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NELSONIOIDEAE (LAMIALES: ACANTHACEAE): REVISION OF GENERA AND CATALOG OF SPECIES

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ABSTRACT

A taxonomic account of Acanthaceae subfamily Nelsonioideae based on morphological and phylogenetic data treats five genera with 172 species: *Anisosepalum* (3), *Elytraria* (21), *Nelsonia* (2), *Saintpauliopsis* (1), and *Staurogyne* (145). Two other currently recognized genera, *Gynocraterium* and *Ophiorrhizophyllum*, are included within *Staurogyne*, and the new combinations, ***Staurogyne guianensis*** and ***S. macrobotrya***, are proposed. Probable apomorphic and other diagnostic macro- and micromorphological characters are discussed relative to the subfamily and genera. Characters of the inflorescence, androecium (especially pollen), and seed show important phylogenetic and diagnostic signal. A key to genera, generic descriptions and discussions, illustrations, and distribution maps are provided. Lists of currently recognized species for each genus include synonymies and distributions by country.

Key words: Acanthaceae, *Anisosepalum*, *Elytraria*, morphology, *Nelsonia*, Nelsonioideae, phylogeny, *Saintpauliopsis*, *Staurogyne*.

INTRODUCTION

Acanthaceae consist of about 190 genera and 4750 species (Daniel unpubl.; vs. 212 genera and 3175 species fide Mabberley 2008). The family is pantropical in distribution, although most genera are restricted to either the New World or the Old World. Recent phylogenetic studies (e.g., McDade et al. 2008; Fig. 1) reveal the family to be monophyletic and divisible into at least three subfamilies that are related as follows: Nelsonioideae (Thunbergioideae + Acanthoideae). Nelsonioideae, the smallest among the currently recognized subfamilies, are here treated as consisting of 172 species in five genera: *Anisosepalum* (3), *Elytraria* (21), *Nelsonia* (2), *Saintpauliopsis* (1), and *Staurogyne* (145). Geographic occurrence and morphological diversity of Nelsonioideae reflect that of the entire family: they are nearly worldwide in distribution and show considerable variation in habit, foliar characteristics, and floral features.

Nelsonioideae have had a convoluted taxonomic history with respect to constituent genera, familial affinities, and taxonomic rank. Nees (1832, 1847a,b) treated genera now known as *Elytraria*, *Nelsonia*, and *Staurogyne* as tribe Nelsonieae of Acanthaceae; these were characterized by having small seeds that were not supported by conspicuous retinacula. Bentham and Hooker (1876) recognized this tribe and also included *Ophiorrhizophyllum* in it. In the most comprehensive and influential account of Acanthaceae to date, Lindau (1895) treated these four genera in subfamily Nelsonioideae, which was characterized by having numerous seeds, papilliform retinacula, and tricolporate pollen. Van Tieghem (1908) segregated all genera lacking retinacula from Acanthaceae as

a new family, Thunbergiaceae, with the nelsonioid assemblage remaining a subfamily. Wettstein (1924) returned Thunbergiaceae to Acanthaceae as a subfamily with the nelsonioids as a tribe of Thunbergioideae. In sequence, Bremekamp treated the nelsonioid genera as a subtribe of Acanthoideae: Acantheae (1938), as a tribe of Acanthoideae (1944), and finally, based primarily on the presence of persistent endosperm in their seeds, as a tribe of Scrophulariaceae: Rhinanthoideae (1953, 1955). In the most extensive treatment of the nelsonioid assemblage to date, Hossain (1971, 1972, 1984, 2004) treated these genera (with the addition of *Anisosepalum*, *Saintpauliopsis* and *Gynocraterium*) as a tribe of Acanthaceae: Acanthoideae. Sreemadhavan (1977) and Lu (1990) have recognized nelsonioids as a distinct family, Nelsoniaceae. Treatment outside Acanthaceae (either as Scrophulariaceae sensu traditionalem or as a distinct family) never received widespread acceptance, and subfamilial rank has been generally utilized for the taxon (e.g., Cronquist 1981; Scotland and Vollesen 2000). Recent molecular phylogenetic studies (e.g., McDade et al. 2008, 2012) confirmed the subfamily as monophyletic, supported recognition of the five genera noted above, and placed the clade as sister to all other Acanthaceae.

Some of the genera now treated as Nelsonioideae have been placed outside Acanthaceae. *Neozenkerina*, *Ophiorrhizophyllum*, and *Zenkerina* (all = *Staurogyne*) were originally described in Scrophulariaceae, and *Saintpauliopsis* was originally described in Gesneriaceae. A further taxonomic complication is that both Nees (1847a) and Lindau (1895) included some genera now treated as Plantaginaceae (*Adenosma* R. Br.) and Orobanchaceae (*Hiernia* S. Moore) in their nelsonioid taxa.

PHYLOGENY

Because patterns of variation in macro- and micro-morphological characters are best contextualized by phylogenetic relationships, we summarize recent phylogenetic results (Wenk and Daniel 2009; McDade et al. 2012) and then discuss

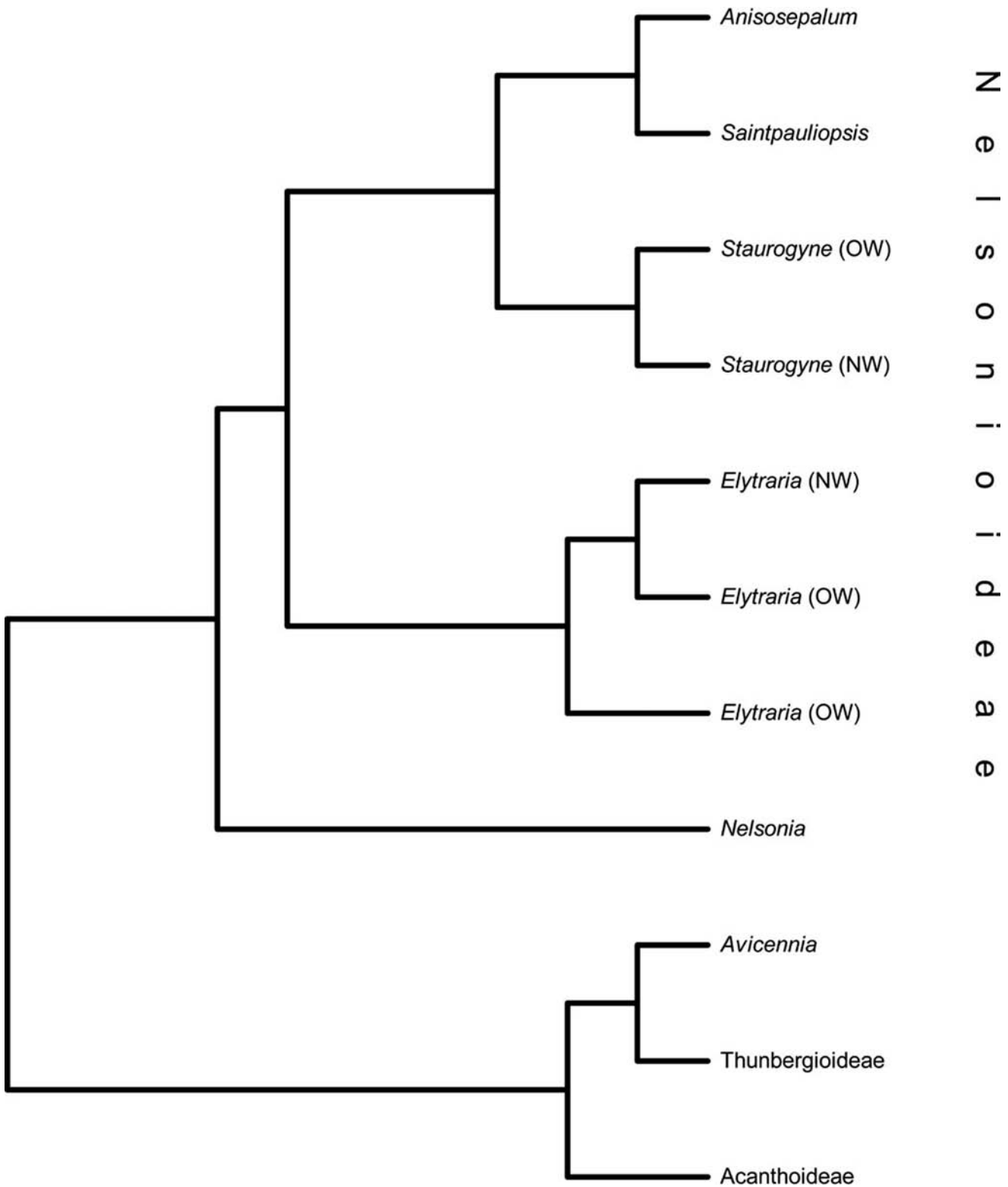


Fig. 1. Summary phylogeny of Acanthaceae showing subfamilies (and *Avicennia*) and relationships among genera of Nelsonioideae based on McDade et al. (2008, 2012); OW = Old World, NW = New World.

plant characteristics. The subfamily is monophyletic and sister to all other Acanthaceae. Monophyly is also supported by at least one shared morphological character (possibly synapomorphic; this trait cannot be polarized with certainty until the

closest relatives of Acanthaceae are clarified), descending-cochlear aestivation of corolla lobes. Aestivation patterns have been shown to be phylogenetically informative among Acanthaceae and, within the family this pattern is known

only among Nelsonioideae (Scotland et al. 1994; Scotland and Vollesen 2000; additional observations by us for each genus). Therefore, there exists a basis for treating Nelsonioideae as a distinct and circumscribable (both morphologically and molecularly) family, as argued by Sreemadhavan (1977). McDade et al. (2012) provided data that support the recognition of at least five of the seven traditionally recognized genera of Nelsonioideae: *Anisosepalum*, *Elytraria*, *Nelsonia*, *Saintpauliopsis*, and *Staurogyne*. Relationships among these genera are summarized in Fig. 1. *Nelsonia* is monophyletic and sister to all other nelsonioids. We propose loss of bracteoles as a morphological synapomorphy for *Nelsonia* (versus paired bracteoles subtending each flower in other nelsonioids and, more broadly, Acanthaceae). *Elytraria* is also monophyletic and is sister to a “staurogynoid” clade consisting of all other genera of Nelsonioideae except *Nelsonia*. *Elytraria* can be delimited by at least three morphological synapomorphies: scaly peduncles, coriaceous to sclerophyllous bracts, and touch-sensitive stigmas. The existence of the “staurogynoid” clade was predicted by Hossain (2004) based on morphological similarities. Within this clade, monotypic *Saintpauliopsis* is sister to *Anisosepalum* and these together are sister to *Staurogyne*. Although no morphological synapomorphy for this “staurogynoid” clade has been identified, there is a tendency toward adnation of bracts to dichasial peduncles (cryptic epiphyllly) in all three genera. Adnation of bracteoles to the base of flowers (i.e., receptacle and calyx tube) is likely synapomorphic for the clade consisting of *Anisosepalum* and *Saintpauliopsis*. Hossain (1972) indicated that *Anisosepalum* and *Saintpauliopsis* (unlike other genera of Nelsonioideae) lack acicular fibers in roots, stems, petioles, and veins; this might represent an anatomical synapomorphy for these two genera. The Asian genus *Ophiorrhizophyllum* was shown to be nested among Asian taxa of *Staurogyne*, and the unispecific American genus *Gynocraterium* is sister to all of the sampled American species of *Staurogyne*. Although a case could be made for treating *Gynocraterium* as a distinct genus based on existing molecular data, this would involve considerable taxonomic renovations (see McDade et al. 2012), and there do not appear to be sufficient morphological grounds for such (see below under *Staurogyne*). As a result, we treat both *Ophiorrhizophyllum* and *Gynocraterium* in an expanded *Staurogyne*. Thus, all genera recognized here are monophyletic based on molecular data and each is morphologically distinguishable. Morphological synapomorphies are known for all genera except for *Staurogyne*.

MORPHOLOGY

The subfamily can be characterized morphologically by several presumed symplesiomorphies and at least one probable synapomorphy (descending-cochlear aestivation of corolla lobes as described below). Traditionally, the lack of cystoliths and of indurate, hooklike structures (retinacula) subtending the seeds have been important in distinguishing Nelsonioideae (e.g., Lindau 1895). These presumably symplesiomorphic attributes are shared with both *Avicennia* and genera of Thunbergioideae. The absence of cystoliths is also shared with the basalmost tribe (Acantheae) of subfamily Acanthoideae. An additional distinguishing character usually associated with Nelsonioideae is the presence of persistent endosperm in their

seeds (versus exalbuminous seeds in other acanthids). Discussion of this and some additional morphological characters, highlighting phylogenetic patterns and variation among Nelsonioideae is presented below.

Habit

Species of Nelsonioideae are either herbs or shrubs. They are mostly terrestrial, but epiphytic or epipetric plants are known in *Anisosepalum* and *Saintpauliopsis* and probably occur sporadically in other genera. Herbs vary in duration from annual to perennial. Annual herbs are apparently not common. Both *Elytraria marginata* and *Nelsonia gracilis* are commonly noted to be annuals (e.g., Morton 1956; Dokosi 1971; Vollesen 2013). Cultivated plants of *E. marginata* (*Daniel 11158cv* at CAS) persisted only for one year and produced viable seeds that yielded plants lasting only a single year. While most collections of *N. gracilis* consist of plants that appear to be annual, some (see below) have larger and somewhat woody roots suggesting that other plants may also become perennial. Perennial herbs, with woody roots, caudices, or stems, are a more common growth form among the subfamily. Herbs vary from acaulescent (i.e., with a basal rosette of leaves) to subcaulescent (i.e., with slight internodal elongation at or just above ground level) to caulescent (up to 1 m or more high). Most herbaceous species are consistent in growth form, but some vary from acaulescent to subcaulescent (e.g., *Elytraria acaulis*, seen in *Thwaites 240* at P), some from subcaulescent to caulescent (e.g., *Elytraria marginata*, seen in *Adam 2058* at P), and some from acaulescent to caulescent (e.g., *Nelsonia canescens*, seen in *Duthie s.n.* from India at UC). Shrubs are uncommon in *Anisosepalum* (e.g., *A. lewalli*), *Elytraria* (e.g., *E. nodosa*), and *Staurogyne* (e.g., *S. minarum*), and do not occur at all in *Nelsonia* or *Saintpauliopsis*. The habit of plants in at least one species (*E. imbricata*) varies from acaulescent herbs to weak shrubs. Thus, there is no clear pattern of evolution of plant habits at the level of genus but the trait merits further examination once a densely sampled phylogeny of the largest genus, *Staurogyne*, is available.

Leaves

Nelsonioideae exhibit greater variation in foliar disposition and arrangement than the other main lineages of Acanthaceae. Plants with leaves \pm evenly disposed along stems occur in all genera; basal clusters of leaves occur in all genera except *Anisosepalum*; and apical/aerial clusters of leaves occur in some *Elytraria*. Arrangement of the leaves varies from alternate (some *Elytraria*, *Nelsonia*, and *Staurogyne*) to subopposite (some *Staurogyne*) to opposite (all genera except *Elytraria*) to whorled (*Anisosepalum*, *Elytraria*).

Leaves of Nelsonioideae are either sessile or petiolate. If petiolate, then the petioles (bladeless portion only) are nearly always shorter than the blade, except in *Saintpauliopsis* and at least one species of *Staurogyne* (*S. chapaensis*), in which the petioles are conspicuously longer than the blades.

Leaf variation is particularly evident in *Elytraria*. In addition to variation in disposition and arrangement as noted above, length of leaf blades in the genus varies from 4 mm (*E. filicaulis*) to 310 mm (*E. caroliniensis*) and the margin varies from entire to sinuate to pinnatisect. Some of the variation in

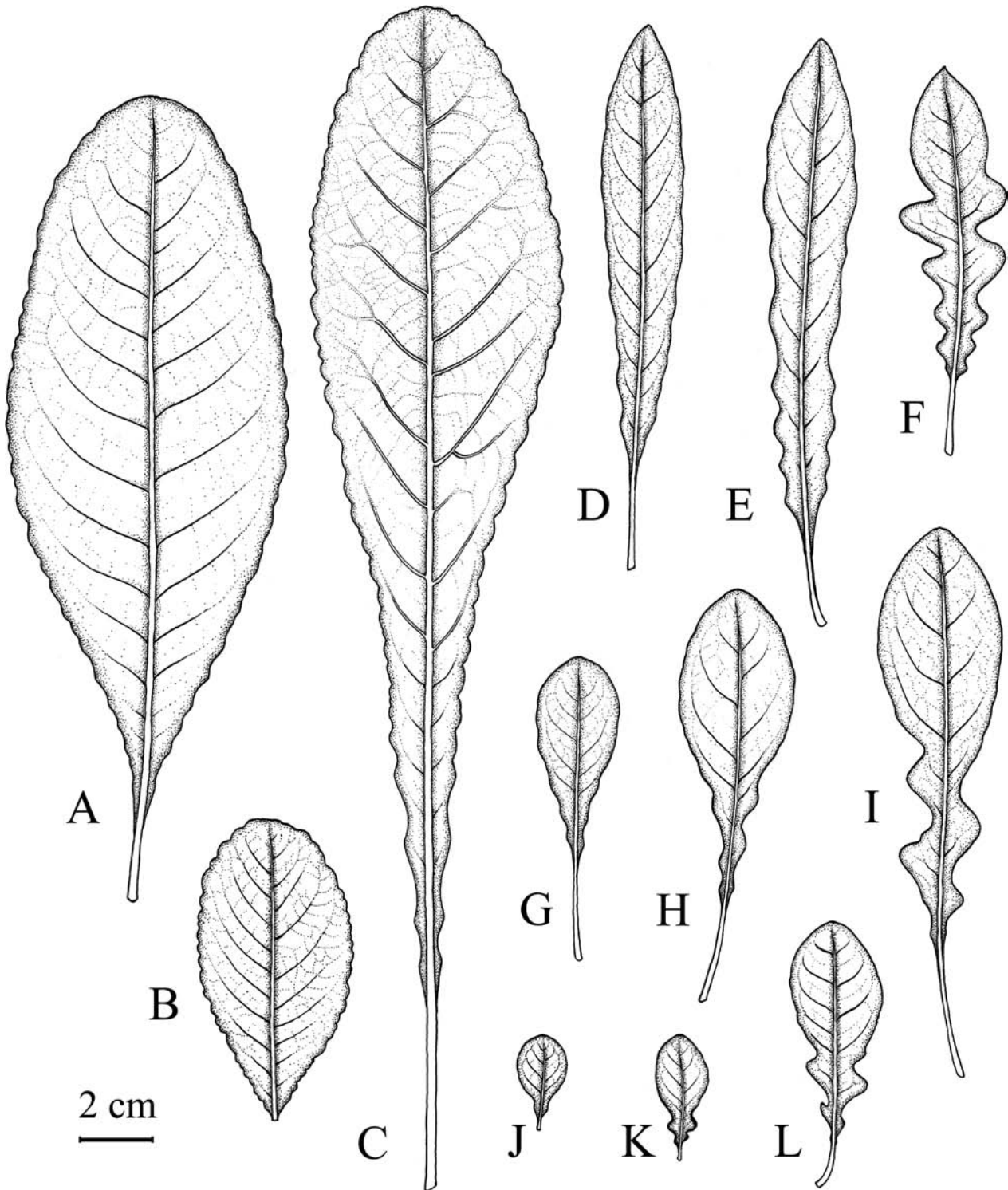


Fig. 2. Leaf variation in *Elytraria acaulis* from India and Sri Lanka.—A. Drummond 26727 (UC).—B. Diraviam & Xavier 20726 (A).—C. Amrita s.n. (ASU).—D. Fagerlind 3925 (S).—E. Kostermans & Wirawan 824 (G).—F. van Beusekom 1653 (US).—G. Dittus WD70012102 (US).—H. Jayasuriy et al. 622 (US).—I. Fosberg 50210 (US).—J. Davidse & Sumithraarachchi 8131 (US).—K. Wight 2174 (NY).—L. Wight 2174 (GH). Drawn by N. Pugh.

shape, size, and margin among leaves of *E. acaulis* from India and Sri Lanka is shown in Fig. 2.

Apical/aerial whorls or clusters of leaves may be synapomorphic for some species within *Elytraria*, but phylogenetic patterns for foliar characteristics are otherwise unclear.

Inflorescences

Inflorescences of Acanthaceae are often complex or highly modified. The basic unit of inflorescences in Nelsonioideae, as in most other Acanthaceae, is a dichasium. The dichasial

nature is reflected by the paired bracteoles that subtend each flower. Throughout the subfamily the dichasium is modified by reduction to a single flower. Dichasia of *Nelsonia* have undergone further reduction by the loss of both bracteoles (although they are very rarely [teratologically?] present below some flowers). Dichasia may be sessile or pedunculate; flowers may be sessile or pedicellate. The dichasia sometimes occur in leaf axils, but more commonly they are subtended by a bract and grouped into sessile to pedunculate spikes (i.e., both dichasia and flowers sessile to subsessile), racemes (i.e., dichasia sessile to subsessile and flowers pedicellate), or thyrses (i.e., dichasia pedunculate and flowers sessile or pedicellate). Each of the spikes, racemes, and thyrses are uncommonly branched to form a panicle. Arrangement of bracts varies from alternate (spirally arranged) in all genera to sometimes subopposite in *Anisosepalum* to sometimes opposite in *Staurogyne*.

Unlike variation in plant habit and leaf disposition, inflorescence traits show considerable phylogenetic pattern. In addition to the synapomorphic absence of bracteoles in *Nelsonia*: 1) scales on inflorescence peduncles are synapomorphic for *Elytraria*; 2) bracts with paired, subapical, winglike teeth are autapomorphic for *E. imbricata*; 3) adnation of bracts to dichasial peduncles may be synapomorphic for *Anisosepalum*, *Saintpauliopsis*, and *Staurogyne* (although this trait is difficult to assess owing to the absence of dichasial peduncles and pedicels in the spicate inflorescences of *Elytraria* and *Nelsonia*); and 4) adnation of bracteoles to the floral receptacle and calyx tube may be synapomorphic for *Saintpauliopsis* + *Anisosepalum*.

Flowers

As in other major lineages of Acanthaceae, floral diversity among Nelsonioideae is particularly evident (Fig. 3). The calyx varies from deeply four- to five-parted. Although calyces of some species of *Staurogyne* have five homomorphic lobes, those of most species are conspicuously heteromorphically lobed (1 + 2 + 2). The posterior lobe is often the largest. The two lateral lobes are often the smallest, internal to the posterior and anterior lobes, and obscured by the adjacent bracteoles (when present). In most plants, the anterior lobes are connate to a greater extent than the other calyx lobes; more rarely they are completely fused into a single lobe or divided nearly to the base. In *Elytraria*, the anterior lobes (irrespective of the degree of fusion) show a conspicuous constriction proximally.

Corollas of all Nelsonioideae appear to share a unique, putatively synapomorphic aestivation pattern, descending-cochlear, with the corolla lobes arranged in bud such that the lower-central lobe is innermost (overlapped on each side by the lateral lobes of the lower lip) and the two lobes of the upper lip are outermost (with one overlapping the other, and each overlapping the lateral lobes of the lower lip; see McDade et al. 2012: Fig. 1A–D). We observed this pattern in buds representing each genus of the subfamily. The corolla tube varies from subcylindric to funnellform and is sometimes divisible into a narrowly cylindrical proximal portion and an expanded (\pm triangular) throat. Much of the floral diversity among Nelsonioideae results from variation in the orientation and form of the limb of the corolla. The limb is usually strongly zygomorphic, but is nearly actinomorphic in some species (e.g., *Elytraria caroliniensis*; Fig. 3B). It consists of a bilobate upper

lip and a trilobate lower lip. The lips may project forward (in line with the tube) or be reflexed at angles to 90° with respect to the tube. Colored markings sometimes occur on some portion of—or throughout—the limb. The variation in size, shape, and color of corollas undoubtedly reflects adaptations to diverse pollinators. Braz (2005) noted two groups of species of *Staurogyne* based on floral morphology and suggested that these corresponded to melitophily and ornithophily. Although she did not provide evidence of visitation to these flowers by bees or hummingbirds, we agree with her assessments based on floral morphology.

Variation in features of the androecium provide important diagnostic characters for distinguishing taxa of Nelsonioideae, but few synapomorphic traits are evident. Two stamens are present in *Nelsonia*, most *Elytraria*, and a few species of *Staurogyne*. Four stamens characterize *Anisosepalum*, Malagasy species of *Elytraria*, *Saintpauliopsis*, and most species of *Staurogyne*. Short and usually inconspicuous staminodes have been noted in all genera except *Nelsonia*. Although up to 3 staminodes have been reported in species of Nelsonioideae, usually only a single staminode (in posterior position) is present. Anthers are bitheous with the thecae equally inserted on the filament in all genera. The connective of the filament is sometimes extended beyond the anthers and appears as an apical appendage (e.g., in some *Elytraria* from the Old World). The thecae are glabrous in all genera except *Anisosepalum* and some *Staurogyne*, in which they are pubescent with eglandular and/or glandular trichomes. The occasional presence of widely divergent anther thecae (i.e., forming a right angle with the filament/connective so that the pair is horizontally positioned with the apex of each theca adjacent, i.e., with stamen T-shaped), as in some *Nelsonia* and *Staurogyne*, is not otherwise common among Acanthaceae. In some *Staurogyne* (e.g., *S. capitata* and *S. macrobotrya*) the thecae are apparently divergent nearly 180° so that they appear upside down (i.e., with stamen Y-shaped). Basal or subbasal appendages are found in at least some species of each genus of Nelsonioideae except *Elytraria* (Fig. 4A–C). Appendages are often flaplike and appear to be associated with dehiscence. Appendages in *Saintpauliopsis* differ from those in other genera by being bifurcate, a probable autapomorphy for the genus. Dehiscence of the anthers appears to be nototribic (i.e., toward the lower lip) in all genera except *Nelsonia*, in which it is pleurotribic (i.e., toward each other).

