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Two new genera of Acanthaceae from tropical Africa

Iain Darbyshire[1], Carrie A. Kiel[2], Thomas F. Daniel[3], Lucinda A. McDade[2] & W. R. Quentin Luke[4]

Summary. DNA sequence data, macro-morphological evidence and pollen analysis are used to clarify the phylogenetic placement of two African species of Acanthaceae: *Schaueria populifolia* C.B.Clarke and *Rhinacanthus ndorensis* Schweinf. The combined data demonstrate that these species are only distantly related to the genera in which they are currently placed and provide strong support for recognition of new genera to accommodate them. Two new genera are therefore proposed and a taxonomic account is provided for each of these. The first, *Champluviera* I.Darbysh., T.F.Daniel & C.A.Kiel, is based primarily on *S. populifolia* but *Chlamydocardia nuda* C.B.Clarke (= *Justicia tigrina* Heine) is also included within this new genus based on shared morphological traits, at least one of which is synapomorphic and restricted to these species. Based on molecular evidence, *Champluviera* is placed in a well-supported clade of several genera that are together sister to the core Isoglossinae lineage of tribe Justicieae. The genus may be recognised morphologically by the combination of a dense spiciform terminal thyrse with the bracts, bracteoles and calyx lobes all slender and closely resembling one another; a bilabiate corolla lacking a rugula and with intricate speckling or striping on the lips; and, in particular, the putatively synapomorphic trait of anther thecae with broad, flattened, basal appendages that have an irregularly toothed fringe. The second new genus, *Kenyacanthus* I.Darbysh. & C.A.Kiel, is based on *R. ndorensis* and is so far thought to be monospecific. It is placed between core Diclipterinae and *Monechma* Group II within the expanded subtribe Diclipterinae in tribe Justicieae. *Kenyacanthus* can be recognised morphologically by having the combination of a trailing or procumbent habit; fasciculate inflorescences; bracts, bracteoles and calyces with hyaline margins; a bilabiate corolla with a slender cylindrical tube longer than the limb and with a shallow rugula; stenotribic flowers, with the stamens held against the lower lip; and anthers with only slightly offset thecae that lack appendages.

Key Words. Floristics, justicioid, phylogeny, taxonomy.

Introduction

With at least 2000 species and a nearly worldwide distribution, the Justicieae lineage of the Acanthaceae has long challenged taxonomists. Considerable progress has been made in the last 20 years in understanding this, the largest of the major lineages of Acanthaceae. However, recent phylogenetic work (e.g., Kiel *et al.* 2006, 2017; Daniel *et al.* 2008; McDade *et al.* 2000, 2018), as well as floristic and taxonomic research (e.g., Côrtes *et al.* 2016; Daniel 1995a, 2015, 2017; Darbyshire & Govaerts 2017; Darbyshire & Goyder 2019), has pointed to a number of outstanding problems that require resolution. Here, we propose solutions for two such taxonomic problems involving the African plants *Schaueria populifolia* C.B.Clarke and *Rhinacanthus ndorensis* Schweinf.

Schaueria populifolia

The genus *Schaueria* Nees (1839: 3) was originally described from the forests of eastern Brazil, and is best known for the species *S. calytricha* (Hook.) A.L.A.Côrtes ("golden plume"), which is popular in botanical gardens (Côrtes *et al.* 2016). *Schaueria* is a member of the "*Tetramerium* lineage" of the tribe Justicieae (Daniel *et al.* 2008; Côrtes *et al.* 2016; McDade *et al.* 2018). The genus is exclusively New World (NW) in distribution with the notable exception of *S. populifolia* C.B.Clarke (1900a: 242), which is found in the lowland rainforests of eastern Nigeria, Bioko and western and southern Cameroon. Daniel *et al.* (2008) noted that there are otherwise no genera of the *Tetramerium* lineage common to both the Old World (OW) and NW. As such, it would be remarkable if this African species were indeed a *Schaueria*.

A recent taxonomic revision of *Schaueria* by Côrtes *et al.* (2016), using both molecular and morphological evidence, demonstrated that *Schaueria* s.l. is polyphyletic. As a result, six species traditionally included in *Schaueria* were excluded following a recircumscription of the genus. The 14 species of *Schaueria* treated in the revision are all restricted to Brazil (Côrtes *et al.* 2016).

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[1] Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK. e-mail: i.darbyshire@kew.org
[2] Rancho Santa Ana Botanic Garden, Claremont Graduate University, 1500 North College Avenue, Claremont, CA, 91711, USA.
[3] California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA, 94118, USA.
[4] East African Herbarium, National Museums of Kenya, P.O. Box 45166, Nairobi, 00100, Kenya.

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Schaueria populifolia was not included in these authors' molecular studies, but they rejected this species from *Schaueria* on the basis that then unpublished molecular data by L. McDade show that *S. populifolia* is more closely related to the Isoglossinae lineage than to the *Tetramerium* lineage. These data have subsequently been published in an expanded sampling of the *Tetramerium* lineage based on six gene regions (McDade *et al.* 2018). These authors showed that *S. populifolia*, represented by *Gereau et al.* 5666 (MO) from Cameroon, was resolved with taxa of Isoglossinae that were sampled as outgroups. However, the authors noted that taxon sampling among outgroups was insufficient for the results to be considered conclusive regarding the placement of *S. populifolia*.

Côrtes *et al.* (2016) did not comment on any morphological differences between *Schaueria* s.s. and *S. populifolia*. The two are superficially similar, sharing many-flowered inflorescences comprising a series of dichasial inflorescence units; long narrow bracts, bracteoles and calyx lobes; a bilabiate corolla lacking a rugula (stylar furrow); two bithecous stamens and stipitate-clavate 4-seeded capsules with tuberculate seeds. However, these similarities are symplesiomorphic or of uncertain phylogenetic status and thus do not constitute evidence of a close relationship.

Rhinacanthus ndorensis

Rhinacanthus ndorensis was described by Schweinfurth (1892) from Ndoro near Mt Kenya. It is restricted to central Kenya where it occurs in grassland and open woodland, typically on seasonally damp black clay soils (Darbyshire *et al.* 2010). The species was maintained within the genus *Rhinacanthus* Nees for the *Flora of Tropical East Africa* account of Acanthaceae (Darbyshire *et al.* 2010) and for related studies on the genus in Africa (Darbyshire & Harris 2006), primarily on the basis of the slender corolla tube that is longer than the lips and the anther thecae of each stamen being offset and basally muticous. However, keys to the species of *Rhinacanthus* presented in those publications identify *R. ndorensis* first due to a number of unique characters including its procumbent or trailing habit, fasciculate inflorescences, hyaline margins to the bracts, bracteoles and calyx lobes and essentially glabrous capsules.

In a phylogenetic study of the 'justicioid' lineage of Justicieae based on six gene regions, Kiel *et al.* (2017) sampled one voucher of *Rhinacanthus ndorensis* (*Young* 3169, EA) together with 10 other accessions of *Rhinacanthus* representing eight additional species. They found that all sampled *Rhinacanthus* are resolved in an expanded Diclipterinae lineage, but that *Rhinacanthus* s.l. is not monophyletic (Kiel *et al.* 2017, Fig. 8). These authors recognised a well-supported *Rhinacanthus* clade comprising seven of the nine species sampled. However, they found that two species of the genus fall outside this clade: *R. virens* (Nees) Milne-Redh. and *R. ndorensis*. The former, a Guineo-Congolian forest species of West Africa, was placed basally among members of the Diclipterinae lineage; it is tentatively maintained in *Rhinacanthus* whilst we await further molecular investigation of this species and the other forest species of *Rhinacanthus* (Darbyshire *et al.* 2018). The latter was placed sister to core Diclipterinae, a lineage that comprises *Dicliptera* Juss., *Peristrophe* Nees (sometimes treated as congeneric with *Dicliptera*; Darbyshire & Vollesen 2007), *Xerothamnella* C.T.White and *Hypoestes* R.Br.

For this study, we combine macro-morphological data, pollen analysis and DNA sequence data for *Schaueria populifolia* and *Rhinacanthus ndorensis* with the goal of clarifying the phylogenetic placement of these two taxa. With regard to the former, we test the hypothesis that this African species is not related to its American congeners in the context of a more expansive sample of OW taxa that was included in earlier studies. Regarding *Rhinacanthus*, we seek to test the hypothesis that *R. ndorensis* is not closely related to *Rhinacanthus* s.s.

Materials & Methods

Morphological Analysis

Herbarium specimens of the focal taxa and related groups held at the BM, K, MO and P herbaria were examined, supported by study of digital images of specimens from the BR, L, LBV and WAG herbaria accessed via their respective online catalogues or by individual request. Abbreviations for herbaria follow *Index Herbariorum* (Thiers 2019). All duplicates of specimens seen are marked in the "Specimens Examined" sections with an exclamation mark (!). Those for which only online images have been seen are marked with an asterisk (*). The herbarium research was supplemented by field studies and photographs of wild plants where possible.

All measurements were made on dried material except for those of the flowers. Dried flowers were soaked in Aerosol OT 5% solution prior to dissection and measurement.

Pollen analysis

For the study of pollen of *Schaueria populifolia*, individual grains were removed from multiple anthers on the specimen *Cheek* 7771 using an insect pin. The grains were mounted onto a SEM stub coated with double-sided sticky tape, sputter coated with gold/palladium and examined under SEM at CAS. Study of pollen of *Rhinacanthus ndorensis* followed a similar methodology except that a whole anther was extracted from a flower bud on *Luke* 17084 and

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dissected to extract the pollen. Also in this case, the SEM stub was sputter coated with platinum before examination under SEM at K.

Molecular analysis

For this study, new sequence data were generated for nine taxa (Appendix 1). These were supplemented by downloading data for an additional 94 accessions from GenBank (Appendix 1). Most of these latter data were generated for previous studies in Justicieae (McDade *et al.* 2000, 2008, 2018; Kiel *et al.* 2006, 2017; Daniel *et al.* 2008). To make the datasets congruent across the five loci sampled, we sequenced an additional 94 samples (Appendix 1) for the final dataset totalling 103 taxa. For the newly generated sequences, leaf tissue was extracted using Doyle & Doyle's (1987) CTAB method. Procedures to amplify the cp *trnT-L*, *trnL-F* and *trnS-G* spacers, and *rps16* intron were as described by Daniel *et al.* (2008). Procedures for amplification of nrITS are found in McDade *et al.* (2000) and Daniel *et al.* (2008). PCR products were cleaned using PEG precipitation (Morgan & Soltis 1993) and the purified PCR products were cycle sequenced with both forward and reverse PCR primers using Applied Biosystems (ABI, Foster City, California) PRISM BigDye version 3.1, according to the manufacturer's specifications. All sequenced reactions were cleaned with Sephadex G50 and sequenced on an ABI 3100 genetic analyzer. Chromatograms were edited and aligned manually in Geneious® version 9.15 (https://www.geneious.com) and alignments were deposited in TreeBASE, 23681.

Data matrices for the five DNA regions were prepared as nexus files for Maximum Likelihood and Bayesian analyses in Geneious 9.1.5. Possible incongruence between the nrITS and cp data sets was examined by comparing the results of majority rule trees from Bayesian inference (analyses conducted as described below). We used a posterior probability value of 0.90 as a conservative threshold for well-supported conflict. Finding no evidence of incongruence between nrITS and cp data, we combined the datasets for further analyses.

Bayesian inference (BI) of phylogenetic relationships with posterior probabilities (BPP) as the support measure was conducted in MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001; Huelsenbeck *et al.* 2001; Ronquist & Huelsenbeck 2003). Models of molecular evolution for the genic regions were selected using the Akaike information criterion (AIC) (Akaike 1974; Posada & Crandall 2001) as implemented in JModelTest 2.1.3 (Posada 2008; Darriba *et al.* 2012). The selected models of nucleotide substitution were GTR + G for the combined plastid dataset and GTR + G + I for nrITS. Each dataset was run with data partitions corresponding to the combined cp and nrITS regions. Two simultaneous runs of four Monte Carlo Markov Chains were run for 20,000,000 generations with a random tree as the starting point and saving trees every 1,000 generations. Results were inspected in Tracer version 1.5 (Rambaut *et al.* 2014) to determine the burn-in period. Analysis of the nuclear + cp dataset reached stationarity (i.e., average standard deviation of split frequencies ≤ 0.01) after approximately 5,000,000 generations and the first 20% of the sampled trees were discarded as burn-in before constructing a majority rule consensus tree.

The three data sets (i.e. cp, nrITS, cp + nrITS) were also analysed using maximum likelihood (ML) using RAxML ver. 8.0.0 (Stamatakis 2014). For analysis, the combined data were partitioned under the same models of evolution as used for Bayesian inference, and 1000 bootstrap replicates were implemented. Each analysis was repeated three times to test the consistency of tree topology and bootstrap values (MLBS).

Species conservation (extinction risk) assessments

The species conservation assessments are based on the Categories and Criteria of the IUCN Red List (2012). The Extent of Occurrence (EOO) was calculated using the Kew Geospatial Conservation Assessment Tool GeoCAT (geocat.kew.org; Bachman *et al.* 2011).

Results

The topologies returned by BI and ML are congruent and are also congruent with the results of all earlier studies of Justicieae (e.g., McDade *et al.* 2000, 2018; Kiel *et al.* 2006, 2017; Daniel *et al.* 2008; Côrtes *et al.* 2016). We emphasise here the placement of the two focal taxa and do not reiterate the relationships established in earlier studies, a more complete review of relationships within Justicieae will be presented in a forthcoming paper (Kiel *et al.* in prep).

The three accessions of *Schaueria populifolia* (Fig. 1) are together monophyletic with strong support (1.00 BPP; 100 MLBS); this clade is in turn part of a well-supported clade (1.00 BPP; 100 MLBS) of several genera that are together sister with weak support (0.75 BBP; 51 MLBS) to the core Isoglossinae lineage (1.00 BPP; 100 MLBS) (Fig. 1). Accessions of *Schaueria* s.s. are placed phylogenetically distant from *S. populifolia* in the *Tetramerium* lineage (Fig. 1).

Two accessions of *Rhinacanthus ndorensis* (Fig. 2) are sister with strong support (1.00 BPP; 99 MLBS) and are together sister to *Dicliptera* s.l. + *Hypoestes* with strong support for this relationship (1.00 BPP; 100 MLBS). *Rhinacanthus virens* is a member of a weakly supported basal lineage (0.96 BPP; 56 MLBS) in Diclipterinae and is sister to *Justicia* aff. *tenuipes* with strong support (1.00 BPP; 98 MLBS). All other sampled *Rhinacanthus* are members of the core *Rhinacanthus* clade (1.00 BPP; 88 MLBS) and are not closely related to *R. ndorensis* (Fig. 2).

