

A PALYNOLOGICAL INVESTIGATION OF
DAPHNE PAPHYRACEA AND *DAPHNE BHOLUA* (THYMELAEACEAE) IN INDIA

Arti Garg

Central National Herbarium
Botanical Survey of India

P.O. Indian Botanic Gardens, Howrah – 711 103, INDIA
kad_arti396@yahoo.com

Zachary S. Rogers

Missouri Botanical Garden
P.O. Box 299

St. Louis, Missouri, 63166-0299, U.S.A.
zachary.rogers@mobot.org

ABSTRACT

The pollen grains of three putative relatives (*Daphne bholua* var. *bholua*, *D. bholua* var. *glacialis*, *D. papyracea*) were studied to explore micromorphological variation aimed at identifying novel taxonomically helpful characters. Based on an examination of specimens collected from India the study taxa differed in several key palynological features, most notably in characters related to the ectoexine. The exine of *D. bholua* var. *glacialis* showed that the baculoidate, dome-shaped structure of the suprategal projections (STP) and the arrangement of the suprategal subunits (4 and free, or 5–6 and fused) were intermediate between *D. bholua* and *D. papyracea*. In addition, the mean grain diameter (29 µm), STP-pattern (semi-crotonoid), and exposed muri of the basal reticulum suggested that the pollen of *D. bholua* var. *glacialis* was more similar to the pollen of *D. papyracea* than to the typical variety of *D. bholua*. Preliminary palynological evidence indicates that the taxonomic status of *D. bholua* var. *glacialis* should be reevaluated with additional palynological and macromorphological data. The first valid publication date and correct authorship of *D. papyracea* is also clarified.

RESUMEN

Se estudió el polen de tres taxones putativamente relacionados (*Daphne bholua* var. *bholua*, *D. bholua* var. *glacialis*, *D. papyracea*) para explorar su variación micromorfológica con el objetivo de identificar nuevos caracteres de utilidad taxonómica. En base al examen de especímenes colectados en India encontramos que el polen de los taxones estudiados difiere en varios caracteres palinológicos, y más notablemente con aquellos relacionados con la ectexina. La exina de *D. bholua* var. *glacialis* presenta proyecciones suprategales (STP) baculoides con estructuras en forma de domo, y subunidades suprategales (4 y libres, o 5–6 y fusionadas) organizadas de un modo intermedio al de *D. bholua* y *D. papyracea*. Adicionalmente, el promedio del diámetro de los granos (29 µm), patrón de STP (semi-crotonoide), y los muros expuestos del retículo basal sugieren que el polen de *D. bholua* var. *glacialis* es más similar al de *D. papyracea* que al de *D. bholua*. Nuestros estudios preliminares indican que la posición taxonómica de *D. bholua* var. *glacialis* debe ser reevaluada con datos palinológicos complementarios y estudios macromorfológicos adicionales. La fecha válida de publicación y autoridades de *D. papyracea* también son clarificadas.

INTRODUCTION

Daphne L., a well-known genus comprising about 100 species distributed across Asia, Europe and North Africa, is one of the largest genera of Thymelaeaceae (ca. 45 genera, 1,000 species; Rogers 2009). Species of *Daphne* are deciduous or evergreen shrubs, shrubs, or small trees, and are often cultivated as showy ornamentals (Brickell & Mathew 1976; Halda 2001). The genus is represented in India by eight species occurring in temperate Himalaya, Khasi Hills, and Manipur (Prasanna, pers. comm.; Rogers, unpubl. data). Most of the Indian species are relatively well-defined and easily distinguishable, but two putative relatives (*D. bholua* Buch.-Ham. ex D. Don and *D. papyracea* Wall. ex G. Don) pose difficult taxonomic problems (Burt 1936). Both of these species are horticulturally important and belong to the “Paper *Daphne*” group (Brickell & Mathew 1976), as they are harvested for their bark, which is used to make paper and ropes (Hodgson 1832; Santapau & Henry 1973).

