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Front view of flower of *Gesneria fruticosa* (from Haiti) featuring fimbriate corolla lobes. Photographed by John L. Clark.
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Back view of flower of *Gesneria ekmanii* (from Haiti) featuring resin deposits. Photographed by John L. Clark.
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The objects of The Gesneriad Society are to afford a convenient and beneficial association of persons interested in the Gesneriad Plant Family (Gesneriaceae); to stimulate a wide-spread interest in; to gather and publish reliable information about the identification, correct nomenclature, culture, propagation, and conservation of gesneriads; and to encourage the origination, introduction, and conservation of species and cultivars.

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The Caribbean Gesneriaceae: an update on the classification of *Gesneria* and *Rhytidophyllum*

John L. Clark ~ Aldo Leopold Distinguished Teaching Chair, Science Department, The Lawrenceville School, Lawrenceville, NJ, USA ~ <jclark@lawrenceville.org>

GESNERIADS ARE BOTANICAL JEWELS of the Caribbean flora. Their broad range of flower shapes and colors do not conform to traditional generic concepts. Habits range from terrestrial shrubs that are more than two meters tall (Fig. 1A) to miniature rosettes that are smaller than a human palm (Fig. 1B) to obligate lithophytes (restricted to rocks or cliffs). Eccentric flower colors are represented by *Gesneria heterochroa*, which has green corolla tubes with white lobes (Figs. 1C & D), and *Gesneria clarensis*, which has orange corolla tubes with green lobes (Figs. 1E & F).

Gesneria and *Rhytidophyllum* share a recent common ancestor (along with *Pheidonocarpa* and *Bellonia*) and are classified in the subtribe Gesneriinae (Weber et al., 2013, 2020). Current estimates suggest that *Gesneria* has 65 species, and *Rhytidophyllum* has 25 species (Clark et al., 2020). The current taxonomy of *Gesneria* is based on a monograph published more than four decades ago (Skog 1976), which is more recent compared to *Rhytidophyllum* that was last monographed in the late 19th century (Hanstein 1865).

The entire Caribbean Gesneriaceae could be considered a taxonomist's nightmare because of ongoing changes in classification. Likewise, this group is a cherished dream for evolutionary biologists because of convergent evolution, remarkable patterns of species diversification, and a broad range of plant-pollinator interactions. A goal of this article is to share information about *Gesneria* and *Rhytidophyllum*, the dominant genera of Caribbean Gesneriaceae. I will describe recent classification changes, and highlight those changes with images, many of which are documented here from live material during recent exploratory research expeditions. A more comprehensive background on the classification of these two genera is found in Wiehler (1983) and Skog (1976). Skog's Ph.D. dissertation focused on a comprehensive taxonomic treatment of *Gesneria* (Skog 1976) that included field expeditions in 1970 to Puerto Rico, Dominica, Dominican Republic, Haiti, and Jamaica. Important discoveries from those expeditions were described in *The Gloxinian*, now *Gesneriads*, by Skog and Talpey (1973).

Gesneria and *Rhytidophyllum* are sister groups (i.e., share a recent common ancestor), and, as a result of their close relationship, they share many distinguishing features. The following list of characters (Fig. 2) differentiates them from all other members of the New World Gesneriaceae.

1) The ovaries are inferior in *Gesneria* and *Rhytidophyllum*. Inferior means that the ovary is below the attachment of the petals and sepals (Fig. 2A). In contrast, most New World Gesneriaceae, with very few exceptions, have superior ovaries. Superior means that the ovary is above the attachment of the petals and sepals (Fig. 2B).