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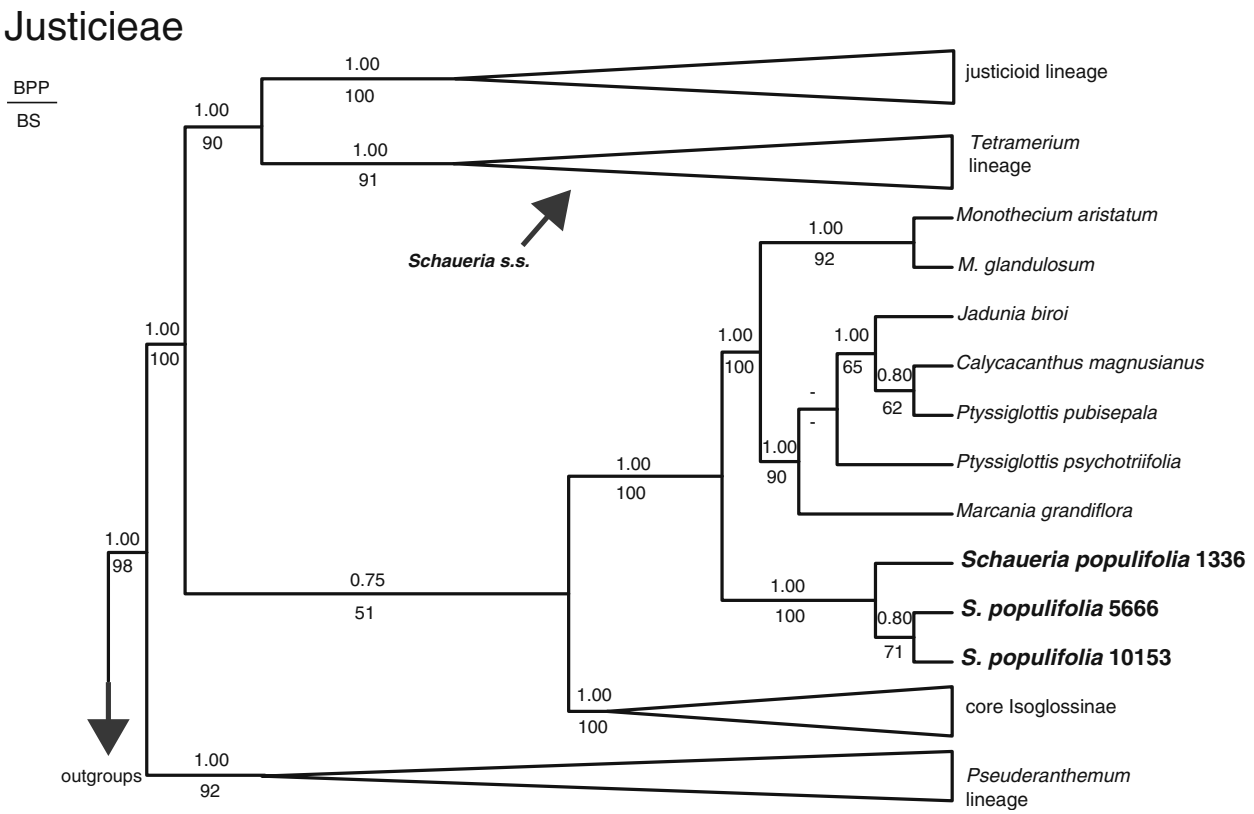


Fig. 1. Summary of phylogenetic relationships among Justicieae highlighting *Schaueria populifolia* (= *Champluviera populifolia*) from Maximum likelihood. BPP = values above branch and MLBS = values below branch.

Analysis of DNA sequence data thus supports recognition of two new genera to accommodate *Schaueria populifolia* and *Rhinacanthus ndorensis*. Supporting evidence from the morphological analyses, including pollen, will be described in detail in the Discussion below.

Discussion and taxonomic treatments

1. *Champluviera* — a new genus from the forests of central Africa

Our study of specimens of *Schaueria populifolia* found notable morphological differences between plants of this African species and Brazilian congeners. Brazilian *Schaueria* (henceforth *Schaueria* s.s.) have white or yellow flowers lacking speckling, whilst those of *S. populifolia* are dull red, red-brown or purple with intricate speckling on at least the lower lip (Fig. 3). More significantly, in *Schaueria* s.s., the anther thecae of each stamen lack basal appendages and are glabrous, whereas those of *S. populifolia* have a broad, flattened and irregularly fringed basal appendage and the upper theca has a fringe of trichomes on the margin that is not adpressed to the second theca.

Pollen of *Schaueria populifolia* is remarkable in that the ora are markedly enlarged in comparison to the colpi and the two pseudocolpi in each mesocolpium curve toward one another equatorially and sometimes fuse at the equator, forming an hour-glass shape or figure eight (Fig. 4). In contrast, pollen of *Schaueria* s.s. have ora that are less markedly enlarged and the pseudocolpi are ± parallel to the apertures such that the two pseudocolpi of each mesocolpium do not form an hour-glass shape (see Côrtes *et al.* 2016, Fig. 6).

These morphological differences indicate that the resemblance between *Schaueria* s.s. and *S. populifolia* is superficial and that they are not closely related, thus supporting the findings of the molecular analysis (Fig. 1).

On studying specimens of *Schaueria populifolia* during her research on the Acanthaceae of West and Central Africa, Dominique Champluvier (formerly of BR) proposed the new combination *Justicia populifolia* (C.B.Clarke) Champl. and annotated specimens at the Kew herbarium as such in April 1999. This name was adopted by Onana (2011, 2013) as an unpublished combination in the checklist of vascular plants of Cameroon, but has never been validly published. This new combination was proposed on the basis that the flowers, and in particular the unique appendages of the anthers described above, bear a close resemblance

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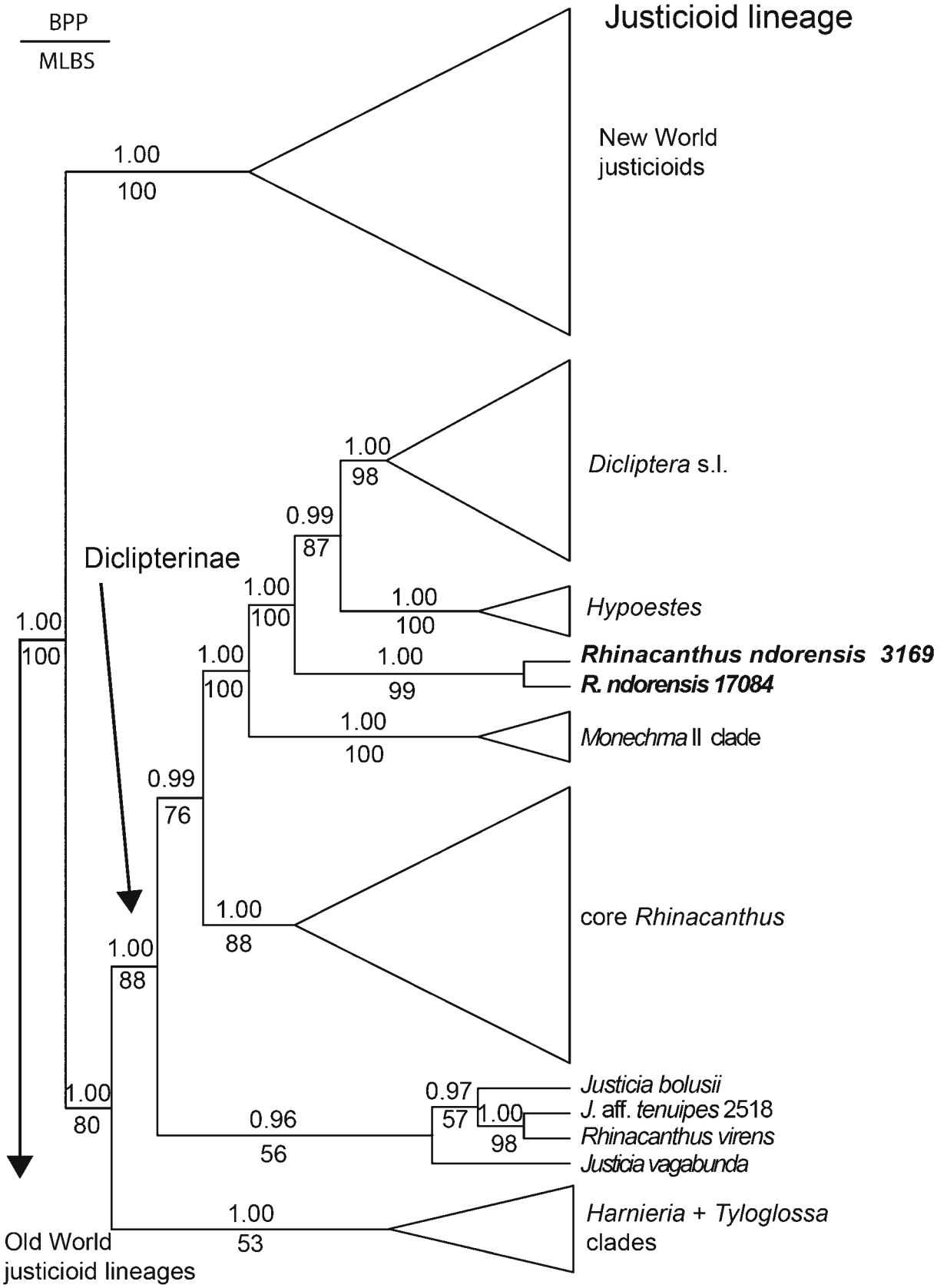


Fig. 2. Summary of phylogenetic relationships among Diclipterinae in the "justicioid" lineage highlighting *Rhinacanthus ndorensis* (= *Kenyacanthus ndorensis*) from Maximum likelihood. BPP = values above branch and MLBS= values below branch.

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Fig. 3. *Champluviera populifolia* in the field, Cameroon. PHOTOS: **A** J. OSBORNE (collected as *Osborne* 97); **B** & **C** M. CHEEK.

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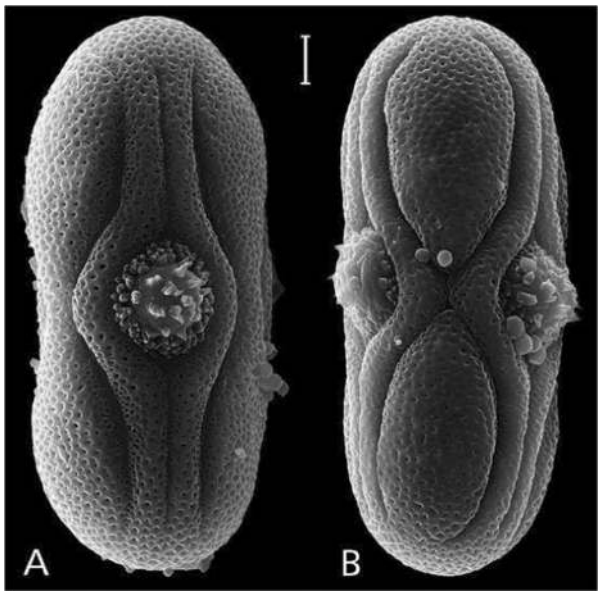


Fig. 4. Pollen of *Champluviera populifolia*. A equatorial view showing the compound aperture and pseudocolpi; B equatorial view showing the mesocolpium with equatorially fused pseudocolpi (from *Cheek* 7771).

to those of *Justicia tigrina* Heine from Gabon (D. Champluvier, pers. comm.). *Justicia tigrina* is based on *Chlamydocardia nuda* C.B.Clarke, a species that Clarke (1900b) had only tentatively placed in *Chlamydocardia*, noting that it lacked the characteristic bracts of that genus (see Darbyshire & Govaerts 2017). Heine (1966) recorded the anther appendage of *J. tigrina* as resembling a chicken's crest ("en forme de crête de poule", p. 220) which is an apt description for the flattened broad appendage with an irregularly toothed fringe. He further noted that this appendage corresponds well to that of the other species of *Justicia* treated in the *Flore du Gabon* account, and it was on this basis that he transferred *C. nuda* to *Justicia*. In doing so, Heine, was obliged to give the species a new name, because the epithet "*nuda*" was already occupied in *Justicia* — *J. nuda* (Nees) O.Schwartz (1939: 259).

We concur with Dr Champluvier that, based on morphological evidence, *Schaueria populifolia* and *Justicia tigrina* are closely allied. They are vegetatively very similar, have a similar inflorescence type and the anther morphology is closely similar except that the thecae are more markedly offset in *J. tigrina*. However, neither the morphological nor the molecular evidence support the placement of these species within *Justicia*. Contrary to Heine's (1966) statement, the anther appendages differ significantly from African species of *Justicia* where often only the lower theca has an appendage (but note that appendages on both thecae is more frequent in New World *Justicia* — see, for example, Daniel 1995b; Kiel *et al.* 2017, Fig. 4E – F) and the appendage is usually longer than it is broad, often markedly so, and is untoothed except sometimes for a forked apex. This is in marked contrast to the broad, short and flattened appendage with an irregularly toothed fringe in *S. populifolia* and *J. tigrina* (Fig. 5). Furthermore, both of these latter species lack a rugula (stylar furrow), whilst species of *Justicia* have rugulate corollas (Kiel *et al.* 2017).

Unfortunately, suitable material for DNA analysis of *Justicia tigrina* was not available for the current study and so we have been unable to test the phylogenetic relationship between *Schaueria populifolia* and *J. tigrina*. However, as just described, the detailed morphological examination conducted in this study strongly supports the hypothesis that they are closely related.

Our results place *Schaueria populifolia* in a well-supported clade of several genera that are together sister to the core Isoglossinae lineage, albeit without strong support (Fig. 1). This result is congruent with morphological evidence. Core Isoglossinae, a clade that includes the large genera *Isoglossa* Oerst. (OW) and *Stenostephanus* Nees (NW), is well-marked by structural synapomorphies: plants have gürtelpollen, i.e. biporate pollen that is circular in apertural view and with a broad marginal girdle (Kiel *et al.* 2006), although this can be modified to 3 (– 4)-porate pollen in *Brachystephanus* Nees (Figueiredo & Keith-Lucas 1996; Champluvier & Darbyshire 2009). In contrast, the clade of genera sister to Core Isoglossinae, including *S. populifolia* and *Ptyssiglottis* T.Anderson, have different pollen types (Kiel *et al.* 2006). This clade includes only one other African representative so far as is known at present, that being *Monothecium* Hochst. *Monothecium* comprises two species in continental Africa one of which extends to India; a third, Malagasy species (*M. leucopterum* Benoist) is unlikely to belong to *Monothecium* in view of several morphological differences (I. Darbyshire, pers. obs.). *Monothecium* is easily separated from *S. populifolia* and *J. tigrina* in, amongst other differences, having monothecous anthers lacking appendages (see Vollesen in Darbyshire *et al.* 2010).