In the literature, *Daphne bholua* (recorded from India, Bangladesh, China, Bhutan, Myanmar, Nepal, Vietnam) and *D. papyracea* (recorded from India, China, Nepal) have most often been distinguished morphologically by differences related to leaf and bract persistence, flower color, fragrance, and hypanthium lobe shape (e.g., Brickell & Mathew 1976; Wang et al. 2007). The best documented distinction between the two species is whether or not the flowers are fragrant (sweetly-scented in *D. bholua* vs. odorless in *D. papyracea*). Differences in flower color have also been discussed in numerous treatments, but the supposed distinctions are often inconsistent or contradictory between reports (cf. Burt 1936; Brickell & Mathew 1976; Halda 2001;

Wang et al. 2007). Flowers of *D. bholua* are generally described as pink, or white and flushed with either pink or purple, whereas flowers of *D. papyracea* are usually characterized as white, greenish-white, or rarely pinkish. Perhaps the apparent overlap in color variation does not occur throughout the entire geographic distribution of each species because in India the flowers of *D. bholua* are reportedly always pink and the flowers of *D. papyracea* are consistently pure white (Prasanna, pers. comm.). The two species are allopatric and probably inhabit different elevation ranges. *Daphne bholua* occurs in the foothills of the Eastern Himalayas, roughly from Arunchachal Pradesh to Darjeeling and West Bengal (Prasanna, pers. comm.), while *D. papyracea* is found in the mountains of the Western Himalayas, from approximately Western Nepal to Uttar Pradesh and Punjab (Brickell & Mathew 1976).

A total of eleven morphological variants have been formally named throughout the wide geographic ranges of both species (*Daphne papyracea*—two subspecies, eight varieties, one form; *D. bholua*—one subspecies, one variety). Some of the infraspecific taxa are now recognized at the species rank, while others have been reduced to synonymy under their respective species. Five of the varieties are still recognized (Wang et al. 2007), but only one, *D. bholua* var. *glacialis* (W.W. Sm. & Cave) B.L. Burt, occurs in India (also recorded from China and Nepal). *Daphne bholua* var. *glacialis*, which was originally described as an extreme alpine variety of *D. cannabina* Lour. (Smith & Cave 1913), reportedly differs from *D. bholua* var. *bholua* by having deciduous (vs. more persistent) leaves (Burt 1936; Halda 2001), less pubescent branchlets (Brickell & Mathew 1976), a creeping (vs. erect) habit, subrhombic (vs. semicircular) leaf scars, and 6–11 (vs. 11–16) pairs of lateral veins per leaf (Wang et al. 2007).

General palynological variation in Thymelaeaceae and *Daphne* pollen

The members of Thymelaeaceae constitute a remarkable stenopalynous assemblage of uniformly spheroidal grains (Mohl 1835) with polyforate (Blaise 1959) and panporate (Archangelsky 1966; cf. pantoporate - Punt et al. 2007) aperture types. The exine strata are formed by a highly specialized crotonoid tectum or a derivative thereof (Nowicke et al. 1985; Herber 2002). The “crotonoid pattern” of the exine was first defined by Erdtman (1952: 173) as being composed of “regularly arranged excrescences (triangular or \pm circular in cross-section), supported (always?) by a baculate, baculoidate, or spongy layer.” Individual subunits are attached to a basal ring-like network of muri (also known as horizontal rods). The shape of the subunits range from basic triangular to a number of other derived shapes (e.g., baculoidate, tetrahedral, pilate), thereby forming a homogenous or heterogeneous pattern over the surface of the exine.

Daphne pollen is classified as “Type IV,” the most common of four categories of Thymelaeaceae pollen (Herber 2002). Archangelsky (1971) published the most comprehensive palynological investigation of *Daphne* using light microscopy, analyzing nearly one-half of the total number of species (ca. 40) in the genus. In that study, some species and groups of species were found to differ in one or more pollen characters (e.g., grain size, exine thickness, pore size, pore shape, pore number). Neither *D. bholua* nor *D. papyracea* have been investigated palynologically judging from available literature.