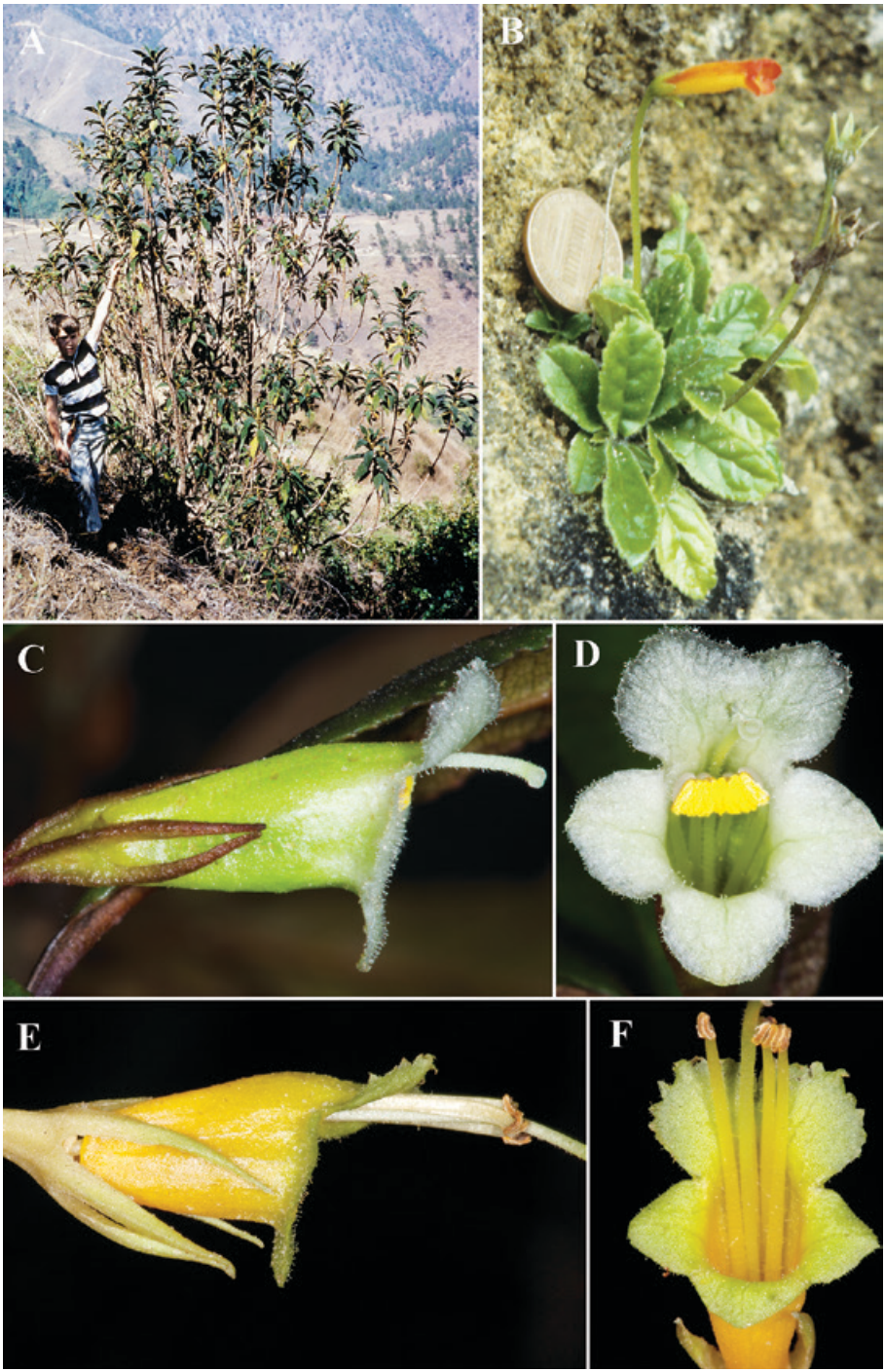

Figure 1. Variation of habit and corolla colors found in *Gesneria* and *Rhytidophyllum*. **A.** Tree habit of *Rhytidophyllum grandiflorum*. **B.** Rosette habit of *Gesneria reticulata*. **C** and **D.** *Gesneria heterochroa*. **E** and **F.** *Gesneria clarensis*.