The other genera allied to *Schaueria populifolia* are confined to Asia: *Calycacanthus* K.Schum., *Jadunia* Lindau, *Marcania* J.B.Imlay and *Ptyssiglottis*. Of these, only the last could potentially be confused with the African plants. *Ptyssiglottis* was most recently revised by Hansen (1992) who recognised 33 species, occurring from Sri Lanka eastwards through Southeast Asia to New Guinea. It differs from *S. populifolia* and *Justicia tigrina* in anther form and inflorescence characteristics. All species of *Ptyssiglottis* have non-appendaged anthers with the exception of *P. mucronata* B.Hansen from Sumatra, which has a sharply mucronate base to each theca (Hansen 1992). However, this is quite different to the broad, irregularly fringed appendages seen in *S. populifolia* and *J. tigrina*. In *Ptyssiglottis*, the inflorescence is

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Fig. 5. Anthers of *Champluviera nuda* (from *Bates* 494, BM). PHOTO: HANNAH ARMER (NATURAL HISTORY MUSEUM, LONDON).

axillary and is a variation of a compound dichasium, usually branched dichotomously. In some species (e.g. *P. pubisepala* (Lindau) B.Hansen, sampled here), a lax compound dichasium with elongate internodes is fully developed, but in many species (e.g. *P. psychotriifolia* (Stapf) B.Hansen, sampled here) the dichasium is reduced and contracted, confined to two (to four) contracted branches, these often bearing several pairs of imbricate, scale-like bracts (Hansen 1992). In *S. populifolia* and *J. tigrina*, in contrast, the inflorescence is a terminal spiciform thyrse, with the dichasial cyme units arranged along a central, indeterminate axis. Pollen morphology is variable in *Ptyssiglottis*, but some pollen types are somewhat similar to that of *S. populifolia*, having the 3-colporate 6-pseudocolpate grains with enlarged ora, although the pseudocolpi are not or only slightly convergent in the mesocolpium (see Hansen 1992, Figs. 10 and particularly 11). *Ptyssiglottis* is not monophyletic in our results but, with only two species sampled, this result must be viewed as preliminary. Further sampling is warranted to investigate this further.

Based on the molecular and morphological evidence presented, our data indicate that a new genus is warranted to accommodate *Schaueria populifolia* within the lineage sister to Core Isoglossinae and we describe the new genus *Champluviera* I.Darbysh., T.F.Daniel & C.A.Kiel below. Further, based on the close morphological similarity between *S. populifolia* and *Justicia tigrina*, we include the latter species within *Champluviera*; this treatment should be tested in future via acquisition of material suitable for DNA analysis.

Taxonomic Treatment

Champluviera *I. Darbysh., T.F.Daniel & C.A.Kiel* **genus nov.** Type species: *Champluviera populifolia* (C.B.Clarke) I.Darbysh. & T.F.Daniel

http://www.ipni.org/urn:lsid:ipni.org:names:77197847-1

Perennial herbs or subshrubs, erect or decumbent; young stems somewhat 4- or 6-angular. *Leaves* opposite-decussate, petiolate, pairs isophyllous, blade ovate or oblong-ovate to elliptic or oblong-elliptic; cystoliths present, linear, numerous, conspicuous in dry state at least on adaxial leaf surface. *Inflorescences* terminal, spiciform, comprising a series of opposite subsessile or shortly pedunculate cymes arranged along an indeterminate axis, i.e. a spiciform thyrse; bracts (excluding those pairs at base of inflorescence spike), bracteoles and calyx lobes subequal in size and shape, linear, linear-spathulate or linear-lanceolate; flowers subsessile or shortly pedicellate. *Calyx* divided almost to base into five lobes, subequal to somewhat unequal in length. *Corolla* intricately speckled and/or striped, rugula absent; aestivation ascending-cochlear, limb bilabiate; upper lip with apex shortly bilobed, lower lip 3-lobed. *Stamens* 2, inserted on interior of corolla tube, anthers exserted, dehiscing toward lower lip (i.e. flowers nototribic), bithecous, thecae parallel or slightly oblique, very slightly to more markedly offset, both thecae with a flattened, broad, irregularly toothed appendage at the base; staminodes absent. *Floral disk* annular, fleshy, 0.5 – 0.7 mm tall. *Ovary* oblong-ellipsoid, 4-ovulate; style filiform; stigma shortly bilobed. *Capsule* (where known) 4-seeded (or fewer by abortion), retinaculate, stipitate; seeds (only seen in immature state) tuberculate.

RECOGNITION. *Champluviera* is recognised by having the combination of a dense spiciform terminal thyrse with the bracts, bracteoles and calyx lobes all slender and closely resembling one another; a bilabiate corolla lacking a rugula and with intricate speckling or striping on the lips; and, in particular, anthers comprising two slightly to more markedly offset thecae each of which has a broad flattened basal appendage with an irregular fringe, and at least the upper theca having a line of trichomes on the exposed side. It differs from *Schaueria* primarily in having appendaged and pubescent anthers and in having speckled or striped corolla lips (vs anthers lacking appendages and glabrous, corollas not speckled or striped). It differs from *Justicia* primarily in the corolla lacking a rugula and in the anther appendages being broad and irregularly

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toothed (vs corolla with a rugula, anther appendages elongate to rounded and smooth except sometimes for a forked apex). *Champluviera populifolia* also has an apparently unique pollen type in which the two pseudocolpi of each mesocolpium converge towards the equator and sometimes meet, forming an hour-glass or figure eight shape. It is not clear, however, whether the second species, *C. nuda*, has the same pollen type (see Note to that species).

ETYMOLOGY. This genus is named in honour of Dr Dominique Champluvier (previously of the BR herbarium), an expert on the Acanthaceae of Africa with a particular interest in the Central African region. Dominique was the first to recognise the close relationship between the two species in this new genus.

Key to species of *Champluviera*

Corolla tube 10 – 14 mm long, clearly longer than limb, corolla glabrous externally except for few trichomes at apex of lower lip; anther thecae only very slightly offset; bracteoles and calyx lobes typically linear-spathulate with a blunt tip, usually with conspicuous glandular trichomes distally [Nigeria, Bioko, Cameroon] . . . . . **C. populifolia**

Corolla tube 6 – 8 mm long, only slightly longer than limb, corolla pubescent externally; anther thecae markedly offset; bracteoles and calyx lobes linear-lanceolate with a sharply acute tip, glandular trichomes minute and inconspicuous [Gabon]. . . . . **C. nuda**

Champluviera populifolia (*C.B.Clarke*) *I.Darbysh. & T.F.Daniel* **comb. nov.**

http://www.ipni.org/urn:lsid:ipni.org:names:77197848-1

Schaueria populifolia C.B.Clarke, *Fl. Trop. Afr.* 5: 242 (1900a); Hutchinson & Dalziel (1931: 263); Heine (1963: 423); Lebrun & Stork (1997: 503); Vollesen in Cable & Cheek (1998: 5); Vollesen & Darbyshire in Cheek *et al.* (2004: 230). Type: Equatorial Guinea, Fernando Po [Bioko], fl. 1862, *Mann* 1426 (K! [K000419169] lectotype, **selected here**). Additional syntypes: Equatorial Guinea, Bioko, in bud Nov. 1841, *Vogel* s.n. (K! [K000419170]); Cameroon, Bipinde, fl. 1896, *Zenker* 1205 (BM! [BM000949851], K!, M* [M0186812], S* [S09-5904], WAG* [WAG0248378]).

Justicia populifolia (C.B.Clarke) Champl. ined. sensu Onana (2011: 31; 2013: 64), nom. nud.

Perennial herb or subshrub, 30 – 200 cm tall, erect or decumbent, sometimes rooting at lower nodes; young stems somewhat 4- or 6-angular, furrowed in dry state, markedly swollen above each node (often shrunken in dry state), with two opposite-decussate lines of short retrorse trichomes most numerous below each node, trichomes multicellular with conspicuous dark cell walls, stems also with numerous minute red-brown sessile glands throughout; mature stems terete. *Leaves* with a strong liquorice odour (*fide Bos* 5548); petioles 18 – 66 mm long, furrowed above, antrorse-puberulous; blade dark green above, sometimes paler or purplish along main veins, pale grey-green to purplish beneath, ovate, oblong-ovate or ovate-elliptic, 6.2 – 19.7 × 3.4 – 10.5 cm (length : width ratio 1.5 – 2.5 : 1), base cordate, sometimes asymmetrically so, margin entire or obscurely undulate, apex acuminate, adaxial surface glabrous or with scattered short multicellular trichomes that appear deflated in dry state, abaxial surface antrorse-puberulous along main veins, margin with few short patent glandular trichomes in proximal half; cystoliths linear, numerous and conspicuous on adaxial surface, most dense along veins, both surfaces also with numerous minute red-brown sessile glands; lateral veins 6 – 9 pairs, brochidodromous, prominent beneath, with ± scalariform tertiary veins. *Inflorescence* a terminal spiciform thyrse with few flowers open at any one time, (1.8 –) 3.5 – 11 × 2 – 2.7 cm, comprising a series of opposite (sub)sessile dichasia, these at first 3-flowered but can become many-flowered with age; rachis greenish-white or purplish, indumentum as that of stem but trichomes can be more dense; bracts along rachis greenish-white or purplish towards base, apical portion darker, linear, linear-spathulate or more rarely linear-lanceolate, 6.5 – 14 × 0.3 – 1.3 mm, pairs divergent, distal portion often ascending, apex usually obtuse or rounded, surface with short antrorse eglandular trichomes and with few to numerous spreading glandular trichomes distally, cystoliths numerous and conspicuous in proximal half or two thirds; bract pair at base of thyrse often somewhat larger, lanceolate, up to 4 mm wide; bracteoles as bracts but usually linear-spathulate, 7.5 – 11.5 × 0.3 – 0.8 mm, apex sometimes slightly recurved; flowers subsessile or on stout glabrous pedicels to 2 mm long. *Calyx* lobes linear or usually linear-spathulate, closely resembling the bracteoles, somewhat unequal in length, 8 – 12.5 × 0.2 – 0.5 mm, apex blunt, often slightly recurved, indumentum like that of bracts. *Corolla* 16 – 21 mm long, dull red, red-brown or purple, lower lip white to pale yellow with red to purple speckling; tube 10 – 14 mm long, basal cylindrical portion 7.5 – 10 mm long, c. 1.2 – 1.7 mm in diam. at midpoint, expanded throat 3 – 4.5 mm long, glabrous externally, minutely puberulous within with mixed eglandular and

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glandular trichomes particularly on roof, with a diffuse broad band of longer eglandular trichomes starting 2.5 – 4.7 mm from base, only sparsely hairy below this; upper lip triangular, 4.5 – 7.3 × 4 – 5 mm when flattened but margins narrowly involute, apex shortly bilobed, lobes 0.5 – 1.3 mm long, tips reflexed; lower lip 4.5 – 7 mm long, deeply 3-lobed, lateral lobes lanceolate, 2.3 – 4.2 × 1 – 2.2 mm when flattened, median lobe broadly rounded, 1.8 – 3 × 3 – 3.6 mm, with two raised, convergent ridges and a central furrow and with prominent reticulate venation, lips glabrous externally except for few short trichomes at apices of lower lobes. *Stamens* inserted 6.3 – 8.7 mm from base of corolla; filaments free for 5 – 7.5 mm, flattened either side of raised central vein, shortly pubescent at base and along fused portion, glabrous distally; anthers bithecous, thecae parallel or slightly oblique, slightly offset by c. 0.15 mm, narrowly oblong, 1.9 – 2.4 mm long, both with broad subsessile glands on adhering surfaces, upper (inner) theca with dense band of short multicellular eglandular trichomes and shorter capitate glandular trichomes dorsally along exposed side, lower (outer) theca glabrous on exposed side, both thecae with broad flattened, slightly protruding appendage below suture with irregular fringe of conical teeth to 0.07 mm long. *Pollen* perprolate, 3-colporate, 6-pseudocolpate, polar diameter (P) 57 – 60 µm, equatorial diameter (E) 24 µm, P:E = 2.37 – 2.5, ora considerably wider than colpi and with membrane echinate (to gemmate), the two pseudocolpi in each mesocolpium curved toward one another equatorially (and sometimes toward poles as well) and sometimes fusing at equator forming an hour-glass or figure eight shape, interaperatural exine reticulate. *Floral disk* annular, fleshy, 0.5 – 0.7 mm tall. *Ovary* black, oblong-ellipsoid, 1.1 – 1.6 mm long, glabrous; style pale orange-brown in dry state, 10 – 13.5 mm long, with few pale eglandular trichomes at base; stigma shortly bilobed. *Capsule* c. 17.5 mm long including stipe 8 mm long, apex shortly attenuate, surface glabrous; immature seeds only seen, flattened, tuberculate. Figs 3, 4 and 6.

DISTRIBUTION. Nigeria (Cross River State), Equatorial Guinea (Bioko), Cameroon (Southwest, Littoral and South Regions); Map 1.

