SYSTEMATICS AND PHYLOGENY

Revised classification of Acanthaceae and worldwide dichotomous keys

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Abstract Acanthaceae are among the most taxonomically diverse, geographically widespread, and morphologically and ecologically variable lineages of flowering plants. Most modern workers have estimated more than 4000 species and potentially more than 5000 species worldwide, thus placing Acanthaceae among the 12 or so most diverse families of angiosperms. This diversity is marked by exceptional morphological variation, particularly with respect to floral forms, growth forms, and pollen types. The present work represents a synthesis of knowledge generated over the past two decades on the taxonomy and systematics of this complex plant family. We place all 191 accepted genera within a revised classification of the family. Dichotomous keys (nine in total) to recognize the major lineages of Acanthaceae are presented together with geographically partitioned keys to all genera, covering (a) Africa, Madagascar, the Mediterranean region, and Arabia; (b) Asia and Australasia; and (c) the Americas. Finally, we validate several new tribes, subtribes, and genera, and provide new combinations for species where generic delimitation has changed. Our hope is that the present contribution serves to benefit future research on the systematics of Acanthaceae and provides a foundation upon which future classification efforts can be built.

Keywords circumscription; keys; molecular phylogeny; nomenclature; reclassification; taxonomy; worldwide

■ INTRODUCTION

On a global scale, the Acanthaceae are a flowering plant family of exceptional taxonomic diversity, morphological and ecological variation, and geographical range (Figs. 1–3) (Daniel, 1993; McDade & al., 2000a; Scotland & Vollesen, 2000; Manktelow & al., 2001; Moylan & al., 2004; Wasshausen, 2006; Vollesen, 2008; Wood & Scotland, 2009; Tripp & Darbyshire, 2017; Kiel & al., 2018; Darbyshire & al., 2020). Estimates of the total number of species vary, but based on checklists, regional treatments, and fieldwork that has recovered many undescribed species, most modern workers have predicted over 4000 species and potentially over 5000 species. In this treatment, we estimate ~4900 species, placing Acanthaceae among the 12 or so most diverse families of flowering plants (McDade & al., 2008; Christenhusz & al., 2017; POWO, 2020; Utteridge & Bramley, 2020). This diversity is parsed among 191 genera recognized herein, with *Justicia* s.l. (n ~ 1000, but non-monophyletic and inclusive of several other genera), *Ruellia* (n ~ 350), *Strobilanthes* (n ~ 350), and *Barleria* (n ~ 300) the most species-rich among these (Wood & Scotland, 2009; Tripp & al., 2013a; Darbyshire & al., 2015, 2019a; Kiel & al., 2017, 2018; Tripp & Darbyshire, 2017).

Taxonomic diversity is concentrated in the Paleo- (Old World, OW) and Neo- (New World, NW) tropics and subtropics, but notable diversity occurs at temperate latitudes, particularly in *Acanthus*, *Justicia*, and *Ruellia* (e.g., Daniel, 2015a). Numerous centers of diversity exist worldwide, the most species-rich among these being the tropical thornscrub, dry forests, and savannas of Brazil and Mexico; the wet forests of the Andean foothills in Bolivia, Peru, Ecuador, Colombia, and Venezuela; the semi-deserts, savannas, dry forests and submontane wet forests of tropical East and northeastern Africa as well as central Africa; the wet and dry forests of Madagascar; the Namib Desert and adjacent grasslands and bushlands of Namibia and Angola; and varied ecosystems

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Fig. 1. Floral diversity among worldwide Acanthaceae. Collector, collection number, location of photograph, and photographer provided where available. **A**, *Dicliptera trifurca*, *Kiel & al. 122* (photo: C. Kiel), Costa Rica; **B**, *Hypoestes phyllostachya*, *Kiel & Tripp 65* (photo: C. Kiel), Mexico (native to Old World, widespread); **C**, *Justicia refractifolia*, *Kiel & al. 137* (photo: C. Kiel), Costa Rica; **D**, *Justicia costaricana, Kiel & al. 81* (photo: C. Kiel), Costa Rica; **E**, *Neuracanthus niveus*, Not vouchered (photo: W. McCleland), Mali; **F**, *Pachystachys spicata*, *Kiel & Velez 258* (photo: C. Kiel), Colombia; **G**, *Tetramerium nervosum*, *Kiel & Tripp 75* (photo: C. Kiel), Mexico; **H**, *Ruelliopsis setosa*, *Tripp & Dexter 799* (photo: E. Tripp), Namibia; **I**, *Petalidium giessii*, *Tripp & Dexter 825* (photo: E. Tripp), Namibia; **J**, *Blepharis pruinosa*, *Tripp & al. 884* (photo: E. Tripp), Namibia; **K**, *Acanthopsis hoffmanseggiana*, *Tripp & al. 2073* (photo: E. Tripp), Namibia; **L**, *Aphelandra aurantiaca*, *Tripp & al. 5739*, Mexico; **M**, *Acanthopale pubescens*, *Ballings & Wursten 1074* (photo: B. Wursten), Mozambique; **N**, *Barleria oenotheroides*, *Tripp & al. 5755* (photo: E. Tripp), Mexico; **O**, *Bravaisia integerrima*, *Tripp & Luján 519* (photo: E. Tripp), Venezuela; **P**, *Brunoniella australis*, *Hosking 2952* (photo: J. Hosking), Australia; **Q**, *Mendoncia aspera*, *Clarke & Tripp s.n.* (photo: D. Clarke), Guyana; **R**, *Dyschoriste repens*, *Tripp & Luján 516* (photo: E. Tripp), Venezuela; **S**, *Barleria lancifolia*, *Tripp & Dexter 781* (photo: E. Tripp), Namibia; **T**, *Louteridium donnellsmithii*, *Tripp & Medina 9680* (photo: E. Tripp), Mexico; **U**, *Calacanthus grandiflorus*, Not vouchered (photo S. Yadav), India; **V**, *Dinteracanthus asper*, *Tripp & al. 2079* (photo: E. Tripp), Namibia; **W**, *Anisosepalum alboviolaceum*, *Bytebier & al. 3279* (photo: Q. Luke), Dem. Repub. Congo; **X**, *Ruellia megasphaera*, *Tripp & al. 5756* (photo: E. Tripp), Mexico; **Y**, *Odontonema glabrum*, *Tripp & al. 5763* (photo E. Tripp), Mexico; **Z**, *Anisotes formosissimus*, *Wursten 2020* (photo: B. Wursten), Mozambique; **AA**, *Lepidagathis fischeri*, Not vouchered (photo: I. Darbyshire), Tanzania; **BB**, *Asystasia malawiana*, *Mphamba 122* (photo: T. Harris), Mozambique.

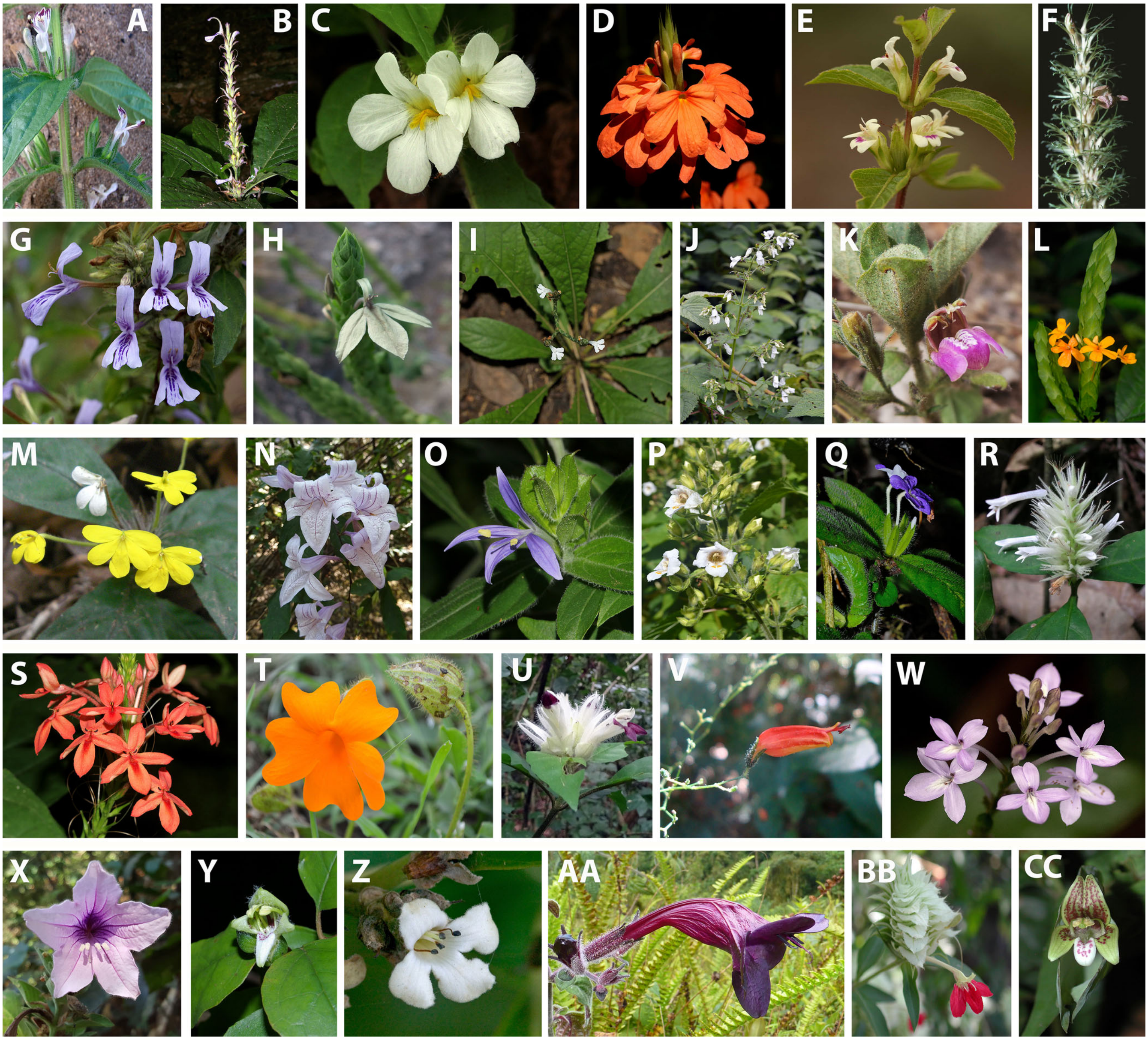

Fig. 2. Floral diversity among worldwide Acanthaceae. Collector, collection number, location of photograph, and photographer provided where available. **A**, *Andrographis echioides*, *Luke & Chidzinga 16414B* (photo: Q. Luke), Kenya (naturalised, native to Asia); **B**, *Cephalophis lukei*, *Hyde 15.119.06* (photo: M. Hyde), Mozambique; **C**, *Crabbea velutina*, *Ballings & Wursten 2391* (photo: B. Wursten), Zimbabwe; **D**, *Crossandra puberula*, *Wursten & al. 1946* (photo: B. Wursten), Mozambique; **E**, *Duosperma crenatum*, Not vouchered (photo: B. Wursten), Mozambique; **F**, *Champluviera populifolia*, *Cheek 7654* (photo: M. Cheek), Cameroon; **G**, *Dyschoriste hildebrandtii*, *Wursten 951* (photo: B. Wursten), Mozambique; **H**, *Ecbolium tanzaniense*, *Suleiman & al. TTSA 235* (photo: I. Darbyshire), Tanzania; **I**, *Elytraria acaulis*, Not vouchered (photo: B. Wursten), Mozambique; **J**, *Isoglossa vulcanicola*, *Darbyshire & al. 1048* (photo: I. Darbyshire), Uganda; **K**, *Justicia salviiflora*, *Tripp & al. 5773* (photo: E. Tripp), Mexico; **L**, *Lankesteria elegans*, Collector/photographer unknown, Cameroon; **M**, *Lankesteria hispida*, *van der Burgt 1406* (photo: X. van der Burgt), Sierra Leone; **N**, *Mackaya bella*, Not vouchered (photo: I. Darbyshire), South Africa (cult.); **O**, *Megalochlamys hamata*, Not vouchered (photo: B. Wursten), Zimbabwe; **P**, *Mimulopsis excellens*, *Darbyshire & al. 1056* (photo: I. Darbyshire), Uganda; **Q**, *Physacanthus batanganus*, *Cheek in Kami 4132* (photo: M. Cheek), Dem. Repub. Congo; **R**, *Schaueriopsis variabilis*, *Luke 12527* (photo: Q. Luke), Dem. Repub. Congo; **S**, *Ruspolia seticalyx*, *Wursten 1859* (photo: B. Wursten), Mozambique; **T**, *Thunbergia gregorii*, Not vouchered (photo: I. Darbyshire), Kenya; **U**, *Whitfieldia orientalis*, *Suleiman & al. 5534* (photo: I. Darbyshire), Tanzania; **V**, *Stenostephanus sessilifolius*, *Hammel & al. 26074* (photo: C. Kiel), Costa Rica; **W**, *Pseuderanthemum subviscosum*, Not vouchered (photo: B. Wursten), Mozambique; **X**, *Ruellia neesiana*, *Tripp & Medina 5957* (photo: E. Tripp), Brazil; **Y**, *Leandriella valvata*, *Thulin & Razafindraibe 11880* (photo: M. Thulin), Madagascar; **Z**, *Avicennia germinans*, *Daniel 11120* (photo: W. Eckerman), São Tomé; **AA**, *Heteradelphia paulowilhelmia*, Not vouchered (photo: T. Daniel), São Tomé; **BB**, *Lepidagathis grandidieri*, *Daniel & al. 11066* (photo: T. Daniel), Madagascar; **CC**, *Chlamydacanthus euphorbioides*, *Daniel & Ranarivelo 10584* (photo: T. Daniel), Madagascar.

of tropical Asia, particularly in India (Daniel, 1993; Carine & Scotland, 1998; Vollesen, 2008; Darbyshire & al., 2010, 2020; Kiel & al., 2017, 2018; Tripp & Darbyshire, 2017; Tripp & al., 2017; Tripp & Luján, 2018; Madagascar Catalogue, 2020). Conversely, the family is noticeably absent or species-poor in several regions at seemingly suitable latitudes including Australia, the Guiana Shield, and Mediterranean climate zones worldwide. These patterns may in part be driven by nutrient-poor edaphic conditions and/or climatic conditions of these regions (e.g., winter rainfall, summer aridity). Centers of endemism largely parallel centers of biodiversity worldwide. Madagascar almost certainly hosts the highest degree of endemism: of over 500 species of Acanthaceae, 93% are considered to be endemic (Onjalalaina & Darbyshire, 2016; Madagascar Catalogue, 2020). In addition to marked taxonomic diversity worldwide, Acanthaceae have a notably rich fossil record (Tripp & McDade, 2014).

As is frequently observed in tropical ecosystems characterized by high alpha diversity, populations of species of Acanthaceae tend to be small, with many consisting of one

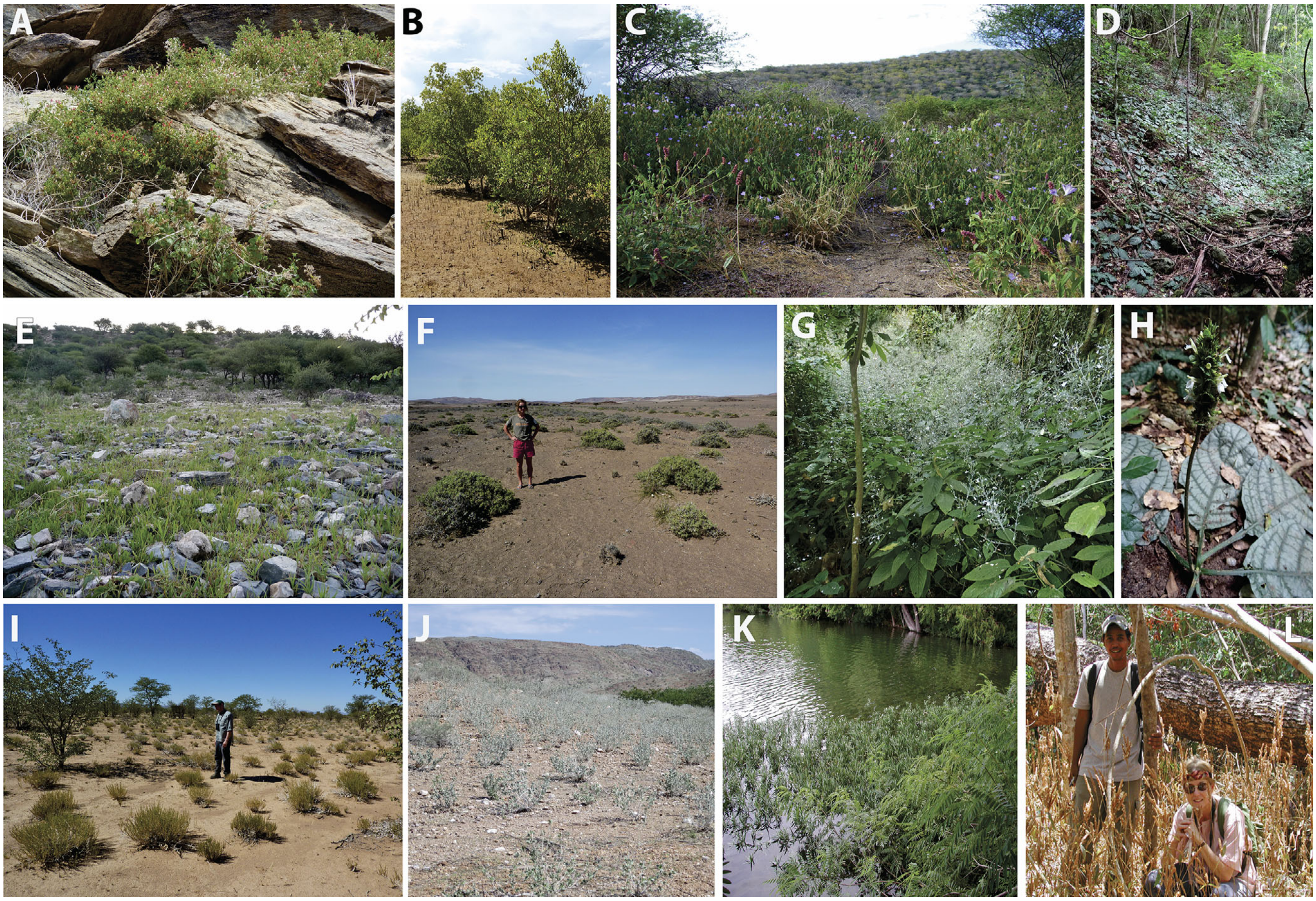

Fig. 3. Examples of habitat diversity among worldwide Acanthaceae. Collector, collection number, location of photograph, and photographer provided where available. **A**, *Petalidium crispum*, *Tripp & Dexter 4087* (photo: E. Tripp), Namibia; plants showing affinity for crevices of near-barren schist rocks and associated slopes, near Van Zyl's Pass; **B**, *Avicennia marina*, Not Vouchered (photo: I. Darbyshire), Tanzania; locally dominant in intertidal mangrove communities near Lindi; note the presence of pneumatophores; **C**, *Barleria aristata*, Not Vouchered [but same location as *Bidgood & al. 5027*] (photo: I. Darbyshire), Tanzania; locally common in dry Somalia-Masai woodland near the Lukosi River; **D**, *Justicia fittonioides*, *Suleiman & al. 5536* (photo: I. Darbyshire), Tanzania; abundant on the floor of seasonally dry coastal forest at Ruawa Forest Reserve near Lindi; **E**, *Ruelliopsis setosa*, *Tripp & Dexter 799* (photo: E. Tripp), Namibia; plants a dominant component of rocky savanna floor, acting as a "grass mimic"; **F**, *Blepharis ferox*, *Tripp & Dexter 4094* (photo: K. Dexter), Namibia; plants comprising one of the most abundant shrubs on barren sand of Namib Desert, near Oropembe; **G**, *Isoglossa dispersa*, Not Vouchered (photo: P.K. Haba), Guinea; a mass-flowering plietesial species of moist lowland and mid-elevation forest, here at Simandou; **H**, *Justicia fittonioides*, *Suleiman & al. 5536* (photo: I. Darbyshire), Tanzania; showing the rosulate habit of the plants in D; **I**, *Pogonospermum salsola*, *Klaassen & al. 2537* (photo: E. Tripp), Namibia; plants represent the dominant shrubs on the floor of the Namib Desert, which is typical of numerous species of this genus and of *Petalidium*, *Blepharis*, and *Barleria* in Namibia; **J**, *Petalidium welwitschii*, *Tripp & Dexter 4091* (photo: E. Tripp), Namibia; total dominance of Namib Desert near Hartmann's Valley in the northwestern Kaokoveld; **K**, *Justicia americana*, *Daniel & Lott 10530* (photo: T. Daniel), U.S.A.; aquatic perennial herb at edge of Town Lake, Austin, Texas; **L**, *Lankesteria glandulosa* Benoist, *Daniel & al. 10453* (photo: T. Daniel), Madagascar; dying perennial herb along trail in seasonally moist forest, Ankarana Special Reserve.

to several (often fewer than 20) plants. This has long challenged tropical botanists in our attempt to understand the natural history of species in these regions. However, exceptions exist: notable areas where species of Acanthaceae comprise some of if not *the* most abundant and ecologically dominant plants across the landscape (Fig. 3) include the Namib Desert and surrounding drylands of Namibia and Angola (Tripp & al., 2017; Darbyshire & al., 2019b, 2020), portions of northeastern tropical Africa such as the *Acacia-Commiphora* woodlands of southern Ethiopia and northern Kenya, and monodominant stands of the Indian species *Strobilanthes kunthiana* (Nees) T.Anderson ex Benth. and *Barleria involucrata* Nees in the Western Ghats (Annaselvam & Parthasarathy, 1999; Krishnan, 2000; Sharma & al., 2008). Although perhaps best known in *Strobilanthes* (e.g., Bremekamp, 1944; Wood, 1994, 1999), synchronized mass-flowering of perennially monocarpic (plietesial) Acanthaceae is a well-documented phenomenon in a number of genera across several clades (e.g., Thomas, 1996; Cheek & al., 2004; Daniel, 2006; Champluvier & Darbyshire, 2009; Darbyshire, 2009; Champluvier & Fischer, 2020), with high ecological significance. Other examples of monodominance in Acanthaceae include species of *Avicennia*, which occur in extensive stands of coastal mangrove communities worldwide (Tomlinson, 1986; Beentje & Bandeira, 2007).

Species of Acanthaceae have long been appreciated for their exceptional morphological diversity, particularly with respect to floral forms, growth forms, and pollen types (Figs. 1, 2). Floral morphological diversity includes a broad spectrum of colors ranging from red to purple, pink, yellow, orange, white, green, and blue-green, and it is not atypical for sister species to have strikingly divergent colors (e.g., Tripp & Manos, 2008; Kiel & al., 2018). Diversity of floral forms among related species is equally marked, with corolla morphology likely reflecting adaptation to a variety of pollinators including bees, birds, butterflies, hawkmoths, flies (especially bombyliids), and bats (Grant, 1983; Hilsenbeck, 1983; Ramamoorthy, 1991; Daniel, 1993; Ezcurra, 1993; Vogel & al., 2004; Holmqvist & al., 2005; Döll & al., 2007; Tripp & Manos, 2008; Heywood & al., 2017; Tripp & Tsai, 2017; Kiel & al. in prep.).

Whereas most species of Acanthaceae are herbs or shrubs, trees have evolved in parallel in several genera including *Aphelandra*, *Barleria*, *Justicia*, and *Louteridium*. In particular, species of *Trichanthera* and *Bravaisia* are nearly or fully arborescent (Daniel, 1988; Daniel & Véliz, 2009; Daniel, 2015b; Darbyshire & Luke, 2016; Daniel & Tripp, 2018), as are members of the mangrove genus *Avicennia*.

Species of *Avicennia* display adaptations to saline environments, such as the presence of pneumatophores (Daniel, 2016). Elsewhere in the family, twining herbs and lianas are frequent in subfamily Thunbergioideae (Borg & al., 2008). Other unusual growth forms include that of African *Dischistocalyx*, which is reported to initiate developmentally as a terrestrial herb before producing climbing shoots that anchor to tree trunks or boulders and then produce epiphytic or lithophytic flowering shoots (Cheek, 1995). This exceptional diversity across growth forms, floral forms, and vegetative morphologies (Figs. 1–3) adds to the family's intrigue for those who study it. However, this morphological diversity is also frustrating owing to clearly homoplasious patterns of evolution that have resulted in the presence of similar features in only distantly related lineages. This evolutionary vagility has long plagued efforts to interpret taxonomy, morphological diversity, and evolution (Moylan & al., 2004; Tripp, 2007; Daniel & al., 2008; Tripp & Manos, 2008; Wood & Scotland, 2009; Kiel & al., 2017, 2018; McDade & al., 2018; Darbyshire & al., 2019a).

Since the 19th century, there has been only one reclassification of the family. Scotland & Vollesen (2000) treated a total of 221 genera, parsed among three subfamilies, two tribes, and four subtribes, with 20 genera remaining unplaced. Their study was made possible largely through comparative morphological (including palynological) interpretation of variation in the family, together with a limited number of early, molecular phylogenetic studies. Since this landmark recircumscription, extensive new knowledge, especially molecular data placed in a phylogenetic context, has accumulated (e.g., Manktelow & al., 2001; Schwarzbach & McDade, 2002; Moylan & al., 2004; McDade & al., 2005, 2008, 2012, 2018; Schmidt-Lebuhn & al., 2005; Kiel & al., 2006, 2017, 2018; Tripp, 2007; Wortley & al., 2007; Borg & al., 2008; Daniel & al., 2008; Tripp & al., 2013a,b; Kiel & McDade, 2014; Fisher & al., 2015; Deng & al., 2016; Tripp & Darbyshire, 2017; Darbyshire & al., 2019a,b). Cumulatively, these and other works have placed nearly all of the 20 genera that were unclassified in Scotland & Vollesen (2000), as well as provided evidence that several genera should be transferred to other tribes or subtribes (e.g., Manktelow & al., 2001; McDade & al., 2008; Tripp & al., 2013a).

Despite the high species richness and a nearly worldwide distribution, surprisingly few professional botanists are actively pursuing and publishing new phylogenetic and taxonomic knowledge in Acanthaceae. Tripp & Darbyshire (2017) lamented this low "scholars to species" ratio and estimated fewer than 20 such individuals worldwide, of whom ~12 are providing regular contributions. This disparity contributed to the placement of Acanthaceae among the worst offenders in an angiosperm-wide synthesis of remaining knowledge gaps, thus challenging full achievement of "Targets" put forward in the Global Strategy for Plant Conservation (Paton & al., 2008). Tripp & Darbyshire (2017) further commented that phylogenetic studies centered around the generation and analysis of new molecular data yield results more quickly, are published in journals with higher impact factors, and have higher citation rates than are taxonomic studies that attempt to translate information coming out of such molecular studies into updated treatments and classifications. Many taxonomic papers are slower to produce, compiled by fewer specialists, and are published in journals with lower impact factors. Scientists are more commonly rewarded for publishing papers in high impact factor journals with high citation rates and may thus find it challenging to devote research time to taxonomic work, hindering taxonomic progress. That said, the years since Scotland

& Vollesen's (2000) classification have witnessed major strides in our understanding of species diversity in Acanthaceae in many parts of the world, from monographic and floristic perspectives in addition to the aforementioned phylogenetic advances. Progress has been most notable in Africa (e.g., Balkwill & Welman, 2000; Darbyshire & Harris, 2006; Ensermu, 2006; Hedrén & Thulin, 2006; Vollesen, 2006, 2007, 2008, 2013; Darbyshire & Vollesen, 2007; Champluvier & Darbyshire, 2009, 2012; Daniel & Figueiredo, 2009; Darbyshire, 2009; Darbyshire & al., 2009, 2010, 2011, 2019c; Balkwill & al., 2017; Magnaghi & Daniel, 2017; Breteler & Wieringa, 2018; Steyn, 2018), the Americas (e.g., Durkee, 2001; Ezcurra, 2002, 2018; Daniel & Acosta, 2003; Daniel, 2004, 2005, 2010, 2015b, 2016; Wasshausen & Wood, 2004; McDade & Tripp, 2007; Kameyama, 2008; Indriunas, 2011; Wasshausen, 2013; Franck & Daniel, 2015; Côrtes & al., 2016a; Braz & Monteiro, 2017; Da Silva Monteiro & al., 2018; Daniel & Tripp, 2018; Tripp & Luján, 2018; Da Costa-Lima & de Oliveira Chagas, 2019; McDade & al., 2019; Zanatta, 2019; Burgos-Hernández & Castillo-Campos, 2020; McDade, 2020; Braz & al., 2021) and, to a lesser extent, in tropical Asia (e.g., Moylan & al., 2002; Wood & al., 2003; Carine & al., 2004; Deng & al., 2006; Wood & Scotland, 2009; Shendage & Yadav, 2010; Hu & al., 2011; Wood, 2014; Gnanasekaran & al., 2016; Bongcheewin & al., 2019; Deng, 2019; Rueangsawang & al., 2020), as well as in groups that are wide-ranging (e.g., Vollesen, 2000; Daniel & McDade, 2014). These works have, in turn, increased the knowledge base for classification of this diverse and complex family.

The present reclassification of Acanthaceae represents our synthesis of information from the last two decades of phylogenetic, floristic, taxonomic, and nomenclatural research in the family. For the first time since Lindau (1895), dichotomous keys to the major lineages and genera of Acanthaceae are presented, along with geographically structured keys. We discuss previously unplaced as well as newly placed genera. We furthermore take a first pass at delimiting the geographical distributions of all recognized genera within the family. We validate a number of names and make several new combinations of names where required. Specifically, our contribution includes the following sections, in addition to the primary text:

I. The classification
II. Keys to the subfamilies, tribes, and genera of Acanthaceae
III. Geographical keys to the genera of Acanthaceae
IV. Validation of names (tribes, subtribes, genera)
V. New synonymies and combinations (species)

Our revised classification reflects a first pass at interpreting and reinterpreting morphological variation in light of molecular results based largely on Sanger sequence data. With anticipation and optimism, we expect that subsequent revisions will emphasize results from next-generation sequencing methods and will incorporate results for previously unsampled or poorly sampled lineages. Phylogenomic analyses primarily emphasizing RADseq datasets for Acanthaceae are growing rapidly and already include *Petalidium* (Tripp & al., 2017), Ruellieae (Tripp & Darbyshire, 2020), *Ruellia* (Tripp & Daniel, in prep.), *Louteridium* (Daniel & Tripp, 2018), *Barleria* (Comito, 2019; Comito & al., in rev.), *Justicia* (Kiel & al., in prep.), and *Monechma* (Darbyshire & al., 2020). The present contribution builds upon the foundation laid by Scotland & Vollesen (2000) to produce a revised classification, which future phylogenetic, taxonomic, and floristic contributions can further refine.

■ METHODS

To facilitate reclassification of Acanthaceae, we surveyed (1) historical literature (i.e., prior to the rise of molecular phylogenetics) followed by (2) more recent studies, primarily but not entirely those utilizing molecular phylogenetic analyses of relationships among various lineages of Acanthaceae. We sought to include studies of lineages that have been treated among other plant families at various times in the past (e.g., *Avicennia*, *Mendoncia*, *Thunbergia*). A list of accepted genera was prepared based on the cumulative opinions of the authors, informed by numerous published contributions. Thorough histories of taxonomic accounts of Acanthaceae (e.g., Bentham & Hooker, 1876) have been provided in numerous prior works and it is not our intention to repeat these accounts here. Likewise, many of the phylogenetic, monographic, and floristic works cited in the Introduction provided extensive evidence of morphological synapomorphies and other suites of traits that were used to inform the taxonomic classification presented herein. Evolution of these traits is not discussed in detail in the current work but can be found in these primary references.

Keys to subfamilies, tribes, and genera of Acanthaceae on a worldwide basis (except for Justicieae) and keys to all genera based on major geographical regions were prepared. We refrained from preparing a key to Justicieae because the tribe includes numerous poorly known genera as well as genera that are inadequately circumscribed and differentiated at present. Following Part I (The classification), twelve dichotomous keys are presented here: Part II contains nine keys, these to the subfamilies, tribes, and genera; Part III contains three keys, these geographically organized. The keys were constructed through a combination of extensive review of available literature (particularly monographs and floristic accounts) and study of herbarium material housed at a wide range of herbaria and botanical gardens, but with most extensive reference to the collections at B, BM, BR, C, CAS, COLO, EA, G, K, L, LISC, MEXU, MO, NY, P, RSA, S, US and WAG. Many images of type specimens were accessed via JSTOR Global Plants (https://plants.jstor.org/).

In citing type material, an exclamation mark (!) is used whenever direct study of specimens was undertaken. An asterisk (*) indicates that study was limited to online images of specimens. Numbers associated with type specimens refer to specimen barcodes.

Pollen terminology largely follows Walker & Doyle (1975), supplemented by Hesse & al. (2009).

■ RESULTS

The present classification of Acanthaceae (Fig. 4) includes four subfamilies: Nelsonioideae, Avicennioideae, Thunbergioideae, and Acanthoideae. In prior works (e.g., McDade & al., 2008), these have together been referred to as Acanthaceae sensu lato (s.l.). Thunbergioideae are divided into two tribes: Mendoncieae and Thunbergieae. Within Acanthoideae, which encompass by far the greatest taxonomic diversity, eight tribes are recognized: Acantheae, Physacantheae, Barlerieae, Andrographideae, Whitfieldieae, Neuracantheae, Ruellieae, and Justicieae. Within these tribes, a total of 19 subtribes are recognized: Acanthinae and Aphelandrinae (Acantheae); Lankesteriinae and Whitfieldiinae (Whitfieldieae); Dinteracanthinae, Erantheminae, Hygrophilinae, Mcdadeinae, Mimulopsidinae, Petalidiinae, Phaulopsidinae, Ruelliinae, Strobilanthinae, and Trichantherinae (Ruellieae); and Graptophyllinae, Isoglossinae, Justiciinae, Monotheciinae, and Tetrameriinae (Justicieae).

In total, 191 genera are recognized in this treatment. Of these, all are placed taxonomically except three members of Ruellieae (*Diceratotheca*, *Stenothyrsus*, *Xylacanthus*), five of Justicieae (*Dolichostachys*, *Ichthyostoma*, *Samuelssonia*, *Streblacanthus*, *Tessmanniacanthus*), and one genus that is currently treated as Acanthaceae Incertae Sedis (*Ritonia*). Four genera are excluded from the classification for varied reasons, as described below: *Gymnophragma*, *Schwabea*, *Sericospora*, and *Strobilacanthus*. Two genera from Madagascar that have been referred to widely in the literature but had not been validly published are validated below: *Dolichostachys* and *Vavara*. Finally, updated generic placements and new combinations are made for numerous species.

The present classification differs from that of Scotland & Vollesen (2000) in several ways. Their subtribes Andrographinae (= Andrographidinae), Barleriinae, Ruelliinae, and Justiciinae have here been elevated to tribal rank within subfamily Acanthoideae. Further, we recognize three additional tribes

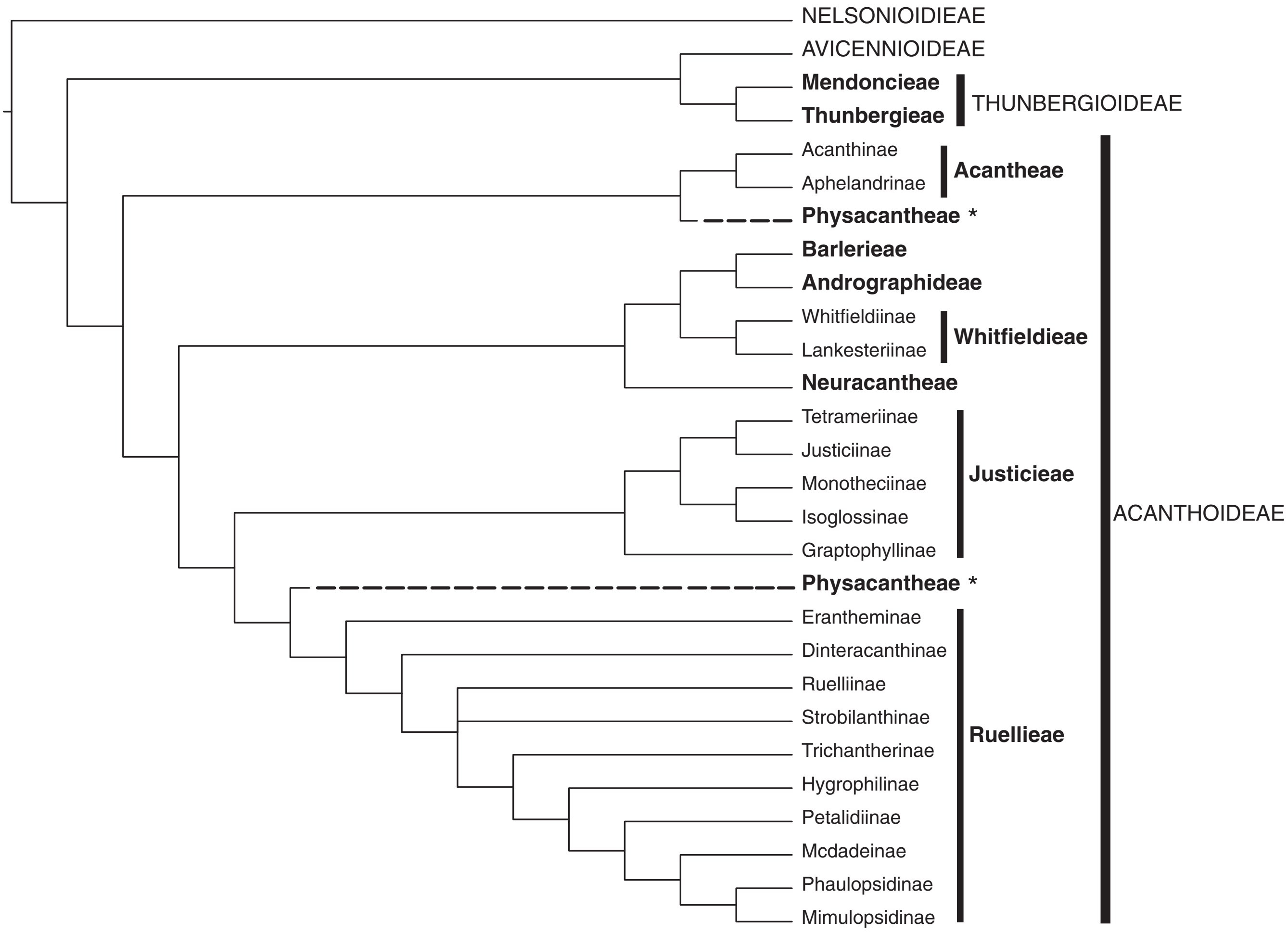

Fig. 4. Schematic molecular phylogeny of the Acanthaceae, which serves as the foundation for the present reclassification. Phylogeny represents current understanding of evolutionary relationships among major lineages of Acanthaceae based on numerous phylogenetic works, as cited throughout this study. Depicted are the 4 subfamilies (capital letters), 10 tribes (bold), and 19 subtribes (not in bold, not in caps) recognized in the present study. Key diagnostic morphological characters for the subfamilies and tribes are provided in Table 1 and Fig. 5. Asterisks and dashed lines indicate uncertain phylogenetic placement of Physacantheae, either within or sister to Ruellieae or Acantheae (see text).

within that subfamily for genera that were either unplaced or (in the case of *Physacanthus*) misplaced in the earlier classification: Neuracantheae, Physacantheae, and Whitfieldieae. In addition, we here subdivide Thunbergioideae into two tribes and recognize 15 subtribes across Justicieae and Ruellieae. Nineteen of the 20 unplaced genera listed by Scotland & Vollesen (2000) have been placed either as accepted genera within the present classification (13 genera) or in synonymy (6 genera). The remaining taxon, "*Idiacanthus* Leonard", was never validly published and thus was a nomen nudum when included by Scotland & Vollesen (2000). We have also revised the placement of a number of genera and placed into synonymy a number of other genera recognized by these authors (Appendix 1).