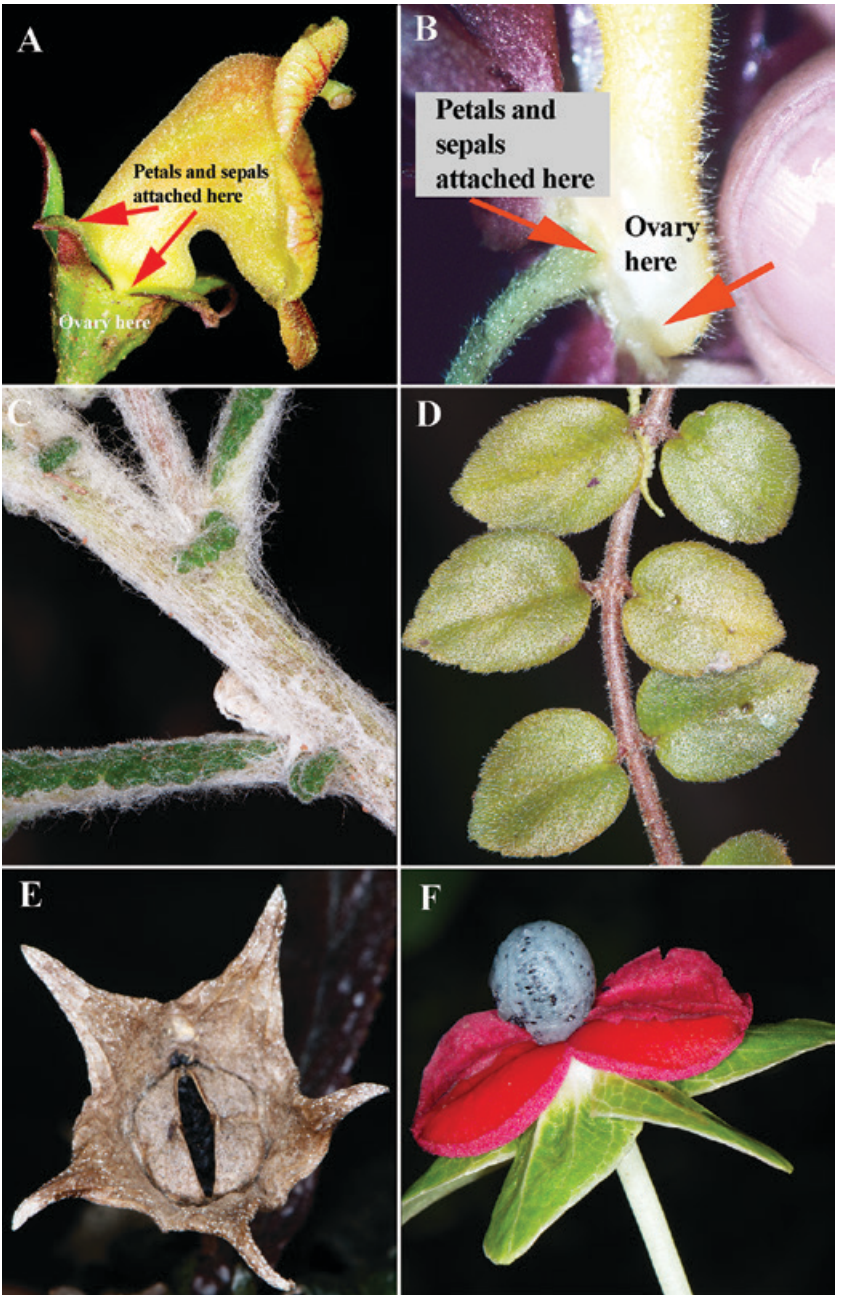

Figure 2. Characters that distinguish *Rhytidophyllum* and *Gesneria* from most New World Gesneriaceae. A, C, and E. are *Gesneria/Rhytidophyllum* and B, D, and F. are other New World Gesneriaceae. **A.** Inferior ovary where ovary is below the attachment of the petals and sepals (*Gesneria bicolor*). **B.** Superior ovary where the ovary is above the attachment of the petals and sepals (*Crantzia cristata*). **C.** Leaf arrangement alternate (*Rhytidophyllum acunae*). **D.** Leaf arrangement opposite (*Neomortonia rosea*). **E.** Subwoody capsule (*Gesneria depressa*). **F.** Fleshy display capsule (*Drymonia brochidodroma*), one of a variety of fleshy fruit types in New World Gesneriaceae.

