offset and oblique anther thecae (*I. sp. aff. gracillima*, here tentatively reidentified as *I. expansa* Benoist), hence the generic distinction based on anther characters

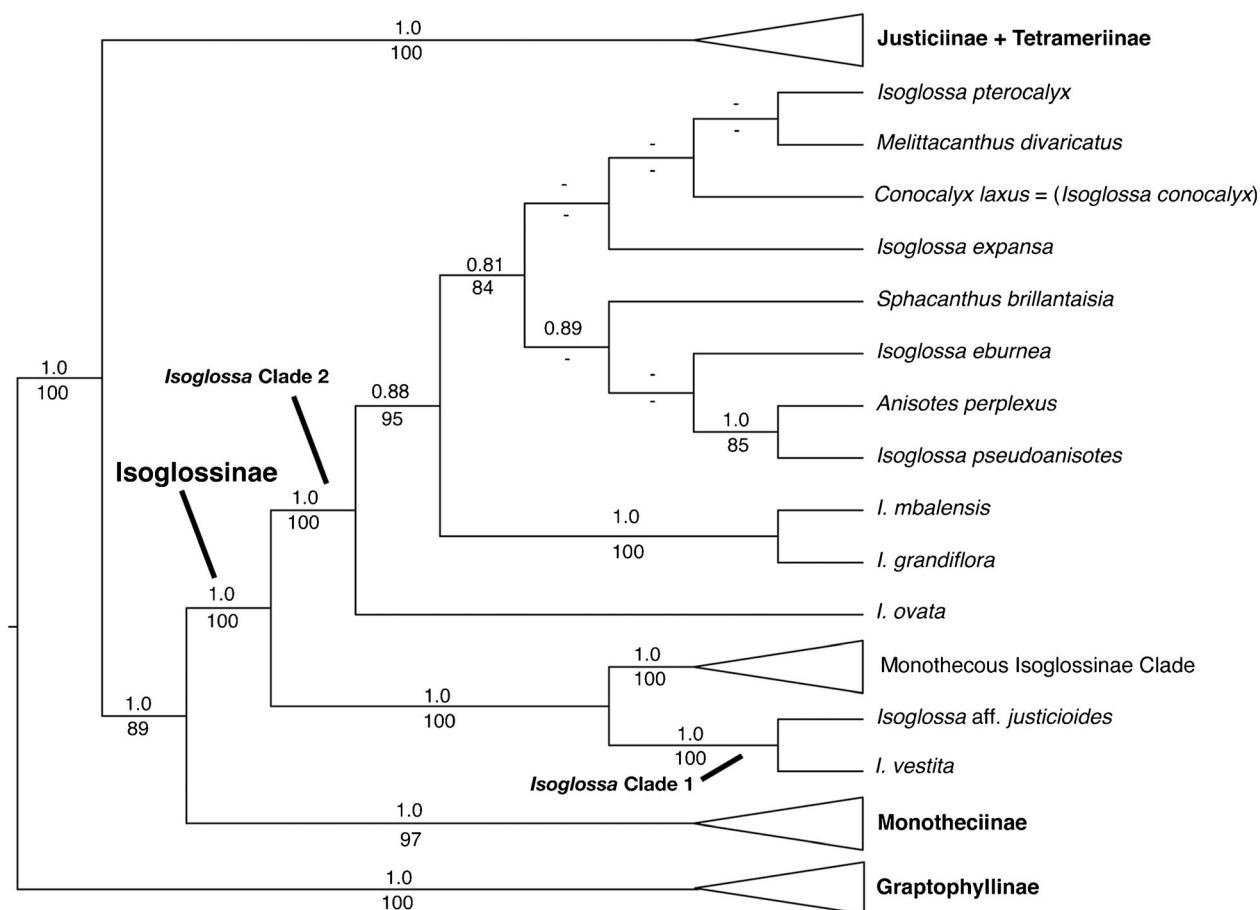


Fig. 1. Details of relationships among members of Isoglossinae summarised from McDade *et al.* (2021), based on five genes: *trnL-F*, *rps16*, *trnT-L*, *trnS-G*, and *nrlTS*. Values above branches are Bayesian posterior probabilities (BEAST analysis); those below are maximum likelihood bootstrap values (IQTree analysis). - = <50% or 0.50.

applied in Madagascar by previous authors does not hold phylogenetically.

An interim solution to generic delimitation in Isoglossinae on Madagascar

Given the morphological and molecular data summarised above, it is clear that generic circumscription is problematic within Isoglossinae (McDade *et al.* 2021). Although a broadly circumscribed *Isoglossa* might be a desirable solution from a morphological perspective, it appears that this could only be achieved by accepting paraphyly. McDade *et al.* (2021) concluded that a densely sampled phylogenetic study using NGS methods is warranted in order to gain better resolution of the clades in Isoglossinae and their constituent species. Recent NGS studies elsewhere in Acanthaceae, using RADseq in particular, have yielded well resolved phylogenies, with considerably improved data resolution compared to traditional Sanger techniques (e.g., Tripp *et al.* 2017; Darbyshire *et al.* 2020; Comito *et al.* 2022). With such a project still to be initiated for Isoglossinae, a pragmatic interim solution is needed to allow the description of the known novelties from Madagascar to proceed. We here propose that all bitheous Isoglossinae be treated at present under *Isoglossa* s.l. and that all new species should be described in *Isoglossa*. In order to avoid unnecessary proliferation of taxonomic names, we refrain from formally transferring existing species from the segregate genera to *Isoglossa* at the present time and will only make new combinations for taxa of Isoglossinae currently placed outside of the subtribe. In this study we first provide an overview of current knowledge on the segregate endemic genera and misplaced species of Isoglossinae in Madagascar to aid understanding of these taxa and how they relate to *Isoglossa*. We then go on to describe three new species in *Isoglossa* as well as validating the species previously treated by Benoist (1967) as *Conocalyx laxus*.

Materials & Methods

Herbarium specimens of the new species were analysed at G, K and P using standard herbarium practices. Specimens from other herbaria, primarily type material, were observed online, mainly via JSTOR Global Plants (<https://plants.jstor.org/>). Prior to dissection, flowers were soaked in Aerosol OT 5% solution; all other characters were measured on dry material. All duplicates seen by one or more of the authors are marked “!”. Those that have only been seen as digital images are marked “*”. Barcodes for duplicates are listed wherever available to facilitate digital access to the specimens. Specimens cited in the “Additional Specimens Examined” section are cited in chronological order of collection, earliest first.

In the “Distribution” section, we include both the Provinces and Regions of Madagascar in which each taxon occurs. The six Provinces still exist as official geographic entities in Madagascar, but no longer have administrative functions; these have now passed to the 23 Regions. DIANA and SAVA Regions are spelled out in capitals as per their official title, because they are based on the initial letters of their sub-regions’ names.

The species conservation assessments follow the Categories and Criteria of IUCN (2012) and the guidelines for their use (IUCN Standards and Petitions Subcommittee 2019). Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated by using the GeoCAT tool (www.geocat.kew.org; Bachman *et al.* 2011).

Taxonomic Account

1. Review of endemic Isoglossinae genera and misplaced species of Isoglossinae in Madagascar

Melittacanthus S.Moore

Moore (1906) described *Melittacanthus* based on a single species and specimen, *M. divaricatus* S.Moore (Deans-Cowan s.n., Ankafana). He noted that this species was “in the neighbourhood of *Isoglossa*” (Moore 1906: 218) but he did not note how they differ. Instead, he went on to compare it to *Populina* Baill., a genus he had not seen. *Populina* is now known to be in subtribe Tetrameriinae, quite unrelated to *Isoglossa* (Daniel *et al.* 2008; McDade *et al.* 2018). *Melittacanthus divaricatus* combines fasciculate inflorescences terminating the branches, conspicuous, lanceolate calyx lobes, and a large, strongly bilabiate corolla with a broadly expanded throat (Fig. 2); the two bitheous stamens have the thecae only slightly offset. Although this inflorescence type has not been observed in continental African *Isoglossa*, inflorescence form is very variable across the genus and it would not be a significant stretch to also include the fasciculate inflorescence of *Melittacanthus*. All other characters observed in *M. divaricatus* are congruous with *Isoglossa*; the calyces are larger than in most species of *Isoglossa* but large calyces are noted in, for example, *I. pawekiae* Brummitt & Feika (1978) from Malawi.

Benoist (1967) described *Melittacanthus divaricatus* var. *minor* based on Perrier de la Bâthie 16844. He differentiated it from typical *M. divaricatus* by the smaller flowers, with calyx lobes 4 – 5 mm long and corolla 22 mm long including tube 12 mm long; Moore (1906) recorded calyx lobes 10 mm long and corolla tube 20 mm long in *M. divaricatus*. In addition to the strikingly smaller corollas, some of the inflorescences of var. *minor* are more elongate and spiciform, very similar to *Celerina seyrigii* Benoist var. *egena* Benoist (see below) with which this taxon should be compared more closely. A collection from ± the same

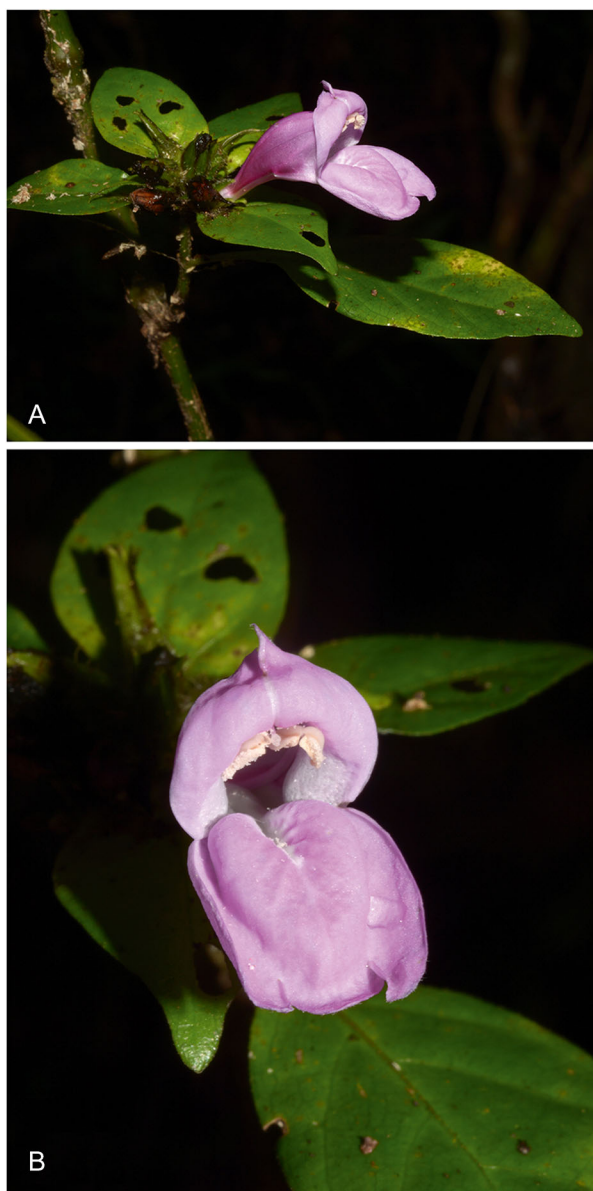


Fig. 2. *Melittacanthus divaricatus*. Analamanga. **A** flowering stem; **B** face view of flower. PHOTOS: DAVID SCHERBERICH.

locality and date (*Perrier de la Bâthie* 16858) appears to be typical *M. divaricatus*, with a considerably longer and more curved corolla tube than var. *minor*. Given these differences, the status of var. *minor* requires further investigation as it may be better treated as a distinct species.

The type of var. *minor* bears the same collector, number and collection details as the type of *Justicia disjuncta* Benoist (although it is a different duplicate and so not homotypic), and the two are clearly conspecific. In earlier describing this taxon in *Justicia*, Benoist (1947) noted biporate pollen and the anthers with barely offset and muticous thecae, both of which point to placement in Isoglossinae; these are both illustrated on the

holotype. *Justicia disjuncta* is synonymised below.

***Melittacanthus divaricatus* S.Moore (1906: 218).** Type: Madagascar, Ankafana, fl. & fr. 1880, *Deans Cowan* s.n. (holotype BM! [BM000931236]).

DISTRIBUTION. This species occurs in east-central Madagascar in the Analamanga and Itasy Regions of Antananarivo Province and Matsiatra Ambony Region of Fianarantsoa Province (Map 1).

HABITAT AND ECOLOGY. This species is a subshrub with pink to mauve flowers, recorded from mixed forest and grassland on slopes and from humid woodland on gneiss.

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Manankazo au NE d'Ankazobe, 1500 m elev., fl. Sept. 1913 *Perrier de la Bâthie* 9178 (P! [P00089889, P00089890, P00089891]); Manerinerina sur le Tampoketsa, entre l'Ikopa et le Betsiboka, 1500 m elev., fl. & fr. Dec. 1924, *Perrier de la Bâthie* 16858 (P! [P03977293]); Antananarivo, Tampoketsa d'Ankazobe, 1 km S of bridge at R. Manankazo, 1590 m elev., fl. & fr. 29 Dec. 1998, *Flores & Andriantiana* 90 (A, K!).

There is also an additional iNaturalist record available for this species: <https://www.inaturalist.org/observations/120312553>, Antananarivo, Analamanga, April 2022 (see Fig. 2).