In Appendix 2, we propose a numeric linear sequence for the 191 accepted genera, informed by phylogenetic and morphological evidence accumulated to date. This is aimed towards assisting curation of herbarium collections of Acanthaceae in herbaria that opt for a systematic rather than alphabetic sequence.

■ DISCUSSION

Acanthaceae s.l.: one family or four? — The delimitation of Acanthaceae has varied considerably over time and continues to be contentious. Lindau (1895), in his major classification of the family, recognized a broadly circumscribed Acanthaceae comprising four subfamilies: Acanthoideae, Nelsonioideae, Thunbergioideae and Mendoncioideae. Bremekamp's later (1965) reclassification excluded groups that lack retinaculate fruits and therefore he recognized Thunbergioideae and Mendoncioideae as separate families (Thunbergiaceae and Mendonciaceae) and transferred Nelsonioideae to Scrophulariaceae. The recent body of systematic studies in Acanthaceae has demonstrated a close relationship between thunbergioids and mendoncioids (Schönenberger & Endress, 1998; Borg & al., 2008) and also shown that nelsonioids are sister to other Acanthaceae and are not closely related to any of the former members of Scrophulariaceae (Hedrén & al., 1995; McDade & al., 2012). In the most recent classification of the Acanthaceae prior to the present work, drawing on available molecular and morphological data, Scotland & Vollesen (2000) adopted a similar delimitation to that of Lindau (1895) and included the clades with non-retinaculate fruits within Acanthaceae. Scotland & Vollesen (2000) recognized three subfamilies (Nelsonioideae, Thunbergioideae, Acanthoideae), with mendoncioids being included within Thunbergioideae. More recently, molecular phylogenetic studies have demonstrated that the woody mangrove genus *Avicennia* is nested within Acanthaceae s.l., sister to Thunbergioideae (Schwarzbach & McDade, 2002). This genus was previously treated either within its own family, Avicenniaceae (e.g., Fernandes, 2005; Brummitt, 2007) or within the Verbenaceae (e.g., Verdcourt, 1992). Results presented in Schwarzbach & McDade (2002), although surprising in view of the morphological differences between *Avicennia* and other Acanthaceae, have been supported consistently by subsequent molecular analyses (e.g., Borg & al., 2008; McDade & al., 2008), and the genus is now widely accepted as belonging to Acanthaceae (Angiosperm Phylogeny Group, 2016), as treated herein.

All major studies on the Lamiales have demonstrated that Acanthaceae, including *Avicennia*, are monophyletic (McDade & al., 2008, 2012; Schäferhoff & al., 2010). McDade & al. (2012) hypothesized that indurate, explosively dehiscent capsules are synapomorphic for Acanthaceae, albeit with autapomorphic leathery, non-explosively dehiscent capsules in *Avicennia* and drupaceous fruits in *Mendoncia* and *Anomacanthus*. This combined molecular and morphological evidence supports recognition of a single family and, indeed, most modern floristic and phylogenetic treatments of Acanthaceae, prior and subsequent to McDade & al. (2012), follow this broad circumscription (e.g., Scotland & Vollesen, 2000; Ensermu, 2006; McDade & al., 2008; Vollesen, 2008, 2013; Darbyshire & al., 2010, 2015), with a few others (e.g., Cronquist, 1981) taking alternative stances.

Nevertheless, under this broad circumscription, it is difficult to diagnose Acanthaceae in relation to a number of the other ~24 families that comprise Lamiales (Stevens, 2001–). This is due in part to the broad range of morphological variation that Acanthaceae encompass and begs the question as to whether a narrower family definition might benefit classification efforts within Lamiales through improved diagnosis of segregate families based on morphological traits. Following Bremekamp's (1965) narrower circumscription, Acanthaceae sensu stricto (s.str.; i.e., here, Acanthoideae), is by far the most species-rich clade within Acanthaceae, containing approximately 90% of the total number of taxa. This clade is easily characterized by the synapomorphy of presence of retinacula (i.e., modified hook-shaped funiculi) contained within explosively dehiscent capsules. There are very few instances of autapomorphic, evolutionary diversions from this morphology (e.g., capsules of a few Justicieae: *Aphanosperma*, *Chalarothyrsus*, and a few *Justicia* species [Kiel & al., 2017] have poorly developed or not clearly discernible retinacula). Retinacula are absent in the remaining subfamilies of Acanthaceae s.l. (but see fig. 9E in Daniel & McDade, 2014 for images of structures in some Nelsonioideae that may represent early stages in the evolution of retinacula). Indeed, among angiosperms, retinacula were thought to be unique to Acanthaceae s.str., except that they are also present in *Thomandersia*, a genus previously treated within Acanthaceae but subsequently found to be more distantly related (Wortley & al., 2007; McDade & al., 2012). *Thomandersia* is thus now treated within its own monogeneric family, Thomandersiaceae; plants of *Thomandersia* differ from Acanthaceae s.str. in lacking explosively dehiscent capsules as well as lacking articulation of the stems (Wortley & al., 2007).

The other major lineages of Acanthaceae s.l. (i.e., Nelsonioideae, Thunbergioideae, and the genus *Avicennia*) are also well delimited based on morphological traits, although morphological synapomorphies have not been determined for all of them. These lineages can be differentiated readily from one another (see key to subfamilies below) and from other families of Lamiales, although the separation of Nelsonioideae from some of the segregate families in the former Scrophulariaceae remains challenging on morphological grounds.

Given the stipulations and exceptions noted above, we here adopt a compromise classification in which we recognize Acanthaceae s.l., which are united by explosively dehiscent capsules, with the exception of the autapomorphic fruit types noted above. We recognize four morphologically distinct clades as separate subfamilies: Nelsonioideae, Avicennioideae, Thunbergioideae, and Acanthoideae. This revised family classification was adopted in Stevens (2001–) as well as by the Angiosperm Phylogeny Group (2016) and is similar to that proposed by Reveal (2012).

An overview of the subfamilies, tribes, and subtribes of Acanthaceae. — Below, we provide abridged descriptions of the four subfamilies and their tribes and subtribes, as a general overview of the phylogeny and upper-level classification of the family (Fig. 4). We caution that several genera of Acanthaceae have yet to be included in phylogenetic analyses such that this synopsis remains a working hypothesis pending further phylogenetic studies. Key diagnostic morphological characters for the subfamilies and tribes are provided in Table 1 and are discussed below.

Nelsonioideae. — This subfamily of mostly herbaceous and subshrubby species (ca. 175 spp.) is united by the following morphological characters: descending-cochlear corolla aestivation (unique in Acanthaceae and proposed as a probable synapomorphy by Daniel & McDade, 2014) (Fig. 5D), presence of persistent endosperm in the seeds (versus usually exalbuminous seeds elsewhere in Acanthaceae, although the trait has yet to be thoroughly studied across the family and exceptions have been noted, e.g., Mohan Ram & Wadhi, 1964), absence of cystoliths and retinacula (both features shared with Thunbergioideae and Avicennioideae), capsules with 6–68 seeds (which separates this group from other non-retinaculate Acanthaceae, where fruits have 1–4 seeds) and, in many species, spirally arranged flowers in the inflorescence (versus opposite or secund in other Acanthaceae). Thus, Nelsonioideae are relatively easy to separate from other Acanthaceae. Explosive capsule dehiscence and the presence of papilliform and/or elongate (but not indurate) modified funiculi are likely to be diagnostic, but this requires further investigation. The generic delimitation and diversity were considered globally by Daniel & McDade (2014; see also Braz & al., 2021). Six genera are currently recognized, and the subfamily is pantropical.

Avicennioideae. — This pantropical subfamily of ca. 8 species comprises the mangrove tree and shrub genus *Avicennia*. Unique in Acanthaceae, plants of *Avicennia* display adaptations to saltwater inundation, including the presence of pneumatophores (Tomlinson, 1986; Verdcourt, 1992; Daniel, 2016). Plants lack cystoliths and have only tardily dehiscent, leathery fruits bearing a single seed (*Mendoncia* and *Anomacanthus* in Thunbergioideae have indehiscent drupaceous fruits). Floral morphology is variable: the *A. marina* group is unusual in having actinomorphic, 4-lobed corollas (number of corolla lobes = number of stamens) with valvate aestivation (Tomlinson, 1986) (Fig. 5E), the only known occurrence of this aestivation pattern in Acanthaceae. However, other species of *Avicennia* have zygomorphic corollas with left-contort aestivation (Tomlinson, 1986; Borg & Schönenberger, 2011) (Fig. 5A). The genus is composed of two monophyletic lineages: one of Atlantic-East Pacific taxa and a second of Indo-West Pacific taxa (Li & al., 2016). A recent study of *Avicennia* (Cornejo, 2020) proposed subdivision of the genus into two distinct genera, *Avicennia* and *Hilairanthus*, on the basis of monophyletic units in combination with morphological distinctiveness. However, the degree of morphological variation between these two lineages is comparable to variation among lineages within many other genera of Acanthaceae, e.g., *Ruellia* and *Barleria*. Moreover, there is comparable variation within the lineage that includes the type alone, *Avicennia marina*. As such, we recognize *Avicennia* as broadly circumscribed, especially given the numerous synapomorphies for the genus, as described above.

Thunbergioideae. — With ca. 260 species in five genera, plants of this pantropical and subtropical subfamily are primarily vines and lianas that climb by twining (Borg & al., 2008), although a significant number of species of *Thunbergia* are perennial herbs or shrubs, presumably secondarily. Clambering and vine-like plants are sometimes encountered elsewhere in the family, but twining climbers appear to be known only in, and synapomorphic for, Thunbergioideae. Other distinguishing characters (and probable synapomorphies) common to all genera in Thunbergioideae include an involucre or epicalyx of paired, large, spathaceous bracteoles subtending each flower, a highly reduced and modified calyx, and anthers that dehisce by pores or short, slit-like openings. In their study of floral development in *Mendoncia*, *Pseudocalyx*, and *Thunbergia*, Schönenberger & Endress (1998) demonstrated that these genera share similar types of inflorescences and features of the anther thecae. Several unusual types of pollen occur among, and are synapomorphic for, genera of Thunbergioideae. The two tribes (Mendoncieae, Thunbergieae) are readily distinguishable by their fruits: fleshy and indehiscent (drupaceous) in Mendoncieae vs. woody and explosively dehiscent (capsular) in Thunbergieae. Like those in Nelsonioideae and Avicennioideae, plants of this subfamily lack cystoliths and retinacula. Based on phylogenetic studies to date, *Pseudocalyx* is sister to *Thunbergia*, and both of these genera together are sister to *Mendoncia* (Borg & al., 2008). *Meyenia* and *Anomacanthus* have yet to be included in a phylogenetic analysis. Among the five genera, only *Mendoncia* occurs natively in the NW, where it has undergone extensive speciation.

• *Thunbergieae.* – This tribe consists of ca. 160 species treated currently among three genera (*Meyenia*, *Pseudocalyx*, *Thunbergia*) native to the Paleotropics and subtropics. Plants share numerous characteristics, including ovoid and prominently beaked capsules with the seeds borne in a subglobose to 4-partite capsular base, up to four seeds, and anther thecae showing considerable diversity in pubescence and appendages.

Table 1. Key morphological characters for the major lineages of Acanthaceae. Table includes some exceptions to general trends within a given lineage but is not comprehensive in terms of all exceptions that exist.

Character	Nelsonioideae	Avicennioideae	Thunbergioideae	Acantheae	Physacantheae	Andrographideae
Cystoliths	Absent	Absent	Absent	Absent	Absent	Present
Corolla aestivation	Descending-cochlear	Left-contort, slightly imbricate, or valvate	Left-contort; rarely ascending-cochlear	Ascending-cochlear or “open”	Left-contort	Ascending-cochlear
No. of fertile stamens	2 or 4	4	4	4	4	2
No. of anther thecae per fertile stamen	2	2	2	1	1	2
Pollen characteristics	3-colpate to 3-colporate, pseudocolpi absent	3-colporate, pseudocolpi absent	Spiraperturate, 3–6-colpate, or 7–9-lobate and -colpate, pseudocolpi absent	Usually 3-colpate, sometimes with numerous short colpus-like apertures dividing grains into polygonal regions, rarely with pseudocolpi	3-colporate, 9-pseudocolpate	3-colporate, 3-pororate, ectoapertural membrane and/or thickened margin often with spines, pseudocolpi absent
Fruit characteristics	Mostly small capsules varying from thin- to thick-walled, sometimes rostrate	Leathery to fleshy capsule that is non-explosive, and tardily dehiscent	Large woody rostrate capsule; OR globose or ellipsoid drupe	Fusiform or shortly rostrate capsule	Linear capsule	Linear and 4-angular or compressed elliptic, oblanceolate or narrowly oblong capsule
Hooked retinacula	Absent	Absent	Absent	Present	Present	Present
No. of ovules*	8 to many	4	1, 2 or 4	4	6–10	4 to many
No. of seeds*	8–30 (–68)	1	1, 2 or 4	2–4	(4–) 6–10	4 to many
Seed sculpture / trichomes	Variably smooth, pitted, with minute protrusions and with or without hygroscopic trichomes (these simple or branched)	Smooth	Smooth or sculptured, with a prominent scar or hole on one side (in drupaceous genera, a woody stone)	Dense hygroscopic trichomes, dense scales or tuberculate, glandular puberulous, smooth or glabrous, or otherwise variable	With pale straight or flexuose papillae-like trichomes	With or without dense hygroscopic trichomes or non-hygroscopic trichomes, smooth or sculptured
Other diagnostic or informative characters	Flowers often alternate to spirally arranged on inflorescence, although can be opposite	Mangrove shrubs or trees with pneumatophores, and plants cryptoviviparous	Often twiners; flowers subtended by paired clasping bracteoles		Leaves often variegated; long-cylindric or inflated calyx with short lobes	

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* Acanthaceae specialists have, in the past, described either the numbers of ovules or the numbers of seeds for a given taxon. We here provide ranges for both the numbers of ovules (i.e., total number, regardless of whether fertilized and later developing into a seed) as well as the number of seeds (i.e., the total number of ovules that were fertilized and later developed to maturity). We note that, for the vast majority of taxa, we are uncertain as to what minimum seed set is required for capsule development to maturation.

ˆ Pollen of *Borneacanthus* and *Pseudodicliptera* are not well known.

Barlerieae	Neuracantheae	Whitfieldieae	Ruellieae	Justicieae	Character
Present	Present	Present	Present	Present	Cystoliths
Quincuncial	Induplicate	Left-contort	Left-contort	Ascending-cochlear	Corolla aestivation
2 or 4	4	2 (*Lankesteria*) or 4	2 or 4	2 or 4	No. of fertile stamens
2, or mixed 2×2-thecous and 2×1-thecous	Mixed 2×2-thecous and 2×1-thecous	2	2	1 or 2; if 4 stamens then 2-thecous or mixed 2×2-thecous, 2×1-thecous	No. of anther thecae per fertile stamen
Mostly 3-colporate or 3-porate, interapertural exine often coarsely reticulate, pseudocolpi absent^	3-colporate, interapertural exine finely perforate, pseudocolpi absent	Usually lenticular, 2-pororate with ectoaperture usually very large, sometimes 3-pororate or spherical and pantoforate, pseudocolpi absent	Diverse; germinal apertures 2 to many, porate to colporate or pantoforate; tectum often raised flanking apertures, pseudocolpi often present and usually more than 2 between germinal apertures	Diverse, germinal apertures 2–6, (porate to) pororate to colporate, pseudocolpi often present but rarely (if ever) more than 2 between germinal apertures	Pollen characteristics
Fusiform or rostrate capsule, rarely stipitate	Fusiform or rostrate capsule	Stipitate or fusiform capsule	Stipitate, linear or fusiform capsule	Stipitate, sometimes also shortly rostrate capsule	Fruit characteristics
Present	Present	Present	Present	Present	Hooked retinacula
4	2 or 4	2 or 4	2–32	2 or 4	No. of ovules*
2–4	2–4	2–4	2–28	2–4	No. of seeds*
Dense hygroscopic trichomes or fine ?non-hygroscopic trichomes, rarely glabrous and smooth	Dense hygroscopic trichomes	Raised concentric rings at least towards the rim; glabrous or (*Lankesteria*) with hygroscopic trichomes	Dense hygroscopic trichomes or these restricted to the rim, rarely absent	Smooth or often sculptured (tubercles, spines, verrucae, etc.), and/or with hygroscopic or non-hygroscopic trichomes	Seed sculpture / trichomes
Cystoliths can occur in adjoining cells	Calyx bilabiate (anterior lip 2-notched, posterior lip 3-notched)	Inflorescence units often subtended by conspicuous paired clasping bracteoles	Filament curtain usually present, and thecae sometimes with basal appendages	Anther thecae sometimes offset to superposed and/or oblique, and one or both thecae sometimes with basal appendages	Other diagnostic or informative characters

These plants differ conspicuously from other Acanthaceae by the spiraperturate pollen of *Pseudocalyx* and *Thunbergia*, and the 7–9-lobate and -colpate pollen of *Meyenia* (Bremekamp, 1942).

• *Mendoncieae.* – Two genera (*Anomacanthus*, *Mendoncia*) are currently treated in this tribe of ca. 100 spp., which occurs in Africa, Madagascar/Mayotte, and the Neotropics. They share the synapomorphy of drupaceous fruits, these most frequently with a single, large seed (perhaps the largest in the family); drupes of *Anomacanthus* are 2-seeded. Schönenberger & Endress (1998) confirmed that, like many other members of the family, the ovary of *Mendoncia* is composed initially of two locules containing four ovules; however, later in development abortion yields a single locule with two fertile ovules, only one of which normally develops into a seed.

Acanthoideae. — Acanthoideae, consisting of ca. 4450 species, comprise by far the greatest morphological diversity and species richness within Acanthaceae. This lineage is readily delimited morphologically by the presence of capsules with retinacula. The global "success" of this group in terms of overall species richness may be explained in part by the evolutionary innovation of retinacula. It has been demonstrated recently that retinacula facilitate efficient launching and backspin of seeds of Acanthaceae at the fastest rate documented to date in nature (Cooper & al., 2018). We speculate that this capacity to launch seeds distant from source parent plants both minimizes intraspecific competition (Janzen, 1970; Connell, 1971) and aids in the establishment of populations in new niches. The following eight tribes are, for the most part, clearly delimited, but at times delimitation requires evidence from multiple characters, as well as study of both microscopic and macroscopic features.

• *Acantheae.* – Acantheae, with some ca. 550 species, are well-delimited morphologically: they are the only clade to combine retinaculate capsules with absence of cystoliths and presence of four monothecous stamens (the monogeneric tribe Physacantheae is the exception, see below). In addition, pollen of members of Acantheae are colpate and lack endoapertures, which are present in almost all other Acanthoideae. Acantheae can be further divided into two lineages: Aphelandrinae consist of species with bilabiate or subrotate corollas that occur primarily in the Neotropics but with representation in the Paleotropics (*Stenandriopsis*), and Acanthinae, which are restricted to the Paleotropics and have flowers with all five corolla lobes directed ventrally (McDade & al., 2005).

• *Physacantheae.* – Physacantheae, with three species currently recognized, comprise the single continental African forest genus *Physacanthus*. Tripp & al. (2013b) hypothesized an ancient origin of "wide hybridization" between members of Acantheae and Ruellieae for *Physacanthus*, and presented molecular and morphological evidence that supported this hypothesis. *Physacanthus* shares with Acantheae four monothecous stamens and absence of cystoliths but shares with Ruellieae colporate pollen and left-contort corolla aestivation. Given the likely hybrid origin of this lineage and intermediate (chimeric) morphologies of species (see Tripp & al., 2013b), it is difficult to place this lineage in either Acantheae or Ruellieae and, as such, a new tribe is proposed here and described formally below.

• *Barlerieae.* – This lineage comprises 13 genera and ca. 500 species, with most of the species diversity occurring in two widespread genera: the largely Paleotropical *Barleria* and the Pantropical *Lepidagathis*. Confirmed and putative members of Barlerieae share the synapomorphy of quincuncial corolla aestivation (Scotland & Vollesen, 2000; McDade & al., 2008; Darbyshire & al., 2019a) (Fig. 5B), but they are otherwise morphologically diverse. For example, species may bear four or five androecial units, comprising variously two stamens plus two or three staminodes, or four stamens with or without one staminode. When there are four stamens, they may all be bithecous or may be configured with two bithecous + two monothecous. With the exception of *Barleria* (Comito & al., in rev.), genera of Barlerieae are among the least-studied lineages of Acanthaceae from a molecular phylogenetic perspective, with several having never been sequenced, and so the circumscription of this tribe must be considered provisional (Darbyshire & al., 2019a). Following further studies, it may be possible to recognize subtribes, with morphological data suggesting at least three taxa: (1) *Barleria*, with strongly zygomorphic calyces that are 4-lobed due to partial or complete fusion of the two anterior lobes; corollas that are variously arranged from subrotate to strongly zygomorphic but always lacking a hooded upper lip; globose, tricolporate, coarsely reticulate pollen; and an androecium usually of two fully developed bithecous stamens and either two minute stamens that seem to function for self-pollination plus one staminode, or three staminodes (Darbyshire & al., 2019a); (2) *Crabbea* and allies, with ± actinomorphic, 5-lobed calyces; weakly zygomorphic corollas without a hooded upper lip; globose to subprolate, tri- (or hexa-) porate, variously gemmate,

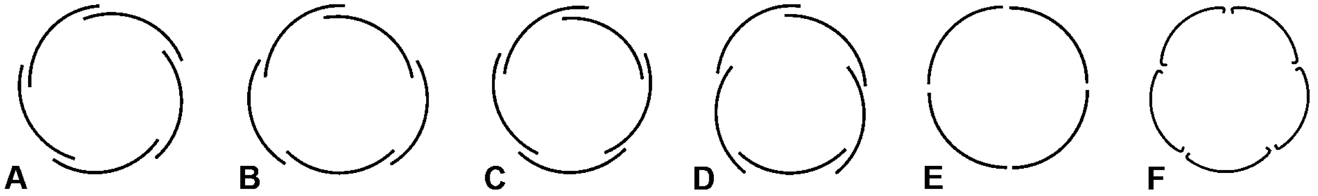

Fig. 5. Corolla aestivation types in Acanthaceae. Note that the "open" aestivation observed in some Acantheae is not illustrated here. **A**, Left-contort (Avicennioideae in part, Thunbergioideae in part, Physacantheae, Whitfieldieae, Ruellieae); **B**, Quincuncial (Barlerieae); **C**, Ascending-cochlear (Thunbergioideae in part, Acantheae, Andrographideae, Justicieae); **D**, Descending-cochlear (Nelsonioideae); **E**, Valvate (Avicennioideae in part); **F**, Induplicate (Neuracantheae).

verrucose, rugose to coarsely reticulate pollen; and an androecium of four bithecous stamens (Thulin, 2007; Onjalalaina & Darbyshire, 2016); and (3) *Lepidagathis* and allies, with often zygomorphic, 5-lobed or sometimes 4-lobed calyces due to partial fusion of the two anterior lobes; bilabiate corollas with a hooded upper lip; prolate, tricolporate, finely reticulate pollen; and an androecium of four bithecous stamens or two bithecous + two monothecous stamens or two bithecous stamens plus two staminodes (Kameyama, 2008; Champluvier & Darbyshire, 2012).

• *Andrographideae.* – This lineage, comprising ca. eight genera and ca. 130 species, is unusual in Acanthaceae in being restricted to tropical Asia. These genera share the synapomorphy of "daubenpollen", i.e., pollen with the apertural margins and/or surfaces conspicuously thickened and intricately ornamented with conical spines (Scotland & Vollesen, 2000; McDade & al., 2008). Although apparently not closely related (McDade & al., 2008), taxa of Andrographideae can otherwise closely resemble members of Justicieae, with these two tribes sharing ascending-cochlear aestivation (Fig. 5C), two stamens with or without two additional staminodes, and zygomorphic, often bilabiate corollas. However, in addition to the unique pollen type of Andrographideae, they are usually also distinguished from Justicieae by ovule and seed number: Andrographideae typically have more than four ovules per ovary and the capsule is usually 6–20-seeded whereas Justicieae have two or four ovules/seeds per capsule. However, 4-seeded capsules are rarely recorded in Andrographideae, specifically occurring in *Andrographis* (*Indoneesiella*) and in *Sphinctacanthus*; the latter genus is only tentatively placed in Andrographideae here and with reference only to the type, *S. griffithii* (T.Anderson) Benth. & Hook.f. (see Hansen, 1985b; McDade & al., 2018; and footnote in the key, below). Molecular phylogenetic studies on Andrographideae have been very limited to date (McDade & al., 2008; Arolla & al., 2015), and generic circumscription is still in a state of flux (Deng & al., 2020). For example, the genus *Haplanthus* was recently reinstated as distinct from *Andrographis* based on morphological evidence (Gnanasekaran & al., 2016).

• *Whitfieldieae.* – This small lineage of eight genera and ca. 33 species is confined to tropical Africa and Madagascar (Grall & Darbyshire, 2021). Manktelow & al. (2001) first recognized the tribe Whitfieldieae to accommodate *Whitfieldia* together with two Afro-Malagasy genera, *Chlamydacanthus* and *Lankesteria*. McDade & al. (2008) recognized a strongly supported core Whitfieldieae clade and found *Lankesteria* to be weakly supported as sister to it: these clades are here treated as subtribes, Whitfieldiinae and Lankesteriinae. Manktelow & al. (2001) proposed several synapomorphies for Whitfieldieae, most notably the presence of concentric rings of ridges protruding from the testa of the seeds and pollen with a densely granular circular area surrounding the pores. The concentric ridges on the seeds are easily observed in Whitfieldiinae where the seeds lack trichomes, but they are hidden by the presence of dense hygroscopic trichomes in Lankesteriinae. Most species for which pollen has been sampled have lenticular, bipororate pollen grains with ectoapertures that are usually very large and pseudocolpi absent, similar to (but homoplasious with) the "gürtelpollen" of Isoglossinae, Justicieae (Manktelow & al., 2001; McDade & al., 2008). Exceptions are *Whitfieldia elongata*, which has pantofororate pollen, and *Lankesteria*, which has triporate pollen with a reticulate exine (Manktelow & al., 2001). Members of Whitfieldieae also combine left-contort aestivation (Fig. 5A) and four androecial elements (usually four stamens in Whitfieldiinae, two stamens + two staminodes in Lankesteriinae), without any basal fusion of filaments and lacking a filament curtain. Ruellieae also have left-contort aestivation, but in that tribe, all but four of the genera have a well-developed filament curtain (see below). We note that Manktelow & al. (2001) reported imbricate aestivation in *Chlamydacanthus*, but we have observed only contorted buds in that genus.

• *Neuracantheae.* – This tribe comprises the enigmatic Paleotropical genus *Neuracanthus* Nees (32 spp.). McDade & al. (2008) found *Neuracanthus* to be monophyletic with strong support but were unable to place it with certainty within the phylogeny of Acanthaceae. Instead, it was found to be weakly supported as sister to a clade comprising (Barlerieae + Andrographideae) + Whitfieldieae. The proposed morphological synapomorphy for *Neuracanthus*, and hence for tribe Neuracantheae, is a bilabiate calyx with three posterior lobes and two anterior lobes (i.e., in a 3 + 2 pattern) (McDade & al., 2008). The arrangement of the corolla is also unique among Acanthaceae: the two posterior lobes are largely fused to form a lobe similar in size and shape to each of the three anterior lobes, and these four broad, shallow lobes are arranged in a ± equidistant manner such that the limb is funnel-shaped and appears only weakly zygomorphic (Bidgood & Brummitt, 1998). Other features are shared with members of Barlerieae and thus tentatively support a close relationship with that tribe. For example, presence of hygroscopic trichomes on the seeds and exstipitate, 2- or 4-seeded capsules. The androecium is composed of four didynamous stamens, the anterior pair being bithecous and the posterior pair monothecous, an arrangement also found in some species of *Lepidagathis* in Barlerieae (Bidgood & Brummitt, 1998). However, the pollen of *Neuracanthus*, which is tricolporate with a perforate tectum, does not closely resemble pollen of any its putative relatives. The corolla aestivation pattern of *Neuracanthus* is described as induplicate by Balkwill & Welman (2000), in which the corolla lobes are folded inwards at the margin and do not overlap (Fig. 5F). This represents a unique aestivation pattern in Acanthaceae. Attempts by the current authors to confirm this from herbarium material have been inconclusive (I. Darbyshire and T.F. Daniel, pers. obs.).

• *Ruellieae.* – With 37 genera and ±1200 species, Ruellieae are pantropical to temperate plants that vary tremendously in growth form, floral morphology, and ecology. Although members of Ruellieae are primarily caulescent herbs (acaulescent in a few species) or shrubs, plants of *Trichanthera* and *Bravaisia* are fully arborescent trees up to at least 9 m tall, extending to 20–25 m tall in *Bravaisia integerrima* (Spreng.)

Standl., *Trichanthera corymbosa* Leonard, and *Trichanthera gigantea* (Bonpl.) Nees (Daniel, 1998, 2015b). Among Acanthoideae, Ruellieae are second only to Justicieae in species richness. Ruellieae are globally widespread, with the diverse genera *Ruellia* and *Strobilanthes* dominating the Western and Eastern Hemispheres, respectively, in taxonomic diversity. Ruellieae have been the focus of detailed phylogenetic investigation (Tripp & al., 2013a). Synapomorphies for the tribe include (1) presence of a filament curtain (evolutionarily lost in some members), (2) left-contort corolla aestivation (Fig. 5A), (3) presence of hygroscopic trichomes that cover seed surfaces (these reduced to the seed margins in some genera and/or species), and (4) bifid, filiform stigma lobes in which the dorsal lobe is often partially or fully reduced. Within Acanthoideae, only members of Whitfieldieae similarly have left-contort corolla aestivation, but genera within that clade possess several other features that separate them from Ruellieae (e.g., concentric ridges on seed surfaces and capitate stigmas). Compared to many other lineages of Acanthaceae, the number of seeds per fruit is exceptionally diverse in Ruellieae, ranging from 2 to over 36 per capsule; seed number may vary markedly even within a single genus (e.g., *Ruellia*). Most Ruellieae have flowers with four stamens, but two stamens plus two staminodes are not uncommon. Ruellieae are most likely to be confused with Justicieae, the sister lineage, with which they share pollen bearing pseudocolpi in many taxa. There is no readily available macromorphological feature to differentiate the two tribes beyond corolla aestivation: left-contort in Ruellieae and ascending-cochlear in Justicieae. However, members of Justicieae more commonly have 2 (vs. 4) stamens and lack a filament curtain (but note that *Asystasia* and allies within Graptophyllinae have four stamens, see below).

• *Justicieae*. – With ca. 100 currently recognized genera and at least 2000 species, Justicieae are the largest of the major sublineages of Acanthaceae. The work of McDade & al. (2000b, 2021) supports the monophyly of Justicieae consisting of four major clades: the Pseuderanthemum lineage, Isoglossinae, the Tetramerium lineage, and the Justicioids, with Isoglossinae further subdivided by McDade & al. (2021) into Isoglossinae s.str. and the Ptyssiglottis lineage. The major clades of McDade & al. (2000b, 2021) are here treated formally among five subtribes: Graptophyllinae, Isoglossinae, Monotheciinae, Tetrameriinae, and Justiciinae. Justicieae are marked by the presence of tricolporate, hexapseudocolpate pollen, a morphology not known in other Acanthaceae. This pollen is known from all major lineages of Justicieae, possibly excepting Isoglossinae (Kiel & al., 2006; McDade & al., 2021), with subsequent evolutionary changes in pollen morphology occurring in all subtribes (Kiel & al., 2017, 2018; McDade & al., 2021). Isoglossinae are marked by "gürtel-pollen", i.e., bipororate (more rarely tri- or tetrapororate), usually lenticular pollen with a pronounced marginal girdle. Among Justiciinae some species retain tricolporate hexapseudocolpate pollen but in many other species, particularly NW Justiciinae, exine ornamentation and aperture number depart considerably. In contrast to Ruellieae, species of which have a wide range in seed number, members of Justicieae typically have two to four seeds per capsule. Justicieae are also notable for their androecial diversity, with staminal elements ranging from two to four, together with additional innovations (see below). Plants of Graptophyllinae have four staminal elements, either as four stamens or as two stamens + two staminodes. In contrast, all other Justicieae have just two stamens and no staminodes, with the exception of *Chalarothyrsus* (Tetrameriinae), which has four stamens. Species of Justiciinae have corollas with a rugula (i.e., a medial furrow in the internal surface of the dorsal corolla lip and tube in which the style lies during anthesis). The rugula is lost secondarily in some genera including *Dicliptera* and *Hypoestes*. Additionally, taxa of Justiciinae often have "anther complexity" in which the thecae are not parallel, not evenly inserted on the filament (i.e., the pair are offset from one another), and/or are basally awned or spurred (Kiel & al., 2017, 2018). Unevenly inserted and/or oblique thecae are also frequent in Isoglossinae but there the thecae are not awned or spurred (Darbyshire, 2009; Darbyshire & al., 2011; McDade & al., 2021). Unevenly inserted and oblique thecae are uncommon elsewhere in Justicieae, although awned or otherwise appendaged thecae are widespread in Graptophyllinae and occasional in Monotheciinae (Darbyshire & al., 2019c; McDade & al., 2021). There are, at present, no known morphological synapomorphies for Tetrameriinae or Monotheciinae (McDade & al., 2018, 2021).

Generic delimitation within Acanthaceae. — Historically, generic delimitation has been a challenge owing to complex patterns of morphological variation exacerbated by scant collections and a paucity of systematists and taxonomists working in such a diverse family. More recently, these challenges have been compounded by a paucity of recently collected material for molecular phylogenetic study. Although resolving the entirety of outstanding issues concerning relationships within and among genera is beyond the scope of the present work, we take the opportunity to remark on some of our most persistent challenges in the footnotes to the keys, below. Genera of Acanthaceae have traditionally been delimited based on morphological traits, with important characters including calyx and corolla morphology, number and characteristics of the androecial units, variation in pollen type, number of ovules/seeds, and capsule morphology. Although many of these traits are phylogenetically informative, reliance on variation in floral morphology to delimit genera has, in some cases, yielded unsatisfactory generic delimitation owing to rampant homoplasy (e.g., Daniel & al., 2008; Tripp & Manos, 2008; Côrtes & al., 2015). This also applies to numerous instances of segregate genera now known to be nested within a larger genus (e.g., *Ruellia*, Tripp, 2007). Recent molecular studies, involving denser sampling than previously achieved, have revealed the magnitude of the problem in some parts of the family. In Tetrameriinae, McDade & al. (2018) refer to a "clade complex", analogous to a species complex but in this case of clades that are very distinctive with regard to molecular data but show no notable macromorphological differences based on current evidence. In Justiciinae, Kiel & al. (2017, 2018) proposed several options for radical changes to generic circumscription in view of the gross non-monophyly of *Justicia*, with subsequent studies inclining towards a narrower circumscription of genera (Darbyshire & al., 2019c, 2020, in press).

Elsewhere in the family, genera within some clades such as Barlerieae (Onjalalaina & Darbyshire, 2016), Whitfieldieae (Grall & Darbyshire, 2021), Isoglossinae (Kiel & al., 2006; McDade & al., 2021), and Graptophyllinae (McDade & al., 2021) remain poorly delimited morphologically. Excessive segregation of genera is sometimes linked to geography and to taxonomists who have focused on those regions. This is most notable in Madagascar, where many of the endemic genera, as currently delimited, are not well differentiated from continental African genera (Onjalalaina & Darbyshire, 2016). Indeed, detailed molecular studies in Ruellieae showed that all three genera of Ruellieae that were previously considered to be endemic to Madagascar were nested within African or pantropical genera (Tripp & al., 2013a). Other genera have long been in flux. For example, the extensive variation in pollen morphology among species of *Strobilanthes* led Bremekamp (1944) to subdivide this lineage into some 54 genera; most of these names have subsequently been synonymized back into *Strobilanthes* (e.g., Wood & Scotland, 2009; Hu & al., 2011; Tripp & al., 2013a; Wood, 2014).

In sum, the most pressing challenge now facing those studying Acanthaceae is to provide a robust generic framework for the family. In the current work, we place all accepted (and disputed) genera within a revised classification of the family. Although this represents our best prediction of relatedness based on available evidence, we emphasize that several issues persist and some aspects of the classification presented below will be further revised following inclusion of as yet unsampled genera in ongoing and future phylogenetic studies and analyses.

■ TAXONOMIC TREATMENT OF ACANTHACEAE

The revised classification of Acanthaceae is organized by subfamily followed by tribe, subtribe, then genus. Subfamilies, tribes, and subtribes are organized phylogenetically. Genera are organized alphabetically (see Appendix 2 for a proposed linear phylogenetic sequence for the genera). Following taxon names, a “ch” denotes changes since, and deviations from, Scotland & Vollesen (2000), including additional genera. We do not mark lineages that have changed rank (e.g., Barleriinae to Barlerieae) or that have been subdivided (e.g., the subtribes of Justicieae and Ruellieae) since Scotland & Vollesen (2000). A “mol” denotes that the taxon has been included in a published phylogenetic study based on molecular sequence data. A “prov” indicates that the classification should be considered provisional.