The gynoecium consists of a cylindrical to conic ovary with a terminal, filiform style bearing an apical, \pm two-parted stigma. Manifestations of the stigma, which can be difficult to observe in some dried and pressed specimens, offer important diagnostic characters among Nelsonioideae. Variation in stigma form for the subfamily was illustrated by Hossain (2004). Stigmas vary from (equally to) subequally to unequally bilobed, or rarely crateriform (Fig. 4D). In all species of *Anisosepalum* the longer of the unequal lobes is equally bifurcate, a probable synapomorphy for the genus although similar bifurcation of stigma lobe(s) occurs in some *Nelsonia* and *Staurogyne*. Stigmas of *Elytraria* are remarkably distinctive. They consist of a broad, flattened lobe that folds over the anthers, rapidly unfolds when touched, and slowly refolds over several minutes. These touch-sensitive stigmas appear to play a role in pollination, as they are located at the mouth of the corolla or in the corolla tube, and must be touched before the

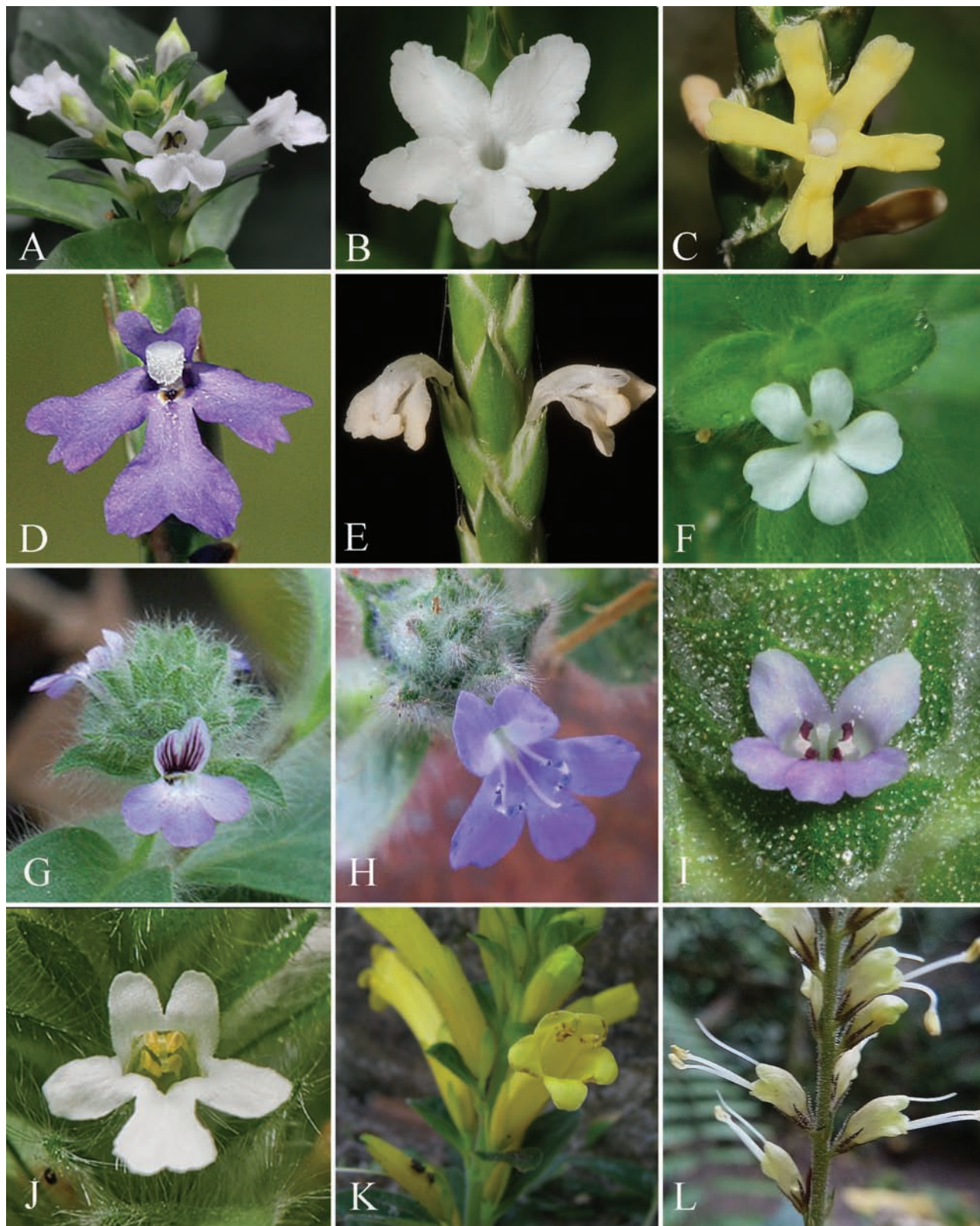


Fig. 3. Flowers of Nelsonioideae.—A. *Anisosepalum alboviolaceum* (Congo-Brazzaville), photo courtesy of Chrisje Horions and Quentin Groom.—B. *Elytraria caroliniensis* (USA), photo by Thomas Daniel.—C. *Elytraria macrophylla* (Mexico), photo by Thomas Daniel.—D. *Elytraria imbricata* (Mexico), photo courtesy of Jon Rebman.—E. *Elytraria marginata* (São Tomé and Príncipe), photo courtesy of Wes Eckerman.—F. *Nelsonia canescens* (Australia), photo courtesy of Russell Cumming.—G. *Nelsonia canescens* (India), photo courtesy of Dinesh Valke.—H. *Nelsonia canescens* (Zambia), photo courtesy of Helen Pickering.—I. *Nelsonia canescens* (Costa Rica), photo courtesy of Barry Hammel.—J. *Staurogyne stolonifera* (South America), photo courtesy of Kris Weinhold.—K. *Staurogyne flava* (Brazil), photo courtesy of Mauro Peixoto—www.brazilplants.com.—L. *Staurogyne* (*Ophiorrhizophyllon*) *macrobotrya* (China), photo courtesy of Erin Tripp.

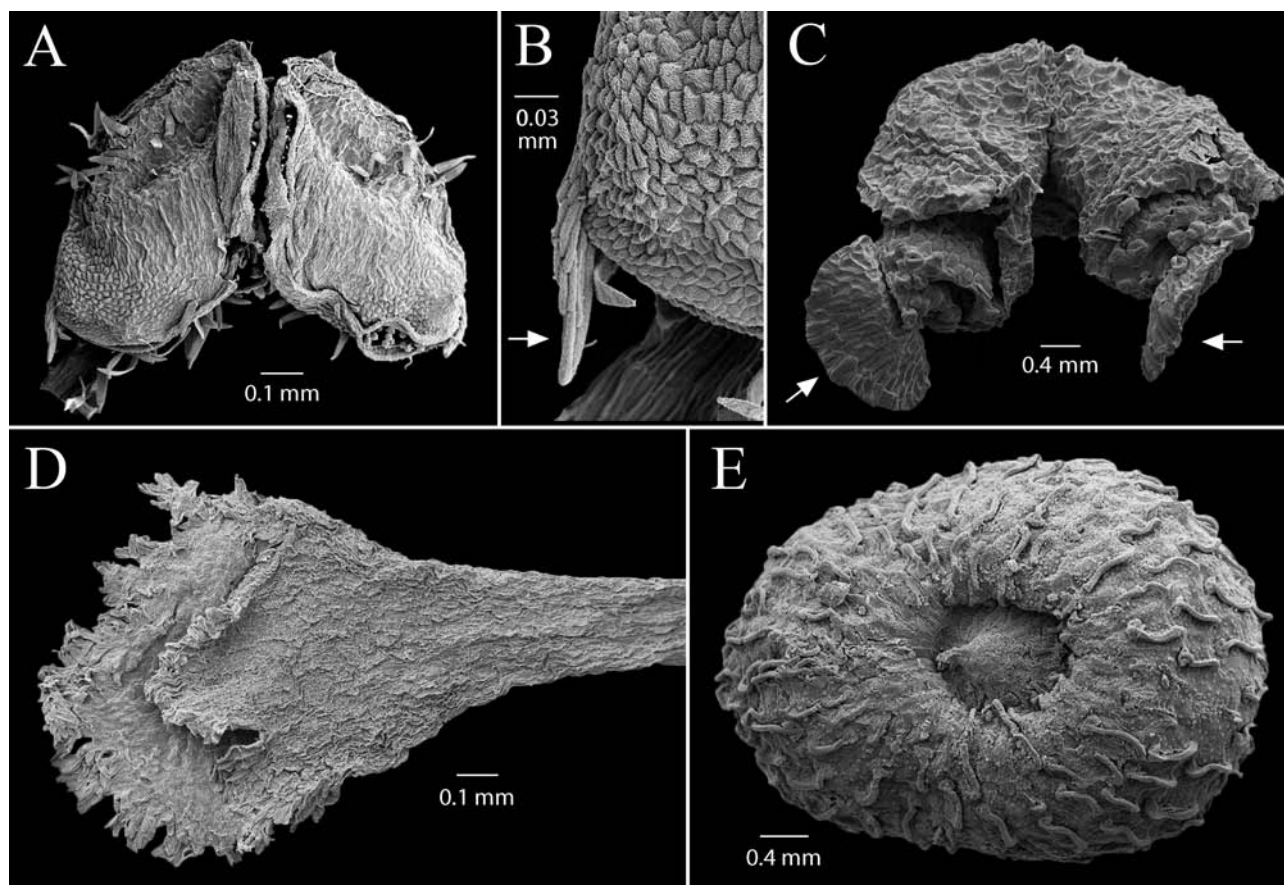


Fig. 4. Reproductive structures (SEM) of Nelsonioideae.—A. Sagittate anther thecae of *Nelsonia canescens* (Daniel 11176) showing eglandular trichomes and basal appendages.—B. Basal portion of theca of *N. canescens* (Daniel 11176) showing basal appendage (arrow).—C. Subsagittate anther thecae of *Stauogyne spatulata* (Toroes 4795) showing flap-like basal appendages.—D. Distal portion of gynoceium of *Stauogyne guianensis* showing unequal lobes of subcrateriform stigma (Jansen-Jacobs 2852).—E. Seed of *Nelsonia gracilis* (Bingham & Mpundu 122660) showing prominent hyalar depression.

pollen from their flower is revealed. A minute and inconspicuous second lobe is often evident near the base of the broad lobe on stigmas of *Elytraria*. These traits of the stigma provide clear synapomorphies for *Elytraria*.

Pollen

Palynological characters have been widely employed in classification of Acanthaceae since the late 19th century (e.g., Radlkofer 1883; Lindau 1895); indeed, the family apparently exhibits more diversity in pollen morphology than any other family of plants (Lindau 1895; Raj 1961). Phylogenetic signal at varying taxonomic levels has been associated with pollen sculptural characters of Acanthaceae (e.g., Scotland 1993; Scotland and Vollesen 2000; McDade et al. 2000; Manktelow et al. 2001; Kiel et al. 2006; Daniel et al. 2008). Published studies comparing pollen from all currently treated genera of Nelsonioideae are lacking.

We sampled pollen of 28 species of Nelsonioideae as follows (see Appendix I): *Anisosepalum* (3), *Elytraria* (13), *Nelsonia* (2), *Saintpauliopsis* (1), and *Stauogyne* (9). Size, shape, and sculpturing of grains were observed in non-acetolyzed samples of dry pollen using scanning electron and some light microscopy. Additional data have been derived from Raj

(1961, 1973), Hossain (1971), Scotland (1990), and Braz (2005). Descriptive terminology for pollen generally follows that of Walker and Doyle (1975), with additional insights from Hesse et al. (2009). Results of our observations are provided in Appendix 1, summarized for the subfamily here, and summarized for each genus in the accounts below.

Pollen of Nelsonioideae (Fig. 5–8) varies in shape from oblate spheroidal to spherical to prolate (P:E = 0.82–2.43) in equatorial views and from round to triangular (planaperturate) in polar view. Variation in size encompasses three size classes, small to large. The polar axis varies from 13–58 μm , and the equatorial axis varies from 11–36 μm . Based on sampling to date, the smallest known grains among Nelsonioideae are in several species of *Stauogyne* (e.g., *S. repens*; P = 13–15 μm , E = 15–18 μm ; Braz 2005); *Elytraria caroliniensis* has the largest grains (P = 56–58 μm , E = 28–36 μm).

All grains are triaperturate. The interapertural exine is (microreticulate to) reticulate, but in some grains (non-acetolyzed) it appears \pm psilate to microfoveolate to foveolate. The muri of the reticulum vary from psilate to microverrucate. Apertures of Nelsonioideae consist of elongate colpi, which may or may not contain a centrally located endoaperture (os). In a developmental study, Johri and Singh (1959: 233) indicated the presence of “three germ pores” each situated in

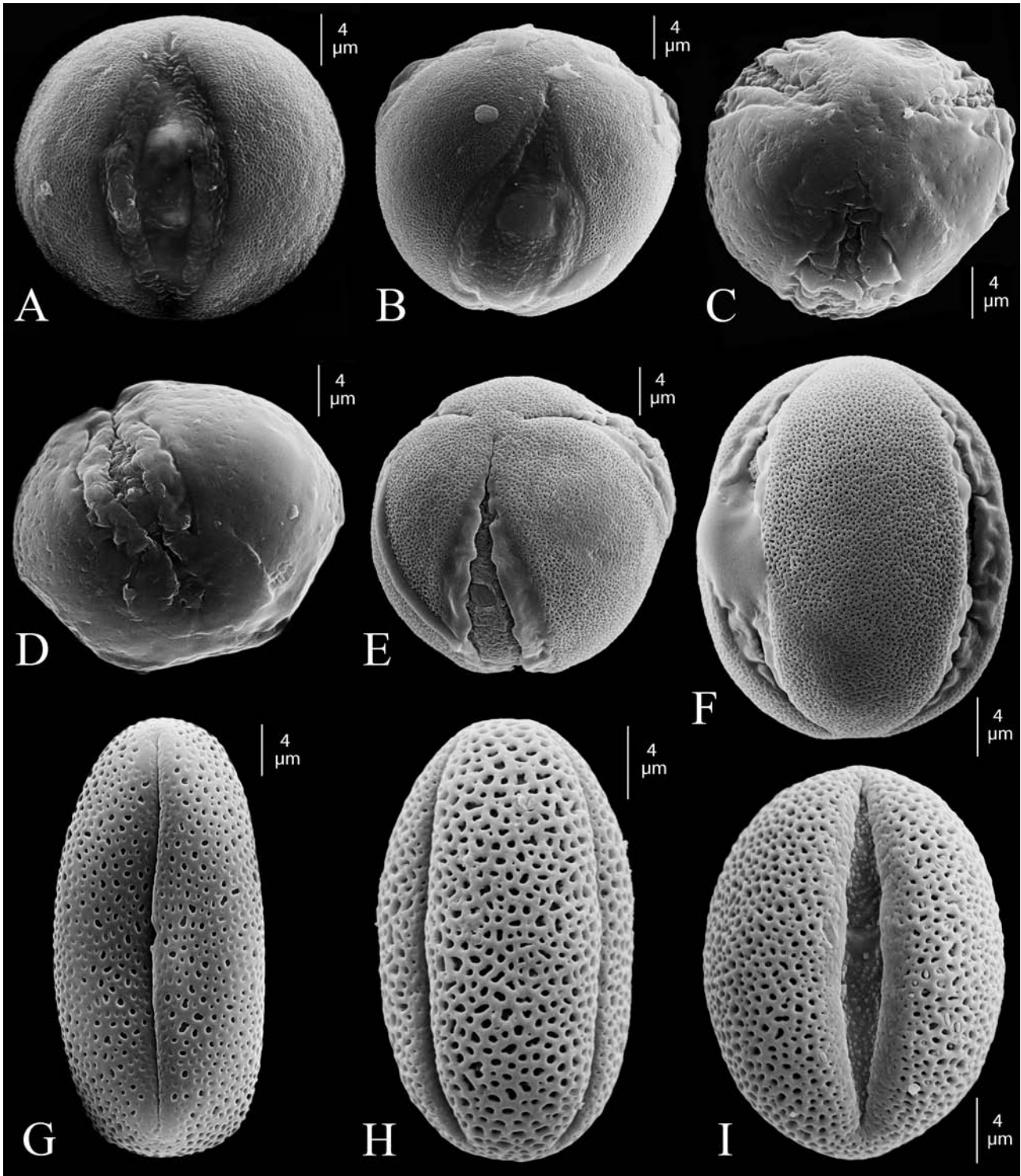


Fig. 5. Pollen of *Anisosepalum* and *Nelsonia*.—A. *Anisosepalum humbertii* (de Witte 7121), apertural view.—B. *Anisosepalum humbertii* (de Witte 7121), subpolar view.—C. *Anisosepalum alboviolaceum* (Louis 12208), polar view.—D. *Anisosepalum alboviolaceum* (Louis 12208), subpolar view, note two differentiated bands along margins of colpi here and in other views of *Anisosepalum* pollen.—E. *Anisosepalum lewallii* (Reekmans 3610), subpolar view.—F. *Anisosepalum lewallii* (Reekmans 3610), interapertural view.—G. *Nelsonia canescens* (Daniel 11186), apertural view.—H. *Nelsonia gracilis* (Bingham & Mpundu 122660), interapertural view.—I. *Nelsonia gracilis* (Bingham & Mpundu 122660), apertural view.

a colpus in young pollen grains of *Elytraria acaulis*. Using light microscopy, Raj (1961) determined that pollen of *Elytraria* (1 sp.), *Nelsonia* (1 sp.), and *Staurogynne* (3 spp.) was tricolpate. In a subsequent examination of additional species (Raj 1973: 96),

S. spatulata (as *S. glauca*) was described as tricolpate, but with “indication of a faint os at each aperture,” and *E. acaulis* was described as tricolpate. Based on acetolyzed grains, Hossain (1971) noted that *Elytraria* (including *E. acaulis*), *Saintpau-*

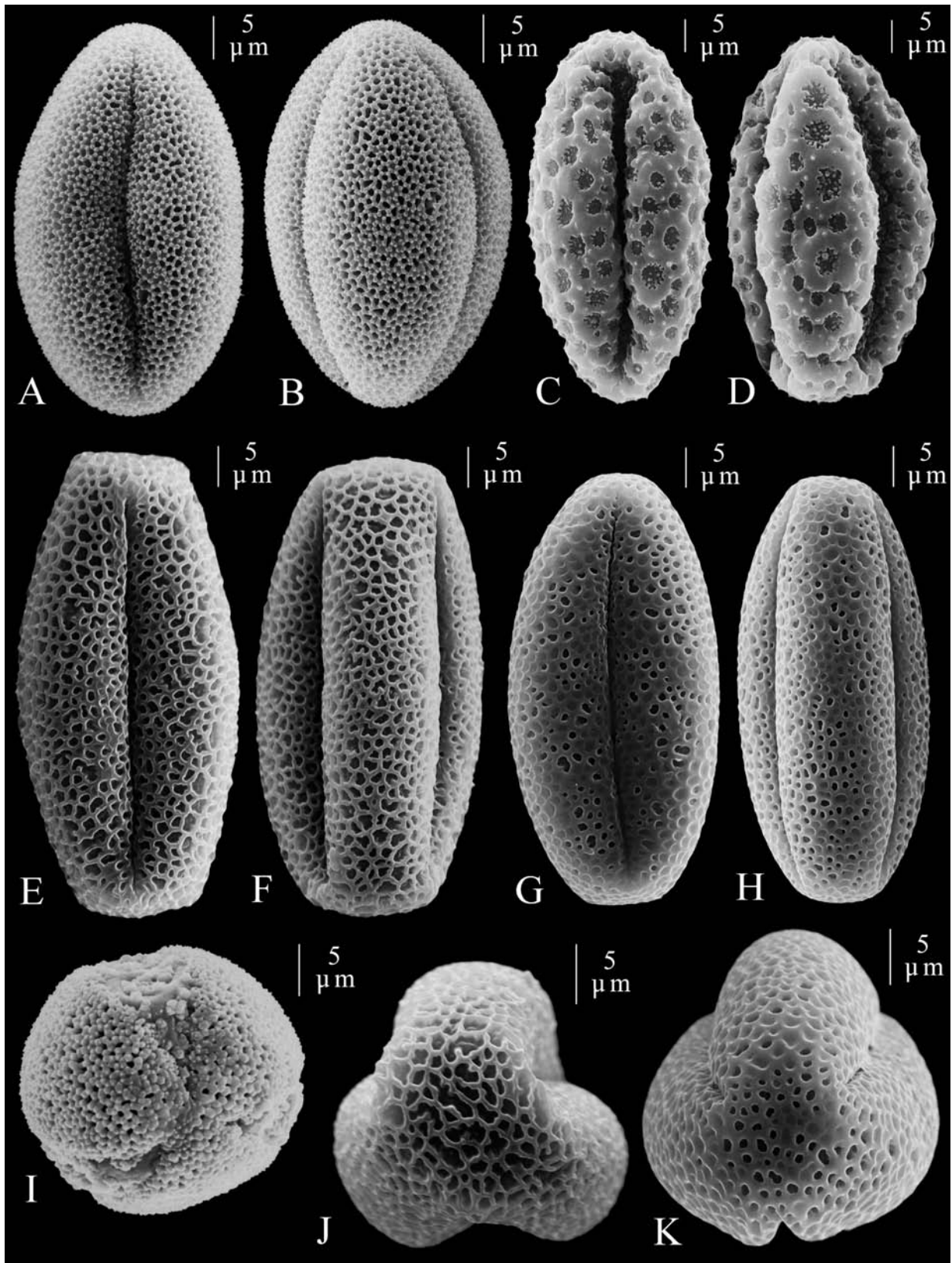


Fig. 6. Pollen of *Elytraria*.—A. *Elytraria imbricata* (Daniel 10184), apertural view.—B. *Elytraria imbricata* (Daniel 10184), interapertural view.—C. *Elytraria caroliniensis* (Daniel s.n.cv-cultivated), apertural view.—D. *Elytraria caroliniensis* (Daniel s.n.cv), interapertural view.—E. *Elytraria marginata* (Daniel 11158), apertural view.—F. *Elytraria marginata* (Daniel 11158), interapertural view.—G. *Elytraria nodosa* (Almeda 9232), apertural view.—H. *Elytraria nodosa* (Almeda 9232), interapertural view.—I. *Elytraria macrophylla* (Dressler 2619), polar view.—J. *Elytraria marginata* (Daniel 11158).—K. *Elytraria nodosa* (Almeda 9232), polar view.

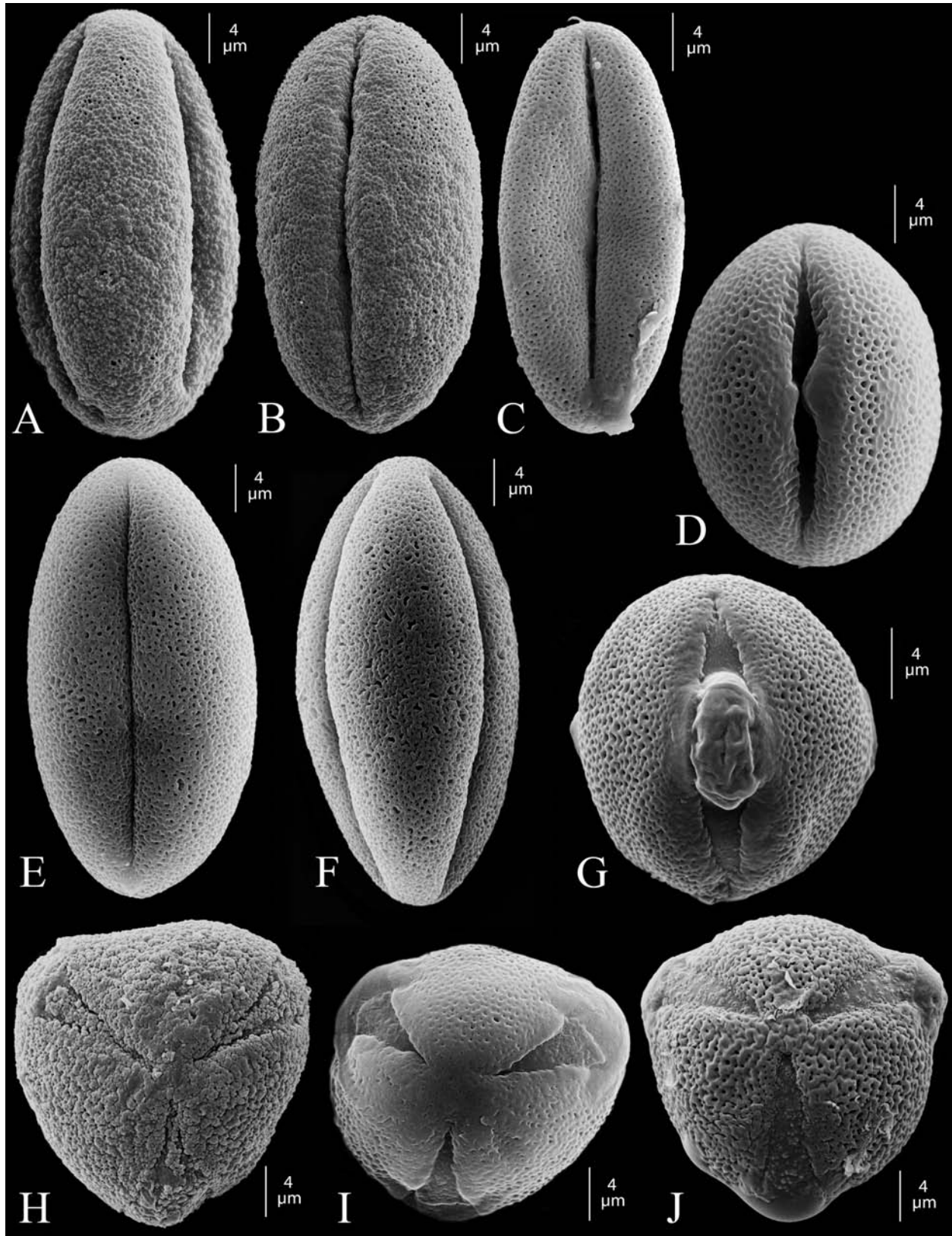


Fig. 7. Pollen of *Saintpauliopsis* and *Staurogyne*.—A. *Saintpauliopsis lebrunii* (Bamps 3270), interapertural view.—B. *Saintpauliopsis lebrunii* (Bamps 3270), apertural view.—C. *Staurogyne macrobotrya* (Hansen & Smitinand 12817), apertural view.—D. *Staurogyne mandioccana* (Cordeiro & Silva 108), apertural view.—E. *Staurogyne concinnula* (Bartholomew & Boufford 6215), apertural view.—F. *Staurogyne concinnula* (Bartholomew & Boufford 6215), interapertural view.—G. *Staurogyne spatulata* (Toroes 4795), apertural view, note prominent endoaperture.—H. *Saintpauliopsis lebrunii* (Gautier et al. 3598), polar view.—I. *Staurogyne spatulata* (Maxwell 94-76), polar view.—J. *Staurogyne major* (Kerr 10264), polar view, note prominent endoapertures.

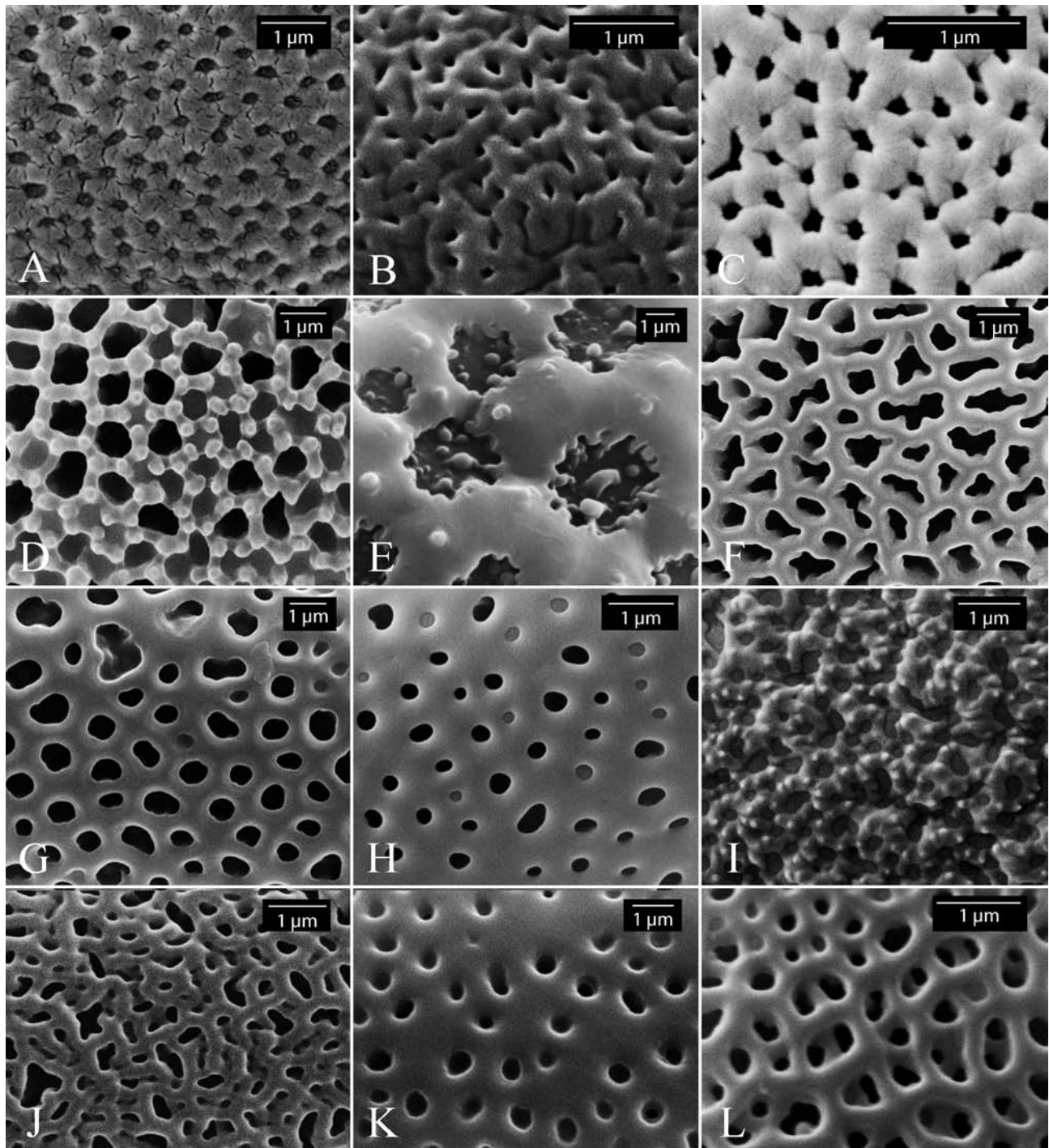


Fig. 8. Interapertural exine surfaces of pollen of Nelsonioideae.—A. *Anisosepalum alboviolaceum* (Champluvier 5295).—B. *Anisosepalum humbertii* (de Witte 7121).—C. *Anisosepalum lewalliei* (Reekmans 3610).—D. *Elytraria imbricata* (Daniel 10184), note microverrucate muri.—E. *Elytraria caroliniensis* (Daniel s.n.cv.cultivated), note microverrucate muri.—F. *Elytraria marginata* (Malaisse & Claes 14802).—G. *Elytraria nodosa* (Almeda 9232).—H. *Nelsonia canescens* (Daniel 11186).—I. *Saintpauliopsis lebrunii* (Bamps 3270), note microverrucate muri.—J. *Staurogyne concinnula* (Bartholomew & Boufford 6215).—K. *Staurogyne guianensis* (Jansen-Jacobs et al. 2346).—L. *Staurogyne mandioccana* (Cordeiro & Silva 108).

liopsis, and *Gynocraterium* have tricolpate pollen whereas the other genera of Nelsonioideae also possess either some—or clear evidence of—endoapertures. He concluded that pollen of Nelsonioideae is basically tricolpate with a trend to tricolporate (via “tricolporoidate”) grains in several genera. Scotland

(1990) contended that in Nelsonioideae colpate pollen was restricted to *Elytraria*. He characterized pollen of three species of *Elytraria* as tricolpate, *E. acaulis* as tricolporate (but with the endoapertures often indistinct with light microscopy), *Nelsonia canescens* and *Saintpauliopsis lebrunii* as tricolporate,

and 17 species of *Staurogyne* (including *Gynocraterium macrobotryum*) from both the Old World and the New World as tricolporate (but with endoapertures often indistinct). Indeed, the indistinctness of endoapertures had led Raj (1961) to describe some of the same species as tricolpate. Twenty-seven Neotropical species of *Staurogyne* were characterized as tricolporate (Braz 2005; Braz and Monteiro 2011), and endoapertures are evident in most of the images provided for these taxa by these authors.