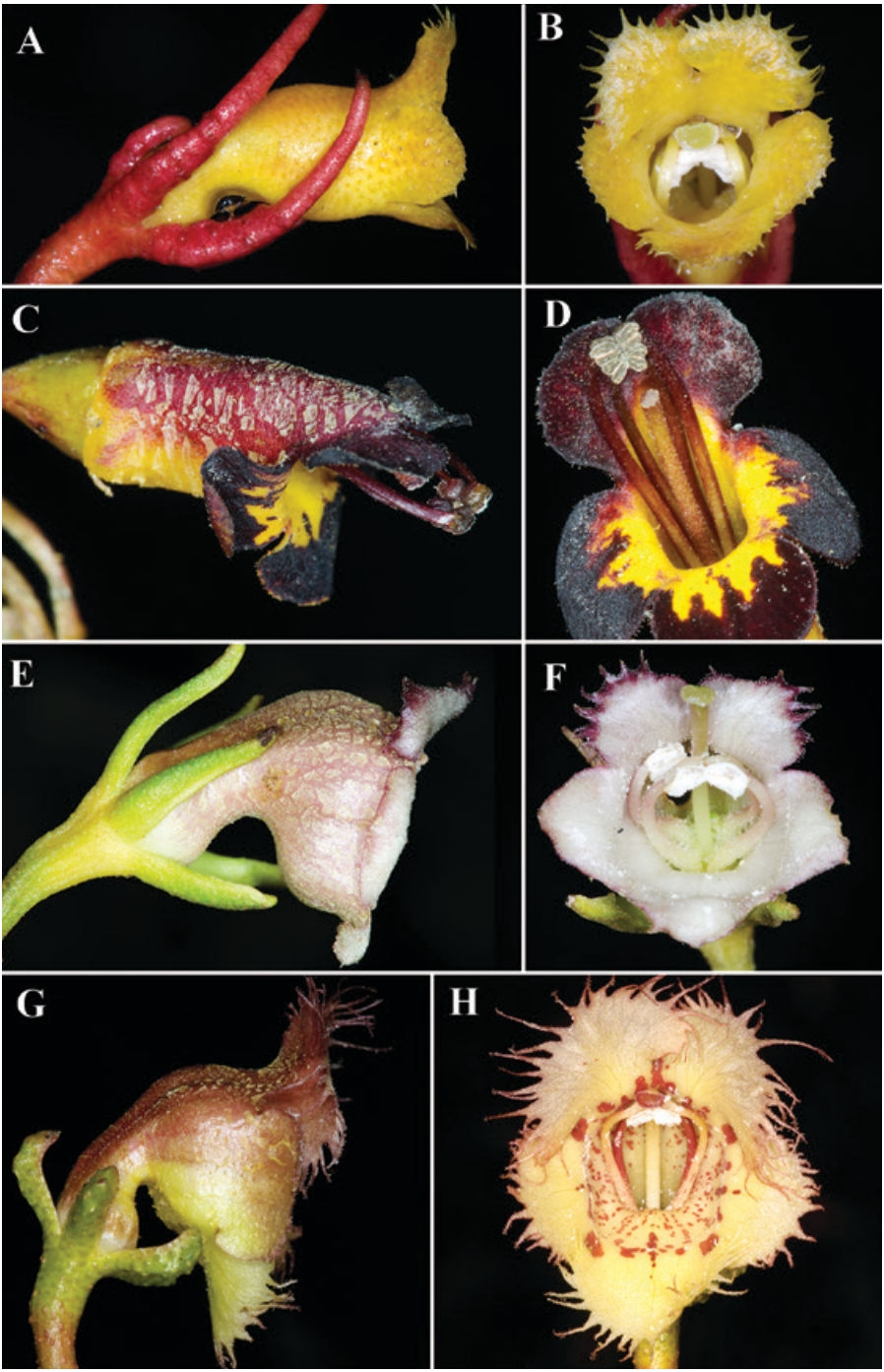

Figure 3. Selection of flowers featuring corolla lobe fimbriations and resin deposits of arborescent (=shrubby) species of *Gesneria*. **A** and **B.** *Gesneria duchartreoides* (from Cuba). **C** and **D.** G*esneria odonotophylla* (from Haiti). **E** and **F.** *Gesneria ekmanii* (from Haiti). **F** and **G.** *Gesneria viridiflora* (from Cuba).

2) The leaf arrangement in *Gesneria* and *Rhytidophyllum* is alternate (Fig. 2C). In contrast, most other New World Gesneriaceae are characterized by opposite leaves (Fig. 2D).

3) The fruits in *Gesneria* and *Rhytidophyllum* have woody capsules (Fig. 2E). In contrast, most fruits of New World Gesneriaceae have fleshy berries or fleshy capsules (Fig. 2F), with few exceptions.

4) The nectary for *Gesneria* and *Rhytidophyllum* is annular (Fig. 4H). In contrast, nectaries for most other New World genera are lobed. Examples include five separate lobes (esp. *Columnea*) to bilobed or single-lobed on the upper surface of the ovary.

Gesneria and *Rhytidophyllum* diversified in the Caribbean, and their presence in South or Central America is rare. They are almost entirely endemic to the Caribbean except for the following two species: 1) *Rhytidophyllum onacaense* is endemic to northern Colombia, where it is known from fewer than ten collections (only three from the last century) at the base of the Sierra Nevada de Santa Marta, a mountain range that is isolated from the Andes; 2) *Rhytidophyllum cumanense* is mostly known from Venezuela.