MATERIAL AND METHODS

One collection was selected for each of the three study taxa. Vouchers were identified by Dr. P. V. Prasanna, a specialist working in India, and specimens are deposited at CAL. For pollen extraction, between two and four anthers were removed from the mature buds of each collection, soaked for four to five hours in 70% alcohol, and then crushed on slides with one drop of distilled water. Extracted pollen grains were acetolyzed following the protocol of Erdtman (1960) and thoroughly washed with distilled water followed by ethanol. Excess ethanol was allowed to evaporate. Pollen grains were mounted on glass slides in glycerine jelly, sealed with molten paraffin wax, and observed with light microscopy (LM). For scanning electron microscopy (SEM) observations, one drop of the pollen-ethanol mixture was transferred to specimen stubs, any excess alcohol was allowed to evaporate, and pollen grains were sputter coated with a thin gold film of ca. 200 Å (at 18 mA current, 0.2 kV voltage for 160 sec.). Grains were viewed under the scanning electron microscope at an accelerating

voltage of 15 kV. Pollen size was measured using a calibrated ocular micrometer under LM. Palynological terminology was based on Erdtman (1952), Nair (1970), and Hesse et al. (2009).

RESULTS

General description of the observed pollen grains

Pollen grains monads, spheroidal, pantoporate, 17–32 μm in diameter. Wall tectate, suprareticulate with supracteal subunits of variable shapes and size; basal layer of ectoexine much thicker than endoexine; ectoexine attached to endoexine by means of columellae that unite to form supracteal projections (STP).

The STP correspond to the projections of the supracteal subunits described in the classification of Thymelaeaceae pollen published by Herber (2002).

Palynological summary of *Daphne bholua* var. *bholua*, *D. bholua* var. *glacialis*, and *D. papyracea* (Table 1; Fig. 1)

The pollen wall is formed by the primary and secondary reticulum, the latter is derived from a complete or partial fusion of supracteal elements. Supracteal elements form trihedral, dome-shaped or circular variously arranged supracteal subunits, which result in a crotonoid (*Daphne bholua* var. *bholua*), or barely detectable, semi-crotonoid pattern of supraornamentation (*D. bholua* var. *glacialis* and *D. papyracea*). The ectoexine is always thicker than the endoexine, and is attached to the endoexine by means of the columellae that unite to form the supracteum. The basic reticulate pattern is thus superimposed by the secondary reticulum of the supracteum and was previously described as cryptostellate by Archangelsky (1966, 1971), an observation that Herber (2002: 117) found to be erroneous. Grains are always spheroidal. Pollen size is small in *D. bholua* var. *bholua* (ca. 19.5 μm mean diameter) and larger in *D. bholua* var. *glacialis* and *D. papyracea* (both ca. 29 μm mean diameter). The supracteal subunits are either free (varying from densely to sparsely arranged), or fused in groups. When free, the individual subunits are distantly spaced, and the muri of the basal reticulum becomes exposed as horizontal rods. However, when these subunits are fused, the muri (i.e., horizontal rods) of the basal reticulum are concealed under the closely packed subunits. In all three taxa, the supracteal subunits are surmounted by a single, central projection (STP). The STP are spinulate and blunt in *D. bholua* var. *bholua*, verrucose and bead-like in *D. bholua* var. *glacialis*, and spinulate and sharply pointed in *D. papyracea*. The outlines and margins of the STP range from circular to angular and sinuous to rounded-angular, respectively, depending on the particular form of the STP.

PALYNOLOGICAL KEY TO TAXA

1. Pollen grain diameter less than 25 μm ; STP fused in groups of 5–7; muri of basal reticulum concealed _____ **1a. *Daphne bholua* var. *bholua***
1. Pollen grain diameter more than 25 μm ; STP free, or sometimes fused in groups of 4–6; muri of basal reticulum exposed.
 2. STP baculoidate; subunits 4–6, free, or sometimes fused, sparsely arranged when free; projections verrucose, bead-like, and blunt _____ **1b. *Daphne bholua* var. *glacialis***
 2. STP trihedral; subunits 5–6, free, densely arranged; projections spinulate and sharply pointed _____ **2. *Daphne papyracea***

1. *Daphne bholua* Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 68. 1825.

1a. *Daphne bholua* var. *bholua* (Fig. 1A–C).

STP baculoidate (STP-B), flattened, mean size: 1 \times 1.1 \times 0.9 μm (height \times base length \times base width), size range: 1.0–1.2 \times 1.1–1.2 \times 0.9–1 μm ; muri of basal reticulum concealed. Muri of secondary tectum forming groups of 5–7 subunits arranged in a crotonoid pattern, and surrounding the lumina of the basal (i.e., primary) reticulum; subunits densely packed, fused or rarely free. STP-B surmounted by minute, blunt spinules; spinule generally centrally located, sometimes displaced off-center, outline circular, margin sinuous; lumina of secondary reticulum 0.9–1 μm in diameter, rounded-angular.