Contradictory reports for the type of apertures (colpi vs. colpori) among taxa of Nelsonioideae undoubtedly reflect 1) the difficulty of seeing endoapertures in grains where the flanks of the colpi are “closed” and do not reveal the interior contents (e.g., Fig. 5G, 6A,E,G, 7B,C,E), and/or 2) their rather weak manifestation, even in “open” colpi compared to most other Acanthaceae with compound apertures (at least in mature grains; e.g., Fig. 5A–F, 7H,I). It is evident from the studies noted above, which have used various techniques (e.g., acetolyzed and non-acetolyzed pollen, whole grains and sectioned grains) and both light and scanning electron microscopy, that acetolysis does not always help to reveal the presence or absence of endoapertures in Nelsonioideae. It is possible that all Nelsonioideae have endoapertures, but that these are cryptic (or become so in later stages of development) in some taxa. Our observations, using non-acetolyzed pollen and both light and scanning electron microscopy, largely agree with those of Hossain (1971). Thus, endoapertures among Nelsonioideae vary from absent (or imperceptible) to inconspicuous to conspicuous.

The apparent taxonomic pattern of aperture type among genera of Nelsonioideae (including colpate and colporate pollen, which also both occur among other Acanthaceae and related families) does not appear to be phylogenetically informative. However, the lack of subsidiary apertures (e.g., pseudocolpi) and other modifications (e.g., biretulate exine, bifurcate colpi, sexine lips) implicate Nelsonioideae (as well as Thunbergioideae, *Avicennia*, and Acanthaceae) as likely more basal in the family. This implication has been confirmed by several molecular phylogenetic analyses (e.g., McDade et al. 2012).

Johri and Singh (1959) indicated that pollen of *Elytraria acaulis* used in their developmental studies was syncolpate. Pollen with colpi fused at one or both poles was not encountered in our studies of Nelsonioideae; however, the syncolpate condition is sometimes variable within species of Acanthaceae (e.g., *Aphelandra*; McDade 1984; Daniel 1991).

Some variation in pollen sculpturing among Nelsonioideae appears to have phylogenetic and/or taxonomic significance. Pollen of all species of *Anisosepalum* differs from that of other genera of Nelsonioideae in two features: conspicuous ridges near margins of colpi (Fig. 5A–F), and microreticulate (i.e., lumina <1 µm in diameter) exine (Fig. 8A–C). In *Elytraria caroliniensis* the reticulum of the exine has much broader muri (Fig. 6C,D, 8E) than encountered elsewhere in the subfamily. Based on this feature and its large size, pollen of *E. caroliniensis* is the most distinctive in the genus. Microverrucate muri (Fig. 8D,E,I) occur only in *Saintpauliopsis* and in *Elytraria* from the New World. Although microverrucate muri are present in all pollen samples of *Elytraria* from the New World examined to date, pollen has yet to be examined for any species from the West Indies (flowers for most species there remain unknown). All species of *Elytraria* from the Old World have psilate muri.

Because phylogenetic work to date indicates that New World species of *Elytraria* (inclusive of the one West Indian species sampled) are monophyletic, we predict that West Indian species will also have pollen with microverrucate muri.

Fruits

Fruits of Nelsonioideae, like most other Acanthaceae, consist of indurate and loculicidal capsules that dehisce explosively into two valves. They show only minor diversity of size and shape among or within genera, unlike other major lineages of Acanthaceae that encompass considerably more variation. Nelsonioid capsules are estipitate, usually ovoid to subconic to linear-ellipsoid in shape, fertile from the base, and sterile apically (Fig. 9). They lack the indurate and hooklike retinacula subtending the seeds that are synapomorphic for subfamily Acanthoideae. The presence of papilliform retinacula has often been noted for genera of Nelsonioideae. This presumably refers to the discolored regions of septum where a papilliform connection (to 0.1 mm long) to the seed sometimes remains (Fig. 9A–D). Hossain (1972) also noted the presence of non-indurate and caducous retinacula in *Anisosepalum*, but he did not describe or illustrate these. In *Anisosepalum alboviolaecum*, we observed coarse, threadlike connections (0.1–0.4 mm long) from discolored regions of septum to ovules and seeds (Fig. 9E). Whether these structures are homologous to the retinacula encountered in Acanthoideae remains to be determined.

Hossain (1971, 2004) noted the rare presence of tardily dehiscent or indehiscent capsules in some *Staurogyne*, and he noted that this characteristic had been the basis for the African genus *Staurogynopsis*. Champluvier (1991) described the African species of *Staurogyne* section *Zenkerina* as having capsules with a membranous (vs. indurate in other species) wall and both delayed and non-explosive dehiscence. Tardily dehiscent or indehiscent capsules are also known elsewhere in the family in genera with otherwise regularly dehiscent capsules (e.g., *Justicia*; Hedrén 1989), and likely represent a specialization that has occurred numerous times in the family.

Seeds, Hygroscopic Trichomes, and Endosperm

Ovules and seeds among Nelsonioideae tend to be more numerous than elsewhere in the family. The number of seeds that develop per capsule varies from six (e.g., *Elytraria* spp., *Staurogyne carvalhoi*) to 68 (e.g., *Staurogyne* spp.). Mature seeds are generally smaller than in other Acanthaceae. The longest axis varies from 0.3 to 2 mm, but in most species is less than 1 mm. *Anisosepalum* has the largest seeds, with the longest axis varying from 1.1 to 2 mm. Dimensions of seeds that have been expelled from the mature capsule can be difficult to attribute to length, width, or height because the hylar scar is not always evident and the seeds are usually irregular in shape (frequently somewhat blocky to oblong to ellipsoid to subhemispheric to cochlear). However, the hylar scar forms a conspicuous depression in *Anisosepalum* and to a lesser extent in *Nelsonia* (Fig. 4E). The surface of seeds varies from smooth to reticulate to foveolate, and sometimes includes minute protrusions (e.g., verrucae, gemmae, baculae, etc.; Fig. 10–12). The presence or absence of seminal trichomes was found to be useful in characterizing the five genera of Nelsonioideae. They are apparently universal in all genera except *Elytraria* and *Anisosepalum*, in which they do not occur.

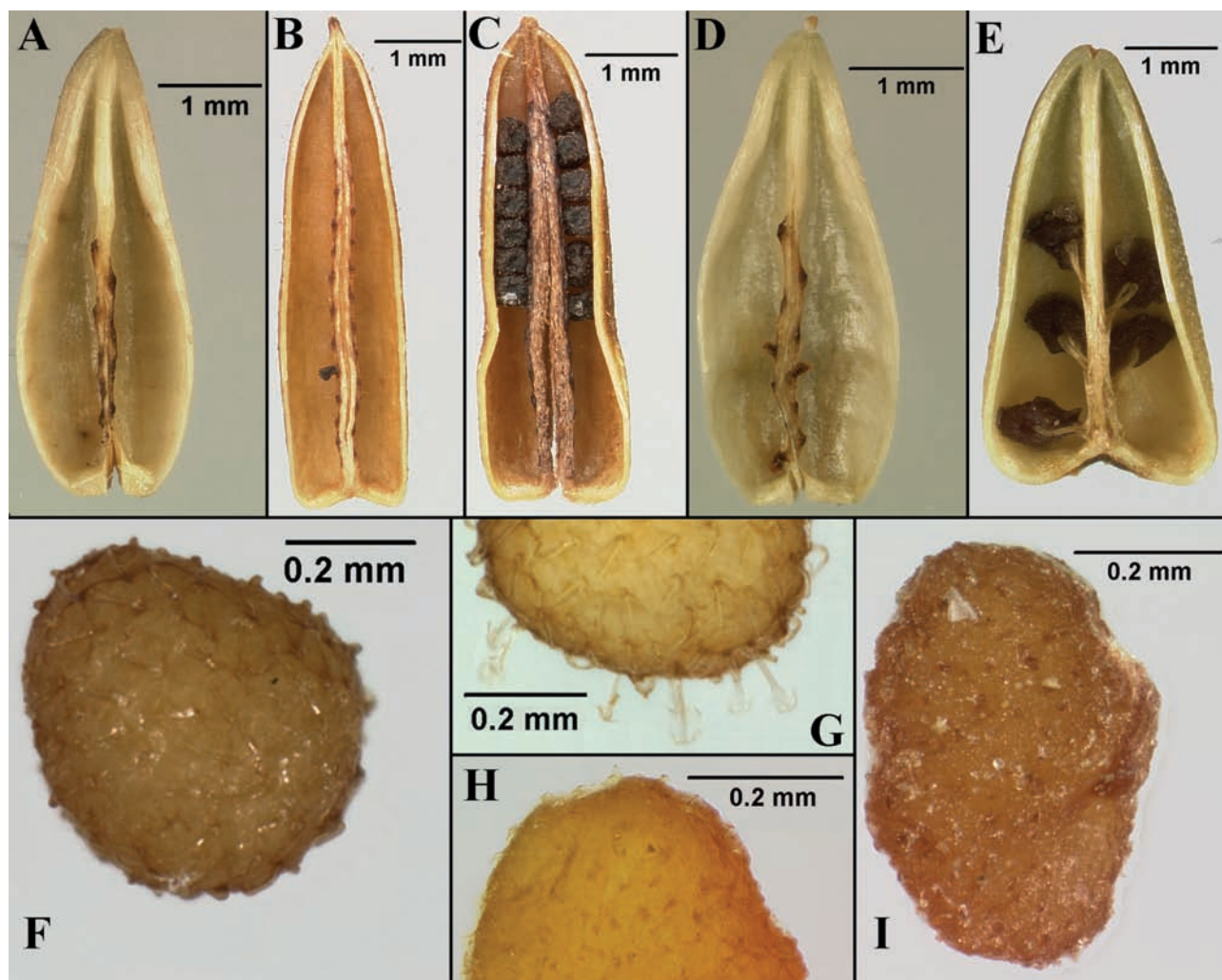


Fig. 9. Capsules and seeds of Nelsonioideae.—A. Capsule valve of *Elytraria caroliniensis* (Cooley et al. 9135) showing darkened funicular regions where nine seeds were attached.—B. Capsule valve of *Staurogyne merguensis* (Maxwell 94-234) showing darkened funicular regions where 24 seeds were attached (with one aborted seed remaining).—C. Capsule valve of *Staurogyne obtusa* (Maxwell 90-362) showing both unejected seeds and funicular regions of ejected seeds.—D. Capsule valve of *Elytraria marginata* (Daniel 11158 cv-cultivated) showing slight funicular elongations from some funicular regions.—E. *Anisosepalum albviolaceum* (Champluvier 5295) showing five immature seeds with non-indurate funicular elongations below each.—F. Dry seed of *Nelsonia canescens* (Daniel 11186) with hygroscopic trichomes appressed.—G. Portion of hydrated seed of *N. canescens* (Daniel 11186) showing strong hygroscopic reaction of trichomes.—H. Portion of hydrated seed of *S. concinnula* (Peng 6777) showing moderate hygroscopic reaction of trichomes.—I. Dry seed of *Staurogyne concinnula* (Peng 6777) with hygroscopic trichomes appressed. See text for details.

Seminal trichomes of Nelsonioideae are simple or usually branched; the number of branches per trichome can vary on a seed. The trichomes are also hygroscopic.

Hygroscopic trichomes in Acanthaceae are usually appressed to the seed surface and expand and/or become erect on being wetted with water; they often discharge mucilage. Such trichomes have long been known among various Acanthaceae (Kippist 1845). They occur on seeds of some taxa in two of the three currently recognized subfamilies (Nelsonioideae and Acanthoideae) and in six of the seven tribes of Acanthoideae: Ruellieae (Tripp et al. 2013), Justicieae (e.g., Daniel 1990; Daniel and Figueiredo 2009), Barlerieae (Manktelow et al. 2001; McDade et al. 2008), Acantheae (Vollesen 2000; McDade et al. 2005), Whitfieldieae (Manktelow et al. 2001; McDade et al. 2008), and Neuracanthaeae (Bidgood and Brummitt 1998; McDade et al. 2008). Whether

hygroscopic trichomes in all of these taxa are homologous remains to be determined. To our knowledge, hygroscopic trichomes are not known to occur on seeds of *Avicennia*, Thunbergioideae, or Acanthoideae: Andrographideae.

Hygroscopic trichomes on seeds of Nelsonioideae were illustrated by Oersted (1855) and Lindau (1895). In this subfamily apically hooked, double-hooked (i.e., anchor shaped), or multi-branched trichomes that lack copious mucilage are appressed to the dry seed surface (Fig. 9F,I, 11G-I, 12); these usually become erect (and clearly visible) upon hydration (Fig. 9G,H). Kippist (1845: 73) noted that whereas trichomes of *Nelsonia* “expand very slowly when wetted,” in two species now treated in *Staurogyne*, a similar reaction to water was inconclusive “owing to [the trichomes’] extreme minuteness, and the very slight action which water has upon them.” Our results (Appendix 2) were similar. Trichomes

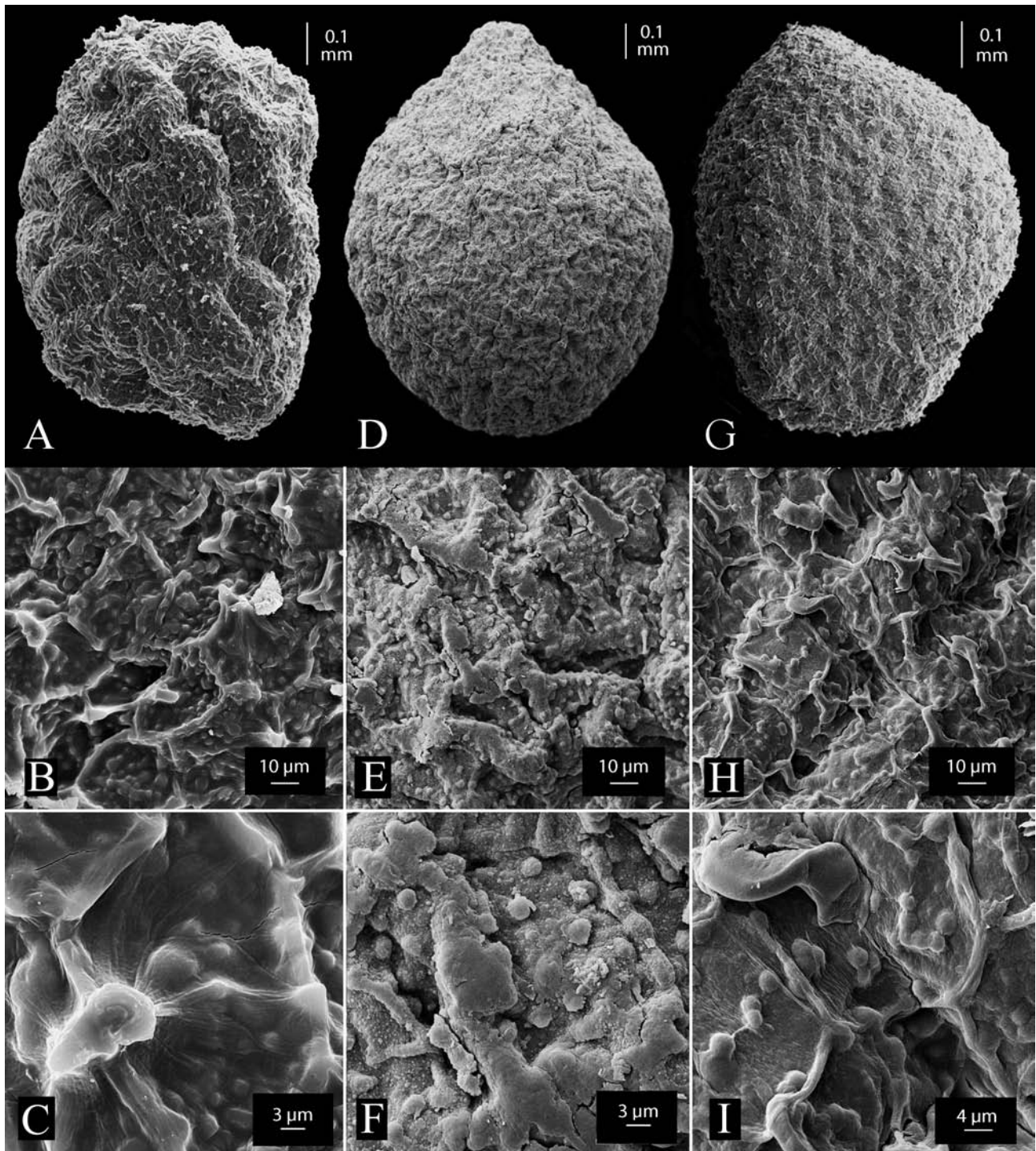


Fig. 10. Seeds of *Anisosepalum* and *Saintpauliopsis*.—A–C. *Anisosepalum alboviolaceum* (Champluvier 5295, CAS).—A. Seed.—B–C. Close-ups of surface.—D–F. *Anisosepalum humbertii* (Raynal 20630, K).—D. Seed.—E–F. Close-ups of surface.—G–I. *Saintpauliopsis lebrunii* (Ndangalasi 0449, C).—G. Seed.—H–I. Close-ups of surface.

are not present on seeds of *Anisosepalum* or *Elytraria* based on SEM observations (Fig. 10A–F, 11A–F) and hydration studies. Trichomes were observed on seeds in all species of *Nelsonia*, *Saintpauliopsis*, and *Staurogyne* examined. Most or all trichomes on seeds of some samples of *Nelsonia* and *Staurogyne* became erect en masse immediately and conspicuously (i.e., trichomes to 0.1 mm long) on hydration (Fig. 9G).

Less dramatic reactions observed in other samples of *Nelsonia*, *Saintpauliopsis*, and *Staurogyne* included: some or most of the trichomes expanded, but the trichomes are short (<0.05 mm long, e.g., *Staurogyne obtusa*; Fig. 9H) and inconspicuous, and the reaction was not immediate (e.g., both samples of *Saintpauliopsis lebrunii*); only some of the trichomes became erect after a minute or more (e.g., some *Nelsonia canescens*);

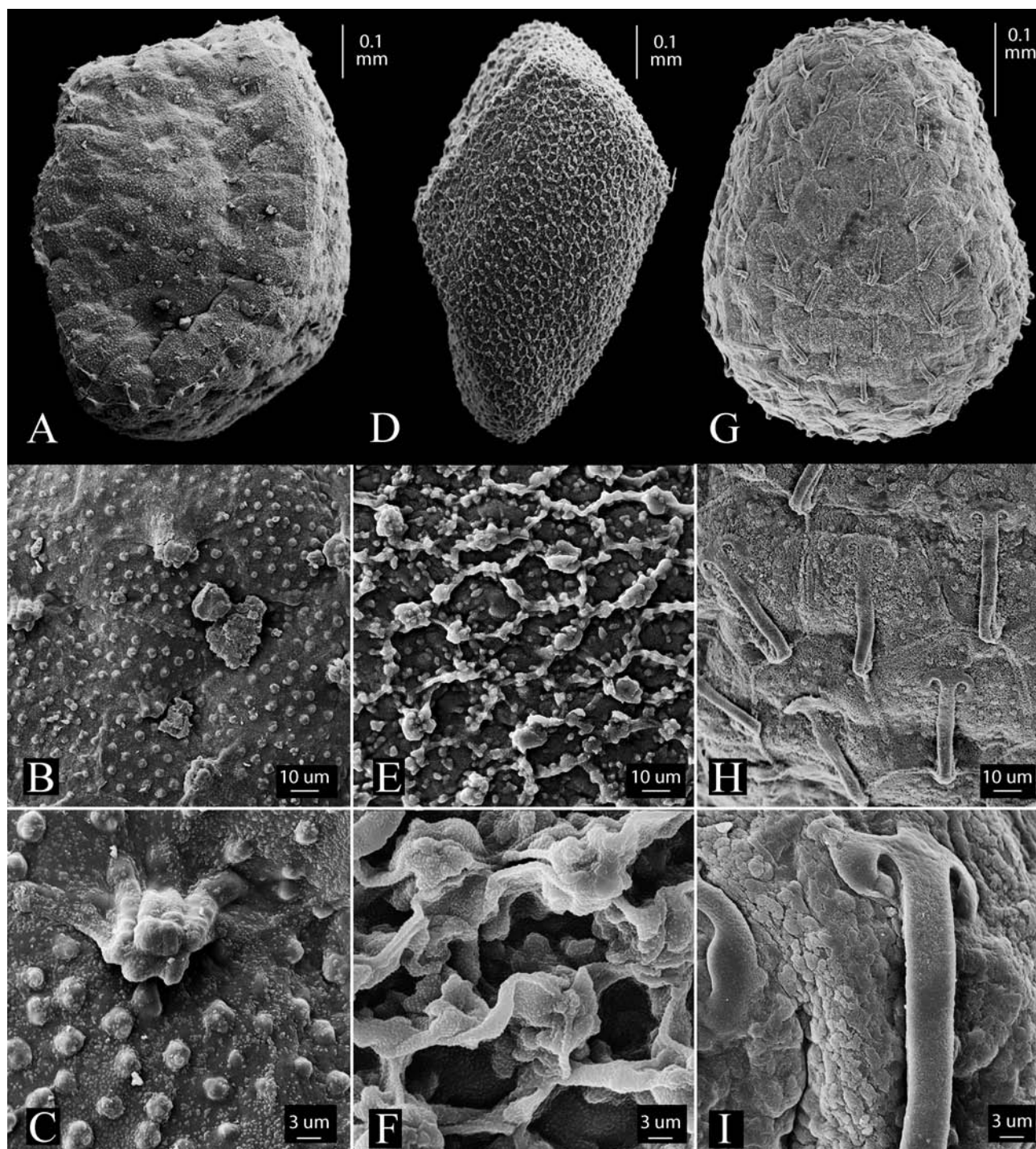


Fig. 11. Seeds of *Elytraria* and *Nelsonia*.—A–C. *Elytraria acaulis* (Iwarsson 664, UPS).—A. Seed.—B–C. Close-ups of surface.—D–F. *Elytraria bromoides* (Daniel 3683, CAS).—D. Seed.—E–F. Close-ups of surface.—G–I. *Nelsonia canescens* (Lewalle 3921, UC).—G. Seed.—H–I. Close-ups of surface (note apically uncinata, anchor-shaped and appressed hygroscopic trichomes).

and no apparent reaction of the trichomes within three minutes (e.g., some seeds of *Staurogyne* spp.). Thus not all of the seminal trichomes were always reactive. Although hygroscopy was observed in all species of *Staurogyne* tested, all trichomes on some, but not all, seeds showed no reactivity. Possible causes of non-reactivity include: age of seed, method of preservation of seed, immaturity of seed, and innate lack of reactivity in some trichomes.

Bremekamp (1953) noted well developed endosperm in Nelsonioideae, and it was largely based on this trait that he considered these plants more closely related to Scrophulariaceae than Acanthaceae (Bremekamp 1955). Hossain (1971) characterized endosperm of Nelsonioideae as usually persistent, oily, and alveolate. Borg et al. (2008) indicated that the presence of persistent (vs. non-persistent) endosperm was one of the characteristics by which the subfamily differs from other

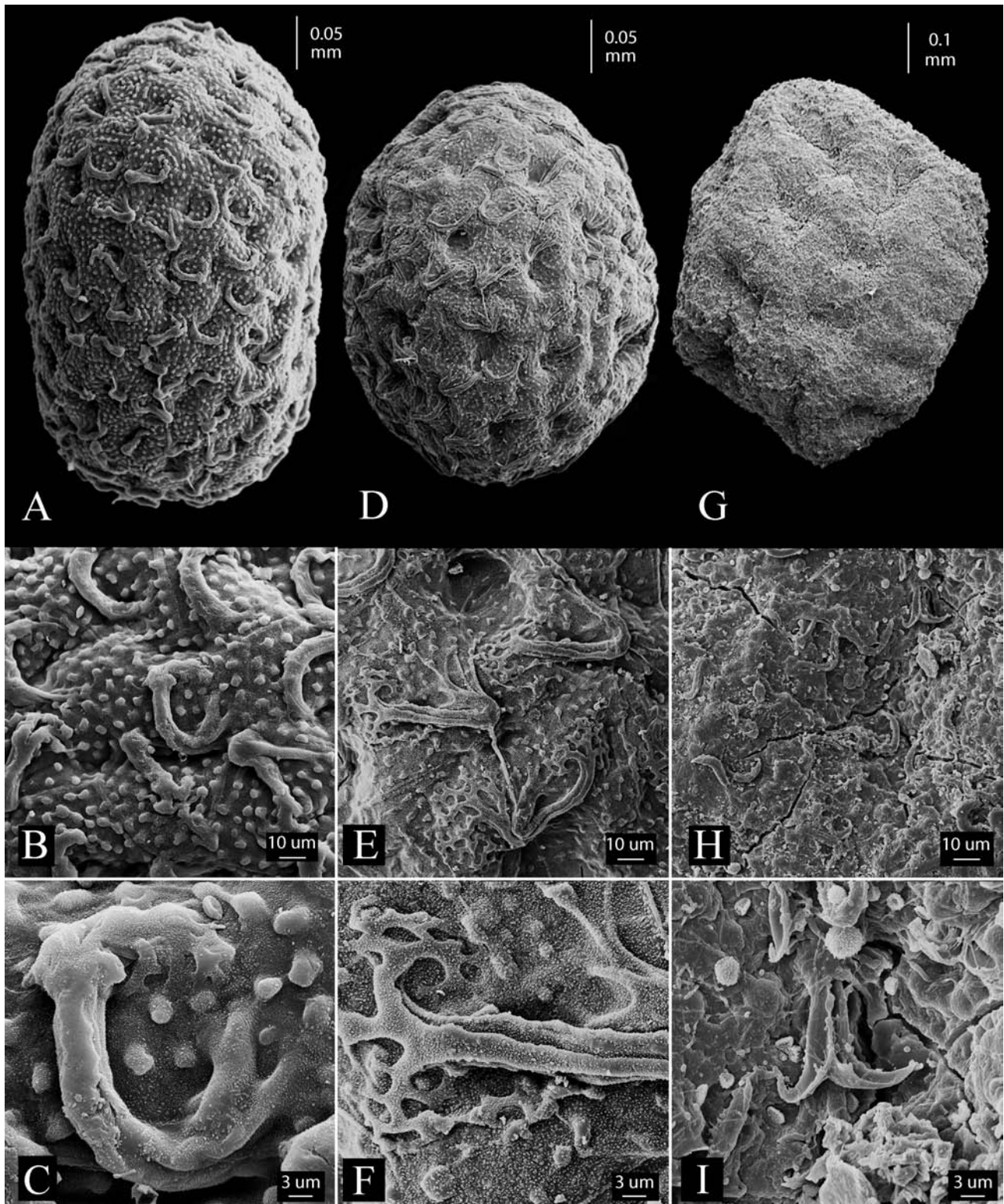


Fig. 12. Seeds of *Staurogyne*.—A–C. *Staurogyne miqueliana* (Lott et al. 3226, CAS).—A. Seed.—B–C. Close-ups of surface (note appressed hygroscopic trichomes).—D–F. *Staurogyne spatulata* (Clemens & Clemens 4006, UC).—D. Seed.—E–H. Close-ups of surface (note appressed hygroscopic trichomes).—G–I. *Staurogyne macrobotrya* (Poilane 20703, P).—G. Seed.—H–I. Close-ups of surface (note short hygroscopic trichomes).