SPECIMENS EXAMINED. NIGERIA. Cross River State: Oban Distr., fl. 1911 – 1912, *Talbot* s.n. (K!); Oban, fl. 1911, *Talbot* 993 (BM, K!); Ogoja Prov., Ikom Distr., Cross River North Forest Reserve, fl. 7 Dec. 1950, *Keay* in FHI 28157 (FHI, K!); Ogoja Prov., Ikom Distr., Afi River Forest Reserve, fl. 13 Dec. 1950, *Keay* in FHI 28238 (FHI, K!). **EQUATORIAL GUINEA. Bioko (unplaced)**: Fernando Po [Bioko], fl. 1862, *Mann* 1426 (K! lectotype). **Bioko Norte**: Fernando Po [Bioko], Clarence Peak [Pico Basilé], in bud Nov. 1841, *Vogel* s.n. (K!). **CAMEROON. Southwest Region**: Meme Div., Southern Bakundu Forest Reserve, near Pete, 28 Nov. 1985, *Thomas & Nemba* 5022 (MO!); Ndian Div., along path from "Fabe Road" towards Fabe, fl. 22 Nov. 1986, *Manning* 916 (K!, MO!); Korup N.P., WCI study area, 35 km W of Nguti, fl. 18 Jan. 1991, *Harris* 2704 (K!); Mabeta-Moliwe, Diculu, fl. 16 Dec. 1993, *Cable* 585 (K!, SCA, YA); Ndian Div., N of Mundemba at second crossing of Moliba R. on Ekundu Kundu road, fl. 12 Dec. 1994, *Gereau et al.* 5666 (K!, MO!); Mt Kupe SW slope, main trail leading to the summit, fl. 11 July 1995, *Ensermu* 3533 (K!, YA); Mt Kupe, path to Kupe rock along Esense R., fl. 2 Nov. 1995, *Cheek* 7654 (BR*, K!, MO!, P, SCA, WAG, YA); Mt Kupe, SW slope, Muanenzum trail, fl. 6 Nov. 1995, *Schoenenberger* 26 (K!, YA); Mt Kupe, main trail to the top from Kupe village, fl. 13 Nov. 1995, *Schoenenberger* 53 (K!, YA); Mt Kupe, path to top of Kupe rock, fl. 14 Nov. 1995, *Cheek* 7771 (BR*, K!, MO!, NY, P*, SCA, US, WAG, YA); Meme Div., Mungo River Forest Reserve, S of Kumba-Tombel road, c. 1 km from Mungo bridge, fl. & fr. 26 Nov. 1999, *Cheek* 10153 (K!, SCA, YA); Ngomboku, on path to Mbombe hill, fl. 9 Dec. 1999, *Mackinder* 292 (BR*, K!, SCA, YA); Banyang-mbo Sanctuary, Research Station path to sanctuary via Nlowoa and Mbu river crossings, fl. 25 Nov. 2000, *Cheek* 10605 (K!, MO, WAG, YA); Mone Forest Reserve, Mokoyong to Tafu path, 2.5 hrs E, 30 Nov. 2000, *Cheek* 13984 (K!). **Littoral Region**: Forêt de Bakaka, 3 km E of Eboné (km 11 Nkongsamba-Loum road), fl. 17 Dec. 1971, *Leeuwenberg* 8913 (K!, WAG); près Yingui II, à 5 km à l'ENE de Yingui, 35 km E de Yabassi, fl. & fr. 8 Jan. 1972, *Letouzey* 10919 (K!, P*); Ebo Proposed N. P., Bekob, fl. 15 Feb. 2006, *Tchiengue* 2486, (K! YA); Ebo Proposed N. P., Ebo Forest Research Station, W transect, fl. 9 Oct. 2006, *Osborne* 97 (K!, WAG, YA); Ebo Proposed N. P., Ebo Bekob forest, fl. 26 Nov. 2013, *Tchiengue* 3613 (K!, MO, P*, WAG, YA); Ebo Proposed N. P., Bekob camp, fl. 2 Dec. 2013, *Ngansop* 187 (K!, WAG, YA). **South Region**: Bipinde, fl. 1896, *Zenker* 1205 (BM!, K!, M*, P*, S*, WAG*); au S de Zingui, 40 km ESE de Kribi, fl. 20 Jan. 1962, *Letouzey* 4072 (K!, P*); Mviglimangalé, 16 km E Nayabesan, 1 km NW village, fl. 15 Feb. 1965, *Raynal* 13411 (P*); près de R. Kienke, au NNW de Nkolbewa, km 35 route Kribi-Ebolowa, fl. 12 March 1968, *Letouzey* 9001 (K!, YA); about 11 km from Kribi, between airfield and Kienke, fl. 27 Oct. 1969, *Bos* 5548 (BR*, WAG); c. 5 km SSE of Bipindi, fl. & fr. 14 Jan. 1987, *Manning* 1336 (K!, MO!, YA*); Efoulan, au sud d'Akom II (mi-chemin entre Ebolowa et Kribi), fl. 11 May 2009, *Lachenaud et al.* 737 (BR*).

HABITAT & ECOLOGY. This species is recorded from 1lowland rainforest in deep shade, sometimes being recorded from swamp and riverine forests. It can also persist in secondary and disturbed forest patches; 70 – 900 m elevation.

PHENOLOGY. *Champluviera populifolia* has been recorded in flower most frequently in the months of

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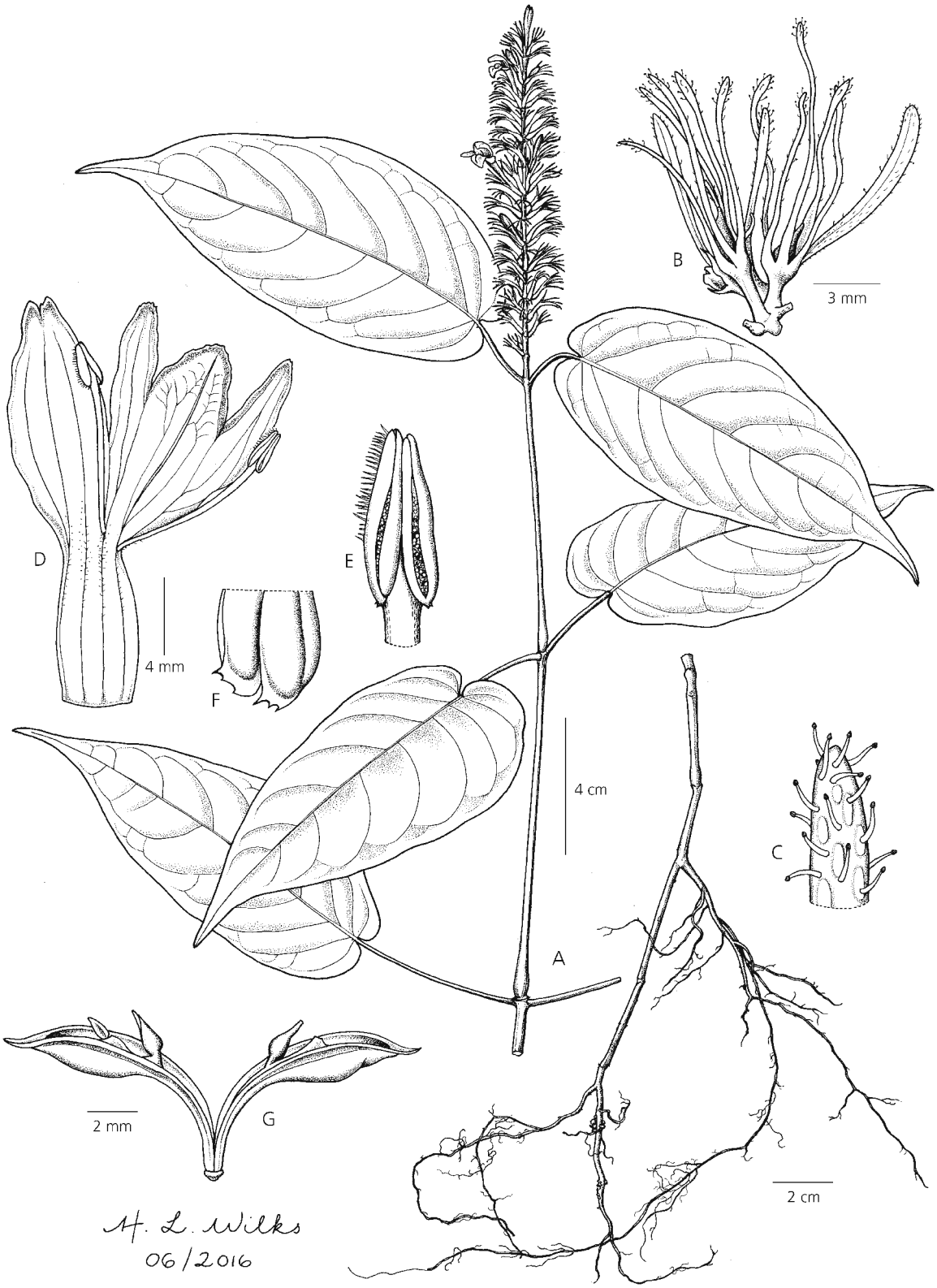
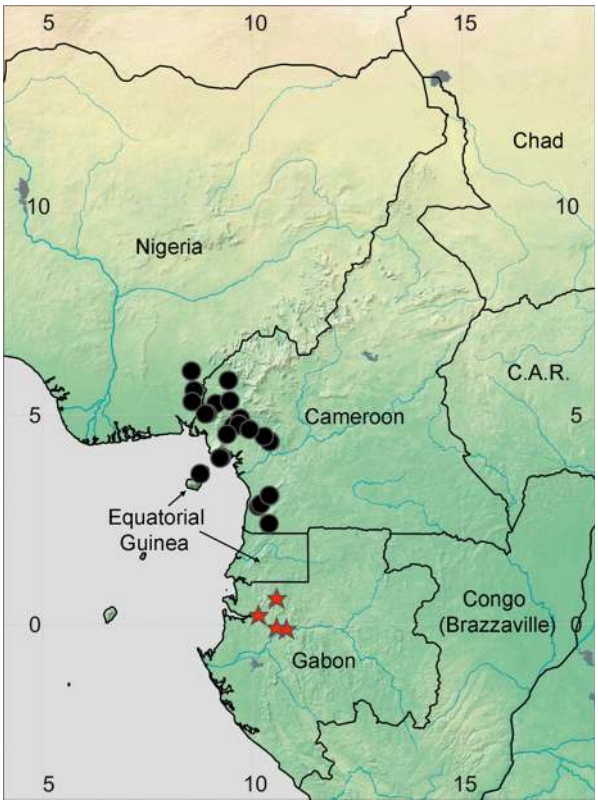


Fig. 6. *Champluviera populifolia.* **A** habit: rootstock and distal portion of flowering stem; **B** dichasial inflorescence unit showing calyces and bracteoles (some bracteoles cut away at base); **C** apex of calyx lobe showing glandular trichomes; **D** dissected corolla with androecium; **E** anther; **F** detail of anther base showing thecal appendages; **G** dehisced capsule. **A** from *Ngansop* 187 with rootstock from *Osborne* 97, **B** from *Cheek* 10153; **C – E** from *Ngansop* 187; **F** from *Gereau et al.* 5666; **G** from *Manning* 1336 and *Cheek* 10153. DRAWN BY HAZEL WILKS.

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Map 1. Distribution of *Champluviera*: *C. populifolia* (black circles), *C. nuda* (red stars).

(October –) November – December (– January) but with occasional records from February, March, May and July. The peak flowering time coincides with the onset of the dry season within this species' range.

CONSERVATION STATUS. This species was recorded as Near Threatened (NT) by Vollesen & Darbyshire (in Cheek *et al.* 2004). It appears to be fairly frequent in the lowland to mid-altitude forests of the Cameroon Highlands and southwestern Cameroon but its favoured habitat is threatened through large parts of its range due to timber extraction and forest clearance for subsistence and commercial agriculture. It has an EOO of 53,797 km^2 which is considerably greater than the 20,000 km^2 threshold for Vulnerable under IUCN criterion B1 and has up to 20 locations historically but some of these are likely to have been lost. The assessment of **Near Threatened** (NT) under criterion B is therefore upheld here.

NOTES. *Mann* 1462 (K) is chosen as the lectotype, as it is the most informative of the three syntypes and, from his annotations and illustrations on this specimen, it is clear that Clarke (1900a) used it as the basis for his description in the protologue.

Champluviera nuda (*C.B.Clarke*) *I.Darbysh. & T.F.Daniel* **comb. nov.**

http://www.ipni.org/urn:lsid:ipni.org:names:60478962-2

Chlamydocardia nuda C.B.Clarke, *Fl. Trop. Afr.* 5: 235 (1900b); Darbyshire & Govaerts (2017: 4). Type: Gabon, Mabam, Como R., 60 miles from Gaboon, fl. 13 July 1896, *Bates* 494 (K! [K000419168] holotype; BM! [BM000931152], L* [L0003054], P! [P00540805] isotypes).

Justicia tigrina Heine, *Fl. Gabon* 13: 219, pl. XXXVIII 10 – 13 (1966); Lebrun & Stork (1997: 489); Sosef (2006: 38). Type as for *Chlamydocardia nuda*.

Perennial herb or subshrub, 70 – 180 cm tall, basal stems trailing and rooting at nodes, decumbent; young stems somewhat 6-angular, ± evenly pubescent with sparse antrorse to appressed eglandular trichomes and with opposite lines of denser trichomes, older internodes glabrescent. *Leaves* petiolate, petioles to 70 mm long, furrowed above, antrorse-puberulous; blade ± concolorous, green or dark glaucous-green, elliptic, oblong-elliptic or ovate-elliptic, 8.5 – 15.5 × 3.6 – 8 cm (length : width ratio (1.75 –) 2.1 – 2.8 : 1), base rounded, shallowly cordate or obtuse, can be somewhat asymmetric, margin entire or irregularly undulate, apex acuminate, surfaces sparsely pubescent on main veins, with antrorse eglandular trichomes; cystoliths linear, numerous and conspicuous on both surfaces when dry, surfaces also with numerous minute red-brown sessile glands; lateral veins 6 – 8 pairs, brochidodromous, pale and prominent beneath. *Inflorescence* a slender erect terminal spike to 15 – 24.5 cm long including peduncle to 0.5 – 1.2 (– 3) cm long, comprising a series of opposite 1 – 3 (potentially more)-flowered cymes, those at base of spikes borne on peduncles to 2.5 mm long, those in distal portion of spike sessile or peduncle to 0.5 mm; rachis ± evenly pubescent with antrorse eglandular trichomes like those of young stems; bracts opposite, green, linear-lanceolate, 6 – 8 mm × c. 1 mm, pubescent abaxially, like rachis; bracteoles similar to bracts in shape and size but can have a more puberulent indumentum and can be purplish (drying brown); pedicels to 1.5 (– 2.5) mm long, puberulent. *Calyx* purple or grey-purple in live state at least towards base and apex, drying brown, divided almost to base into five subequal to ± unequal linear-lanceolate lobes resembling the bracteoles, 7.5 – 11 mm long, puberulent externally with mixed erect glandular and eglandular trichomes to 0.05 mm long. *Corolla* ± 11 – 14 mm long, yellow with dark purple stripes on upper lip and dark purple speckling on lower lip, pubescent externally with erect eglandular trichomes; tube ± 6 – 8 mm long, cylindrical; limb bilabiate with lips ± 5.5 – 6 mm; upper lip hooded, apex shortly bilobed; lower lip pendant, shortly 3-lobed. *Stamens* 2; filaments ± 4 mm long (*fide* Heine 1966), glabrous; anthers with thecae unequally

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inserted, overlapping by 0.8 – 0.9 mm, thecae narrowly elliptic, 1.3 – 1.6 mm long, with multicellular eglandular trichomes along the exposed side more numerous on upper theca, and both with a flattened, broad appendage at base below suture with irregularly toothed fringe. *Pollen* not seen (see note). *Floral disk* annular, ± 0.5 mm tall. *Ovary* ± 2 mm long, glabrous; style ± 11 mm long (*fide* Heine 1966), with eglandular trichomes towards base; stigma shortly bilobed. *Capsule* not seen. Fig. 5.