Following each genus is a geographical code to represent our best understanding of approximate native distributions of genera, as follows: AA (Southeast Asia, Australasia, Oceania, and greater Pacific), AF (continental sub-Saharan Africa and associated islands but excluding Madagascar and the Mascarenes), AR (Arabian Peninsula including Socotra, through Iran), EU (Europe, Mediterranean region, Middle East), IC (India and Pakistan through China and Japan), MA (Madagascar and the Mascarenes), NW (New World), PAN (representation in both the OW and the NW). Instances where there is uncertainty surrounding native status of taxa in a given region, for example, whether *Nelsonia* is or is not native to the NW, we default to the former. Dichotomous keys are organized by taxonomy as well as by geography. For purposes of the geographical keys to genera, several regions were combined. We present a total of three keys: (1) AA + IC, (2) AF + AR + EU + MA, and (3) NW.

I. The classification

ACANTHACEAE Juss.

NELSONIOIDEAE Pfeiff. **(6 genera)**
Anisosepalum E.Hossain (AF); mol
Aymoreana Braz, T.F.Daniel & Kiel (NW); ch, mol
Elytraria Michx. (PAN); mol
Nelsonia R.Br. (PAN); mol
Saintpauliopsis Staner (AF, MA); mol
Staurogyne Wall. (PAN); mol

AVICENNIOIDEAE Miers **(1 genus)**
Avicennia L. (PAN); ch, mol

THUNBERGIOIDEAE T.Anderson
Mendoncieae Meisn. **(2 genera)**
Anomacanthus R.D.Good (AF)
Mendoncia Vell. ex Vand. (AF, MA, NW); mol

Thunbergieae Dumort. **(3 genera)**
Meyenia Nees (IC)
Pseudocalyx Radlk. (AF, MA); mol
Thunbergia Retz. (AA, AF, IC, MA); mol

ACANTHOIDEAE Eaton
Acantheae Dumort.
Acanthinae Nees **(8 genera)**
Acanthopsis Harv. (AF); mol
Acanthus L. (AA, AF, AR, EU, IC); mol
Blepharis Juss. (AA, AF, IC); mol
Crossandra Salisb. (AF, AR, IC, MA); mol
Crossandrella C.B.Clarke (AF); mol
Cynarospermum Vollesen (IC); mol
Sclerochiton Harv. (AF); mol
Streptosiphon Mildbr. (AF); mol

Aphelandrinae Bremek. **(7 genera)**
Aphelandra R.Br. (NW); mol
Cyphacanthus Leonard (NW)
Holographis Nees (NW); mol
Neriacanthus Benth. (NW); mol
Salpixantha Hook. (NW); mol
Stenandriopsis S.Moore (AF, MA); ch, mol
Stenandrium Nees (NW); mol

Physacantheae E.Tripp & I.Darbysh., **tr. nov. (1 genus)**
Physacanthus Benth. (AF); ch, mol

Neuracantheae Reveal **(1 genus)**
Neuracanthus Nees (AA, AF, IC, MA); ch, mol

Barlerieae Nees **(13 genera)**
Barleria L. (PAN); mol
Barleriola Oerst. (NW)
Borneacanthus Bremek. (AA)
Boutonia DC. (MA)
Chroesthes Benoist (AA, IC)
Crabbea Harv. (AF); mol
Hulemacanthus S.Moore (AA)
Lasiocladus Bojer ex Nees (MA); ch, mol
Lepidagathis Willd. (PAN); mol
Pericalypta Benoist (MA); ch
Podorungia Baill. (MA); ch
Pseudodicliptera Benoist (MA); ch, mol
Schaueriopsis Champl. & I.Darbysh. (AF); ch, mol

Andrographideae Endl. **(8 genera)**
Andrographis Wall. ex Nees (AA, IC); mol
Diotacanthus Benth. (IC)
Graphandra J.B.Imlay (AA)
Gymnostachyum Nees (AA, IC); mol
Haplanthodes Kuntze (IC)
Haplanthus Nees (AA, IC); ch
Phlogacanthus Nees (AA, IC); mol
Sphinctacanthus Benth. (IC); ch, prov

Whitfieldieae Bremek. ex Reveal
Lankesteriinae I.Darbysh. & E.Tripp, **subtr. nov. (1 genus)**
Lankesteria Lindl. (AF, MA); ch, mol

Whitfieldiinae I.Darbysh. & E.Tripp, **subtr. nov. (7 genera)**
Camarotea Scott Elliot (MA); ch, mol
Chlamydacanthus Lindau (AF, MA); ch, mol
Forcipella Baill. (MA); ch, mol
Leandriella Benoist (MA); ch, mol
Vindasia Benoist (MA); ch
Whitfieldia Hook. (AF); ch, mol
Zygoruellia Baill. (MA); ch, mol

Ruellieae Dumort.
Erantheminae Nees **(5 genera)**
Brunoniella Bremek. (AA); mol
Eranthemum L. (AA, IC); mol
Kosmosiphon Lindau (AF); mol
Leptosiphonium F.Muell. (AA); mol
Pararuellia Bremek. & Nann.-Bremek. (AA, IC); mol

Dinteracanthinae E.Tripp & I.Darbysh. **(1 genus)**
Dinteracanthus Schinz (AF); ch, mol

Ruelliinae Nees **(5 genera)**
Acanthopale C.B.Clarke (AA, MA); mol
Calacanthus T.Anders. ex Benth. (IC); mol
Dischistocalyx T.Anderson ex Benth. (AF); mol
Ruellia L. (PAN); mol
Satanocrater Schweinf. (AF); mol

Trichantherinae Benth. & Hook.f. **(6 genera)**
Bravaisia DC. (NW); mol
Louteridium S.Watson (NW); mol
Sanchezia Ruiz & Pav. (NW); mol
Suessenguthia Merxm. (NW); mol
Trichanthera Kunth (NW); mol
Trichosanchezia Mildbr. (NW); mol

Strobilanthinae T.Anderson **(1 genus)**
Strobilanthes Blume (AA, IC); mol

Hygrophilinae Nees **(2 genera)**
Brillantaisia P.Beauv. (AF, MA); mol
Hygrophila R.Br. (PAN); mol

Petalidiinae Benth. & Hook.f. **(6 genera)**
Duosperma Dayton (AF); mol
Dyschoriste Nees (PAN); mol
Echinacanthus Nees (IC, AA); mol
Petalidium Nees (AF, IC); mol
Ruelliopsis C.B.Clarke (AF); mol
Strobilanthopsis S.Moore (AF); mol

Mcdadeinae E.Tripp & I.Darbysh. **(1 genus)**
Mcdadea E.Tripp & I.Darbysh. (AF); ch, mol

Phaulopsidinae E.Tripp & I.Darbysh. (**1 genus**)
Phaulopsis Willd. (PAN); mol

Mimulopsidinae E.Tripp **(4 genera)**
Eremomastax Lindau (AF); mol
Heteradelphia Lindau (AF); mol
Mellera S.Moore (AF); mol
Mimulopsis Schweinf. (AF, MA); mol

Ruellieae incertae sedis (3 genera)
Diceratotheca J.R.I.Wood & Scotland (AA); ch
Stenothyrsus C.B.Clarke (AA)
Xylacanthus Aver. & K.S.Nguyen (AA); ch

Justicieae Dumort.
Graptophyllinae T.Anderson **(27 genera)**
Afrofittonia Lindau (AF); mol
Asystasia Blume (AA, AF, AR, IC, MA); mol
Ballochia Balf.f. (AR); mol
Chamaeranthemum Nees (NW); mol
Chileranthemum Oerst. (NW); mol
Codonacanthus Nees (IC); mol
Cosmianthemum Bremek. (AA, IC); mol

Filetia Miq. (?AF, AA); mol
Glossochilus Nees (AF); mol
Graptophyllum Nees (AA, AF); mol
Herpetacanthus Nees (NW); mol
Isotheca Turrill (NW)
Linariantha B.L.Burtt & R.M.Sm. (AA)
Mackaya Harv. (AF, IC); mol
Odontonema Nees (NW); mol
Oplonia Raf. (MA, NW); mol
Phialacanthus Benth. (AA, IC)
Pranceacanthus Wassh. (NW); mol
Pseuderanthemum Radlk. (PAN); mol
Psilanthele Lindau (NW); mol
Pulchranthus V.M.Baum, Reveal & Nowicke (NW); mol
Ruspolia Lindau (AF, MA); mol
Ruttya Harv. (AF, AR, MA); mol
Sapphoa Urb. (NW)
Spathacanthus Baill. (NW); mol
Thysanostigma J.B.Imlay (AA)
Wuacanthus Y.F.Deng, N.H.Xia & H.Peng (IC); ch, mol

Monotheciinae Lindau **(8 genera)**
Ambongia Benoist (MA); prov
Calycacanthus K.Schum. (AA); mol
Champluviera I.Darbysh., T.F.Daniel & Kiel (AF); ch, mol
Cyclacanthus S.Moore (AA); prov
Jadunia Lindau (AA); mol
Marcania J.B.Imlay (AA); mol
Monothecium Hochst. (AF, IC); mol
Ptyssiglottis T.Anderson (AA, IC); mol

Isoglossinae Lindau **(7 genera)**
Brachystephanus Nees (AF, MA); mol
Celerina Benoist (MA)
Isoglossa Oerst. (AA, AF, AR, IC, MA); mol
Melittacanthus S.Moore (MA); mol
Sebastiano-Schaueria Nees (NW); mol
Stenostephanus Nees (NW); mol
Sphacanthus Benoist (MA); ch, mol

Tetrameriinae T.F.Daniel, Kiel & McDade, **subtr. nov. (27 genera)**
Ancistranthus Lindau (NW); mol
Angkalanthus Balf.f. (AR); mol
Anisacanthus Nees (NW); mol
Aphanosperma T.F.Daniel (NW); mol
Carlowrightia A.Gray (NW); mol
Cephalophis Vollesen (AF); ch, prov
Chalarothyrsus Lindau (NW); mol
Chlamydocardia Lindau (AF); mol
Chorisochora Vollesen (AF, AR); mol
Clinacanthus Nees (AA, IC); mol
Ecbolium Kurz (AF, AR, IC, MA); mol
Fittonia Coem. (NW); mol
Gypsacanthus E.J.Lott, V.Jaram. & Rzed. (NW); mol
Henrya Benth. (NW); mol
Hoverdenia Nees (NW); mol
Kudoacanthus Hosok. (IC); ch, mol
Leptostachya Nees (AA, IC); ch, prov
Megalochlamys Lindau (AF, AR); mol
Mexacanthus T.F.Daniel (NW); mol
Mirandea Rzed. (NW); mol
Pachystachys Nees (NW); mol
Populina Baill. (MA); mol
Schaueria Nees (NW); mol
Tetramerium Nees (NW); mol
Thyrsacanthus Moric. (NW); ch, mol
Trichaulax Vollesen (AF); mol
Yeatesia Small (NW); mol

Justiciinae Nees **(23 genera)**
Anisostachya Nees (AF, MA); ch, mol
Anisotes Nees (AF, AR, MA); mol
Ascotheca Heine (AF); mol
Cephalacanthus Lindau (NW); mol
Clistax Mart. (NW); mol
Dasytropis Urb. (NW); prov
Dichazothece Lindau (NW); prov
Dicladanthera F.Muell. (AA); prov
Dicliptera Juss. (PAN); mol
Harpochilus Nees (NW); mol
Hypoestes Sol. ex R.Br. (AA, AF, AR, IC, MA); mol
Justicia L. (PAN); mol
Kenyacanthus I.Darbysh. & Kiel (AF); ch, mol
Megaskepasma Lindau (NW); mol
Meiosperma Raf. (AF, IC); ch, mol
Metarungia Baden (AF); mol
Pogonospermum Hochst. (AF); ch, mol
Poikilacanthus Lindau (NW); mol
Rhinacanthus Nees (AA, AF, AR, IC, MA); mol
Rungia Nees (AA, AF, AR, IC, MA); mol
Trichocalyx Balf.f. (AR); mol
Vavara Benoist (MA); ch
Xerothamnella C.T.White (AA); mol

Justicieae incertae sedis (5 genera)
Dolichostachys Benoist (MA); ch
Ichthyostoma Hedrén & Vollesen (AF); mol
Samuelssonia Urb. & Ekman (NW)
Streblacanthus Kuntze (NW); mol
Tessmanniacanthus Mildbr. (NW)

ACANTHACEAE incertae sedis (1 genus)
Ritonia Benoist (MA); ch

Excluded names. — *Gymnophragma* Lindau was validly published with two syntypes (both collected by C. Ledermann, Papua New Guinea) described in the protologue. However, neither appear to be extant, and there is apparently no additional extant material representing this genus. Based on the protologue it is furthermore unclear as to what taxon this name likely applies. We thus here exclude the name.

Idiacanthus Leonard was not validly published but rather applied only to herbarium material (McDade & al., 2008). It is likely that this name refers to *Stenostephanus* (McDade & al., 2008).

Schwabea Endl. was previously treated as congeneric with *Monechma* Hochst. but the description in the protologue does not fit with the latter "genus" (now segregated into *Meiosperma* and *Pogonospermum*), most notably in the androecium of four stamens. The genus was described from cultivated plants grown from an unnumbered collection made by T. Kotschy in "Nubia", and no extant original material has been traced.

Sericospora Nees was based on a single species, *S. crinita* Nees, which belongs within Justicieae, but the type material at GZU is a mixed collection with one of the shoots being non-Acanthaceae. It is possible that the capsule and seeds in the packet do not pertain to the shoot of Acanthaceae. The plant may belong within *Justicia* but this requires confirmation.

Strobilacanthus Griseb. probably refers to cultivated *Crossandra* (McDade & al., 2005).

II & III. Dichotomous keys

Here, we present a series of keys (12 in total) for identification of Acanthaceae. Keys to subfamilies, tribes, and genera (Part II) are followed by geographical keys to genera (Part III). Specifically, Part II (9 keys) consists of: Key to the subfamilies of Acanthaceae, Key to the tribes of Acanthoideae, Key to the genera of Nelsonioideae, Key to the genera of Thunbergioideae, Key to the genera of Acantheae, Key to the genera of Barlerieae, Key to the genera of Andrographideae, Key to the genera of Whitfieldieae, and Key to the genera of Ruellieae. Part III (3 keys) consists of: Key to genera in Africa, Madagascar, the Mediterranean region, and the Arabian Peninsula; Key to genera in Asia and Australasia (excluding the Arabian Peninsula and Mediterranean region); and Key to genera in the Americas. In Part II, the only major lineage for which we have not yet produced a worldwide key to the genera is Justicieae, which remains taxonomically problematic. Genera of Justicieae are, however, included within the geographical keys in Part III.

This effort represents the first such attempt since Lindau (1895) to introduce globally useful keys but has not been without challenges. These challenges arise because there remains much work to be done to adequately resolve generic circumscription in several lineages of the family, with many future generic changes likely. We have tried, where possible, to address most of the known exceptions to typical morphological features of a genus either through use of endnotes (numbers in square brackets) or, in some cases, through separation of a particular taxon or group of taxa elsewhere in the key.

At the generic rank, several morphological characters, such as the number of stamens, the presence or absence of staminodes, the number, arrangement and ornamentation of anther thecae, the number of ovules and seeds, and the arrangement of the calyx and corolla, are both taxonomically informative and easily observable. As such, these characters are broadly employed in the dichotomous keys below, even when exceptions require that genera be keyed more than once. This helps to avoid the use of less readily observable characters. However, in some instances, we have needed to resort to using more technical characters (e.g., corolla aestivation, pollen morphology) where such features are of primary importance in taxon delimitation. Future attempts to delimit taxa may avoid the use of such subtle features through development of multi-access keys to the genera.

The following set of keys emphasizes taxa native to respective geographical regions. Thus, species that have been introduced to a given region but are not native there are generally not included in the key to that region. Geographical ranges are included in the keys in Parts II and III where they are useful in the separation of morphologically similar genera or where taxa have a notably restricted distribution; in Part III, if specific geography is not listed, it can be taken that the genus is widespread in that geographical region.

For the 12 keys presented below, we define the following terms:

(1) Types of **corolla aestivation**, or the orientation of petals to one another during the mature bud stage: refer to Fig. 5 for a schematic of all types used in keys.

(2) A **filament curtain** is a physical partition within the corolla formed by elaboration of the synstapetal zone to form flanges of tissue that partition the corolla obliquely into two compartments and enclose a nectar chamber behind this physical partition.

(3) A **rugula** is a groove formed by elaborations of the inner surface of the corolla, often derived from veins along the dorsal side of the corolla to form a channel that generally retains the style within the tube and oftentimes upper lip. This structure is sometimes referred to as a "stylar furrow".

(4) **Fracturing placentae** refer to fruits in which the placentae and retinacula fracture away from the capsule walls during fruit dehiscence. This is sometimes referred to as "elastic dehiscence" in other works. In some cases, the lateral walls of the capsule (which can be modified and thinned) also rupture as the placentae fracture.

(5) **Cystoliths** are mineralized structures of unknown substance in Acanthaceae (putatively calcium oxalate) that are visible generally as hyaline or white streaks or dots on dried herbarium material on the upper and/or lower leaf surfaces, and sometimes on other vegetative surfaces (e.g., commonly on stems). These structures characterize Acanthoideae except for members of Acantheae and Physacantheae.

(6) **Nototribic flowers** have stamens positioned near or appressed to the upper lip of the corolla and anthers dehiscing toward the lower lip; this is the most typical condition in Acanthaceae. **Sternotribic flowers** have stamens positioned near or appressed to the lower lip of corolla and anthers dehiscing toward the upper lip. **Pleurotribic flowers** have stamens positioned between the two lips of the corolla and anthers dehiscing toward the center of the floral axis and each other.

(7) **Zygomorphic** corollas are those with an overall single plane of symmetry (i.e., bilaterally symmetric). **Bilabiate** corollas are zygomorphic but with two distinct lips, i.e., an upper and a lower lip.

(8) **Hygroscopic trichomes** are typical of seed surfaces on many genera of Acanthaceae; such trichomes become inflated and elongated when moistened and many are additionally mucilaginous when inflated.

II. Keys to the subfamilies, tribes, and genera of Acanthaceae

Key to the subfamilies of Acanthaceae

1 Fruit a capsule with seeds held on hooked retinacula (retinacula malformed or not discernible in *Aphanosperma* and *Chalarothyrsus* and seeds permanently retained in capsule valves); cystoliths present or if absent then anthers monothecous .... **Acanthoideae**
1 Fruit a capsule or a drupe; if a capsule, then without hooked retinacula; cystoliths absent; anthers bithecous 2
2 Mangrove trees or shrubs with pneumatophores; fruit a leathery 1-seeded capsule .... **Avicennioideae**
2 Herbs, shrubs or lianas, not mangrove trees or shrubs, pneumatophores absent; fruit a capsule with 2 or more seeds, or a 1–2-seeded drupe ... 3
3 Herbs or shrubs, not twining; paired bracteoles present or absent but never large and conspicuous; flowers usually alternate or spirally arranged in few- to many-flowered inflorescences; calyx deeply 4- or 5-lobed; fruit a many-seeded (usually >10 seeds) capsule .... **Nelsonioideae**
3 Climbing herbs or lianas, less frequently free-standing shrubs or perennial herbs; flowers subtended by conspicuous clasping or partially connate (at anthesis) paired bracteoles; flowers solitary or in fascicles or racemes of mostly opposite flowers, never spirally arranged; calyx a subentire or undulate rim or with irregular teeth, or shallowly 5-lobed; fruit either a 1–2-seeded drupe or a 2–4-seeded woody capsule...................................... **Thunbergioideae**

Key to the tribes of Acanthoideae

1 Cystoliths absent; stamens 4, monothecous................................. 2
1 Cystoliths present; stamens 2 or 4, if 4 then at least 2 of these bithecous 3
2 Calyx long-tubular, cylindrical to inflated; pollen colporate; capsule with more than 4 seeds; corolla aestivation left-contort.................... ....**Physacantheae** [1]
2 Calyx not as above; pollen colpate; capsule with up to 4 seeds; corolla aestivation ascending-cochlear .... **Acantheae**
3 Calyx strongly bilabiate, with a 2-lobed or -toothed anterior lip and a 3-lobed or -toothed posterior lip; androecium usually of 2 bithecous stamens and 2 monothecous stamens (rarely 4 bithecous stamens); corolla with a funnel-shaped limb comprising equal anterior and lateral lobes and partially (or almost completely) fused dorsal pair of lobes, not strongly bilabiate........................**Neuracantheae**
3 Above combination of characters lacking; if androecium of 2 bithecous stamens and 2 monothecous stamens then corolla strongly bilabiate 4
4 Corolla with left-contort aestivation in bud 5
4 Corolla with either quincuncial or ascending-cochlear aestivation in bud 6
5 Corolla tube with a filament curtain present (in all but 4 genera); seeds with trichomes either covering entire surfaces or along rim, often hygroscopic, seed surface without concentric ridges............ ....**Ruellieae**
5 Corolla tube lacking a filament curtain; seeds sculptured with concentric ridges at least towards the rim, lacking trichomes, or if hygroscopic trichomes covering the seed surface (*Lankesteria* only) then with the unique combination of: corolla salverform with a long narrowly cylindrical tube and a spreading 5-lobed limb, sometimes with the sinus between the anterior pair of lobes broader than the other sinuses ....**Whitfieldieae**
6 Corolla with quincuncial aestivation.............................**Barlerieae**
6 Corolla with ascending-cochlear aestivation................................ 7
7 Capsule 6–20-seeded or rarely 4-seeded; pollen with apertural margin or surface conspicuously thickened and often intricately ornamented with conical spines, pseudocolpi absent....................... .... **Andrographideae**
7 Capsule 2- or 4-seeded; pollen variable but without conspicuously thickened and ornamented apertural margins or surfaces, pseudocolpi often present ....**Justicieae**

Key to the genera of Nelsonioideae [2]

1 Peduncles (if present) bearing alternate to spirally arranged, clasping scale-like sterile bracts; bracts sclerophyllous to coriaceous; leaves alternate and diffuse along stems or in rosettes or whorls either basally or terminating branches; stigma scarcely divided, touch-sensitive, folded over and enclosing anthers in undisturbed flowers, becoming erect when touched...........................***Elytraria***
1 Peduncles (if present) without clasping scale-like bracts; bracts membranous or foliaceous; leaves opposite (sometimes subopposite or alternate in *Nelsonia* and *Staurogyne*), at least some pairs dispersed along the stems; stigma usually conspicuously lobed, neither folded over nor enclosing anthers, not touch-sensitive 2
2 Bracteoles absent; inflorescence of dense ± cylindrical spikes with imbricate bracts; calyx 4-lobed, the anterior lobe with bifid apex (rarely more deeply divided into 5 lobes); stamens 2, staminodes absent...***Nelsonia***
2 Bracteoles present; inflorescence variable but if spikes cylindrical then not so dense (except in *Anisosepalum*); calyx 5-lobed; stamens 4, adaxial staminode often also present (rarely reduced to 2 stamens + 2–3 staminodes).. 3
3 Pairs of bracteoles inserted below receptacle, not adnate to it or to base of calyx tube (leaves not ternate and corollas usually less than 3 cm long)...***Staurogyne***
3 Pairs of bracteoles partially adnate to receptacle and sometimes also to base of calyx tube (or if bracteoles sometimes free in *Anisosepalum lewallei*, then leaves mostly ternate and corollas 3–4 cm long) 4
4 Calyx lobes subequal but similar to one another and not hidden by bracteoles; ovary asymmetric with style arising on one side, stigma 1-lobed, lobe apically subcapitate; Brazil .... ***Aymoreana***
4 Lateral 2 calyx lobes markedly shorter than other lobes and often hidden by the bracteoles; gynoecium not with the above combination of characters; Africa, Madagascar 5
5 Plants delicate trailing herbs; petiole usually longer than leaf blade; anther thecae with a basal appendage, this often forked; corolla widened almost to the base into a campanulate throat, palate of lower lip not bullate, i.e., without raised bosses .... ***Saintpauliopsis***
5 Plants erect or procumbent herbs or subshrubs; petiole usually shorter than leaf blade; anther thecae with basal appendages absent or short, apiculate, not forked; corolla with a cylindrical basal tube, and ± gradually widened throat, not appearing campanulate, palate of lower lip bullate, i.e., with raised bosses............... ***Anisosepalum***

Key to the genera of Thunbergioideae

1 Fruit a fleshy drupe with 1 or 2 seeds... 2
1 Fruit a woody capsule with 2 or 4 seeds..................................... 3
2 Drupe 2-seeded, large (3–10 cm in diam.) .... ***Anomacanthus***
2 Drupe 1-seeded, not so large ....***Mendoncia***
3 Stigma ± equally 2-lobed, each lobe subdivided into 2 unequal lobes; pollen 7–9-lobate and -colpate .... ***Meyenia***
3 Stigma funnel-shaped, capitate, unequally 2-lobed or if equally lobed then not subdivided; pollen spiraperturate and unlobed 4
4 Anthers opening by apical pores; seed with a scar on the proximal face; indumentum stellate, bracteoles with a dense orange, red or mustard-yellow stellate indumentum covering the external surface ....***Pseudocalyx***

4 Anthers opening by longitudinal slits; seed hollow on the proximal face; indumentum rarely stellate, bracteoles without a very dense orange, red or mustard-yellow indumentum externally.... ***Thunbergia***

Key to the genera of Acantheae

1 Corolla regularly 5-lobed or bilabiate, not comprising a single lip.... 2

1 Corolla lobes comprising a single lip, entire or 3- or 5-lobed, held either ventrally or dorsally, or if (rarely) not markedly 1-lipped [3] then at least with the sinus between the 2 uppermost (outermost) lobes clearly at a wider angle than that of the other sinuses 8

2 Plants of tropical Africa and Madagascar........ ***Stenandriopsis*** [4]

2 Plants of the Americas 3

3 Corolla zygomorphic, the lobes dissimilar in form 4

3 Corolla usually subactinomorphic, the lobes more or less similar in form (or nearly zygomorphic with lobes of upper lip dissimilar from those of lower lip in some *Stenandrium*) 6

4 Calyx deeply 3-partite.. ***Cyphacanthus***

4 Calyx 5-partite 5

5 Leaves opposite (rarely subopposite), not quaternate; bracts entire or dentate, green or often brightly colored; corollas rarely with linear nectar guides, mostly 25–85 mm long; at least distal portion of filaments of stamens usually exserted from corolla tube; pollen with colpi not expanded or bifurcating (usually narrowed) toward poles, interapertural exine usually heterogeneously sculptured; plants typically of wet habitats; widespread in NW................. ***Aphelandra*** [5]

5 Leaves opposite (rarely subopposite) or quaternate; bracts entire and usually green; corolla often with colored linear nectar guides, 6.5–24 mm long (or if longer [to 40 mm], then plants with quaternate leaves); filaments of stamens often entirely included in corolla tube; pollen with colpi sometimes expanded or bifurcating toward poles, interapertural exine homogeneously sculptured; plants of dry habitats; Mexico .... ***Holographis***

6 Pollen 3-colpate with each colpus longitudinally bisected by an operculum (elongate band of exine), opercula either isolated within the colpi (operculate) or connected at each end to the interapertural exine (pontoperculate); Jamaica.............................. ***Salpixantha*** [6]

6 Pollen 3-colpate with colpi not bisected by elongate bands of exine or pollen pantoforate (i.e., sometimes in *Stenandrium dulce*) or pollen pantoaperturate (rugate) with rugae arranged ± tangentially or irregularly over surface or pollen 3-colpate and with prominent margines and mesocolpial ridges (appearing 9-colpate); widespread, but not in Jamaica.. 7

7 Plants usually small, up to 25(–70) cm; leaves often borne at or near ground level (plants acaulescent to subcaulescent); bracts usually green; widespread .... ***Stenandrium***

7 Plants usually shrubby, up to 1.5 m tall; leaves disposed along conspicuous stems; bracts whitish, pinkish, or reddish-brown; Central America and South America.............................. ***Neriacanthus*** [6]

8 Corolla tube twisted through 180°, the single corolla lip held dorsally, entire or 3-lobed; Tanzania............................ ***Streptosiphon***

8 Corolla tube not twisted, corolla lip held ventrally, 3- or 5-lobed or sometimes only undulate 9

9 Stamens included in corolla tube, anthers subsessile, not inserted on a thickened flange.. 10

9 Stamens exserted from corolla tube, with flattened bone-like filaments, inserted on a thickened flange...................................... 11

10 Calyx 4-lobed, anterior lobe bifid; bracts not imbricate, smaller than bracteoles; bracteoles conspicuous, elliptic or obovate, diverging widely from inflorescence axis; corolla tube not narrowly cylindrical, limb obscurely 5-lobed or erose .... ***Crossandrella***

10 Calyx 5-lobed; bracts usually imbricate, larger than and enclosing bracteoles; bracteoles linear to lanceolate, not diverging widely from inflorescence axis; corolla tube narrowly cylindrical, limb 5-lobed.. ***Crossandra***

11 Calyx 5-lobed; seeds sculpted with pectinate scales or concentric rings; bracts, bracteoles and calyx lobes glumaceous ... ***Sclerochiton***

11 Calyx 4-lobed; seeds either covered in hygroscopic trichomes, puberulous or glabrous, or seeds tuberculate, without scales or concentric rings; bracts, bracteoles and calyces only rarely glumaceous 12

12 Anterior pair of staminal filaments flattened and either with an obtuse or acute tooth-like appendage or truncate to rounded towards apex ventrally 13

12 Anterior staminal filaments lacking appendages, if flattened then gradually narrowed towards apex 14

13 Leaves opposite; flowers solitary or paired in leaf axils, each subtended by 2 pairs of bracteoles, outer pair entire, inner pair trifid; ovary without apical tufts of glandular trichomes; seeds tuberculate; India .... ***Cynarospermum***

13 Leaves in pseudowhorls of (3) 4; inflorescences variable but not with single or paired flowers in leaf axils; bracteoles entire or toothed, not trifid; ovary with 2 apical tufts of glandular trichomes; seeds with branched hygroscopic trichomes; widespread............. .... ***Blepharis***

14 Seeds glabrous or sericeous-puberulous; stigma bilobed; bracts terminating in a single spine; plants often robust, ± tall perennial herbs, shrubs or small trees; widespread ....***Acanthus***

14 Seeds covered in long hygroscopic trichomes; stigma 1-lobed; bracts terminating in 3 or 5 simple or compound spines; plants often compact shrublets or acaulescent perennial herbs, if taller then slender; SW Africa .... ***Acanthopsis***

Key to the genera of Barlerieae

1 Calyx 4-lobed, anterior lobe entire or bifid for less than half its length; anterior and posterior lobes typically larger and broader than lateral lobes and often enclosing them; corolla limb variously arranged, lobes subregular or in a 4 + 1 or 2 + 3 configuration, without hooded upper lip; staminal filaments ?always twisted and crossing near the base ....***Barleria***

1 Calyx 5-lobed, if lobes unequal then lateral lobes not enclosed; if calyx 4-partite with largely fused anterior lobes then corolla strongly bilabiate with hooded upper lip; stamens not twisted and crossing near the base.. 2

2 Androecium of 4 stamens, didynamous, with or without 1 staminode.. 3

2 Androecium of 2 stamens, usually with 2 or 3 staminodes 14

3 All anthers bithecous 4

3 Anthers of longer pair of stamens bithecous, those of shorter pair of stamens monothecous.. 12

4 Stamens included within corolla tube; stigma flattened, fan-shaped or rhombic; corolla weakly bilabiate, posterior pair of lobes partially fused but not forming a hooded upper lip 5

4 Longer pair of stamens exserted from corolla tube or clearly visible at corolla mouth; stigma capitate-bilobed; corolla strongly bilabiate, posterior pair of lobes largely or wholly fused to form a ± hooded upper lip.. 10

5 Flowers in often large spherical heads with several whorls of bracts, outermost bracts with a spiny or bristly margin and/or large, 20 mm long or more; continental Africa .... ***Crabbea***

5 Flowers arranged in smaller, non-spherical heads or in spikes, glomerules or panicles; bracts not spiny, smaller; Madagascar [7] 6

6 Inflorescences pedunculate axillary heads, spikes, umbels or dichasial panicles, or if fasciculate then inflorescence units held within paired clasping bracts 7

6 Inflorescences sessile, axillary glomerules, inflorescence units not held within paired clasping bracts 9

7 Flowers subtended by a whorl of (3) 4 bracts, these connate for at least half their length to form a 3–4-lobed epicalyx; corolla 37–50 mm long..***Boutonia***

7 Flowers or inflorescence units subtended by a pair of bracts; bracts not connate or only basally so; corolla up to 25 mm long 8

8 Inflorescences of spikes, dichasial panicles or heads; pairs of bracts subtending each inflorescence unit often unequal, not adpressed, variously shaped .... ***Podorungia*** [8]

8 Inflorescences of umbels (sometimes fasciculate) or lax dichasia; pairs of bracts subtending each inflorescence unit subequal, adpressed, ovate or elliptic .... ***Pseudodicliptera***

9 All bracts of glomerules linear or lanceolate, without recurved apices; plants often with dense pale indumentum on stems and/or abaxial surface of leaves .... ***Lasiocladus***

9 Outermost bracts of glomerules broader, foliaceous, sometimes with recurved apices; plants without dense pale indumentum....... .... ***Pericalypta***

10 Anther thecae conspicuously spurred at base; China to Malaysia .... ***Chroesthes***

10 Anther thecae not spurred at base, either obtuse or at most minutely apiculate 11

11 Capsule stipitate; seeds glabrous; calyx lobes homomorphic; bracts and bracteoles small and inconspicuous; Borneo..... ***Borneacanthus***

11 Capsule not or barely stipitate; seeds with hygroscopic trichomes; calyx lobes ± markedly heteromorphic, posterior lobe broadest, lateral lobes narrowest; bracts and bracteoles usually conspicuous, often similar to calyx lobes in shape and size; widespread .... ***Lepidagathis***

12 Plants spiny with axillary spines and/or spinose leaf margins; Caribbean.. ***Barleriola***

12 Plants without axillary spines or spinose leaf margins 13

13 Stamens exserted beyond corolla lobes; corolla limb very short and not strongly bilabiate (although posterior pair of lobes is fused); inflorescence a many-flowered thyrse with flowers in dense whorls at each node; bracts and bracteoles inconspicuous; New Guinea...... .... ***Hulemacanthus***

13 Stamens not exserted beyond corolla lobes; corolla limb strongly bilabiate; inflorescence a secund spike, spikes sometimes compounded into dense heads; bracts and bracteoles usually conspicuous; widespread .... ***Lepidagathis***

14 Calyx lobes unequal, posterior lobe clearly broadest (2 + 2 + 1 configuration); seeds covered in long hygroscopic trichomes; inflorescences markedly secund; widespread .... ***Lepidagathis***

14 Calyx lobes subequal, all linear; seeds with minute trichomes towards the rim only; inflorescence a congested spiciform thyrse, not secund; D.R. Congo .... ***Schaueriopsis***

Key to the genera of Andrographideae

1 Filaments swollen (pouched) distally; corolla subequally 5-lobed, not clearly bilabiate... 2

1 Filaments not swollen or pouched; corolla bilabiate or subequally 5-lobed 3

2 Cladodes (reduced abortive branches) present in the inflorescence, terminated by paired small spines; seeds not compressed, with 2 distinct grooves, surface with hygroscopic trichomes .... ***Haplanthodes***

2 Cladodes absent in inflorescence; seeds somewhat compressed, not distinctly grooved, surface lacking trichomes, verrucose .... ***Haplanthus*** [9]

3 Ovules 2 per locule; anthers glabrous, dehiscent by longitudinal slit in central half or 2/3 of each theca........ ***Sphinctacanthus*** [10]

3 Ovules 3 or more per locule, or if 2 then anthers conspicuously penicillate at base and dehiscent by longitudinal slit in distal half extending to apex.. 4

4 Capsule compressed perpendicular to the septum, elliptic, oblanceolate or narrowly oblong in face view; seeds subglobose, ellipsoid or block-like, not compressed, often pitted or rugose and grooved; anthers often penicillate at base .... ***Andrographis*** [11]

4 Capsule not compressed, narrow throughout and 4-angled; seeds markedly compressed, smooth and lacking trichomes, or covered in trichomes; anthers not penicillate 5

5 Calyx 4-lobed; slender procumbent herbs .... ***Graphandra***

5 Calyx 5-lobed; habit variable but not procumbent herbs 6

6 Staminodes present .... ***Phlogacanthus*** [12]

6 Staminodes absent 7

7 Corolla tube shorter than limb; upper lip ± curved.... ***Diotacanthus***

7 Corolla tube longer than limb; upper lip not curved..................... .... ***Gymnostachyum***

Key to the genera of Whitfieldieae

1 Seeds covered in hygroscopic trichomes that obscure the seed surface; androecium of 2 stamens and (usually) 2 staminodes; corolla salverform (or sinus between the anterior pair of lobes broader than the other sinuses), tube narrowly cylindrical throughout.............. .... ***Lankesteria***

1 Seeds lacking trichomes, surface with concentric rings at least towards rim; androecium of 4 stamens (very rarely reduced to 2 stamens plus 2 staminodes in occasional flowers); corolla form various but not salverform with tube narrowly cylindrical throughout........ 2

2 Flowers in well-developed racemes or spikes, these sometimes branched to form panicles; tropical Africa and Madagascar 3

2 Flowers in axillary or subterminal fascicles, glomerules or short umbels; Madagascar [13].. 4

3 Each inflorescence unit 1-flowered; calyx ≥9 mm long, usually extending beyond or subequal in length to bracteoles, often showy and can be colored similar to corolla.......................... ***Whitfieldia***

3 Each inflorescence unit either 1-flowered or 2–3-flowered; calyx up to 8 mm long, hidden within paired bracteoles, not colored similar to corolla.. ***Chlamydacanthus***

4 Peduncle of each inflorescence unit conspicuous, filiform, 7–14 mm long, considerably longer than bracteoles and calyces .. ..***Zygoruellia***

4 Inflorescence units either sessile or peduncles shorter than or equal in length to bracteoles and calyces, not filiform.......................... 5

5 Corolla bright orange-red or scarlet, tube markedly curved; stamens exserted well beyond corolla lobes.................... ***Camarotea***

5 Corolla variously colored but not bright orange-red or scarlet, tube straight or curved; stamens not or only slightly exserted beyond corolla lobes.. 6

6 Corolla tube subequal in length to limb, limb strongly bilabiate, lobes of upper lip partially fused, all lobes with long wispy white trichomes internally .... ***Leandriella*** [14]

6 Corolla tube longer than limb, often markedly so, limb not strongly bilabiate, lobes of upper lip more deeply divided, or limb subequally 5-lobed, all lobes lacking long white trichomes internally .... ***Forcipella/Vindasia*** [15]