Acanthaceae. Several species of *Andrographis* (Acanthoideae: Andrographideae) have both persistent and ruminant endosperm, like that described for species of *Elytraria* and *Nelsonia* (Mohan Ram and Wadhi 1965), and the presence of one or more layers of persistent endosperm in mature seeds was noted for diverse taxa throughout the family by Mohan Ram and Wadhi (1964). However, as noted by Scotland and Vollesen (2000), this trait remains poorly documented in the family and merits further study.

CHROMOSOME NUMBERS

Knowledge of chromosome numbers has been helpful in understanding the systematics, evolution, and biogeography of some taxa of Acanthaceae (e.g., Daniel 2000, 2006; McDade et al. 2000, 2005). To date, chromosome numbers have been reported for seven species of *Elytraria* (Appendix 3). Among them, the three Mexican taxa sampled have relatively low (presumably diploid) numbers of $n = (11) 12$ whereas taxa from the southeastern United States and the Old World have higher (presumably polyploid) numbers of $n = (17) 19, 22, 23,$ and 25. The only other genus of Nelsonioideae for which counts have been reported is *Nelsonia* (Appendix 3), with all counts ($n = 14, 16-18$) presumably attributable to *N. canescens*. It remains to be seen how useful chromosome data will be for understanding patterns of relationships among these taxa, but the diversity of numbers reported for the small sample of *Elytraria* is encouraging. Additional counts for species of *Elytraria* and *Nelsonia*, and initial counts for all other genera of Nelsonioideae are highly desirable.

DISTRIBUTIONS, BIOTIC COMMUNITIES, AND BIOGEOGRAPHY

The distribution of Nelsonioideae is nearly pantropical with incursions into temperate regions in North America (northern Mexico, southern United States to ca. lat. 33°N), South America (southeastern Brazil), Africa/Madagascar (northern South Africa to ca. lat. 27.5°S, southern Madagascar), and Asia (China, India, Japan-southern Ryukyu Islands, Nepal). The subfamily does not appear to be present on tropical Pacific islands located east of the Solomon Islands. All genera occur in Africa, with *Anisosepalum* restricted to that continent and *Saintpauliopsis* occurring only in Africa and Madagascar. Three genera (*Elytraria*, *Nelsonia*, *Staurogyne*) also occur in Asia, with *Nelsonia* and *Staurogyne* also distributed eastward to Australia. Two genera (*Elytraria* and *Staurogyne*) are native to—and have radiated in—the New World. The native range of *Nelsonia* is not known with certainty; the genus may not be native to the New World, but the non-native range of *N. canescens* there appears to be expanding (cf. Franck and Daniel 2012).

A comparative study of biotic communities in which Nelsonioideae occur has not been attempted based on the information available in floristic accounts and on herbarium specimens. However, it is clear from those sources and from our own field observations that some species occur in very wet communities (e.g., wet evergreen forest) and others occur in dry communities (e.g., tropical deciduous forest). Species of *Anisosepalum* and *Saintpauliopsis* appear to occur only in wet evergreen forests. Plants treated herein as *Nelsonia canescens* occur in a wide range of biotic communities from wet evergreen forest (in western Africa) to grasslands (in Southern

Africa) to arid scrub (in southern Madagascar). Most species of *Staurogyne* appear to occur in moist to wet communities (e.g., all African species occur in wet evergreen forest), but Mexican plants of *S. miqueliana* (Daniel and Lott 1993; as *S. agrestis*) were collected along a dry streambed in a region of dry forest (tropical subdeciduous forest). *Elytraria* contains species that are restricted to wet evergreen forest (e.g., *E. marginata*) and others that occur only in seasonally arid tropical deciduous forest (e.g., *E. mexicana*). The widespread *E. imbricata* occurs in diverse biotic communities from desert to mesophytic montane forest and at elevations from sea level to 2200 m.

Biogeographic analyses of *Elytraria* (Wenk and Daniel 2009; McDade et al. 2012) optimized Africa as the area of origin for the genus with dispersals to Madagascar, the Indian subcontinent, and the New World. At least three subsequent dispersal events within the New World could account for the current distribution of species of *Elytraria* there. Wenk and Daniel (2009) proposed rafting as the mode of dispersal for seeds or plants of the genus between landmasses. Dispersal by rafting may be most plausible for genera that lack the apically hooked and hygroscopic trichomes (e.g., *Elytraria*), which possibly play a role in zoochoric dispersal. *Saintpauliopsis* + *Anisosepalum* retain the symplesiomorphic African distribution, with dispersal to Madagascar within *Saintpauliopsis lebrunii*.

The richest genus of Nelsonioideae, *Staurogyne*, apparently dispersed to the New World early in its evolutionary history as the New World clade is sister to a clade comprising all other species. A subsequent dispersal from Africa to Asia resulted in a major radiation that is today represented on the southeastern mainland of that continent and islands to the east. Interestingly, only five species are present in Africa today, far fewer than in the New World or in Asia. Whether this represents a decrease in richness over time due to climatic changes (e.g., increasing aridity) in Africa or relatively little speciation during its history on that continent remains an interesting question.

There have been at least three colonizations of Madagascar by Nelsonioideae. Presumably because of Madagascar's lengthy isolation from Africa (separation of Indo-Madagascar began ca. 165 mybp; Krause 2003), there are relatively few species of Acanthaceae common to both landmasses (Benoist 1967; Daniel unpubl. data). It is therefore of interest that whereas *Elytraria* is represented on the island by two very distinctive endemic species, the other genera of Nelsonioideae are each represented by a species that also occurs in Africa: *Nelsonia canescens* and *Saintpauliopsis lebrunii*. We hypothesize that future phylogenetic work to date these dispersal events will show that *Elytraria* arrived considerably earlier than the two other Nelsonioideae.

FUTURE STUDIES

With Braz's (2005) account of the American species and Champluvier's (1991) treatment of the African species of *Staurogyne*, a modern revision of the Asian species of that genus remains the most urgent taxonomic priority among Nelsonioideae. Bremekamp's (1955) detailed study of the Malesian species serves as a useful starting point in this regard. Additional molecular studies of *Nelsonia* on a worldwide basis will likely be useful in resolving both the number and rank of taxa that would be appropriate to recognize in that genus.

Such studies linked to a time-calibrated phylogeny should determine whether putatively native populations of the genus in the New World are indeed pre-Columbian. Collections of *Elytraria* with flowers and fruits from Cuba and Haiti are much desired to better resolve the taxonomy of the genus in the West Indies.

TAXONOMY

The following account is intended to delimit monophyletic genera of nelsonioids, to characterize each one, and to tabulate currently recognized species. It provides the known geographic distribution (by country), synonyms, and relevant taxonomic or nomenclatural notes for each genus and species.

NELSONIOIDEAE Pfeiff., Nomencl. Bot. 1(1): 10 (1871) (as "*Nelsonieae*"). *Nelsonieae* Nees in N. Wallich, Pl. Asiat. Rar. 3: 74 (1832). *Nelsoniinae* Bremek., Recueil Trav. Bot. Néerl. 35: 134 (1938). *Nelsoniaceae* Sreem., Phytologia 37: 412 (1977).—TYPE. *Nelsonia* R. Br.

Elytrarieae Dumort., Anal. Fam. Pl. 23 (1829).—TYPE. *Elytraria* Michx.

Annual or perennial, acaulescent to caulescent, and terrestrial (to epiphytic or epipetric) herbs or shrubs, cystoliths absent. Leaves opposite or whorled or alternate, sometimes clustered at ground level or at apex of branches or along stems, sessile to petiolate, margin of blade entire to sinuate-crenate to shallowly dentate to pinnately lobed. Inflorescence of dichasia in leaf axils or more commonly consisting of sessile or pedunculate, axillary or terminal dichasiate spikes or racemes or thyrses (or if branched then panicles of these), peduncles naked or with alternate (spirally disposed) clasping scales; dichasia opposite or alternate (sometimes spirally disposed), sessile or pedunculate, 1-flowered, subtended by a (leaf or) bract. Bracts subfoliose or usually greatly reduced in size relative to leaves, not overlapping to densely imbricate, borne along rachis or sometimes adnate at base to dichasial peduncle and becoming free along peduncle. Flowers sessile to pedicellate, homostylous, flower or flower + pedicel subtended by paired bracteoles (except in most *Nelsonia*). Bracteoles of a pair homomorphic, sometimes with basal portion partially adnate to calyx tube. Calyx deeply 4–5-parted, lobes heteromorphic (1 + 2 + 2) or rarely subequal, posterior lobe often largest, lateral lobes usually shortest, interior to posterior and anterior lobes, and often obscured by bracteoles, anterior lobes sometimes longest and sometimes connate to a greater extent than other lobes. Corolla entirely white or variously colored, tube subcylindric to funnellform, narrow proximal portion \pm cylindric, throat (if present) expanded toward mouth of corolla, limb (subactinomorphic to) strongly zygomorphic (2-labiate), upper lip entire or 2-lobed, lower lip 3-lobed, central lobe usually largest, corolla lobes with descending cochlear aestivation. Stamens 2 or 4, if 4 then didynamous (or if \pm equal in length then inserted at different heights), included in or exerted from mouth of corolla, anthers not surpassing lips or extended well beyond lips, 2-theous, thecae dehiscing toward lower lip (i.e., flower nototribic) or toward each other (i.e., flower pleurotribic), those of a pair equally inserted, with or without a basal appendage; pollen oblate spheroidal to spherical to perprolate (P:E = 0.82–2.43), round to triangular

in polar view, 3-colpate (endoapertures, if present, not evident) to 3-colporoidate (endoapertures evident but indistinct) to 3-colporate (endoapertures distinct), exine reticulate (sometimes appearing foveolate in non-acetolyzed grains), muri smooth or microverrucate; staminodes 0–2 (–3). Style included in or exerted from mouth of corolla. Capsule estipitate, ovoid to subconic to linear-ellipsoid, lacking retinacula. Seeds (6–) 12–68 per capsule, variable in shape (often \pm blocky or irregularly shaped), hygroscopic trichomes present or absent, endosperm present.

We recognize five genera with 172 species in the subfamily. They are nearly pantropical in distribution, and occur to a lesser extent in temperate regions. All genera occur in Africa; *Elytraria*, *Nelsonia*, and *Staurogyne* are also native to Asia; and at least *Elytraria* and *Staurogyne* are native in the New World.

Key to Genera of Nelsonioideae

1. Peduncles of inflorescence (if present) bearing alternate (spirally arranged) clasping scales; bracts coriaceous to sclerophyllous; abaxial surface of calyx lobes with veins obscured or not evident; seeds lacking hygroscopic trichomes; stigma inconspicuously and scarcely divided (if at all), folded over and enclosing anthers in undisturbed flowers, unfolding and becoming erect when touched . . .
 *Elytraria*
1. Peduncles of inflorescences (if present) lacking clasping scales; bracts membranaceous; abaxial surface of calyx lobes with veins evident to prominent; seeds (except for *Anisosepalum*) with hygroscopic trichomes; stigma usually conspicuously 2 (or more)-lobed, neither folded over nor enclosing anthers, not touch-sensitive.
 2. Bracteoles absent; inflorescence of dense, cylindric spikes 5–14 mm in diameter near midpoint (excluding corollas), with bracts imbricate and corollas 2.5–7 mm long; androecium of 2 stamens, staminodes absent; bracts borne on inflorescence rachis only *Nelsonia*
 2. Bracteoles present; inflorescence not with the combination of characters noted above; androecium of 4 stamens (rarely with 2 stamens in some *Staurogyne*), staminodes absent or 1 (–3); bracts borne on inflorescence rachis or fused to and emerging from dichasial peduncle along its length or at its apex.
 3. Anther thecae with a bifurcate (forked) appendage at base; petiole usually longer than blade of leaves; corolla \pm pendant and appearing \pm campanulate; bracts adnate to (and indistinguishable from) dichasial peduncles for 91–98% the length of the peduncle (emerging near apex of peduncle); pollen with muri of reticulate exine beset with microverrucae *Saintpauliopsis*
 3. Anther thecae lacking an appendage or (rarely) with a short, non-forked subbasal or basal appendage; petiole usually shorter than blade of leaves; corolla neither pendant nor campanulate; bracts borne on inflorescence rachis or adnate to (and distinguishable or indistinguishable from) dichasial peduncle for 11–100% the length of the peduncle (usually emerging well below apex of peduncle); pollen with muri of reticulate exine smooth.

4. Base of bracteoles adnate (for up to 2 mm) to floral receptacle and sometimes base of calyx (or sometimes free in *A. lewallei*); corolla with a conspicuous bullate palate on lower lip; seeds with longest axis 1.1–2 mm, shortest axis 0.9–1.2 mm, lacking trichomes . . . *Anisosepalum*
4. Base of bracteoles not adnate to floral receptacle or calyx; corolla lacking a palate on lower lip; seeds with longest axis 0.3–1 mm, shortest axis 0.2–0.8 mm, pubescent with hygroscopic trichomes *Staurogyne*

ANISOSEPALUM E. Hossain, Notes Roy. Bot. Gard. Edinburgh 31: 377 (1972).—TYPE. *Anisosepalum humbertii* (Mildbr.) E. Hossain (*Staurogyne humbertii* Mildbr.)

Caulicent, erect to spreading perennial herbs or shrubs (sometimes epiphytic) to 1.5 (–3) m long or tall. Young stems subterete to subquadrate to quadrate-sulcate or becoming ± flattened on drying, internodes glabrous or pubescent with eglandular trichomes or glabrate. Leaves opposite or ternate, ± evenly disposed along younger stems, subsessile to petiolate, petiole shorter than blade, margin of blade entire to sinuate to sinuate-dentate. Inflorescence usually of subsessile to pedunculate loose to dense terminal raceme-like thyrses, peduncles lacking scales, fertile portion of spike neither dense nor cylindrical or dense and ± cylindrical, 9–30 mm in diameter (excluding corollas) near midpoint, not branching, rachis clearly visible to not visible; dichasia (subopposite to) alternate, pedunculate. Bracts (subopposite to) alternate, not imbricate to ± densely imbricate, green, membranaceous, basal portion adnate to dichasial peduncle for 50–96% the length of the peduncle, free portion linear to elliptic to oblanceolate to obovate or subfoliose, 4.3–17 mm long, 1–4 mm wide, 3-veined. Bracteoles borne at base of flower and usually basally adnate to receptacle and calyx tube for up to 2 mm (sometimes free in *A. lewallei*) and appearing much like the longer calyx lobes, each positioned exterior to and usually obscuring the short lateral calyx lobes, green to at least partially hyaline, subulate to lanceolate, 3.1–16.5 mm long, 0.3–2 mm wide. Flowers sessile (i.e., pedicels absent). Calyx deeply 5-lobed, 3.5–19 mm long, green to hyaline, accrescent and becoming somewhat brownish and bony at or following fruiting, lobes heteromorphic (1 + 2 + 2), posterior lobe 2.5–15 mm long, 3-veined (at least basally), lateral lobes shortest, 1.1–9 mm long, usually ≤ ½ the length of anterior lobes, 1-veined, anterior lobes longest, 3.5–18 mm long, 3-veined (at least basally). Corolla dark reddish or greenish white with brownish pink markings or white with purplish markings or blue or purplish or maroon internally and pale purple with violet striations externally, 6.5–39 mm long, externally pubescent with stipitate glandular (sometimes sparse) and/or eglandular trichomes or glabrous, tube cylindrical for ½ or more of its length, expanded into a throat for distal ¼–½ its length, limb 2-labiate, upper lip entire to shallowly bifid, lower lip with a conspicuous bullate palate proximally. Stamens 4, didynamous, inserted at or distal to base of throat, 1 or both pairs exerted from mouth of corolla, anthers not extending beyond lips, thecae dehiscing toward lower lip (i.e., flower nototribic), elongate, ellipsoid, 0.7–2 mm long, those of a pair

subsagittate to sagittate, equal in length, dorsally pubescent with flexuose eglandular and glandular trichomes, each with a subtriangular and flaplike basal appendage; staminode 0–1; pollen oblate spheroidal to spherical to euprolate (P:E = 0.90–1.36; polar axis 22–31 µm, equatorial axis 22–32 µm), 3-colpate to 3-colporoidate, exine microreticulate (or appearing ± psilate to microreticulate to microfoveolate in *A. alboviolaceum*), muri smooth. Style exerted from mouth of corolla, not extending beyond lips of corolla, stigma not touch-sensitive, subequally to unequally 2-lobed, lobes linear (to inrolled), 0.3–2 mm long, 0.2–0.4 mm wide, longer lobe equally 2-furcate at apex into lobes 0.1–0.7 mm long. Capsule ovoid, 4–13.5 mm long, glabrous or sometimes glandular punctate. Seeds mostly 12–16 per capsule, oblong to ellipsoid to subhemispheric, longest axis 1.1–2 mm, shortest axis 0.9–1.2 mm, deeply excavated on one side, surface coarsely foveolate- to rugose-reticulate, microverrucate to microgemmate, and usually microreticulate as well, lacking trichomes; (Fig. 13).

Three species from tropical Africa (Fig. 14) are recognized in this genus. All of them are well collected and morphologically documented. Detailed taxonomic accounts of the genus were provided by Champluvier (1991) and Vollesen (2008). The two species initially treated by Hossain (1972: 378) were segregated from *Staurogyne* based on differences in the calyx (“form of calyx . . . approaches *Saintpauliopsis*”), corolla (palate on lower lip), number of ovules (6 to 8 vs. 12 or more), and seeds (with a large hilar excavation and rugose testa, and lacking “hooks on their testa cells”). We recognize *Anisosepalum* as morphologically distinct among Nelsonioideae by a unique combination of characters: bracteoles fused to the base of the calyx (like *Saintpauliopsis*), corollas with a conspicuous palate (likely synapomorphic), thecae with an undivided and flaplike basal appendage (like *Nelsonia*), seeds lacking hygroscopic trichomes (like *Elytraria*) and with a conspicuous and deep hilar excavation (likely synapomorphic), and pollen with conspicuous ridges near the colpal margins (synapomorphic).

Currently Recognized Species of *Anisosepalum*

1. *Anisosepalum alboviolaceum* (Benoist) E. Hossain (Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Gabon, Rwanda, Uganda, Zambia)

Staurogyne alboviolacea Benoist; synonyms fide Vollesen (2008, 2013): *Anisosepalum alboviolaceum* subsp. *grandiflorum* (Napper) E. Hossain, *Staurogyne alboviolacea* subsp. *grandiflora* Napper

Champluvier (1991) recognized two subspecies, *alboviolaceum* and *gracilius* (Heine) Champluvier, based on habit and pubescence of the external surface of the corolla. Within subsp. *alboviolaceum* she treated five informal groups based on geographic distribution and differences in shape, size, and pubescence of the corolla. Vollesen (2008) noted variation in size of the corollas in different parts of the geographic range of the species, but he did not recognize formal infraspecific taxa; he also did not specifically include subsp. *gracilius* as a synonym. However, he did include the distribution of subsp. *gracilius* within the geographic range of the single taxon recognized.

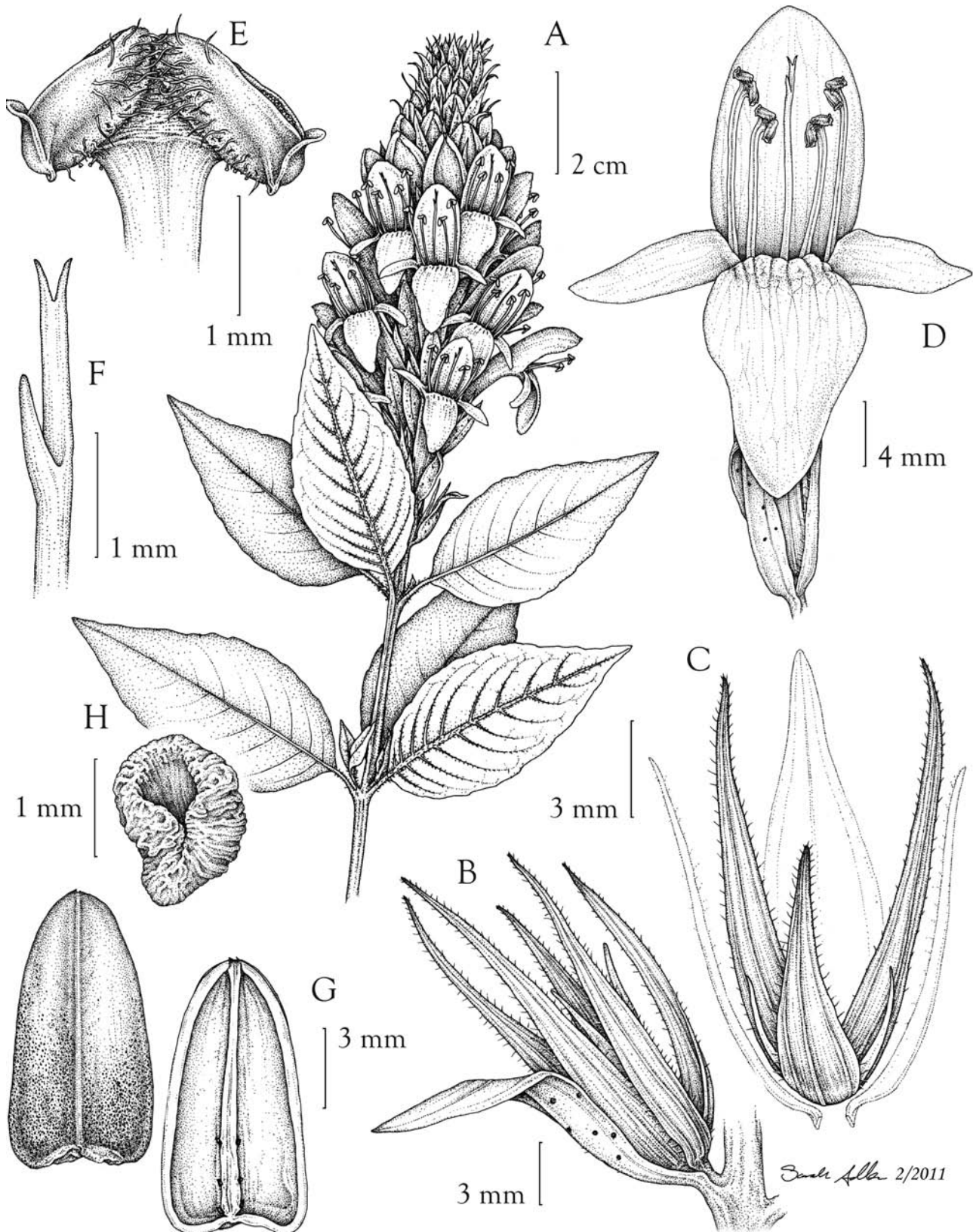


Fig. 13. *Anisosepalum lewallei*.—A. Habit (Bidgood et al. 4570; Tanzania).—B. Inflorescence node (Bidgood et al. 4570).—C. Calyx subtended by paired bracteoles (on sides) and bract (background) (Bidgood et al. 4728; Tanzania).—D. Flower (Bidgood et al. 4570).—E. Apex of stamen with anthers (Bidgood et al. 4570).—F. Apex of style with stigma (Bidgood et al. 4570).—G. Capsule (exterior view on left, interior view on right) (Bidgood et al. 4728).—H. Seed (Bidgood et al. 4728). Drawn by S. Adler.



Anisosepalum

Fig. 14. Map of Africa showing the distribution by country of *Anisosepalum*.

2. *Anisosepalum humbertii* (Mildbr.) E. Hossain (Burundi, Congo-Kinshasa, Rwanda, Tanzania, Uganda, Zambia)

Staurogyne humbertii Mildbr.

Champluvier (1991) recognized two subspecies: *humbertii* and *zambiense* Champluvier. These were based on position of the ring of trichomes inside the corolla tube and the width of the corolla tube below the lips. Vollesen (2008, 2013) maintained these subspecies and noted that subsp. *zambiense* has a longer corolla tube with the ring of hairs on its internal surface located more distally. Based on our observations, the subspecies appear very similar (the differences being relatively

minor and not mutually exclusive), but their geographic ranges apparently do not overlap.

3. *Anisosepalum lewallei* P. Bamps (Burundi, Tanzania)

This is a highly distinctive species with generally ternate leaves. Although opposite leaves occur, at least some nodes (usually most) per shoot bear three leaves. Corollas of this species (3–3.9 cm long; Fig. 13D) are the largest in the genus.

ELYTRARIA Michx., Fl. Bor.-Amer. 1: 8 (1803), nomen conserv.—TYPE. *Elytraria virgata* Michx., nomen illegit.

(*E. caroliniensis* (Walter ex J.F. Gmel.) Pers.; *Tubiflora caroliniensis* Walter ex J.F. Gmel.)

Anonymos Walter, Fl. Carol. 91 (1788), excluded name (McNeill et al. 2012: Article 20.4(a)).—TYPE. *Anonymos caroliniensis* Walter

Tubiflora J.F. Gmel., Syst. Nat., ed. 13[bis]. 2(1): 27 (1791), nomen rej.—TYPE. *Tubiflora caroliniensis* J.F. Gmel.

Acaulescent to caulescent, erect to spreading annual or perennial herbs to shrubs to 0.5 (–1) m tall. Young stems subterete to 3-angulate to subquadrate, sometimes \pm flat on drying, glabrous, pubescent with eglandular trichomes, or glabrate. Leaves alternate or whorled, \pm diffuse along stems or borne in basal rosettes (usually from a subterranean caudex or rhizome) or aerial whorls or aerial clusters (up to 11 leaves per cluster), sessile to petiolate, petiole (if present) usually shorter than blade, margin of blade entire to crenate to pinnatifid. Inflorescence of (sessile to) pedunculate axillary and terminal densely bracteate spikes, peduncles (if present) covered with imbricate or remote coriaceous clasping scales, fertile portion of spike cylindric, 1.8–17 mm in diameter (excluding corollas) near midpoint, simple or sometimes branched, rachis not or only partially visible; dichasia alternate (spirally disposed), sessile. Bracts alternate (spirally disposed), imbricate, green or partially hyaline, not fused to other structures, coriaceous to sclerophyllous, lanceolate to ovate to broadly ovate to elliptic to hour-glass shaped to obovate, 2.5–11 mm long, 1–5.8 mm wide, 1- or 3-veined or veins not evident, sometimes apically toothed and/or winged. Bracteoles borne at base of (but not adnate to) flower, positioned near edges of posterior calyx lobe and \pm conduplicate there, often mostly hyaline, narrowly elliptic to linear to lanceolate to lance-lunate to subulate, 1.6–7.5 mm long, 0.2–1.7 mm wide. Flowers sessile. Calyx usually appearing deeply 4-lobed, mostly hyaline, 1.8–8.5 mm long, lobes heteromorphic, \pm equal in length, posterior lobe 1.8–7.5 mm long, lateral lobes 1.7–7 mm long, anterior lobe 1.9–8 mm long, 2-dentate to \pm deeply 2-cleft from apex, all lobes obscurely veined abaxially. Corolla pinkish or blue or yellow or entirely white or dark purple and white, sometimes with colored markings near mouth, 3–17 mm long, externally glabrous or pubescent, tube cylindric or slightly expanded near mouth, throat indistinct or evident only near mouth, limb (subactinomorphic to) 2-labiate, upper lip 2-lobed, lower lip lacking a bullate palate, corolla lobes often apically divided or 2-cleft. Stamens 2 (or 4 in species native to Madagascar), inserted at/near apex of corolla tube or near midpoint of tube, anthers included in corolla tube or partially exerted from mouth of corolla, not extending beyond lips of corolla, thecae (covered by folded stigma during anthesis) dehiscent toward lower lip (i.e., flower nototribic), oblong to broadly ellipsoid, 0.3–1.7 mm long, those of a pair parallel, equal to subequal in size, glabrous, lacking basal appendages, connective sometimes with an apical appendage (in some Old World spp.); staminodes 0–2, minute; pollen suboblate to spherical to perprolate (P:E = 0.82–2.43; polar axis 25–58 μ m, equatorial axis 14–36 μ m), 3-colpate to 3-colporoidate, exine reticulate (sometimes appearing \pm foveolate in non-acetylated grains), muri psilate or microverrucate. Style included in corolla tube or if exerted from mouth of corolla then not extending beyond lips of corolla, stigma folded over anthers during

anthesis and straightening when touched (touch-sensitive) and gradually refolding, appearing non-lobed but usually with a minute and inconspicuous lobe (to 0.3 mm long) borne on an expanded, flat, subelliptic to subspatulate lobe (rarely subcrateriform), 0.4–2.5 mm long, 0.2–1.2 mm wide. Capsule conic to ovoid to linear-ellipsoid, sometimes irregularly constricted proximally, 2.1–9 mm long, glabrous (rarely inconspicuously glandular punctate, but lacking elongate trichomes). Seeds to 26 per capsule, irregularly shaped (often blocky or reniform or ellipsoid), longest axis 0.3–1.7 mm, shortest axis 0.3–1.5 mm, surface (smooth to) lumpy- to rugose- to foveolate-reticulate, microverrucate to microbaculate and with smaller rounded to pointed protrusions that sometimes form chains or a microreticulum, lacking trichomes; $x = 11$ or 12?; (Fig. 15).