Voucher specimen: **INDIA. Assam:** Shillong, 3000 ft, 25 Oct 1938, K. Biswas 3733 (CAL).

1b. *Daphne bholua* var. *glacialis* (W.W. Sm. & Cave) B.L. Burtt, Bull. Misc. Inform. Kew 1936: 438. 1936. (Fig. 1D–F).

TABLE 1. Pollen morphology of the three study taxa. H: Height of projection; B_L: Base width for longest axis; B_S: Base width for shortest axis.

Pollen Feature	<i>D. bholua</i> var. <i>bholua</i>	<i>D. bholua</i> var. <i>glacialis</i>	<i>D. papyracea</i>
Full grain count	30	28	25
Sum total of counts	589	820	708
Mean grain diameter (µm)	19.5	29	29
Standard deviation in size	3	3	2
Aperture type	pantoporate	pantoporate	pantoporate
Muri of basal reticulum	concealed	exposed	exposed
Lumina of secondary reticulum diameter (µm)	0.9–1	0.6–1.8	1–2
Supratrectal projections (STP)			
STP Shape	baculoidate, flattened (STP-B)	baculoidate, dome-shaped (STP-B)	trihedral, dome-shaped (STP-T)
Projections	spinulate, blunt	verrucose, blunt-beaded	spinulate, sharply pointed
STP pattern	crotonoid	semi-crotonoid	semi-crotonoid
Arrangement of subunits	fused, in groups of 5–7, rarely free, densely packed	4 and free, sparsely spaced, or 5–6 fused	5–6, free, densely packed
Outline/margin	circular/sinuuous	irregularly angular/wavy	circular/rounded- angular
Mean size (µm) [H×B _L ×B _S]	1 × 1.1 × 0.9	2.5 × 2.8 × 1.8	1.15 × 1.25 × 1.15
Height (H, µm)	1–1.2	2.4–2.6	1.1–1.2
Base-longest width (B _L , µm)	1.1–1.2	2.6–3.0	1.1–1.3
Base-shortest width (B _S , µm)	0.9–1.0	1.6–2.0	1.0–1.19

STP baculoidate (STP-B), dome-shaped, mean size: 2.5 × 2.8 × 1.8 µm (height × base length × base width), size range: 2.4–2.6 × 2.6–3 × 1.6–2 µm; muri of basal reticulum exposed as horizontal rods, ca. 0.8 µm wide. Muri of secondary tectum forming groups of 4–6 subunits and situated at the joining points of the muri of the basal reticulum; individual subunits 4 and free (distance between adjacent STP: 0.8–1.6 µm) or 5–6 fused, surrounding the lumina of the basal reticulum; arranged in a scattered semi-crotonoid pattern. STP-B surmounted by centrally located, circular, bead-like, verrucose projections, outline irregularly angular, straight-sided, margins wavy; lumina of secondary reticulum 0.6–1.8 µm in diameter, broadly angular.

Voucher specimen: **INDIA. Sikkim:** lumlong, 6500 ft, 30 Apr 1876, *C.B. Clarke 27716* (CAL).

2. *Daphne papyracea* Wall. ex G. Don, Hort. Brit. 156. 1830. (Fig. 1G–I).

STP trihedral (STP-T), dome-shaped, mean size: 1.15 × 1.25 × 1.15 µm (height × base length × base width), size range: 1.1–1.2 × 1.1–1.3 × 1–1.19 µm; muri of basal reticulum exposed as horizontal rods, 0.3–0.9 µm wide. Muri of secondary reticulum (composed of the supratrectum) forming groups of 5–6 subunits, arranged in a scattered semi-crotonoid pattern, surrounding the lumina of basal reticulum; subunits densely packed, free. STP-T surmounted by central, pointed, spinules, outline circular, margins rounded-angular; lumina of secondary reticulum 1–2 µm in diameter, unevenly rounded.