DISTRIBUTION. Gabon (Estuaire, Moyen-Ogooué and Woleu-Ntem Provinces); Map 1.

SPECIMENS EXAMINED. GABON. Estuaire Province: Mabam, Como R., 60 miles from Gaboon, fl. 13 July 1896, *Bates* 494 (K! holotype; BM!, L*, P! isotypes); Abanga Chantier C.E.T.A., fl. 3 June 1963, *N. Hallé* 2176 (P! [P03616770, P03616771]); *idem*, fl. 8 June 1963, *N. Hallé* 2362 (P! [P03616769]). **Moyen-Ogooué Province:** 15 km NE of Ndjolé, Exploitation road, 31 Jan. 1991, *de Wilde & Sosef* 10329 (WAG [WAG0130200], n.v.). **Woleu-Ntem Province**: Crystal Mts, Tchimbélé, fl. 23 Jan. 2001, *Mayombo-Nzengue* 271 (LBV* [LBV0019437]).

HABITAT & ECOLOGY. This species is recorded from primary wet forest, shaded river margins and in alluvial silts by streams; the elevation range is estimated at 10 – 630 m.

PHENOLOGY. Phenology information on this species is very limited; three of the four flowering specimens seen by the current authors were collected in June or July, during the short dry season; the fourth was collected in January during the wet season.

CONSERVATION STATUS. This species is clearly scarce, being known with certainty from only four herbarium collections, despite Gabon being one of the best explored countries botanically in Africa according to Sosef *et al.* (2017). It appears to have a highly restricted range with an EOO of 2890 km^2 based on current knowledge. Of the four known localities, Ndjolé is an area of gold and manganese mining (https://mining-atlas.com/project/Ndjole-Mangenese-Gold-Mine-Project.php) and the footprint of this mining activity along the Ogooué River is clearly visible on Google Earth™ imagery (accessed 15th August 2018). This is likely to have impacted upon habitat suitable for this species. There is still extensive intact forest habitat elsewhere within its range, and this species is likely to occur at other localities within this small range. However, based on current knowledge, with an EOO of less than 5000 km^2, fewer than five locations and an inferred decline in extent and quality of habitat due to mining activities, this species is provisionally assessed as **Endangered** - EN B1ab(iii).

NOTES. This species is well illustrated in Heine (1966: pl. XXXVIII 10 – 13). The anthers are illustrated in Fig. 5 here.

Sosef (2006) also lists *Mayombo-Nzengue* 390 (LBV) under this species but this collection number is listed as a Zingiberaceae in the LBV database and only *Mayombo-Nzengue* 271 is housed under *Justicia tigrina* at LBV (P. Bissiengou, pers. comm.). Further, Sosef *et al.* (l.c.) list *Arends* 570 (WAG) as *Justicia* cf. *tigrina* but this specimen was redetermined by D. Champluvier as *J. tristis* T.Anderson, and we concur with this identification.

We have not seen the pollen of this species. Clarke (1900b) recorded the pollen as "globose with 12 equidistant ribs not reaching the pores" (p. 235) and illustrated it as such on a sheet of paper attached to the holotype specimen. He thought that there were 6 equidistant pores on the grains which supported the placement of this species in *Chlamydocardia* (see Darbyshire & Govaerts 2017), but this does not seem to fit with the presence of 12 'ribs.' If the grains are colporate and pseudocolpate, then 12 ribs would suggest four germinal apertures — if Clarke (1900b) was correct then these grains are quite different to those of *C. populifolia* described above.

Heine (1966) notes the presence of "sterile floral buds" in this species — these are presumably cleistogamous flowers, which are not uncommon in some genera of Acanthaceae, for example in *Isoglossa* (Darbyshire *et al.* 2012).

Asystasia lindauiana Hutchinson & Dalziel (1931: 257) could potentially be confused with *Champluviera* on morphological grounds and has a sympatric distribution, hence is worthy of mention here. The two are superficially very similar both in vegetative characters and inflorescence form, sharing a terminal many-flowered spiciform thyrse. Indeed, Clarke (1900b) remarked on this close superficial similarity when describing *Chlamydocardia nuda*. However, *A. lindauiana* is easily separated from *Champluviera* in having four stamens (a character shared by all species of *Asystasia*), and in the anthers having thecae markedly offset and lacking basal appendages. Molecular evidence confirms that these genera are not closely related, with *Asystasia* falling within the "*Pseuderanthemum* lineage" of Justicieae (McDade *et al.* 2000).

2. *Kenyacanthus* — a new monotypic genus endemic to Kenya

Notable morphological differences exist between *Rhinacanthus ndorensis* and species of *Rhinacanthus* s.s. In particular, *R. ndorensis* is unique in *Rhinacanthus* in the positioning of stamens, these being held against the lower lip of the corolla with thecae dehiscing towards the upper lip (i.e. flowers are stenotribic; Kiel *et al.* 2017). In *Rhinacanthus* s.s., the stamens are held between the two lips and dehisce toward the lower lip

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(i.e. flowers are nototribic). The two lips of the corolla in *R. ndorensis* are subequal in size, whilst in other *Rhinacanthus* the upper lip is markedly smaller and usually much narrower than the lower lip (Darbyshire & Harris 2006; Darbyshire *et al.* 2018). In addition, as noted in the Introduction, *R. ndorensis* can be separated by its procumbent or trailing habit, fasciculate inflorescences, hyaline margins to the bracts, bracteoles and calyx lobes and essentially glabrous capsules. In other species of *Rhinacanthus*, plants are erect, decumbent or straggling, the inflorescences are usually lax panicles or spikes (although fascicled in *R. rotundifolius* C.B.Clarke), the bracts, bracteoles and calyces lack hyaline margins and the capsules are variously puberulous to pubescent with eglandular and/or glandular trichomes (Darbyshire & Harris 2006). These morphological differences support the findings of the molecular analysis (Fig. 2) that *R. ndorensis* is not closely related to *Rhinacanthus* s.s.

Rhinacanthus ndorensis has 3-colporate, 6-pseudocolpate pollen (Fig. 7), a pollen type that is hypothesised to be synapomorphic for Justicieae as a whole (Kiel *et al.* 2017) and that thus does not contribute to assessing the phylogenetic position of *R. ndorensis* within Justicieae.

The placement of *Rhinacanthus ndorensis* sister to core Diclipterinae, as confirmed in our analysis here (Fig. 2), is not surprising on morphological grounds, as this species could easily be confused with a member of the genus *Dicliptera*. Indeed, the general corolla morphology, with the lips being widely divergent and subequal in size, is very similar to that of African *Dicliptera*. Inflorescences of *Dicliptera* are typically of monochasial units (cymules) with conspicuous paired clasping bracts that are often umbellately arranged (Balkwill *et al.* 1996; Darbyshire 2009). However, some species have solitary or fascicled axillary inflorescences

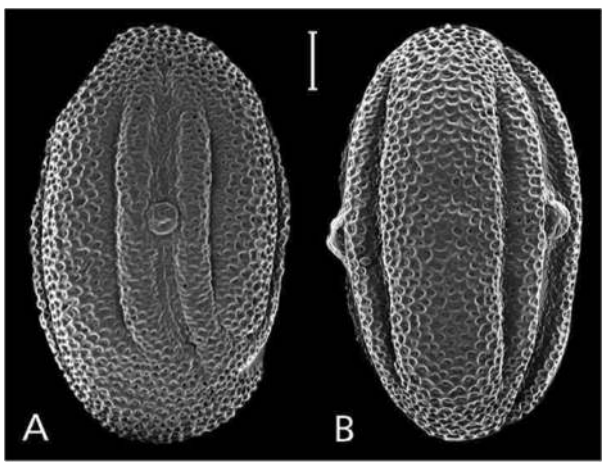


Fig. 7. Pollen of *Kenyacanthus ndorensis*. **A** equatorial view showing the compound aperture and pseudocolpi; **B** equatorial view showing the mesocolpium (from *Luke* 17084).

with reduced cymule bracts (e.g. *D. minutifolia* Ensermu from Ethiopia and Kenya; Ensermu 2003; Darbyshire *et al.* 2010) which are similar to the inflorescences of *R. ndorensis*. Furthermore, hyaline margins on the bracts, bracteoles and calyces are fairly widespread in *Dicliptera* (see, for example, Balkwill *et al.* 1996; Darbyshire *et al.* 2010). However, *R. ndorensis* differs significantly from *Dicliptera* in floral morphology. In *R. ndorensis* the corolla tube is straight, not twisted, and, as noted above, the flowers are stenotribic with the stamens held against the lower, 3-lobed lip of the corolla (Fig. 8). All OW species and many NW species of *Dicliptera* (and all species in the related genus *Hypoestes*) have a resupinate corolla, in which the tube is twisted through ± 180°, thus the 3-lobed "lower" lip is held in the upper position, although Daniel & Figueiredo (2009) note that in "*D. verticillata* (Forssk.) C.Chr." (possibly = *D. hyalina* Nees) from São Tomé the tube can be twisted by only 90° such that the limb is held on its side. In these resupinate-flowered species, the flowers are effectively stenotribic. However, the positionally lower 2-lobed lip that the stamens are held against is actually the upper lip morphologically. In his synopsis of the species of *Dicliptera* in the Nueva Galicia region of western Mexico, Daniel (2009) noted three distinct floral forms: tube twisted through 180°, tube twisted through 360° and tube untwisted. The latter two cases both result in non-resupinate corollas in which the 3-lobed lip is in the "normal" lower position. In these non-resupinate forms, the flowers are nototribic with the stamens held close to the upper corolla lip, quite different to those of *R. ndorensis*. The species of *Dicliptera* with non-resupinate flowers in the NW have large, brightly coloured and unspeckled red, orange-yellow or purple corollas that appear to be adapted for bird pollination (Daniel 2009; Kiel *et al.* 2017). These are quite unlike the small, pink flowers of *R. ndorensis*. The stamens of *Dicliptera* are usually exserted well beyond the corolla mouth and not appressed to the corolla lip as in *R. ndorensis*. Further, *R. ndorensis* differs from all African members of *Dicliptera* in having only slightly offset as opposed to fully superposed anther thecae. This character is, however, more variable in some species of NW *Dicliptera* (Kiel *et al.* 2017).

Rhinacanthus ndorensis is further separated from most taxa in core Diclipterinae by the presence of a rugula (stylar furrow), which in *R. ndorensis* comprises two raised ciliate bands of tissue running dorsally along the corolla tube and base of the upper lip (Fig. 9F), similar to the rugula seen in *Rhinacanthus* s.s. Whilst rugulas are widespread in the justicioid lineage, they are mainly lacking or indistinct in the core Diclipterinae lineage including *Dicliptera* (Balkwill & Welman 2000; Darbyshire & Vollesen 2007). The rugula is hypothesised to hold the style in position during anthesis, and it has been suggested that the loss

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of the rugula in core Diclipterinae occurred as a correlate of corolla resupination (Kiel *et al.* 2017), where the twisting of the corolla tube may hold the style in position. That said, recent observations on putatively bird-pollinated species of *Hypoestes* from Madagascar with elongate, expanded corolla tubes such as *H. isalaensis* Benoist have revealed the presence of a shallow rugula of two raised, ciliate lines not dissimilar to the rugula in *R. ndorensis* (I. Darbyshire, pers. obs.). It may be that this character is more widespread in taxa of Diclipterinae with enlarged corolla tubes.

Monechma Group II is sister to (*Rhinanthus ndorensis* (*Hypoestes* + *Dicliptera* s.l.)) (Fig. 2); the former is one of two widely separated clades comprising the non-monophyletic genus *Monechma* Hochst. (= *Justicia* L. sect. *Monechma* (Hochst.) T.Anderson). However, *R. ndorensis* is unlikely to be confused morphologically with species of *Monechma* Group II as these plants have broader cylindrical corolla tubes, usually subequal in length to the limb, a markedly hooded upper corolla lip, stamens with a conspicuous appendage on the lower anther theca, capsules with two seeds and the seeds having a smooth testa. *Rhinacanthus ndorensis*, on the other hand, has a narrowly cylindrical tube clearly longer than the limb, the upper corolla lip is not hooded, the stamens lack appendages, the capsule is 4-seeded and the seeds are sculptured (Fig. 9J).

In summary, phylogenetically, *Rhinacanthus ndorensis* forms an isolated clade composed of, so far as known, a single species that is placed between (*Hypoestes* + *Dicliptera* s.l.) and the *Monechma* Group II (Fig. 2). Regarding morphological traits, *R. ndorensis* appears to be intermediate between plants belonging to the core Diclipterinae and those of the other clades that are part of the expanded Diclipterinae as recognised by Kiel *et al.* (2017), as described above (Figs 8 and 9). Thus, morphology and phylogenetic relationships based on DNA data are congruent.

Kiel *et al.* (2017) reviewed the potential taxonomic implications of their findings on the complex relationships within the "justicioid" lineage, and five potential solutions were offered. They noted that in order to maintain a broadly circumscribed *Justicia* as is currently widely accepted (see, for example, Graham 1988; Vollesen in Darbyshire *et al.* 2010), the entire "justicioid" lineage would potentially have to be treated as a single genus. This is highly undesirable as it would mean subsuming several genera that are easily separated by morphological differences, including those within Diclipterinae. The most credible solution offered therefore appears to be to divide *Justicia* s.l. into a number of segregate genera and to uphold the morphologically distinct genera such as *Dicliptera*, *Hypoestes* and *Rhinacanthus* s.s. Whilst the taxon sampling in Kiel *et al.* (2017) was insufficiently dense to support full revision of generic delimitations among justicioids, the strong morphological and molecular evidence presented here supports the recognition of a new genus to accommodate *R. ndorensis*, allied to but clearly separated from *Dicliptera, Monechma* and *Rhinacanthus*. In consequence, the new genus *Kenyacanthus* I.Darbysh & C.A.Kiel is described below.