NOTES. From the very limited material seen to date, this species appears to be rather variable in the length of the corolla tube; *Perrier de la Bâthie* 9178 and 16858 have a longer, more gradually expanded and curved tube than the type specimen and *Flores & Andriantiana* 90.

This species, including var. *minor*, is assessed as Endangered [EN B2ab(i,ii,iii,iv,v)] on the IUCN Red List (Faranirina & Rabarimanarivo 2019).

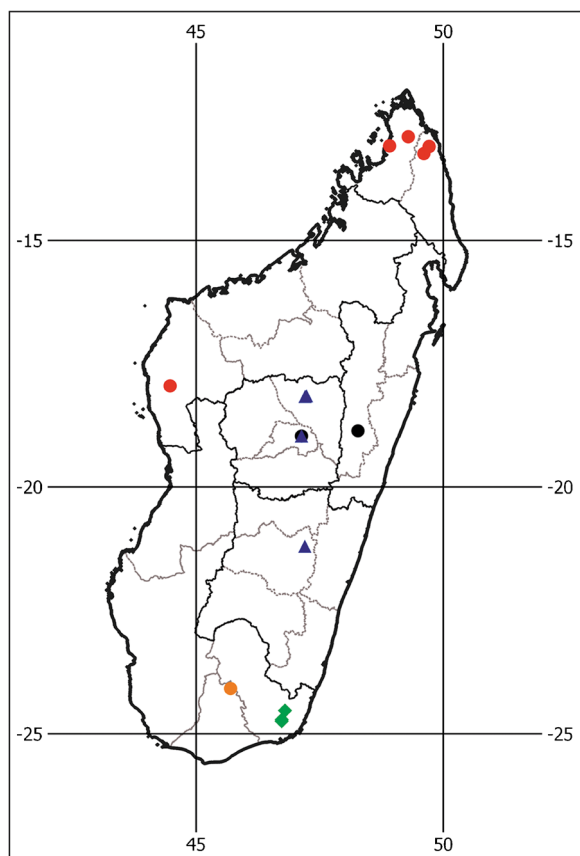
***Melittacanthus divaricatus* S.Moore var. *minor* Benoist (1967: 534).** Type Madagascar, Manerinerina sur le Tampoketsa, entre l'Ikopa et le Betsiboka, 1500 m elev., fl. & fr. Dec. 1924, *Perrier de la Bâthie* 16844 (holotype P! [P00089892]).

Justicia disjuncta Benoist (1947: 122). Type: Madagascar, Manerinerina sur le Tampoketsa, entre l'Ikopa et le Betsiboka, 1500 m elev., fl. & fr. Dec. 1924, *Perrier de la Bâthie* 16844 (holotype P! [P00089619]), **synon. nov.**

DISTRIBUTION. This variety occurs in east-central Madagascar in Alaotra-Mangoro Region of Toamasina Province and Itasy Region of Antananarivo Province (Map 1).

HABITAT AND ECOLOGY. This variety is recorded from woodland on slopes and forest “on crust”.

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Toamasina, Alaotra-Mangoro Region, Moramanga, Andasibe, Menalamba, Ampitambe, Ambatovy forest,



Map 1. Known distribution of *Melittacanthus divaricatus* var. *divaricatus* (blue triangles), *M. divaricatus* var. *minor* (black circles), *Celerina seyrigii* var. *seyrigii* (orange circle), *C. seyrigii* var. *egena* (green diamonds) and *Isoglossa eburnea* (red circles).

Dynatec Camp, fl. 15 Dec. 2005, *Antilahimena et al.* 4395 (K!, MO, P! [P03960550], TAN).

NOTES. As noted above, this variety appears to be closely allied to *Celerina seyrigii* var. *egena* from southeast Madagascar and the relationship between the two requires further scrutiny as they may be conspecific. The flowers of *C. seyrigii* var. *egena* tend to be more conspicuously pedicellate but there is some overlap in this character, and *Antilahimena et al.* 4395 has clearly pedicellate flowers.

Sphacanthus Benoist

Benoist (1939) described *Sphacanthus* based on *S. brillantaisia* Benoist which features a long slender spiciform inflorescence, markedly bilabiate corollas resembling *Salvia* L. or *Brillantaisia* P.Beauv., and anther thecae that are parallel and barely offset. Benoist (1945) later added a second species, *S. humbertii*, which has smaller corollas than *S. brillantaisia* and has characteristic oblanceolate, imbricate calyx lobes, those of *S. brillantaisia* being linear-lanceolate and not imbricate. *Justicia excalcea* Benoist (1947) is here considered to be a synonym of *S. humbertii*.

Sphacanthus is morphologically very similar to some members of continental African *Isoglossa*, notably *I. grandiflora* S.Moore, *I. floribunda* C.B.Clarke and allies which include the former segregate genus *Schliebenia* Mildbr. (Mildbraed 1934; Brummitt 1985; Darbyshire 2009). However, in the phylogenetic study of McDade *et al.* (2021) *Sphacanthus* (represented by *S. brillantaisia*) was resolved within the Madagascar Sub-clade of *Isoglossa* Clade 2, whilst the continental African “*Schliebenia*” group (represented by *I. grandiflora* and *I. mbalensis* Brummitt), was resolved as sister to the Madagascar Sub-clade (Fig. 1).

***Sphacanthus brillantaisia* Benoist (1939: 157).** Type: Madagascar, vallée moyenne du Mandrare, près d’Anadabolava, 200 – 250 m elev., fl. & fr. Dec. 1933, *Humbert* 12583 (lectotype P! [P00089895], selected here; isolectotypes G! [G00341402], K! [K000379189], P! [P00089893, P00089894], S* [S09-2253], TAN* [TAN000238], US* [US00730930]).

DISTRIBUTION. Occurs widely across southern Madagascar, in Androy, Anosy and Atsimo-Andrefana Regions of Toliara Province (Map 2).

HABITAT AND ECOLOGY. This is a species of xerophytic bush and “dry forest” on calcareous or gneissic rocks and sands, often occurring in rocky areas. It is a (sub)shrub 50 – 150 cm tall, with pale lilac-pink to rose-violet corollas.

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Vallée de la Mandrasi, fl. Nov. 1905, *Alleizette* s.n. (CLF* [CLF072947]); Ambovombe, Antanimora, fl. 12 May 1925, *Decary* 3795 (P! [P00089896]); vallée de la Sakamalio, affluent de la Manambolo (bassin du Mandrare), 500 – 800 m elev., fl. & fr. Dec. 1933, *Humbert* 13313 (K!, P! [P03297973]); vallée de la Sakamalio, affluent de la Manambolo (bassin de Mandrare), 900 – 1100 m elev., in bud, Dec. 1933, *Humbert* 13366 (P! [P03297971, P03297972]); gorges de la Manombo (sud-ouest), 100 – 350 m elev., fl. 25 – 26 Jan. 1947, *Humbert* 19989 (K!, P! [P03297969, P03297970]); plateau au sud des gorges du Fiherenana entre Andranohinaly et Andranovory, fl. 3 – 4 Feb. 1947, *Humbert* 20111 (K!, P! [P00089900]); vallée de l’Onilahy près de Tongobory, vallon d’Andranolahy, 50 – 200 m elev., fl. 5 Feb. 1947, *Humbert* 20170 (K!, P! [P00089901]).

NOTES. The gürtelpollen of this species is well illustrated by Muller *et al.* (1989); see their plates 182/XXXV and 182/XXXVI.

***Sphacanthus humbertii* Benoist (1945: 14).** Type: Madagascar, forêt d’Analafanja, au nord du Fiherenana, sur plateau calcaire, 950 – 1000 m elev., fl. March 1934, *Humbert* 14289 (lectotype P! [P00089897], selected here; isolectotypes G! [G00341403], K! [K000379188], P! [P00089898, P00089899], TAN* [TAN000221]).

Justicia excalcea Benoist (1947: 123). Type: Madagascar, forêt d'Analavelona, entre le Fiherenana et le Manombo, 1000 m elev., fl. & fr. May 1933, *Perrier de la Bâthie* 19193 (holotype P! [P00089622]), **synon. nov.**

DISTRIBUTION. Occurs in Atsimo-Andrefana Region of Toliara Province (Map 2).

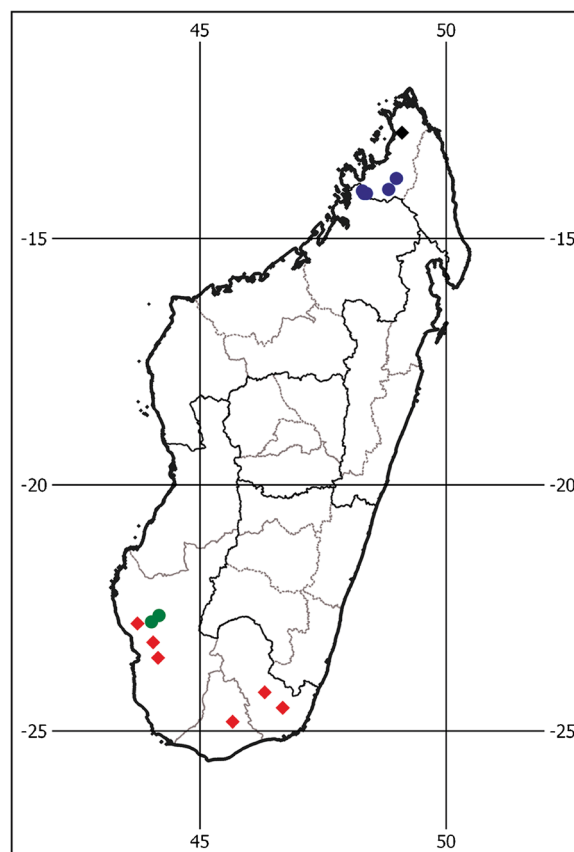
HABITAT AND ECOLOGY. This species is a shrub that occurs on both calcareous and basaltic substrates according to specimen labels.

NOTES. This species is known only from the two collections cited; their collection localities are close, hence it appears to be a highly restricted species. The flower colour is unknown. The epithet *humbertii* is already occupied in *Isoglossa* (Mildbraed 1937), hence if this species were to be transferred to *Isoglossa*, the epithet *excalcea* would have precedence. The imbricate, oblanceolate calyx lobes with acuminate tips are characteristic for this species.

Celerina Benoist

Benoist (1964) described *Celerina* based on *C. seyrigii*, with two varieties, var. *seyrigii* and var. *egena*. The protologue does not specify that the pollen is biporate, but it is described as spherical and smooth which suggests gürtepollen (McDade *et al.* 2021). *C. seyrigii* s.s. is very similar to *Sphacanthus* in combining spiciform inflorescences, subsessile flowers, markedly bilabiate, *Salvia*-like corollas, and anther thecae that are parallel and barely offset. Indeed, a second sheet of the type specimen of *C. seyrigii* at P (Seyrig 494, P06490663), apparently not seen by Benoist, has been filed under *Sphacanthus humbertii* until now. *Celerina seyrigii* has broad calyx lobes similar to those in *S. humbertii* but they are more elliptic, and *C. seyrigii* is also more hairy throughout; the two species are apparently distinct but their morphology suggests a close relationship. The second variety, var. *egena*, is very different to var. *seyrigii*. It has conspicuously pedicellate flowers that are held in fascicles, these being spaced along a racemose inflorescence and/or sometimes in separate fascicles in the distalmost leaf axils. The plants are also largely glabrous except along the stems and inflorescence rachises and the calyx lobes are linear-lanceolate. It bears much more resemblance to *Melittacanthus divaricatus* var. *minor* than to *C. seyrigii* s.s. and it is difficult to understand why Benoist united them under the same species.

Justicia subpaniculata Benoist (1947) was earlier described from the same area as the type of *Celerina seyrigii* var. *egena* and it bears a very close resemblance. Further, although not mentioned in the protologue, an illustration on the type specimen of *J. subpaniculata* shows this species to have gürtepollen as in *Celerina*. Indeed, a second sheet of the type of *J. subpaniculata* at



Map 2. Known distribution of *Sphacanthus brilliantaisia* (red diamonds), *S. humbertii* (green circles), *Isoglossa perplexa* (blue circles) and *I. pseudoanisotes* (black diamond).

P (Humbert 6595, P00089182) is currently filed under *C. seyrigii*. We here consider *J. subpaniculata* and *C. seyrigii* var. *egena* to be conspecific and they should be treated as a separate species from *C. seyrigii* s.s., with the epithet “*subpaniculata*” having priority. However, given the uncertainty over generic circumscription and over the relationship between var. *egena* and *Melittacanthus divaricatus* var. *minor*, we refrain from making the new combination here.

Celerina is yet to be included in any molecular phylogenetic studies (McDade *et al.* 2021), and so should be considered a priority for inclusion in future molecular studies of Isoglossinae.

***Celerina seyrigii* Benoist (1964: 404).** Type: Madagascar, forêt de Belambo près d'Ampandrandava, 1000 m elev., fl. 1945, Seyrig 494 (holotype P! [P00089181]; isotype P! [P06490663]).

DISTRIBUTION. Occurs in Androy Region of Toliara Province (Map 1).

HABITAT AND ECOLOGY. This species is a subshrub with pale violet flowers, known only from the type locality,

where it was recorded from degraded areas in (presumably dry) forest.

Celerina seyrigii Benoist var. **egena** Benoist (1964: 404). Type: Madagascar, bassin supérieur de la Mandrare (sud est), col et sommet de Marosoui, 1000 – 1400 m elev., fl. & fr. 14 – 15 Nov. 1928, *Humbert* 6595 (holotype P! [P00089183]).