Key to the genera of Ruellieae

1 Filament curtain lacking 2

1 Filament curtain present 5

2 Anther filament connective tissue positioned lateral to thecae, thecae facing outward in a 180° configuration from connective tissue 3

2 Anther filament connective tissue positioned dorsal to thecae, thecae held parallel (i.e., side-by-side) as typical in Acanthaceae.... 4

3 Plants with basal rosettes of leaves .... ***Pararuellia***

3 Plants upright, with cauline leaves... .... “***Pseudosiphonium*** ined.” [16]

4 Plants with long, tubular flowers (≥5 cm total length), these yellow to white, narrow, unexpanded portions of tubes ≥2× longer than expanded portions; leaves not in a basal rosette; Papuasia............... .... ***Leptosiphonium***

4 Plants with short, infundibuliform flowers (<5 cm total length), these mostly purple, narrow unexpanded portions of tubes ± equal to expanded portions (or marginally different in length, not as above); leaves typically held in a basal rosette; Australia, New Caledonia, New Guinea .... ***Brunoniella***

5 Pollen with coarse reticulate exine; corolla with a very long, narrow, unexpanded portion of tube; androecium of 2 stamens + 2 staminodes; ovary with 4 ovules 6

5 Pollen, corolla, androecium, and ovule number various, but not in the above combination 7
6 Dichasia of 2 flowers typically arranged in terminal spikes, each flower subtended by a single leaf-like bract; pollen colporate; tropical Asia ..... ***Eranthemum***
6 Dichasia typically of 2 flowers, axillary and not arranged into terminal spikes, each flower subtended by pair of leaf-like bracts; pollen porate; west-central Africa ..... ***Kosmosiphon***
7 All anther thecae lacking basal awns or appendages 8
7 One or more anther thecae with basal awns or appendages 27
8 Corolla with a rugula and with rows of trichomes on the inner surface of posterior corolla; transverse fusion of filaments creating a ridge or "strobilanthoid" type of filament curtain 9
8 Corolla lacking a rugula or rows of trichomes; filament curtain not "strobilanthoid" 10
9 Ovaries with ≤4 ovules ..... ***Strobilanthes***
9 Ovaries with >4 ovules ..... ***Strobilanthes*** s.l. [incl. ***Hemigraphis*/*Clarkeasia*/*Stenosiphonium***] [17]
10 Androecium of 2 stamens + 2 staminodes 11
10 Androecium of 4 stamens 14
11 Ovaries with 2 ovules; pollen with sexine lips, 12-pseudocolpate; plants usually strongly odoriferous with a creosote-like smell ..... ***Duosperma***
11 Ovaries with >2 ovules; pollen lacking sexine lips and not 12-pseudocolpate; plants not typically strongly odoriferous 12
12 Corolla very large, gullet-shaped, pale green to greenish-yellow (sometimes with maroon tinges), cream-colored, or entirely dark maroon; primarily nocturnal, and adapted to bat pollinators; calyx 3-lobed; pollen lacking pseudocolpi ..... ***Louteridium***
12 Corolla various but not in the above character combination, and rarely yellow; calyx not 3-lobed; pollen with 4 pseudocolpi 13
13 Plants usually large herbs to large shrubs; corolla strongly bilabiate, hooded; leaf bases decurrent onto the petiole and forming a wing; plants typically of forests and woodlands or their margins ..... ***Brillantaisia***
13 Plants typically small herbs; corolla usually more weakly bilabiate, typically not hooded; leaf bases not typically decurrent onto the petiole thus not forming a wing; plants typically of riparian corridors ..... ***Hygrophila***
14 Plants with large, inflated calyces with calyx lobes fused nearly to the apex (thus appearing tubular); all plant surfaces covered with large, prominent glands ..... ***Satanocrater***
14 Plants lacking large, inflated, nearly completely fused calyces; plant surfaces with or without glands but not to the extent and size as above 15
15 Corolla with all 5 lobes comprising the lower lip (thus 1-lipped) ..... ***Eremomastax*** [18]
15 Corolla not 1-lipped 16
16 Corolla with conspicuous "herring-bone" pattern characterizing lower throat and/or lip surfaces; transverse folds of corolla forming an additional fold (in addition to transverse fusion of filaments), or "corolla fold" type of filament curtain; corolla typically strongly bilabiate but weakly bilabiate in a few species 17
16 Corolla lacking "herring-bone" patterning; filament curtain not of the "corolla fold" type; corolla typically rotate to zygomorphic, only distinctly bilabiate in a few species 18
17 Large herbs typically >1 m in height; leaves drying blackish in color; pollen grains 2-aperturate ..... ***Calacanthus*** [19]
17 Small herbs typically <1 m in height; leaves not drying blackish in color; pollen grains 4-aperturate ..... ***Hygrophila***
18 Calyx 3-lobed ..... ***Louteridium***
18 Calyx not 3-lobed 19
19 Corolla with flattened, apically rounded, uni- or bicellular trichomes lining inner corolla surfaces; pollen spherical, echinate, lacking ring of echinae surrounding the apertures ..... ***Acanthopale***
19 Corolla lacking trichomes as described above; pollen various but not spherical, echinate, and lacking the ring of echinae 20
20 Ovary with 2 ovules; pollen with sexine lips and 12-pseudocolpate; plants usually strongly odoriferous with a creosote-like smell ..... ***Duosperma***
20 Ovary with >2 ovules (rarely reduced to 2); pollen lacking sexine lips and not 12-pseudocolpate; plants not typically strongly odoriferous 21
21 Calyx conspicuously zygomorphic 22
21 Calyx typically actinomorphic or at most weakly zygomorphic 23
22 Calyx with 3 anterior lobes fused to varying degrees, 2 posterior lobes mostly free; dorsalmost lobe lacking conspicuous marginal veins; pollen spherical, echinate, and with conspicuous ring of echinae surrounding the apertures ..... ***Dischistocalyx*** [20]
22 Calyx in a 2 + 2 + 1 configuration with dorsalmost lobe the largest, the 2 ventral lobes intermediate in size, the 2 lateral lobes the smallest, and all lobes free to the receptacle; dorsalmost lobe with conspicuous marginal veins; pollen spherical, coarsely reticulate, ring of echinae absent ..... ***Dinteracanthus***
23 Shrubs or trees to 25 m tall and usually >4 m in height at maturity; plants often used as fence posts; restricted to southern Central America and northern South America ..... ***Trichanthera***
23 Herbs, shrubs, or treelets, but clearly not true trees; plants not used as fenceposts to our knowledge; widespread 24
24 Plants covered in dense tomentum of golden-yellow pubescence; pollen bicolporate with numerous bands of pseudocolpi oriented perpendicular to opposing face ..... ***Trichosanchezia***
24 Plants not as above; pollen not as above 25
25 Pollen spherical, exine coarsely reticulate, lacking pseudocolpi and lacking sexine lips ..... ***Ruellia***
25 Pollen 3-porate, 12-pseudocolpate, pores flanked by sexine lips 26
26 Capsule with fracturing placentae ..... ***Phaulopsis***
26 Capsule remaining intact post-dehiscence, lacking fracturing placentae ..... ***Heteradelphia***
27 Plants creeping or trailing herbs characterized most frequently by near linear leaves, giving overall gestalt a "grass-like" appearance (rarely elliptical to obovate); restricted to Namib and Kalahari Deserts ..... ***Ruelliopsis***
27 Plant habit various but not creeping with linear leaves and "grass-like" in appearance; widespread 28
28 Capsule with fracturing placentae 29
28 Capsule with placentae that remain attached to capsular wall at time of dehiscence 30
29 Flowers lacking pair of conspicuously leaf-like bracts; pollen grains with sexine lips ..... ***Phaulopsis***
29 Conspicuous pair of relatively large, leaf-like bracts subtending each flower; pollen grains with 4 areas of raised tectum, triangular in polar view ..... ***Petalidium***
30 Anther thecae each with 2 appendages ..... ***Diceratotheca***
30 Anther thecae otherwise 31
31 Pollen polypseudocolpate with 40+ pseudocolpi ..... "***Sinoacanthus*** ined." [21]
31 Pollen otherwise 32
32 Calyx lobes fused for at least 1/3 of their length and usually over half of their length, with hyaline regions bordering each lobe 33
32 Calyx lobes unfused or variously fused but rarely over 1/3 of their length, lacking hyaline regions bordering each lobe 34
33 Ovary with 4 ovules, capsule with (up to) 4 seeds ..... ***Dyschoriste*** [22]
33 Ovary with 8 ovules, capsule with more than 4 seeds ..... ***Echinacanthus***
34 Leaves conspicuously dentate or crenate 35
34 Leaves entire or weakly dentate to crenate, but not conspicuously so 36
35 Outermost theca of each of longer pair of stamens with a conspicuous appendage, other thecae with much shorter appendages or rounded ..... ***Mimulopsis*** [23]

35 Either both thecae or one of each pair of thecae of all anthers with an appendage ... ***Mellera*** [24]

36 Plants with long tubular, bird-pollination adapted flowers, often bright red, pink, orange, or yellow in color; pollen bicolporate with numerous bands of pseudocolpi oriented perpendicular to opposing face ... 37

36 Plants with various flowers and pollen, but not as above ... 38

37 Androecium of 2 stamens + 2 staminodes ... ***Sanchezia***

37 Androecium of 4 stamens ... ***Suessenguthia***

38 Capsules usually 2-seeded ... 39

38 Capsules with >2 seeds ... 40

39 Corolla bilabiate, 10–12.5 mm long, tube cylindrical, without a clearly expanded throat; lower lip with long bristly trichomes internally; pollen with 12 pseudocolpi; SW Angola ... ***Mcdadea***

39 Corolla subactinomorphic, not strongly bilabiate, 22–45 mm long, tube clearly differentiated into a narrow basal tube and an expanded throat; pollen with 18+ pseudocolpi; Angola to D.R. Congo and to Zimbabwe ... ***Strobilanthopsis***

40 Inflorescences of very long, terminal spikes, these commonly 30 cm in length; Malaysia ... ***Stenothyrsus***

40 Inflorescences variable, primarily of racemes, less commonly of spikes or solitary flowers, but if a spike, these not so elongate, consistently <15 cm long ... 41

41 Evergreen shrubs or trees, precocious flowering absent; ultimate branches not as below; pollen bicolporate with numerous bands of pseudocolpi oriented perpendicular to opposing face; Neotropics ... ***Bravaisia***

41 Deciduous tree to 5 m tall, flowering before the leaves appear (precocious flowering); ultimate branches numerous and curved-ascending; pollen not as above; karst hills of Laos ... ***Xylacanthus*** [25]

III. Geographical keys to the genera of Acanthaceae

Key to the genera of Acanthaceae in Africa, Madagascar, the Mediterranean region, and the Arabian Peninsula

1 Mangrove trees or shrubs with pneumatophores present; fruit a leathery 1-seeded capsule ... ***Avicennia***

1 Herbs, shrubs, woody twiners or small trees, not mangrove trees, without pneumatophores; fruit an explosively dehiscent capsule, not leathery, with (1) 2 or more seeds, or a 1–2-seeded drupe ... 2

2 Seeds not borne on hook-shaped retinacula, retinacula lacking or papilliform; plants without cystoliths; anthers bithecous ... 3

2 Seeds borne on prominent hook-shaped retinacula; plants with or without cystoliths, if cystoliths absent then anthers monothecous [8] ... 11

3 Herbs or shrubs, not twining; paired bracteoles present or absent but not large and conspicuous; flowers usually alternate or spirally arranged in few- to many-flowered inflorescences; calyx deeply 4- or 5-lobed; fruit a many-seeded (usually >10 seeds), capsule, not woody ... 4

3 Herbaceous twiners or lianas, less frequently free-standing shrubs or herbs; flowers solitary or in fascicles or racemes of opposite flowers, not spirally arranged; flowers subtended by conspicuous clasping or partially connate paired bracteoles; calyx a subentire or undulate rim or with irregular teeth, or obscurely 5-lobed; fruit either a 1–2-seeded drupe or a 2–4-seeded woody capsule ... 8

4 Peduncles bearing alternate clasping scale-like sterile bracts; all bracts sclerophyllous; leaves held in rosettes or whorls ... ***Elytraria***

4 Peduncles (if present) without clasping scale-like bracts; bracts membranous or foliaceous; leaves opposite, at least some pairs dispersed along the stems ... 5

5 Bracteoles absent; inflorescence of dense ± cylindrical spikes with imbricate bracts; calyx 4-lobed, the anterior lobe with bifid apex (rarely more deeply divided into 5 lobes); stamens 2, staminodes absent ... ***Nelsonia***

5 Bracteoles present; inflorescence variable but if spikes cylindrical then not so dense; calyx 5-lobed; stamens 4, adaxial staminode often also present (rarely reduced to 2 stamens + 2–3 staminodes) ... 6

6 Pairs of bracteoles inserted below receptacle, not adnate (leaves not ternate; corollas <3 cm long); lateral 2 lobes of calyx can be somewhat shorter than other lobes but not markedly so and not hidden by the bracteoles; W and C Africa ... ***Staurogyne***

6 Pairs of bracteoles partially adnate to receptacle and sometimes base of calyx (or if bracteoles sometimes free in *Anisosepalum lewallei*, then leaves mostly ternate and corollas 3–4 cm long); lateral 2 calyx lobes markedly shorter than other lobes and largely hidden by the bracteoles ... 7

7 Plants delicate trailing herbs; petiole usually longer than leaf blade; anther thecae with a basal appendage, this often forked; corolla widened almost from the base into a campanulate throat, palate of lower lip not bullate, i.e., without raised bosses; Gabon to Tanzania, Madagascar ... ***Saintpauliopsis***

7 Plants erect or procumbent herbs or subshrubs; petiole usually shorter than leaf blade; anther thecae with basal appendages absent or short, apiculate, not forked; corolla with a cylindrical basal tube, and ± gradually widened throat, not appearing campanulate, palate of lower lip bullate, i.e., with raised bosses; C and E Africa ... ***Anisosepalum***

8 Fruit a fleshy drupe with 1 or 2 seeds ... 9

8 Fruit a 2–4-seeded woody capsule ... 10

9 Drupe with 2 seeds, large (3–10 cm in diam.); leaves with a characteristic ± long narrow basal portion above an abruptly rounded or cordate base, can appear as a winged petiole; Congo Rep., D.R. Congo ... ***Anomacanthus***

9 Drupe with a single seed, not so large; leaves without base as above; widespread ... ***Mendoncia***

10 Anthers opening by apical pores; seed with a scar on proximal face; indumentum stellate, bracteoles with a dense orange, red or mustard-yellow stellate indumentum covering external surface ... ***Pseudocalyx***

10 Anthers opening by longitudinal slits; seed hollowed on proximal face; indumentum usually not stellate, bracteoles without a very dense orange, red or mustard-yellow indumentum externally ... ***Thunbergia***

11 Stamens 4, sometimes with an additional staminode ... 12

11 Stamens 2, with or without additional staminodes ... 61

12 Anthers all monothecous; plants without cystoliths ... 13

12 Either anthers all bithecous or 2 anthers bithecous and 2 anthers monothecous; plants with cystoliths ... 21

13 Calyx long-tubular, cylindrical to inflated, with short lobes; capsule with more than 4 seeds; corolla aestivation left-contort; W and C Africa ... ***Physacanthus***

13 Calyx not markedly tubular, deeply divided into 4 or 5 lobes; capsule with up to 4 seeds; corolla aestivation not contorted ... 14

14 Corolla lobes not comprising a single lip, either regularly 5-lobed or bilabiate; corolla not yellow ... ***Stenandriopsis*** [4]

14 Corolla limb comprising a single lip, entire or 3- or 5-lobed, held either ventrally or dorsally, or at least with the sinus between the 2 uppermost (or outermost) lobes at a markedly wider angle than that of the other lobe sinuses, if only weakly so then corolla yellow (*Crossandra flava*) ... 15

15 Corolla tube twisted through 180°, the single corolla lip held dorsally, entire or 3-lobed; Tanzania ... ***Streptosiphon***

15 Corolla tube not twisted, corolla lip held ventrally, 3- or 5-lobed or sometimes only undulate ... 16

16 Stamens included in corolla tube, subsessile, not inserted on a thickened flange ... 17

16 Stamens exserted from the corolla tube, with flattened bone-like filaments, inserted on a thickened flange ... 18

17 Calyx 4-lobed, anterior lobe bifid; bracts not imbricate, smaller than bracteoles, these conspicuous, elliptic or obovate, diverging widely from inflorescence axis; corolla tube not narrowly cylindrical, limb obscurely 5-lobed or erose; Liberia to Tanzania .... ***Crossandrella***

17 Calyx 5-lobed; bracts usually imbricate, larger than and enclosing bracteoles, these linear to lanceolate, not diverging widely from inflorescence axis; corolla tube narrowly cylindrical, limb 5-lobed; widespread .... ***Crossandra***

18 Calyx 5-lobed; seeds sculptured with pectinate scales or concentric rings; bracts, bracteoles and calyx lobes glumaceous .... ***Sclerochiton***

18 Calyx 4-lobed; seeds covered in hygroscopic trichomes, puberulous or glabrous, without scales or concentric rings; bracts, bracteoles and calyces rarely glumaceous 19

19 Anterior pair of staminal filaments each with an obtuse or acute tooth-like appendage towards the apex ventrally .... ***Blepharis***

19 Anterior staminal filaments lacking appendages 20

20 Seeds glabrous or sericeous-puberulous; stigma bilobed; bracts terminating in a single spine; plants often robust, ± tall perennial herbs, shrubs or treelets; widespread .... ***Acanthus***

20 Seeds covered in long hygroscopic trichomes; stigma 1-lobed; bracts terminating in 3–5 simple or compound spines; plants often compact shrublets or acaulescent perennial herbs, if taller then slender; Namibia, western South Africa .... ***Acanthopsis***

21 Longer 2 stamens bithecous, shorter 2 stamens monothecous but sometimes with vestigial second theca, or if rarely (in few *Neuracanthus*) all stamens bithecous then shorter pair with anthers almost sessile and corolla with short tube and funnel-shaped limb comprising equal anterior and lateral lobes and partially to almost completely fused dorsal pair of lobes 22

21 All stamens bithecous, filaments present; corolla not as above 24

22 Calyx bilabiate, with a 2-lobed or -toothed anterior lip and a 3-lobed or -toothed posterior lip; corolla with a funnel-shaped limb comprising equal anterior and lateral lobes and partially (or almost completely) fused dorsal pair of lobes, not bilabiate .... ***Neuracanthus***

22 Calyx 5-lobed, lobes either equal or with posterior lobe widest (2 + 2 + 1 configuration); corolla bilabiate 23

23 Bracts obovate with rounded apex, often with conspicuous darker pinnate-anastomosing venation; calyx ± equally 5-lobed, markedly shorter than bracteoles; small trailing herbs of rainforest; Nigeria, Bioko, Cameroon .... ***Afrofittonia***

23 Bracts variously shaped but apex acute to acuminate, 3- to palmately veined or venation inconspicuous; calyx unequally 5-lobed, posterior lobe clearly broadest (2 + 2 + 1 configuration), not or only slightly shorter than bracteoles; habit and habitat various but often in drier habitats; widespread .... ***Lepidagathis***

24 Calyx 4-lobed, anterior lobe entire or bifid for less than half its length; anterior and posterior lobes typically much broader than lateral lobes and often enclosing them; corolla variously arranged, lobes subregular or in a 4 + 1 or 2 + 3 (rarely 1 + 3) configuration, without a hooded upper lip; filaments of anterior (long) pair of stamens ?always twisted and crossing near the base .... ***Barleria***

24 Calyx (3-) 5-lobed, or if anterior pair of lobes partially fused and lobes of unequal width then corolla markedly bilabiate with a ± hooded upper lip; staminal filaments not twisted and crossing near the base 25

25 Stamens in 2 pairs with filaments fused at base, sometimes forming a filament curtain within the corolla tube 26

25 Stamens not in 2 pairs, filaments not fused, filament curtain absent 49

26 Seeds usually tuberculate or rugose, often with a thickened and irregularly crenate or serrate margin, more rarely smooth and rounded, lacking trichomes; corolla bilabiate (sometimes weakly so), with ascending-cochlear aestivation 27

26 Seeds with hygroscopic trichomes present throughout or at least along the rim; or if (rarely) glabrous then corolla subactinomorphic; corolla with left-contort aestivation 29

27 Flowers solitary in leaf axils; Botswana, South Africa .... ***Glossochilus***

27 Flowers held in well-developed spikes or racemes, sometimes compounded into panicles 28

28 Anthers with thecae offset, rounded at the base; inflorescence a slender racemose thyrse with opposite cymose units; west-central Africa .... ***Filetia*** [26]

28 Anthers with thecae held at an equal or subequal height, usually basally spurred or apiculate; inflorescence often a secund spike or raceme, more rarely with opposite cymose units; widespread .... ***Asystasia*** [27]

29 All anther thecae ± rounded at base, lacking basal appendages 30

29 One or both thecae of at least 2 of the 4 anthers with basal appendages 42

30 Calyx large, inflated, fused nearly to the apex with only short lobes; all plant surfaces covered in large, prominent scale-like glands; Guinea, NE Africa .... ***Satanocrater***

30 Calyx not large and inflated, not fused nearly to the apex; plant surfaces with or without glands but not covered in dense scale-like glands 31

31 Corolla 1-lipped, with all 5 lobes comprising the lower lip (or rarely lip held in upper position due to floral resupination resulting from twisting of the tube) .... ***Eremomastax***

31 Corolla not 1-lipped 32

32 Calyx with 3 posterior lobes fused for half their length or more, 2 anterior lobes free to the receptacle (2 + 3 configuration); Guineo-Congolian forests 33

32 Calyx without 3 posterior lobes conspicuously fused 34

33 Pollen coarsely reticulate; corolla tube cylindrical, only narrowly widened towards mouth, geniculate; W and C Africa .... ***Ruellia*** [*Endosiphon*] [20]

33 Pollen echinate, not coarsely reticulate; corolla tube infundibuliform, not markedly geniculate; Nigeria to D.R. Congo .... ***Dischistocalyx***

34 Calyx strongly zygomorphic, posterior lobe conspicuously broader than the other lobes, ovate, elliptic or rhombic, the other lobes linear-lanceolate to oblanceolate, the 2 anterior lobes slightly broader than the 2 lateral lobes (2 + 2 + 1 configuration), all divided ± to the receptacle 35

34 Calyx (sub)actinomorphic or if zygomorphic then not as above; posterior lobe not markedly broader than other lobes 36

35 Capsule with fracturing placentae; flowers held in strobilate to more lax spikes, usually dorsiventral, with flowers and fertile bracts ventrally and sterile bracts dorsally, or rarely flowers solitary and axillary; pollen prolate, 12(+)-pseudocolpate, exine finely reticulate; widespread .... ***Phaulopsis***

35 Capsule without fracturing placentae; inflorescences simple or compound dichasia, not strobilate or dorsiventral; pollen spherical, lacking pseudocolpi, exine coarsely reticulate; Angola, Namibia .... ***Dinteracanthus*** [28]

36 Capsule 2-seeded 37

36 Capsule 4- to many-seeded 38

37 Calyx divided almost to the receptacle into 5 subequal (posterior sometimes longer) lobes; corolla with flattened, apically rounded, uni- or bicellular trichomes lining inner surface, tube usually ± markedly curved; stigma with 1 linear lobe, second lobe reduced to a short tooth; plants without a creosote-like smell; widespread .... ***Acanthopale***

37 Calyx with fused basal portion and zygomorphic limb due to partial fusion of anterior pair of lobes; corolla without such trichomes internally, tube straight; stigma bilobed; plants usually strongly odiferous with a creosote-like smell; E and S Africa, Arabia .... ***Duosperma***

38 Calyx lobes fused for at least 1/3 of their length and usually over half their length, with marginal hyaline regions, lobes linear(-lanceolate); capsule 4-seeded; stigma lobe with flat straight margin; pollen prolate with 12+ pseudocolpi and with sexine lips around the short apertures .... ***Dyschoriste***

38 If calyx fused for over 1/3 of their length and with linear lobes and capsule 4-seeded (some *Ruellia* in Madagascar), then calyx lacking hyaline margins, stigma lobe with involute irregular margin and pollen spheroid, coarsely reticulate, lacking pseudocolpi and sexine lips 39

39 Corolla typically strongly bilabiate with 2-lobed hooded upper lip and 3-lobed lower lip often with conspicuous "herring-bone" patterning, or if corolla only weakly bilabiate then less than 1 cm long; plants of (seasonal) wetlands............................. ***Hygrophila***

39 Corolla subactinomorphic or if zygomorphic then not strongly bilabiate with hooded 2-lobed upper lip, lacking or with only faint "herring-bone" patterning on lower lip; corolla usually >1 cm long; plants not of wetlands... 40

40 Pollen spherical, exine coarsely reticulate or rarely (in our region only known in *Ruellia togoensis*) with large verrucae, lacking pseudocolpi or sexine lips; flowers usually axillary, solitary or in fascicles, more rarely in lax axillary dichasia or (in *R. dissidens* only) a slender terminal spike... ***Ruellia***

40 Pollen prolate, 3-porate and 12-pseudocolpate, pores flanked by sexine lips; flowers held in a terminal thyrse or panicle............ 41

41 Corolla limb either zygomorphic, with 1 lobe splitting from the tube earlier than and considerably longer than the other 4 lobes, or if subactinomorphic then lobes narrowly oblong with rounded apices and staminal filaments puberulous; Tanzania .... ***Mimulopsis*** [*Epiclastopelma*] [29]

41 Corolla limb subactinomorphic, lobes elliptic or oblong with emarginate apices; staminal filaments glabrous; Guinea to Ivory Coast, São Tomé .... ***Heteradelphia***

42 Flowers subtended by a pair of conspicuous, ± large bracteoles, these papery to leathery and often with conspicuous reticulate venation, enclosing the calyx and base of the corolla; southern Africa.. ***Petalidium***

42 Flowers not subtended by a pair of conspicuous bracteoles...... 43

43 Capsules with fracturing placentae; calyx strongly zygomorphic, posterior lobe ovate or elliptic, markedly broader than other lobes, these linear-lanceolate to oblanceolate (2 + 2 + 1 configuration); inflorescences often dorsiventral spikes, with flowers and fertile bracts ventrally and differently shaped sterile bracts dorsally, rarely radially symmetrical .... ***Phaulopsis***

43 Capsules without fracturing placentae or with placentae easily dislodged but lateral walls of capsule not tearing; calyx actinomorphic or only weakly zygomorphic, posterior lobe not markedly broader than other lobes; inflorescences not dorsiventral spikes........ 44

44 Corolla limb subactinomorphic, throat lacking "herring-bone" patterning; plants with trailing or procumbent stolons from a woody rootstock sometimes rooting adventitiously, with clusters of leaves or short erect leafy stems along the stolons, leaves linear to narrowly elliptic or obovate, plant often with a "grass-like" gestalt; southern Africa .... ***Ruelliopsis***

44 Corolla limb zygomorphic or weakly so, throat often with prominent "herring-bone" patterning; plant habit not as above, not grass-like 45

45 Calyx lobes fused for at least 1/3 of their length and usually over half their length, with hyaline margins between the lobes, lobes linear(-lanceolate); ovary with 2 ovules per locule, capsule 4-seeded... ***Dyschoriste***

45 Calyx lobes divided to the receptacle or shortly fused, lacking hyaline margins; lobes linear or often spathulate; ovary with 2–8 ovules per locule; capsule often either >4-seeded or 2-seeded...... 46

46 Outermost theca of each of longer pair of stamens with a conspicuous curved appendage, other thecae with much shorter appendages or rounded .... ***Mimulopsis***

46 Either all thecae or 1 of each pair of thecae of all anthers with an appendage... 47

47 Leaves conspicuously dentate or crenate; capsule with >4 and usually ≥8 seeds; seeds with hygroscopic trichomes largely restricted to the rim, surfaces with or without short non-hygroscopic trichomes; E and S Africa .... ***Mellera*** [24]

47 Leaves entire or with a single tooth on each side; capsule usually 2-seeded, hygroscopic trichomes covering entire seed surface 48

48 Corolla bilabiate, 10–12.5 mm long, tube cylindrical, without a clearly expanded throat; lower lip with long bristly trichomes internally; pollen with 12 pseudocolpi; SW Angola............. ***Mcdadea***

48 Corolla subactinomorphic, not strongly bilabiate, 22–45 mm long, tube clearly differentiated into a narrow basal tube and an expanded throat; pollen with 18+ pseudocolpi; Angola to D.R. Congo and Zimbabwe .... ***Strobilanthopsis***

49 Seeds (where known) sculptured with concentric rings at least towards the rim, lacking trichomes; corolla with left-contort aestivation..... 50

49 Seeds not sculptured with concentric rings, either covered in trichomes or, if glabrous, then surface smooth; corolla with quincuncial aestivation 55

50 Flowers held in well-developed racemes or spikes, sometimes branched to form panicles; continental Africa and Madagascar............ 51

50 Flowers held in axillary or subterminal fascicles, glomerules or short umbels; Madagascar [13] 52

51 Inflorescence units 1-flowered; calyx ≥9 mm long, usually extending beyond or subequal in length to bracteoles, often showy and colored similar to corolla; widespread in tropical continental Africa... ***Whitfieldia***

51 Inflorescence units 1- or 2–3-flowered; calyx short, up to 8 mm long, hidden within paired bracteoles, not colored similar to corolla; Kenya, Tanzania, Madagascar ....***Chlamydacanthus***

52 Peduncle of inflorescence units conspicuous, filiform, 7–14 mm long, considerably longer than bracteoles and calyces .... ***Zygoruellia***

52 Inflorescence units either sessile or peduncles shorter than or equal in length to bracteoles and calyces, not filiform....................... 53

53 Corolla bright orange-red or scarlet, tube markedly curved; stamens exserted well beyond corolla lobes .... ***Camarotea***

53 Corolla variously colored but not bright orange-red or scarlet, tube straight or curved; stamens not or barely exserted beyond corolla lobes 54

54 Corolla tube subequal in length to limb, limb strongly bilabiate, lobes of upper lip partially fused, all lobes with long wispy white trichomes internally ....***Leandriella*** [14]

54 Corolla tube longer than limb, often markedly so, limb not so strongly bilabiate, lobes of upper lip more deeply divided, or limb subactinomorphic, all lobes lacking long white trichomes internally .... ***Forcipella/Vindasia*** [15]

55 Longer pair of stamens exserted from corolla tube or clearly visible at corolla mouth; stigma capitate-bilobed; corolla strongly bilabiate with 2 posterior lobes largely or completely fused to form a hooded upper lip.. ***Lepidagathis***

55 Stamens included within corolla tube; stigma flattened, fan-shaped or rhombic; corolla not so strongly bilabiate, posterior pair of lobes fused somewhat higher than other lobes but not forming a hooded upper lip... 56

56 Flowers held in ± spherical heads surrounded by several whorls of bracts, outermost bracts with a spiny or bristly margin and/or long, ≥20 mm long; E and S Africa... ***Crabbea***

56 Flowers arranged in smaller, non-spheroidal heads or in spikes, glomerules or panicles; bracts not spiny, smaller; Madagascar [7] 57

57 Inflorescences pedunculate axillary heads, spikes, umbels or dichasial panicles, or if fasciculate then inflorescence units held within paired clasping bracts 58

57 Inflorescences sessile axillary glomerules, inflorescence units not held within paired clasping bracts 60

58 Flowers subtended by a whorl of (3) 4 bracts connate for at least half their length to form a 3–4-lobed epicalyx; corolla 37–50 mm long ...... ***Boutonia***

58 Flowers or inflorescence units subtended by a pair of bracts; bracts not connate or only basally so; corolla up to 25 mm long 59

59 Inflorescences of spikes, dichasial panicles or heads; bracts subtending each inflorescence unit paired but the pairs often unequal, not adpressed, variously shaped ...... ***Podorungia***

59 Inflorescences of umbels (sometimes fasciculate) or lax dichasia; bracts subtending each inflorescence unit paired, subequal, adpressed, ovate or elliptic ...... ***Pseudodicliptera***

60 All bracts of glomerules linear or lanceolate, without recurved apices; plants often with dense pale indumentum on stems and/or abaxial surface of leaves ...... ***Lasiocladus***

60 Outermost bracts of glomerules broader, foliaceous, sometimes with recurved apices; plants without dense pale indumentum ...... ***Pericalypta***

61 Anthers monothecous 62

61 Anthers bithecous 67

62 Corolla resupinate through ±180° twist in corolla tube; flowers held between paired clasping or partially fused ± conspicuous bracts ...... ***Hypoestes***

62 Corolla not resupinate, tube not twisted; pairs of bracts neither clasping nor partially fused 63

63 Corolla either subregularly 5-lobed or if bilabiate then upper lip conspicuously 2-lobed and lower lip deeply divided into 3 lobes; staminodes 2, sometimes basally fused to filaments of fertile stamens; seeds either smooth on both faces, or smooth on outer face and irregularly ridged on inner face, this with or without a raised rim 64

63 Corolla strongly bilabiate, upper lip undivided or at most shortly notched, lower lip only partially divided into 3 lobes or almost undivided; staminodes absent; seeds tuberculate, rugulose or with concentric ridges, without a raised rim 66

64 Corolla tube much longer than limb, markedly curved and gradually expanded towards mouth; Socotra ...... ***Ballochia***

64 Corolla tube either shorter than limb or if longer than limb then narrowly cylindrical throughout except for slight expansion at the mouth; not on Socotra **65**

65 Corolla tube narrowly cylindrical, longer than limb; limb either subequally 5-lobed or bilabiate with posterior 2 lobes partially fused, anterior 3 corolla lobes not reflexed or widely divergent ...... ***Ruspolia*** [30]

65 Corolla tube more broadly cylindrical or saccate, shorter than or subequal to limb; posterior pair of lobes partially fused and erect, anterior 3 corolla lobes either reflexed and held against the tube, or widely divergent ...... ***Ruttya***

66 Corolla with tube up to 10 mm long, upper lip lanceolate, hooded, largely enclosing the staminal filaments (flower nototribic); C and E Africa ...... ***Monothecium*** [31]

66 Corolla with tube longer than 10 mm or, if shorter, then upper lip subulate, oblong-lanceolate or elliptic, not hooded, often recurved or inrolled, stamens held between the 2 lips (flower pleurotribic); widespread ...... ***Brachystephanus***

67 Staminodes present, sometimes basally fused to the adjacent staminal filament 68

67 Staminodes absent 81

68 Calyx 4-lobed, anterior lobe entire or bifid for less than half its length; anterior and posterior lobes typically much broader than lateral lobes and often enclosing them; corolla arrangement variable, lobes subregular or in a 4 + 1 or 2 + 3 configuration, without hooded upper lip; staminal filaments ?always twisted and crossing near the base ...... ***Barleria***

68 Calyx 5-lobed or equally 4-lobed, or if anterior pair of lobes partially fused (less than half their length) and lobes of unequal width then corolla markedly bilabiate with ± hooded upper lip; staminal filaments not twisted and crossing near the base 69

69 Pollen bipororate, circular in apertural view, with a broad marginal girdle-like ring of sexine; flowers held in axillary and subterminal glomerules on largely leafless woody stems; corolla with dense tuft of yellow trichomes on palate of lower lip immediately proximal to the lobes; Madagascar ...... ***Ritonia*** [32]

69 Pollen and macromorphological characters not in the above combination 70

70 Seeds with hygroscopic trichomes present throughout or at least around the rim; corolla either with left-contort or quincuncial aestivation 71

70 Seeds without hygroscopic trichomes, sculptured with tuberculae, echinae or verruculae, or smooth; corolla with ascending-cochlear aestivation 78

71 Corolla salverform, with narrowly cylindrical tube markedly longer than spreading 5-lobed limb; limb subactinomorphic or with sinus between 2 adaxial lobes wider than the other sinuses 72

71 Corolla not salverform, often markedly bilabiate or, if limb subactinomorphic, then tube not long and narrowly cylindrical 73

72 Corolla blue or violet; flowers held in (1)2(3)-flowered dichasia in the axils of leaves, each flower subtended by a pair of conspicuous ovate foliaceous bracteoles held on a winged pedicel; Cameroon, Central African Republic, D.R. Congo ...... ***Kosmosiphon***

72 Corolla yellow, orange or white; flowers held in terminal spikes or dense thyrses, often with conspicuous imbricate bracts, or bracts linear; bracteoles linear; winged pedicels absent; widespread ...... ***Lankesteria***

73 Filament curtain absent; corolla aestivation quincuncial 74

73 Filament curtain present; corolla aestivation left-contort 75

74 Inflorescences dense secund spikes with unequal fertile and sterile bracts; calyx lobes markedly unequal in 2 + 2 + 1 configuration, posterior lobe broadest, ovate or elliptic; seeds with long hygroscopic trichomes; Madagascar [33] ...... ***Lepidagathis***

74 Inflorescences dense terminal thyrses, not secund, pairs of bracts equal; calyx of 5 subregular linear lobes; seeds with minute trichomes only; D.R. Congo ...... ***Schaueriopsis***

75 Capsule 2-seeded; 2 anterior calyx lobes fused more distally than 3 posterior lobes, inflorescences not subtended by spines ...... ***Duosperma***

75 Capsule 4- to ca. 30-seeded; anterior calyx lobes not fused more distally than posterior lobes or, if so, then fascicles of flowers subtended by hard spines 76

76 Leaf base decurrent onto petiole, forming a ± marked wing; corolla strongly bilabiate with laterally compressed and curved hooded upper lip and basally hinged lower lip ...... ***Brillantaisia***

76 Leaf base not winged; corolla not so strongly bilabiate, upper lip may be hooded but not laterally compressed nor so strongly curved, lower lip not basally hinged 77

77 Capsule 4-seeded; lower corolla lip lacking stiff retrorse bristles; anther thecae usually spurred; plants usually of dry habitats ...... ***Dyschoriste***

77 Capsule 8–20+-seeded; lower lip of corolla with numerous stiff retrorse bristles; anther thecae not spurred; plants of (seasonal) wetlands ...... ***Hygrophila***

78 Inflorescence of curved secund spikes, with the flowers held upright, 1 flower per inflorescence node; corolla tube markedly infundibuliform, with basal cylindrical portion and abruptly widened throat; South Africa, Eswatini ...... ***Mackaya***

78 Inflorescences of axillary solitary flowers or fascicles, or of slender spikes with opposite flowers or fascicles at each inflorescence node; corolla tube cylindrical throughout or, if with an expanded throat, then throat gradually widened 79

79 Corolla tube curved and gradually widened distally, 7–10 mm in diam. at mouth; dorsal pair of corolla lobes largely fused to form hooded upper lip; Nigeria, Bioko, Cameroon ...... ***Graptophyllum***

79 Corolla tube cylindrical to narrowly so or at most narrowly campanulate, up to 3 mm in diam. at mouth, straight or ± abruptly bent

distally; dorsal pair of corolla lobes not largely fused, upper lip not hooded 80