It should be noted that authors of modern taxonomic treatments (e.g., *Flora Malesiana*, Hou 1960; *Flore du Cambodge du Laos et du Vietnam*, Hô 1992; *Flora of China*, Wang et al. 2007) have incorrectly credited Steudel (1840) as the validating author of *Daphne papyracea*, a name based on the illegitimate *D. cannabina* Wall. (1820), non Lour. (1790). Wallich's (1820) name was actually validated by George Don 10 years before Steudel's work in *Loudon's Hortus Britannicus* (Loudon 1830: 156) via the direct reference below *D. papyracea* to Wallich's name and description as "*Daphne cannabina* (sensu) Wall., *Asiat. Res.* 13:315 [typ. err. 385], ic. 1820 (non Lour. 1790)." To avoid unnecessary confusion regarding authorship, it should also be noted that Loudon, as editor of *Hortus Britannicus*, explicitly credited G. Don entirely for part I of the work (i.e., the "Linnean Arrangement"), which included the name *D. papyracea* (see page iv of the preface).

Voucher specimen: **INDIA. West Bengal:** Darjeeling, 6500 ft, 20 May 1949, *N. Narayanaswamy & Party 2770* (CAL).

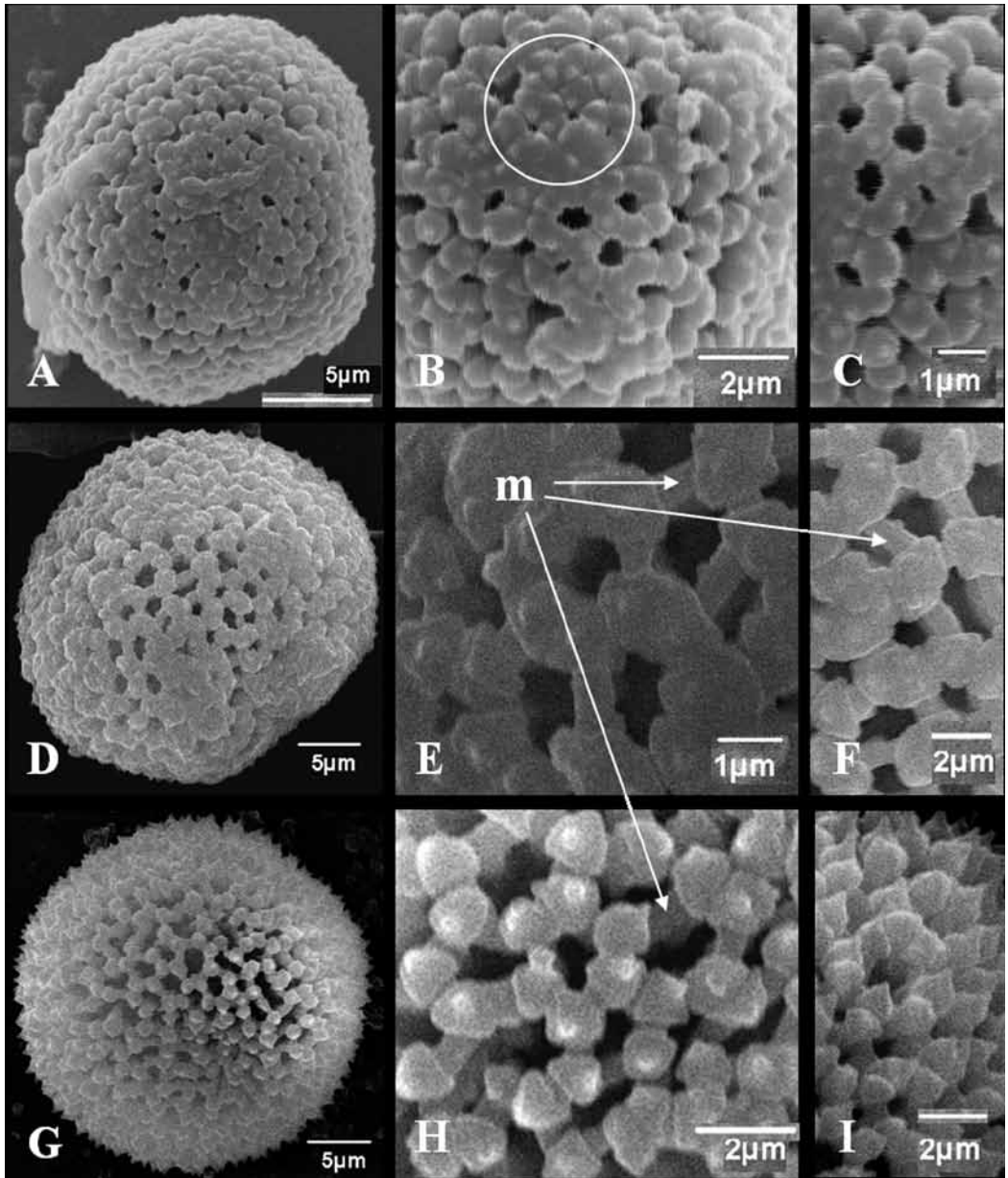


FIG. 1. Scanning Electron Micrographs of acetolyzed pollen (m: muri of basal reticulum). A–C. *Daphne bholua* var. *bholua*, A. Pollen grain, B–C. Surface with groups of fused supratectate projections surrounding lumina (encircled portion in B showing one unit of seven fused subunits). D–F. *Daphne bholua* var. *glacialis*, D. Pollen grain, E–F. Surface with free and fused groups of fused supratectate projections surrounding lumina. G–I. *Daphne papyracea*, G. Pollen grain, H. Surface with groups of supratectate projections surrounding lumina, I. Trihedral subunits with pointed spinule.

DISCUSSION

All three study taxa share a fundamentally similar exine structure formed by basic elements of regularly arranged excrescences (i.e., projections), which are supported by a baculate, baculoidate, or spongy layer of secondary (supra-) tectum. The resulting architecture forms the double reticulum and is a characteristic of Thymelaeaceae and Euphorbiaceae (Erdtman 1952). Pollen grains of Thymelaeaceae generally possess mural ridges that anastomose variously to form the horizontal rods of the basal reticulum and are surmounted by a very elaborate system of suprategal subunits (i.e., STP), which are organized into various patterns. These patterns display a wide range of variation in the arrangement, degree of fusion, shape, and size, and are of diagnostic value in the delineation of some taxa.