Justicia subpaniculata Benoist (1947: 124). Type: Madagascar, bassin de réception de la Mananara, affluent du Mandrare, sur les pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, à l'Aniampanga (rive gauche de la rivière Akaramy) en amont de Mahamavo, 800 – 900 m elev., fl. & fr. Jan. – Feb. 1934, *Humbert* 13947 (lectotype P! [P00089762], selected here; islectotype P! [P00089182]), **synon. nov.**

DISTRIBUTION. Occurs in southeast Anosy Region of Toliara Province (Map 1).

HABITAT AND ECOLOGY. This variety is a herb or subshrub to 0.5 – 1.5 m of (sub)humid forest on gneiss and laterite, with pale lilac to purple corollas.

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Mont Itrafanomby (Ankazondrano) et ses contreforts SW (Haut-Mandrare), 1600 – 1800 m elev.; fl. Dec. 1933, *Humbert* 13445 (G! [G00379515], P! [P03977292]); Toliara, Anosy, Ambatoabo, Mahamavo, Ankazomena, 660 m elev., fl. 29 April 2009, *Rakotonasolo* 1259 (K!, MO, TAN).

NOTES. See also the note to *Melittacanthus divaricatus* var. *minor* for comparison to that taxon, which is closely allied morphologically.

Ritonia poissonii Benoist and *Justicia onilahensis* Benoist

Ritonia Benoist (1962) was unplaced in the recent reclassification of Acanthaceae, but Manzitto-Tripp *et al.* (2021) noted that *Ritonia s.l.* is not a natural grouping. *Ritonia humbertii* Benoist, the type species, and *R. barbiger* Benoist potentially belong within Whitfieldiinae, whilst *R. rosea* Benoist is considered to be a synonym of *Populina perrieri* Benoist in Tetramerinae (Manzitto-Tripp *et al.* 2021; Madagascar Catalogue 2022). The fourth species, *R. poissonii*, combines bilabiate corollas with prominent raised venation on the lower lip, two bithecous stamens with the thecae barely offset, no staminodes, and gürtelpollen. This combination places *R. poissonii* within Isoglossinae with little doubt. Unfortunately, recent attempts to include *R. poissonii* within a phylogenetic study of Acanthaceae have been unsuccessful as the available material did not yield sufficient DNA (I. Darbyshire & A. Zuntini, pers. data). *Ritonia poissonii* is an illegitimate name

and is also predated by the name *Justicia onilahensis* Benoist which refers to the same taxon (see note below). With this in mind, it is considered most appropriate to transfer *J. onilahensis* to *Isoglossa*, with *R. poissonii* in synonymy, so that this species is at least placed in the correct subtribe pending final circumscription of genera within Isoglossinae.

Isoglossa onilahensis (Benoist) I. Darbysh. **comb. nov.**

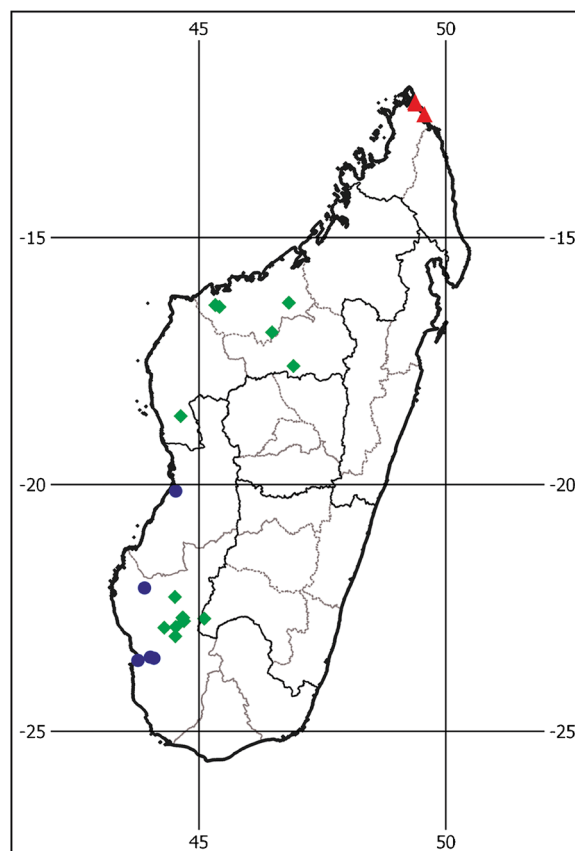
<http://www.ipni.org/urn:lsid:ipni.org:names:77307258-1>

≡ *Justicia onilahensis* Benoist, *Notul. Syst. (Paris)* 13: 130 (1947). Type: Madagascar, vallée inférieure de l'Onilahy, alt. 25 – 200 m, fl. 12 Aug. 1928, *Humbert* & *Swingle* 5234 (holotype P! [P00089700]).

Ritonia poissonii Benoist (1967: 533), nom. illegit., **synon. nov.** — see note.

Fig. 3

DISTRIBUTION. Occurs in Atsimo-Andrefana and Menabe Regions of Toliara Province (Map 3).



Map 3. Known distribution of *Isoglossa conocalyx* (green diamonds), *I. pterocalyx* (red triangles) and *I. onilahensis* (blue circles).



Fig. 3. *Isoglossa onilahensis*. Near Ifanato village (Madjid & Vanomena MHA93). A habit with precocious flowering; B & C flowers. PHOTOS: HARITHI ASSANE MADJID.

HABITAT AND ECOLOGY. This species occurs on calcareous hills within dry forest on sandy soil. It is a shrub or small tree, 1.5–5 m tall and can have a trunk up to 50–60 cm in diam. with dense wood. The pink or pink-violet flowers are produced in masses before the leaves (see Fig. 3).

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Bord de l'Onilahy à Manassa près de Tongobory, fl. 21 Nov. 1921, *Poisson* [2nd voyage] 358 (P! [P00089223]); forêt de Marofandelia, entre Morondava et la Tsiribihina, 10–20 m elev., fl. Oct. 1933, *Humbert* 11430 (G! [G00341744], K!, P! [P00089225, P00089224]); Befandriana-Sud, c. 10 km N, 150 m elev., fl. 2 Dec. 1961, *Appert* 34 (K!, Z); Atsimo Andrefana, près du village d'Ifanato, fl. 1 Nov. 2020, *Madjid & Vanomena* MHA93 (P! [P01069700], TAN); without locality or date, *Montagnac* s.n. (P! [P02857419]).

NOTES. The name *Ritonia poissonii* is illegitimate because two specimens — *Humbert* 11430 and *Poisson* [2nd voyage] 358 — were cited in the protologue without a type being designated (Benoist 1967). The type of *Justicia onilahensis* is a poor specimen but appears a good match for *R. poissonii* and is collected from along the Onilahy River, close to one of the two localities recorded by Benoist (1967) for *R. poissonii*.

Some variation is noted between the few available specimens of this species in terms of calyx indumentum, this

being very sparse in the type of *Justicia onilahensis* and in *Madjid & Vanomena* MHA93, both from the Onilahy, whilst it is more developed in *Poisson* 358 and the *Montagnac* collection. Further material is desirable to assess this variation.

Anisotes perplexus T.F.Daniel, Letsara & Martín-Bravo
Anisotes perplexus was described by Daniel *et al.* (2013) from the highland forests of the Manongarivo massif in northern Madagascar. *Anisotes* Nees belongs in subtribe Justiciinae of the Justicieae and is characterised by its floral form where the corollas are large, typically brightly coloured and the lobes are $\pm$ longer than the tube, the upper lip being strongly hooded, the lower lip being narrowly strap-shaped and becoming recurved to recoiled at anthesis. The epithet “*perplexus*” was applied to this species because, although it matches *Anisotes* Nees in floral form, it has gürtelpollen, as opposed to the prolate, bi- or tri-colporate tetra- or hexa-pseudocolpate pollen of other *Anisotes* species. *Anisotes perplexus* was included along with other species of *Anisotes* in molecular phylogenetic studies by Kiel *et al.* (2017) and McDade *et al.* (2021) in both of which *Anisotes* was found to be polyphyletic, occurring in several clades of Justiciinae and with *A. perplexus* being resolved in Isoglossinae. In the latter study, *A. perplexus* was placed within the Madagascar clade of *Isoglossa* clade 2, and sister

with reasonable support to an undescribed species (*Isoglossa* sp. 1022) which again combines an *Anisotes*-type floral morphology with gürtelpollen. McDade *et al.* (2021) noted that large, brightly-coloured corollas with the morphology described for *Anisotes* above have evolved multiple times across Justicieae and that this is hypothesised to be as an adaptation to passerine bird pollination. Whilst this corolla form has not previously been reported in *Isoglossa*, corolla morphology is variable across continental African *Isoglossa* and does include putative bird-pollinated taxa, for example *I. ixodes* Lindau from the Uluguru Mountains of Tanzania (Darbyshire 2008). Other characters in *A. perplexus*, including the weakly offset, muticous anther thecae, and the spiciform inflorescences with conspicuous pairs of bracts are all congruent with *Isoglossa* s.l. The presence of a rugula (stylar furrow) is of note in this species, as this character is mainly known from Justiciinae (Kiel *et al.* 2017). However, Balkwill & Welman (2000) have previously recorded presence of a rugula in *Isoglossa*, and this character is also noted in some of the new species described below. Further research is clearly needed on the rugula and its taxonomic significance within Justicieae.

Given that *Anisotes perplexus* is currently placed in the wrong subtribe of Justicieae, we here provide the new combination in *Isoglossa* so that it is at least placed within the correct subtribe, pending recircumscription of genera within Isoglossinae. *Isoglossa* sp. 1022 of McDade *et al.* (2021) is described in part 2 of the taxonomic treatment below as *I. pseudoanisotes* I.Darbysh.

Isoglossa perplexa (T.F.Daniel, Letsara & Martín-Bravo) I.Darbysh. & Kiel **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77307259-1>

≡ *Anisotes perplexus* T.F.Daniel, Letsara & Martín-Bravo, *Novon* 22: 402 (2013). Type: Madagascar, Antsiranana, E of Ankaramy, Réserve Spéciale, Manongarivo, Antsatroto, SE of summit, river valley between Antsatroto and massif, 1470 – 1570 m elev., fl. 14 – 15 April 1992, Malcomber, Hutcheon, Razafimanantsoa & Zjhra 1481 (holotype MO* [MO-2758543]; isotypes BR, G! [G00444734], K! [K001090217]).

Anisotes sp. 1 sensu Gautier (2002: 133).

DISTRIBUTION. Occurs in DIANA Region of Antsiranana Province (Map 2).

HABITAT AND ECOLOGY. This species occurs in upland moist forest; it is a clambering shrub up to 3.4 m tall.

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Mt Tsaratanana, fl. April 1924, Perrier de la Bâthie 16151 (P! [P00089850, P00089851, P00089852]); Distr. D'Ambilobe, Massif de Marivorahona au SW de Manambato (Haute Mahavavy du Nord), fl. 18 – 26

March 1951, Humbert & Capuron 25721 (K!, MO [MO-2758546], P! [P00089849]); Bekolosy, vallon en amont de la chute de la rivière Bekolosy, fl. 25 June 1994, Gautier *et al.* LG 2458 (G, K!, MO, P! [P04404235]); Manongarivo Massif, above village of Ambodisakoana, E of Ankaramy, fl. & fr. 18 Oct. 1994, McPherson & van der Werff 16400 (K!, MO [MO-2758541]).

NOTES. The flowers of this species are variously described as lemon-yellow with a darker yellow upper lip (Humbert & Capuron 2571) or with the upper lip bright red (Perrier de la Bâthie 16151) or the whole corolla yellow with orange veins (Gautier *et al.* LG 2458). The flowers are held in spikes with conspicuous bracts.

2. New species of *Isoglossa* from Madagascar

All of the new species described below were included in the molecular phylogenetic study of McDade *et al.* (2021) and were resolved within *Isoglossa* Clade 2 of Isoglossinae, together with other, though not all, bitheous species of Isoglossinae from Madagascar. However, as noted above, data resolution within this Madagascar sub-clade was generally low and so evolutionary relationships among the taxa are not well defined at present.

Isoglossa eburnea Onjalal. & I.Darbysh. **sp. nov.** Type: Madagascar, Antsiranana, SAVA Region, Iharana (Vohémar), Daraina, Bekaraoka forest, North part, 530 m elev., fl. 15 Jan. 2005, Ranirison & Nusbaumer PR 890 (holotype K!; isotypes G! [G00019629], P! [P00853198], TEF).

<http://www.ipni.org/urn:lsid:ipni.org:names:77307490-1>

Isoglossa sp. PR890 *sensu* McDade *et al.* (2021).