Taxonomic Treatment

Kenyacanthus *I.Darbysh. & C.A.Kiel* **genus nov.** Type species: *Kenyacanthus ndorensis* (Schweinf.) I.Darbysh. & C.A.Kiel.

http://www.ipni.org/urn:lsid:ipni.org:names:77197855-1

Perennial herbs, with trailing or procumbent branches radiating from a small woody base; stems markedly angular with 2 opposite pairs of ridges. *Leaves* opposite-decussate, sessile or very shortly petiolate, pairs isophyllous, blade obovate or obovate-elliptic; cystoliths present, shortly linear, numerous but often inconspicuous. *Inflorescences* axillary, sessile or shortly pedunculate fasciculate cymes of (1 –) 2 – 3 flowers, bracts and bracteoles paired, linear-lanceolate, green with hyaline margins. *Calyx* shortly tubular, deeply

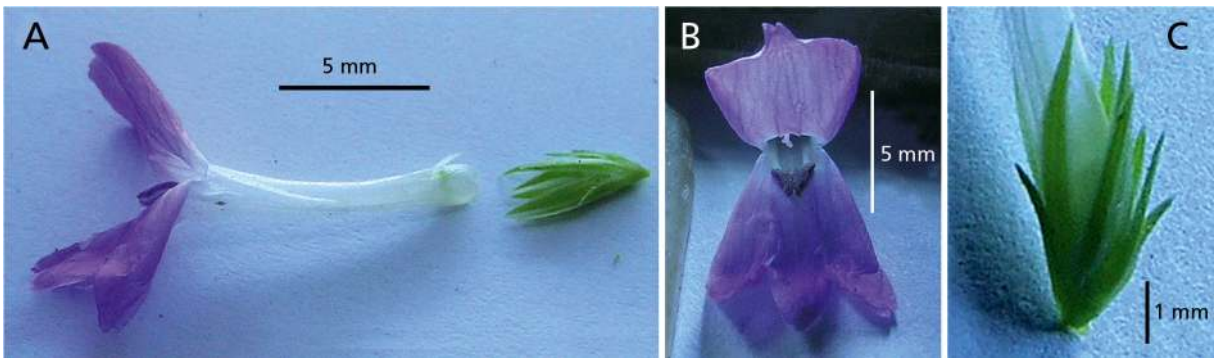


Fig. 8. *Kenyacanthus ndorensis*. A flower, lateral view; B flower, face view; C bracts, bracteoles and calyx with corolla base (photographed from plant cultivated by W. R. Q. Luke).

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divided into five lobes, these subequal, linear-lanceolate with hyaline margins, shorter than the bracteoles. *Corolla* with rugula present, comprising two slender ciliate ridges extending from near base of corolla tube to proximal portion of upper lip; tube slender, longer than limb, gradually widened towards the mouth; aestivation ascending-cochlear, limb bilabiate; upper lip ovate or elliptic, apex shortly bilobed or emarginate, lower lip conspicuously 3-lobed, palate with faint raised venation. *Stamens* 2, inserted on ventral side of corolla tube just below the corolla mouth; filaments short; anthers shortly exserted, held ± adpressed to the lower lip, dehiscing toward upper lip (i.e. flowers stenotribic), bithecous, thecae ± parallel, slightly offset, lacking basal appendages; staminodes absent. *Floral disk* cupular, ± 0.5 mm tall, with unevenly undulate margin. *Ovary* oblong-ellipsoid, 4-ovulate; style filiform; stigma minutely bilobed, one lobe slightly larger than the other. *Capsule* 4-seeded (or fewer by abortion), retinaculate, stipitate and with attenuate apex; seeds tuberculate.

RECOGNITION. *Kenyacanthus* is recognised by having the combination of a trailing or procumbent habit; fasciculate inflorescences; bracts, bracteoles and calyces with hyaline margins; a bilabiate corolla with a slender cylindrical tube longer than the limb and with a shallow rugula; and two stamens held against the lower corolla lip and anthers with slightly offset thecae, the flowers being stenotribic. It differs from *Rhinacanthus* primarily in the trailing or procumbent habit; hyaline margins to the bracts, bracteoles and calyx lobes; two corolla lips of subequal size; stenotribic flowers and essentially glabrous capsules (vs plants erect, decumbent or straggling; bracts etc. lacking hyaline margins; upper corolla lip markedly smaller and narrower than the lower lip; flowers nototribic and capsules puberulous to pubescent in *Rhinacanthus*). It differs from *Dicliptera* primarily in the combination of a straight, untwisted corolla tube and stenotribic flowers (vs corolla tube twisted through ± 180° such that the corolla is resupinate, or if corolla tube untwisted then flowers nototribic in *Dicliptera*); it also differs from all African *Dicliptera* in the anther thecae being only partially offset (vs fully superposed).

ETYMOLOGY. *Kenyacanthus* is named in honour of the Republic of Kenya, to which this genus is apparently endemic based on current evidence.

Kenyacanthus ndorensis (*Schweinf.*) *I.Darbysh. & C.A.Kiel* **comb. nov.**

http://www.ipni.org/urn:lsid:ipni.org:names:60478965-2

Rhinacanthus ndorensis Schweinfurth in Höhnel, *Zum Rudolph-See und Stephanie-See*: 858 (1892); Engler (1892: 394), nom. nud.; Schweinfurth (1894: 357); Clarke (1900a, 1900b: 225); Mildbraed (1926: 504); Agnew (2013: 327, pl. 129C); Lebrun & Stork (1997: 500) as "sont mal connus"; Darbyshire *et al.* (2010: 602). Type: Kenya, Ndoro, foot of Mt Kenya, fr. 1887 – 1888, *Höhnel* s.n. [*Höhnel* 76 per Engler 1892] (B† holotype; BM! [BM001011739] lectotype, **selected here** — see note); Nyeri County, Nanyuki-Naromoru, near pt. 866 (Ndoro?), fl. & fr. 7 Feb. 2016, *Luke* 17084 (EA! epitype, **selected here**; K! isoepitype).

Procumbent or trailing perennial herb, branching widely from a small woody base and rootstock, forming small mats in the ground layer; young stems with two prominent pairs of opposite ridges and two broader opposite ridges, glabrous except for tufts of multicellular trichomes along the nodal lines. *Leaves* sessile or on a poorly defined petiole to 3 mm long; blade fleshy, obovate (-elliptic), 0.8 – 1 (– 1.4) × 0.45 – 0.6 (– 0.75) cm, base cuneate, margin entire, apex obtuse or rounded, surfaces glabrous except for minute trichomes along the margin; lateral veins 3 (– 4) pairs. *Inflorescences* axillary, fasciculate, (1 –) 2 – 3-flowered; peduncle 0 – 3 mm long, glabrous; bracts linear-lanceolate, 5.5 – 9 mm long, green with narrow hyaline margin at least in the proximal half, ciliate with trichomes of variable length, midrib prominent abaxially, apex minutely apiculate; bracteoles resembling bracts but 5 – 8.5 mm long, more gradually narrowed towards apex, margin more conspicuously hyaline; flowers sessile. *Calyx* with short basal tube 0.7 – 0.8 mm long; lobes linear-lanceolate, 3.7 – 5.5 mm long, margins narrowly hyaline, ciliate, surfaces with sparse short ascending trichomes. *Corolla* (13 –) 15 – 18.5 mm long, bright pink to mauve, rather densely retrorse-pubescent externally; tube (8 –) 10 – 11 mm long, 1 – 1.5 mm in diam. centrally, widening somewhat towards mouth, with scattered minute glandular trichomes on internal surface, rugula of two raised lines of trichomes on dorsal side of tube and barely extending onto upper lip; lips widely divergent, upper lip suberect, ovate or elliptic, 5 – 7 × 3 – 3.7 mm, glabrous internally, apex shortly bilobed or emarginate; lower lip pendant, 6 – 7.5 mm long, glabrous internally, lobes oblong, 2.5 – 3 × 1.4 – 1.8 mm, apices obtuse or rounded with irregular margins, median lobe slightly longer and narrower than lateral pair. *Stamens* with filaments 1.2 – 2.3 mm long, glabrous; anther thecae offset by 0.25 – 0.3 mm, each theca 1 – 1.5 mm long, basally muticous. *Pollen* prolate, 3-colporate, 6-pseudocolpate, polar diameter (P) 35 – 37 µm, equatorial diameter (E) 20 – 22.5 µm, P:E = 1.57 – 1.8, ora ± the same width as the colpi, the pseudocolpi parallel to the colpi, interaperatural exine reticulate. *Ovary* ± 1.5 mm long, glabrous; style ± 8.5 mm long, ± sparsely appressed-pubescent or glabrous. *Capsule* 8 – 10 mm long,

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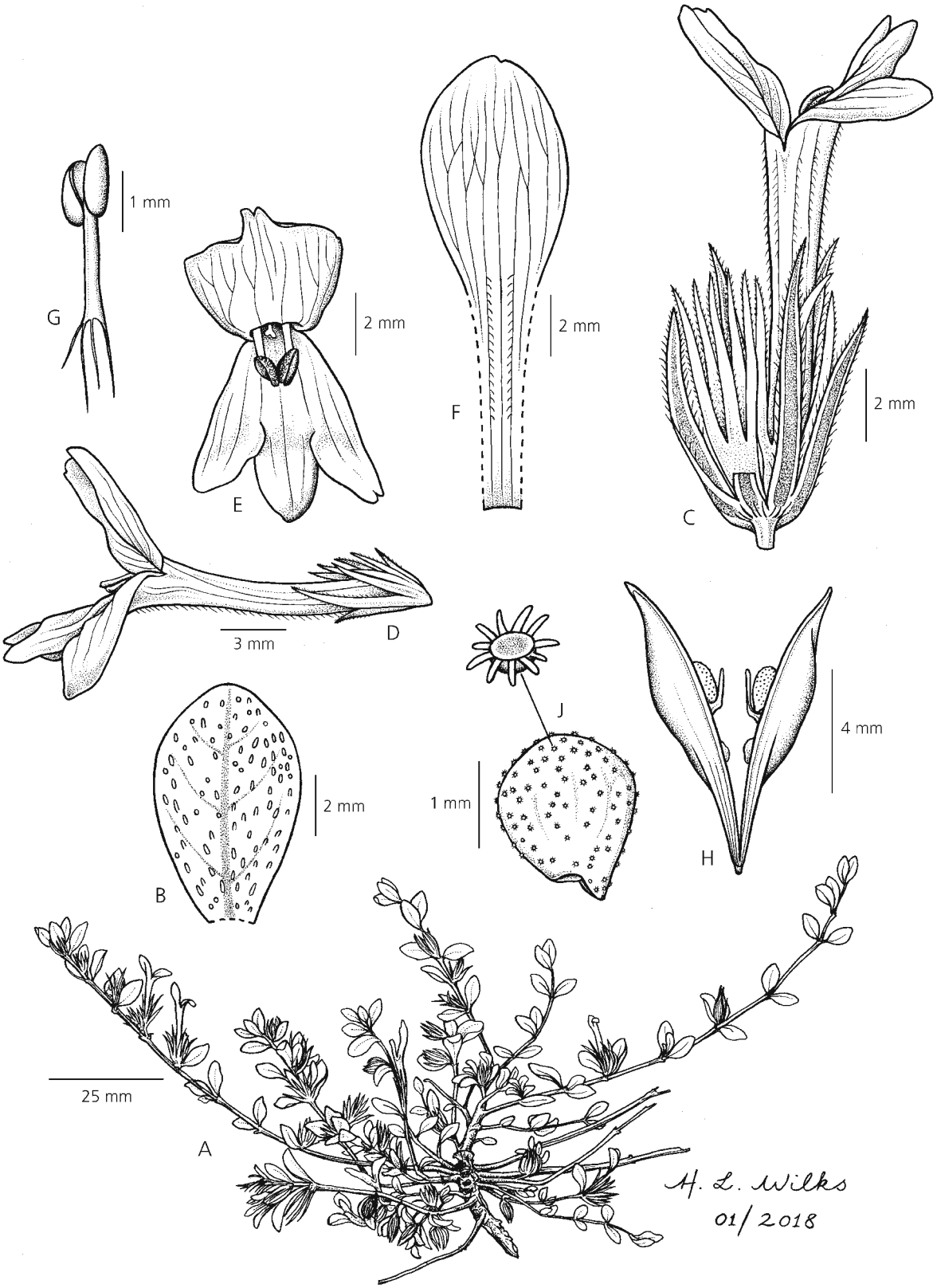


Fig. 9. *Kenyacanthus ndorensis*. **A** habit; **B** leaf, adaxial surface with cystoliths; **C** inflorescence, with one bracteole cut away at base to show the calyx; **D** flower, lateral view; **E** flower, face view showing position of stamens; **F** upper lip and dorsal side of corolla tube, showing the rugula; **G** stamen; **H** capsule; **J** seed, with detail of one tubercle. Drawn from *Battiscombe* 721 except **J** from *Luke* 17084 and **D** & **E** from photos. by W. R. Q. Luke. DRAWN BY HAZEL WILKS.

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glabrous or with very few inconspicuous trichomes towards apex; seeds blackish at maturity, 1.3 – 1.8 mm in diameter, tuberculate, the tubercles short, rounded with minute glochidia. Figs. 8, 9 and 10.

DISTRIBUTION. Kenya (Laikipia and Nyeri Counties; *Flora of Tropical East Africa* floristic regions K3 and K4); Map 2.