The morphological variation observed in several pollen grain characters (e.g., grain size, muri exposure, subunit arrangement, STP structure) allow all three study taxa to be distinguished palynologically (Table 1; Fig. 1). The baculoidate, dome-shaped STP of *Daphne bholua* var. *glacialis* pollen, is intermediate between the pollen of *D. bholua* var. *bholua* (STP baculoidate, flattened) and *D. papyracea* (STP trihedral and dome-shaped). The structure and arrangement of the STP in *D. bholua* var. *glacialis* with its semi-crotonoid pattern usually composed of free subunits (rarely fused) are characteristics of *D. papyracea*, whereas the presence of groups of 5–7 fused subunits (mixed with free subunits on the same pollen grain) is the usual form of *D. bholua* var. *bholua* pollen. Moreover, the mean pollen grain diameter was the same (29 µm) for *D. bholua* var. *glacialis* and *D. papyracea*, and both taxa have exposed muri of the basal reticulum. When taken together, the data suggest that *D. bholua* var. *glacialis* has a closer palynologic, if not taxonomic, affinity to *D. papyracea*. In addition to the novel pollen differences identified here, the three taxa differ in one or more readily available characters (e.g., floral scent, flower color, geographic distribution). Nevertheless, we refrain from taking formal nomenclatural action until our palynological results can be tested by further analyses utilizing additional pollen samples from more populations occurring throughout the widespread distributional ranges of all three taxa. So far none of the Paper Daphnes have been investigated using molecular phylogenetic analyses so it would also be worthwhile to add a DNA component to an expanded morphological study. Furthermore, future analyses of the Paper Daphnes would benefit from the inclusion of several more taxa such as *D. sureil* W.W. Sm. & Cave (recorded from India, Bangladesh, Bhutan, China, Nepal, Thailand), a putative relative, and the four currently recognized Chinese varieties of *D. papyracea*.

Lastly our palynological findings disagree with previous studies based on other genera of Thymelaeaceae, in which pollen was reportedly homogenous between species (e.g., Hawaiian *Wikstroemia*, Mayer 1991; *Lachnaea* – ca. 40 South African species, Beyers 2001), or variable in a few characters but still not deemed taxonomically useful at the species rank (e.g., *Passerina* – ca. 25 South African species, Bredenkamp & Van Wyk 1996).

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