Perennial herb or shrub, 30 – 150 cm tall; stems with internodes 1.5 – 4.5 cm long on leafy branches; young stems grey to greyish-green, glabrous or sometimes with sparse short brown eglandular retrorse hairs in two opposite lines below the nodes; mature stems ± woody. *Leaves* dark green on both surfaces, lanceolate or elliptic, 3 – 10.5 × 1 – 3.6 cm, base attenuate, margin crenate or sometimes subentire, apex bluntly acuminate or immature leaves sometimes obtuse; upper surface glabrous, lower surface sparsely pubescent along main veins, hairs brown, soon glabrescent; cystoliths dense, conspicuous; lateral veins 4 – 7 pairs, brochidodromous; petiole 1.5 – 4 mm long, glabrous. *Inflorescences* terminal, spiciform, 5.5 – 12.5 cm long, spike comprising a series of opposite, single-flowered, sessile units, internodes of the rachis 5.5 – 10 mm long at midpoint of spike, occasionally with retrorse hairs at each node; bracts paired, dark green, pairs subequal, ensiform, often curved, 1.5 – 2.7 × 0.5 – 0.7 mm, surface with conspicuous cystoliths, margin with short

eglandular hairs; bracteoles as bracts but 1.3 – 1.8 mm long, sometimes curved. *Calyx* divided almost to the base into 5 subequal lobes, dark green, tube 1.4 – 1.9 × 1.2 – 1.5 mm, lobes linear-lanceolate, 3 – 4 × 0.5 – 0.8 mm, external surface with conspicuous cystoliths, margin with sparse short eglandular brown hairs, internal surface with glandular hairs. *Corolla* pale greenish-yellow or lip white with pink in the throat, ± 15 – 16 mm long in situ, glabrous externally; tube ± 5 mm long, divided equally between basal cylindrical portion and expanded throat; upper lip hooded, elliptic when flattened, 12.5 – 13.5 × 4.5 – 6 mm, margin recurved, apex minutely 2-lobed, internal surface with short rugula towards base, the ridges puberulous; lower lip elliptic when flattened, 10.3 – 10.6 × 9.4 – 9.5 mm, palate with two raised, rounded ridges and central furrow, glabrous, apex 3-lobed, lateral lobes somewhat ovate, 1.6 × 1.4 mm, median lobe rounded, 1.2 × 2.6 mm. *Stamens* inserted ± 2.4 mm from base of corolla; filaments 10 – 10.5 mm long, glabrous; anthers with thecae slightly offset and slightly oblique, elliptic, upper theca 1.9 – 2.2 mm long, lower theca 1.8 – 1.9 mm long. *Ovary* dark brown, 1.2 × 0.5 – 0.7 mm, glabrous; style brown, 11.5 – 13.5 mm long, glabrous, curved; stigma yellow, with two flattened equal lobes 0.3 × 0.4 mm. *Capsule* not seen. Figs 4 & 5.

RECOGNITION. Similar to members of the segregate genus *Sphacanthus* but differs from both *S. brillantaisia* and *S. humbertii* in having single-flowered cyme units at each inflorescence axil on the spike (vs flowers in subsessile cymes of 2 – 5 or more flowers at each axil at maturity). It additionally differs from *S. brillantaisia* in the inflorescence rachis, bracts, bracteoles, and calyx being largely glabrous externally except for inconspicuous hairs along the bract and calyx margins and sometimes at the nodes (vs inflorescence conspicuously pubescent); the calyx lobes being shorter, 3 – 4 mm long (vs 4.5 – 7.5 mm long); the corolla being white to pale greenish-yellow with or without a pink flush on the lower lip and being glabrous externally (vs corolla pale lilac-pink to rose-violet, pubescent externally); and the corolla being smaller, 15 – 16 mm long (vs 25 – 30 mm long). It additionally differs from *S. humbertii* in the calyx lobes being linear-lanceolate, 0.5 – 0.8 mm wide, not imbricate and not paler towards the base and margin (vs calyx lobes oblanceolate-acuminate, 1.3 – 1.8 mm wide, imbricate, paler towards the base and margin). The species is also similar to *Melittacanthus divaricatus* var. *minor* and *Celerina seyrigii* var. *egena* but the flowers are subsessile and in opposite single-flowered cymes along the spike (vs at least some flowers pedicellate to conspicuously so, inflorescences fasciculate or if spiciform then flowers usually in fascicles along the spike) and the corollas are white to

pale greenish-yellow with or without pink on the lower lip (vs corollas lilac to purple).

DISTRIBUTION. *Isoglossa eburnea* occurs in northern Madagascar, known primarily from DIANA and SAVA Regions of Antsiranana Province, but with one record from Melaky Region in Mahajanga Province (Map 1).

ADDITIONAL MATERIAL STUDIED: MADAGASCAR. Antsiranana: Ambilobe, Ankarana, fl. Feb. 1960, *Humbert* 32493 (P*); Binara forest, 720 m, fl. 5 Dec. 2005, *Nusbaumer & Ranirison* LN 1734 (G! [G00090118], K!, P! [P00853205], TEF) — see note; Antsiranana II, Andrafiarana, forest around Anjahakely, 431 m, fl. 20 Dec. 2010, *Burivalova* ZB 110 (G! [G00304081], K!, P! [P00853197], TEF). Mahajanga, Maintirano, Ambinda, Beanka, centrale part, 234 m, fl. 9 Feb. 2012, *Bolliger et al.* RFB 192 (CAS, G! [G00340189], K!, TEF).

There are two additional iNaturalist records available for this species: <https://www.inaturalist.org/observations/37807588>, Antsiranana, Ambatobe-Andavakoera, 6 Dec. 2019, and <https://www.inaturalist.org/observations/86831122>, Antsiranana, Montagne des Français, 12 Dec. 2020.

HABITAT AND ECOLOGY. This species is recorded from dry forest and semi-deciduous humid forest mostly on limestone, at 200 – 750 m elevation. The flowering period is between December and February, during the rainy season in this Region of Madagascar (Moat & Smith 2007).

CONSERVATION STATUS. *Isoglossa eburnea* is known from dry deciduous forests in two disjunct Regions in the western and northern parts of the island, and has an EOO of 34,502 km² and a minimum AOO of 24 km². It is known from six localities, five of which are encompassed in the Protected Area network (Ambohitr'Antsingy Montagne des Français, Ankarana, Beanka, and Loky-Manambato, the lattermost with two localities). However, throughout its range, this species is threatened by the loss of habitat through illegal woodcutting for firewood, construction and precious wood, for slash and burn agriculture and for mining. Even where it occurs within protected areas, the level of threat remains high. It is known from five threat-defined locations, but we strongly suspect that this is an under-representation of the true number of locations (see below) and so prefer to record that it is currently known from fewer than 10 locations. Therefore, based on current knowledge, this species should be assessed as **Vulnerable – VU B2ab(ii,iii,iv)**. However, given its rather wide geographic range, more populations may well be discovered in remnant dry forest in northern and northwestern Madagascar and the apparent disjunction in its range may be an artefact of under-collecting, hence the extinction risk of this species may be downgraded in the future.

ETYMOLOGY. The epithet “*eburnea*”, meaning “ivory”, denotes the pale yellowish-white corollas of most

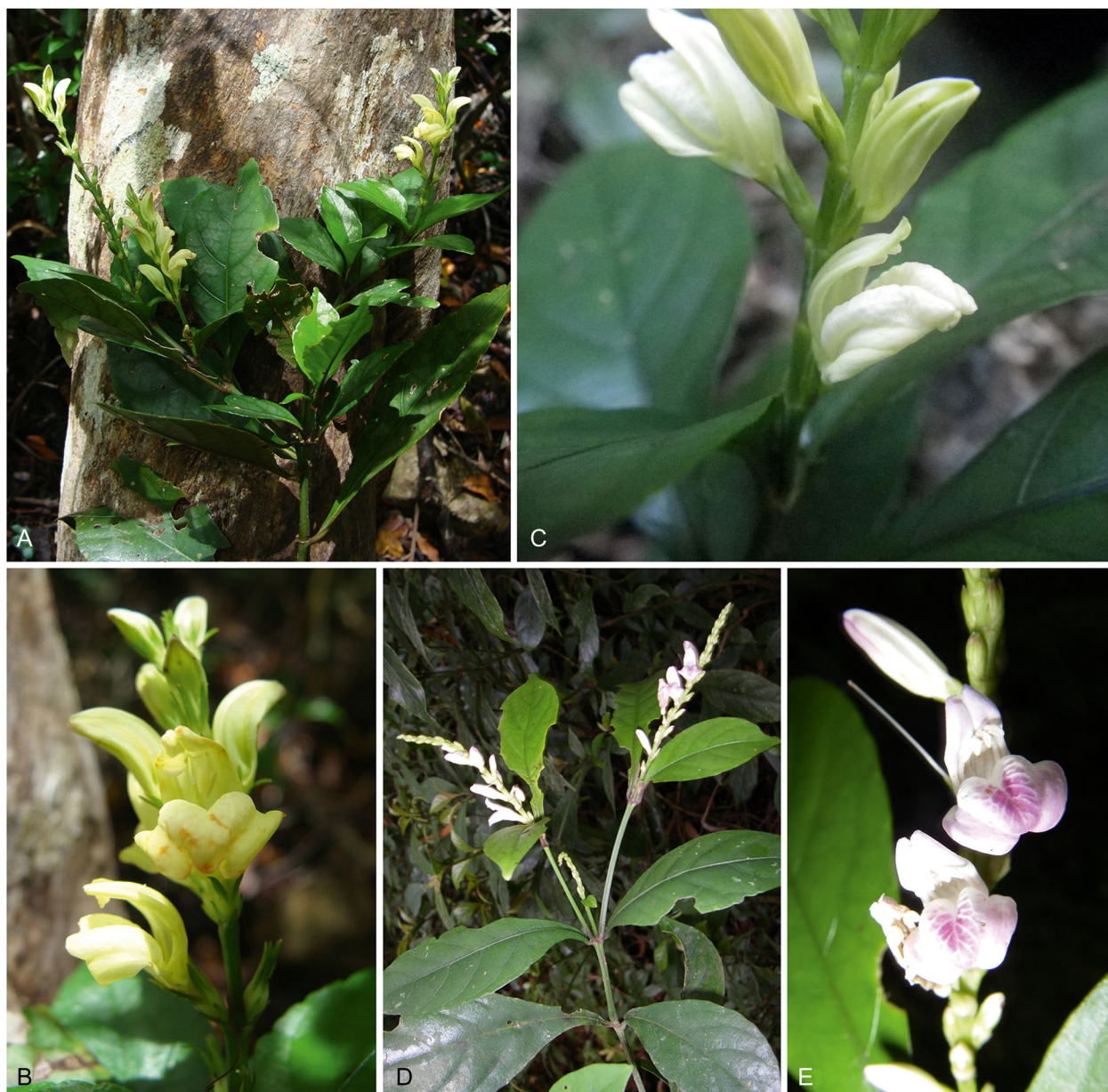


Fig. 4. *Isoglossa eburnea*. A & B forest around Anjahakely (*Burivalova* ZB 110); C Beanka (*Bolliger et al.* RFB 192); D & E Variant with pink tinge on lower lip; Binara forest (*Nusbaumer & Ranirison* LN 1734). PHOTOS: A & B Z. BURIVALOVA; C R. BOLLIGER; D & E L. NUSBAUMER. REPRODUCED WITH PERMISSION FROM CONSERVATOIRE ET JARDIN BOTANIQUES, GENÈVE.

specimens of this species, which help differentiate it from similar taxa in Madagascar.

NOTES. The combination of pale corollas with an arcuate upper lip and strongly raised and veined lower lip, the slender spiciform inflorescence with subsessile opposite flowers at each inflorescence node, and plants being largely glabrous readily separate this species from all other *Isoglossinae* on Madagascar. It is most likely to be confused with members of *Sphacanthus* but is easily separated by the characters listed in the Recognition section.

Although always pale, corolla colour is rather variable in this species (see Fig. 4). In *Burivalova* ZB 110 and *Bolliger et al.* RFB 192 the corollas are pale yellow to yellowish-green tinged and lack any pink colouring, whereas in *Nusbaumer & Ranirison* LN 1734 they are white with a pink flush on the lower lip. More collections are needed to see if discrete colour forms are recognisable that could be treated as separate taxa. Similar variation in flower colour has been encountered in some Neotropical *Justicia* species but, thus far, without molecular signal for separate taxa (C. A. Kiel, pers. obs.).