80 Inflorescences long slender spikes; corolla tube usually much longer than limb, rarely shorter than limb; widespread .... ***Pseuderanthemum***

80 Inflorescence axillary (but branches can be largely leafless at flowering), flowers solitary or in fascicles; corolla tube shorter than limb; Madagascar .... ***Oplonia*** [34]

81 Corolla resupinate through ±180° twist in corolla tube 82

81 Corolla not resupinate or if so, then due to twisting of pedicel, corolla tube not twisted 84

82 Thecae of each anther widely separated by extension of the connective tissue; Madagascar .... ***Vavara*** [35]

82 Anther thecae immediately superposed or slightly overlapping 83

83 Capsule with fracturing placentae, placenta base and thin walls tearing away from thickened flanks .... ***Dicliptera***

83 Capsule without fracturing placentae, walls and placenta base remaining attached at dehiscence .... [***Peristrophe***] [36]

84 Corolla strongly bilabiate with lips markedly longer than tube (often 2× longer or more), upper lip strongly hooded, straight to gradually curved, lower lip narrowly oblong, strap-shaped or narrowly cylindrical, usually recoiled at anthesis 85

84 Corolla limb various, if bilabiate, then lips usually not markedly longer than tube or if so then lower lip broader and not recoiled at anthesis 87

85 Pollen bipororate, circular in apertural view, with a broad marginal girdle-like ring of sexine (“gürtelpollen”); inflorescence spikes slender with rachis sometimes visible between the pairs of bracts; Madagascar .... ***Anisotes perplexus*** [37]

85 Pollen 2-, 3- or 4-colporate with pseudocolpi flanking each aperture, prolate, without a marginal girdle; inflorescences variable but if spikes then more contracted with usually imbricate bracts, not so slender 86

86 Capsule with fracturing placentae; Nigeria, E and S Africa .... ***Metarungia*** [38]

86 Capsule without fracturing placentae; widespread .... ***Anisotes***

87 Flowers sternotribic; trailing or procumbent herb with axillary fascicles of flowers; bracts, bracteoles and calyx lobes with pale-hyaline margins; Kenya .... ***Kenyacanthus***

87 Plants without the above combination of characters 88

88 Pollen bipororate, circular in apertural view, with a broad marginal girdle-like ring of sexine (“gürtelpollen”); corolla bilabiate; anthers with thecae either held at an equal height and parallel or offset to fully superposed and/or oblique, basally muticous, if offset then the upper theca slightly longer than the lower theca .... ***Isoglossa*/*Melittacanthus*/*Sphacanthus*/*Celerina*** [39]

88 Pollen variable but not as above; if anther thecae offset to superposed then often with a basal appendage on the lower theca or both thecae, and the upper theca slightly shorter than the lower theca 89

89 Anther thecae each with a broad flattened appendage with irregular projections along the rim (resembling a “chicken’s crest”); corolla intricately speckled or striped, lacking a rugula; Nigeria, Bioko, Cameroon, Gabon .... ***Champluviera***

89 Anther thecae either without appendages or if appendages present then not as above, appendages apiculate to well-developed and elongate, often curved, sometimes with a bifid apex but without projections along the rim; corolla coloring various; if anther appendages present, then corolla with a rugula 90

90 Corolla lacking a rugula; anther thecae held at an equal height (but sometimes unequal in size) and parallel or sagittate; anther appendages absent 91

90 Corolla with a rugula present on upper lip and dorsal side of tube; anther thecae usually strongly offset to fully superposed and/or oblique; lower theca or both thecae often with a well-developed appendage 101

91 Corolla 9–12 mm long, with narrowly cylindrical tube longer than the limb; corolla lobes all reflexed at anthesis; anther thecae held at ± equal height but 1 theca larger than the other; pollen 6-colporate, sculptured with verruculae arranged in ± well-defined longitudinal lines; W and C Africa .... ***Chlamydocardia***

91 If corolla with narrowly cylindrical tube then considerably longer than 12 mm; corolla lobes not all reflexed at anthesis but apices can be recurved or recoiled; anther thecae not unequal in size; pollen not as above 92

92 Upper lip of corolla curved and laterally compressed, very narrow; lower lip lacking raised “herring-bone” pattern; seeds covered in glochidiate tubercles; D.R. Congo, Kenya, Mozambique .... ***Cephalophis***

92 Plant not with the above combination of characters; if upper lip of corolla curved and laterally compressed then lower lip with conspicuous raised “herring-bone” pattern and seeds not covered in glochidiate tubercles 93

93 Upper lip of corolla not hooded, sometimes apically recurved or recoiled; lower lip without raised “herring-bone” pattern; seeds discoid with a raised rim 94

93 Upper lip of corolla ± hooded; lower lip often with raised “herring-bone” pattern; seeds less strongly flattened, without a marginal rim 100

94 Inflorescences pendulous; corolla ascending-sigmoid-shaped in bud, tube strongly expanded apically; lower lip shortly 3-lobed; Socotra .... ***Angkalanthus***

94 Inflorescences erect; corolla not ascending-sigmoid-shaped in bud, tube cylindrical or only slightly widened upwards; lower lip deeply 3-lobed 95

95 Upper corolla lip broadly elliptic with rounded or slightly emarginate apex; leaves lanceolate with length: width ratio 7–9: 1, longest leaves 11–15 cm long; Madagascar .... ***Dolichostachys***

95 Upper corolla lip linear-lanceolate to narrowly elliptic, apex acute or notched; leaves variable, if narrow then less than 10 cm long 96

96 Corolla tube narrowly cylindrical, barely widened at mouth, often longer than lobes; upper lip markedly smaller than lower lip; stamens held close to upper lip of corolla with short filaments (flower nototribic), anthers parallel to filament .... ***Ecbolium*** [40]

96 Corolla tube cylindrical to somewhat campanulate but not narrowly cylindrical, shorter than or subequal in length to lobes; upper lip ± equal in length to lower lip; stamens held ± equidistant between the upper and lower lips (flower pleurotribic), anthers often held perpendicular to filaments 97

97 Corolla lobes spreading or recurved but not recoiled at anthesis; pollen 3-colporate with only weakly defined colpi and lacking pseudocolpi; E and S Africa, Arabian Peninsula .... ***Megalochlamys***

97 Corolla lobes, at least on lower lip, becoming apically recoiled at anthesis; pollen 3–6-colporate, colpi conspicuous, pseudocolpi present 98

98 Inflorescence 4-angular with imbricate slightly concave bracts; pollen (4) 5 (6)-colporate, with pseudocolpi fused towards one or both poles to form arcs, circles or ellipses; coastal Kenya and Tanzania .... ***Trichaulax***

98 Inflorescence not conspicuously 4-angular, if bracts imbricate then convex; pollen 3-colporate, pseudocolpi not fused towards poles, parallel to the colpi 99

99 Plants from Madagascar .... ***Populina*** [41]

99 Plants from Socotra, Somalia, Botswana, South Africa .... ***Chorisochora***

100 Calyx zygomorphic (2 + 2 + 1 configuration), lobes oblong-elliptic to oblong-oblanceolate, posterior lobe broadest, 4–7 mm wide; Madagascar .... ***Ambongia***

100 Calyx not or barely zygomorphic, lobes linear or lanceolate, less than 4 mm wide; Ethiopia, Somalia .... ***Ichthyostoma***

101 Corolla tube narrowly cylindrical throughout or ventrally abruptly expanded in distal half, usually considerably longer than lips except in *R. pulcher* where lower lip >20 mm long; upper lip linear-lanceolate to shortly ovate, not hooded; anthers with thecae muticous or lower theca apiculate .... ***Rhinacanthus***

101 Corolla tube not so narrowly cylindrical throughout nor abruptly expanded on ventral side of tube, if tube longer than lips then upper lip hooded; anthers usually with well-developed basal appendages 102

102 Capsule with fracturing placentae; inflorescences strobilate secund spikes, bracts often with conspicuous and abrupt white- or pinkish hyaline margins 103

102 Capsule with placentae not fracturing; inflorescences variable, if strobilate, secund spikes then bracts without abrupt pale hyaline margins (margins sometimes gradually paler)........................ 104

103 Anthers dehiscing by basal pores; Nigeria, Cameroon, Equatorial Guinea, Gabon .... ***Ascotheca***

103 Anthers dehiscing by longitudinal slits; widespread .... ***Rungia***

104 Capsule 2-seeded (rarely 4-seeded), seeds smooth, glabrous or white-sericeous, or with 2 tufts of moniliform trichomes 105

104 Capsule usually 4-seeded, more rarely 2-seeded, seeds variously sculptured or with short trichomes, rarely smooth 106

105 Inflorescences of axillary or both axillary and terminal spikes; bracts elliptic, ovate or obovate, often imbricate, inflorescence units at each axil often >1-flowered; seeds 2–3 mm in diam., lenticular with a sharp rim, ± symmetrical in cross section and lacking a prominent ridge on one side, glabrous .... ***Meiosperma*** [42]

105 Inflorescences either axillary and 1-flowered (bracts undifferentiated from the leaves) or in well-defined, mostly terminal spikes (bracts highly modified), rarely in axillary pedunculate fascicles; bracts in species with well-defined spikes usually narrow, linear to lanceolate, or rarely (in one species) broadly elliptic to obovate; seeds variable, often larger than 3 mm in diam. with a rounded rim (including in the single species with broad bracts) and/or variously pubescent, or if small and with sharp rim then asymmetric in cross section and with a prominent ridge on one side .... ***Pogonospermum***

106 Corolla red or orange with tube somewhat curved and gradually widened, longer than lips; anthers with both thecae appendaged; Socotra .... ***Trichocalyx***

106 Corolla variable but usually with ± straight tube; if corolla red and with curved, gradually widened tube, then anthers with only the lower theca appendaged 107

107 Inflorescences secund spikes with usually imbricate, obovate, spathulate or lanceolate bracts, these green, white or pink; seeds subglobose, with hygroscopic or papillose trichomes; mainly Madagascar, 1 sp. widespread in tropical Africa............. ***Anisostachya***

107 Inflorescences variable; if secund spikes with imbricate bracts then seeds not as above, primarily without (rarely with) hygroscopic or papillose trichomes; widespread................ ***Justicia*** [43]

Key to the genera of Acanthaceae in Asia and Australasia (excluding the Arabian Peninsula and Mediterranean region)

1 Mangrove trees or shrubs with pneumatophores present; fruit a leathery 1-seeded capsule .... ***Avicennia***

1 Herbs, shrubs, woody twiners, or small trees, not mangrove trees (although occasionally mangrove shrubs in *Acanthus*), without pneumatophores; fruit a woody or thin-walled capsule with (1) 2 or more seeds 2

2 Seeds not borne on hook-shaped retinacula, either retinacula lacking or papilliform; plants without cystoliths; all anthers bithecous 3

2 Seeds borne on prominent hook-shaped retinacula; plants with or without cystoliths, if cystoliths absent then anthers monothecous... 7

3 Herbs or shrubs, not twining; paired bracteoles present or absent but not large and conspicuous; calyx deeply 4- or 5-lobed; fruit a many-seeded (usually >10 seeds) capsule 4

3 Herbaceous twiners or lianas, less frequently free-standing shrubs or herbs; flowers solitary or in fascicles or racemes of opposite flowers, not spirally arranged; calyx a subentire or undulate rim or with irregular teeth, or obscurely 5-lobed; fruit a 2–4-seeded capsule 6

4 Peduncles bearing spirally arranged, clasping, scale-like sterile bracts; all bracts sclerophyllous; leaves held in rosettes or basal whorls; India, Sri Lanka ....***Elytraria***

4 Peduncles (if present) without clasping scale-like bracts; bracts membranous or foliaceous; leaves mostly opposite, at least some pairs dispersed along the stems.. 5

5 Stamens 2, staminodes absent; bracteoles absent (rarely present); inflorescence of dense ± cylindrical spikes with imbricate bracts; calyx 4-lobed, the anterior lobe with bifid apex (rarely more deeply divided into 5 lobes) ....***Nelsonia***

5 Stamens 4, adaxial staminode often also present, or rarely reduced to 2 stamens +2–3 staminodes; bracteoles present; inflorescence variable but, if spikes cylindrical, then not so dense; calyx 5-lobed..***Staurogyne***

6 Stigma ± equally 2-lobed, each lobe subdivided into 2 unequal lobes; pollen 7–9-lobate and -colpate; India.................... ***Meyenia***

6 Stigma funnel-shaped, unequally 2-lobed or if equally so then not subdivided; pollen spiraperturate and unlobed; widespread ....***Thunbergia***

7 Stamens 4, sometimes with an additional staminode.................. 8

7 Stamens 2, with or without additional staminodes 39

8 Anthers all monothecous; plants without cystoliths; corolla 1-lipped... 9

8 Either anthers all bithecous or 2 anthers bithecous and 2 anthers monothecous; plants with cystoliths; arrangement of corolla lobes various but not 1-lipped... 12

9 Stamens included in corolla tube, subsessile, not inserted on a thickened flange; India and Sri Lanka to Myanmar............. ***Crossandra***

9 Stamens exserted from corolla tube, with flattened bone-like filaments, inserted on a thickened flange....................................... 10

10 Anterior staminal filaments lacking appendages, if flattened then gradually narrowed towards apex; seeds glabrous or sericeous-puberulous ....***Acanthus***

10 Anterior pair of staminal filaments flattened and either with an obtuse or acute tooth-like appendage or truncate to rounded towards apex ventrally; seeds with branched hygroscopic trichomes or tuberculate 11

11 Leaves opposite; flowers solitary or paired in the leaf axils, each flower or pair of flowers subtended by 2 pairs of bracts, outer pair entire, inner pair trifid; ovary without apical tufts of glandular trichomes; seeds tuberculate; India ....***Cynarospermum***

11 Leaves in pseudowhorls of (3) 4; inflorescences variable but not consisting of solitary or paired flowers in leaf axils; bracts entire or toothed, not trifid; ovary with 2 apical tufts of glandular trichomes; seeds with branched hygroscopic trichomes; widespread .... ***Blepharis***

12 Calyx distinctly bilabiate, with a 2-lobed or -toothed anterior lip and a 3-lobed or -toothed posterior lip; corolla with a funnel-shaped limb comprising equal anterior and lateral lobes and partially (or almost completely) fused dorsal pair of lobes; India to Laos ....***Neuracanthus***

12 Calyx not distinctly bilabiate (although can appear so in *Barleria*), either 4- or 5-lobed, lobes can be equal or unequal in shape and size; if calyx appears bilabiate then corolla not as above 13

13 Calyx 4-lobed, anterior lobe entire or bifid for less than half its length; anterior and posterior lobes typically much broader than lateral lobes and often enclosing them; corolla variously arranged, lobes subregular or in a 4 + 1 or 2 + 3 configuration, without hooded

upper lip; filaments of anterior (long) pair of stamens ?always twisted and crossing near the base..***Barleria***

13 Calyx 5-lobed, or if anterior pair of lobes partially fused and lobes of unequal width then corolla strongly bilabiate with ± hooded upper lip; staminal filaments not twisted and crossing near the base.... 14

14 Seed surfaces smooth or sculptured, lacking trichomes; corolla aestivation ascending-cochlear 15

14 Seed surfaces either covered by trichomes or with trichomes at least along margins and/or near the apices (trichomes minute in a few genera, such as *Hulemacanthus*, absent in *Borneacanthus*); corolla aestivation left-contort or quincuncial 19

15 One pair of stamens with bithecous anthers, the other pair with monothecous anthers; Thailand, Malaysia............ ***Thysanostigma***

15 Both pairs of stamens with bithecous anthers 16

16 Corolla strongly bilabiate with upper two lobes almost completely fused into a hooded or erect, apically notched lip; either stamens included in corolla tube or if exserted then anthers usually with thecae unevenly inserted on the filament and offset by ca. half their length.. 17

16 Corolla not so strongly bilabiate, 5 lobes often subequal although arranged in a 2 + 3 configuration and upper two lobes can be partially fused; stamens exserted, anther thecae held at a subequal height.. 18

17 Mouth of corolla closed due to raised, rounded palate of lower lip, upper lip held erect; stamens included in corolla tube, filaments very short, anthers with thecae held at a subequal height; calyx lobes apically reflexed; Borneo .... ***Linariantha***

17 Mouth of corolla not closed, palate of lower lip can be raised but not so strongly bulging, upper lip hooded, not erect; stamens exserted and held within hooded upper lip, filaments well developed; calyx lobes not markedly reflexed apically; Malaysia, Sumatra, Borneo ....***Filetia*** [44]

18 Calyx with a ± distinct tubular portion, the tube sometimes longer than the lobes; inflorescences often with opposite cymose units, pedicels widely divergent from inflorescence axis and can be thickened; India, Malaysia.............................***Phialacanthus*** [45]

18 Calyx divided ± to the base; inflorescences often secund, pedicels not so widely diverging from the axis and not thickened; widespread...***Asystasia***

19 Corolla lacking a filament curtain 20

19 Corolla with a conspicuous filament curtain 27

20 One pair of stamens with bithecous anthers, the other pair with monothecous anthers 21

20 Both pairs of stamens with bithecous anthers 22

21 Stamens exserted beyond corolla lobes, corolla limb very short and not strongly bilabiate (although posterior pair of lobes are partially fused); inflorescence a many-flowered thyrse with flowers in dense whorls at each node, not secund; bracts and bracteoles inconspicuous; New Guinea ....***Hulemacanthus***

21 Stamens not exserted beyond corolla lobes, corolla limb strongly bilabiate; inflorescence a secund spike, spikes sometimes compounded into dense heads; bracts and bracteoles usually conspicuous; widespread ....***Lepidagathis***

22 Corolla bilabiate, with ± hooded upper lip; corolla aestivation quincuncial 23

22 Corolla subactinomorphic or weakly zygomorphic, not strongly bilabiate with hooded upper lip; corolla aestivation left-contort 25

23 Anther thecae conspicuously spurred at base; China to Malaysia .... ***Chroesthes***

23 Anther thecae not spurred at base, either obtuse or at most minutely apiculate... 24

24 Capsule stipitate; seeds glabrous; calyx lobes all linear or linear-lanceolate; bracts and bracteoles small and inconspicuous; Borneo ....***Borneacanthus***

24 Capsule not or barely stipitate; seeds with hygroscopic trichomes; calyx lobes ± markedly unequal, posterior lobe broadest, lateral lobes narrowest (2 + 2 + 1 configuration); bracts and bracteoles usually conspicuous, often similar to calyx lobes in shape and size; widespread..***Lepidagathis***

25 Flowers with "X-shaped anthers" (i.e., thecae extend outwardly in a 180° configuration from expanded filament connective tissue); China ....***Pararuellia***

25 Anthers various but not "X-shaped" as above........................... 26

26 Plants with long-tubed, pale-colored corollas; leaves not held in a basal rosette; Papuasia ....***Leptosiphonium***

26 Corollas not long-tubed and pale-colored, typically short infundibuliform, primarily purple; leaves typically held in a basal rosette; Australia, New Caledonia, New Guinea.................... ***Brunoniella***

27 Corolla strongly bilabiate 28

27 Corolla infundibuliform, campanulate or other shapes, not strongly bilabiate 29

28 Plants large herbs or weak shrubs to 2.5 m tall; capsule oblong or obovate, not with noticeably thin walls; ovules 4 or fewer per ovary; India...***Calacanthus***

28 Plants herbaceous, typically <1 m tall (very rarely to 1.5 m tall); capsule cylindrical, with noticeably thin walls; ovules >8 per ovary, capsule typically polyspermous (≥16 seeds); widespread ....***Hygrophila***

29 Capsule with fracturing placentae 30

29 Capsules with non-fracturing placentae.................................... 31

30 Inflorescences complex, densely bracteate and compact, with numerous, small flowers; flowers not subtended by large, conspicuous, paired leaf-like bracts; corolla small (<10 mm long); anther thecae without appendages; widespread......................***Phaulopsis***

30 Inflorescences axillary, solitary or in simple dichasia, not complex and dense as above; flowers subtended by a large, conspicuous, pair of leaf-like bracts; corolla >34 mm long; anther thecae with appendages; India and Nepal.......................................***Petalidium***

31 Anthers with at least some thecae with basal appendages......... 32

31 Anthers lacking basal appendages.. 36

32 Deciduous tree to 5 m tall, flowering before the leaves appear; ultimate branches numerous and curved-ascending; karst hills of Laos ....***Xylacanthus*** [25]

32 Herbs or shrubs, habit not as above... 33

33 Leaf pairs strongly and consistently anisophyllous, the smaller leaf about 1/3 of the size of the larger; each anther theca with a pair of appendages; Thailand .... ***Diceratotheca***

33 Leaf pairs sometimes slightly dissimilar in size but not strongly (nor consistently) anisophyllous; anther thecae variously appendaged but not with 2 appendages per theca.............................. 34

34 Inflorescences of very long, terminal spikes, these commonly 30 cm in length; Malaysia ....***Stenothyrsus***

34 Inflorescences variable, primarily of racemes, less commonly of spikes or solitary flowers, if spikes, consistently <15 cm long..... 35

35 Ovary with 8 ovules; India, China....................... ***Echinacanthus***

35 Ovary with 4 ovules (occasionally fewer); widespread .... ***Dyschoriste***

36 Ovary with 16 ovules.......................................***Strobilanthes*** [46]

36 Ovary primarily with fewer than 16 ovules (with rare exceptions) 37

37 Corolla resupinate via twisting of the tube through 180°; inflorescences thyrsoid with secondary flowers in the axils of bracteoles; corolla with a ventricose throat.........................***Strobilanthes*** [47]

37 Corolla usually not resupinate via twisting of the tube (except in *Strobilanthes dyeriana*, *S. autapomorpha*, and *S. steenisiana*), but corolla distortions sometimes achieved by bending of the corolla throat; if resupinate, then not in combination with above additional features...38

38 Corolla internally with prominent rows of trichomes along posterior surface, these functioning to retain the style (very rarely secondarily lost); corolla typically with thin but prominent ridge between pairs of stamens, representing vestigial staminode.......... .... ***Strobilanthes***

38 Corolla internally lacking prominent rows of trichomes along posterior surface; corolla lacking a ridge between pairs of stamens.. ***Ruellia***

39 Anthers monothecous.. 40

39 Anthers bithecous (one theca sometimes reduced in size)........ 43

40 Corolla tube twisted through 180°, limb resupinate with the 3-lobed lower lip held in the upper position and unlobed or emarginate upper lip held in the lower position; India to China and Thailand.. ***Hypoestes***

40 Corolla tube not twisted; if flower resupinate then this achieved through geniculation of corolla tube.. 41

41 Corolla 30–60 mm long, bright red-orange; clambering shrubs; China to Indonesia.. ***Clinacanthus***

41 Corolla up to 10 mm long, white or pale blue, with or without red or mauve markings; perennial herbs or small shrubs, not clambering.. 42

42 Corolla with 4-lobed upper lip and unlobed lower lip; each anther with theca terminal and transverse, sometimes also with a vestigial second theca observed as a bump below the fertile theca; flowers axillary and solitary, held on lateral branches; Australia.. ***Xerothamnella*** [48]

42 Corolla with shortly bilobed, hooded upper lip and 3-lobed lower lip; each anther with theca dorsifixed and ± parallel to filament, without a vestigial second theca; inflorescence a small, dense secund spike; India, Sri Lanka.. ***Monothecium***

43 Staminal filament divided at apex, the thecae separated widely by an elongate connective perpendicular to the filament; corolla subactinomorphic with 5 ± equal lobes; Australia.. ***Dicladanthera***

43 Stamens not as above, if thecae widely separated then vertically offset to superposed; arrangement of corolla lobes various, but corolla usually ± zygomorphic.. 44

44 Staminodes present, either free or basally fused to the adjacent staminal filament.. 45

44 Staminodes absent.. 59

45 Calyx 4-lobed, anterior lobe entire or bifid for less than half its length, anterior and posterior lobes typically much broader than lateral lobes and often enclosing them; corolla arrangement variable, lobes subregular or in a 4 + 1 or 2 + 3 configuration, without a hooded upper lip; staminal filaments ?always twisted and crossing near the base.. ***Barleria***

45 Calyx 5-lobed, or if anterior pair of lobes largely fused then corolla markedly bilabiate with ± hooded upper lip; staminal filaments not twisted and crossing near the base.. 46

46 Seeds with hygroscopic trichomes present throughout or at least around the rim; corolla either with left-contort or quincuncial aestivation.. 47

46 Seeds without hygroscopic trichomes, variously tuberculate, echinate, verruculate, puberulous, tomentellous or smooth; corolla with ascending-cochlear aestivation.. 51

47 Filament curtain absent; corolla with quincuncial aestivation; inflorescences dense secund spikes that can be compounded into complex heads, often with dimorphic fertile and sterile bracts; calyx lobes highly unequal, posterior lobe broadest, lateral lobes narrowest (2 + 2 + 1 configuration).. ***Lepidagathis***

47 Filament curtain present; corolla with left-contort aestivation; inflorescences variable but not dense secund spikes with dimorphic bracts; calyx lobes (sub)equal to somewhat unequal, not in 2 + 2 + 1 configuration.. 48

48 Corolla tube much longer than lobes, tube either narrowly cylindrical throughout (corolla salverform) or with long cylindrical basal portion and gradually expanded throat; inflorescences a series of spikes, bracts often imbricate and often with conspicuous reticulate patterning.. ***Eranthemum***

48 Corolla without such a long basal cylindrical tube, not salverform; inflorescences not as above.. 49

49 Corolla internally with prominent rows of trichomes along posterior surface, these functioning to retain the style; corolla typically with thin but prominent ridge between pair of stamens.. ***Strobilanthes***

49 Style not held in place by trichomes on corolla tube; corolla without a prominent ridge between pair of stamens.. 50

50 Ovary with 4 ovules; lower corolla lip lacking stiff retrorse bristles; anther thecae usually spurred; plants usually of dry ground.. ***Dyschoriste***

50 Ovary with 8–20+ ovules; lower lip of corolla with numerous stiff retrorse bristles; anther thecae not spurred; plants of (seasonal) wetlands.. ***Hygrophila***

51 Ovary with 8 or more ovules, capsule 8–16-seeded; pollen with aperture margins conspicuously thickened and intricately ornamented with conical spines.. ***Phlogacanthus*** [12]

51 Ovary with 2 or 4 ovules; capsule 2- or 4-seeded; pollen without thickened and ornamented aperture margins.. 52

52 Leaves strongly anisophyllous (appearing alternate), larger leaf of a pair 9.5–19 × 2.5–6.7 cm, smaller leaf of a pair reduced to a minute lanceolate blade 4–6 × 1–2 mm; Borneo.. ***Ptyssiglottis staminodifera***

52 Leaves isophyllous or not so markedly anisophyllous.. 53

53 Corolla salverform, tube longer than limb and narrowly cylindrical throughout or only slightly widened distally, limb either subequally 5-lobed or only weakly bilabiate, if the posterior pair of lobes partially fused then not forming a hooded upper lip.. ***Pseuderanthemum*** [49]

53 Corolla not salverform, if tube longer than limb and cylindrical, then limb markedly bilabiate with posterior pair of lobes largely fused and sometimes forming a hooded upper lip.. 54

54 Corolla small, up to 15 mm long but often ≤10 mm long.. 55

54 Corolla much larger, >25 mm long.. 58

55 Leaves with toothed, spinose or sinuate margin; inflorescences axillary, 1-flowered or simple dichasia or fascicles; Australia, New Guinea, Fiji.. ***Graptophyllum*** [50]

55 Leaves with ± entire margin; inflorescences spikes or racemes, often terminal.. 56 [51]

56 Corolla campanulate, limb only weakly bilabiate; tube shorter than limb and widened almost from the base; India to Japan and Vietnam.. ***Codonacanthus***

56 Corolla strongly bilabiate; tube longer than or subequal to limb, not widened from the base.. 57

57 Anther thecae basally muticous; corolla tube sometimes with a dorsal pouch distally; China to Borneo.. ***Cosmianthemum***

57 Anther thecae with paired basal spurs; corolla tube without a dorsal pouch; China.. ***Wuacanthus***

58 Corolla tube markedly infundibuliform, with basal cylindrical portion and abruptly widened throat; limb only weakly bilabiate, the 5 lobes subequal, upper lip not strongly hooded; corolla white or rose-colored, with intricate darker veins; India, Bhutan, Myanmar, China.. ***Mackaya***

58 Corolla tube more gradually widened from base to apex and ± strongly curved; limb bilabiate with posterior pair of lobes forming a hooded upper lip; corolla red or bright pink; Australia, New Guinea, Pacific Is., naturalized elsewhere.. ***Graptophyllum***

59 Corolla resupinate through ±180° twist in corolla tube; flowers held between paired clasping bracts.. 60

59 Corolla not resupinate or, if so, then due to twisting of pedicel, corolla tube not twisted; flowers not held between paired clasping bracts.. 61

60 Capsule with fracturing placentae; anther thecae rounded or elliptic.. ***Dicliptera***

60 Capsule without fracturing placentae; anther thecae (in Asia) typically linear-oblong, rarely rounded or elliptic.. [***Peristrophe***] [36]

61 Anthers with thecae superposed and held patent to one another; corolla with a conspicuously 2-lobed upper lip, each lobe forked; Australia.. ***Xerothamnella*** [52]

61 If anthers superposed and oblique then corolla with a shortly 2-lobed or emarginate upper lip, the lobes not forked.............. 62

62 Pollen disc-shaped, bipororate with a broad marginal girdle of sexine [53]; anthers with thecae ± markedly offset to fully superposed and often highly oblique, sometimes 1 or both thecae perpendicular to filament, lacking basal appendages; rugula absent .... ***Isoglossa***

62 Pollen very variable but never disc-shaped with a marginal girdle; anthers with thecae variously held at an equal height to strongly offset, if offset then often with the lower theca or both thecae with a basal appendage, and rugula present 63

63 Rugula absent; anther thecae held at the same height or only slightly offset, parallel to each other and to the filament or slightly sagittate; thecae without appendages or with short uncurved appendages....64

63 Rugula present; anther thecae usually offset by at least half their length or fully superposed, sometimes markedly oblique; lower theca or more rarely both thecae often with a conspicuous ± curved appendage, this typically pale.. 79

64 Ovary with 6 or more ovules, capsule 6- to many-seeded, or if 2 ovules per locule and capsule 4-seeded then anthers penicillate at base or thecae only dehiscing via a short slit in central half to 2/3; pollen with aperture margins and/or aperture surface conspicuously thickened and often intricately ornamented with conical spines... 65

64 Ovary with 2 or 4 ovules; capsule 2- or 4-seeded; anthers not penicillate at base, thecae dehiscing along ± their full length; pollen without thickened and ornamented aperture margins or surfaces 72

65 Filaments swollen (pouched) distally; corolla subequally 5-lobed, not clearly bilabiate 66

65 Filaments not swollen or pouched; corolla bilabiate or subequally 5-lobed... 67

66 Cladodes (reduced abortive branches) present in the inflorescence, terminated by paired small spines; seeds not compressed, with 2 distinct grooves, surface with hygroscopic trichomes; India .... ***Haplanthodes***

66 Cladodes absent in inflorescence; seeds somewhat compressed, not distinctly grooved, surface without trichomes, verrucose; widespread .... ***Haplanthus*** [9]

67 Ovary with 4 ovules; anthers glabrous, dehiscent via longitudinal slit in central half or 2/3 of each theca; India, Myanmar.............. .... ***Sphinctacanthus*** [10]

67 Ovary with 6 or more ovules, or if 4 then anthers conspicuously penicillate at base and dehiscent via longitudinal slit in distal half extending to apex.. 68

68 Capsule linear and 4-angled, not compressed; seeds markedly compressed, smooth, can be covered in trichomes; anthers not penicillate 69

68 Capsule compressed perpendicular to the septum, elliptic, oblanceolate or narrowly oblong in face view; seeds subglobose, ellipsoid or block-like, not compressed, often pitted or rugose and grooved; anthers often penicillate at base...71

69 Calyx 4-lobed; slender procumbent herbs; Thailand....... ***Graphandra***

69 Calyx 5-lobed; habit variable but not procumbent herbs........... 70

70 Corolla tube shorter than limb; upper lip ± curved; India .... ***Diotacanthus***

70 Corolla tube longer than limb; upper lip not curved; widespread .... ***Gymnostachyum***

71 Capsule 6–20-seeded; India and Sri Lanka to Myanmar, introduced elsewhere.. ***Andrographis***

71 Capsule 4-seeded; India, Sri Lanka .... [***Indoneesiella***] [11]

72 Corolla blue-green or livid-green, tube narrowly cylindrical throughout with only very short expanded throat, usually longer than limb, upper lip linear-lanceolate, much smaller than lower lip; India and Sri Lanka to Myanmar.. ***Ecbolium***

72 Corolla variously colored but not shades of green, tube variously shaped but if longer than limb then more gradually expanded and lips not so unequal.. 73

73 Inflorescences often on leafless portion of branches or on mature woody stems (ramiflorous or cauliflorous), in fascicles or short spikes; shrubs or small trees 74

73 Inflorescences either terminal or axillary on leafy portion of branches; herbs or shrubs 75

74 Corolla lips conspicuously longer than tube; lower lip strap-shaped with 3 short rounded apical lobes; New Guinea............. .... ***Calycacanthus***

74 Corolla tube longer than lips; lower lip deeply divided into 3 linear-lanceolate lobes; Vietnam...................................... ***Cyclacanthus***

75 Calyx lobes lanceolate, with 3 or more parallel veins prominent at maturity; corolla with ± markedly saccate throat above short basal cylindrical tube 76

75 Calyx lobes linear to linear-lanceolate, usually only the midrib prominent or veins inconspicuous; corolla without markedly saccate throat.. 77

76 Inflorescences 1-flowered, these sometimes clustered towards branch tips; anther thecae pubescent; pollen 3-colporate, 6-pseudocolpate; Thailand .... ***Marcania***

76 Flowers held in branched thyrses; thecae glabrous; pollen 5-colporate, 10-pseudocolpate; New Guinea .... ***Jadunia*** [54]

77 Inflorescences axillary, varying from lax dichasia to reduced and contracted dichasia with 2(–4) contracted branches that can bear several to many pairs of imbricate, scale-like bracts, or sometimes reduced to single flowers; inflorescences not spiciform; Sri Lanka to New Guinea... ***Ptyssiglottis***

77 Inflorescences terminal, spiciform or, if branched, then branches spiciform.. 78

78 Corolla with strongly curved and hooded upper lip, upper lip either shortly 2-lobed or 4-lobed, lower lip 3-lobed or 1-lobed; inflorescence often branched with branches spiciform, or sometimes unbranched; India and China to Indonesia .... ***Leptostachya***

78 Corolla with a ± straight and not conspicuously hooded upper lip, upper lip shortly 2-lobed, lower lip 3-lobed; inflorescence spiciform, unbranched; Taiwan............................. ***Kudoacanthus*** [55]

79 Corolla tube narrowly cylindrical, considerably longer than lips; upper lip lanceolate or narrowly so, not hooded; anthers with thecae lacking appendages; widespread .... ***Rhinacanthus***

79 Corolla tube not so narrowly cylindrical, if tube longer than lips then upper lip hooded; anther thecae with or (rarely) without basal appendages, often with a conspicuous curved pale appendage on the lower theca.. 80

80 Capsule with fracturing placentae; inflorescences usually secund spikes with imbricate bracts; bracts with or without conspicuous white or pinkish hyaline margins...................................... ***Rungia***

80 Capsule without fracturing placentae; inflorescences variable, if secund spikes with imbricate bracts then bracts without abrupt pale hyaline margins 81

81 Capsule 2-seeded, seeds smooth, discoid; India........ ***Meiosperma***

81 Capsule usually 4-seeded, seeds variously sculptured or rarely smooth; widespread .... ***Justicia*** [43]

Key to the genera of Acanthaceae in the Americas

1 Mangrove trees or shrubs with pneumatophores present; fruit a leathery 1-seeded capsule .... ***Avicennia***

1 Herbs, shrubs, lianas or small trees, if (rarely) mangrove trees or shrubs then pneumatophores lacking (can have aerial prop roots); fruit either a ± woody or thin-walled capsule with 2 or more seeds, or a 1-seeded drupe... 2

2 Seeds not borne on hook-shaped retinacula, retinacula lacking or papilliform; plants without cystoliths; all anthers bithecous......3

2 Seeds borne on prominent hook-shaped retinacula (retinacula indistinct in *Aphanosperma* and *Chalarothyrsus*, with seeds permanently retained in capsule valves); plants with or without cystoliths, if cystoliths absent then anthers monothecous 7

3 Herbaceous twiners or lianas; flowers subtended by conspicuous clasping or partially connate paired bracteoles; calyx a subentire

or undulate rim or with irregular teeth, or obscurely 5-lobed; fruit a 1-seeded drupe ... ***Mendoncia*** [56]

3 Herbs or shrubs, not twining; paired bracteoles present or absent but not large and conspicuous; calyx deeply 4- or 5-lobed; fruit a many-seeded capsule (usually >10 seeds) ... 4

4 Peduncles bearing clasping scale-like sterile bracts; all bracts sclerophyllous; leaves in rosettes or whorls either basally or terminating branches (sometimes dispersed along stems in *E. imbricata* and *E. mexicana*) ... ***Elytraria***

4 Peduncles (if present) without clasping scale-like sterile bracts; bracts membranous or foliaceous; leaves opposite, at least some pairs dispersed along the stems ... 5

5 Bracteoles absent; inflorescence of dense ± cylindrical spikes with imbricate bracts; calyx 4-lobed, the anterior lobe with bifid apex (rarely more deeply divided into 5 lobes); stamens 2, staminodes absent ... ***Nelsonia*** [57]

5 Bracteoles present; inflorescence variable but, if spikes cylindrical, then relatively lax; calyx 5-lobed; stamens 4, adaxial staminode often also present (rarely 2 stamens +2–3 staminodes) ... 6

6 Plants subcaulescent (internodes indistinct or short); inflorescence of axillary, long-pedunculate (peduncles 9.8–22 cm long) panicles of spikes; ovary asymmetric with style arising on one side, stigma 1-lobed, subcapitate; Brazil ... ***Aymoreana***

6 Plants caulescent (internodes distinct, usually elongate); inflorescence of terminal, sessile to short-pedunculate (peduncles 0.2–4 cm long) racemes or spikes (rarely panicles); ovary symmetric, stigma 2-lobed (one lobe usually bifid) or subcrateriform (in *S. guianensis*), lobes not subcapitate; widespread ... ***Staurogyne***