SPECIMENS EXAMINED. KENYA. Unplaced: West Kenya plains, fl. & fr. 29 July 1913, *Battiscombe* 721 (K! 2 sheets, EA photo!). **Laikipia County:** Rumuruti, NE slope Aberdare Mts, fl., without date [received at K: 22 Sept. 1915], *Dowson* 561 (EA!, K!); Nanyuki, fl. May 1932, *Napier* 2093 (EA!); Solio Ranch, 20 miles SW of Nanyuki, fl. 4 April 1973, *Elliott* 33 (EA!); Laikipia Distr., Rumuruti, fl. & fr. 5 Nov. 1978, *Hepper & Jaeger* 6626 (EA!, K!); Mpala, 1800 m, fl. & fr. 5 Nov. 1992, *Young* 3169 (EA!); Laikipia Distr., Nanyuki, Batuk, Laikipia Airbase, 5 km NW Nanyuki town, fl. 18 March 2010, *Malombe & Kimeu* BATUK 1594 (EA!). **Nyeri County:** Ndoro, foot of Mt Kenya, fr. 1887 – 1888, *Höhnel* s.n. (BM! lectotype); Cole's Mill, fl. 17 Jan. 1922, *Fries* 1001 (BM!); Nyeri, Amboni R., fl. & fr. 18 Jan. 1933, *Napier* 2579 (EA!, K!); Nanyuki, fl. Dec. 1933, *Minns* s.n. [in Coryndon Museum 5881] (EA!); 3 miles SE Nanyuki Station, fl. 19 June 1943, *Moreau & Moreau* 34 (EA!); North Nyeri Distr., Nyeri to Nanyuki, c. 40 km S Nanyuki, fl. 3 April 1975, *Hepper & Field* 4838 (K!); Nanyuki-Naromoru, near pt. 866 (Ndoro?), fl. & fr. 7 Feb. 2016, *Luke* 17084 (EA! epitype, K! isoepitype).

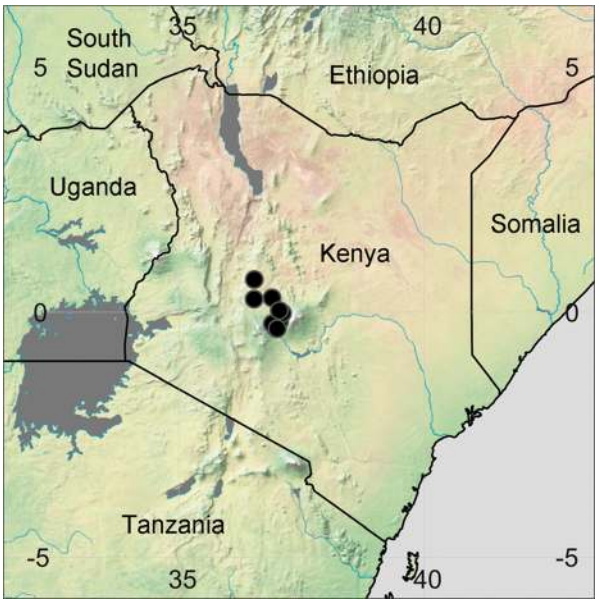
HABITAT & ECOLOGY. This species occurs in upland grassland and open woodland, including *Acacia drepanolobium* Harms ex Y.Sjöstedt woodland, where it can form small mats amongst the grasses in the ground layer of the vegetation (Fig. 10). These mats are conspicuous during the dry season, appearing green amongst the dried brown grasses (Odadi *et al.* 2013). It can also sometimes be found along road verges. It often grows on seasonally damp black clay soils; 1700 – 2150 m elevation.

PHENOLOGY. From the limited information available, mainly derived from specimen data, this species appears to have a prolonged flowering season, recorded from early November through to late July. This



Fig. 10. Habit of *Kenyacanthus ndorensis* in the field, collected as *Luke* 17084. PHOTO: W. R. Q. LUKE.

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Map 2. Distribution of *Kenyacanthus ndorensis* (black circles).

spans the period of the two rains — the first rains occur primarily in October and November whilst the peak rains fall in April to May. The intervening period is dry, with January being the driest month.

CONSERVATION STATUS. Darbyshire *et al.* (2010) considered this species to be Near Threatened (NT) based on its very restricted range (the EOO is approx. 3050 km^2), with few collections known, and with potential loss of habitat due to expansion of agriculture. It can be locally frequent to abundant in suitable habitat (W. R. Q. Luke, pers. obs.) and is regularly consumed by cattle as an important fodder during dry periods (Odadi *et al.* 2013). However, in some parts of its range it is threatened by widespread habitat loss through conversion to commercial pastoral agriculture and the global population is considered to be declining. This species has, therefore, recently been provisionally assessed as **Endangered** (EN B1ab(ii,iii,iv)+2ab(ii,iii,iv)) by the East African Plant Red List Authority (W. R. Q. Luke *et al.*, unpubl. data). This assessment is awaiting publication on the IUCN Red List.

NOTES. From Fig. 8 and the discussion above, it is apparent that during at least a significant portion of anthesis (if not throughout) the stamens and anthers are held adjacent to the lower lip whereas the style and stigma are adjacent to the upper lip. This poses the question as to how pollen is transferred by pollinators from the anthers to the stigma, when these two organs are held on opposite sides of the corolla mouth. Field observations are required to document the position of the anthers and stigma throughout anthesis and also to document pollinator interactions in order to resolve this issue.

The author for *Rhinacanthus ndorensis* has sometimes been given as Schweinf. ex Engl. (e.g. see Klopper *et al.* 2006: 18). This is based on Engler (1892: 394) who recorded "*Rhinacanthus ndorensis* Schweinf. nov. spec. msc." then cited the proposed type specimen, which he listed as *v. Höhnel* 76. However, the only description provided states "Gebüschpfl." (i.e. bushy plant), a phrase applied to multiple taxa within Engler's work and not considered to be sufficient to constitute a description as per Article 38.1 of the Botanical Code, hence Engler (1892) did not validly publish the name *R. ndorensis*. A short but sufficient description was provided by Schweinfurth (1892: 858) together with the type citation, which validated the name.

The extant material of the *Höhnel* type specimen at BM is only a very small scrap with a few leaves, an inflorescence and an immature fruit; the holotype specimen at B is believed to have been destroyed during World War II. An epitype is therefore selected to supplement the lectotype, and *Luke* 17084 is chosen as it was collected from a site near Naromoru which a local informant said had previously been known as 'Mukiri wa Ndoro' (translated as "valley of mud" in Kikuyu); this is quite likely to be the same as the Ndoro of the original type locality.

The general habit, of trailing stems with axillary (sub)sessile clusters of flowers, is superficially most reminiscent of trailing members of the genus *Dyschoriste* Nees which is distantly related, in tribe Ruellieae of Acanthaceae (Tripp *et al.* 2013). Indeed, both Mildbraed (1926) and Agnew (2013) remark upon this potential confusion. However, *Dyschoriste* is easily separated from *Kenyacanthus* in, amongst other differences, having a markedly tubular calyx, an androecium comprising 4 fertile stamens or 2 fertile stamens + 2 staminodes, left-contorted corolla aestivation and seeds with hygroscopic trichomes.

Acknowledgements

We are highly indebted to Dominique Champluvier (formerly of BR) for providing useful information on the species of *Champluviera* treated here. We thank Hazel Wilks for the line drawings of *Champluviera populifolia* and *Kenyacanthus ndorensis*, and Martin Cheek and Jo Osborne (both K) for allowing us to use their photographs of *C. populifolia*. Heather Lindon is thanked for her assistance with the nomenclatural history of *Rhinacanthus ndorensis*. Aurélie Grall (R.B.G. Kew) assisted with the SEM analysis of pollen grains of *R. ndorensis* and Hannah Armer (Manager of the Light Microscopy Imaging Suite, Natural History Museum, London) very kindly photographed the stamens of *Champluviera nuda* presented in Fig. 5. We thank the curators of the herbaria visited for providing access to the collections of the study taxa, notably Itambo Malombe (EA) and Ranee Prakesh (BM). Pulchérie Bissiengou kindly checked for specimens

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of *J. tigrina* at the LBV herbarium on our behalf and sent scanned images of *Mayombo-Nzengue* 271 which were very helpful. This work was supported by grants from the U.S. National Science Foundation to CAK (DEB1754845); TFD (DEB0743273, DEB 0108589, BSR 8304790) and LAM (DEB 9707693, DEB 0108589, DEB 0743178, DEB 1754845).

Appendix 1

Taxa, sources of plant materials from which DNA was extracted for sequencing and GenBank accession numbers (*trnS-G*, *trnT-L*, *rps16*, *trnL-F*, nrITS; – = sequence not obtained); when a given taxon is not depicted by name as a terminal in Figs. 1 or 2, the last entry indicates the clade where that taxon is placed in our results (clade names are as given in Figs 1 and 2). Taxa are listed in alphabetical order by genus and species. When plants in cultivation were used, we provide information on native range in parentheses. GenBank numbers beginning with MF and MK are new to this study.

Ancistranthus harpochiloides Lindau; Cuba, *Shafer* 13404 (US) MF670371, MF768291, MF678397, MF768343, MF768396; *Tetramerium* lineage. *Angkalanthus oligophylla* Balf.f.; Yemen (Socotra), *Miller* M10292 (UPS) EU081105, EU081172, EU087533, EU087567, EU087478; *Tetramerium* lineage. *Anisacanthus gracewoodiae* Hammel & McDade; Costa Rica, *Hammel et al.* 26865 (RSA) MF670359, MF768281, MF678386, MF768327, MF768385; *Tetramerium* lineage. *Anisotes formosissimus* Milne-Redh.; cultivated, Lowveld National Botanical Garden, South Africa: Mpumalanga (native to South Africa), *Daniel* 9382 (CAS) KY584162, KY632232, MK282280, MK282352, KY632576; Old World justicioid lineages. *Anisotes macrophyllus* (Lindau) Heine; Uganda, *Synnott* 488 (EA) KY584141, KY632212, –, MK282353, MK282341; Old World justicioid lineages. *Anisotes madagascariensis* Benoist; Madagascar, *Daniel & Butterwick* 6736 (CAS) KY584157, KY632227, MK282280, MK282354, AF289772; Old World justicioid lineages. *Anisotes rogersii* S.Moore; South Africa, *McDade* 1265 (J) KY584140, KY632211, MK282282, MK282355, KY632560; Old World justicioid lineages. *Aphelandra leonardii* McDade; Costa Rica, *McDade* 310 (DUKE) DQ059287, EU529071, DQ059205, AF063112, AF169761; outgroup.

Barleria lupulina Lindl.; cultivated, San Francisco Conservatory of Flowers, San Francisco, U.S.A. (native to Madagascar), *Daniel* s.n. (CAS) EU528946, EU529075, EU529010, AF289758, AF169751; outgroup. *Brachystephanus africanus* S.Moore; Tanzania, *Luke et al.* 6704 (US) DQ372491, DQ372446, EU087537, MF768374, DQ372469; core Isoglossinae. *Calycacanthus magnusianus* K.Schum.; cultivated, Royal Botanic Gardens, Sydney (native to Papuasia), *Daniel* 10072 (CAS) EU081108, EU081175, EU087536, MK282356, EU087481. *Thyrsacanthus sulcatus* (Nees) C.Ezcurra & A.L.A.Côrtes; Paraguay, *Schinini & Bordas* 18098 (MO) MF670373, MF768293, MF678398, MF768346, MF768399; *Tetramerium* lineage. *Cephalacanthus maculatus* Lindau; Peru, *Veja & Dillon* 8517 (F) KY584123, KY632195, KY632029, KY632353, KY632505, KY632545; New World justicioid lineage. *Chlamydocardia buettneri* Lindau; cultivated, National Botanic Garden of Belgium (native to Cameroun, Gabon, Ivory Coast and Nigeria), Accession No. 95-0034-44 (BR) EU081107, EU081174, EU087535, EU087569, EU087480; *Tetramerium* lineage. *Chlamydostachya spectabilis* Mildbr.; *Poest Knox* 88192/4 (K) KY584160, KY632230, MK282283, MK282357, KY632574; Old World justicioid lineages. *Chorisochora transvaalensis* (A.Meeuse) Vollesen; South Africa, *Daniel* 9379 (CAS) EU081100, EU081167, EU087528, EU087565, EU087474; *Tetramerium* lineage. *Clinacanthus siamensis* Bremek.; cultivated, National Botanic Garden of Belgium (native to Thailand), Accession No. 1979-0344 (BR) EU081106, EU081173, EU087534, EU087568, EU087479; *Tetramerium* lineage. *Clistax brasiliensis* Mart., Brazil, *Lombardi* 2257 (US) KY584112, KY632186, MK282284, MK282358, KY632537; New World justicioid lineage. *Conocalyx laxus* Benoist; Madagascar, *Leandri* 3033 (P); DQ372485, DQ372440, –, MK282359, MK282342; core Isoglossinae.

Dicliptera extenta S.Moore; South Africa, *McDade* 1306 (J) EU528955, EU529084, EU529018, AF289724, KC420542; *Dicliptera* s.l. *Dicliptera insularis* Benoist; Madagascar, *Daniel* 9194 (CAS) KY584194, –, MK282285, AF289723, AF289764; *Dicliptera* s.l. *Dicliptera magaliesbergensis* K.Balkwill; South Africa, *Daniel* 9357 (CAS) KY584192, MK282273, –, AF289725, KY632607; *Dicliptera* s.l. *Dicliptera resupinata* Juss.; United States, *Boyd* s.n. (ARIZ); KY584189, EU529084, EU529019, MK282360, AF169841; *Dicliptera* s.l. *Dicliptera suberecta* (André) Bremek., cultivated, University of Arizona (native to Argentina, Bolivia, Paraguay), *McDade* 1176 (ARIZ) KY584188, KY632257, MK282286, AF289722, AF289763; *Dicliptera* s.l.

Henrya insularis Nees ex Benth; Mexico, *Jenkins* 89-432 (ARIZ) EU081071, EU081142, EU087507, AF063125, AF169843; *Tetramerium* lineage. *Hoverdenia speciosa* Nees; Mexico, *Daniel & Baker* 3739 (CAS) EU081089, EU081157, EU087519, AF289738, AF289777; *Tetramerium* lineage. *Hypoestes sp.*; Madagascar, *Daniel & McDade* 10433 (CAS) KY584203, KY632274, MK282287, MK282361, –; *Hypoestes* clade. *Hypoestes*

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aristata (Vahl) Sol. ex Roem. & Schult.; cultivated, San Francisco Conservatory of Flowers (East Africa, South Africa, Madagascar), *Daniel* s.n. (CAS) KY584208, KY632279, MK282288, AF289726, KY632625; *Hypoestes* clade. *Hypoestes phyllostachya* Baker, cultivated University of Arizona (widespread in OW tropics), *McDade* 1232 (ARIZ) KY584207, KY632278, EU529025, AF195520, AF169842; *Hypoestes* clade.

Isoglossa gracillima Baker; Madagascar, *Daniel* 9106 (CAS) DQ372488, DQ372443, MK282289, AF289746, AF289789; core Isoglossinae. *Isoglossa grandiflora* C.B.Clarke; Cultivated, San Francisco Conservatory of Flowers, San Francisco, CA, U.S.A. (Malawi, Tanzania, Zambia), *Daniel* s.n. (CAS) DQ372490, DQ372445, MK282290, AF289745, AF289788; core Isoglossinae. *Isoglossa ovata* (Nees) Lindau; South Africa, *Daniel* 9336 (CAS) DQ372487, DQ372442, EU529027, MK282362, DQ372468; core Isoglossinae.