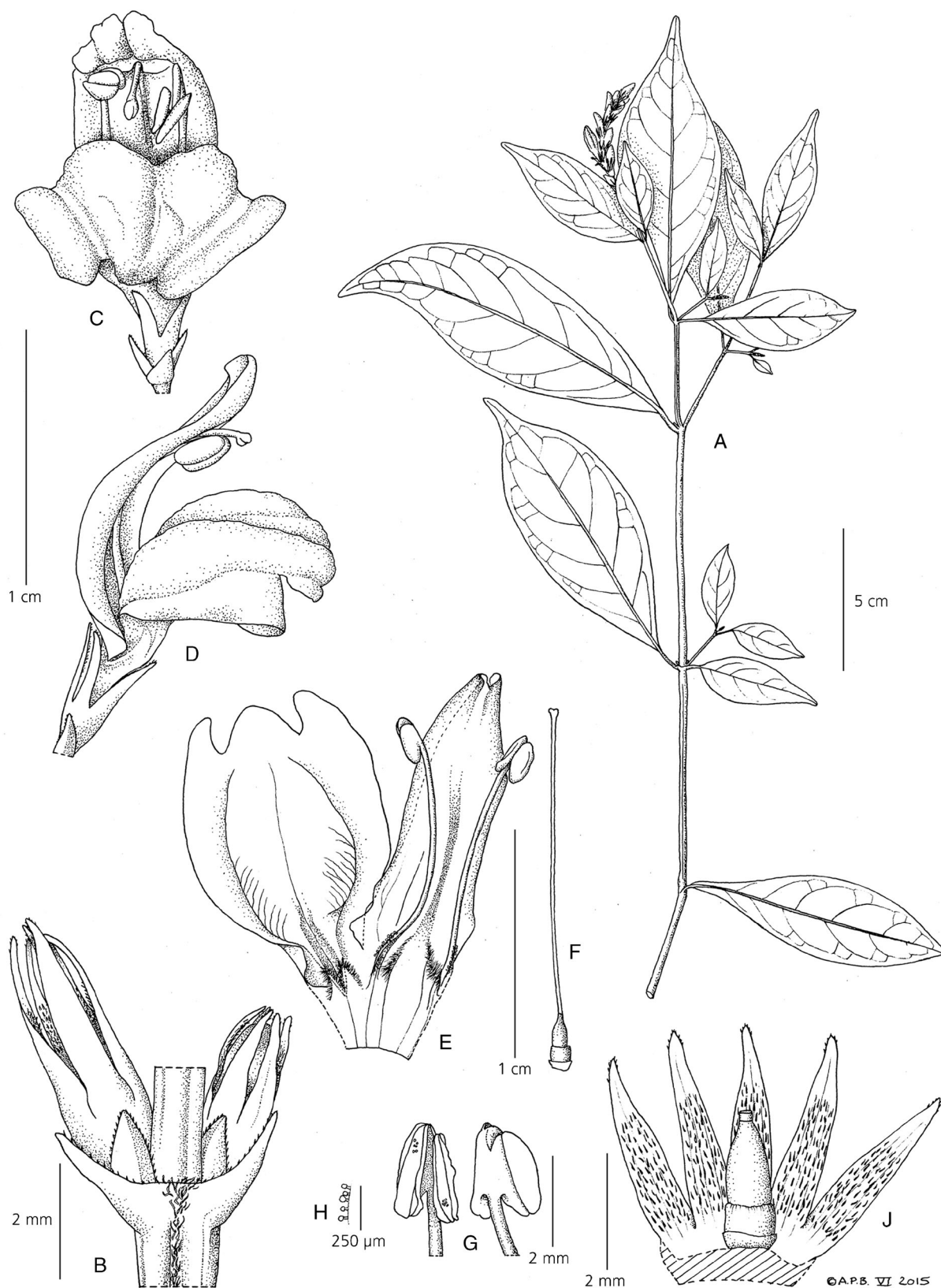


Fig. 5. *Isoglossa eburnea*. A habit with young inflorescence; B inflorescence node showing bracts, bracteoles and calyces; C flower, face view; D flower, lateral view; E dissected corolla with androecium; F pistil; G anthers in ventral and dorsal view; H details of glands on connective; J ovary within dissected calyx. A, B & J from Nusbaumer & Ranirison LN 1734; C & D from photographs of live plants; E – H from Ranirison & Nusbaumer PR 890. DRAWN BY ANDREW BROWN.

Isoglossa conocalyx *I. Darbysh. & Callm. sp. nov.* Type: Madagascar, Mahajanga, Betsiboka Region, Firingalava, fl. Feb. 1898, *Perrier de la Bâthie* 482 (holotype P! [P00089902]; isotypes P! [P00089903, P00089904]).

<http://www.ipni.org/urn:lsid:ipni.org:names:77307642-1>

Conocalyx laxus Benoist (1967: 534), nom. illegit. — see note.

Perennial herb or suffrutescent shrub, 30 – 100 cm tall, basal stems can be trailing and rooting; young stems subangular and with narrow, darker green furrows, with pale antrorse or mixed antrorse and retrorse hairs most dense or exclusively on two opposite sides, sometimes sparse or glabrescent; mature stems more terete and sometimes softly woody. *Leaves* green on both surfaces or drying greyish-green beneath, pairs anisophyllous, ovate, 2 – 9 × 1.2 – 3.7 cm, base asymmetric, rounded or obtuse in small-leaved plants but becoming more attenuate-cuneate in larger-leaved plants, margin subentire or obscurely crenate, apex (sub)attenuate; surfaces sparsely pubescent mainly on midrib, main veins beneath and sometimes on margin, or largely glabrous; cystoliths numerous, conspicuous, linear; lateral veins 3 – 6 pairs; petiole 4 – 24 mm long, antrorse-pubescent or sparsely so. *Inflorescences* axillary in the upper axils and also subterminal; cymes single-flowered, opposite or one per node; bracts foliaceous; bracteoles paired, usually lanceolate and falcate, 1.5 – 2.7 × 0.7 – 1 mm, midrib green, margins pale-hyaline, external surface sparsely puberulous on margin and midrib, rarely oblanceolate and up to 7.5 × 1.4 mm with a broader green area; pedicels 0.7 – 2 (– 6) mm long, glabrous. *Calyx* green, becoming paler at fruiting, appearing pale green in dry state due to dense cystoliths, 8 – 11.5 mm long, in bud curved and “beak-like” with the lobes appearing slightly winged, lobes straightening at anthesis; tube 1.5 – 3 mm long, lobes lanceolate, 5.5 – 10 × 1.8 – 3 mm, lobe margins paler in dry state, surfaces glabrous. *Corolla* (31 –) 52 – 58 mm long at maturity, white or limb pale pink to mauve, glabrous externally; tube (24 –) 42 – 43 mm long, narrowly cylindrical throughout, ± 2 mm wide, barely widened at mouth, presence of rugula unknown; upper lip (7 –) 10 – 16 mm long, oblong-lanceolate, curved at least when young, apex and margins slightly recurved, apex minutely 2-lobed; lower lip (7 –) 15 – 18.5 mm long, broadly obovate when flattened, palate with a markedly raised area and central depression leading into throat, glabrous, apex with 3 rounded lobes, the median lobe much broader than the lateral lobes. *Stamens* inserted near mouth of corolla tube; filaments ± 11 – 14.5 mm long, glabrous; anthers with thecae held at a ± equal height, slightly divergent (subsagittate), 2 – 3 mm long. *Ovary* dark

brown in dry state, ± 2.2 mm long, glabrous or with few short hairs at apex; style ± 39 – 48 mm long, glabrous; stigma capitate-bilobed, 0.7 – 1.1 mm diam. *Capsule* 9 – 12 mm long, base shortly stipitate, glabrous; seeds ± 3.1 × 2.3 mm, rugose-tuberculate. Fig. 6.

RECOGNITION. Differs from all other known species of *Isoglossa* in having the combination of a long, narrowly cylindrical corolla tube > 2 times longer than the limb; single-flowered axillary and subterminal cymes with a conspicuous calyx which is curved and “beak-like” in bud and has broadly lanceolate lobes 1.8 – 3 mm wide; and in the anthers having thecae held at a ± equal height and subsagittate.

DISTRIBUTION. This species is recorded from Western Madagascar. It occurs in Atsimo-Andrefana Region of Toliara Province, Betsiboka, Boeny and Melaky Regions of Mahajanga Province and just extends into Ihorombe Region of Fianarantsoa Province (Map 3).

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Tsingy de Namoroka (8e Réserve), fr., without date, *Service Forestier* 20 (G! [G00379543], K! [K001514182], P! [P03977294]); Firingalava, fl. Feb. 1898, *Perrier de la Bâthie* 482 (P! [P00089902, P00089903, P00089904]); Bois de KamaKama sur le causse d’Ankara, fl. Aug. 1901, *Perrier de la Bâthie* 9437 (P! [P00089905]); vallée du Fiherenana, près de Manera, fl. March 1934, *Humbert* 14199 (P! [P00089910, P00089911]); forêt de Zombitsy (Sakaraha), plateaux et vallées de l’Isalo a l’Ouest de Ranohira, haut vallée de la Malio, fl. 29 Jan. – 2 Feb. and 8 – 10 April 1955, *Humbert* 28671 (P! [P03977291, P00573478]); aux confins des bassins du Fiherenana et de l’Onilahy, fr. 26 – 29 March 1955, *Humbert et al.* 29601 (K! [K000379186, K000379187], MO* [MO-934623], P! [P00089912]); Sakaraha, fl. Feb. 1956, *Bosser* 9118 (K!, P! [P00089906, P03977296], WAG* [WAG1281292]), pro parte, mixed coll.; Antsingy, vers Andobo (E d’Antsalova), sentier vers l’est, fl. bud 5 – 8 Feb. 1960, *Leandri & Saboureau* 3033 (G! [G00379542], P! [P00089913], WAG* [WAG1281293]); Lambomakasadro, fl. Feb. 1962, *Bosser* 15755 (P! [P00089907]); Ankazoabo (Ouest), fl. Feb. 1963, *Bosser* 17331 (K!, P! [P00089908], WAG* [WAG1281291]); Forêt de Zombitsy, Sakaraha, fr. March 1964, *Bosser* 19323 (P! [P00089909]); Soalala, Andranomavo, Vilanandro, Ambatofolaka RN8, fl. 24 Feb. 1970, *Service Forestier* 26983 (P! [P03977302]); *idem*, fr. 25 March 1970, *Service Forestier* 26983 (P! [P03977303]); Tsaramasao, 20 km S of Sakaraha, fl. March 1970, *Morat* 3499 (P! [P03977297]); Forêt Besaka Zombitsy, 15 – 20 km E of Sakaraha, W of Tulear on route #7, fl. 4 Feb. 1975, *Croat* 30713 (P! [P03977295]); Mahajanga, Marovoay, near Ravelobe lake, fl. 27 Feb. 2013, *Rakotonasolo* RNF 2181 (K!, TAN).

HABITAT AND ECOLOGY. This species is recorded from the understorey of dry deciduous and semi-deciduous forest and moist woodland on sandy and alluvial soils,

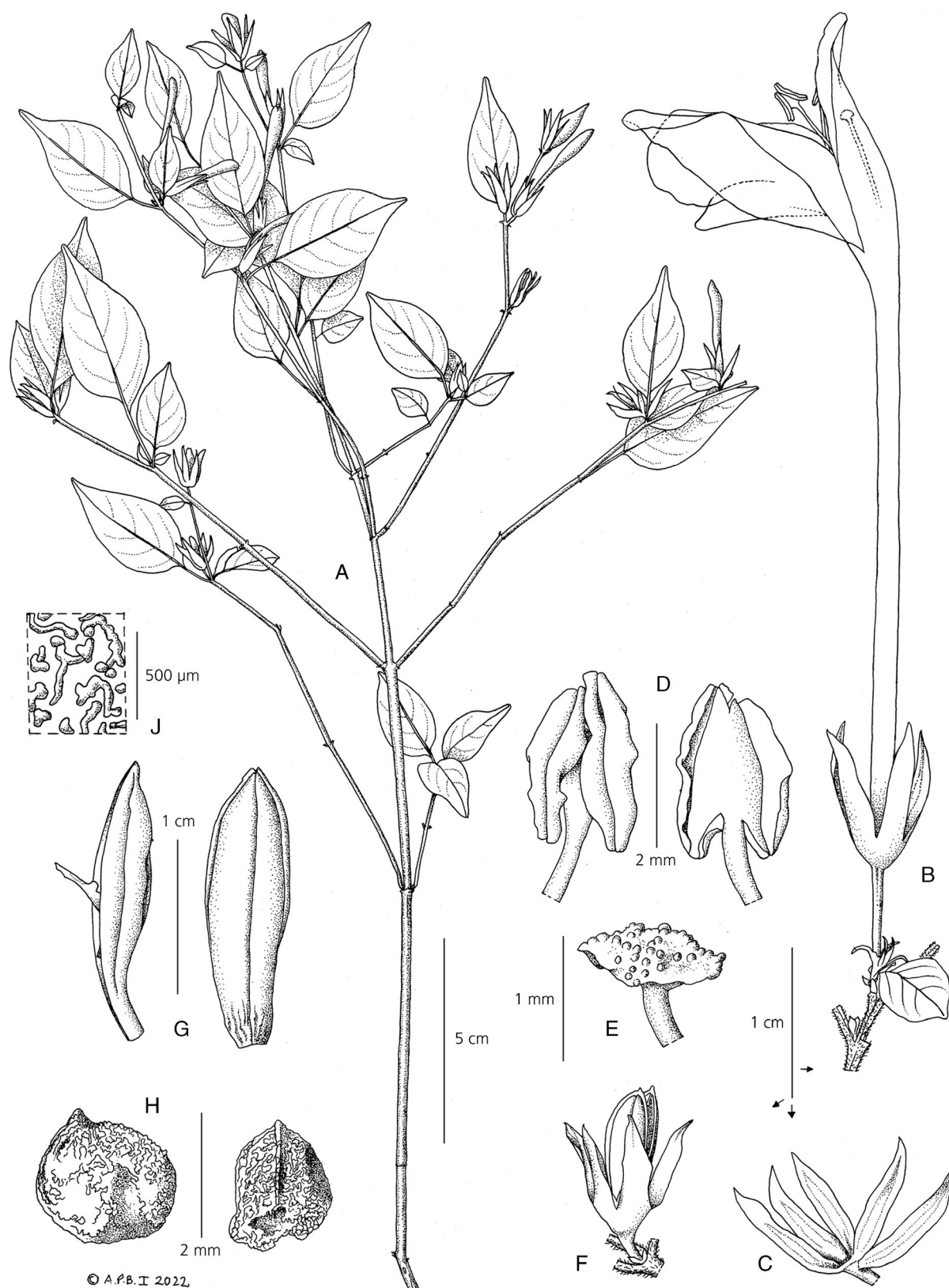


Fig. 6. *Isoglossa conocalyx*. A habit, with flowers in bud; B mature flower with subtending bract and bracteoles; C dissected calyx, inner surface; D anther, anterior and posterior views; E stigma; F capsule within calyx; G capsule valves, lateral and face views; H two immature seeds; J detail of sculpturing on seed surface. A from Bosser 9118; B & C from Rakotonasolo RNF 2181; D & E from Bosser 17731; F – J from Humbert 29601. DRAWN BY ANDREW BROWN.

and on calcareous substrates; 300 – 850 (– 1250) m elevation.