7 Stamens 4, sometimes also with an additional staminode ... 8

7 Stamens 2, sometimes also with (1) 2 (3) staminodes ... 30

8 Anthers all monothecous; plants without cystoliths ... 9

8 Anthers all bithecous or 2 bithecous and 2 monothecous; plants with cystoliths ... 14

9 Corolla zygomorphic, the lobes dissimilar in form ... 10

9 Corolla usually subactinomorphic, the lobes more or less similar in form ... 12

10 Calyx deeply 3-partite; Colombia ... ***Cyphacanthus***

10 Calyx 5-partite ... 11

11 Leaves opposite (rarely subopposite); bracts entire or dentate, green or often brightly colored; corolla rarely with linear nectar guides, mostly 25–85 mm long; at least distal portion of filaments of stamens usually exserted from corolla tube; pollen with colpi not expanded or bifurcating (usually narrowed) toward poles, interapertural exine usually heterogeneously sculptured; widespread ... ***Aphelandra*** [5]

11 Leaves opposite (rarely subopposite) or quaternate; bracts entire and usually green; corolla often with colored linear nectar guides, 6.5–24 mm long (or if larger, to 40 mm, then plants with quaternate leaves); filaments of stamens often entirely included in corolla tube; pollen with colpi sometimes expanded or bifurcating toward poles, interapertural exine homogeneously sculptured; Mexico ... ***Holographis***

12 Pollen 3-colpate with each colpus longitudinally bisected by an operculum (elongate band of exine), opercula either isolated within the colpi (operculate) or connected at each end to the interapertural exine (pontoperculate); Jamaica ... ***Salpixantha***

12 Pollen 3-colpate with colpi not bisected by elongate bands of exine or pollen pantoforate (i.e., sometimes in *Stenandrium dulce*) or pollen pantoaperturate (rugate) with rugae arranged ± tangentially over surface or pollen 3-colpate and with prominent margines and mesocolpial ridges (appearing 9-colpate); widespread, but not in Jamaica ... 13

13 Plants usually small, up to 25(–70) cm; leaves often borne at or near ground level (plants acaulescent to subcaulescent); bracts usually green; pollen 3-colpate or pantoforate (i.e., sometimes in *S. dulce*) ... ***Stenandrium***

13 Plants usually shrubby, up to 1.5 m tall; leaves disposed along conspicuous stems; bracts whitish, pinkish, or reddish-brown; pollen pantoaperturate (rugate) with rugae arranged ± tangentially or pollen 3-colpate and with prominent margines and mesocolpial ridges (appearing 9-colpate) ... ***Neriacanthus*** [6]

14 Stamens with 2 anthers bithecous and 2 anthers monothecous ... 15

14 Stamens with all anthers bithecous ... 20

15 Seeds with hygroscopic trichomes; corolla with quincuncial aestivation ... 16

15 Seeds without hygroscopic trichomes; corolla with ascending-cochlear aestivation ... 17

16 Calyx lobes ± homomorphic; plants with axillary spines and/or spiny leaf margins; West Indies ... ***Barleriola***

16 Calyx lobes heteromorphic in 2 + 2 + 1 configuration, posterior lobe broadest, lateral lobes narrowest, anterior lobes often partially fused; plants lacking axillary spines and/or spiny leaf margins; widespread ... ***Lepidagathis*** [58]

17 Corolla red, colored markings on limb absent, 34–48 mm long, ± tubular or clarinet shaped with the tube elongate, relatively slender but gradually expanded distally and the limb shallow, inconspicuous, tube 6–11× longer than limb; Bolivia, Brazil ... ***Pranceacanthus***

17 Corolla white, pinkish or purple, often with colored markings on limb, 10–45 mm long, infundibuliform to salverform and with a ± conspicuous limb (at least the upper lip in *Isotheca*), tube 1–2.6 (–3.6) × longer than limb (or if 6 or more times longer than limb as in *Isotheca*, then corolla white) ... 18

18 Corolla white, apparently lacking colored markings on limb, 35–45 mm long, downward curved and “cobralike” in bud; stamens conspicuously exserted beyond limb of corolla; inflorescence a ± open, terminal dichasiate raceme (i.e., dichasia sessile and flowers pedicellate); pollen 4-aperturate, echinate; Trinidad, Venezuela ... ***Isotheca***

18 Corolla white, pinkish or purple, usually with colored markings on limb, 10–30 mm long, usually straight, not “cobralike” in bud; stamens included in corolla tube or exserted from it, but not extending beyond limb; inflorescence of axillary or usually terminal dichasiate spikes (sometimes very reduced) or panicles of spikes; pollen usually 3-aperturate ... 19

19 Corolla ± salverform with subactinomorphic limb, upper lip deeply lobed; bracts ± inconspicuous, ca. 1 mm wide; Costa Rica, Brazil, Panama ... ***Chamaeranthemum***

19 Corolla infundibuliform with bilabiate limb, upper lip entire to shallowly lobed; bracts conspicuous, (2–) 5–20 mm wide; widespread ... ***Herpetacanthus***

20 Corolla with ascending-cochlear aestivation; pollen 3-colporate, 6-pseudocolpate ... 21

20 Corolla with quincuncial or left-contort aestivation; pollen otherwise ... 22

21 Perennial herbs or shrubs to 1.5 m tall; calyx to 5 mm long, 5-lobed, lobes homomorphic; corolla red, 15–21 mm long; capsule 12–18 mm long; seeds permanently retained in capsule and partially fused to inner capsule wall; western Mexico ... ***Chalarothyrsus***

21 Large shrubs to small trees to 8 m tall; calyx 15–40 mm long, 2-lipped, the 2 segments entire or variously lobed at apex; corolla white to yellow; 23–97 mm long; capsule 40–85 mm long; seeds expelled from mature capsule, not fused to inner capsule wall; eastern and southern Mexico to Costa Rica ... ***Spathacanthus***

22 Corolla with quincuncial aestivation, lacking a filament curtain; inflorescences mostly secundiflorus ... ***Lepidagathis***

22 Corolla with left-contort aestivation, with a filament curtain; inflorescences rarely (if ever) secundiflorus ... 23

23 Calyx 3-lobed; corolla very large, gullet-shaped, pale green to greenish-yellow (sometimes with maroon tinges), cream-colored, or entirely dark maroon; Mexico and Central America ... ***Louteridium***

23 Calyx 5-lobed; corolla variable but not as above ... 24

24 Corolla subcylindrical or, if with an expanded/ampliate throat, then flowers borne in headlike clusters subtended by several pairs of bracts ... 25

24 Corolla campanulate, throat ampliate; flowers not borne in head-like clusters, not subtended by several pairs of bracts 26

25 Thecae awned basally; western South America..... ***Suessenguthia***

25 Thecae awnless; Peru... ***Trichosanchezia***

26 Calyx lobes fused for at least 1/3 of their length and usually over half of their length, with hyaline regions bordering each lobe; anther thecae usually appendaged at base, these sometimes inconspicuous or rarely absent; plants herbaceous or subshrubby .... ***Dyschoriste***

26 Calyx lobes deeply divided, or if with a conspicuous fused portion then lacking hyaline regions bordering each lobe; anther thecae lacking basal appendages or if basally awned (*Bravaisia*) then plants large shrubs or trees 27

27 Thecae awned with a single, subulate projection ....***Bravaisia***

27 Thecae awnless... 28

28 Shrubs or trees up to 25 m tall and usually ≥4 m tall; corolla woolly pubescent externally ....***Trichanthera***

28 Herbs, shrubs, sometimes clambering, or treelets, <4 m tall; corolla various but not woolly pubescent externally........................ 29

29 Corolla usually ≤10 mm long, conspicuously bilabiate; plants usually aquatic or semi-aquatic; pollen 4-colporate and 8- (or more? [59]) pseudocolpate, exine usually more or less finely and irregularly reticulate ....***Hygrophila***

29 Corolla usually >10 mm long, subactinomorphic and not conspicuously bilabiate; plants not aquatic but can be riparian; pollen 3-aperturate, lacking pseudocolpi, exine coarsely reticulate .... ***Ruellia***

30 Corolla with left-contort or quincuncial aestivation, with or without a filament curtain.. 31

30 Corolla with ascending-cochlear aestivation, lacking a filament curtain... 34

31 Corolla with quincuncial aestivation, lacking a filament curtain..... 32

31 Corolla with left-contort aestivation, with a filament curtain.... 33

32 Corolla red, strongly bilabiate, upper lip ± hooded, entire or shallowly 2-lobed, lower lip 3-lobed; Mexico ....***Lepidagathis***

32 Corolla bright yellow (drying dark purplish), consisting of 5, large, spreading lobes, 4 posterior, 1 anterior; widespread ....***Barleria***

33 Calyx 3-partite; corolla very large, gullet-shaped, pale green to greenish-yellow (sometimes with maroon tinges), cream-colored, or entirely dark maroon; primarily nocturnal; shrubs to trees; pollen spherical and pantoforate; Mexico and Central America......... ....***Louteridium***

33 Calyx 5-partite; corolla long and tubular, primarily red or orange, but can be yellow or white; shrubs; pollen not spherical, 2-colporate and polypseudocolpate, the apertural faces oriented 90° from one another; mostly South America......................................***Sanchezia***

34 Androecium of 2 stamens (bithecous) and 2 staminodes; flowers sometimes heterostylous.. 35

34 Androecium of 2 stamens (bithecous or monothecous) and 0 staminodes; flowers not heterostylous 41

35 Corolla ca. 5 mm long; upper lip divided less than 1/3 its length (i.e., shallowly 2-lobed); Ecuador....................... ***Psilanthele*** [60]

35 Corolla (at least of chasmogamous flowers) >5 mm long (up to 45 mm long and usually >10 mm long); upper lip divided 1/2 or more its length (shallowly 2-lobed in *Chileranthemum* and some species of *Odontonema*) 36

36 Corolla with purplish spots on limb, the 2 lobes of upper lip strongly laterally divergent from each other; stamens conspicuously exposed between lips of corolla (not appressed to upper lip of corolla), filaments arched toward lower lip of corolla; plants not heterostylous; South America..***Pulchranthus***

36 Corolla with or without spots on limb, the 2 lobes of upper lip not laterally divergent from each other; stamens appressed to upper lip of corolla or exposed between lips, filaments straight (not curved toward lower lip of corolla); plants often heterostylous..................37

37 Corolla ± salverform, tube elongate and cylindric (or throat becoming slightly expanded) or sometimes narrowed distally, limb ± rotate, usually subactinomorphic.................***Pseuderanthemum***

37 Corolla infundibuliform, tube expanding gradually or ± abruptly toward mouth (sometimes subcylindric), limb extending forward to reflexed, bilabiate 38

38 Trailing or clambering shrubs; leaves coriaceous, blades 10–25 mm long; corolla 13–17 mm long; serpentine substrates in Cuba .... ***Sapphoa***

38 Plants lacking the above combination of characters 39

39 Armature usually present in leaf axils (absent in some plants or in some species); leaves usually coriaceous; corolla usually bluish to purple (rarely red or white); Argentina, Bolivia, Peru, West Indies .... ***Oplonia*** [61]

39 Spines absent; leaves membranaceous; corolla red, purplish, pink, yellow, or white 40

40 Corolla purplish to pinkish to whitish with colored markings on the lower lip, tube subcylindric to ± abruptly expanded distally, shorter to only slightly longer than limb, upper lip shallowly 2-lobed, erect, lower lip horizontally spreading (i.e., lips 90° apart with lower lip forming a conspicuous "landing platform"); plants not clambering; Mexico to El Salvador...................................***Chileranthemum***

40 Corolla red, pinkish, or purplish (rarely yellow or white), usually lacking colored markings, tube usually gradually expanded distally and longer (often >1.5× longer) than limb, upper lip shallowly to ± deeply 2-lobed, upper and lower lips variously oriented; plants sometimes clambering; widespread .... ***Odontonema***

41 Anthers monothecous 42

41 Anthers bithecous 43

42 Inflorescence of terminal spikes; corolla violet, tube cylindric, limb deeply 5-lobed with equal lobes; Brazil ....***Sebastiano-Schaueria*** [62]

42 Plants not with the above combination of characters; widespread ....***Stenostephanus***

43 Stems usually hexagonal; flowers in bracteate dichasia bearing 1 or more cymules, cymules of 1 or more flowers subtended by an involucre of 2 or more pairs of bracteoles (outer pair usually conspicuous and larger than inner pair(s)); capsules with fracturing placentae, dehiscent capsule conspicuously ruptured near base of head; corolla resupinate (180° or 360°) in some species; widespread ....***Dicliptera***

43 Stems terete to quadrate to quadrate-sulcate (rarely subhexagonal); flowers rarely borne in cymules but, if so, then not as described above; capsules without fracturing placentae (or retinacula slightly separating from inner wall in *Henrya* and *Tetramerium*, but then not rising to protrude prominently from each capsule valve on/after dehiscence); corolla not resupinate... 44

44 Corolla subsalverform, purplish; stamens 2–2.5 mm long, filaments apically pubescent with flexuose eglandular trichomes, thecae superposed (0.3–0.5 mm apart), distal theca fertile, proximal theca sterile (appendage-like); seeds ca. 5 mm in diam., papillose, margin swollen...***Streblacanthus***

44 Plants not with the above combination of characters................ 45

45 Upper lip of corolla with a rugula on the internal surface (not confirmed for all taxa); flowers nototribic; anther thecae with or without basal appendages, the pair parallel to perpendicular and equally to unequally inserted on the filament; pollen 2–6 (or more?)-aperturate, pseudocolpi present or absent, insulae (i.e., ± isolated [sometimes linked in *Poikilacanthus*] [63] gemmate regions enclosed by thick, smooth marginal walls) and/or peninsulae (attached on one side to the interapertural exine), when present, usually restricted to 1 or more rows flanking apertures or entire interapertural surface either reticulate or covered with smooth and subconic to rounded verrucae..46

45 Upper lip of corolla lacking a rugula; flowers sternotribic, nototribic or pleurotribic; anther thecae lacking basal appendages, the pair parallel to subsagittate and equally to subequally inserted on the filament; pollen 3-colporate and 6-pseudocolpate (pseudocolpi sometimes fused, inconspicuous, or rarely absent; 2-colporate, 4-pseudocolpate in *Mexacanthus*), insulae and peninsulae absent ... 53

46 Shrubs or epiphytic herbs; flowers subtended by an involucre of conspicuous, basally fused bracteoles; corolla red or lilac; calyx highly reduced, cupular, entire to shallowly dentate; Brazil .... ***Clistax*** [64]

46 Plants not with the above combination of characters................. 47

47 Inflorescence of short, axillary, pedunculate, subcapitate spikes; bracts oblanceolate to obovate; thecae of a pair superposed and perpendicular; corolla yellow-green with purplish spots on lower lip, ca. 9 mm long; Andean Peru ....***Cephalacanthus***

47 Plants not with the above combination of characters................. 48

48 Trees to 5 m tall; leaves with globose (appearing hemispheric on surfaces) concretions 0.3–0.7 mm in diam.; thecae of a pair equally inserted, parallel to subsagittate, lacking basal appendages; calyx 25–32 mm long, lobes oblong to oblanceolate, widely spreading at maturity; capsule 22–29 mm long; Haiti ....***Samuelssonia***

48 Plants not with the above combination of characters................. 49

49 Pollen 4–6 (or more?)-porate, interapertural surfaces either covered with discrete insulae or with insulae linked by sharing common end-walls and arranged in loops that enclose a row or band of linked insulae 50

49 Pollen 2–4-aperturate (colporate or porate), apertures flanked by pseudocolpi or by 1 or more rows of ± discrete insulae and/or peninsulae, or the entire interapertural surface covered with smooth and subconic to rounded verrucae 51

50 Inflorescence large, usually longer than 7 cm, and very showy with conspicuous subfoliose red to maroon to pinkish bracts and bracteoles; corolla white (sometimes turning pinkish with age); pollen covered with discrete insulae; frequently cultivated, presumably native in Venezuela .... ***Megaskepasma*** [65]

50 Inflorescence various, but not as described above, usually less than 7 cm long; corolla red, orangish, pink, pinkish-purple, greenish-yellow, or white; pollen covered with discrete insulae or pollen otherwise; widespread ....***Poikilacanthus***

51 Erect shrubs to 3 m; corolla primarily nocturnal, greenish, pale yellow, or cream, 38–95 mm long, upper lip arched, lobes of lower lip usually dangling and somewhat twisted; thecae 5–7.6 mm long; pollen 3-colporate and with either a pseudocolpus or 1 row of insulae flanking each colporus; Brazil ....***Harpochilus*** [66]

51 Plants not with the above combination of characters................. 52

52 Subscandent shrubs; corolla greenish white, 13–14 mm long, upper lip erect (i.e., continuous with tube) and lower lip horizontal at maturity (i.e., spreading 90° from upper lip); pollen 4-colporate, mesocolpia "occasionally" [fide Raj, 1961] with 2 pseudocolpi; Cuba.. ***Dasytropis***

52 Plants not with this combination of characters and extremely variable in vegetative, floral, and palynological morphologies; widespread ....***Justicia*** [67]

53 Inflorescence a terminal thyrse; corolla bud strongly arched (i.e., curved downward and appearing like an upside-down hook), open corolla with the limb curved downward forming an upside-down "U" or semi-circle; thecae 5–6 mm long; Cuba ..... ***Ancistranthus***

53 Plants not with the above combination of characters; not occurring in Cuba 54

54 Bracteoles of a pair fused along one side from base to near apex forming a sheathing involucre around flower; pollen with colpi broad, far exceeding the width of the centrally positioned ora; septa and attached retinacula separating slightly from inner wall of mature capsules near base of head; U.S.A. (Arizona) to Costa Rica.......................***Henrya***

54 Bracteoles of a pair not fused, or if so only at base up to 1 mm; pollen with colpi narrow, not or only slightly exceeding width of centrally positioned ora; septa and attached retinacula not separating from inner wall of mature capsules (except in *Tetramerium*) 55

55 Capsules progressively reflexing during maturation (upside-down at maturity), distal portion of capsule expanded, truncate and widest at apex, basal portion of capsule densely pubescent with apically hooked (uncinate) trichomes; seeds 2, permanently enclosed in capsule valves; northwestern Mexico .... ***Aphanosperma***

55 Capsules not reflexed at maturity, distal portion of capsule tapering to a point or rounded at apex, basal portion lacking uncinate trichomes; seeds 2–4, free from capsule valves when mature 56

56 Flowers sternotribic (i.e., stamens positioned near lower lip of corolla and anthers dehiscing toward upper lip) or pleurotribic (i.e., anthers dehiscing toward center of floral axis and each other); primarily North and Central America 57

56 Flowers nototribic (i.e., stamens positioned near upper lip of corolla and anthers dehiscing toward lower lip) or sternotribic in *Schaueria litoralis* from South America; mostly South America 61

57 Flowers pleurotribic; seeds usually 2 per capsule...................... 58

57 Flowers sternotribic; seeds 2–4 per capsule............................... 59

58 Corolla 6.5–11 mm long, cream with maroon markings; pollen 3-colporate, 6-pseudocolpate; southern Mexico .... ***Gypsacanthus***

58 Corolla 17–26 mm long, bicolored with upper lip red and lower lip yellow; pollen 2-colporate, 4-pseudocolpate; west-central Mexico ....***Mexacanthus***

59 Inflorescence of usually densely bracteate, 4-sided spikes; bracts conspicuous, usually concealing the calyx; septa and attached retinacula separating slightly from inner wall of mature capsules near base of head ....***Tetramerium***

59 Inflorescence neither densely bracteate nor 4-sided; bracts inconspicuous and sometimes caducous, not concealing the calyx; septa and attached retinacula not separating from inner wall of mature capsules 60

60 Shrubs to 4 m tall, rarely dying back to woody caudices; corolla (white) pink, red, or orange (yellowish), lacking conspicuous colored markings, (24–) 30–65 mm long, tube usually conspicuously ampliate toward apex, (10–) 14–31 mm long; thecae 2.2–4.8 mm long; U.S.A. to Costa Rica ....***Anisacanthus***

60 Perennial herbs to weak shrubs up to 1 (–1.5) m tall, usually dying back to woody caudices; corolla white, yellow, blue, purple, or pinkish, usually with conspicuous colored markings on the limb, 5.5–23 (–27) mm long, tube not or only slightly ampliate toward apex, 1.5–8.5 (–13) mm long; thecae 0.5–1.9 mm long; widespread.................................***Carlowrightia***

61 Creeping perennial herbs; leaves with conspicuous white, pink, or red veins; corolla yellow, 10–15 mm long; inflorescence of densely bracteate terminal spikes; Colombia and Brazil to Bolivia ....***Fittonia***

61 Plants not with the above combination of characters................. 62

62 Inflorescence of axillary and terminal, densely bracteate spike-like thyrses to 15 cm long; bracts and calyx lobes distally dark maroon; corolla yellow, (28–) 35–47 mm long, throat abruptly and broadly expanded from subcylindric tube, appearing saccate; northeastern Mexico...***Hoverdenia***

62 Plants not with the above combination of characters [68]......... 63

63 Shrubs; bracts and bracteoles inconspicuous and often caducous, 0.8–3 mm long, 0.2–1 mm wide; corolla red, 20–45 mm long; seasonally dry forests of Argentina, Bolivia, Brazil, Paraguay .... ***Thyrsacanthus*** (in part, excl. *T. sulcatus*)

63 Plants not with the above combination of characters................. 64

64 Corolla subsalverform, tube elongate, 1.3–8.5× longer than limb, narrow (up to 1.5 mm in diam. near midpoint, measured flat), and cylindric for most of its length (± abruptly expanded only near apex, if at all).. 65

64 Corolla infundibuliform, tube ± gradually expanded distally, 0.7–3 (–3.6) × longer than limb, mostly neither conspicuously narrow ([1.2–] 1.5–6.3 mm in diam. near midpoint, measured flat) nor cylindric through most of its length 67

65 Inflorescence of open and elongate spikes, bracts inconspicuous, rachis clearly visible; corolla tube 3–8.5× longer than limb; Costa Rica to Argentina......................***Pachystachys*** (in part [69])

65 Inflorescence of densely and conspicuously bracteate ± 4-sided spikes, rachis not visible; corolla tube 1.3–3× longer than limb..... 66

66 Bracts lanceolate, 2–4 mm wide; Argentina, Paraguay, Uruguay .... ***Thyrsacanthus sulcatus***

66 Bracts ovate, broadly ovate, subdeltate, elliptic or subcircular, 5–18 mm wide; U.S.A. to Mexico .... ***Yeatesia***

67 Corolla bluish or purplish, 11–21 mm long; arid regions of northern Mexico................ ***Mirandea*** (in part, excluding *M. sylvatica*)

67 Corolla white, yellow, orangish, red or pink, 8–70 mm long; plants of moist to wet forests in southern Mexico to South America 68

68 Corolla yellow to white, 8–31 mm long; Mexico, Guatemala 69

58 Corolla white, yellow, orangish, red or pink, 10–70 mm long; South America and the West Indies 70

69 Bracts 1–4 mm long, 0.5–0.8 mm wide; calyx 2–3.7 mm long; corolla 8–13.5 mm long; southern Mexico..........***Mirandea sylvatica*** [70]

69 Bracts 9–22 mm long, 1.2–2.2 mm wide; calyx 10–25 mm long; corolla 22–31 mm long; Mexico, Guatemala ....***Schaueria parviflora*** [71]

70 Corolla yellow or white; bracts narrow, 0.5–2.5 mm wide, mostly yellow in species with yellow corollas and green in species with white corollas; Atlantic forests of Brazil .... ***Schaueria***

70 Corolla mostly red, orange-red or pink (white in *P. lutea*, and yellow in *P. azaleiflora*); bracts (4–) 6–18 mm wide in most species (1–1.5 mm wide in *P. azaleiflora*, *P. badiospica*, *P. gracilis* and *P. linearibracteata*), green to yellowish-green (bright yellow to orange-yellow in *P. lutea* and brownish red in *P. badiospica*); West Indies and Amazonian South America, especially Peru .... ***Pachystachys***

Notes corresponding to keys

[1] Physacantheae is here recognized for the first time (see Validation of Names) to accommodate three species of *Physacanthus*, a lineage of proposed wide-hybrid origin (Tripp & al., 2013b) between unknown progenitors of Acantheae and Ruellieae.

[2] See also the keys in Daniel & McDade (2014) and Braz & al. (2021), which provide additional information useful for identifying genera in this lineage, especially with respect to bract, seed, and pollen morphology.

[3] This condition occurs for example in *Crossandra flava* Hook. and *Sclerochiton uluguruensis* Vollesen from continental Africa.

[4] Molecular evidence (McDade & al., 2005) indicates that the Afro-Malagasy species of *Stenandrium*, including the Malagasy segregate genus *Achyrocalyx*, form a clade distinct from NW *Stenandrium* and should be treated under the genus *Stenandriopsis*. However, no morphological characters have so far been identified to support the separation of *Stenandriopsis* from caulescent species of *Stenandrium*, which was the basis for Vollesen's (1992) uniting of the two.

[5] Plants previously treated in *Encephalosphaera*, *Geissomeria*, *Rhombochlamys*, *Orophochilus*, and *Xantheranthemum* cannot reliably be differentiated from those of *Aphelandra* using either micro- or macromorphological means; moreover, phylogenetic (McDade & al., 2005) evidence suggests some of these taxa are likely to be best considered under *Aphelandra* (some have already been combined in prior works), hence these genera are here treated within *Aphelandra* s.l. (see also Wasshausen, 1996).

[6] The type of *Neriacanthus*, *N. purdieanus* Benth. & Hook.f., is congeneric with *Salpixantha*. The Central and South American species of "*Neriacanthus*" as keyed out here may need to be accommodated under a new generic name unless *Neriacanthus* is conserved with a different type (see Franck & Daniel, 2015). More molecular work for the continental taxa is needed prior to taxonomic re-assignments.

[7] The five genera allied to *Crabbea* that are considered to be endemic to Madagascar are poorly delimited morphologically and may ultimately be united under a single genus; they are, however, here upheld pending further molecular phylogenetic evidence (see Onjalalaina & Darbyshire, 2016).

[8] Preliminary observations including chemical treatments on leaves of the genus *Podorungia* from Madagascar indicate a potential absence of cystoliths in two species (I. Darbyshire, unpub. data), but further study is needed.

[9] *Haplanthus* has recently been resurrected from *Andrographis* based on morphological characters (Gnanasekaran & al., 2016) but this merits evaluation via phylogenetic analyses of molecular data.

[10] Only the type of *Sphinctacanthus*, *S. griffithii*, is here included in our concept of this genus (see Hansen, 1985b; McDade & al., 2018).

[11] *Andrographis* here includes *Indoneesiella*, which was previously separated on the basis of having 2 ovules per locule (capsule 4-seeded), versus 3 or more ovules per locule (capsule 6–20-seeded) in *Andrographis* s.str. The two are separated in the key to Asian genera as *Indoneesiella* is upheld by some authors.

[12] *Phlogacanthus* here includes *Cystacanthus*; they were previously separated (e.g., in Hu & al., 2011) by differences in the shape of the corolla tube: cylindrical and gradually widened towards the mouth and straight in *Phlogacanthus*, abruptly saccate and geniculate above the middle in *Cystacanthus*. However, emerging molecular evidence indicates that these two genera are congeneric (see Deng & al., 2020).

[13] Genera of Whitfieldiinae are not well circumscribed, particularly in Madagascar where the endemic genera *Camarotea*, *Forcipella*, *Leandriella*, *Vindasia*, and *Zygoruellia* are very close morphologically. These entities may ultimately be best treated under a single genus, and *Zygoruellia* has nomenclatural priority.

[14] An unmatched Malagasy species with corollas similar to *Leandriella* (but lacking long white trichomes on the internal surface of the corolla lobes) has not yet been reliably placed to genus.

[15] We have been unable to uncover any morphological characters to separate *Forcipella* and *Vindasia* (see note 13).

[16] "*Pseudosiphonium* ined." was a tentative descriptor proposed in Tripp & al. (2013a) to accommodate plants from China previously ascribed to *Ruellia venusta* Hance or *Leptosiphonium venustum* (Hance) E.Hossain that differ from the latter in several features. It has not yet been formally described and is here mentioned only within the Key to Genera of Ruellieae. That is, the inclusion of this name in the present study *does not* indicate acceptance of the name by the authors of this paper.

[17] Genera within Strobilanthinae have remained poorly delimited, and phylogenetic evidence (Moylan & al., 2004) suggests *Strobilanthes* is best delimited to include previously segregated genera (i.e., *Clarkeasia*, *Hemigraphis*, and *Stenosiphonium*, which appear to differ from *Strobilanthes* s.str. primarily in having >4 ovules per ovary). As such, we here recognize a broadened concept of *Strobilanthes*—one that includes these three genera. However, we refrain from making a long series of necessary combinations, for which additional, focused, phylogenetic and nomenclatural work outside the scope of the present study will be required.

[18] The lip of *Eremomastax* can sometimes be held in the upper position (i.e., is resupinate) due to twisting of the corolla tube.

[19] *Calacanthus* is resolved as sister to *Acanthopale* in the RADseq results of Tripp & Darbyshire (2020) with strong support and so is tentatively placed within Ruelliinae in the current classification. However, morphological characters point towards a closer affinity to Hygrophilinae (Tripp & al., 2013a). The placement of *Calacanthus* within Ruelliinae should therefore be considered provisional.

[20] *Endosiphon primuloides* T.Anderson ex Benth. was transferred to *Ruellia* by Heine (1966) as they share the same pollen type (spheroid, coarsely reticulate) but the zygomorphic calyx of *Endosiphon* is very close to *Dischistocalyx*, and *E. primuloides* is a forest species like members of *Dischistocalyx* and unlike most African species of *Ruellia*. This species needs to be included in a future phylogenetic analysis to confirm its placement. *Endosiphon* may ultimately need to be resurrected.

[21] "*Sinoacanthus* ined." was a tentative descriptor proposed in Tripp & al. (2013a) to accommodate plants from China previously ascribed to *Echinacanthus* that differ from the latter in several features including pollen morphology. "*Sinoacanthus* ined." has not

yet been formally described and as such is here mentioned only within the Key to genera of Ruellieae. That is, the inclusion of this name in the present study *does not* indicate acceptance of the name by the authors of this paper.

[22] In limited instances, species of *Dyschoriste* lack anther appendages, such as *D. mutica*.

[23] We here include *Ionacanthus* within *Mimulopsis* for the first time, and provide the new combination. In Tripp & al. (2013a), *Ionacanthus* was synonymized within *Mellera*, but subsequent RADseq data (Tripp & Darbyshire, 2020) demonstrated that *Ionacanthus* is instead nested within *Mimulopsis*, with which it more closely aligns morphologically, particularly with regard to stamen morphology.

[24] *Mellera congdonii* Vollesen is excluded from the circumscription of *Mellera* here as it has traits more closely allied to *Mcdadea*; see Tripp & Darbyshire (2020).

[25] Filaments of flowers of *Xylacanthus* were not described in the protologue. However, its morphological affinity to *Strobilanthes* as well as to *Echinacanthus* suggests high likelihood of phylogenetic placement of this lineage within core Ruellieae (i.e., among the subtribes phylogenetically derived with respect to Erantheminae, whose members lack filament curtains except for *Eranthemum* and *Kosmosiphon*). Additionally, although pollen morphology of *Xylacanthus* was not depicted in the protologue, the authors describe it as similar to that of *Echinacanthus* (Averyanov & al., 2018).

[26] This entry refers to *Filetia africana* Lindau, currently treated under *Asystasia lindauiana* Hutch. & Dalziel, but the anthers with offset thecae and the slender racemose thyrse are quite different to other species in *Asystasia*, and show similarities with Asian *Filetia* (for which, see the note in the key to Asian genera).

[27] *Asystasia* is here treated in the broad sense and includes a number of previously separated small genera, including *Salpinctium* and *Asystasiella*. *Asystasia* encompasses considerable variation in inflorescence form, corolla morphology, and pollen type. *Glossochilus* may also be included within *Asystasia* in the future, but we maintain it in this work, pending further molecular analyses.

[28] *Ruellia heterosepala* Benoist from Madagascar would key out here, but is otherwise very different to *Dinteracanthus*, for example, in being largely glabrous, having anisophyllous leaves, and bearing smaller corollas. It is likely to represent an as yet undescribed genus.

[29] Two species of *Mimulopsis* from the Uluguru Mts. of Tanzania, *M. macrantha* (Mildbr.) E.Tripp and *M. marronina* (Vollesen) E.Tripp (previously treated in the segregate genus *Epiclastopelma*), lack spurred outer thecae on the two longer stamens, which are otherwise characteristic of *Mimulopsis*. These two species are morphologically close to *Heteradelphia* and the relationship between these taxa requires further investigation. Note that the type of *Epiclastopelma*, *E. glandulosum* Lindau (= *Mimulopsis volleseniana* E.Tripp & T.F.Daniel), does have spurred anthers and is morphologically similar to some Malagasy species of *Mimulopsis*.

[30] It is not certain that the Malagasy species *Ruspolia humbertii* Benoist is best treated within this genus; it differs from other species of *Ruspolia* in having clearly exserted stamens, a markedly bilabiate corolla with the upper two lobes partially fused, and a curved corolla tube.

[31] *Monothecium leucopterum* Benoist from Madagascar would key here but this species is morphologically very different from the two continental African species, and probably belongs within *Anisostachya*.

[32] *Ritonia* is a poorly known genus and its tribal placement is unclear. The combination of glomerules of flowers each with small subtending clasping pairs of bracteoles and spheroid, 2-porate pollen suggest affinity with Whitfieldiinae but the corollas are unlike anything in that subtribe. The fruits are unknown, and corolla aestivation of *Ritonia* is not clear from specimens. Therefore, potential affinity with Isoglossinae cannot be entirely dismissed. This description refers only to *R. humbertii* Benoist (the type of the genus) and *R. barbigera* Benoist. The other two species described by Benoist are quite different. *Ritonia rosea* Benoist is considered to be a synonym of *Populina perrieri* (Madagascar Catalogue, 2020), while *R. poissionii* Benoist is considered to belong in core Isoglossinae (I. Darbyshire, pers. obs.).

[33] To our knowledge, only one species of *Lepidagathis* in Africa and Madagascar has 2 stamens + 2 staminodes: *L. grandidieri* Benoist from Madagascar.

[34] Stearn (1971) included *Forsythiopsis* from Madagascar within *Oplonia* from the NW. While the two have similar floral morphologies, molecular evidence indicates that they do not form a monophyletic clade (McDade & al., 2021). Morphologically, Malagasy *Oplonia* is similar to *Pseuderanthemum*, particularly to the short-tubed *P. campylosiphon* Mildbr. from Tanzania, differing primarily in inflorescence form.

[35] *Vavara* is very close to *Dicliptera* and may prove to be a member of that genus, but the anther character is a notable morphological difference.

[36] *Peristrophe* is not recognized as separate from *Dicliptera* in this classification but is included in the key here as it is maintained by some scholars. Most Asian members of *Peristrophe* have linear anther thecae, quite different from the elliptic to rounded thecae of *Dicliptera* and African *Peristrophe*. This Asian group of *Peristrophe* may be a distinct taxon.

[37] Molecular evidence places *Anisotes perplexus* T.F.Daniel, Letsara & Martín-Bravo and a second, undescribed species with a matching corolla form from Madagascar in Isoglossinae and this is supported by pollen morphology (Kiel & al., 2017; McDade & al., 2021). The similar corolla form to *Anisotes* in Justiciinae is almost certainly an adaptation to bird pollination in both lineages.

[38] Species currently placed in *Anisotes* and *Metarungia* share the same corolla form, which is likely an adaptation to bird pollination. *Metarungia* is not upheld as distinct from *Anisotes* by some authors, but Kiel & al. (2017) find that members of *Metarungia* form a clade with *Rungia*, with which they share capsules with fracturing placentae.

[39] The genera within core Isoglossinae from Africa and Madagascar with bithecous stamens are not well differentiated and may be best treated as a single genus (*Isoglossa*), but preliminary molecular results indicate that *Isoglossa* is paraphyletic. The Malagasy segregate genera *Celerina*, *Melittacanthus*, and *Sphacanthus* are not keyed out separately here.

[40] Vollesen (1989) noted that in one specimen of *Ecbolium flanaganii* C.B.Clarke (*Comins 1309*) some of the flowers have 2 well-developed staminodes with antherodes in addition to the fertile stamens; however, this appears to be an aberrant specimen.

[41] We have not been able to reliably distinguish *Chorisochora* from *Populina* on morphological grounds, in part because of the variation within each of these two genera. Species of *Chorisochora* from Socotra and Somalia have anthers held ± perpendicular to the filament, unlike in *Populina* where they are parallel or slightly oblique (although becoming more markedly oblique with age). The South African *C. transvaalensis* (A.Meeuse) Vollesen has ± parallel thecae. Daniel & al. (2008) found *P. richardii* Baill., the type of the genus, to be included within a well-supported *Ecbolium* clade and sister to two Malagasy species of *Ecbolium*; they therefore concluded that *P. richardii* should be treated within *Ecbolium*. McDade & al. (2018) placed the second species of *Populina, P. perrieri*, sister to *P. richardii* and confirmed placement with the Ecbolium clade. However, the floral morphology is markedly different to *Ecbolium*, although the broadly ovate, palmately veined leaves are similar to those of some Malagasy species of that genus. The flowers of *P. perrieri* look somewhat different to those of *P. richardii* and are highly reminiscent of *Megalochlamys* but, unlike in *Megalochlamys*, the pollen has pseudocolpi (Muller & al., 1989).

[42] *Meiosperma* and *Pogonospermum* were previously united within *Monechma* or *Justicia* sect. *Monechma*. This group has been the focus of recent phylogenetic and nomenclatural studies

(Darbyshire & al., 2020, in press), which revealed that two separate clades are involved, and that *Monechma* s.str. is a later synonym of *Meiosperma*. Some species of *Justicia* s.l. with smooth seeds may key out to one of the two leads in couplet 105, e.g., *J. crebrinodis* Benoist from Madagascar, but these few exceptions are markedly different morphologically from *Meiosperma* and *Pogonospermum*.

[43] Generic circumscription around OW *Justicia* is problematic and is likely to change significantly in the future (see Kiel & al., 2017). For the present time, we key out only the most commonly segregated genera.

[44] *Filetia* is only doubtfully distinct from *Asystasia*. To date, only one species (*F. ridleyi* C.B.Clarke) has been included in a phylogenetic study (McDade & al., 2021) and it was resolved to be nested within the *Asystasia* clade.

[45] The tubular calyx is variable in *Phialacanthus*; it is most striking in the type from India, *P. griffithii* Benth. & Hook.f., where the lobes are shorter than the tube. Species with a more deeply divided calyx such as *P. minor* C.B.Clarke appear very similar to *Asystasia*.

[46] Plants that key here were formerly treated in the genus *Clarkeasia*, which is now considered a synonym of *Strobilanthes*.