Jadunia biroi (Lindau & K.Schum.) Lindau, Papua New Guinea, *Daniel et al.* 6603 (CAS) MK282333, MK282274, MK282291, MK282363, MK282343. *Justicia sp.;* Cameroon, *Tchiengue* 2518 (K) MK282268, MK282269, MK282270, MK282271, MK282344. *Justicia sp.*; Madagascar, *Daniel* 9024 (CAS) KY584182, KY632251, MK282292, AF289729, AF289768; Old World justicioid lineages. *Justicia sp.*; Madagascar, *Daniel et al.* 10446 (CAS) KY584138, KY632210, MK282293, MK282365, KY632559; Old World justicioid lineages. *Justicia aconitiflora* (A.Meeuse) Cubey; cultivated, San Francisco Conservatory of Flowers (native to South Africa), *Daniel et al.* 9361 (CAS) KY584161, KY632231, MK282294, AF289735, AF289774; Old World justicioid lineages. *Justicia adhatoda* L.; cultivated, University of Arizona (native to South Africa), *Barr* 60-393 (ARIZ) KY584158, EU081109, DQ059214, AF289734, AF289773; Old World justicioid lineages. *Justicia americana* (L.) Vahl; United States, *Daniel & Lott* 10530 (CAS) KY584096, KY632173, MK282295, MK282366, KY632522; New World justicioid lineage. *Justicia anagalloides* (Nees) T.Anderson; cultivated NBI Garden, South Africa (native to Africa), *McDade & Balkwill* 1239 (J) KY584151, KY632221, MK282296, MK282367, MK282345; Old World justicioid lineages. *Justicia andromeda* (Lindau) J.C.Manning & Goldblatt; South Africa, *Balkwill et al.* 11660 (J) KY584146, KY632216, MK282297, MK282368, KY632563; Old World justicioid lineages. *Justicia anselliana* (Nees) T.Anderson; Tanzania, *Kiel et al.* 155 (RSA) KY584181, KY632250, MK282298, MK282369, KY632594; Old World justicioid lineages. *Justicia betonica* L.; cultivated, Johannesburg, Gauteng, South Africa (widespread tropical Africa), *Daniel* 9369 (CAS) KY584165, KY632235, MK282299, AF289731, AF289770; Old World justicioid lineages. *Justicia bolusii* C.B.Clarke; cultivated, South Africa (native to South Africa), *Balkwill* s.n. (J) KY584246, KY632313, –, –, KY632656. *Justicia brandegeeana* Wassh. & L.B.Sm.; cultivated, University Arizona (native to Mexico), *Starr* c. 32 (ARIZ) KY584130, KY632203, MK282300, MK282370, KY632553; New World justicioid lineage. *Justicia brasiliana* Roth; Paraguay, *Zardini & Aguayo* 9523 (CAS) KY584118, KY632190, MK282301, MK282371, KY632542; New World justicioid lineage. *Justicia cavernarum* F.Muell.; Australia, *Forster* 28601 (CAS) KY584143, KY632214, MK282302, MK282372, KY632562; Old World justicioid lineage. *Justicia comata* (L.) Lam.; Costa Rica, *Kiel & McDade* 138 (CAS) KY584088, KY632165, MK282303, MK282373, KY632515; New World justicioid lineage. *Justicia flava* (Forssk.) Vahl; South Africa, *McDade et al.* 1256 (J) KY584235, KY632302, MK282304, MK282374, KY632648; *Harnieria* & *Tyloglossa* clades. *Justicia gendarussa* Burm.f.; cultivated, San Francisco Conservatory of Flowers (native to tropical Asia), *Daniel* s.n. (CAS) KY584166, KY632236, MK282305, MK282375, KY632580; Old World justicioid lineages. *Justicia grossa* C.B.Clarke; Thailand, *Von Bousekom & Santisuk* 2699 (L) KY584171, KY632241, MF678390, MF768371, KY632585; *Tetramerium* lineage. *Justicia hassleri* (Lindau) V.A.W.Graham; Bolivia, *Wood* 19750 (CAS) KY584131, KY632204, MK282306, MK282376, KY632554; New World justicioid lineage. *Justicia hyssopifolia* L.; cultivated Kew 1991-1486 (native to Canary Islands) (K) KY584250, KY632317, MK282307, MK282377, KY632659; Old World justicioid lineages. *Justicia linifolia* (Lindau) V.A.W.Graham; South Africa, *Balkwill* 10860 (J) KY584238, KY632305, MK282308, MK282378, KY632651; Old World justicioid lineages. *Justicia longii* Hilsenb.; United States, Arizona, *Van Devender* 87-307 (ARIZ) KY584107, KY632182, MK282309, MK282379, KY632532; New World justicioid lineage. *Justicia odora* (Forrsk.) Lam.; South Africa, *Daniel & Butterwick* 9364 (CAS) KY584241, KY632308, MK282310, MK282380, KY632653; *Harnieria* & *Tyloglossa* clades. *Justicia pacifica* Hemsl.; Mexico, *Kiel et al.* 74 (RSA) KY584103, KY632179, MF678421, MF768367, KY632529; New World justicioid lineage. *Justicia prominens* Benoist; Laos, *Klackenberg* 1383 (S) KY584177, KY632246, MF678395, MF768370, KY632590; *Tetramerium* lineage. *Justicia rhodoptera* Baker; Madagascar, *Daniel & Butterwick* 6741 (CAS) KY584136, KY632208, MK282272, MK282381, KY632557; Old World justicioid lineages. *Justicia ruwenzoriensis* C.B.Clarke; Zaire, *de Witte* 2862 (CAS) KY584164, KY632234, MK282311, MK282382, KY632578; Old World justicioid lineages. *Justicia*

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vagabunda Benoist; China, *Tripp* 1547 (COLO) MK282334, MK282275, MK282312, MK282383, –.

Lepidagathus formosensis C.B.Clarke ex Hayata; Taiwan, *Bartholomew et al.* 7654 (CAS) EU528973, EU529101, EU529034, EU528930, EU529101; outgroup.

Marcania grandiflora J.B.Imlay; Thailand, *Van Beusekom et al.* 3985 (L) MK282335, MK282276, MK282313, MK282384, MK282346. *Megalochlamys revoluta* (Lindau) Vollesen; South Africa, *McDade & Balkwill* 1264 (J) EU081099, EU081166, EU087527, EU087564, EU087473; *Tetramerium* lineage. *Megaskepasma erythrochlamys* Lindau; Costa Rica, *Hammel et al.* 26088 (RSA) KY584120, KY632192, MK282314, MK282385, KY632544; New World justicioid lineage. *Metarungia galpinii* (Baden) Baden; cultivated, Johannesburg, Gauteng, South Africa (native to South Africa), *Daniel* 9322 (CAS) KY584168, KY632238, EU529046, AF289737, KY632582; Old World justicioid lineages. *Metarungia longistrobus* Baden; cultivated, Witwatersrand National Botanic Garden, Roodepoort, South Africa (native to South Africa), *Daniel et al.* 9355 (CAS) KY584169, KY632239, MK282315, MK282386, KY632583; Old World justicioid lineage. *Mirandea huastecensis* T.F.Daniel; Mexico, *Manktelow* 706 (UPS) EU081099, EU081166, EU087527, EU087564, EU087473: *Tetramerium* lineage. *Monechma divaricatum* C.B.Clarke; South Africa, *McDade* 1275 (J) KY584209, KY632280, MK282316, MK282387, KY632626; *Monechma* II clade. *Monechma divaricatum* C.B.Clarke; South Africa, *Daniel et al.* 9373 (CAS) KY584210, KY632281, MK282317, MK282388, KY632627; *Monechma* II clade. *Monechma mollissimum* P.G.Mey.; South Africa, *Balkwill et al.* 11787 (J) KY584211, KY632282, MK282318, MK282389, KY632628; *Monechma* II clade. *Monothecium aristatum* (Nees) T.Anderson; Tanzania, *Abdallah et al.* 512 (US) MK282336, MK282277, MK282319, MK282390, MK282348. *Monothecium glandulosum* Hochst.; Ethiopia, *Friis et al.* 9498 (C) MK282337, MK282278, MK282320, MK282391, MK282347.

Odontonema tubaeforme (Bertol.) Kuntze; cultivated Duke University greenhouse (native to Mexico and Central America), *McDade* 1182 (ARIZ) KY584172, DQ372462, DQ059215, AF063127, AF169748; *Pseuderanthemum* lineage.

Pachystachys lutea Nees; cultivated, Duke University greenhouse (native to Peru), *McDade* 1181 (DUKE) EU081082, EU081151, EU087516, AF063128, AF169844; *Tetramerium* lineage. *Peristrophe brassii* R.M.Barker; Australia, *Forster* 28600 (CAS) KY584201, KY632272, MK282321, MK282392, KY632618; *Dicliptera* s.l. *Peristrophe hyssopifolia* (Burm.f.) Bremek., cultivated, Missouri Botanical Garden, St. Louis, Missouri, U.S.A., MBG861410 (native to Indonesia), *MacDougal* 5047 (MO) KY584202, KY632273, MK282322, MK282393, KY632620; *Dicliptera* s.l. *Peristrophe speciosa* (Roxb.) Nees, cultivated San Francisco Conservatory of Flowers (native to Asia), *Daniel* s.n. (CAS) KY584200, KY632271, MK282323, MK282394, KY632617; *Dicliptera* s.l. *Poikilacanthus macranthus* Lindau; Costa Rica, *Kiel et al.* 85 (RSA) KY584127, KY632200, MK282324, MK282395, KY632550; New World justicioid lineage. *Populina richardii* Baill.; Madagascar, *Kerardren* 1671 (P) EU081104, EU081171, EU087532, EU087566, EU087477; *Tetramerium* lineage. *Pseuderanthemum floribundum* T.F.Daniel; cultivated, San Francisco Conservatory (native to Mexico), *Daniel* 5381cv (CAS) KY584173, –, MK282325, MK282396, DQ37247; *Pseuderanthemum lineage. Ptyssiglottis psychotriifolia* (Stapf) B.Hansen; Borneo, *Poulsen* 40 (C) DQ372484, DQ372439, MK282326, MK282397, DQ372466. *Ptyssiglottis pubisepala* (Lindau) B.Hansen; Papua New Guinea, *Daniel* 6630 (CAS) DQ372483, DQ372438, EU529055, AF289744, AF289787.

Razisea spicata Oerst; Costa Rica, *Hammel* 7974 (DUKE) DQ372502, DQ372457, EU529056, AF063131, AF169848; core Isoglossinae. *Rhinacanthus angulicaulis* I.Darbysh.; Kenya, *Kiel et al.* 170 (RSA) KY584226, KY632293, –, –, KY632639; core *Rhinacanthus*. *Rhinacanthus dichotomus* (Lindau) I.Darbysh. var. *dichotomus*; Tanzania, *Mfinanga* 17 (US) KY584223, KY632290, –, –, KY632636; core *Rhinacanthus*. *Rhinacanthus latilabiatus* (K.Balkwill) I.Darbysh.; cultivated San Francisco Conservatory of Flowers (native to South Africa), *Daniel* s.n. (CAS) KY584222, KY632289, MK282327, MK282398, KY632635; core *Rhinacanthus*. *Rhinacanthus nasutus* (L.) Kuntze; Thailand, *Nanakorn* 880081 (US) KY584229, KY632296, –, –, KY632642; core *Rhinacanthus*. *Rhinacanthus ndorensis* Schweinf.; Kenya, *Yovng* 3169 (EA) KY584221, KY632288, –, –, –. *Rhinacanthus ndorensis* Schweinf.; Kenya, *Luke* 17084 (EA) MK282338, MK282279, MK282328, MK282399, MK282349. *Rhinacanthus pulcher* Milne.-Redh.; Kenya, *Gilbert & Thulin* 1081 (EA) KY584225, KY632292, –, –, KY632638; core *Rhinacanthus*. *Rhinacanthus rotundifolius* C.B.Clarke; Kenya, *Luke et al.* TPR60 (EA) KY584227, KY632294, –, –, KY632640; core *Rhinacanthus*. *Rhinacanthus virens* (Nees) Milne-Redh.; Uganda, *Lye* 3875 (EA) KY584220, –, –, –, KY632634. *Rhinacanthus xerophilus* A.Meeuse; South Africa, *McDade* 1277 (J) KY584224, KY632291, MK282329, MK282400, KY632637; core *Rhinacanthus*. *Ruellia californica* (Rose) I.M.Johnst.; Cultivated, Univ. Arizona campus, Tucson, Arizona, U.S.A. (native to northwest Mexico), *McDade* 1157 (ARIZ) EU528996, EU529123, EU529058, AF063115, AF167704; outgroup. *Rungia klossii* S.Moore; Papua New Guinea, *Daniel et al.* 6561 (CAS) KY584170, KY632240, MK282330, MK282401, KY632584; Old World justicioid lineages.

Schaueria gonatistachya Nees; Brazil, *Paixao et al.* 67 (CAS) MF670378, MF768297, MF678389, MF768352,

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MF768404; *Tetramerium* lineage. *Schaueria populifolia* C.B.Clarke; Cameroon, *Gereau et al.* 5666 (MO) MF670388, MF768309, MF678381, MF768372, MF768415. *Schaueria populifolia* C.B.Clarke; Cameroon, *Cheek* 10153 (K) MK282339, –, –, MK282402, MK282351. *Schaueria populifolia* C.B.Clarke; Cameroon, *Manning* 1336 (K) MK282340, –, –, MK282403, MK282350.

"*Tetramerium* lineage" indet.; Malaysia, *Hansen & Smitinand* 12005 (L) MF670389, MF768307, MF678404, MF768368,–; *Tetramerium* lineage. *Tetramerium nervosum* Nees; United States, *McDade & Jenkins* 1154 (ARIZ) EU081058, EU081126, EU087493, AF063133, AF169847; *Tetramerium* lineage. *Trichocalyx obovatus* Balf.f.; Socotra, Yemen, *Thulin & Gifri* 8503 (UPS) KY584176, KY632245, MK282331, MK282404, KY632589; *Harnieria* & *Tyloglossa* clades. *Xerothamnella herbacea* C.T.White; Australia, *Daniel* 10066 (CAS) KY584204, KY632275, MK282332, MK282405, KY632621; *Dicliptera* s.l.

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