CONSERVATION STATUS. *Isoglossa conocalyx* has a wide geographic range in the form of an EOO of 125,545 km² and a minimum AOO of 56 km². It is known from an estimated thirteen threat-defined locations, six of which are encompassed in the Protected Area network (Ankarafantsika, Bemaraha, Isalo, Namoroka, Zombitse-Vohibasia). *Isoglossa conocalyx* is therefore assessed as of **Least Concern – LC**.

ETYMOLOGY. The epithet “*conocalyx*” is taken from the earlier generic name applied to this taxon by R. Benoist, and refers to the distinctive calyx which is connate in bud before splitting into lobes above a connate base.

NOTES. When describing *Conocalyx laxus*, Benoist (1967) listed four specimens (Perrier de la Bâthie 482 and 9437; Humbert 14199; Humbert *et al.* 29601) but did not select a type specimen from amongst these, thus the names of the genus and species were not validly published under Art. 40 of the Shenzhen Code (Turland *et al.* 2018). Rather than validate the genus here, it is considered more prudent to place this species under *Isoglossa* pending further molecular phylogenetic studies in Isoglossinae.

The corolla morphology, in which the tube is narrowly cylindrical throughout and markedly longer than the limb, is very distinctive in this species. In Madagascar, the only other *Isoglossa* with a long slender corolla tube is *I. longiflora* Benoist, but in that species the tube is gradually (though narrowly) widened upwards, the anthers have superposed, clearly separated thecae, the inflorescence is a lax, slender terminal panicle and the calyx lobes are linear-lanceolate; it could not be confused with *I. conocalyx*. The corolla morphology of *I. conocalyx* is similar to that of *I. hypoestiflora* Lindau and *I. cooperi* C.B. Clarke from South Africa, these two species having been placed in their own subgenus *Ramusia* by Clarke (1901). However, these two species differ from *I. conocalyx* in having, amongst other differences, anthers with almost superposed parallel thecae and a terminal, shortly spiciform inflorescence with subulate bracts.

Rakotonasolo RNF 2181 is unusual for this species in having long pedicels to 4 – 6 mm long; this specimen is also at the smallest end of the size range for plant height. However, it appears to be a good match for other material of *I. conocalyx*.

The gürtelpollen of this species is well illustrated by Muller *et al.* (1989); see their plates 182/XXVII and 182/XXIX. The holotype also includes an illustration of the pollen, presumably drawn by Benoist. Muller *et al.* (1989) treated the pollen of *Conocalyx* as a distinct type from that of *Isoglossa*, *Melittacanthus* and *Sphacanthus* but it is not clear on what grounds, as the illustrations of the pollen of *I. gracillima* Baker and *S. brillantaisia* in the same publication appear very similar to that of *I. conocalyx*, and the pollen of this

latter species is well within the variation recorded in *Isoglossa* s.l. (see, for example, Darbyshire *et al.* 2011).

***Isoglossa pterocalyx* I.Darbysh. & Phillipson sp. nov.**

Type: Madagascar, Antsiranana, DIANA, Diego-Suarez, Baie des Sakalaves, fl. 13 March 1988, Cheek *et al.* B1492 (holotype K sheet 1!; isotypes K sheet 2!, TAN).

<http://www.ipni.org/urn:lsid:ipni.org:names:77307656-1>

Isoglossa sp. B1492 *sensu* McDade *et al.* (2021).

Perennial herb or suffrutescent shrub, with scrambling or arching branches 100 – 200 cm tall; young stems slightly angular and with narrow furrows, with short pale antrorse and retrorse hairs mainly on two opposite sides, soon becoming sparse or glabrescent; mature stems more terete and can be woody, to 6 mm in diam. Leaves green above, grey-green beneath, pairs ± isophyllous, elliptic to broadly ovate-elliptic, 5 – 8 × 2.2 – 4.2 cm, base attenuate or cuneate, margin subentire, apex acuminate; upper surface glabrous, lower surface shortly antrorse-pubescent along main veins and margin; cystoliths numerous, conspicuous on upper leaf surface in dry state, linear to more dot-like; lateral veins 4 – 7 pairs, pale and prominent beneath in dry state, these and midrib occasionally purple beneath when fresh; petiole 9 – 24 mm long, antrorse-pubescent mainly on adaxial groove. Inflorescences axillary in the upper axils or together forming a loose, leafy terminal spike on main or short lateral branches; cymes 1 – 2 (– 3)-flowered; bracts as leaves at lower fertile nodes but ± reducing in size in the distal portion of the stems and becoming more elliptic or suborbicular with attenuate or obtuse apex, then typically 6 – 28 × 3 – 23 mm; cymes sessile or with a peduncle up to 3.5 mm long; bracteoles paired, foliaceous, held close to the pedicel, ovate to elliptic, often slightly asymmetric, (4 –) 6.5 – 16 × (2.8 –) 3.5 – 8.5 mm, puberulous mainly on margin or glabrous; pedicels (1.2 –) 4.5 – 12.5 (– 17.5) mm long, sometimes curved towards apex and attached to calyx at an oblique angle, pale retrorse-puberulous. Calyx pale bright green in fresh state, appearing glaucous-green in dry state due to dense cystoliths, markedly tubular and saccate towards the rounded base, somewhat curved and beak-like in bud, mature calyx 15 – 23.5 mm long, each lobe lanceolate, 3 – 5 mm wide but concave, the fused edges of the lobes forming wings, lobe fusion varying in length (the sinus between the lateral and anterior pairs of lobes often deeper) but at least some lobes fused for (4.5 –) 6 – 13.5 mm, lobe margins and fusion lines paler in dry state, lobe apices acute or attenuate, usually brown at tip, surfaces largely glabrous except for few short fine hairs along

lobe margins. *Corolla* 38 – 43 mm long, base of tube and throat greenish-white, lips purple to lavender-pink, glabrous externally except for few inconspicuous hairs towards apex of median lobe of lower lip; tube 24 – 26 mm long, with basal cylindrical portion 9 – 11 mm long and markedly funnel-shaped throat, somewhat dorso-ventrally compressed, dorsal side with shallow rugula extending onto upper lip, white-villose at base of rugula which starts $\pm$ at the point of expansion into the throat; upper lip 10 – 12 mm long, somewhat recurved with reflexed apices and margins, broadly triangular when flattened, apex with two rounded lobes $\pm$ 4 mm long; lower lip 12.5 – 16 mm long, broadly elliptic when flattened, palate with a markedly raised area and central depression leading into throat, glabrous, apex with 3 broadly rounded lobes. *Stamens* inserted $\pm$ 14 mm from base of corolla tube; filaments $\pm$ 11 – 12 mm long, glabrous; anthers white, with thecae held at an equal height, parallel or divergent towards base (subsagittate), 2.5 – 3.5 mm long. *Ovary* black, $\pm$ 2.5 mm long, glabrous; style $\pm$ 27 mm long, glabrous; stigma white, shallowly bilobed. *Capsule* largely hidden within persistent calyx, 12.5 – 13.5 mm long, base shortly stipitate, glabrous; only immature seeds seen, irregularly tuberculate particularly towards the rim. Figs 7 & 8.

RECOGNITION. Differs from *Isoglossa conocalyx* in having a markedly different corolla form, the tube being broadly infundibuliform with the expanded throat longer than the basal cylindrical portion (vs corolla tube narrowly cylindrical throughout with only a very short expanded throat); in the calyx being larger, 15 – 23.5 mm long and with a longer fused portion, at least some lobes being fused for (4.5 –) 6 – 13.5 mm (vs calyx 8 – 11.5 mm long and with fused portion 1.5 – 3 mm long); in the pedicels being retrorse-puberulous (vs glabrous); in the bracteoles being green, ovate or elliptic, (4 –) 6.5 – 16 mm long, asymmetric but not falcate (vs pale-hyaline except for darker midrib, lanceolate or rarely oblanceolate, 1.5 – 2.7 (– 7.5) mm long, often falcate); and in the leaves being $\pm$ isophyllous (vs anisophyllous in *I. conocalyx*).

DISTRIBUTION. This species is confined to DIANA Region in the northern portion of Antsiranana Province (Map 3).

ADDITIONAL SPECIMENS EXAMINED. MADAGASCAR. Antsiranana, Diego-Suarez, forêt d'Orangea, fl. 22 Jan. 1960, *Cours & Humbert* 5389 (P! [P00853289]); *idem*, *Humbert* 32296 (P! [P00853290]); Diégo-Suarez, Orangéa, fl. 16 April 1970, *Bosser* 20200 (G [G00379541], P! [P00853288]); forêt de Orangea, along path E of entrance to military camp, fl. 17 Jan. 2003, *Miller* 10661 (MO [MO-2974310], P! [P01069699]); Ramena, Baie des Sakalava, 5 km E d'Ankorikahely, fl. & fr. 15 Aug. 2004, *Be et al.* 73 (CNARP, K!, MO [MO-2974011], P! [P00853291],

TAN); Andrafiabe, presqu'île entre Ambolobozobe et Ambolobozokely, fl. 9 Feb. 2005, *Ratovoison et al.* 972 (CNARP, K!, MO [MO-1059806], TAN); Orangea, Ramena, fl. & fr. 12 Feb. 2005, *Schatz et al.* 4222 (MO! [MO-1441587], P! [P00853292]); Diego II, Ramena, Ankorikahely, NAP Oranjia, fl. 17 Feb. 2015, *Andriamiharimanana et al.* 12 (K!, MO!, P!, TAN!).

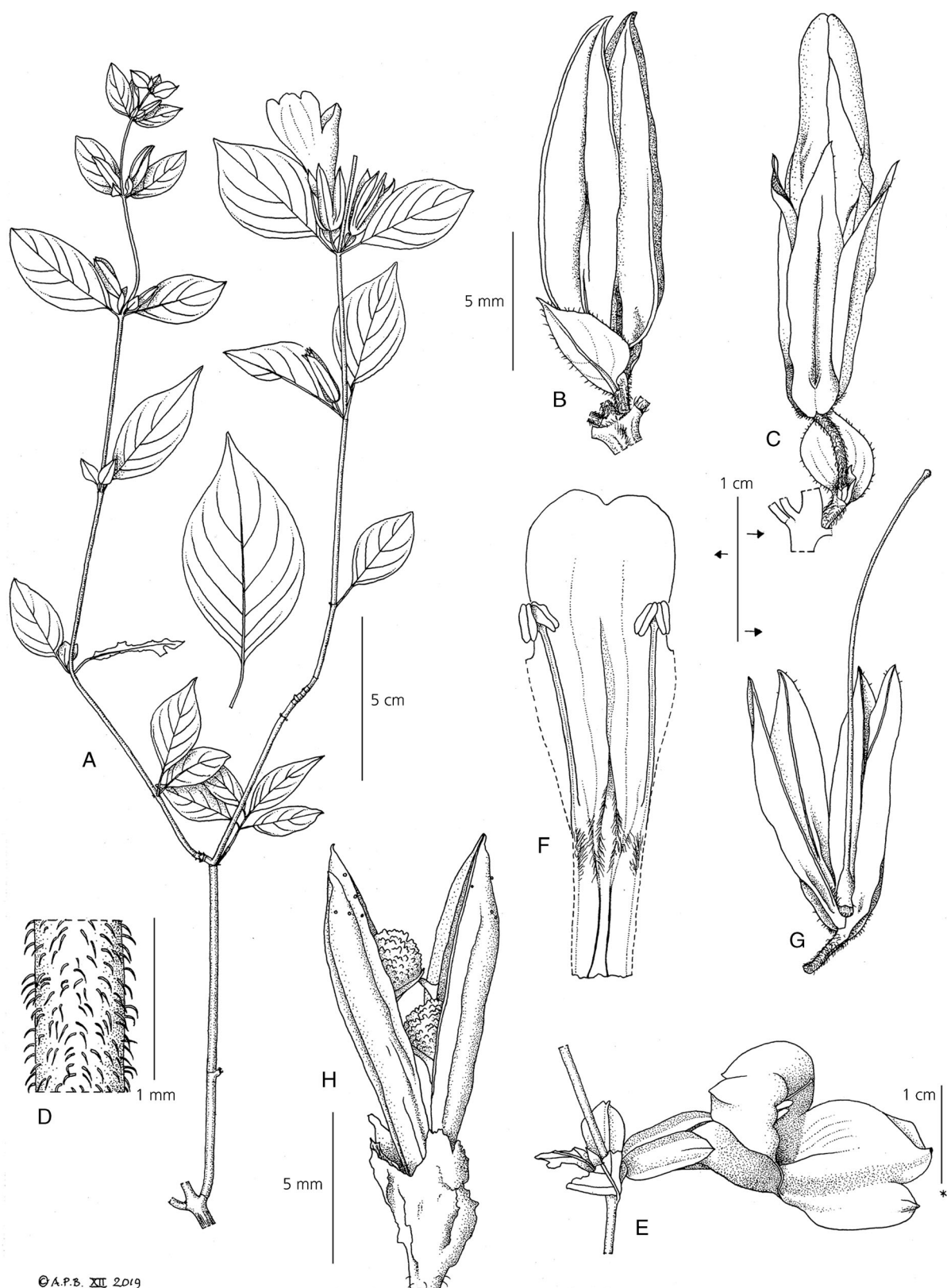
HABITAT AND ECOLOGY. This species is recorded from dry deciduous coastal forest including heavily degraded forest areas and in coastal thicket, on sandy soils at or near to sea level.