The genus consists of 21 species occurring in the tropics, subtropics, and warm deserts of both the Old World and the New World (Fig. 16). The majority of species are American (14), but species also occur in Africa (5), Madagascar (2), and the Indian subcontinent (1). Except for the naturalized presence of weedy *Elytraria imbricata* in Madagascar, southeastern Asia, and Malesia, there are no species common to the Old World and the New World. North American and African species are well collected and fully documented morphologically (e.g., Morton 1956; Dokosi 1970, 1971, 1979; Daniel and Acosta C. 2003; Vollesen 2008; Daniel in press). Species endemic to South America and Madagascar are poorly collected but reasonably well known (e.g., Benoist 1967; Wenk 2008). The seven species endemic to the West Indies remain very poorly collected, morphologically documented, and taxonomically resolved; indeed, corollas remain unknown for most of those species (e.g., Borhidi and Muñiz 1978). A monograph of the entire genus is currently in preparation.

Hossain (1972) recognized two subgenera: *Tetrandra* E. Hossain consisting of the two species endemic to Madagascar (characterized by woody habit, whorled leaves, and four stamens), and *Elytraria* consisting of all other species (characterized by mostly herbaceous habit; alternate, whorled, or clustered leaves; and two stamens). Molecular phylogenetic results (Wenk and Daniel 2009; McDade et al. 2012) reveal that the subgenera are not monophyletic.

Elytraria is distinctive among Nelsonioideae by having peduncles (absent only in *E. madagascariensis*) covered with alternate (spirally arranged) scales, coriaceous to sclerophyllous bracts, and touch-sensitive stigmas. All three traits appear to be synapomorphic for the genus. Another significant character of *Elytraria* is the absence of minute, hooklike, and hygroscopic trichomes on its seeds (shared with *Anisosepalum*). Variation in several morphological attributes is notable for the genus. Habit varies from acaulescent herbs from a woody caudex or rhizome (most species) to monocaulous or branched herbs (e.g., *E. marginata*, *E. imbricata*) to shrubs (e.g., *E. nodosa*). Most species have either a taproot or fibrous roots, but one (*E. tuberosa*) has fibrous roots that bear elongate and conspicuously swollen tubers. Tuberos roots are otherwise unknown among Nelsonioideae, but they are known elsewhere among Acanthaceae (e.g., *Ruellia tuberosa*). Leaf margin varies (sometimes intraspecifically) from entire to crenate to lobed to subpinnatisect. Floral diversity in *Elytraria* encompasses size, color, and form of the limb of corollas. The West Indian endemic, *E. shaferei*, has the smallest known

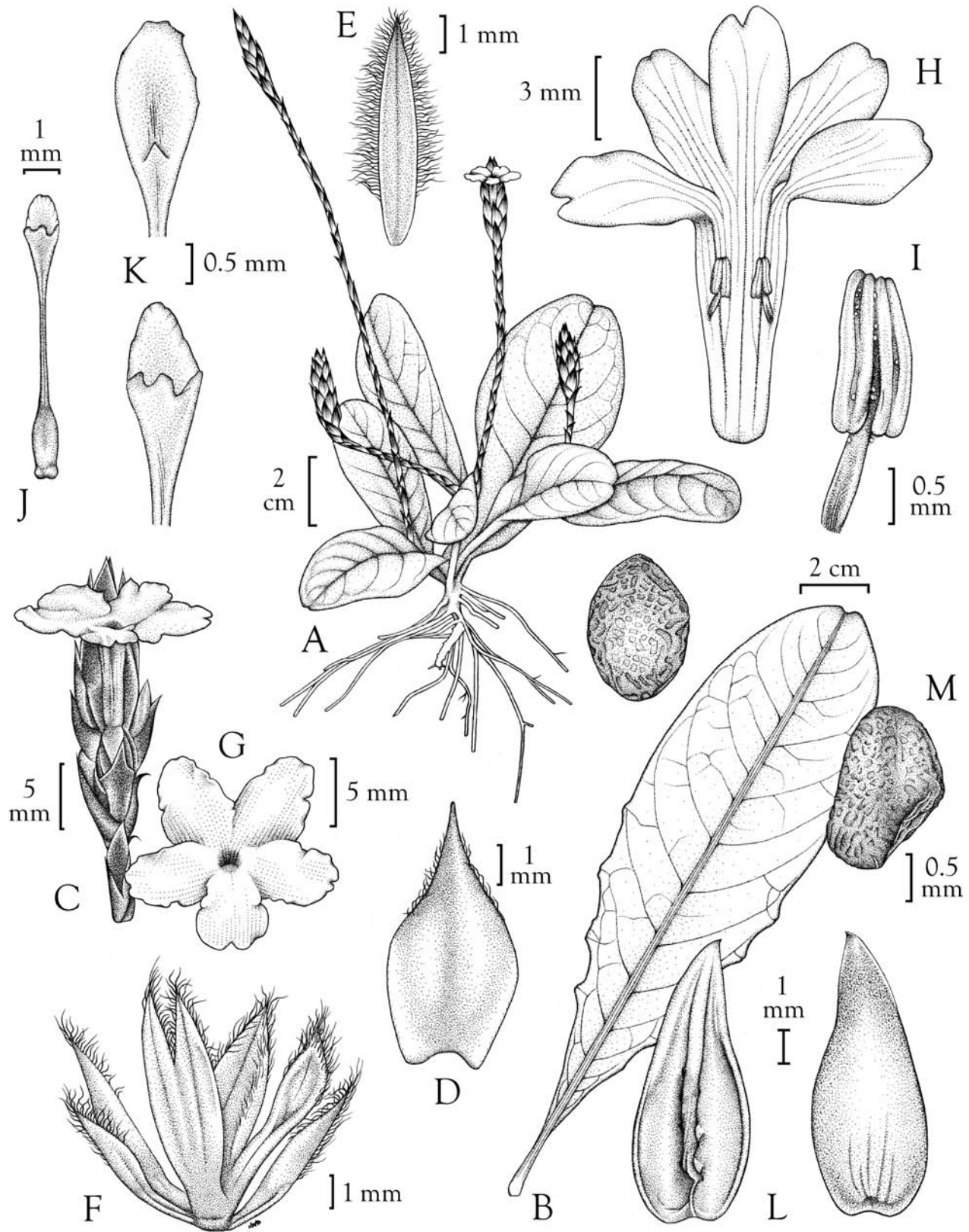


Fig. 15. *Elytraria caroliniensis* (*Daniel s.n.cv*, cultivated from plants from the USA, except as noted).—A. Habit (based on *Daniel s.n.cv* and *Curtis 5947*; USA).—B. Leaf (*Wiggins 19812*; USA).—C. Inflorescence with flower (bract, bracteoles, and calyx subtending flower removed).—D. Bract.—E. Bracteole.—F. Calyx subtended by bracteoles.—G. Limb of corolla from above.—H. Corolla opened to show androecium.—I. Stamen.—J. Gynoecium.—K. Variation in stigmas (one lobe highly reduced at top, crateriform at bottom).—L. Capsule valves (internal view on left, external view on right).—M. Seeds (top view to left of leaf, side view to right of leaf). Drawn by N. Bollinger.

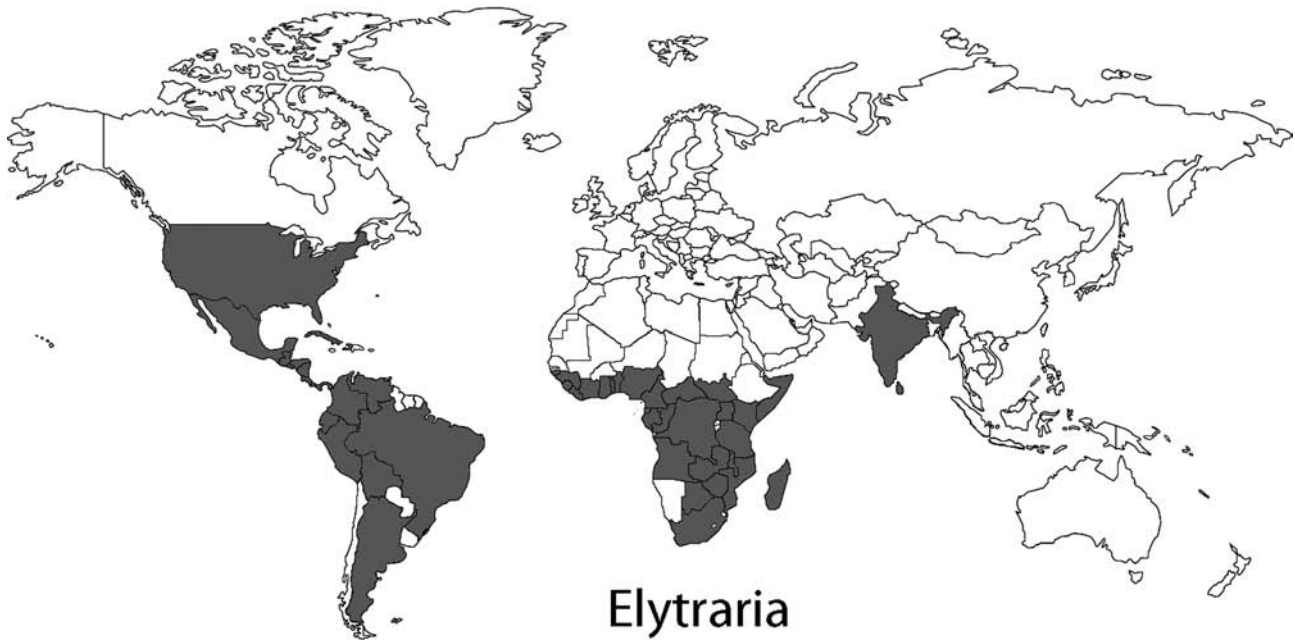


Fig. 16. Map showing the worldwide distribution by country of *Elytraria*.

corollas (3 to 3.7 mm long), and the continental American species *E. caroliniensis* and *E. mexicana* have the largest (up to 17 mm long). Although the color(s) of corollas for several species in South America and the West Indies remains unknown, so far as is known, all species endemic to the Old World (with possible exception of *E. madagascariensis*, which is reported to have white-pink corollas fide Benoist 1967), South America, and West Indies have white to cream corollas. Among North American (United States, Mexico, and Central America) species, corolla color varies from white (*E. caroliniensis*) to pink (*E. bromoides*) to blue (*E. imbricata*) to yellow (*E. macrophylla*) to white and purple (*E. mexicana*). Limb form varies from bilabiate with lips little opened (e.g., *E. marginata*) to bilabiate with lips widely spreading (e.g., *E. macrophylla*) to subactinomorphic (e.g., *E. caroliniensis*). Androecial diversity in *Elytraria* is greater than in any other genus of Nelsonioideae (except perhaps *Staurogyne* in which various numbers of staminodes have been reported). The following combinations of number of stamens and staminodes are represented: two stamens + no staminodes, two stamens + two staminodes, and four stamens + no staminodes.

Currently Recognized Species of *Elytraria*

This list is based on Wenk and Daniel (2009) and on a revision of the genus that is currently in preparation.

1. *Elytraria acaulis* (L.f.) Lindau (Angola, Botswana, Congo-Kinshasa, Ghana, India, Kenya, Malawi, Mozambique, Nigeria, Somalia, South Africa, Sri Lanka, Tanzania, Uganda, Zambia, Zimbabwe)

Justicia acaulis L.f., *Tubiflora acaulis* (L.f.) Kuntze; synonyms fide Vollesen (2008): *Elytraria acaulis* var. *lyrata* (Vahl) Bremek., *E. crenata* Vahl, *E. crenata* var. *lyrata* (Vahl) Nees, *E. indica* Pers., *E. lyrata* (Vahl) Vahl, *Justicia acaulis* var. *lyrata* Vahl

This is the most widely distributed species of *Elytraria* in Africa, the southernmost-occurring species of Nelsonioideae (to ca. lat. 27.5°S), and the only Old World species of the genus with an apparently natural intercontinental (Africa and Asia), disjunct distribution.

2. *Elytraria bissei* H. Dietr. (Cuba)

3. *Elytraria bromoides* Oerst. (Guatemala, Mexico, USA)

Synonyms fide Daniel (1995): *Elytraria acuminata* (Small) Cory, *Tubiflora acuminata* Small

4. *Elytraria caroliniensis* (Walter ex J.F. Gmel.) Pers. (USA)

Tubiflora caroliniensis Walter ex J.F. Gmel., *Anonymos caroliniensis* Walter; synonyms fide Daniel (in press): *Elytraria angustifolia* (Fernald) Leonard, *E. caroliniensis* var. *angustifolia* (Fernald) S.F. Blake, *E. caroliniensis* var. *vahliana* (Nees) D.B. Ward, *E. virgata* Michx., *E. virgata* var. *angustifolia* Fernald, *E. virgata* var. *latifolia* Nees, *E. virgata* var. *vahliana* Nees, *Tubiflora caroliniensis* var. *angustifolia* (Fernald) Small

This species, which occurs in subtropical (southern Florida) and temperate regions of the southeastern USA, is the northernmost-occurring species of Nelsonioideae (to ca. 33°N latitude). Its flowers are unusual in their subsalverform shape with a subactinomorphic limb.

5. *Elytraria cubana* Alain (Cuba)

Synonym fide Alain (1956): *Elytraria crenata* Leonard

6. *Elytraria filicaulis* Borhidi & O. Muñiz (Cuba)

7. *Elytraria imbricata* (Vahl) Pers. (Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Netherlands Antilles-Curaçao, Nicaragua, Panama, Peru, Trinidad and Tobago, USA, Venezuela)

Justicia imbricata Vahl; synonyms fide Daniel (1995): *Elytraria apargiifolia* Nees, *E. fasciculata* Kunth, *E. frondosa* Kunth, *E. microstachya* Oerst., *E. pachystachya* Oerst., *E. ramosa* Kunth, *E. scorpioides* Roem. & Schult., *E. squamosa* (Jacq.) Lindau, *E. tridentata* Vahl, *Stachytarpheta squamosa* (Jacq.) Vahl, *Tubiflora pachystachya* (Oerst.) Kuntze, *Tubiflora squamosa* (Jacq.) Kuntze, *Verbena squamosa* Jacq.

Although native to, and widespread in, the New World, this weedy species has been introduced into several Paletropical regions (e.g., Madagascar, Philippines, Vietnam). It is the only species in the New World to occur in both North America and South America.

8. *Elytraria ivorensis* Dokosi (Ghana, Ivory Coast)

9. *Elytraria klugii* Leonard (Peru)

10. *Elytraria macrophylla* Leonard (Mexico)

11. *Elytraria madagascariensis* (Benoist) E. Hossain (Madagascar)

Tubiflora madagascariensis Benoist

12. *Elytraria marginata* Vahl (Angola, Congo-Kinshasa, Cameroon, Equatorial Guinea-Bioko and Río Muni, Gabon, Ghana, Ivory Coast, Liberia, Nigeria, São Tomé and Príncipe, Sierra Leone, South Sudan, Togo, Uganda)

Synonym fide Vollesen (2008): *Tubiflora paucisquamosa* De Wild. & T. Durand

This is the most widespread, and a rather common, species in western Africa.

13. *Elytraria maritima* J.K. Morton (Ghana, Ivory Coast)

14. *Elytraria mexicana* Fryxell & S.D. Koch (Mexico)

15. *Elytraria minor* Dokosi (Kenya, Tanzania)

16. *Elytraria nodosa* E. Hossain (Madagascar)

17. *Elytraria planifolia* Leonard (Cuba)

Borhidi and Muñiz (1978) recognized *Elytraria planifolia* subsp. *acunae* Borhidi, the status of which remains unresolved.

18. *Elytraria prolifera* Leonard (Haiti)

19. *Elytraria shaferi* (P. Wilson) Leonard (Cuba)

Tubiflora shaferi P. Wilson; synonym fide León and Alain (1974): *Elytraria tridentata* var. *wrightii* Gomez

20. *Elytraria spathulifolia* Borhidi & O. Muñiz (Cuba)

21. *Elytraria tuberosa* Leonard (Ecuador)

So far as is known, this is the only species of *Elytraria* that has conspicuously tuberous roots.

NELSONIA R. Br., Prodr. Fl. Nov. Holland. 480 (1810).—
TYPE. *Nelsonia campestris* R. Br. (lectotype designated in 1955 by Bremekamp, ING card 00749)

Acaulescent to caulescent (usually low and often mat-forming and rooting at nodes), annual to perennial herbs to 2.5

dm tall and up to 7 dm long. Young stems subterete or ± flattened on drying, pubescent with glandular and/or eglandular (often silky and up to 4.5 mm long) trichomes. Leaves opposite (to alternate), ± clustered in a basal rosette to evenly disposed, sessile to petiolate, petiole (if present) shorter than blade, margin of blade entire. Inflorescence of sessile to pedunculate axillary and terminal densely bracteate spikes, peduncles (if present) lacking scales, fertile portion of spike dense and cylindrical, 5–14 mm in diameter (excluding corollas) near midpoint, not branching, rachis mostly not visible, often bearing elongate, silky trichomes, especially at base of dichasia; dichasia alternate (± spirally disposed), sessile. Bracts alternate (± spirally disposed), imbricate, green, membranaceous, not fused to other structures, broadly ovate to ovate to elliptic to subcircular to oblate to obovate, 4–8 (–10) mm long, 2.5–5.2 (–6) mm wide, (1– or) 3– or 5–veined (lateral veins sometimes indistinct). Bracteoles absent (see discussion). Flowers sessile to subsessile (i.e., with pedicels to 1 mm long). Calyx usually deeply 4-lobed, green to hyaline, 3.3–7 mm long, lobes heteromorphic (sometimes equal in length, but differing in shape and width), posterior lobe 3–6 mm long, sometimes largest, 3– or 5– or 7–veined, lateral lobes 2.5–5 mm long, 1– or 3– or 5–veined, anterior lobe 2.5–5 mm long, 2– (or 5–) veined, (entire) 2– (or more–) cleft at apex (or rarely divided almost to tube). Corolla whitish (usually with lobes suffused with shades of pink or purple) or pink or blue or purple, sometimes with differently colored striations or spots, (2.5–) 4–7 mm long, externally glabrous, tube ± funnellform, narrow proximal portion ± constricted (or narrowest) at apex thence expanded into a short throat, limb 2-labiate, upper lip 2-lobed, lower lip lacking a bullate palate. Stamens 2, inserted near base of corolla throat, anthers included in throat or partially exerted from mouth of corolla, not extending beyond lips of corolla, thecae dehiscing toward each other (i.e., flowers pleurotribic), subellipsoid, 0.2–0.5 (–1) mm long, those of a pair parallel to widely divergent (i.e., thecae ± end to end and horizontal), ± equal in size, glabrous, with a subbasal flaplike appendage associated with dehiscence; staminode 0; pollen subprolate to perprolate (P:E = 1.28–2.18; polar axis 20–39 µm, equatorial axis 15–21 µm), 3-colpate to 3-colporoidate, exine reticulate, muri smooth. Style included in corolla tube or if exerted from mouth of corolla then not extending beyond lips of corolla, stigma not touch-sensitive, unequally 2-lobed (sometimes with at least one lobe again divided), lobes 0.1–0.2 mm long, 0.1–0.2 mm wide. Capsule ovoid-conic, 2.8–5 mm long, lacking trichomes or with inconspicuous sessile to subsessile glands (especially near apex). Seeds to 30 per capsule, subglobose to subhemispheric to subellipsoid, one face somewhat flattened and with a shallow pore, longest axis 0.3–0.6 mm, shortest axis 0.3–0.5 mm, surface coarsely lumpy to nearly smooth, microreticulate and microverrucate, pubescent with inconspicuous, hygroscopic, anchor-shaped trichomes (expanding to 0.2 mm long on moistening); (Fig. 17).

Opinion varies as to whether a single variable species (e.g., Hossain 1984; McDade et al. 2012) or several species (e.g., Bremekamp 1964; Morton 1979; Vollesen 1994) should be recognized. Although the genus appears to be native in Africa, Asia, and Australia, it remains unknown whether it is native or introduced in tropical America (Fig. 18). Bremekamp (1955) indicated that *Nelsonia* was a Paletropical

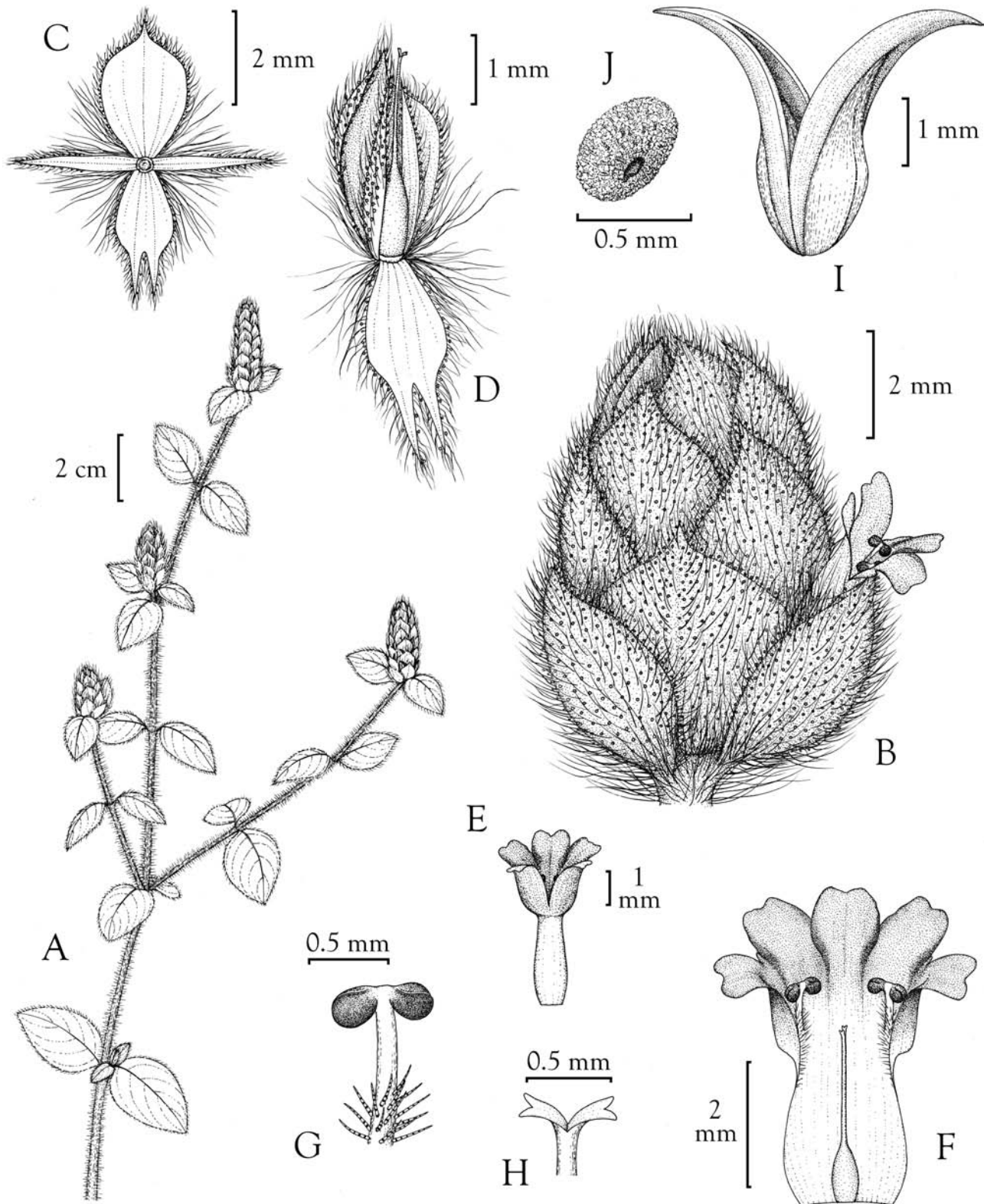


Fig. 17. *Nelsonia canescens*.—A. Habit (Palmer 583; Mexico).—B. Spike with flower (Daniel et al. 5452gh; cultivated from plants from Panama).—C. Calyx flattened and with anterior lobe lowermost.—D. Calyx with anterior lobe bent to show gynoecium.—E. Corolla (view from above).—F. Corolla cut open to show androecium and gynoecium.—G. Apex of stamen with anthers.—H. Apex of style with stigma.—I. Dehiscent capsule (Palmer 583).—J. Seed (Palmer 583). Drawn by M. Tenorio.

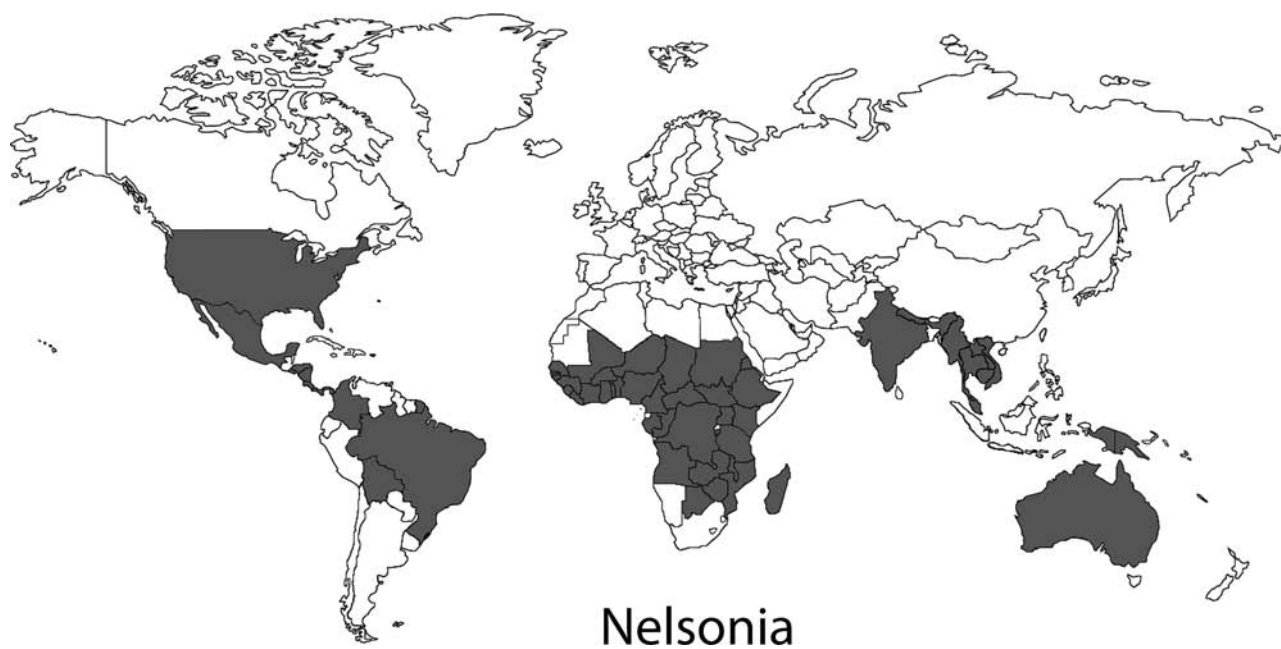


Fig. 18. Map showing the worldwide distribution by country of *Nelsonia* (some or all of the New World distribution represents naturalized occurrences).

genus that has spread to the New World in post-Columbian times. Vollesen (1994) indicated that there are likely five species of *Nelsonia*, three in Africa (*N. canescens*, *N. gracilis*, and *N. smithii*), one in southern Asia (*N. canescens*), one in Australia (*N. campestris*), and two in the New World (*N. canescens*-introduced and *N. pohlii*-native). In addition to species that have been described, Champluvier has annotated a large number of specimens at BR as a new species, "*N. feracissima* Champl.," from Burundi, Cameroon, Congo-Kinshasa, Equatorial Guinea-Bioko, Malawi, Mozambique, Rwanda, and Tanzania. Molecular phylogenetic studies that included plants sampled from multiple continents led McDade et al. (2012) to suggest that only a single species was likely represented. However, these authors did not include *N. gracilis*, and that species appears rather distinctive morphologically. Major questions that remain to be resolved in this genus include the number of species deserving recognition and whether any of the occurrences in the New World represent native (i.e., pre-Columbian) populations.