[47] Plants that key here were formerly treated in the genus *Stenosiphonium*, which is now considered a synonym of *Strobilanthes*.

[48] This refers only to *Xerothamnella parvifolia* C.T.White; the second species in the genus is keyed elsewhere.

[49] Generic delimitation in Graptophyllinae in Asia (and indeed globally) is not well circumscribed and there are likely to be fewer genera than currently recognized in couplets 53–58 here.

[50] Most species of *Graptophyllum* have large, bird-adapted corollas (see key), but at least three species from Australia, New Guinea, and Fiji have much smaller, likely insect-pollinated flowers.

[51] *Jadunia racemiflora* Bremek. from New Guinea would also key out here; it clearly does not belong within *Jadunia* s.str., which is a member of Monotheciinae and lacks staminodes (see key), but the generic placement of *J. racemiflora* within Graptophyllinae remains uncertain.

[52] This refers only to *Xerothamnella herbacea* R.M.Barker; the second species in the genus is keyed elsewhere.

[53] Hansen (1985a) assigned several species with tricolporate-pseudocolpate pollen to *Isoglossa*; he later transferred some of these to *Ptyssiglottis* but others currently remain in *Isoglossa*. We consider these unlikely to be correctly placed here.

[54] This refers only to *Jadunia biroi* Lindau; see [61] regarding the second species treated in *Jadunia*, which is not considered to be closely related to *J. biroi*.

[55] Hu & al. (2011) in *Flora of China* suggest that *Kudoacanthus* may not be distinct from *Leptostachya*.

[56] Although not included in the NW key, some species of *Thunbergia*, e.g., *T. alata* Bojer ex Sims and *T. fragrans* Roxb., are naturalized in the Neotropics and, in some locations, extremely weedy; these would key here with *Mendoncia*, if included, and can be readily separated from the latter genus by fruit type.

[57] Whether *Nelsonia* is native or not in the NW remains unresolved.

[58] We follow Kameyama (2008), who provided the combinations necessary for recognizing species formerly ascribed to *Lophostachys* within *Lepidagathis*.

[59] *Hygrophila* remains a rather poorly studied genus; as such, the full range of variation of pollen morphology in this genus remains to be fully understood.

[60] Generic inconsistencies and species with characteristics intermediate between several genera of American Graptophyllinae (e.g., *Pseuderanthemum*, *Odontonema*, *Chileranthemum*, *Pulchranthus*, *Oplonia*) have been noted by several authors (e.g., Baum, 1982; Daniel, 1995; Daniel & Carrión, 2015; Stearn, 1971). Molecular phylogenetic studies (McDade & al., 2021) of these and other morphologically similar genera in that subtribe (e.g., *Psilanthele*, *Pulchranthus, Sapphoa*) reveal that several of the larger genera (*Graptophyllum*, *Oplonia*, *Pseuderanthemum*) are not monophyletic as currently circumscribed. These authors indicated that taxa and clades of Graptophyllinae are in need of considerable additional taxonomic and phylogenetic research to resolve monophyletic genera in that subtribe.

[61] It remains to be confirmed that two species of *Oplonia* occurring in South America (i.e., *O. grandiflora* (Lindau) Stearn and *O. hutchisonii* Wassh.) are correctly placed generically, although a third South American species, *O. jujuyensis* Wassh. & Ezcurra, is confirmed to belong in the Oplonia clade (McDade & al., 2021).

[62] American genera of Isoglossinae (e.g., *Kalbreyeriella*, *Sebastiano-Schaueria*, *Stenostephanus*, *Razisea*) are not distinct either as currently circumscribed or based on current taxonomic compositions of species (see discussions by, e.g., Leonard, 1958; Daniel, 1999; Wood, 2009; McDade & al., 2018), but *Sebastiano-Schaueria* is retained tentatively here, pending further study.

[63] The linked or isolated "insulae" in *Poikilacanthus* cover the entire interapertural surface (cf. Daniel, 1991: fig. 1; Daniel, 1998).

[64] Preliminary molecular phylogenetic studies (McDade & al., 2018) suggest that most (or all) of the NW genera of Justiciinae (e.g., *Cephalacanthus*, *Clistax*, and excluding *Dicliptera*; couplets 46–52) are likely not distinct from *Justicia* in the broad sense in which that genus is currently recognized. Additionally, based on molecular phylogenetic data (Kiel & al., 2018) from two of the three species of *Clistax*, this genus does not appear to be monophyletic.

[65] In his treatment of Nicaraguan Acanthaceae, Durkee (2001) suggested that *Perenideboles* Ram.Goyena is likely to be a synonym of *Megaskepasma* based on descriptive information in the protologue, but there is no indication in the protologue of the specimens seen by M. Ramírez Goyena. We follow Durkee's suggestion here.

[66] *Harpochilus* is now restricted to two species both of which have bat-pollinated flowers fide da Costa-Lima & de Oliveira Chagas (2019).

[67] Based on information available, no characters are known to distinguish *Dichazothece* (Brazil) from *Justicia* and it may belong here, but further research is required; this genus was recognized by Scotland & Vollesen (2000). Monospecific *Tessmanniacanthus* from Peru very likely pertains to *Justicia* (or possibly Tetrameriinae), but characters that might confirm its placement are not evident either via characters noted in the protologue or on images of type specimens at G and NY. It is not keyed out separately here, but is tentatively retained in our classification.

[68] South American species described in *Thyrsacanthus*, *Pachystachys*, and *Schaueria* remain in need of additional studies. Côrtes & al. (2016a) and McDade & al. (2018) note some of the remaining problems among clades containing species placed in these (and other) genera.

[69] Species previously recognized as *Streblacanthus* (excluding *S. monospermus* Kuntze; see Côrtes & al. 2016b).

[70] Molecular phylogenetic data suggest that the southern Mexican wet-forest species *Mirandea sylvatica* Acosta is not closely related to northern Mexican species of this genus, which occur in arid communities (Kiel & McDade, 2014).

[71] Molecular phylogenetic data suggest that *Schaueria parviflora* (Leonard) T.F.Daniel is not closely related to the South American species of *Schaueria* (Côrtes & al., 2015; McDade & al., 2018).

IV. Validation of names (tribes, subtribes, genera)

Below, we propose one new tribe (Physacantheae) and three new subtribes (Lankesteriinae, Whitfieldiinae, Tetrameriinae) of Acanthaceae along with their validating descriptions. We also provide emended descriptions for two resurrected and recircumscribed subtribes in Justicieae: Graptophyllinae and Monotheciinae. Finally, a note on the correct name for the tribe Barlerieae is provided.

Physacantheae E.Tripp & I.Darbysh. **tr. nov.** – Type: *Physacanthus* Benth.

= Haselhoffiinae Lindau in Engler & Prantl, Nat. Pflanzenfam., Nachtr. 1: 305. 1897 – Type: *Haselhoffia* Lindau (= *Physacanthus*).

Trailing, decumbent or weakly erect herbs, cystoliths absent; leaves opposite but sometimes closely spaced and rosette-forming, often variegated; inflorescences terminal, 1- to several-flowered; calyces cylindrical or inflated, lobes fused for most of their length; corolla white to purple, tube narrowly cylindrical, geniculate at apex, limb subactinomorphic with 5 equal lobes, aestivation left-contort; androecium of 4 stamens with monothecous anthers plus 1 staminode; stigma clavate, 2-lobed; capsule cylindrical, (4–) 6–9-seeded, retinacula present, seeds with papillose processes on the surface; pollen with compound germinal apertures, prolate, 3-colporate with 3 interapertural pseudocolpi.

Barlerieae Nees in Martius, Fl. Bras. 9: 7, 65. 1847 – Type: *Barleria* L.

= Russeggereae Meisn., Pl. Vasc. Gen., Tab. Diagn.: 293 & Comm.: 202. 1840 – Type: *Russeggera* Endl. (= *Lepidagathis* Willd.).

Perennial, herbs, shrubs or rarely small trees, with cystoliths, these sometimes occurring in adjacent cells to form "double cystoliths"; leaves opposite, sometimes subrosulate; inflorescences terminal or axillary, varying from flowers solitary to held in complex dichasial or monochasial cymes or thyrses; flowers subtended by paired bracteoles, bracts and/or bracteoles inconspicuous or conspicuous, sometimes with multiple whorls of bracts subtending the flowers; calyces varying from equally to highly unequally 5-lobed or reduced to 4 highly unequal lobes through fusion of the anterior pair of lobes; corollas variable in size, shape and color, strongly bilabiate to subactinomorphic, rugula absent, aestivation quincuncial (i.e., lateral lobes outermost in bud); androecium either of 4 stamens, then didynamous to strongly so, or of 2 stamens plus 2–3 staminodes, anthers in taxa with 2 stamens bithecous, anthers in taxa with 4 stamens either all bithecous or with 2 pairs bithecous and 2 pairs monothecous, thecae in bithecous stamens ± equally inserted on filament, parallel or slightly sagittate, with or more often without short basal appendages; stigma either 2-lobed or with only 1 lobe developing, this either linear or enlarged and flattened; capsule fusiform or conspicuously rostrate, or sometimes stipitate, 2–4-seeded, retinacula present, without fracturing placentae; seeds discoid to lenticular, surfaces often covered in hygroscopic trichomes, these rarely sparse or absent; pollen variable, frequent forms include (1) globose, 3-porate or 3-colporate with a coarsely reticulate exine, (2) prolate, 3-colporate with a finely reticulate exine, or (3) globose to subprolate 3-porate (to 6-porate), with a gemmate, verrucose or rugose sculpturing of the exine.

Note. – The tribal name Russeggereae predates Barlerieae by seven years and so has nomenclatural priority. Russeggereae was described by Meisner to accommodate two genera described by Endlicher, *Russeggera* (= *Lepidagathis*) and *Schwabea*, the latter of which is an excluded name in the current classification. This name has never been used since its first description, whereas the name Barlerieae has been applied frequently to this tribe as currently circumscribed (e.g., Manktelow & al., 2001; McDade & al., 2008; Champluvier & Darbyshire, 2012; Darbyshire & al., 2019a,c; Comito & al., in rev.), and a comparison of citations on Google Scholar reveals 124 references to Barlerieae but 0 references to Russeggereae. There is no option under the *Code* (Turland & al., 2018) to conserve names between the ranks of family and genus, but under Art. 56, rejection of a name at any rank can be proposed. The current authors are therefore preparing a proposal to reject the name Russeggereae, given that abandoning Barlerieae would be a "disadvantageous nomenclatural change" (Art. 56.1). In the meantime, we maintain Barlerieae over Russeggereae in the current classification. A description of Barlerieae is provided above to clarify the circumscription of this tribe.

Lankesteriinae I.Darbysh. & E.Tripp **subtr. nov.** – Type: *Lankesteria* Lindl.

Perennial herbs or shrubs with cystoliths; leaves opposite; inflorescences of dense terminal spikes or thyrses, often with conspicuous imbricate bracts or the bracts linear in some species, paired bracteoles linear and inconspicuous; corolla yellow, orange, or white, salverform, subactinomorphic or with sinus between the two adaxial lobes at a wider angle than the other lobe sinuses, with trifurcating traces to the lobes, filament curtain absent, aestivation left-contort; androecium of 2 stamens plus (typically) 2 staminodes, anthers bithecous, thecae inserted equally on the filament and held at an equal height; stigma capitate, the lobes oblique; capsule 2-seeded, seeds with hygroscopic trichomes covering the surfaces, surface with concentric rings of ridges, the trichomes attached to (and hiding) these ridges (fide Manktelow & al., 2001); pollen 3-porate, triangular in polar view with flattened apertural faces, pores surrounded by a granular circular area, interapertural areas otherwise reticulate.

Whitfieldiinae I.Darbysh. & E.Tripp, **subtr. nov.** – Type: *Whitfieldia* Hook.

Perennial herbs or shrubs with cystoliths; leaves opposite; inflorescences variously spiciform or racemoid thyrses, sometimes compounded into a panicle, or fasciculate, glomerulate or shortly umbellate; individual flowers or floral units subtended by paired bracts (or bracteoles), these often conspicuous, clasping and sometimes partially connate at least in bud; calyces equally to somewhat unequally 5-lobed; corolla ranging from subactinomorphic to bilabiate, with traces trifurcating in the lobes, filament curtain absent, aestivation left-contort (also reported as ascending-cochlear but this not observed by the current authors); androecium of 4 stamens (rarely reduced to 2 stamens plus 2 staminodes in some flowers), with or without an additional staminode, anthers bithecous, thecae inserted equally on the filament and held at an equal height; stigma capitate, the lobes symmetrical; capsule 2- to 4-seeded, seeds (where known) with concentric rings of coarse scales at least towards margin, surfaces lacking trichomes; pollen lenticular, 2-pororate, with a pronounced marginal girdle (this typically psilate), or rarely globose and pantoforate, areas around the pores granular or micro-echinate.

Note. – If *Ritonia* Benoist proves to be a member of Whitfieldiinae, then the description of the androecium must be modified to include 2 stamens plus 2 staminodes as a non-aberrant trait.

Tetrameriinae T.F.Daniel, Kiel & McDade, **subtr. nov.** – Type: *Tetramerium* Nees.

Perennial herbs or shrubs with cystoliths; leaves opposite; inflorescences in 1- to many-flowered dichasia, these borne in leaf axils or in axils of bracts along spikes, racemes, or thyrses, which are sometimes branched into panicles, flowers subtended by paired bracteoles, bracts and/or bracteoles inconspicuous or conspicuous; corollas variable in size, shape and color, rugula absent; androecium of 2 stamens and no staminodes (4 stamens in *Chalarothyrsus*), anthers bithecous (monothecous in *Clinacanthus*), thecae of a pair equally or subequally inserted on filament, parallel to sagittate, lacking basal appendages; stigma usually 2-lobed; capsule clavate, 2–4-seeded, retinacula present and usually not separating from inner capsule wall at maturity (separating slightly in *Henrya* and *Tetramerium*); seeds distinct and expelled from capsule on dehiscence (indistinct by fusion with retinacula and capsule wall, and not expelled from capsule valves in *Aphanosperma* and *Chalarothyrsus*); seeds compressed, surfaces and margin smooth or variously ornamented, trichomes usually absent (hygroscopic trichomes present in *Henrya insularis*); pollen usually 3-colporate, 6-pseudocolpate (see Daniel & al., 2008 for rare variants).

Graptophyllinae T.Anderson in J. Proc. Linn. Soc., Bot. 7: 17. 1863, **emend.** Kiel, McDade, I.Darbysh. & T.F.Daniel – Type: *Graptophyllum* Nees.

Perennial (rarely annual) herbs or shrubs or small trees with cystoliths; leaves opposite; inflorescences terminal to axillary, form highly variable, inflorescences consisting of 1- to many-flowered dichasia in leaf axils or in axils of bracts in axillary and/or terminal spikes, racemes, or thyrses (or, when branched, in panicles of these), flowers subtended by paired bracteoles, bracts and/or bracteoles inconspicuous or conspicuous; corollas variable in size, shape and color, bilabiate to only weakly zygomorphic, rugula absent; androecium either of 4 stamens or of 2 stamens plus 2 staminodes, 2 pairs of stamens (or pairs comprising 1 stamen plus 1 staminode) sometimes with filaments basally fused, anthers in taxa with 2 stamens either bithecous or monothecous, anthers in taxa with 4 stamens either all bithecous or with 1 pair bithecous and 1 pair monothecous, thecae of a pair subequally or unequally inserted on filament, parallel or slightly oblique, with or without short basal appendages; stigma usually bilobed, but sometimes subfunnelform (e.g., some *Chileranthemum*); capsule clavate, (2–) 4-seeded, retinacula present and not separating from inner capsule wall at maturity; seeds (where known) discoid to lenticular, surfaces variously ornamented or smooth, trichomes absent; pollen most frequently prolate and 3-colporate, 6-pseudocolpate but can be 4-colporate, 8-pseudocolpate or sometimes 4-por(or)ate and echinate (in *Isotheca* and some *Herpetacanthus*).

Monotheciinae Lindau in Bot Jahrb. Syst. 18: 56. 1893, **emend.** Kiel, I.Darbysh. & T.F.Daniel – Type: *Monothecium* Hochst.

Perennial herbs, shrubs or small trees with cystoliths; leaves opposite, isophyllous to strongly anisophyllous; inflorescences varying from terminal to axillary or sometimes ramiflorous or cauliflorous, inflorescence form highly variable, ranging from open dichasia to spicate or paniculate thyrses, to contracted few-branched dichasia or flowers solitary, flowers subtended by paired bracteoles, bracts and/or bracteoles inconspicuous or conspicuous; corollas variable in size, shape and color, bilabiate, upper lip often hooded, rugula absent, lower lip often with 2 raised ridges and a central furrow running into the throat; androecium of 2 stamens and no staminodes (except in *Ptyssiglottis staminodifera* where 2 staminodes present), anthers bithecous or (*Monothecium* only) monothecous, thecae of a pair subequally or unequally inserted on filament, parallel or slightly oblique, with or more commonly without basal appendages; stigma 2-lobed; capsule (where known) clavate, 4-seeded, retinacula present and not separating from inner capsule wall at maturity; seeds (where known) lenticular, surfaces variously ornamented, often tuberculate, trichomes absent; pollen most frequently prolate and 3-colporate, 6-pseudocolpate but with variation up to 4- or 5-colporate, 8- or 10-pseudocolpate, and also spheroidal pantoporate.

Below, we validate names for two genera from Madagascar that have been applied in the literature and in various databases for several decades now but were not validly published at the time of original description. The status of these genera within the classification of Acanthaceae remains to be further researched. These validations thus serve to facilitate future discussion. Small diagnostic descriptions are provided to aid identification of these two poorly known taxa; full descriptions are available in the original publications (Benoist, 1962).

Dolichostachys Benoist, **gen. nov.** – Type: *Dolichostachys elongata* Benoist, sp. nov.

Validating description in Bull. Soc. Bot. France 109: 133. 1962.

Resembling *Populina* Baill. and allied genera in Tetrameriinae but differing in the very short corolla tube 4.5 mm long (fide Benoist, 1962), in the broad, elliptic upper lip of the corolla with a rounded apex, and in the long, narrowly elliptic leaves 11–15 cm long when mature.

Dolichostachys elongata Benoist, **sp. nov.** – Holotype: Madagascar: Fénérive, fl. 1912, *Perrier de la Bâthie 9448* (P [P00089215]*).

Validating description in Bull. Soc. Bot. France 109: 133. 1962.

Additional material seen. – Madagascar, R. Mananara, fl. Aug. 1912, *Perrier de la Bâthie 9445* (P [P00089214]*).

Notes. – When describing *Dolichostachys elongata*, Benoist (1962) cited the two specimens listed above but did not designate a type specimen, thus the names of the genus and species were not validly published under Art. 40 of the *Code* (Turland & al., 2018). This is rectified here by selection of a type specimen. As Benoist provided full descriptions for the genus and species (in Latin), the names can continue to be attributed to him but with priority from the present publication.

Dolichostachys remains unplaced within Justicieae. The combination of an androecium comprising two stamens with parallel thecae and (apparently) lacking staminodes, a 2-lipped corolla with the lower lip deeply divided into 3 lobes and lacking raised venation in the throat, and a slender spiciform inflorescence suggests possible affinity to Tetrameriinae, but Isoglossinae cannot be ruled out. Benoist (1962) described the pollen as spherical and smooth with three pores. Triporate pollen is observed in some Isoglossinae, notably in *Brachystephanus* (Champluvier & Darbyshire, 2009), but in those cases the grains are still conspicuously “girdled” as in other Isoglossinae. It is possible that Benoist misinterpreted this pollen type.

Vavara Benoist, **gen. nov.** – Type: *Vavara breviflora* (Benoist) Benoist ex I.Darbysh. & E.Tripp, comb. nov.

Validating description in Bull. Soc. Bot. France 109: 134. 1962.

Resembling *Dicliptera* Juss. in its corolla tube twisted through ±180° resulting in a resupinate corolla limb and sternotribic flower but differing in the anther thecae of each stamen being widely separated by long extension of the anther connective (versus thecae immediately superposed or slightly overlapping).

Vavara breviflora (Benoist) Benoist ex I.Darbysh. & E.Tripp, **comb. nov.** ≡ *Rhinacanthus breviflorus* Benoist in Notul. Syst. (Paris) 12: 140. 1946 – **Lectotype (designated here):** Madagascar, bassin supérieur du Mandrare (Sud-Est), col de Vavara, fl. 10 Nov 1928, *Humbert 6532* (P [P00089211]*; isolectotypes: BM [BM013867026]!, K [K000378866]!, P [P00089210]*, TAN [TAN000434]*).

Additional material seen. – Madagascar, chaine du Vohibory (a l’ouest d’Ivohibe), fl. 1 Nov 1924, *Humbert 3071* (P [P00089213]*); Prov. de Farafangana, entre Vondrozo et Ivohibe, fl. 18 Sep 1926, *Decary 5373* (P [P00089212]*).

Notes. – Benoist (1946) described *Rhinacanthus breviflorus* based on three collections (*Decary 5373*; *Humbert 3071*, *6532*) of which he designated *Humbert 6532* as the type. As there are several specimens of this gathering, we designate (above) one of those at P as lectotype. When Benoist (1962) later described his new genus *Vavara* containing the single species *V. breviflora*, he failed to record that it was based on *R. breviflorus* despite citing the same three collections (without any type designation on this occasion). Therefore, *Vavara* was not validly published under Art. 41 of the *Code* (Turland & al., 2018). This is rectified here by formalizing the new combination.

Vavara breviflora closely resembles some species of *Dicliptera*, most notably in corolla morphology, but the unique arrangement of the anthers with the two thecae widely separated by 0.8–1 mm appears to be diagnostic. Benoist (1946) recorded the corolla as being sulphur-yellow, which would be an additional diagnostic character, as *Dicliptera* has corollas that range from white to purple or red. However, on *Decary 5373*, the flower color is recorded as “white, slightly pink”. We therefore consider it likely that Benoist’s (1946) record of the flower color is erroneous. We are confident that this genus belongs within Justicieae-Justiciinae but molecular data are needed to reveal its position in relation to *Dicliptera* and allied genera.

V. New synonymies and combinations (species)

Below we provide new combinations and synonymies in support of the proposed classification. Numerous other actions (e.g., subsequent combinations at the species level) remain to be advanced, pending further study, for example the many new combinations needed in the expanded concept of *Strobilanthes*.

Asystasia Blume in Bijdr. Fl. Ned. Ind.: 796. 1826 – Type: *Asystasia intrusa* (Forssk.) Blume (= *A. gangetica* (L.) T.Anderson subsp. *micrantha* (Nees) Ensermu).

Salpinctium was separated from *Asystasia* by Edwards & Getliffe Norris (1989) on the basis of having compressed bicolporate pollen and an elongate linear corolla tube. However, Ensermu & al. (1992) noted that bicolporate pollen is also recorded in at least one species of *Asystasia* in Africa, and pollen is quite variable in the genus. Whilst the corolla tube in *Asystasia* is usually infundibuliform, the length and width of the tube is variable and in *A. vogeliana* from West and Central Africa it is long and slender. *Salpinctium* was not upheld by Ensermu & Vollesen (in Darbyshire & al., 2015) and this decision is followed here. Combinations in *Asystasia* are already available for two of the three species treated in *Salpinctium* by Edwards & Getliffe Norris (1989); below we make the new combination for the third species, which is endemic to Eswatini.

Asystasia hirsuta (T.J.Edwards) I.Darbysh. & E.Tripp, **comb. nov.** ≡ *Salpinctium hirsutum* T.J.Edwards in S. African J. Bot. 55: 9. 1989 – Holotype: Eswatini, 3 miles S of Stegi, fl. 25 Nov 1958, *Compton 28397* (PRE [PRE0130612-0]*).

Aphelandra R.Br. in Prodr.: 475. 1810 – Type: *Aphelandra cristata* (Jacq.) R.Br. ex W.T.Aiton (= *A. pulcherrima* (Jacq.) Kunth).

= *Orophochilus* Lindau in Bull. Herb. Boissier 5: 657. 1897, **syn. nov.** – Type: *Orophochilus stipulaceus* Lindau.

= *Rhombochlamys* Lindau in Bull. Herb. Boissier 5: 659. 1897, **syn. nov.** – Type: *Rhombochlamys rosulata* Lindau (≡ *Aphelandra rosulata* (Lindau) Wassh.).
= *Encephalosphaera* Lindau in Bull. Herb. Boissier, ser. 2, 4: 322. 1904, **syn. nov.** – Type: *Encephalosphaera vitellina* Lindau.

Although not sampled phylogenetically in McDade & al. (2005), the monospecific genus *Orophochilus* is allied to spiny members of *Aphelandra*. As such, we provide the necessary combination below.

The genus *Rhombochlamys* was shown by McDade & al. (2005) to be nested within *Aphelandra* with strong bootstrap support, even though placed phylogenetically by only a single locus. Nonetheless, those data in combination with morphological attributes discussed in McDade & al. (2005) suggest that *Rhombochlamys* belongs within *Aphelandra*, and we provide the necessary combination below. Note that *R. rosulata* Lindau was previously transferred into *Aphelandra* by D. Wasshausen in 1996.

The genus *Encephalosphaera* was shown by McDade & al. (2005) to be nested within *Aphelandra* with strong bootstrap support. As such, we provide the necessary combinations for all species here. Note that no new combination is needed for *Encephalosphaera puberula* (Leonard) Wassh., as this was first published under *Aphelandra puberula* Leonard.

The genus *Xantheranthemum* was previously included within *Aphelandra* (Wasshausen, 1996), which we follow here.

Aphelandra elata (Lindau) McDade & E.Tripp, **comb. nov.** ≡ *Rhombochlamys elata* Lindau in Bull. Herb. Boissier 5: 661. 1897 – Holotype: Colombia, prov. Cauca, über La Vitrera bei Palmira, fl. 17 Jun 1883, *Lehmann 2891* (B†, photo at F [neg. no. 8723]*; isotype: G [G00226595]*).

Aphelandra lasiandra (Mildbr.) McDade & E.Tripp, **comb. nov.** ≡ *Encephalosphaera lasiandra* Mildbr. in Notizbl. Bot. Gart. Berlin-Dahlem 11: 68. 1930 – Holotype: Brazil, Rio Acre, Seringal Saraguassu, fl. Feb 1911, *Ule 9810* (B†, photo at F [neg. no. 8721]*; isotype: K [K000534546]!).

Aphelandra stipulacea (Lindau) McDade & E.Tripp, **comb. nov.** ≡ *Orophochilus stipulaceus* Lindau in Bull. Herb. Boissier 5: 658. 1897 – Holotype: Peru, Peruviae orientalis, prope Tarapoto, fl., 1855–1856, *Spruce 4324* (B†, photo at F [neg. no. 8720]*; isotypes: BR [000006951306]*, C [C10005068]*, G [G00236408]*, GH [00094151, 00094152]*, K [K000202098, K000202099]!, NY [00312235]*, P [P00719696]*).

Aphelandra vitellina (Lindau) McDade & E.Tripp, **comb. nov.** ≡ *Encephalosphaera vitellina* Lindau in Bull. Herb. Boissier, ser. 2, 4: 323. 1904 – Holotype: Colombia, Prov. Popayan, "prope Agua Clara in Andibus occidentalis", fl. Jan 1899, *Lehmann 9048* (B†, photo at F [neg. no. 8722]*; isotypes: K [K000534568]!, NY [00311968]!).

Mimulopsis Schweinf. in Verh. K. K. Zool.-Bot. Ges. Wien 18: 677. 1868 – Type: *Mimulopsis solmsii* Schweinf.
= *Ionacanthus* Benoist in Notul. Syst. (Paris) 9: 65. 1940, **syn. nov.** – Type: *Ionacanthus calcaratus* Benoist.

The Malagasy monospecific genus *Ionacanthus* was synonymized with *Mellera* by Tripp & al. (2013a) on the basis of phylogenetic data derived from Sanger sequencing but was later included within a RADseq dataset (Tripp & Darbyshire, 2020) where it was resolved within *Mimulopsis* (including *Epiclastopelma*). This latter result better aligns with morphological features, as *Ionacanthus* shares with *Mimulopsis* the unique arrangement of the anthers in which the outermost theca of each of the longer pair of stamens has a conspicuous curved appendage, while the other thecae have much shorter appendages or lack appendages. *Ionacanthus* is therefore here transferred to *Mimulopsis*.

Mimulopsis calcarata (Benoist) E.Tripp & I.Darbysh., **comb. nov.** ≡ *Ionacanthus calcaratus* Benoist in Notul. Syst. (Paris) 9: 65. 1940 ≡ *Mellera calcarata* (Benoist) E.Tripp in Int. J. Pl. Sci. 174: 128. 2013 – Holotype: Madagascar, massif du Tsaratanana et haute vallée du Sambirano (réserve naturelle no. 4), fl. & fr. Nov–Dec 1937, *Humbert 18317* (P [P00435417]*; isotypes: K [K000394123]!, P [P00435418]*, TAN [TAN000225]*).

Stenandriopsis S.Moore in J. Bot. 44: 153. 1906 – Type: *Stenandriopsis thompsonii* S.Moore.
= *Achyrocalyx* Benoist in Bull. Soc. Bot. France 76: 1036. 1930, **syn. nov.** – Type: *Achyrocalyx decaryi* Benoist.

Vollesen (1992) transferred OW species previously treated within *Stenandriopsis* to *Stenandrium*, which had previously been treated as a NW genus, citing a lack of morphological evidence for their separation. However, the NW and OW clades are clearly separated phylogenetically (McDade & al., 2005) and so *Stenandriopsis* is resurrected here. Combinations are available for all but two of the species of OW *Stenandrium*; as such, the new combinations are made below.

McDade & al. (2005) sampled one of the three species of *Achyrocalyx* in their phylogenetic analysis of Acanthoideae and found it to be resolved within the *Stenandriopsis* clade, related to the two sampled species of Malagasy *Stenandriopsis*. *Achyrocalyx* was separated from *Stenandriopsis* by Benoist (1930) on the basis of having a bilabiate corolla versus corolla with five subequal lobes. However, McDade & al. (2005) noted that several species of *Stenandriopsis* have a zygomorphic corolla and, further, that plants of *Achyrocalyx* share with Malagasy *Stenandriopsis* the character of having leaves in pseudowhorls, a trait that Vollesen (1992) used in placing African and Malagasy species of *Stenandriopsis* into different sections. Hence, *Achyrocalyx* is best placed in *Stenandriopsis* and the new combinations are made here.

Stenandriopsis decaryi (Benoist) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Achyrocalyx decaryi* Benoist in Bull. Soc. Bot. France 76: 1037. 1930 – Holotype: Madagascar, district d'Ambovombe, Ampasimpolaka, fl. 10 Jun 1924, *Decary 2819* (P n.v.; isotypes: P n.v.).

= *Achyrocalyx vicinus* Benoist in Notul. Syst. (Paris) 8: 153. 1939 – Holotype: Madagascar, environs de Tuléar, fl. 7 Aug 1928, *Humbert & Swingle 5215* (P n.v.; isotypes: G [G00008600]*, K [K000394662]!, LISC [LISC 011410]*, US [00664183]*).

Stenandriopsis grandiflora (Vollesen) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Stenandrium grandiflorum* Vollesen in Kew Bull. 55: 967. 2000 – Holotype: Tanzania, Southern Udzungwa Escarpment, Kihansi River Gorge, fl. & fr. 22 Jun 1995, *Lovett 5053* (K [K000394700]!; isotypes: DSM n.v., NHT [NHT000000436]*).

Stenandriopsis gossypina (Benoist) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Achyrocalyx gossypinus* Benoist in Notul. Syst. (Paris) 8: 154. 1939 – Holotype: Madagascar, Manampetsa, fl. Apr 1933, *Perrier de la Bâthie 19185* (P [P00089282]*; isotype: P [P00089283]*).

Stenandriopsis pauciflora (Vollesen) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Stenandrium pauciflorum* Vollesen in Kew Bull. 47: 201. 1992 – Holotype: Madagascar, le long de la piste d'Ampanihy à Ampotaka, fl. Mar 1960, *Keraudren 902* (P [P00083699]*; isotypes: K [K000394697]!, P [P00083700]*).

Stenandriopsis pungens (Benoist) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Achyrocalyx pungens* Benoist in Notul. Syst. (Paris) 12: 11. 1945 – Holotype: Madagascar, plateau de Miandraraha dans le bassin du Manombo, fl. May 1910, *Perrier de la Bâthie 9507* (P [P00089284]*; isotypes: P [P00089285, P00089286]*).

Stenostephanus Nees in Martius, Fl. Bras. 9: 91. 1847 – Type: *Stenostephanus lobeliiformis* Nees.

= *Kalbreyeriella* Lindau in Notizbl. Bot. Gart. Berlin-Dahlem 8: 143. 1922, **syn. nov.** – Type: *K. rostellata* Lindau.

Kalbreyeriella has been distinguished from morphologically similar genera (i.e., most NW Isoglossinae, which are now included in *Stenostephanus*) by the combination of its spicate inflorescences, rostrate corolla buds, relatively long and narrow upper lip of the corolla, and triangular and apically acute (minutely 3-lobed) lower lip of the corolla (e.g., Leonard, 1958; Wasshausen, 2013). However, based on morphological similarities, species of *Razisea* and *Kalbreyeriella* have been suggested as better placed in *Stenostephanus* (Daniel, 1999). Phylogenetic results of Kiel & al. (2006) support the inclusion of *Kalbreyeriella* in *Stenostephanus*. *Stenostephanus* can be characterized by bilabiate, more or less tubular corollas lacking a rugula, two stamens with monothecous anthers, these held with the style adjacent to the upper lip of the corolla, staminodia lacking, and capsular fruits with the retinacula remaining attached to the fruit wall. These plants also share pollen that is banded or "girdled" (i.e., "Gürtelpollen" sensu Lindau, 1895). More recently, McDade & al. (2019) subsumed a species of Costa Rican *Kalbreyeriella* into *Stenostephanus*.

Stenostephanus cabrerae (Leonard) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Kalbreyeriella cabrerae* Leonard in Contr. U. S. Natl. Herb. 31: 408. 1958 – Holotype: Colombia, Putumayo, Mocoa and vicinity, fl. & fr. 16 Mar 1953, *Schultes & Cabrera 19093* (US [00136986]*).

Stenostephanus gigas (Leonard) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Kalbreyeriella gigas* Leonard in Contr. U. S. Natl. Herb. 31: 412. 1958 – Holotype: Colombia, Putumayo, entre Achipayacoy Mocoa, fl. & fr. 25 Dec 1940, *Cuatrecasas 11271* (US [00136987]*; isotypes: COL [COL000004528]*, F [V0047452F = No. 1334109]*).

Stenostephanus rostellatus (Lindau) T.F.Daniel, McDade & Kiel, **comb. nov.** ≡ *Kalbreyeriella rostellata* Lindau in Notizbl. Bot. Gart. Berlin-Dahlem 8: 143. 1922 – Holotype: Colombia, Dep. Antioquia, Plateado, fl. 31 Mar 1880, *Kalbreyer 1524* (B†, photo at F [neg. no. 8801]*; isotype: K [K000529532]!).

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EAMT and ID conceptualized the project. EAMT, ID, and TFD wrote the manuscript and keys. EAMT, ID, TFD, CAK, and LAM revised the manuscript. — EAMT, https://orcid.org/0000-0001-9340-8723; ID, https://orcid.org/0000-0002-5514-9561, i.darbyshire@kew.org; TFD, https://orcid.org/0000-0002-4497-0506, tdaniel@calacademy.org; CAK, https://orcid.org/0000-0002-6773-2519, carrie.kiel@cgu.edu; LAM, https://orcid.org/0000-0001-6504-8775, lucinda.mcdade@cgu.edu

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Appendix 1. List of accepted genera and generic synonyms based on the present reclassification. Some of the synonyms included below are illegitimate or not validly published but we include them here because they have been mentioned in relevant literature.

Key: (Ac), Acantheae; (An), Andrographideae; (Av), Avicennioideae; (B), Barlerieae; (J), Justicieae; (Nel), Nelsonioideae; (Neu), Neuracantheae; (P), Physacantheae; (Ru), Ruellieae; (T), Thunbergioideae; (W), Whitfieldieae; (IS), Incertae sedis.
Bold italics refers to genera recognized in the present work; *italics* refers to genera treated as synonyms in the present work.
* change in generic status since Scotland & Vollesen (2000); ** not recorded by Scotland & Vollesen (2000).

Acanthodium Delile = ***Blepharis***
Acanthodus* Raf. = ***Acanthus
Acanthopale C.B.Clarke (Ru)
Acanthopsis Harv. (Ac)
Acanthostelma* Bidgood & Brummitt = ***Crabbea*
Acanthura* Lindau = ***Lepidagathis*
Acanthus L. (Ac)
Acelica Rizzini = ***Justicia***
Achyrocalyx* Benoist = ***Stenandriopsis*
Adatoda* Raf. = ***Justicia
Adelaster Lindl. ex Veitch = ***Fittonia***
Adeloda* Raf. = ***Justicia
Adenacanthus Nees = ***Strobilanthes***
Adenosma* Nees = ***Hygrophila
Adenostachya Bremek. = ***Strobilanthes***
Adhatoda Mill. = ***Justicia***
Aechmanthera* Nees = ***Strobilanthes*
Aetheilema* N.Br. = ***Phaulopsis
Afrofittonia Lindau (J)
Afromendoncia Gilg ex Lindau = ***Mendoncia***
Aldelaster* K.Koch = ***Pseuderanthemum
Alvarezia* Pav. ex Nees = ***Ruellia
Amathea Raf. = ***Aphelandra***
Ambongia Benoist (J)
Amphiestes S.Moore = ***Hypoestes***
Amphiscopia Nees = ***Justicia***
Ancalanthus Balf.f. = ***Angkalanthus***
Ancistranthus Lindau (J)
Ancistrostylis T.Yamaz. = ***Staurogyne***
Ancylacanthus Lindau = ***Ptyssiglottis***
Ancylogyne* Nees = ***Sanchezia
Androcentrum Lem. = ***Bravaisia***
Andrographis Wall. ex Nees (An)
Angkalanthus Balf.f. (J)
Anisacanthus Nees (J)
Anisosepalum E.Hossain (Nel)
****Anisostachya*** Nees (J) [treated by some authorities as = ***Justicia***]
Anisotes Nees (J)
Anomacanthus R.D.Good (T)
Anthacanthus* Nees = ***Oplonia*
Antheilema* Raf. = ***Phaulopsis
Antheliacanthus Ridl. = ***Pseuderanthemum***
Anthocometes* Nees = ***Monothecium
Apassalus* Kobuski = ***Dyschoriste*
Aphanandrium Lindau = ***Neriacanthus***
Aphanosperma T.F.Daniel (J)
Aphelandra R.Br. (Ac)
Aphelandrella* Mildbr. = ***Aphelandra*
Aphelandros* St.-Lag. = ***Aphelandra
Aphragmia Nees = ***Ruellia***

Appendix 1. Continued.