CONSERVATION STATUS. *Isoglossa pterocalyx* has a very narrow geographic range in the form of an EOO of 41 km² and a minimum AOO of 20 km². It is known from nine collections but only up to four localities in littoral forest and thicket along the far north east coast of Madagascar, three of which are encompassed in the Protected Area of Oranjia. Therefore, two threat-defined locations are recognised for this species. Littoral forests in Madagascar are threatened by deforestation (Consiglio *et al.* 2006). Outside of the Oranjia protected area (and possibly also within it), it is threatened by fire, forest clearing for agriculture and grazing resulting in continuing decline. *Isoglossa pterocalyx* can therefore be assessed as **Endangered – EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)**.

ETYMOLOGY. The epithet “*pterocalyx*” refers to the calyx which appears winged in this species due to the broad abutting lobes, an unusual character in *Isoglossa*.

NOTES. The affinity of this species must lie with the former genus *Conocalyx* Benoist (nom. illegit.), here transferred to *Isoglossa*. It shares with *I. conocalyx* the same inflorescence type of usually single-flowered axillary cymes in the distal portion of the stems, the flowers clearly pedicellate and with an enlarged calyx which is “beak-like” in bud and has a conspicuous fused portion and broad lobes that have pale margins and fusion lines. However, these two species are otherwise very different, not least in the corolla morphology, with *I. pterocalyx* having a broadly infundibuliform corolla tube and large lips whilst *I. conocalyx* has a very narrow long-cylindrical corolla, barely expanded in the throat and with only small lips. The other differences are highlighted in the Recognition section above. In the phylogenetic study of McDade *et al.* (2021), this species was placed in a clade with *Melittacanthus divaricatus* and *I. conocalyx* but with low support. It is similar to *M. divaricatus* in corolla morphology (see Fig. 2) but differs in having solitary or laxly spaced, single-flowered cymes (rather than in having fascicles of flowers) and larger and more saccate, winged calyces.

***Isoglossa pseudoanisotes* I.Darbysh. sp. nov.** Type: Madagascar, Antsiranana, Ankarana, road towards Lac Vert, 82 m elev., fl. & fr. 26 May 1999, *De Block*,



© A.P.S. XII 2019

Fig. 7. *Isoglossa pterocalyx*. A habit; B single-flowered cyme showing calyx and bracteoles, pictured upright; C flower bud pictured upright, one bracteole removed so that pedicel is visible; D detail of indumentum on pedicel; E open flower in situ; F portion of dissected flower showing dorsal side of tube, upper lip and androecium; G calyx partially dissected to show pistil; H capsule with remains of calyx. A & B from Schatz *et al.* 4222; C, D & G from Cheek *et al.* B1492; E from photograph of live plant by G. Schatz; H from Be *et al.* 73. DRAWN BY ANDREW BROWN.



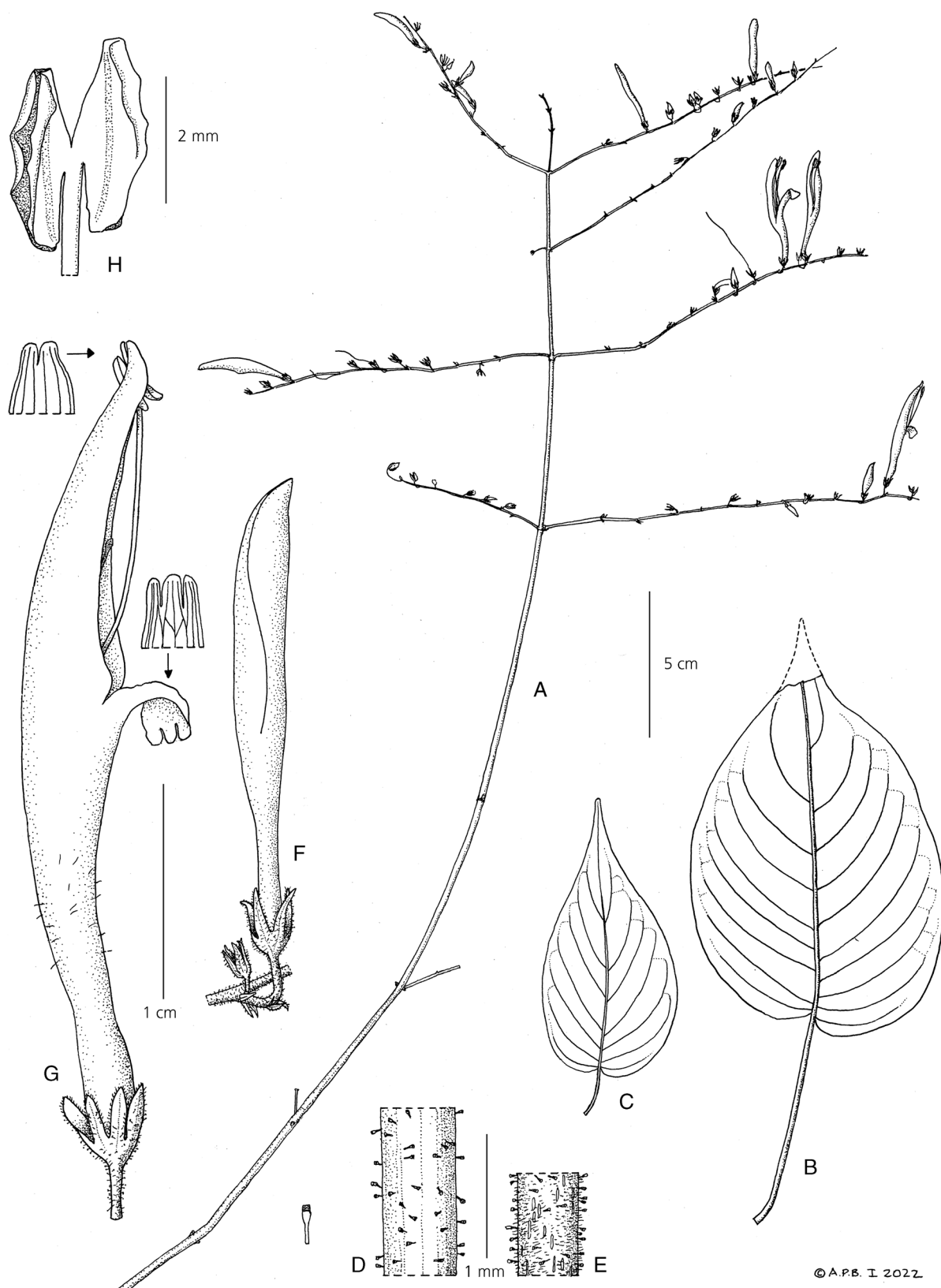
Fig. 8. *Isoglossa pterocalyx*. A and C NAP Oronjia (*Andriamiharimanana et al.* 12); B Orangea [Oronjia], Ramena (*Schatz et al.* 4222). PHOTOS: A & C FIDY RATOVOSON, B GEORGE SCHATZ.

Rapanarivo & Randriamboavonjy 1022 (holotype K!; isotypes BR! [BR00000908784; spirit collection 6102012542296], MO, TAN).

<http://www.ipni.org/urn:lsid:ipni.org:names:77307658-1>

Isoglossa sp. 1022 *sensu* McDade *et al.* (2021).

Shrub $\pm$ 125 cm tall; stems dark green tinged red/purple, drying glaucous-green, at first subangular, darker along the angles, becoming more terete below, glabrous. *Leaves* pale green with main veins tinged reddish, somewhat paler beneath and with main veins tinged dark red/purple, ovate, c. 13.5 – 15 $\times$ 6.7 – 9 cm when mature, base shallowly cordate, asymmetric, margin subentire, apex acuminate; upper surface antrorse-pubescent mainly on midrib, lateral veins and margin, sparsely so elsewhere, lower surface largely glabrous except few hairs along midrib; cystoliths dense, conspicuous; lateral veins c. 9 – 11 pairs; petiole dark red/purple, drying glaucous-green, 67 – 92 mm long on mature leaves, antrorse-pubescent in the groove above. *Inflorescences* terminal, a lax panicle of spikes, internodes of central axis 28 – 60 mm long, the lateral spiciform branches held $\pm$ patent to the central axis, proximal branches sometimes secondarily patent-branched, branches to 13.5 cm long, lax, internodes between flowers typically 7 – 9 mm long, each node 1- or 2-flowered, rachis glandular-puberulous, hairs to c. 0.2 mm long, becoming mixed glandular- and eglandular-puberulous distally; bracts subtending inflorescence branches early-caducous, not seen; bracts at flowering nodes minute, triangular-ensiform, green, 0.9 – 1.2 $\times$ 0.5 – 0.7 mm; bracteoles as bracts but slightly smaller and narrower; pedicels conspicuous, 2.5 – 3.5 mm long, indumentum as on inflorescence branches. *Calyx* dark green, margin narrowly paler in dry state, tube 0.8 – 1.1 mm long, lobes equal, lanceolate, 2.3 – 3.1 $\times$ 0.5 – 0.75 mm, external surface glandular- and eglandular-puberulous, eglandular hairs most numerous along lobe margins. *Corolla* 36 – 40 mm long in situ, tube white, lobes white tinged purplish-red in distal half both internally and externally, glabrous externally; tube 22 – 23 mm long, slightly sigmoid shaped, gradually expanded in the distal half, basal portion 2.3 – 2.7 mm wide, mouth 4.5 – 5 mm wide, internal surface puberulous particularly in proximal half, rugula absent; upper lip hooded, triangular-lanceolate when flattened, 17 – 17.5 mm long, apex minutely 2-lobed for $\pm$ 0.5 mm; lower lip strap-shaped, tightly recoiled at anthesis, $\pm$ 16.5 $\times$ 3.7 mm when flattened, apex minutely 3-lobed for $\pm$ 1.2 mm, palate lacking “herring-bone” venation. *Stamens* inserted $\pm$ 7.5 mm below mouth of corolla, white; filaments 15.5 – 21 mm long, glabrous; anthers with thecae only slightly offset, parallel or slightly oblique, elliptic, $\pm$



© A.P.B. I 2022

Fig. 9. *Isoglossa pseudoanisotes*. A inflorescence; B mature leaf (apex reconstructed); C young leaf; D inflorescence indumentum, at base of branch, with sketch of one glandular hair; E inflorescence indumentum at mid-branch; F cyme unit with flower bud; G flower with corolla at anthesis, with detail of apices of upper and lower lips; H anther. All from de Block et al. 1022. DRAWN BY ANDREW BROWN.

2.6 – 3.2 mm long. *Ovary* dark brown when dry, $\pm$ 2.3 mm long, glabrous; style white, drying brown, 34 – 37 mm long, glabrous; stigma purplish, with two lobes 0.25 – 0.3 mm long. *Capsule* only seen in immature state, $\pm$ 14.5 mm long, glabrous. Fig. 9.

RECOGNITION. Resembles *Isoglossa perplexa* in corolla shape and size but otherwise differing markedly in, for example, having ovate leaves, 6.7 – 9 cm wide, length: width ratio 1.6 – 2: 1, with a shallowly cordate base and a long petiole up to 92 mm (vs leaves lanceolate to narrowly elliptic, < 3 cm wide with length: width ratio 4.2 – 7.8: 1, base cuneate to attenuate and petiole short, to 15 mm long); minute triangular-ensiform floral bracts up to 1.2×0.7 mm and lacking ciliate margins (vs floral bracts conspicuous, ovate-, elliptic- or obovate-acuminate, (5 –) 7 – 11 $\times$ 3 – 6 mm, margins ciliate); flowers pedicellate for 2.5 – 3.8 mm (vs sessile); flowering branches, pedicels and calyces being mixed glandular- and eglandular-puberulous (vs antrorse-pubescent); calyces smaller, lobes lanceolate, 2.3 – 3.1 mm long (vs lobes linear-lanceolate, 4 – 7 mm long); and corollas white, the lobes tinged purplish-red distally, glabrous externally (vs corolla lemon-yellow with darker yellow to red or orange-veined upper lip, puberulous externally).

DISTRIBUTION. *Isoglossa pseudoanisotes* is known only from the type collection from northern Madagascar in DIANA Region of Antsiranana Province (Map 2).

HABITAT AND ECOLOGY. The type collection was recorded from dry semi-deciduous forest with a canopy of 10 – 12 m and emergent trees to 25 m tall, on limestone tsingy; 82 m elevation.

CONSERVATION STATUS. *Isoglossa pseudoanisotes* is known only from a single location in the historically well collected Ankarana Special Reserve. Despite its long-established protection in 1956, the Reserve lost nearly 20% of its dry deciduous forests and 85% of its moist evergreen forest from 1996 to 2016 (Goodman *et al.* 2018). Since 2000, the threat is mainly due to sapphire mining and demand from wood products (Goodman *et al.* 2018). Due to its highly restricted geographic range and threats, *I. pseudoanisotes* is assessed as **Critically Endangered – CR 2ab(i,ii,iii,iv,v)**.

ETYMOLOGY. The epithet “*pseudoanisotes*” refers to the fact that this species could be mistaken for the genus *Anisotes* on the basis of the corolla morphology.