Nelsonia exhibits a unique synapomorphy within Nelsonioideae, the absence of bracteoles below the flowers. The rare (teratological?) presence of bracteoles in some *Nelsonia* (Daniel and Figueiredo 2009) permits recognition of the homology of its flowers to those of the one-flowered dichasial units in other nelsonioids. The inflorescences of the genus (i.e., with peduncles, if present, lacking scales and with dense, cylindric spikes bearing imbricate bracts and small corollas) are also unlike those of other Nelsonioideae. With *Staurogynne* and *Saintpauliopsis*, *Nelsonia* shares the characteristic of seeds bearing hooked or branched hygroscopic trichomes.

Currently Recognized Species of *Nelsonia*

1. *Nelsonia canescens* (Lam.) Spreng. (Angola, Australia, Benin, Botswana, Burkina Faso, Burundi, Cambodia,

Cameroon, Central African Republic, Chad, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea-Bioko, Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, India, Indonesia-Papua, Ivory Coast, Kenya, Laos, Liberia, Madagascar, Malawi, Malaysia, Mali, Mozambique, Myanmar, Nepal, Niger, Nigeria, Papua New Guinea, São Tomé & Príncipe, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, Thailand, Togo, Uganda, Vietnam, Zambia, Zimbabwe).

Justicia canescens Lam.; synonyms fide Vollesen (1994): *Justicia bengalensis* Spreng., *J. hirsuta* Vahl, *J. lamiifolia* Roxb., *J. nummulariifolia* Vahl, *J. organoides* Vahl, *J. tomentosa* Roxb. ex C.B. Clarke, *J. vestita* Roem. & Schult., *N. albicans* Kunth, *N. campestris* R. Br. var. *vestita* (Roem. & Schult.) C.B. Clarke, *N. canescens* var. *vestita* (Roem. & Schult.) E. Hossain, *N. hirsuta* (Vahl) Roem. & Schult., *N. lamiifolia* (Roxb.) Spreng., *N. nummulariifolia* (Vahl) Roem. & Schult., *N. organoides* (Vahl) Roem. & Schult., *N. pohlii* Nees, *N. senegalensis* Oerst., *N. tomentosa* (Roxb.) Dietr., *N. villosa* Oerst.; synonyms fide Hossain (1984): *N. campestris* R. Br., *N. rotundifolia* R. Br.; synonyms fide Daniel (in press): *N. canescens* var. *smithii* (Oerst.) E. Hossain, *N. smithii* Oerst.

The species is native to several regions in the Old World (Africa, Asia, Australia), but due to its propensity to spread into disturbed habitats, its overall natural distribution is not known with certainty and may be less extensive than the list of nations, noted above, in which it is currently found. Its numerous occurrences in the New World (e.g., Bolivia, Brazil, Colombia, Costa Rica, El Salvador, French Guiana, Honduras, Mexico, Nicaragua, Panama, Puerto Rico, United States) possibly contain some native populations (e.g., Colombia, where the species was collected near Cartagena in 1801 [without collector at P], and Brazil, where the species was collected in Goiás as early as 1821 [*Saint-*

Hilaire cat. num. 766 at K and PJ). The species was collected in southern Central America (Costa Rica and Panama) and the West Indies (Puerto Rico) during the 1850s. Other collections from the New World are clearly of recent origin (e.g., Florida in the USA; Franck and Daniel 2012). Both Morton (1979) and Hossain (1984) noted the likely adventive occurrence of *N. canescens* on many islands in the Pacific. We have not been able to locate records of *Nelsonia* from Pacific islands (other than New Guinea), nor have such been reported in numerous floras covering the region (e.g., Yuncker 1959; Heine 1976; Smith 1991; Fosberg et al. 1993; Meyer and Lavergne 2004).

Hossain (1984) noted considerable variation in habit, leaves, bracts, and pubescence for this species, but he reported insignificant correlations among the major morphological characters. We observed additional variation in the color of corollas as noted on herbarium specimen labels and observed by us in the field or in photographs. Plants may have corollas with the limb entirely white (Australia), white with pink to maroon coloration on the distal portion of the lobes (Africa, America), blue to purple (Africa, America, Asia), purple with dark purple striations on the upper lip (Africa, Asia), and purple with dark purple spots on the lower lip (America; Fig. 3F–I). A similar case among Acanthaceae of a widespread species with multiple color patterns on corollas was noted for *Henrya insularis* Nees ex Benth. (Daniel 1990). We also noted variation in the division of the anterior calyx lobe. Most plants have calyces with the anterior lobe shallowly cleft or divided up to $\frac{1}{3}$ the length of the lobe. In some plants from Australia the anterior lobe is entire (Barker 1986) whereas in others it is divided more than $\frac{3}{4}$ its length (e.g., *Lazarides 9080* at L from Australia: Northern Territory).

Discussions about whether to recognize *N. smithii* as distinct from *N. canescens* include those of Morton (1979), Hossain (1984), Vollesen (1994), Daniel and Figueiredo (2009), Franck and Daniel (2012), and McDade et al. (2012). Observations made on plants occurring in three different habitats in the vicinity of Lagos, Nigeria showed slight differences in characters, but it was not determined whether those differences were genetically fixed or correlated with the different habitats (Hossain and Emumwen 1981). Morton (1979) noted that presumably native plants from Brazil that were described as *N. pohlii* are intermediate between *N. smithii* and *N. canescens* in most of the morphological characters he used to distinguish the two species. Until additional studies provide more convincing insights, Hossain's (1984) broad interpretation of this species is utilized here.

Fongod et al. (2010) reported efficacy of *N. canescens* as a beneficial cover crop (especially in weed suppression) in banana plantations.

2. *Nelsonia gracilis* Vollesen (Angola, Malawi, Zambia)

This species of annual duration with sessile to subsessile leaves and bluish flowers appears rather distinctive, but some plants (e.g., *Bingham 10092* at K from Zambia) appear to be perennial, and flowers of some collections of *N. canescens* are also described as "blue." Some apparently annual (or first-year perennial) plants of the latter species (e.g., *Henty & Foreman NGF 49370* from Papua New Guinea at L) are similar to *N. gracilis* with their wiry stems and small, elliptic, and subsessile to short-petiolate leaves.

Excluded Name

Nelsonia brunelloides (Lam.) Kuntze

Justicia brunelloides Lam.

Although it is often cited as a synonym of *N. canescens*, this name pertains to *Hemigraphis* (Bremekamp 1944).

SAINTPAULIOPSIS Staner, Bull. Jard. Bot. Brux. 13: 8 (1934).—

TYPE. *Saintpauliopsis lebrunii* Staner (*Staurogyne lebrunii* (Staner) B.L. Burttt)

Terrestrial, epiphytic, or epipetric acaulescent or caulescent stoloniferous perennial herbs to 4 dm tall or long, often trailing, rooting at nodes and forming mats on forest floor or rosellate clumps on rocky walls. Young stems subquadrate to quadrate-sulcate, evenly pubescent with conspicuously (or inconspicuously) multi-septate flexuose eglandular trichomes, septae maroon. Leaves opposite, evenly disposed along young stems or sometimes \pm congested into subrosettes, petiolate, petiole usually longer than blade, margin of blade entire to sinuate-crenate. Inflorescence of pedunculate loose terminal raceme-like modified thyrses (or panicles of modified thyrses; see discussion), peduncles lacking scales, fertile portion of inflorescence neither dense nor cylindrical, 8–15 mm in diameter (excluding corollas) near midpoint, not branching, rachis clearly visible; dichasia alternate (sometimes resulting in a zig-zag inflorescence), pedunculate. Bracts alternate, not imbricate, greenish, membranaceous, adnate to (and indistinguishable from) dichasial peduncle for 91–98% the length of the peduncle, free portion of bract (arising near apex of peduncle) linear to lance-linear, 2–3.7 mm long, 0.3–0.5 mm wide, 1-veined. Bracteoles borne at base of flower where partially adnate basally to receptacle and calyx tube, greenish, lance-linear to lanceolate to elliptic (to obovate), 1.8–5 mm long, 0.3–0.7 mm wide. Flowers sessile. Calyx deeply 5-lobed, greenish (or lateral lobes hyaline), 3.3–5 (–6.5 in fruit) mm long, lobes heteromorphic (1 + 2 + 2), 3 larger lobes (posterior and 2 anterior) lanceolate to linear to elliptic (to obovate), 3.2–4.2 (–6) mm long, 3-veined, 2 smaller (lateral) lobes often hidden by bracteoles, lanceolate to subulate, 1.1–2 mm long, 1-veined. Corolla white to pink with darker pink striations to pale blue, \pm pendant, 4.5–8.5 mm long, externally glabrous (margins of lobes ciliolate), tube \pm campanulate, narrow proximal portion \pm cylindrical, distally widely spreading into throat, limb 2-labiate, upper lip 2-lobed, shorter than lower lip, lower lip lacking a bullate palate. Stamens 4, didynamous, inserted at \pm different heights or equally inserted, presented at different heights, longer (anterior) pair inserted near base of throat, exerted from mouth of corolla but anthers not extending beyond limb, shorter (posterior) pair inserted near base of throat (often distal to anterior pair) and with anthers included in throat, thecae apparently dehiscent toward lower lip (i.e., flower nototribic), ellipsoid, 0.7–1 mm long, those of a pair parallel to subsagittate, equal in length, glabrous, each with a slender, straight or curved, bifurcate (forked) basal appendage 0.2–0.4 mm long; staminode not evident or 1, to 0.5 mm long; pollen oblate spheroidal to euprolate (P:E = 0.88–1.87; polar axis 21–43 μ m, equatorial axis 21–26 μ m), 3-colpate to 3-colporoidate, exine reticulate (sometimes appearing \pm foveolate in non-acetolyzed grains), muri

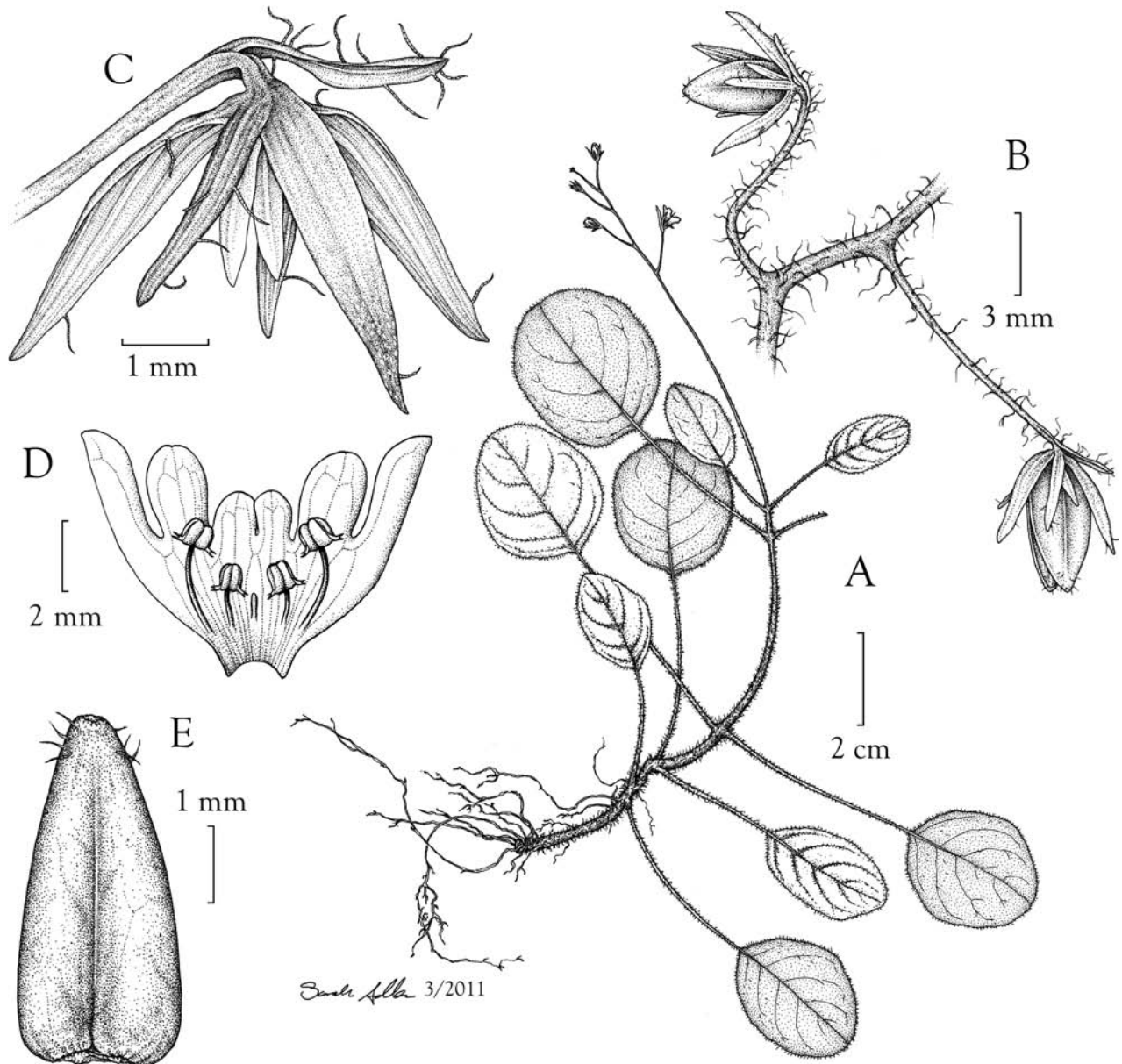


Fig. 19. *Saintpauliopsis lebrunii*.—A. Habit (Reekmans 10955; Burundi).—B. Inflorescence nodes with two flowers in fruit (Lewalle 753; Burundi).—C. Dichasium with bract, bracteoles, and calyx (Lewalle 753).—D. Corolla opened to show androecium (redrawn from sketch on *d'Alleizette* 1107 at P; Madagascar).—E. Capsule (Lewalle 753). Drawn by S. Adler and N. Pugh.

verrucate. Style exerted from mouth of corolla, equaling or extending beyond upper lip, usually not exceeding lower lip, stigma not touch-sensitive, subequally to unequally 2-lobed, lobes somewhat flattened and spreading, 0.1–0.6 mm long, 0.1–0.3 mm wide. Capsule ovoid, 3.5–5.3 mm long, glabrous proximally, sparsely pubescent distally with flexuose to antrorse eglandular trichomes. Seeds up to 26 per capsule (ovules (12–) 28–36 per capsule), \pm blocky to oblong, longest axis 0.5–1 mm, shortest axis 0.4–0.7 mm, surfaces coarsely rugose- to lumpy- to foveolate-reticulate, pubescent with hygroscopic, uncinuate to anchor- or Y-shaped trichomes <0.05 mm long; (Fig. 19).

A single species from tropical Africa and Madagascar (Fig. 20) is recognized in this genus. Plants are often mistaken

for Gesneriaceae (indeed, the genus was originally treated in that family; Staner 1934), and often grow in habitats (e.g., mossy banks) typical of many gesneriads. The species shows similarities to, and has been treated in, *Staurogyne* (Burt 1958). Indeed, leaves and inflorescences of *Saintpauliopsis lebrunii* greatly resemble those of *Staurogyne chapaensis* from south-eastern Asia (although the bracteoles are not fused to the flower in the latter species). If *Saintpauliopsis* were to be treated in an expanded concept of *Staurogyne*, *Anisosepalum* also would have to be included in that genus in order to maintain monophyly of genera. *Saintpauliopsis* differs from *Staurogyne* and *Anisosepalum* by the characters noted in the key above.

In addition to the distinctive habit and leaves of *Saintpauliopsis*, the inflorescence is unusual among Nelsonioideae. It is



Saintpauliopsis

Fig. 20. Map of Africa showing the distribution by country of *Saintpauliopsis*.

sometimes noted to be a raceme. It is not treated here as such because the lateral branches are presumed to be modified dichasia on peduncles. The combination of alternate dichasia (sometimes resulting in a zig-zag rachis), a thin (<0.5 mm in diameter on flattened specimens) and wiry rachis, partial adnation of the bract with the dichasial peduncle and its emergence near the apex of the peduncle on the anterior side (i.e., farthest from rachis) of the dichasium, and partial adnation of the bracteoles to the floral receptacle and calyx tube is unique among Nelsonioideae. According to Dickinson (1978; where *Saintpauliopsis* is cited as an example), flower-bract associations

of this type are examples of cryptic epiphyly. Adnation of bracteoles with the base of the flower also occurs in *Anisosepalum*, and appears to represent a morphological synapomorphy for the clade consisting of these two genera.

A bifurcate basal appendage on each anther theca was reported by Hossain (2004) and was observed on specimens with visible stamens that we examined. The bifurcate nature of the appendage was not noted by Staner (1934), Champluvier (1991), or Vollesen (2008). Whether it is indeed ubiquitous in plants of the genus or not remains unknown.

Currently Recognized Species of *Saintpauliopsis*

1. *Saintpauliopsis lebrunii* Staner (Burundi, Congo-Kinshasa, Gabon, Madagascar, Rwanda, Tanzania)

Synonyms fide Vollesen (2008): *Saintpauliopsis lebrunii* var. *obtusa* Staner, *Staurogyne lebrunii* (Staner) B.L. Burtt

We found no morphological differences between plants from Madagascar and those from the African continent. Detailed label notes on *Perrier de la Bâthie* 9257 (P) from Madagascar indicated flowers as having two stamens and two staminodes. It is unknown whether this represents an error of observation (no corollas are extant on the specimen at P) or variation in the androecium of this species. Other collections from Madagascar have four stamens and a single staminode.

STAUROGYNE Wall., Pl. Asiat. Rar. 2: 80 (1831).—LECTOTYPE (designated by Leonard, Contr. U.S. Natl. Herb. 31: 5 (1951). *Staurogyne argentea* Wall.

Ancistrostylis T. Yamaz., J. Jap. Bot. 55: 1 (1980).—TYPE. *Ancistrostylis harmandii* (G. Bonati) T. Yamaz. (*Herpestis harmandii* G. Bonati)

Ebermaiera Nees in Wall., Pl. Asiat. Rar. 3: 75 (1832).—LECTOTYPE (designated by Leonard, Contr. U.S. Natl. Herb. 31: 5 (1951). *Ebermaiera humilis* Nees

Erythracanthus Nees in Wall., Pl. Asiat. Rar. 3: 75 (1832).—TYPE. *Erythracanthus racemosus* (Roxb.) Nees (*Ruellia racemosa* Roxb.)

Gynocraterium Bremek. in Sandwith, Kew Bull. 1939: 557 (1939).—TYPE. *Gynocraterium guianense* Bremek.

Neozenkerina Mildbr., Notizbl. Bot. Gart. Berlin-Dahlem 7: 491 (1921).—TYPE. *Neozenkerina bicolor* Mildbr.

Ophiorrhizophyllum Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40: 76 (1871).—TYPE. *Ophiorrhizophyllum macrobotryum* Kurz

Phyllophiorhiza Kuntze in Post and O. Kuntze, Lex. Gen. Phan. 435 (1903).—TYPE. *Ophiorrhizophyllum macrobotryum* Kurz

Staurogynopsis Mangenot & Aké Assi, Bull. Jard. Bot. État 29: 27 (1959).—TYPE. *Staurogynopsis paludosa* Mangenot & Aké Assi

Stiftia Pohl ex Nees in Alph. de Candolle, Prodr. 11: 70 (1847), nomen non rite publicatum

Zenkerina Engl., Bot. Jahrb. Syst. 23: 497 (1897).—TYPE. *Zenkerina kamerunensis* Engler

Acaulescent to caulescent, prostrate to decumbent or ascendant to erect annual or perennial herbs or rarely shrubs. Younger stems subterete to subquadrate or becoming \pm flattened on drying, subglabrous or pubescent with eglandular and/or glandular trichomes. Leaves opposite (or distal ones sometimes subopposite or alternate), evenly disposed along stems or in a basal cluster, sessile to petiolate, petiole usually shorter than blade, margin of blade entire to sinuate-crenate or shallowly dentate. Inflorescence of dichasia in leaf axils or usually of pedunculate axillary and/or terminal spikes, racemes, or thyrses, these sometimes branched and forming panicles, fertile portion of inflorescence loose or dense, not cylindrical to cylindrical, peduncles lacking clasping scales (rarely

with a few scattered non-clasping sterile bracts); dichasia opposite or alternate, sessile to pedunculate. Bracts opposite or alternate, imbricate or not, green or otherwise colored, membranaceous, borne along inflorescence rachis or adnate to dichasial peduncle for 11–80 (–100%) the length of the peduncle, subfoliose or triangular to subulate to elliptic to subcircular to obovate-elliptic to oblanceolate, 2–35 mm long, 0.5–11 mm wide, 1-, 3-, 5-, or 7-veined. Bracteoles borne at apex of dichasial peduncle or at base of flower (but not adnate to receptacle or calyx), green or otherwise colored, subulate to narrowly elliptic to elliptic to oblanceolate, 1.5–19 mm long, 0.4–5.7 mm wide. Flowers sessile to pedicellate. Calyx deeply 5-lobed, green or otherwise colored or at least partially hyaline, 3–36 mm long, lobes \pm heteromorphic (1 + 2 + 2; rarely subequal), posterior lobe 3–35 mm long, 1-, 3-, 5-, or 7-veined, usually larger than others, lateral lobes 1–22 mm long, 1- or 3-veined, anterior lobes sometimes fused to a greater extent than other lobes, 2–31 mm long, 1-, 3-, or 5-veined. Corolla white, yellow, pinkish, red, bluish, or purple, sometimes with colored markings within limb, 3.8–47 mm long, externally glabrous or pubescent, tube subcylindric to funnellform, throat inconspicuous or conspicuous and \pm equal to or longer than cylindrical narrow proximal portion of tube, limb subactinomorphic to 2-labiate, upper lip 2-lobed, sometimes shorter than lower lip, lower lip lacking a bullate palate. Stamens 4 (rarely 2), usually didynamous, inserted in corolla tube, anthers included in tube or if slightly exerted from mouth of corolla then usually not (or but barely) extending beyond lips of corolla (rarely long-exserted, see discussion of *S. macrobotrya* below), thecae dehiscing toward lower lip (i.e., flower nototribic), broadly ellipsoid, 0.3–2.9 mm long, those of a pair parallel to widely divergent (i.e., thecae \pm end to end and horizontal [stamen T-shaped] to “upside-down” [stamen Y-shaped]), equal to subequal in length, glabrous or pubescent, sometimes minutely mucronate near base (with mucro on side of theca opposite dehiscing side), connective sometimes expanded; staminode 0 or 1 (posterior) or rarely 2–3, inconspicuous; pollen oblate spheroidal to perprolate (P:E = 0.95–2.31; polar axis 13–47 μ m, equatorial axis 11–36 μ m), 3-colpate to 3-colporoidate to 3-colporate, exine reticulate (sometimes appearing \pm foveolate in non-acetolyzed grains), muri smooth. Style included in corolla tube or if exerted from mouth of corolla then usually not extended beyond lips of corolla (except in *S. macrobotrya*), stigma not touch-sensitive, equally to unequally 2-lobed (sometimes appearing subcrateriform), 1 lobe again 2-parted (in some species), lobes linear (to broadly ovate-triangular), 0.2–2 mm long, 0.05–0.8 mm wide. Capsule subellipsoid to subcylindric to ovoid, 3–12 (–20) mm long, glabrous or pubescent (usually with glandular trichomes). Seeds up to 68 per capsule, spheric to ellipsoid to oblong to blocky or irregularly shaped, longest axis 0.3–1 mm, shortest axis 0.2–0.8 mm, surface coarsely lumpy- to foveolate- to rugulate-reticulate, microverrucate to microbaculate, pubescent with \pm hygroscopic trichomes, trichomes anchor-shaped to apically multibranched or sometimes trichomes branched throughout; (Fig. 21, 22).

This, the richest genus of Nelsonioideae, contains 145 currently recognized species in tropical regions (Fig. 23) of the Americas (30 spp.), Africa (5 spp.), and mainland Asia to the Solomon Islands (110 spp.). The genus is especially well represented in southeastern Asia, Malesia, and Brazil. Due to a

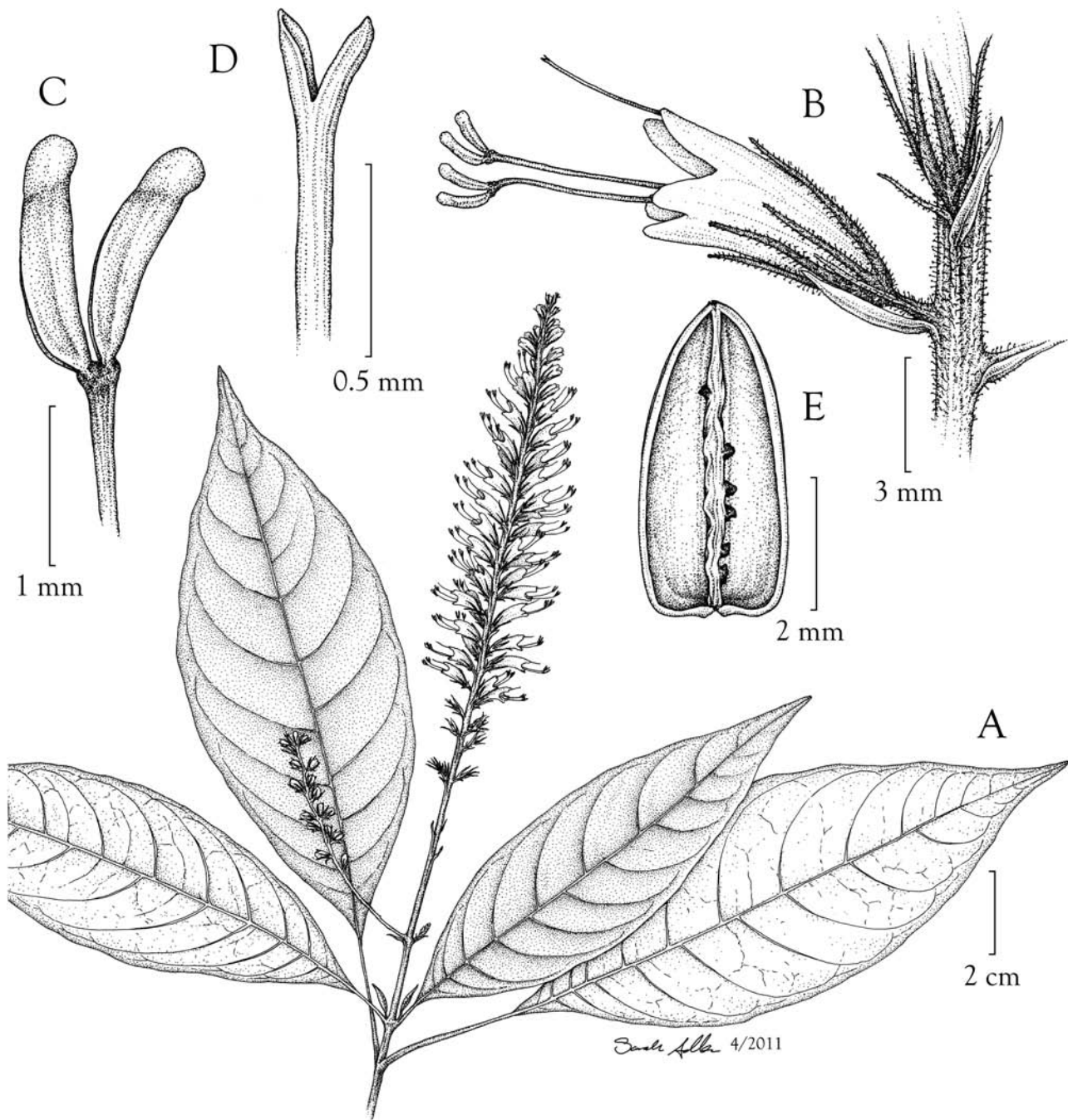


Fig. 21. *Staurogyne macrobotrya* (*Ophiorrhizophyllum macrobotryum*).—A. Habit (Maxwell 97-170; Thailand).—B. Inflorescence nodes with flower (Maxwell 97-170).—C. Apex of stamen with anther (Maxwell 97-170).—D. Apex of style with stigma (Garrett 654; Thailand).—E. Capsule with aborted seeds (Maxwell 95-211; Thailand). Drawn by S. Adler.

lack of recent studies of Acanthaceae from throughout Asia, the distributions of species occurring there, as noted in the catalog below, is not as complete as for species from other regions. The Malesian species were treated by Bremekamp (1955); African species, which are restricted to the Gulf of Guinea region, were treated by Champluvier (1991); and the New World species were revised by Braz (2005). No species are common to both the New World and the Old World; and no species occurs in both Africa and the Asia-Malesian region.