Apolepsis* Hassk. = ***Strobilanthes*
Aporuellia* C.B.Clarke = ***Ruellia
Arrhostoxylum Mart. ex Nees = ***Ruellia***
Ascotheca Heine (J)
Asteracantha Nees = ***Hygrophila***
Asystasia Blume (J)
Asystasiella Lindau = ***Asystasia***
Athlianthus* Endl. = ***Justicia
Aubletia* Neck. = ***Ruellia
Aulojusticia Lindau = ***Justicia***
Averia Leonard = ***Tetramerium***
*****Avicennia*** L. (Av)
*****Aymoreana*** Braz, T.F.Daniel & Kiel (Nel)
Bahel* Adans. = ***Hygrophila
Baillonacanthus* Kuntze = ***Henrya
Ballochia Balf.f. (J)
Baphicacanthus Bremek. = ***Strobilanthes***
Barleria L. (B)
Barleriacanthus Oerst. = ***Barleria***
Barlerianthus Oerst. = ***Barleria***
Barleriola Oerst. (B)
Barleriopsis* Oerst. = ***Barleria
Barleriosiphon Oerst. = ***Barleria***
Barlerites Oerst. = ***Barleria***
Barreliera* J.F.Gmel. = ***Barleria
Belantheria Nees = ***Brillantaisia***
Beloperone Nees = ***Justicia***
Beloperonides* Oerst. = ***Justicia
Benoicanthus* Heine & A.Raynal = ***Ruellia*
Bentia Rolfe = ***Justicia***
Berginia Harv. ex Benth. & Hook.f. = ***Holographis***
Birnbaumia* Kostel. = ***Anisacanthus
Blechum* P.Browne = ***Ruellia*
Blepharacanthus Nees ex Lindl. = ***Blepharis***
Blepharis Juss. (Ac)
Bontia* L. = ***Avicennia
Borneacanthus Bremek. (B)
Boutonia DC. (B)
Brachystephanus Nees (J)
Bravaisia DC. (Ru)
Bremekampia Sreem. = ***Haplanthodes***
Brillantaisia P.Beauv. (Ru)
Brochosiphon Nees = ***Dicliptera***
Brunoniella Bremek. (Ru)
Buceragenia Greenm. = ***Pseuderanthemum***
Butayea De Wild. = ***Sclerochiton***
Buteraea Nees = ***Strobilanthes***
Calacanthus T.Anderson ex Benth. (Ru)
Calasias* Raf. = ***Anisotes
Caldenbachia* Pohl ex Nees = ***Stenandrium
Calliaspidia Bremek. = ***Justicia***
Calophanes D.Don = ***Dyschoriste***
Calophanoides (C.B.Clarke) Ridl. = ***Justicia***
Calycacanthus K.Schum. (J)
Calymmostachya Bremek. = ***Justicia***
****Camarotea*** Scott-Elliot (W)
Campylostemon* E.Mey. = ***Justicia
Cardanthera Buch.-Ham. ex Benth. = ***Hygrophila***
Cardiacanthus Nees & Schauer = ***Carlowrightia***
Carima* Raf. = ***Justicia
Carlowrightia A.Gray (J)
Carvia Bremek. = ***Strobilanthes***
Celerina Benoist (J)
Centrilla* Lindau = ***Justicia*
Cephalacanthus Lindau (J)
*****Cephalophis*** Vollesen (J)
Chaetacanthus Nees = ***Dyschoriste***
Chaetochlamys Lindau = ***Justicia***
Chaetothylax Nees = ***Justicia***
Chaetothylopsis Oerst. = ***Justicia***
Chalarothyrsus Lindau (J)
Chamaeranthemum Nees (J)
Championella Bremek. = ***Strobilanthes***
*****Champluviera*** I.Darbysh., T.F.Daniel & Kiel (J)
Cheilopsis Moq. = ***Acanthus***
Chileranthemum Oerst. (J)
Chiloglossa Oerst. = ***Justicia***
Chingiacanthus Hand.-Mazz. = ***Isoglossa***
****Chlamydacanthus*** Lindau (W)
Chlamydocardia Lindau (J)
Chlamydostachya* Mildbr. = ***Anisotes*
Chorisochora Vollesen (J)
Chrestienia Montrouz. ex Beauvis. = ***Pseuderanthemum***
Chroesthes Benoist (B)
Citharella* Noronha = ***Eranthemum
Clarkeasia* J.R.I.Wood = ***Strobilanthes*
Clinacanthus Nees (J)
Clistax Mart. (J)
Codonacanthus Nees (J)
Conocalyx* Benoist = ***Isoglossa*
Copioglossa Miers = ***Ruellia***
Corna* Noronha = ***Avicennia
Corymbostachys Lindau = ***Anisostachya***
Corythacanthus* Nees = ***Clistax
Cosmianthemum Bremek. (J)
Crabbea Harv. (B)
Crateola* Raf. = ***Oplonia
Croftia Small = ***Carlowrightia***
Crossandra Salisb. (Ac)
Crossandrella C.B.Clarke (Ac)
Cryphiacanthus Nees = ***Ruellia***
Cryptophragmium Nees = ***Gymnostachyum***
Ctenopaepale Bremek. = ***Strobilanthes***
Cuenotia* Rizzini = ***Aphelandra
Cyclacanthus S.Moore (J)
Cylindrosolen* Kuntze = ***Stenostephanus
Cylindrosolenium* Lindau = ***Stenostephanus*
Cynarospermum Vollesen (Ac)
Cyphacanthus Leonard (Ac)
Cyphisia Rizzini = ***Justicia***
Cyrtacanthus* Mart. ex Nees = ***Ruellia
Cyrtanthera Nees = ***Justicia***
Cyrtantherella Oerst. = ***Justicia***
Cystacanthus* T.Anderson = ***Phlogacanthus*
Dactylostegium Nees = ***Dicliptera***
Daedalacanthus T.Anderson = ***Eranthemum***
Danguya* Benoist = ***Anisotes*
Dasytropis Urb. (J)
Delphinacanthus Benoist = ***Pseudodicliptera***
Dianthera L. = ***Justicia***
Diapedium* J.Koenig = ***Dicliptera
Diateinacanthus Lindau = ***Odontonema***
Dicentranthera T.Anderson = ***Asystasia***
****Diceratotheca*** J.R.I.Wood & Scotland (Ru)
Dichazothece Lindau (J)
Dicladanthera F.Muell. (J)
Dicliptera Juss. (J)
Dicranacanthus Oerst. = ***Barleria***
Didyplosandra Wight ex Bremek. = ***Strobilanthes***
Diflugossa Bremek. = ***Strobilanthes***
Digyroloma* Turcz. = ***Justicia
Dilicaria* T.Anderson = ***Acanthus
Dilivaria* Juss. = ***Acanthus
Dimanisa Raf. = ***Justicia***
****Dinteracanthus*** Schinz (Ru)
Diotacanthus Benth. (An)
Diplanthera* Gled. = ***Justicia
Diplocalymma* Spreng. = ***Thunbergia
Diptanthera* Schrank ex Steud. = ***Justicia
Dipteracanthus Nees = ***Ruellia***
Dischistocalyx T.Anderson ex Benth. (Ru)
Disperma J.F.Gmel. = ***Duosperma***
Distichocalyx Benth. = ***Dischistocalyx***
Ditrichospermum Bremek. = ***Strobilanthes***
Dizygandra* Meisn. = ***Ruellia
****Dolichostachys*** Benoist (J)
Donatia* Loefl. = ***Avicennia
Dossifluga Bremek. = ***Strobilanthes***
Drejera* Nees = ***Thyrsacanthus*
Drejerella Lindau = ***Justicia***
Drupina* L. = ***Mendoncia
Duosperma Dayton (Ru)
Duvernoia E.Mey. ex Nees = ***Justicia***
Dyschoriste Nees (Ru)
Dyspemptemorion Bremek. = ***Justicia***
Earlia* F.Muell. = ***Graptophyllum
Eberlea* Riddell ex Nees = ***Hygrophila
Ebermaiera Nees = ***Staurogyne***
Ecbolium* Kuntze = ***Justicia
Ecbolium Kurz (J)
Echinacanthus Nees (Ru)
Echinopaepale Bremek. = ***Strobilanthes***
Ecteinanthus T.Anderson = ***Isoglossa***
Elytraria Michx. (Nel)
Emularia Raf. = ***Justicia***
Encephalosphaera* Lindau = ***Aphelandra*
Endomelas* Raf. = ***Thunbergia
Endopogon Nees = ***Strobilanthes***
Endosiphon T.Anderson ex Benth. = ***Ruellia***
Engelia* H.Karst. ex Nees = ***Mendoncia
Epiclastopelma* Lindau = ***Mimulopsis*
Eranthemum L. (Ru)
Eremomastax Lindau (Ru)
Erianthera* Nees = ***Andrographis
Eriostrobilus Bremek. = ***Strobilanthes***
Erythracanthus Nees = ***Staurogyne***
Ethesia Raf. = ***Justicia***
Eurychanes Nees = ***Ruellia***
Eusiphon* Benoist = ***Ruellia*
Fabria* E.Mey. = ***Ruellia
Filetia Miq. (J)
Fittonia Coem. (J)
Flavicoma* Raf. = ***Schaueria
Flemingia* Roxb. ex Rottler = ***Thunbergia
****Forcipella*** Baill. (W)
Forsythiopsis Baker = ***Oplonia***
Galeottia Nees = ***Stenostephanus***
Gantelbua* Bremek. = ***Strobilanthes*
Gastranthus Moritz ex Benth. & Hook.f. = ***Stenostephanus***
Gatesia A.Gray = ***Yeatesia***
Geissomeria* Lindl. = ***Aphelandra*
Gendarussa Nees = ***Justicia***
Gerardia L. = ***Stenandrium***
Geunsia* Neck. ex Raf. = ***Dicliptera
Gilletiella De Wild. & T.Durand = ***Anomacanthus***
Glockeria Nees = ***Stenostephanus***
Glosarithys Rizzini = ***Justicia***
Glossochilus Nees (J)
Golaea* Chiov. = ***Crabbea*
Goldfussia Nees = ***Strobilanthes***
Graphandra J.B.Imlay (An)
Graptophyllum Nees (J)
Gromovia* Regel = ***Justicia
Gutzlaffia Hance = ***Strobilanthes***
Gymapsis Bremek. = ***Strobilanthes***
Gymnacanthus* Nees = ***Ruellia
Gymnacanthus Oerst. = ***Ruellia***
**Gymnophragma* Lindau [excluded]
Gymnostachyum Nees (An)

Appendix 1. Continued.

Gynocraterium* Bremek. = ***Staurogyne*
Gypsacanthus E.J.Lott, V.Jaram. & Rzed. (J)
Habracanthus Nees = ***Stenostephanus***
Haemacanthus S.Moore = ***Satanocrater***
Hallieracantha Stapf = ***Ptyssiglottis***
Halodendron* Roem. & Schult. = ***Avicennia
Halodendrum* Thouars = ***Avicennia
Hansteinia Oerst. = ***Stenostephanus***
Haplanthera Hochst. = ***Ruttya***
Haplanthodes Kuntze (An)
Haplanthoides* H.W.Li = ***Haplanthus*
****Haplanthus*** Nees (An)
Harnieria Solms = ***Justicia***
Harpochilus Nees (J)
Harrachia Jacq. = ***Crossandra***
Haselhoffia Lindau = ***Physacanthus***
Heinzelia Nees = ***Justicia***
Hemiadelphis Nees = ***Hygrophila***
Hemichoriste Nees = ***Justicia***
Hemidelphus* Nees = ***Hygrophila
Hemigraphis* Nees (Ru) = ***Strobilanthes*
Hemisandra Scheidw. = ***Aphelandra***
Hemitome* Nees = ***Aphelandra
Hemonacanthus* Nees = ***Ruellia
Henrya Benth. (J)
****Herpetacanthus*** Nees (J)
Hesperanthemum* Kuntze = ***Oplonia
Heteradelphia Lindau (Ru)
Heteraspidia Rizzini = ***Justicia***
Hexacentris* Nees = ***Thunbergia
Hilairanthus* Tiegh. = ***Avicennia
Himantochilus T.Anderson ex Benth. = ***Anisotes***
Holographis Nees (Ac)
Holtzendorffia* Klotzsch & H.Karst. ex Nees = ***Ruellia
Homilacanthus* S.Moore = ***Isoglossa
Homotropium* Nees = ***Dyschoriste
Hoverdenia Nees (J)
Hulemacanthus S.Moore (B)
Hydromestus Scheidw. = ***Aphelandra***
Hygrophila R.Br. (Ru)
Hymenochlaena Bremek. = ***Strobilanthes***
Hypoestes Sol. ex R.Br. (J)
Ichthyostoma Hedrén & Vollesen (J)
Idanthisa* Raf. = ***Anisacanthus
Indoneesiella* Sreem. = ***Andrographis*
Intrusaria* Raf. = ***Asystasia
Ionacanthus* Benoist = ***Mimulopsis*
Isacanthus Nees = ***Sclerochiton***
Isaloa Humbert = ***Barleria***
Isochoriste Miq. = ***Asystasia***
Isoglossa Oerst. (J)
Isotheca Turrill (J)
Ixtlania M.E.Jones = ***Justicia***
Jacobinia Nees ex Moric. = ***Justicia***
Jadunia Lindau (J)
Janasia* Raf. = ***Phlogacanthus
Jungia* Boehm. = ***Justicia
Juruasia* Lindau = ***Herpetacanthus*
Justicia L. (J)
Kalbreyeracanthus Wassh. = ***Stenostephanus***
Kalbreyeriella* Lindau = ***Stenostephanus*
Kanjarum Ramam. = ***Strobilanthes***
*****Kenyacanthus*** I.Darbysh. & Kiel (J)
Kita A.Chev. = ***Hygrophila***
Kjellbergia Bremek. = ***Strobilanthes***
Kolobochilus Lindau = ***Razisea***
Kosmosiphon Lindau (Ru)
****Kudoacanthus*** Hook. (J)
Kuestera Regel = ***Justicia***
Kuniria* Raf. = ***Dicliptera
Lagochilium Nees = ***Aphelandra***
Lamiacanthus Kuntze = ***Strobilanthes***
****Lankesteria*** Lindl. (W)
Larsenia Bremek. = ***Strobilanthes***
Larysacanthus* Oerst. = ***Ruellia
****Lasiocladus*** Bojer ex Nees (B)
****Leandriella*** Benoist (W)
Leda C.B.Clarke = ***Isoglossa***
Leiophaca Lindau = ***Whitfieldia***
Lepidacanthus C.Presl = ***Aphelandra***
Lepidagathis Willd. (B)
Leptacanthus Nees = ***Strobilanthes***
Leptosiphonium F.Muell. (Ru)
*****Leptostachya*** Nees (J)
Leucobarleria Lindau = ***Neuracanthus***
Leucorhaphis Nees = ***Brillantaisia***
Liberatia* Rizzini = ***Lepidagathis*
Libonia K.Koch = ***Justicia***
Linariantha B.L.Burtt & R.M.Sm. (J)
Lindauea Rendle = ***Lepidagathis***
Linocalix* Lindau = ***Chlamydocardia*
Linostylis* Fenzl ex Sond. = ***Dyschoriste
Lirayea Pierre = ***Mendoncia***
Lissospermum Bremek. = ***Strobilanthes***
Listrobanthes Bremek. = ***Strobilanthes***
Lophostachys* Pohl = ***Lepidagathis*
Lophothecium Rizzini = ***Justicia***
Louteridium S.Watson (Ru)
Loxanthus* Nees = ***Phlogacanthus
Lundellia Leonard = ***Holographis***
Lustrinia Raf. = ***Justicia***
Lychniothyrsus* Lindau = ***Ruellia*
Mackaya Harv. (J)
Mackenziea Nees = ***Strobilanthes***
Macrorungia C.B.Clarke = ***Metarungia***
Mananthes Bremek. = ***Justicia***
Marama* Raf. = ***Graptophyllum
Marcania J.B.Imlay (J)
*****Mcdadea*** E.Tripp & I.Darbysh. (Ru)
Megalochlamys Lindau (J)
Megalostoma* Leonard = ***Justicia*
Megaskepasma Lindau (J)
*****Meiosperma*** Raf. (J)
Melittacanthus S.Moore (J)
Mellera S.Moore (Ru)
Mendoncia Vell. ex Vand. (T)
Mendozia* Ruiz & Pav. = ***Mendoncia
Meninia* Fua ex Hook.f. = ***Phlogacanthus
Metarungia Baden (J)
Mexacanthus T.F.Daniel (J)
Meyenia Nees (T)
Micraea* Miers = ***Ruellia
Micranthus J.C.Wendl. = ***Phaulopsis***
Microstrobilus Bremek. = ***Strobilanthes***
Mimulopsis Schweinf. (Ru)
Mirandea Rzed. (J)
Monachochlamys Baker = ***Mendoncia***
Monechma* Hochst. = ***Meiosperma*
Monothecium Hochst. (J)
Morsacanthus* Rizzini = ***Pseuderanthemum*
Neesiella* Sreem. = ***Andrographis
Nelsonia R.Br. (Nel)
Neohallia Hemsl. = ***Justicia***
Neolindenia Baill. = ***Louteridium***
Neowedia* Schrad. = ***Ruellia
Neozenkerina Mildbr. = ***Staurogyne***
Neriacanthus Benth. (Ac)
****Neuracanthus*** Nees (Neu)
Nicoteba Lindau = ***Justicia***
Nigrolea* Noronha = ***Staurogyne
Nilgirianthus Bremek. = ***Strobilanthes***
Nomaphila Blume = ***Hygrophila***
Nothoruellia Bremek. = ***Ruellia***
Odontonema Nees (J)
Odontonemella Lindau = ***Mackaya***
Odontophyllum Sreem. = ***Aphelandra***
Odontostigma Zoll. & Moritzi = ***Gymnostachyum***
Onus Gilli = ***Mellera***
Onychacanthus Nees = ***Bravaisia***
Ophiorrhiziphyllon* Kurz = ***Staurogyne*
Ophthalmacanthus* Nees = ***Ruellia*
Oplonia Raf. (J)
Oreacanthus* Benth. = ***Brachystephanus*
Oreothyrsus Lindau = ***Ptyssiglottis***
Orophochilus* Lindau = ***Aphelandra*
Orthotactus Nees = ***Justicia***
Oryzetes* Salisb. = ***Hygrophila
Pachystachys Nees (J)
Pachystrobilus Bremek. = ***Strobilanthes***
Panemata* Raf. = ***Dicliptera
Parabarleria Baill. = ***Barleria***
Parachampionella Bremek. = ***Strobilanthes***
Paragoldfussia Bremek. = ***Strobilanthes***
Paragutzlaffia H.P.Tsui = ***Strobilanthes***
Parajusticia* Benoist = ***Gymnostachyum*
Pararuellia Bremek. & Nann.-Bremek. (Ru)
Parastrobilanthes Bremek. = ***Strobilanthes***
Parasympagis Bremek. = ***Strobilanthes***
Parasystasia Baill. = ***Asystasia***
Pattersonia* J.F.Gmel. = ***Ruellia
Paulowilhelmia Hochst. = ***Eremomastax***
Pelecostemon* Leonard = ***Justicia*
Pentstemonacanthus Nees = ***Ruellia***
Perenideboles* Ram.Goyena = ***Megaskepasma*
Periblema DC. = ***Boutonia***
****Pericalypta*** Benoist (B)
Periestes Baill. = ***Hypoestes***
Perilepta Bremek. = ***Strobilanthes***
Peristrophe* Nees = ***Dicliptera* [maintained as distinct by some authorities]
Petalanthera Raf. = ***Justicia***
Petalidium Nees (Ru)
Petracanthus Nees = ***Gymnostachyum***
Phaulopsis Willd. (Ru)
Phaylopsis Willd. = ***Phaulopsis***
Phialacanthus Benth. (J)
Phidiasia Urb. = ***Odontonema***
Phillipsia Rolfe = ***Dyschoriste***
Phlebophyllum Nees = ***Strobilanthes***
Phlogacanthus Nees (An)
Phyllophiorhiza* Kuntze = ***Staurogyne
Physacanthus Benth. (P)
Physichilus* Nees = ***Hygrophila
Pigafetta* Adans. = ***Eranthemum
Plaesianthera (C.B.Clarke) Livera = ***Hygrophila***
Plagiacanthus Nees = ***Justicia***
Plagiotheca Chiov. = ***Isoglossa***
Planetanthemum* (Endl.) Kuntze = ***Pseuderanthemum
Plegmatolemma Bremek. = ***Justicia***
Pleimeris* Raf. = ***Thunbergia
Pleocaulus Bremek. = ***Strobilanthes***
Pleuremidis* Raf. = ***Thunbergia
Pleuroblepharis Baill. = ***Crossandra***
****Podorungia*** Baill. (B)
Poecilocnemis* Martius ex Nees = ***Aphelandra
****Pogonospermum*** Hochst. (J)
Poikilacanthus Lindau (J)
Polyechma* Hochst. = ***Hygrophila
Polylychnis* Bremek. = ***Ruellia*
Polythrix Nees = ***Crossandra***
Polytrema C.B.Clarke = ***Ptyssiglottis***
Populina Baill. (J)
Porphyrocoma Scheidw. ex Hook. = ***Justicia***

Appendix 1. Continued.

Pounguia Benoist = ***Whitfieldia***
Pranceacanthus Wassh. (J)
Pringleophytum A.Gray = ***Holographis***
Prionitis Oerst. = ***Barleria***
Psacadocalymma Bremek. = ***Justicia***
Psacadopaepale Bremek. = ***Strobilanthes***
Pseudacanthopale Benoist = ***Strobilanthopsis***
Pseudaechmanthera Bremek. = ***Strobilanthes***
Pseuderanthemum Radlk. (J)
Pseudobarleria Oerst. = ***Barleria***
Pseudobarleria T.Anderson = ***Petalidium***
Pseudoblepharis Baill. = ***Sclerochiton***
Pseudocalyx Radlk. (T)
****Pseudodicliptera*** Benoist (B)
Pseudoruellia* Benoist = ***Ruellia*
Pseudostenosiphonium Lindau = ***Strobilanthes***
Psilanthele Lindau (J)
Psiloesthes* Benoist = ***Dicliptera*
Pteracanthus (Nees) Bremek. = ***Strobilanthes***
Pteroptychia Bremek. = ***Strobilanthes***
Ptyssiglottis T.Anderson (J)
Pulchranthus V.M.Baum, Reveal & Nowicke (J)
Pupilla Rizzini = ***Justicia***
Pyrrothrix Bremek. = ***Strobilanthes***
Racka* Bruce ex J.F.Gmel. = ***Avicennia
Racua* J.F.Gmel. = ***Avicennia
Ramusia* Nees = ***Isoglossa*
Razisea* Oerst. = ***Stenostephanus*
Rhacodiscus Lindau = ***Justicia***
Rhaphidosperma G.Don = ***Justicia***
Rhaphidospora Nees = ***Justicia***
Rhinacanthus Nees (J)
Rhombochlamys* Lindau = ***Aphelandra*
Rhyticalymma Bremek. = ***Justicia***
Rhytiglossa Nees ex Lindl. = ***Isoglossa***
****Ritonia*** Benoist (IS)
Rodatia Raf. = ***Justicia***
Roslinia* Neck. = ***Justicia
Rostellaria Nees = ***Justicia***
Rostellularia Rchb. = ***Justicia***
Ruellia L. (Ru)
Ruelliola Baill. = ***Brillantaisia***
Ruelliopsis C.B.Clarke (Ru)
Rungia Nees (J) [treated by some authorities as = ***Justicia***]
Ruspolia Lindau (J)
Russeggera* Endl. = ***Lepidagathis
Ruttya Harv. (J)
Saglorithys Rizzini = ***Justicia***
Saintpauliopsis Staner (Nel)
Salpinctium T.J.Edwards = ***Asystasia***
Salpingacanthus S.Moore = ***Ruellia***
Salpingantha Lem. = ***Salpixantha***
Salpinxantha Urb. = ***Salpixantha***
Salpixantha Hook. (Ac)
Salviacanthus Lindau = ***Justicia***
Samuelssonia Urb. & Ekman (J)
Sanchezia Ruiz & Pav. (Ru)
Santapaua N.P.Balakr. & Subram. = ***Hygrophila***
Sapphoa Urb. (J)
Sarcanthera* Raf. = ***Gymnostachyum
Sarojusticia Bremek. = ***Justicia***
Sarotheca Nees = ***Justicia***
Satanocrater Schweinf. (Ru)
Sautiera* Decne. = ***Dyschoriste*
Sceura* Forssk. = ***Avicennia
Schaueria Nees (J)
*****Schaueriopsis*** Champl. & I.Darbysh. (B)
Schliebenia Mildbr. = ***Isoglossa***
Schmidia* Wight = ***Thunbergia
Schultzia* Nees = ***Herpetacanthus
Schwabea Endl. [excluded]
Sciaphyllum Bremek. = ***Pachystachys***
Sclerocalyx Nees = ***Ruellia***
Sclerochiton Harv. (Ac)
Scorodoxylum* = ***Ruellia
Sebastiano-Schaueria Nees (J)
Sebschauera* Kuntze = ***Sebastiano-Schaueria
Semnostachya Bremek. = ***Strobilanthes***
Semnothyrsus Bremek. = ***Strobilanthes***
Senkebergia* Neck. ex Raf. = ***Mendoncia
×*Sericobonia* Linden & André = ***Justicia*
Sericocalyx Bremek. = ***Strobilanthes***
Sericographis Nees = ***Justicia***
***Sericospora* Nees [excluded]
Simonisia Nees = ***Justicia***
Sinthroblastes Bremek. = ***Strobilanthes***
Siphonacanthus Nees = ***Ruellia***
Siphoneranthemum* (Oerst.) Kuntze = ***Pseuderanthemum
Siphonoglossa Oerst. = ***Justicia***
Solaenacanthus* Oerst. = ***Ruellia
Solenochasma* Fenzl = ***Dicliptera*
Solenoruellia Baill. = ***Henrya***
Somalia* Oliv. = ***Barleria
Sooia* Pócs = ***Mimulopsis*
Soubeyrania* Neck. = ***Barleria
Spathacanthus Baill. (J)
****Sphacanthus*** Benoist (J)
****Sphinctacanthus*** Benth. (An)
Spirostigma* Nees = ***Ruellia*
Sreemadhavana Rauschert = ***Aphelandra***
Stachyacanthus* Nees = ***Ruellia
Standleyacanthus Leonard = ***Herpetacanthus***
Staurogyne Wall. (Nel)
Staurogynopsis Mangenot & Aké Assi = ***Staurogyne***
Steirosanchezia Lindau = ***Sanchezia***
Stemonacanthus Nees = ***Ruellia***
****Stenandriopsis*** S.Moore (Ac) [treated by some authorities as = ***Stenandrium***]
Stenandrium Nees (Ac)
Stenoschista Bremek. = ***Ruellia***
Stenosiphonium* Nees = ***Strobilanthes*
Stenostephanus Nees (J)
Stenothyrsus C.B.Clarke (Ru)
Stephanophysum Pohl = ***Ruellia***
Stethoma Raf. = ***Justicia***
Stiftia* Pohl ex Nees = ***Staurogyne
Streblacanthus Kuntze (J)
Strepsiphus* Raf. = ***Dicliptera
Streptosiphon Mildbr. (Ac)
Strobilacanthus* Griseb. [excluded, possibly = ***Crossandra*]
Strobilanthes Blume (Ru)
Strobilanthopsis S.Moore (Ru)
Strobilorhachis Klotzsch = ***Aphelandra***
Strophacanthus Lindau = ***Isoglossa***
Styasasia S.Moore = ***Asystasia***
Stylarthropus Baill. = ***Whitfieldia***
Suessenguthia Merxm. (Ru)
Supushpa Suryan. = ***Strobilanthes***
Sympagis (Nees) Bremek. = ***Strobilanthes***
Symplectochilus Lindau = ***Anisotes***
Synandra Schrad. = ***Aphelandra***
Synchoriste Baill. = ***Lasiocladus***
Synnema Benth. = ***Hygrophila***
Syringidium Lindau = ***Stenostephanus***
Tabascina Baill. = ***Justicia***
Tacoanthus Baill. = ***Ruellia***
Taeniandra Bremek. = ***Strobilanthes***
Talbotia S.Moore = ***Afrofittonia***
Tarphochlamys Bremek. = ***Strobilanthes***
Teliostachya Nees = ***Lepidagathis***
Tenoria* Dehnh & Giord. = ***Hygrophila
Tessmanniacanthus Mildbr. (J)
Tetraglochidium Bremek. = ***Strobilanthes***
Tetragoga Bremek. = ***Strobilanthes***
Tetragompha Bremek. = ***Strobilanthes***
Tetramerium Nees (J)
Thalestris Rizzini = ***Justicia***
Thamnojusticia Mildbr. = ***Justicia***
Theileamea* Baill. = ***Phaulopsis*
Thelepaepale Bremek. = ***Strobilanthes***
Thunbergia Retz. (T)
****Thyrsacanthus*** Moric. (J)
Thyrsacanthus Nees = ***Odontonema***
Thysanostigma J.B.Imlay (J)
Tremacanthus S.Moore = ***Ruellia***
Triaenacanthus Nees = ***Strobilanthes***
Trichacanthus Zoll. & Moritzi = ***Blepharis***
Trichanthera Kunth (Ru)
Trichaulax Vollesen (J)
Trichocalyx Balf.f. (J)
Trichosanchezia Mildbr. (Ru)
Trixanthera* Raf. = ***Trichanthera
Trybliocalyx Lindau = ***Chileranthemum***
Tubiflora J.F.Gmel. = ***Elytraria***
Tyloglossa Hochst. = ***Justicia***
Ulleria Bremek. = ***Ruellia***
Upata* Adans. = ***Avicennia
Upudalia* Raf. = ***Eranthemum
Vada-kodi* Adans. = ***Justicia
Valentiana* Raf. = ***Thunbergia
****Vavara*** Benoist (J)
****Vindasia*** Benoist (W)
Volkensiophyton Lindau = ***Lepidagathis***
Warpuria Stapf = ***Podorungia***
****Whitfieldia*** Hook. (W)
*****Wuacanthus*** Y.F.Deng, N.H.Xia & H.Peng (J)
Xantheranthemum* Lindau = ***Aphelandra*
Xanthostachya Bremek. = ***Strobilanthes***
Xenacanthus Bremek. = ***Strobilanthes***
Xerothamnella C.T.White (J)
*****Xylacanthus*** Aver. & K.S.Nguyen (Ru)
Yeatesia Small (J)
Zahlbrucknera* Pohl ex Nees = ***Lepidagathis
Zenkerina Engl. = ***Staurogyne***
Zonablepharis* Raf. = ***Acanthus
****Zygoruellia*** Baill. (W)

Appendix 2. A proposed linear sequence for the currently accepted genera of Acanthaceae for use in systematically arranged natural history collections.

1 *Nelsonia* R.Br.
2 *Elytraria* Michx.
3 *Aymoreana* Braz, T.F.Daniel & Kiel
4 *Anisosepalum* E.Hossain
5 *Saintpauliopsis* Staner
6 *Staurogyne* Wall.
7 *Avicennia* L.
8 *Mendoncia* Vell. ex Vand.
9 *Anomacanthus* R.D.Good
10 *Pseudocalyx* Radlk.
11 *Thunbergia* Retz.
12 *Meyenia* Nees
13 *Crossandra* Salisb.
14 *Crossandrella* C.B.Clarke
15 *Streptosiphon* Mildbr.
16 *Sclerochiton* Harv.
17 *Cynarospermum* Vollesen
18 *Blepharis* Juss.
19 *Acanthopsis* Harv.
20 *Acanthus* L.
21 *Stenandriopsis* S.Moore
22 *Stenandrium* Nees
23 *Salpixantha* Hook.
24 *Neriacanthus* Benth.
25 *Holographis* Nees
26 *Aphelandra* R.Br.
27 *Cyphacanthus* Leonard
28 *Physacanthus* Benth.
29 *Neuracanthus* Nees
30 *Barleria* L.
31 *Crabbea* Harv.
32 *Lasiocladus* Bojer ex Nees
33 *Pericalypta* Benoist
34 *Podorungia* Baill.
35 *Pseudodicliptera* Benoist
36 *Boutonia* DC.
37 *Lepidagathis* Willd.
38 *Schaueriopsis* Champl. & I.Darbysh.
39 *Chroesthes* Benoist
40 *Hulemacanthus* S.Moore
41 *Borneacanthus* Bremek.
42 *Barleriola* Oerst.
43 *Andrographis* Wall. ex Nees
44 *Haplanthus* Nees
45 *Haplanthodes* Kuntze
46 *Graphandra* J.B.Imlay
47 *Phlogacanthus* Nees
48 *Gymnostachyum* Nees
49 *Diotacanthus* Benth.
50 *Sphinctacanthus* Benth.
51 *Lankesteria* Lindl.
52 *Whitfieldia* Hook.
53 *Chlamydacanthus* Lindau
54 *Zygoruellia* Baill.
55 *Camarotea* Scott Elliot
56 *Forcipella* Baill.
57 *Vindasia* Benoist
58 *Leandriella* Benoist
59 *Brunoniella* Bremek.
60 *Leptosiphonium* F.Muell.
61 *Pararuellia* Bremek. & Nann.-Bremek.
62 *Eranthemum* L.
63 *Kosmosiphon* Lindau
64 *Dinteracanthus* Schinz
65 *Dischistocalyx* T.Anderson ex Benth.
66 *Satanocrater* Schweinf.
67 *Acanthopale* C.B.Clarke
68 *Ruellia* L.
69 *Calacanthus* T.Anders. ex Benth.
70 *Louteridium* S.Watson
71 *Bravaisia* DC.
72 *Trichanthera* Kunth
73 *Trichosanchezia* Mildbr.
74 *Sanchezia* Ruiz & Pav.
75 *Suessenguthia* Merxm.
76 *Strobilanthes* Blume
77 *Hygrophila* R.Br.
78 *Brillantaisia* P.Beauv.
79 *Strobilanthopsis* S.Moore
80 *Dyschoriste* Nees
81 *Echinacanthus* Nees
82 *Petalidium* Nees
83 *Duosperma* Dayton
84 *Ruelliopsis* C.B.Clarke
85 *Mcdadea* E.Tripp & I.Darbysh.
86 *Phaulopsis* Willd.
87 *Eremomastax* Lindau
88 *Heteradelphia* Lindau
89 *Mellera* S.Moore
90 *Mimulopsis* Schweinf.
91 *Stenothyrsus* C.B.Clarke
92 *Xylacanthus* Aver. & K.S.Nguyen
93 *Diceratotheca* J.R.I.Wood & Scotland
94 *Spathacanthus* Baill.
95 *Chamaeranthemum* Nees
96 *Pranceacanthus* Wassh.
97 *Herpetacanthus* Nees
98 *Isotheca* Turrill
99 *Afrofittonia* Lindau
100 *Thysanostigma* J.B.Imlay
101 *Glossochilus* Nees
102 *Asystasia* Blume
103 *Phialacanthus* Benth.
104 *Filetia* Miq.
105 *Mackaya* Harv.
106 *Cosmianthemum* Bremek.
107 *Codonacanthus* Nees
108 *Chileranthemum* Oerst.
109 *Pulchranthus* V.M.Baum, Reveal & Nowicke
110 *Odontonema* Nees
111 *Sapphoa* Urb.
112 *Oplonia* Raf.
113 *Psilanthele* Lindau
114 *Linariantha* B.L.Burtt & R.M.Sm.
115 *Pseuderanthemum* Radlk.
116 *Graptophyllum* Nees
117 *Wuacanthus* Y.F.Deng, N.H.Xia & H.Peng
118 *Ruspolia* Lindau
119 *Ballochia* Balf.f.
120 *Ruttya* Harv.
121 *Champluviera* I.Darbysh., T.F.Daniel & Kiel
122 *Monothecium* Hochst.
123 *Marcania* J. B.Imlay
124 *Jadunia* Lindau
125 *Calycacanthus* K.Schum.
126 *Cyclacanthus* S.Moore
127 *Ptyssiglottis* T.Anderson
128 *Ambongia* Benoist
129 *Ichthyostoma* Hedrén & Vollesen
130 *Isoglossa* Oerst.
131 *Sphacanthus* Benoist
132 *Celerina* Benoist
133 *Melittacanthus* S.Moore
134 *Brachystephanus* Nees
135 *Stenostephanus* Nees
136 *Sebastiano-Schaueria* Nees
137 *Chlamydocardia* Lindau
138 *Leptostachya* Nees
139 *Kudoacanthus* Hook.
140 *Clinacanthus* Nees
141 *Angkalanthus* Balf.f.
142 *Chorisochora* Vollesen
143 *Ecbolium* Kurz
144 *Populina* Baill.
145 *Megalochlamys* Lindau
146 *Trichaulax* Vollesen
147 *Cephalophis* Vollesen
148 *Mirandea* Rzed.
149 *Yeatesia* Small
150 *Hoverdenia* Nees
151 *Thyrsacanthus* Moric.
152 *Pachystachys* Nees
153 *Fittonia* Coem.
154 *Schaueria* Nees
155 *Ancistranthus* Lindau
156 *Aphanosperma* T.F.Daniel
157 *Chalarothyrsus* Lindau
158 *Henrya* Benth.
159 *Gypsacanthus* E.J.Lott, V.Jaram. & Rzed.
160 *Carlowrightia* A.Gray
161 *Tetramerium* Nees
162 *Anisacanthus* Nees
163 *Mexacanthus* T.F.Daniel
164 *Streblacanthus* Kuntze
165 *Dolichostachys* Benoist
166 *Justicia* L.
167 *Ascotheca* Heine
168 *Rungia* Nees
169 *Metarungia* Baden
170 *Anisotes* Nees
171 *Anisostachya* Nees
172 *Trichocalyx* Balf.f.
173 *Meiosperma* Raf.
174 *Pogonospermum* Hochst.
175 *Kenyacanthus* I.Darbysh. & Kiel
176 *Rhinacanthus* Nees
177 *Hypoestes* Sol. ex R.Br.
178 *Dicliptera* Juss.
179 *Vavara* Benoist
180 *Xerothamnella* C.T.White
181 *Dicladanthera* F.Muell.
182 *Cephalacanthus* Lindau
183 *Poikilacanthus* Lindau
184 *Megaskepasma* Lindau
185 *Clistax* Mart.
186 *Harpochilus* Nees
187 *Dasytropis* Urb.
188 *Samuelssonia* Urb. & Ekman
189 *Dichazothece* Lindau
190 *Tessmanniacanthus* Mildbr.
191 *Ritonia* Benoist