NOTES. The floral form of this highly distinctive new species is similar to that of *Isoglossa perplexa* in having long, narrow lips, the lower lip being strap-shaped and recoiled at anthesis (see notes under that species above). However, these two species are otherwise very different in a wide range of characters, the most obvious of which are provided in the Recognition section above; some of the measurements and observations for *I. perplexa* are taken from Daniel *et al.* (2013). In addition, *I. perplexa* is a species of upland moist forest, whereas *I. pseudoanisotes* is found in low-

elevation dry forest. It is notable that these species are resolved with reasonable support as sister species in the molecular phylogeny of McDade *et al.* (2021). They are the only two species in *Isoglossa s.l.* to have this *Anisotes*-like corolla morphology.

Acknowledgements

We are highly grateful to the curators of the herbaria we consulted during this study, most notably at BM, BR, G, K, and P. We thank Andrew Brown for the illustrations of the new species, and David Scherberich, Harithi Assame Madjid, Fidy Ratovoson, George Schatz, Zuzana Burivalova, Ralph Bolliger, Louis Nusbaumer and the Conservatoire et Jardin Botaniques, Genève for permission to reproduce their field photographs of species pertaining to this study. Franck Rakotonasolo of the Kew Madagascar Conservation Centre and Petra de Block of the Botanic Garden Meise are thanked for helpful correspondence regarding their collections relevant to this study.

Declarations

Conflicts of interests/competing interests. The authors declare no conflicts of interest / competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Bachman, S., Moat, J., Hill, A. W., de la Torre, J. & Scott, B. (2011). Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117 – 126. <https://doi.org/10.3897/zookeys.150.2109>
- Balkwill, K., Sebola, R. J. & Poriazis, D. L. (2017). Taxonomic revision of white-flowered *Isoglossa* Oerst. (Acanthaceae) in southern Africa. *S. African*

- J. Bot.* 108: 48 – 80. <https://doi.org/10.1016/j.sajb.2016.09.013>
- & Welman, W. G. (2000). Acanthaceae, pp. 34 – 45. In: O. A. Leistner (ed.), *Seed plants of southern Africa: families and genera. Strelitzia* 10. National Botanical Institute, Pretoria.
- Benoist, R. (1939). Nouvelles Acanthacées malgaches. *Notul. Syst. (Paris)* 8: 135 – 161.
- (1945). Description de nouvelles Acanthacées malgaches. *Notul. Syst. (Paris)* 12: 4 – 16.
- (1947). Contribution à la connaissance des *Justicia* de Madagascar. *Notul. Syst. (Paris)* 13: 118 – 131.
- (1962). Nouvelles Acanthacées de Madagascar. *Bull. Soc. Bot. France* 109: 129 – 135. <https://doi.org/10.1080/00378941.1962.10835351>
- (1964). Contribution à la connaissance des Acanthacées malgaches. *Bull. Soc. Bot. France* 110: 397 – 404. <https://doi.org/10.1080/00378941.1963.10835411>
- (1967). Contribution à la connaissance des Acanthacées malgaches. *Bull. Soc. Bot. France* 113: 531 – 536 [1966, publ. June 1967]. <https://doi.org/10.1080/00378941.1966.10835562>
- Brummitt, R. K. (1985). Additions to the tropical African species of *Isoglossa* (Acanthaceae). *Kew Bull.* 40: 785 – 791. <https://doi.org/10.2307/4109860>
- & Feika, A. M. B. (1978). Two new species of *Isoglossa* (Acanthaceae) from Malaŵi and Zambia. *Kew Bull.* 32: 595 – 599. <https://doi.org/10.2307/4109665>
- Champluvier, D. & Darbyshire, I. (2009). A revision of the genera *Brachystephanus* and *Oreacanthus* (Acanthaceae) in tropical Africa. *Syst. Geogr. Pl.* 79: 115 – 192.
- & Fischer, E. (2020). *Isoglossa darbyshirei* (Acanthaceae), a new plietesial species from the Albertine Rift (Rwanda, Burundi). *Phytotaxa* 438: 276 – 288. <https://doi.org/10.11646/phytotaxa.438.5.1>
- Cheek, M., Nic Lughadha, E., Kirk, P., Lindon, H., Carretero, J., Looney, B., Douglas, B., Haelewaters, D., Gaya, E., Llewellyn, T., Ainsworth, A. M., Gafforov, Y., Hyde, K., Crous, P., Hughes, M., Walker, B. E., Campostrini Forzza, R., Khoon Meng Wong & Niskanen, T. (2020). New scientific discoveries: Plants and fungi. *Plants, People, Planet* 2: 371 – 388. <https://doi.org/10.1002/ppp3.10148>
- Clarke, C. B. (1901). *Isoglossa*. In: W. T. Thiselton-Dyer (ed.), *Flora Capensis*. Vol. 5 (Pt. 1): 79 – 84. L. Reeve & Co., London.
- Comito, R., Darbyshire, I., Kiel, C., McDade, L. & Fisher, A. E. (2022). A RADseq phylogeny of *Barleria* (Acanthaceae) resolves fine-scale relationships. *Molec. Phylogenet. Evol.* 169: 107428. <https://doi.org/10.1016/j.ympev.2022.107428>
- Consiglio, T., Schatz, G. E., McPherson, G., Lowry, P. P., Rabenantoandro, J., Rogers, Z. S., Rabevohitra, R. & Rabehevitra, D. (2006). Deforestation and plant diversity of Madagascar's littoral forests. *Conserv. Biol.* 20: 1799 – 1803. <https://doi.org/10.1111/j.1523-1739.2006.00562.x>
- Daniel, T. F. (1999). Revision of *Stenostephanus* (Acanthaceae) in Mexico. *Contr. Univ. Michigan Herb.* 22: 47 – 93.
- , McDade, L. A., Manktelow, M. & Kiel, C. A. (2008). The “*Tetramerium* Lineage” (Acanthaceae: Acanthoideae: Justicieae): delimitation and intra-lineage relationships based on cp and nrITS sequence data. *Syst. Bot.* 33: 416 – 436. <https://doi.org/10.1600/036364408784571581>
- , Letsara, R. & Martín-Bravo, S. (2013). Four new species of *Anisotes* (Acanthaceae) from Madagascar. *Novon* 22: 396 – 408. <https://doi.org/10.3417/2012054>
- Darbyshire, I. (2008). Notes on the genus *Dicliptera* (Acanthaceae) in Eastern Africa. *Kew Bull.* 63: 361 – 383. <https://doi.org/10.1007/s12225-008-9053-7>
- (2009). Taxonomic notes and novelties in the genus *Isoglossa* (Acanthaceae) from East Africa. *Kew Bull.* 64: 401 – 427. <https://doi.org/10.1007/s12225-009-9123-5>
- , Kiel, C. A., Astroth, C. M., Dexter, K. G., Chase, F. M. & Tripp, E. A. (2020). Phylogenomic study of *Monechma* reveals two divergent plant lineages of ecological importance in the African savanna and succulent biomes. *Diversity* 12, 237: 1 – 26. <https://doi.org/10.3390/d12060237>
- , Pearce, L. & Banks, H. (2011). The genus *Isoglossa* (Acanthaceae) in west Africa. *Kew Bull.* 66: 425 – 439. <https://doi.org/10.1007/s12225-011-9292-x>
- Faranirina, L. & Rabarimanarivo, M. (2019). *Melittacanthus divaricatus*. The IUCN Red List of Threatened Species 2019: e.T102820542A102820550. <https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T102820542A102820550.en>
- Gautier, L. (2002). Liste commentée des phanérogames de la Réserve Spéciale de Manongarivo, Madagascar. *Boissiera* 59: 105 – 239.
- Goodman, S. M., Raherilalao, M. J. & Wohlhauser, S. [eds] (2018). *The terrestrial protected areas of Madagascar: their history, description, and biota*. Vol. 2. Association Vahatra, Antananarivo.
- Grall, A. & Darbyshire, I. (2021). A synopsis of the African genus *Whitfieldia* (Acanthaceae: Whitfieldieae) and a key to the species. *Kew Bull.* 76: 191 – 221. <https://doi.org/10.1007/s12225-021-09941-8>
- IUCN (2012). *IUCN Red List Categories and Criteria*. Version 3.1. Second Edition. IUCN Species Survival Commission, Gland & Cambridge.
- IUCN Standards and Petitions Subcommittee (2019). *Guidelines for Using the IUCN Red List Categories and Criteria*. Version 14. Prepared by the Standards and Petitions Subcommittee. Available at: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>. [Accessed Jan. 2022]

- Kiel, C. A., Daniel, T. F., Darbyshire, I. & McDade, L. A. (2017). Unraveling relationships in the morphologically diverse and taxonomically challenging “justicioid” lineage (Acanthaceae: Justicieae). *Taxon* 66: 645 – 674. <https://doi.org/10.12705/663.8>
- _____, McDade, L. A., Daniel, T. F. & Champluvier, D. (2006). Phylogenetic delimitation of Isoglossinae (Acanthaceae: Justicieae) and relationships among constituent genera. *Taxon* 55: 683 – 694. <https://doi.org/10.2307/25065644>
- Madagascar Catalogue (2022). *Catalogue of the plants of Madagascar*. Missouri Botanical Garden, St. Louis & Antananarivo. Available at: <http://legacy.tropicos.org/Project/Madagascar>. [Accessed Jan. 2022]
- Manktelow, M., McDade, L. A., Oxelman, B., Furness, C. A. & Balkwill, M.-J. (2001). The enigmatic Tribe Whitfieldieae (Acanthaceae): delimitation and phylogenetic relationships based on molecular and morphological data. *Syst. Bot.* 26: 104 – 119.
- Manzitto-Tripp, E. A., Darbyshire, I., Daniel, T. F., Kiel, C. A. & McDade, L. A. (2021). Revised classification of Acanthaceae and worldwide dichotomous keys. *Taxon* 71: 103 – 153. <https://doi.org/10.1002/tax.12600>
- McDade, L. A., Daniel, T. F. & Kiel, C. A. (2008). Toward a comprehensive understanding of phylogenetic relationships among lineages of Acanthaceae s.l. (Lamiales). *Amer. J. Bot.* 95: 1136 – 1152. <https://doi.org/10.3732/ajb.0800096>
- _____, _____ & _____ (2018). The *Tetramerium* lineage (Acanthaceae, Justicieae) revisited: phylogenetic relationships reveal polyphyly of many New World genera accompanied by rampant evolution of floral morphology. *Syst. Bot.* 43: 97 – 116. <https://doi.org/10.1600/036364418X697003>
- _____, Kiel, C. A., Daniel, T. F. & Darbyshire, I. (2021). Justicieae II: Resolved placement of many genera and recognition of a new lineage sister to Isoglossinae. *Aliso* 38 (1): Article 2, 1 – 31. <https://doi.org/10.5642/aliso.20213801.02>
- Mildbraed, J. (1934). Neue und seltene Arten aus Ostafrika (Tanganyika-Territ. Mandat) leg. H.J. Schlieben, VI. *Notizbl. Bot. Gart. Berlin-Dahlem* 12: 79 – 108.
- _____. (1937). Neue und seltene Acanthaceen aus dem oestlichen Belgischen Kongo. *Bull. Jard. Bot. État Bruxelles* 14: 353 – 361. <https://doi.org/10.2307/3666567>
- Moat, J. & Smith, P. (eds) (2007). *Atlas of the vegetation of Madagascar / Atlas de la vegetation de Madagascar*. Royal Botanic Gardens, Kew.
- Moore, S. le M. (1906). *Alabastra Diversa*, Part XIII. Sertulum Mascarense. *J. Bot.* 44: 217 – 224.
- Muller, J., Schuller, M., Straka, H. & Friedrich, B. (1989). Palynologia Madagassica et Mascarenica. Familien 182: Acanthaceae. *Trop. Subtrop. Pflanzenwelt* 67: 138 – 187.
- Onjalalaina, G. E. & Darbyshire, I. (2016). An endangered new species of *Podorungia* (Acanthaceae), with notes on the tribe Barlerieae in Madagascar. *Kew Bull.* 71: 44 (7 pages). <https://doi.org/10.1007/s12225-016-9657-2>
- Phillipson, P. B., Andriamahefarivo, L., Callmander, M. W., Daniel, T. F., Darbyshire, I., Kiel, C. A., Letsara, R., McDade, L. & Manzitto-Tripp, E. (in press). Acanthaceae. In: S. M. Goodman (ed.), *The New Natural History of Madagascar*. Princeton University Press.
- Tripp, E. A., Tsai, Y. E., Zhuang, Y. & Dexter, K. G. (2017). RADseq dataset with 90% missing data fully resolves recent radiation of *Petalidium* (Acanthaceae) in the ultra-arid deserts of Namibia. *Ecol. Evol.* 7: 7920 – 7936. <https://doi.org/10.1002/ece3.3274>
- Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W. H., Li, D. Z., Marhold, K. & May, T. W. (eds) (2018). International Code of Nomenclature for algae, fungi, and Plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Veg.* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- Wood, J. R. I. (2019a). *Stenostephanus* (Acanthaceae) in Peru. *Kew Bull.* 74: 64 (24 pages) <https://doi.org/10.1007/s12225-019-9843-0>
- _____. (2019b). A synopsis of *Stenostephanus* Nees (Acanthaceae) in Bolivia. *Kew Bull.* 74: 65 (13 pages). <https://doi.org/10.1007/s12225-019-9844-z>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.