Given the size of this genus, which is about four times as species rich as all other nelsonioid genera combined, and its

broad distribution, the morphological diversity noted in the description above is not surprising. Diversity in habit, leaf shape, pubescence, inflorescence type, and floral characters has resulted in the recognition of numerous genera in a staurogynoid alliance. Only two of these are recognized here. Both *Anisosepalum* and *Saintpauliopsis* have been, and could with some justification yet be, included in *Staurogyne*; together, the former genera are sister to the geographically wide-ranging sample of 25 species of *Staurogyne* studied by McDade et al. (2012). Each of those genera also shares some morphological characteristics with *Staurogyne*, but each also

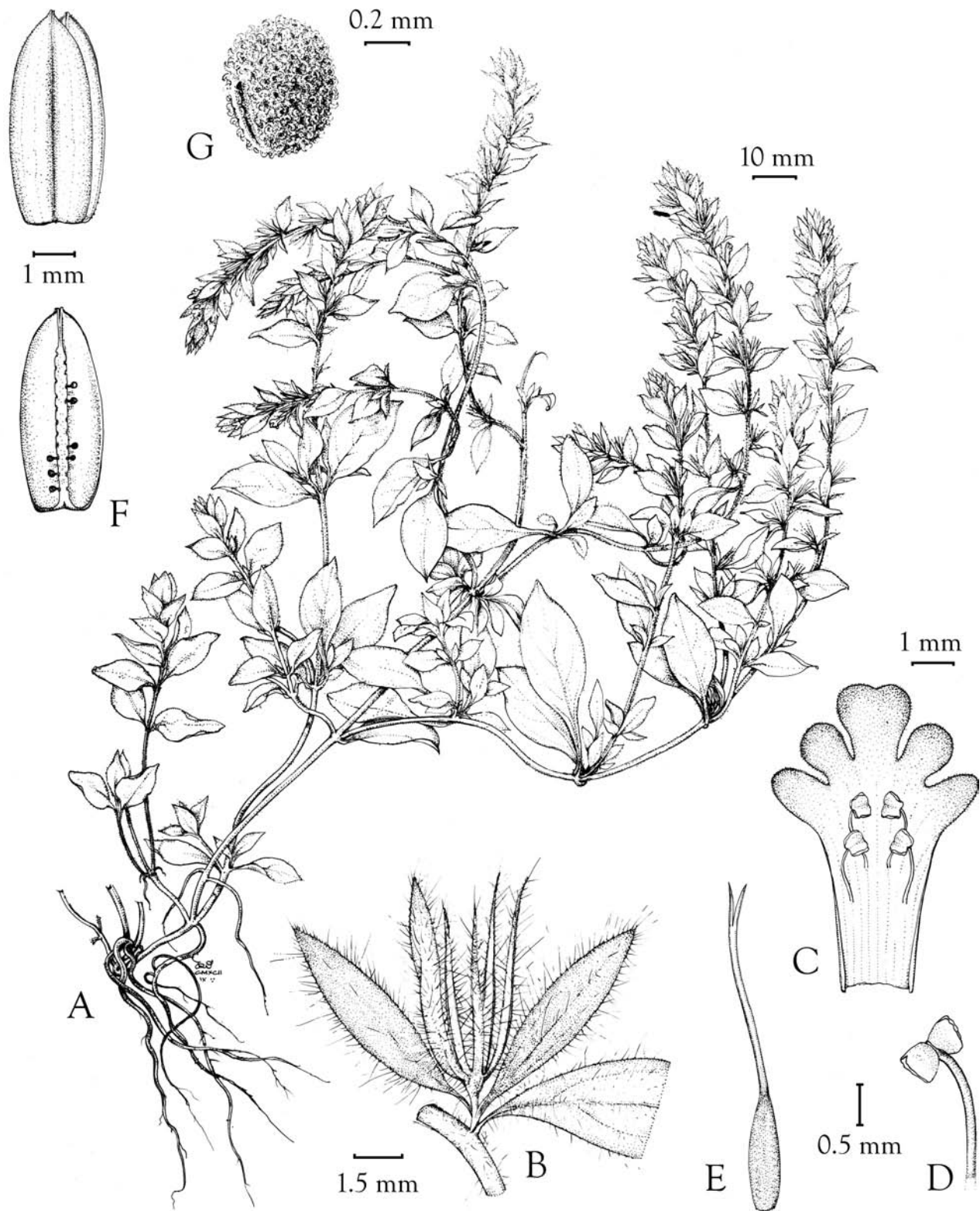


Fig. 22. *Staurogyne miqueliana*.—A. Habit (Lott et al. 3396; Mexico).—B. Inflorescence node with bract, bracteoles, and calyx (Lott et al. 3396).—C. Corolla opened to show androecium (Lott et al. 3226; Mexico).—D. Stamen (Lott et al. 3226).—E. Gynoecium (Lott et al. 3226).—F. Capsule (external view at top, internal view at bottom) (Lott et al. 3396).—G. Seed (Lott et al. 3396). Drawn by K. Douthit (copyright reserved to University of Michigan Herbarium, used with permission).

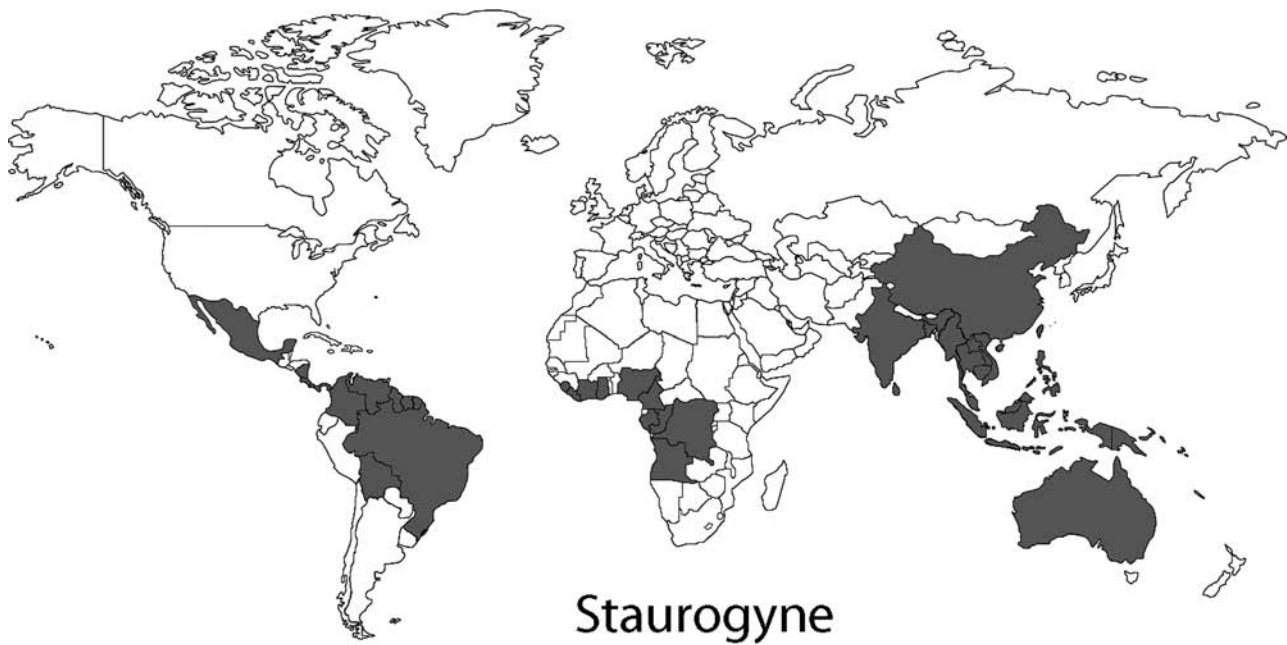


Fig. 23. Map showing the worldwide distribution by country of *Staurogyne*.

differs in several diagnostic features noted in the key above. Because of these diagnostic and unusual features, we prefer to recognize both *Anisosepalum* and *Saintpauliopsis*. Older names that are now treated as synonymous with *Staurogyne* were discussed by Bremekamp (1955) and Hossain (2004). *Ancistrostylis* T. Yamaz., a unispecific genus originally described in Scrophulariaceae based on a collection from Laos (Yamazaki 1980), was treated as congeneric with *Staurogyne* by Scotland and Vollesen (2000). Morphological characters enumerated in the protologue agree well with those of *Staurogyne*. The sole species has not been transferred to *Staurogyne*; whether it corresponds to a previously described species of that genus from southeastern Asia remains to be determined.

Bremekamp (1955) noted that *Gynocraterium* was very similar to *Staurogyne*, from which it differed by its crateriform stigma and fewer number of ovules. Braz and Monteiro (2011) also noted the distinctive, elongate, and subulate bracts, bracteoles, and calyx lobes of the sole species, *G. guianense*. Subulate bracts and bracteoles are known elsewhere among *Staurogyne* (e.g., *S. setigera*). Braz and Monteiro (2011) noted between six and ten ovules per locule in their description of *G. guianense*, a range that does not distinguish the genus from other genera of Nelsonioideae in South America. Form of the stigma would appear to be the primary morphological character for distinguishing *Gynocraterium* from *Staurogyne*. Stigmas of *Jansen-Jacobs 2852* (at U) that were hydrated and studied have two unequal (0.4 and 0.7 mm long) and broadly (1–1.2 mm wide) ovate-triangular lobes that result in a subcrateriform or funnel-shaped aspect. Although form of the stigma is not well documented among species of *Staurogyne*, and is often not well preserved on herbarium specimens, bilobed stigmas occur in the genus. Indeed, Hossain's (2004: Fig. 1L17) illustration of the stigma of *S. subcordata* showing two broad and flattened lobes are similar to those of *G. guianense*. Subcrateriform stigmas sometimes also occur in at least one species of *Elytraria* (i.e.,

E. caroliniensis; Fig. 15K). Intermediates or variations between funnel-shaped stigmas and bilobed stigmas in another genus of Acanthaceae (*Thunbergia* Retz.) are illustrated by Retief and Reyneke (1984: Fig. 3) and Schönenberger (1999: Fig. 118). Given other similarities between *G. guianense* and species of *Staurogyne* and the molecular phylogenetic results of McDade et al. (2012), this putative morphological distinction would not seem sufficient to be the basis of a separate genus. Further, because current phylogenetic results (McDade et al. 2012) indicate that *Gynocraterium* is sister to all species of *Staurogyne* in the New World, if the former genus were to be recognized as distinct from the latter, then either all Neotropical species of *Staurogyne* would have to be transferred to *Gynocraterium* or a new genus would have to be recognized for them. Because morphological synapomorphies remain unknown for species of *Staurogyne* in the New World, neither of these alternatives seems prudent at present.

Bremekamp (1955) also noted a close alliance between *Ophiorrhizophyllum* and *Staurogyne*. He contended that the sole distinction for *Ophiorrhizophyllum* was the exertion of the stamens, and he noted “this can hardly be regarded as sufficient to justify the maintenance of the genus” (Bremekamp 1955: 160). Hossain (2004) further noted that several species of *Staurogyne* have shortly exerted stamens. Another unusual character of *O. macrobotryum*, the type of *Ophiorrhizophyllum*, is the relationship between the anther connective and the two thecae. Among Nelsonioideae, the thecae are attached to the connective distally and are sometimes free from it (to a lesser or greater extent) proximally. Among species of *Staurogyne* both narrow and broad connectives are encountered, and the pair of thecae varies from parallel to sagittate to horizontal (i.e., each perpendicular to the connective and oriented apex to apex, thus stamen T-shaped). In *O. macrobotryum* the thecae are attached only at one end (presumably the distal end), and are divergent and erect (stamen Y-shaped) so that they appear “upside-down.” Somewhat similar

thecae among species of *Staurogyne* were observed by us in *S. setosa* (Toroës 2320 at MICH), illustrated by Hossain (2004: 22, Fig. 1A) in *S. subcordata*, and illustrated by Champluvier (1991: 107, Fig. 3G) in *S. capitata*. Although the shapes and sizes of connectives and thecae differ among these four species, in all of them the thecae appear to be attached only at the apex and oriented “upside-down.” Because anthers are rarely described for species of *Staurogyne*, this unusual arrangement of thecae might be more common than is known. Considering phylogenetic relationships (McDade et al. 2012) and the apparent lack of significant morphological distinctions, there appears to be insufficient basis for recognition of *Ophiorrhizophyllum* as distinct from *Staurogyne*.

Bremekamp (1955) created an infrageneric classification for the Asian species of the Malesian region. He indicated that the classification of African and American species would have to await further studies, but suggested that they were not affiliated with the subgenera he recognized for Asian species. He recognized two subgenera, *Staurogyne* and *Tetrastichum* Bremek., based on the number of ovules, number of rows of ovules in each ovary cell, and inflorescence characters. Subgenus *Staurogyne* was divided into sections, subsections, and series based on differences in habit, inflorescence, bract, and calyces. Hossain (1971, 1972) dealt with the species on a worldwide basis, and proposed (but only partially published) a more extensive infrageneric treatment. Hossain (1972) published sect. *Zenkerina* (Engl.) E. Hossain in subgen. *Tetrastichum*, and he proposed three unnamed series in subgen. *Staurogyne*, sect. *Staurogyne*, subsect. *Staurogyne* (as “*Macrosepala* Bremek.”) to account for species not treated by Bremekamp (1955) and/or that could not be accommodated in his classification for Malesian taxa.

Champluvier (1991) provided descriptions of, and a key to, the five African species of *Staurogyne*. These all occur in tropical western Africa, primarily around the Gulf of Guinea in wet evergreen forests. Champluvier (1991) also discussed the disposition of the African species relative to Hossain’s classification. She treated *S. letestuana* in subgenus *Staurogyne* and noted problems and inconsistencies in characters of other African species vis-à-vis their treatment by Hossain in sect. *Zenkerina*. She questioned the recognition of sect. *Zenkerina* based on its circumscription, but noted that the African species assigned to this section differ from *S. letestuana* by having: 1) capsules with a membranous wall, and that are tardily and apparently not explosively dehiscent, and 2) calyx lobes that converge and rest upon the capsule (even after dehiscence). At least the membranous wall of capsules in these species is apparently unique in the genus. Thus, additional studies are necessary to determine an appropriate taxonomic placement for most of the African species.

Braz (2005) provided descriptions of, and a key to, 28 species of *Staurogyne* in the Neotropics. Profice (2000) described an additional Neotropical species, *Staurogyne carvalhoi* Profice, which according to Braz (2005) likely represents an undescribed genus of Acanthaceae with hypocrateriform corollas and three seeds per locule. This species was excluded from Braz’s study, and we have not seen specimens of it. Braz (2005) noted two centers of richness for New World *Staurogyne*: southeastern Brazil (especially in the mata Atlântica biome where 19 of the Neotropical species are restricted) and northern South America (especially in the

Amazon forest biome of northern Brazil, the Guianas, and Venezuela). Braz (2005) concluded that based on Hossain’s (1972) infrageneric taxa, all New World species of *Staurogyne* pertain to subsect. *Staurogyne* (as “*Macrosepala*”).

Hossain’s (1971) mostly unpublished infrageneric account of *Staurogyne* is particularly uninformative because he assigned most species to infrageneric taxa, which permits testing of his taxonomic hypotheses using molecular sequence data. Also, Braz (2005) used morphological data of mostly Neotropical species to construct a phylogeny for the species she studied. She concluded that *Staurogyne* was monophyletic, but that the Neotropical species were not (i.e., two Asian species were nested among those from the New World). Infrageneric relationships based on molecular phylogenetic data of McDade et al. (2012) confirm that *Staurogyne* is monophyletic (inclusive of *Ophiorrhizophyllum* and *Gynocraterium*), and reveal the Neotropical species to be monophyletic and sister to those from the Old World. Although additional phylogenetic work is required to fully understand the relationships of species in the Old World, there is some support for those sampled from Asia as also being monophyletic (McDade et al. 2012).

Currently Recognized Species of *Staurogyne*

For this list the following sources provided most of the information about species currently recognized and their synonymies: Benoist (1935; southeastern mainland Asia), Bremekamp (1955; Malesia), Hossain (1971, 1972; worldwide), Champluvier (1991; Africa), Hô (1993; Vietnam), Braz (2005; New World), and Hu et al. (2011; China). Numerous additional local floras in Asia, Malesia, Papuasia, and Australia were also consulted. Where there were conflicts, the most recent taxonomic interpretations were generally given preference. The list undoubtedly lacks some synonyms. Although all African (Champluvier 1991) and New World (Braz 2005) species have been revised recently, the majority of species occur in southern Asia and Malesia, and there is no recent comprehensive account of the genus in either of those regions.

1. *Staurogyne alba* Braz & R. Monteiro (Brazil)
2. *Staurogyne amboinica* Bremek. (Indonesia)
3. *Staurogyne amoena* Benoist (Vietnam)
4. *Staurogyne anigozanthus* (Nees) Kuntze (Brazil)
Ebermaiera anigozanthus Nees
5. *Staurogyne anomala* Bremek. (Indonesia)
6. *Staurogyne arcuata* C.B. Clarke (Malaysia)
7. *Staurogyne argentea* Wall. (India, Myanmar)

Synonyms fide Hossain (1971): *Ebermaiera argentea* (Wall.) Nees, *E. staurogyne* Nees

Hossain (1972) recognized *Staurogyne argentea* var. *angustifolia* (Wall.) E. Hossain based on *S. angustifolia* Wall. (= *Ebermaiera staurogyne* Nees var. *angustifolia* (Wall.) Nees, *E. angustifolia* (Wall.) T. Anderson).

8. *Staurogyne aristata* E. Hossain (Thailand)

9. *Staurogyne athroantha* Bremek. (Philippines)
10. *Staurogyne atropurpurea* E. Hossain (Thailand)
11. *Staurogyne axillaris* S. Moore (Malaysia)
12. *Staurogyne balansae* Benoist (Malaysia, Vietnam)
13. *Staurogyne batuensis* Bremek. (Indonesia)
14. *Staurogyne beddomei* (C.B. Clarke) Kuntze (Myanmar)
- Ebermaiera beddomei* C.B. Clarke
Bremekamp's (1961) combination for this name would appear to be superfluous.
15. *Staurogyne bella* Bremek. (Thailand, Vietnam)
16. *Staurogyne bicolor* (Mildbr.) Champluvier (Cameroon)
- Neozenkerina bicolor* Mildbr.
17. *Staurogyne brachiata* (Hiern) Leonard (Brazil)
- Ebermaiera brachiata* Hiern; synonyms fide Braz (2005): *Ebermaiera gracilis* Wawra, *S. wawrana* Leonard
18. *Staurogyne brachystachya* Benoist (China, Vietnam)
19. *Staurogyne brevicaulis* Benoist (Laos, Vietnam)
20. *Staurogyne bullata* Bremek. (Indonesia)
- Didissandra parviflora* Ridl. (non *S. parviflora* (T. Anderson ex C.B. Clarke) Kuntze)
21. *Staurogyne burbridgei* C.B. Clarke ex Bremek. (Malaysia)
22. *Staurogyne cambodiana* (Benoist) E. Hossain (Cambodia, Laos)
- Staurogyne polybotrya* Nees var. *cambodiana* Benoist
23. *Staurogyne capillipes* Bremek. (Philippines)
24. *Staurogyne capitata* E.A. Bruce (Ghana, Ivory Coast, Liberia, Sierra Leone)
- Synonyms fide Champluvier (1991): *Staurogyne paludosa* (Mangenot & Aké Assi) Heine, *Staurogynopsis capitata* (E.A. Bruce) Mangenot & Aké Assi, *Staurogynopsis maiana* Mangenot & Aké Assi, *Staurogynopsis paludosa* Mangenot & Aké Assi
25. *Staurogyne carvalhoi* Profice (Brazil)
- Braz (2005) noted that this species likely represented an undescribed genus of Acanthaceae, near or pertaining to Nelsonioideae. She noted several putative distinctions with respect to *Staurogyne* (e.g., corollas hypocrateriform and seeds three per locule). We have not seen specimens of it.
26. *Staurogyne chapaensis* Benoist (China, Vietnam)
27. *Staurogyne ciliata* Elm. (Philippines)

- Hossain (1971) indicated that this taxon should be treated as a variety of *S. debilis*, but did not publish a combination for it.
28. *Staurogyne citrina* Ridl. (Indonesia)
29. *Staurogyne comosa* Kuntze (Malaysia)
- Ebermaiera axillaris* Nees (non *S. axillaris* S. Moore); synonym fide Hossain (1971): *Staurogyne cremostachya* Bremek.
Hossain (1971) indicated that *Staurogyne comosa* (Wall.) Kuntze, based on *Ruellia comosa* Wall., is illegitimate, and he treated it as a synonym of *S. cremostachya*. Although *R. comosa* Wall. (non Vell. 1829) is illegitimate, Kuntze's name, *S. comosa* Kuntze, which he equated with both *R. comosa* Wall. and *Ebermaiera axillaris*, dates from 1891 and is legitimate.
30. *Staurogyne concinnula* (Hance) Kuntze (China, Japan-southern Ryukyu Islands, Taiwan)
- Ebermaiera concinnula* Hance
Matsumura's (1912) combination for this name would appear to be superfluous.
31. *Staurogyne condensata* (Ridl.) Bremek. (Malaysia)
- Staurogyne longifolia* var. *condensata* Ridl.
32. *Staurogyne coriacea* (T. Anderson ex C.B. Clarke) Kuntze (Myanmar)
- Ebermaiera coriacea* T. Anderson ex C.B. Clarke
Bremekamp's (1961) combination for this name would appear to be superfluous.
33. *Staurogyne cuneata* Imlay (Thailand)
34. *Staurogyne dasyphylla* Bremek. (Malaysia)
35. *Staurogyne debilis* (T. Anderson) C.B. Clarke ex Merr. (Indonesia, Malaysia, Philippines, Solomon Islands, Taiwan, Vietnam)
- Ebermaiera debilis* T. Anderson
Bremekamp (1955) recognized *Staurogyne debilis* vars. *angustifolia* Bremek., *longifolia* Bremek., *pubifolia* Bremek., and *tomentosa* Bremek.
36. *Staurogyne densifolia* Bremek. (Thailand)
37. *Staurogyne diandra* E. Hossain (Vietnam)
- Hossain (1972) noted that this species was unique among *Staurogyne* by having only two stamens and two or three staminodes, and that its taxonomic relationship was uncertain. It was treated by Xin et al. (2010) as *Ophiorrhizophyllum diandrum* (E. Hossain) H.J. Xin, D.V. Hai & Y.F. Deng. This taxon has not been included in phylogenetic work and further studies of it are warranted.
38. *Staurogyne diantheroides* Lindau (Bolivia, Brazil)
39. *Staurogyne dispar* Imlay (Thailand)
40. *Staurogyne elegans* (Nees) Kuntze (Brazil)
- Ebermaiera elegans* Nees

41. *Staurogyne elongata* (Blume) Kuntze (Indonesia)
Adenosma elongata Blume, *Ebermaiera elongata* (Blume) Hassk., *Erythracanthus elongatus* (Blume) Nees; synonym fide Bremekamp (1955): *Ebermaiera subpaniculata* Hassk.
 Bremekamp (1955) recognized *Staurogyne elongata* var. *sumatrana* Bremek.
42. *Staurogyne ericoides* Lindau (Brazil)
 Synonym fide Braz (2005): *Ebermaiera minarum* var. *microphylla* Nees
43. *Staurogyne euryphylla* E. Hossain (Brazil)
 Synonym fide Hossain (1972): *Ebermaiera riedeliana* Nees var. *latifolia* Nees (non *S. latifolia* Bremek., 1969)
44. *Staurogyne eustachya* Lindau (Brazil)
45. *Staurogyne expansa* Bremek. (Thailand)
46. *Staurogyne fastigiata* (Nees) Kuntze (Brazil, Venezuela)
Ebermaiera fastigiata Nees
47. *Staurogyne filipes* E. Hossain (Laos, Thailand)
 Hossain (1972) noted two geographic variants but refrained from naming them.
48. *Staurogyne flava* Braz & R. Monteiro (Brazil)
49. *Staurogyne glutinosa* (Wall. ex C.B. Clarke) Kuntze (Bangladesh, India)
Ebermaiera glutinosa Wall. ex C.B. Clarke
50. *Staurogyne gracilis* (T. Anderson) Kuntze (Myanmar)
Ebermaiera gracilis T. Anderson
51. *Staurogyne grandiflora* E. Hossain (Myanmar)
52. *Staurogyne griffithiana* (Nees) Kuntze (Indonesia, Malaysia, Thailand)
Erythracanthus griffithianus Nees, *Ebermaiera griffithiana* (Nees) T. Anderson; synonym fide Hossain (1971): *Staurogyne setisepala* C.B. Clarke
53. *Staurogyne guianensis* (Bremek.) T.F. Daniel & McDade, comb. nov. (Brazil, French Guiana, Guyana, Suriname)
Gynocraterium guianense Bremek., Bull. Misc. Inform. Kew 1939: 557 (1940).
54. *Staurogyne hainanensis* C.Y. Wu & H.S. Lo (China)
55. *Staurogyne havilandii* C.B. Clarke ex Bremek. (Indonesia, Malaysia)
56. *Staurogyne helferi* (T. Anderson) Kuntze (Myanmar)
Ebermaiera helferi T. Anderson
57. *Staurogyne hirsuta* (Nees) Kuntze (Brazil)
Ebermaiera hirsuta Nees; synonym fide Braz (2005): *Staurogyne glutinosa* Lindau (non Kuntze)
58. *Staurogyne humifusa* Bremek. (Indonesia)
59. *Staurogyne hypoleuca* Benoist (China, Vietnam)
Ophiorrhizophyllum hypoleucum (Benoist) Benoist
60. *Staurogyne inaequalis* E. Hossain (Thailand)
61. *Staurogyne incana* (Blume) Kuntze (Indonesia, Myanmar)
Ruellia incana Blume, *Ebermaiera incana* (Blume) Hassk., *Lepidagathis incana* (Blume) Nees
62. *Staurogyne itatiaiae* (Wawra) Leonard (Brazil)
Ebermaiera itatiaiae Wawra
63. *Staurogyne jaherii* Bremek. (Indonesia, Malaysia)
 Synonym fide Hossain (1971): *Staurogyne maschalostachys* Bremek.
 Bremekamp (1955) recognized *Staurogyne jaherii* var. *angustifolia* Bremek.
64. *Staurogyne kamerunensis* (Engl.) Benoist (Cameroon, Nigeria)
Zenkerina kamerunensis Engl.
 Champluvier (1991) recognized *Staurogyne kamerunensis* subsp. *calabarensis* Champl.
65. *Staurogyne kerrii* E. Hossain (Thailand)
66. *Staurogyne kinabaluensis* Bremek. (Malaysia)
 Hossain (1971) indicated that this taxon should be treated as a variety of *Staurogyne jaherii*, but did not publish such a renovation. Bremekamp (1955) recognized *S. kinabaluensis* var. *angustifolia* Bremek.
67. *Staurogyne kingiana* C.B. Clarke (Indonesia, Malaysia)
 Bremekamp (1955) recognized *Staurogyne kingiana* vars. *angustifolia* Bremek., *magnifolia* Bremek., and *pubicalyx* Bremek.
68. *Staurogyne lanceolata* (Blume) Kuntze (Cambodia, Indonesia, Laos, Malaysia, Myanmar, Vietnam)
Adenosma lanceolata Blume; *Ebermaiera lanceolata* (Blume) Hassk.
 Bremekamp (1955) recognized *Staurogyne lanceolata* var. *scabridula* Bremek.
69. *Staurogyne lasiobotrys* (Nees) Kuntze (Malaysia, Myanmar, Thailand)
Ebermaiera lasiobotrys Nees
70. *Staurogyne latifolia* Bremek. (Thailand)
71. *Staurogyne lepidagathoides* Leonard (Brazil, Colombia, Guyana, Suriname, Venezuela)

72. *Staurogyne letestuana* Benoist (Angola, Congo-Brazzaville, Congo-Kinshasa, Gabon)
Ebermaiera letestuana (Benoist) Benoist; synonym fide Champluvier (1991): *Staurogyne congoensis* S. Moore
73. *Staurogyne linearifolia* Bremek. (Brazil, French Guiana, Guyana, Suriname)
74. *Staurogyne longeciliata* Bremek. (Thailand)
75. *Staurogyne longibracteata* E. Hossain (Myanmar)
76. *Staurogyne longicuneata* H.S. Lo (China)
77. *Staurogyne longifolia* (Nees) Kuntze (Malaysia)
Ebermaiera longifolia Nees
78. *Staurogyne longispica* (Ridl.) Ridl. (Indonesia, Malaysia)
Ebermaiera longispica Ridl.
79. *Staurogyne maccllellandii* (T. Anderson) Kuntze (Myanmar)
Ebermaiera maccllellandii T. Anderson
80. ***Staurogyne macrobotrya*** (Kurz) T.F. Daniel & McDade, comb. nov. (China, Laos, Myanmar, Thailand, Vietnam)
Ophiorrhizophyllum macrobotryum Kurz, J. Asiat. Soc. Bengal, pt. 2, Nat. Hist. 40: 76. 1871; synonym fide Hu et al. (2011): *Ophiorrhizophyllum poilanei* Benoist
81. *Staurogyne macrophylla* (T. Anderson ex C.B. Clarke) Kuntze (Myanmar)
Ebermaiera macrophylla T. Anderson ex C.B. Clarke
82. *Staurogyne major* Benoist (Vietnam)
83. *Staurogyne malaccensis* C.B. Clarke (Cambodia, Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam)
Bremekamp (1955) recognized *Staurogyne malaccensis* var. *stenophylla* Bremek.
84. *Staurogyne mandioccana* (Nees) Kuntze (Brazil)
Ebermaiera mandioccana Nees; synonym fide Braz (2005): *Ebermaiera mandioccana* var. *triandra* Hiern
85. *Staurogyne merguensis* (T. Anderson) Kuntze (Malaysia, Myanmar, Thailand, Vietnam)
Ebermaiera merguensis T. Anderson
86. *Staurogyne merrillii* Bremek. (Philippines)
87. *Staurogyne minarum* (Nees) Kuntze (Brazil)
Ebermaiera minarum Nees
88. *Staurogyne miqueliana* Kuntze (Brazil, Costa Rica, French Guiana, Guyana, Mexico, Nicaragua, Panama, Suriname, Venezuela)
Ebermaiera humilis Miq. (non *S. humilis* (Nees) Kuntze); synonyms fide Braz (2005): *Staurogyne agrestis* Leonard, *S. fockeana* Bremek., *S. stahelii* Bremek., *S. wulschlaegeliana* Bremek.
This is the most widespread species of the genus in the New World.
89. *Staurogyne monticola* Benoist (Cambodia, Thailand)
Synonym fide Hossain (1971): *S. kradengensis* Bremek.
90. *Staurogyne neesii* (S. Vidal) Merr. (Philippines)
Ebermaiera neesii S. Vidal
Benoist (1913) treated this species as *Staurogyne glauca* var. *neesii* (Vidal) Benoist.
91. *Staurogyne novoguineensis* (Kaneh. & Hatys.) B.L. Burt (Indonesia)
Didissandra novoguineensis Kaneh. & Hatys.; synonym fide Hossain (1971): *Staurogyne dasystachya* Bremek.
92. *Staurogyne obtusa* (Nees) Kuntze (Myanmar, Thailand)
Erythracanthus obtusus Nees, *Ebermaiera obtusa* (Nees) T. Anderson
93. *Staurogyne ophiorrhizoides* Elm. (Philippines)
94. *Staurogyne panayensis* Bremek. (Philippines)
95. *Staurogyne paniculata* (Wall. ex T. Anderson) Kuntze (India, Myanmar)
Ebermaiera paniculata Wall. ex T. Anderson
Karthikeyan et al. (2009) recognized *Staurogyne paniculata* var. *glabrior* (C.B. Clarke) Karthik. & Moorthy based on *Ebermaiera paniculata* var. *glabrior* C.B. Clarke.
96. *Staurogyne paotingensis* C.Y. Wu & H.S. Lo (China)
97. *Staurogyne papuana* Laut. (Indonesia)
Bremekamp (1955) recognized *Staurogyne papuana* var. *glabrifolia* Bremek.
98. *Staurogyne parva* D.M. Braz & R. Monteiro (Brazil)
99. *Staurogyne parviflora* (T. Anderson ex C.B. Clarke) Kuntze (Myanmar)
Ebermaiera parviflora T. Anderson ex C.B. Clarke
Bremekamp's (1961) combination for this name would appear to be superfluous.
100. *Staurogyne perpusilla* A.N. Henry & N.P. Balakr. (India)
101. *Staurogyne petelotii* Benoist (China, Vietnam)
102. *Staurogyne polybotrya* (Nees) Kuntze (India, Myanmar, Thailand)
Ebermaiera polybotrya Nees
Hossain (1972) recognized *Staurogyne polybotrya* var. *humilis* (Nees) E. Hossain (based on *Ebermaiera humilis* Nees

- = *S. humilis* (Nees) Kuntze) and *S. polybotrya* var. *thorelii* (Benoist) E. Hossain (based on *S. neesii* var. *thorelii* Benoist).
103. *Staurogyne pseudocapitata* Champluvier (Cameroon, Gabon)
- Champluvier (1991) recorded this species only from Cameroon. In 2004, she annotated a specimen at P from Gabon (*N. Hallé* 424) as this species.
104. *Staurogyne punctata* J.B. Imlay (Thailand)
105. *Staurogyne racemosa* (Roxb.) Kuntze (Cambodia, Indonesia, Malaysia)
- Ruellia racemosa* Roxb., *Ebermaiera racemosa* (Roxb.) Miq., *Erythracanthus racemosus* (Roxb.) Nees
- Benoist (1935) recognized *Staurogyne racemosa* “var. *pierrei*” Benoist but the “name” was not validly published because it lacked a Latin description. A subsequent valid publication of this variety has not been seen.
106. *Staurogyne ranaiensis* Bremek. (Indonesia)
107. *Staurogyne repens* (Nees) Kuntze (Brazil)
- Ebermaiera repens* Nees
108. *Staurogyne riedeliana* (Nees) Kuntze (Brazil)
- Ebermaiera riedeliana* Nees
109. *Staurogyne rosulata* Bremek. (Thailand)
110. *Staurogyne rubescens* D.M. Braz & R. Monteiro (Brazil)
111. *Staurogyne samarensis* Bremek. (Philippines)
112. *Staurogyne sandakanica* Bremek. (Malaysia)
113. *Staurogyne scandens* Benoist (Vietnam)
114. *Staurogyne scopulicola* Kiew (Malaysia)
115. *Staurogyne sesamoides* (Hand.-Mazz.) B.L. Burt (China, Laos, Vietnam)
- Loxostigma sesamoides* Hand.-Mazz.; synonym fide Hu et al. (2011): *Staurogyne dolichocalyx* E. Hossain
116. *Staurogyne setigera* (Nees) Kuntze (Indonesia, Malaysia, Philippines, Singapore, Thailand)
- Ebermaiera setigera* Nees; synonyms fide Benoist (1935): *Ebermaiera subcapitata* C.B. Clarke, *E. trichocephala* Miq.; synonym fide Hossain (1971): *Adenosma uliginosa* R. Br. var. *erecta* Nees
- Bremekamp (1955) recognized *Staurogyne setigera* var. *grandis* Bremek., based on *S. balabacensis* Quisumb.
117. *Staurogyne shanica* W.W. Sm. (Myanmar)
118. *Staurogyne sichuanica* H.S. Lo (China)
119. *Staurogyne simonsii* (T. Anderson) Kuntze (India, Vietnam)
- Ebermaiera simonsii* T. Anderson
120. *Staurogyne singularis* Bremek. (Thailand)
- Hossain (1972) recognized *Staurogyne singularis* var. *longipedicellata* (Bremek.) E. Hossain, based on *S. bella* var. *longipedicellata* Bremek.
121. *Staurogyne sinica* C.Y. Wu & H.S. Lo (China)
- Synonym fide Hu et al. (2011): *Titanotrichum parviflorum* X.B. Ye & W.T. Lin
122. *Staurogyne spatulata* (Blume) Koord. (Australia, Cambodia, China, India, Indonesia, Laos, Myanmar, Papua New Guinea, Philippines, Thailand, Vietnam)
- Adenosma spatulata* Blume, *Ebermaiera glauca* var. *spatulata* (Blume) C.B. Clarke; synonyms fide Benoist (1935): *Ebermaiera glauca* Nees, *E. ligulata* Bedd., *Herpestis cochinchinensis* Bonati; synonyms fide Hossain (1971): *Staurogyne candelabrum* Bremek., *S. flexicaulis* Bremek., *S. glauca* (Nees) Kuntze, *S. glauca* var. *siamensis* (C.B. Clarke) Benoist, *S. latibracteata* Bremek., *S. leptocaulis* Bremek., *S. polycaulis* Bremek., *S. rivularis* Merr., *S. siamensis* C.B. Clarke
- Barker (1986) recognized *Staurogyne leptocaulis* subsp. *decumbens* R.M. Barker.
123. *Staurogyne spiciflora* (Miq.) Bremek. (Indonesia)
- Ebermaiera spiciflora* Miq.
- Bremekamp (1955) recognized *Staurogyne spiciflora* vars. *glabricaula* Bremek. and *stenosepala* Bremek.
124. *Staurogyne spiciformis* E. Hossain (Cambodia)
125. *Staurogyne spraguei* Wassh. (Bolivia, Brazil, Colombia, Guyana, Venezuela)
- Synonym fide Wasshausen (1992): *Staurogyne leptocaulis* Leonard (non Bremek.)
126. *Staurogyne stenophylla* Merr. & Chun. (China)
127. *Staurogyne stolonifera* (Nees) Kuntze (Brazil, Suriname)
- Ebermaiera stolonifera* Nees
128. *Staurogyne strigosa* C.Y. Wu & H.S. Lo (China)
129. *Staurogyne subcapitata* Bremek. (Philippines)
130. *Staurogyne subcordata* Benoist (Vietnam)
- Staurogyne subcordata* (Elm.) Bremek., based on *Gymnostachyum subcordatum* Elm., is a later homonym, and likely pertains to a different species.
131. *Staurogyne subglabra* C.B. Clarke (Indonesia, Malaysia)
- Bremekamp (1955) recognized *Staurogyne subglabra* var. *prianganensis* (Bremek.) Bremek. based on *S. prianganensis* Bremek.
132. *Staurogyne subrosulata* E. Hossain (Thailand)

133. *Staurogyne sundana* Bremek. (Indonesia)
134. *Staurogyne sylvatica* Lindau ex Braz & R. Monteiro (Brazil)
135. *Staurogyne tenera* Benoist (Vietnam)
136. *Staurogyne tenuispica* Bremek. (Thailand)
137. *Staurogyne thyrsoides* (Nees) Kuntze (Cambodia, India, Myanmar, Vietnam)
Ebermaiera thyrsoides Nees
138. *Staurogyne trinitensis* Leonard (Brazil, Guyana, Suriname, Trinidad & Tobago, Venezuela)
Synonym fide Braz (2005): *Staurogyne versteegii* Bremek.
139. *Staurogyne vauthieriana* (Nees) Kuntze (Brazil)
Ebermaiera vauthieriana Nees; synonym fide Hossain (1971) and Braz (2005): *Staurogyne macrantha* Lindau (non C.B. Clarke)
140. *Staurogyne veronicifolia* (Nees) Kuntze (Brazil)
Ebermaiera veronicifolia Nees
141. *Staurogyne vicina* Benoist (China, Vietnam)
142. *Staurogyne viscida* (Ridl.) Bremek. (Malaysia)
Linnophila viscida Ridl.
143. *Staurogyne warmingiana* (Hiern) Leonard (Brazil)
Ebermaiera warmingiana Hiern
144. *Staurogyne yunanensis* H.S. Lo (China)
145. *Staurogyne zeylanica* (Nees) Kuntze (India, Sri Lanka)
Ebermaiera zeylanica Nees; synonym fide Kramer (1998): *Ebermaiera glauca* T. Anderson (non Nees)

Excluded or Unresolved Names

This list includes some nomina nuda that have appeared in the literature cited.

Ancistrostylis harmandii (G. Bonati) T. Yamaz.

Scotland and Vollesen (2000) included the genus in *Staurogyne*, but no combination has been proposed for the sole species from Laos. It remains to be determined if the name corresponds to a previously described species of *Staurogyne* from southeastern Asia.

Ebermaiera nelsonioides Miq.

Hossain (1971) noted that this was the basionym of *Adenosma nelsonioides* (Miq.) Hallier f. ex Bremek. in Scrophulariaceae.

Ebermaiera nitida Rchb.f.

Hossain (1971) indicated that this name did not pertain to *Staurogyne*.

Ebermaiera sanctae-catharinae Nees

Wasshausen and Smith (1969) treated this name, based on a Tweedie collection from Santa Catarina, Brazil in Hooker's herbarium at K, as a synonym of *S. mandioccana*. Braz (2005) did not place this name, and restricted *S. mandioccana* to the Brazilian states of Rio de Janeiro and Minas Gerais. Its placement remains unresolved. Hossain (1971) indicated that it did not pertain to *Staurogyne*.

Ebermaiera velutina Nees

This name was validly published based on a Griffith collection from Mergui, India in Hooker's herbarium at K. A valid combination for it has not been made in *Staurogyne* (see below), and its taxonomic status remains unknown.

Ophiorrhizophyllum laxum Lindau

Hossain (1971) referred this name to an unidentified species of *Justicia*.

“*Staurogyne* cf. *densa* Benoist”

Hô's (1993) use of this name for a Vietnamese plant was undoubtedly an error for *Strobilanthes densa* Benoist (= *Strobilanthes atropurpurea* Nees var. *atropurpurea*), which occurs in Vietnam.

“*Staurogyne floribunda* Rizzini”

This nomen nudum was used by Rizzini (1951, 1954), but was never validly published.

“*Staurogyne glabrata* Braz”

This unpublished name was used by Braz (2005) for the species subsequently published as *S. alba* Braz & R. Monteiro.

Staurogyne javanica Lindau

This name was treated by Hossain (1971) as a synonym of *Pararuellia napifera* (Zoll.) Bremek.

Staurogyne macrantha C.B. Clarke, nomen illegit.

Clarke's name is a later homonym. Hossain (1971) indicated that this name pertains to a species of Gesneriaceae.

“*Staurogyne minor* (Kraenzl.) B.L. Burt”

This “name” was included by Hossain (1971), who indicated that he had not seen the species, but no publication of it has been located. It was likely to be based upon *Hexatheca minor* Kraenzl. (Gesneriaceae from Borneo). Its taxonomic status remains unknown, and the combination is not accepted here.

Staurogyne nudispica (C.B. Clarke) Bremek.

This name was treated by Hossain (1971) as a synonym of *Pararuellia nudispica* (C.B. Clarke) Bremek.

Staurogyne palawanensis (Elmer) Bremek.

This name was treated by Hossain (1971) as a synonym of *Gymnostachyum palawanense* Elmer.

Staurogyne pauper C.B. Clarke

This name was treated by Hossain (1971) as a synonym of *Phialacanthus pauper* (C.B. Clarke) Bremek.

"Staurogyne pedicellata E. Hossain"

A description in English of a collection from Indonesian Borneo, *Kostermans 12998*, was treated as a new species under this name in Hossain (1971), but the name was not subsequently validly published.

Staurogyne serrulata C.B. Clarke

This name was treated by Hossain (1971) as a synonym of an unidentified species of *Didymocarpus* (Gesneriaceae).

"Staurogyne tenuicaulis E. Hossain"

Hossain (1971) used, but did not publish, this "name" as a new name for the illegitimate *Staurogyne leptocaulis* Leonard (non Bremek.), to which Wasshausen (1992) gave the replacement name *S. spraguei*.

"Staurogyne velutina (Nees) E. Hossain"

Hossain (1971) cited this "name" as a new combination based on *Ebermaiera velutina* Nees, but did not subsequently validate it. The combination is not accepted here.

"Zahlbrucknera fruticosa Pohl ex Nees"

This "name" was listed by Nees (1847*a,b*), Wasshausen and Smith (1969), and Hossain (1971) as pertaining to *Staurogyne mandioccana*. It was based on a drawing and specimen (Pohl 4740 at W). Because it was published as a synonym, the name was not validly published.

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APPENDIX 1

Pollen of Nelsonioideae studied with SEM. The name of each taxon studied is followed by collection data (country, collector's number, herbarium of deposit), measurements (not all measurements could be made on all grains), and observations on endoapertures (not evident, evident but not prominent, prominent). n = number of grains measured, P = polar diameter (µm), E = equatorial diameter (µm). Pollen of additional samples and species (e.g., *Elytraria klugii*) was also

studied, but was not in a suitable orientation or condition for accurate measurements. Collection numbers with “cv” or “gh” refer to cultivated collections.

Anisosepalum alboviolaceum (Congo-Brazzaville, *Champluvier 5295*, CAS): n = 2; P = 30–31; E = 22–23; P:E = 1.35–1.36; endoapertures not evident.

Anisosepalum alboviolaceum (Congo-Kinshasa, *Louis 12208*, CAS): n = 5; P = 22; E = 23–25; P:E = 0.92–0.96; endoapertures not evident.

Anisosepalum humbertii (Congo-Kinshasa, *de Witte 7121*, CAS): n = 2; P = 24; E = 26–32; P:E = 0.90–0.92; endoapertures evident but not prominent.

Anisosepalum humbertii (Tanzania, *Congdon 591*, K): n = 3; P = 28–30; E = 22–25; P:E = 1.27–1.36; endoapertures evident but not prominent.

Anisosepalum lewallei (Burundi, *Reekmans 3610*, WAG): n = 2; P = 27; E = 23–24; P:E = 1.17; endoapertures not evident.

Elytraria acaulis (India, *Haines 3435*, K): n = 2; P = 40–41; E = 23–26; P:E = 1.58–1.74; endoapertures not evident.

Elytraria acaulis (Tanzania, *Iversen et al. 86369*, UPS): n = 3; P = 44–46; E = 24; P:E = 1.83–1.92; endoapertures not evident.

Elytraria bromoides (Mexico, *Daniel 303*, CAS): n = 1; P = 50; E = 27; P:E = 1.85; endoapertures not evident.

Elytraria bromoides (Mexico, *Daniel & Baker 3683*, CAS): n = 1; P = 51; E = 25; P:E = 2.04; endoapertures not evident.

Elytraria caroliniensis (USA, *Daniel s.n. cv*, CAS): n = 3; P = 56–58; E = 28–36; P:E = 1.56–2.07; endoapertures not evident.

Elytraria imbricata (Bolivia, *Daniel 10184*, CAS): n = 3; P = 42–44; E = 25–30; P:E = 1.47–1.76; endoapertures not evident.

Elytraria imbricata (Mexico, *Daniel & Butterwick 3259gh*, CAS): n = 2; P = 45; E = 27–35; P:E = 1.67; endoapertures not evident.

Elytraria imbricata (Mexico, *Porter 297*, CAS): n = 1; P = 44; E = 25; P:E = 1.76; endoapertures not evident.

Elytraria ivorensis (Ghana, *Enti GC42410*, WAG): n = 2; P = 35; E = 27–31; P:E = 1.30; endoapertures not evident.

Elytraria macrophylla (Mexico, *Carranza 2397*, CAS): n = 2; P = 42–43; E = 27; P:E = 1.56–1.59; endoapertures not evident.

Elytraria macrophylla (Mexico, *Dressler 2619*, DUKE): n = 1; P = not determined; E = 28; P:E = not determined; endoapertures not evident.

Elytraria madagascariensis (Madagascar, *Humbert & Cours 32602*, P): n = 3; P = 28–29; E = 34; P:E = 0.82; endoapertures evident but not prominent.

Elytraria marginata (Guinea-Bissau, *Malaisse & Claes 14802*, CAS): n = 6; P = 31–35; E = 30–33; P:E = 0.97–1.13; endoapertures not evident.

Elytraria maritima (Ivory Coast, *de Wilde 877*, WAG): n = 3; P = 30–32; E = 29–33; P:E = 0.91–1.10; endoapertures not evident.

Elytraria mexicana (Mexico, *Daniel & Butterwick 3263gh*, CAS): n = 5; P = 49–53; E = 29–31; P:E = 1.65–1.83; endoapertures not evident.

Elytraria minor (Kenya, *Greenway & Rawlins 9366*, K): n = 4; P = 31–33; E = 26–29; P:E = 1.14–1.19; endoapertures not evident.

Elytraria nodosa (Madagascar, *Almeda 9232*, CAS): n = 5; P = 44–52; E = 23–26; P:E = 1.69–2.26; endoapertures not evident.

Elytraria nodosa (Madagascar, *Daniel 11838*, CAS): n = 4; P = 28–49; E = 20–31; P:E = 0.90–2.25; endoapertures not evident to evident but not prominent.

Elytraria nodosa (Madagascar, *Goudot s.n.*, P): n = 3; P = 33–34; E = 14–16; P:E = 2.06–2.43; endoapertures not evident.

Elytraria tuberosa (Ecuador, *Eggers 15405*, S): n = 4; P = 25–31; E = 17–28; P:E = 0.96–1.82; endoapertures not evident.

Nelsonia canescens (Panama, *Daniel 5452*, CAS): n = 3; P = 34–35; E = 17–18; P:E = 1.94–2.00; endoapertures not evident.

Nelsonia canescens (Panama, *Daniel 5452cv*, CAS): n = 3; P = 34–39; E = 19–21; P:E = 1.62–2.05; endoapertures not evident.

Nelsonia canescens (São Tomé & Príncipe, *Daniel 11186*, CAS): n = 2; P = 37–38; E = 17–18; P:E = 2.11–2.18; endoapertures not evident.

Nelsonia gracilis (Zambia, *Bingham & Mpundu 122660*, K): n = 5; P = 23–28; E = 15–18; P:E = 1.28–1.87; endoapertures not evident.

Saintpauliopsis lebrunii (Congo-Kinshasa, *Humbert 7625*, CAS): n = 2; P = 21; E = 24–26; P:E = 0.88; endoapertures not evident.

Saintpauliopsis lebrunii (Madagascar, *Gautier et al. 3598*, P): n = 1; P = not determined; E = 26; P:E = not determined;

Saintpauliopsis lebrunii (Rwanda, *Bamps 3270*, BR): n = 2; P = 38–43; E = 21–23; P:E = 1.81–1.87; endoapertures not evident.

Staurogyne concinnula (Taiwan, *Bartholomew & Boufford 6215*, CAS): n = 2; P = 36–40; E = 19–20; P:E = 1.89–2.00; endoapertures not evident.

Staurogyne guianensis (Guyana, *Jansen-Jacobs et al. 2346*, US): n = 1; P = 42; E = 19; P:E = 2.21; endoapertures not evident.

Staurogyne macrobotrya (China, *Henry 11627*, US): n = 1; P = not determined; E = 18; P:E = not determined; endoapertures not evident.

Staurogyne macrobotrya (Thailand, *Hansen & Smitinand 12817*, C): n = 2; P = 27–29; E = 13–14; P:E = 1.93–2.23; endoapertures not evident.

Staurogyne major (Thailand, *Kerr 10264*): n = 1; P = not determined; E = 26; P:E = not determined; endoapertures prominent.

Staurogyne mandiocana (Brazil, *Cordeiro & Silva 108*, CAS): n = 4; P = 22–29; E = 16–21; P:E = 1.10–1.81; endoapertures not evident.

Staurogyne miqueliana (Mexico, *Lott et al. 3226*, CAS): n = 3; P = 27–30; E = 13; P:E = 2.08–2.31; endoapertures not evident.

Staurogyne miqueliana (Mexico, *Lott et al. 3396*, MEXU): n = 1; P = 24; E = 25; P:E = 0.96; endoapertures prominent.

Staurogyne spatulata (Indonesia, *Toroes 4795*, MICH): n = 4; P = 19–25; E = 14–18; P:E = 1.11–1.79; endoapertures not evident to prominent.

Staurogyne spatulata (Thailand, *Maxwell 94-76*, CAS): n = 3; P = 21; E = 22; P:E = 0.95; endoapertures evident but not prominent.

Staurogyne stolonifera (unknown, *Daniel s.n. cv*, CAS): n = 2; P = 32–36; E = 15–17; P:E = 2.12–2.13; endoapertures not evident.

APPENDIX 2

Results of tests for hygroscopic trichomes among Nelsonioideae by hydration of seeds from herbarium specimens. At least two seeds per collection were submerged in tap water and observed under a dissecting microscope at 64× for at least 3 minutes; some samples were photographed with an automontage camera system in both the dry and wet states (Fig. 9); these and/or additional samples were observed with SEM (Fig. 10–12) to observe seed surface features, including trichomes. The name of each taxon is followed by the collection/herbarium sampled, date of the collection, and the reaction observed. No reaction = no change observed in hydrated seeds vs. dry seeds; moderate reaction = only some trichomes become erect on hydrated seeds and/or this reaction is not immediate; strong reaction = most or all trichomes become erect immediately upon hydration. Collection numbers with “cv” or “gh” refer to cultivated collections.

Anisosepalum alboviolaceum (*Champluvier 5295/CAS*, 1995): no reaction.

Anisosepalum lewallei (*Bidgood et al. 4728/CAS*, 2000): no reaction.

Elytraria caroliniensis (*Daniel s.n. cv/CAS*, 2007): no reaction.

Elytraria imbricata (*Daniel & Butterwick 3201/CAS*, 1983): no reaction.

Elytraria macrophylla (*Daniel 11773 cv/CAS*, 2013): no reaction.

Elytraria marginata (*Daniel 11158 cv/CAS*, 2013): no reaction.

Nelsonia canescens (*Daniel 11186/CAS*, 2008): strong reaction.

Nelsonia canescens (*Balakrishnan 998/L*, 1974): moderate reaction.

Nelsonia canescens (*Rosales 111/CAS*, 2000): moderate reaction in some seeds and strong reaction in others.

Nelsonia gracilis (Henriquez 663/BM, 1965): strong reaction.
Saintpauliopsis lebrunii (Humbert & Capuron 28443/P, 1955): moderate reaction.
Saintpauliopsis lebrunii (Perrier de la Bathie 17106/P, 1925): moderate reaction.
Staurogyne concinnula (Peng 6777/CAS, 1984): moderate reaction.
Staurogyne debilis (Merrill 1215/MO, 1913): no reaction in some seeds and moderate reaction in others.
Staurogyne diantheroides (Wasshausen 2181/CAS, 1998): moderate reaction.
Staurogyne kamerunensis (McPherson 13913/MO, 1989): no reaction in some seeds and moderate reaction in others.
Staurogyne letestuana (Arends et al. 358/MO, 1984): no reaction in some seeds and moderate reaction in others.
Staurogyne longeciliata (Maxwell 76-7/MO, 1976): moderate reaction in some seeds and strong reaction in others.
Staurogyne macrobotrya (Poilane 20703/CAS, 1932): moderate reaction.
Staurogyne merguensis (Maxwell 94-254/CAS, 1994): moderate reaction.
Staurogyne miqueliana (Lott et al. 3226/CAS, 1991): strong reaction.
Staurogyne obtusa (Maxwell 90-362/CAS, 1990): moderate reaction in some seeds and strong reaction in others.
Staurogyne setigera (Toroës 4798/MICH, 1933): moderate reaction.

Staurogyne spatulata (Tsang 126/MO, 1928): no reaction in some seeds and moderate reaction in others.

APPENDIX 3

Chromosome numbers reported for Nelsonioideae. All counts for a taxon are shown as meiotic (i.e., haploid or *n*) numbers, followed by the author(s) reporting the count.

Elytraria acaulis (**17**, Kaur 1969; **19**, Morton 1956 [as *E. lyrata*]; **22**, Govindarajan and Subramanian 1983; **23**, Subramanian and Govindarajan 1980).
Elytraria bromoides (**12**, Daniel et al. 1990).
Elytraria caroliniensis (**25**, Grant 1955 [as *E. virgata*]).
Elytraria imbricata (**11**, Ward 1984; **12**, Daniel et al. 1990).
Elytraria marginata (**19**, Morton 1956; **22**, Mangelot and Mangelot 1962).
Elytraria maritima (**19**, Morton 1956).
Elytraria mexicana (**12**, Daniel et al. 1990).
Nelsonia canescens (**16**, Joseph 1964 [as *N. campestris*]; **14**, Sarkar et al. 1980 [as *N. campestris*]; **17 + B**, Saggoo and Bir 1982 [as *N. campestris*]; **17 + B**, Saggoo 1983; **17 + B**, Saggoo and Bir 1983; **18**, Daniel and Chuang 1993).