Recognizing *Gesneria* and *Rhytidophyllum* is relatively easy because of many shared derived characters (Fig. 2). In contrast, the distinction between *Gesneria* and *Rhytidophyllum* involves more careful evaluation. Taxonomists have differed on whether they should be combined as one large genus or retained as separate genera. Wiehler (1983) preferred a system of one genus (i.e., lumping "*Rhytidophyllum*" as a subgroup of *Gesneria*). The primary reason for Wiehler's support of a single genus classification was based on the absence of a unifying character that defined or differentiated *Gesneria* and *Rhytidophyllum*.

In contrast, Skog (1976) had published a comprehensive treatment of *Gesneria* where he recognized *Gesneria* and *Rhytidophyllum* as distinct genera. Also, Skog (1976) described the new genus, *Pheidonocarpa,* to accommodate a single species that did not fit the currently accepted genera. Although not the focus of this article, the recognition of *Pheidonocarpa* is supported as a monophyletic lineage based on molecular phylogenetic studies (Joly et al., 2017; Marten-Rodriguez et al., 2010; Watson 2015).

Gesneria flowers in the wild are different from what is known in horticulture

There are many flower types in *Gesneria*, but most of the species readily available in horticulture are characterized by red tubular flowers and rosette habits (e.g., *G. reticulata* and *G. cuneifolia*). The shrub habit of *Gesneria* is rare in cultivation, and the flowers of these species are not typical of material that is more readily available in cultivation. Many shrubs of *Gesneria* have campanulate (bell-shaped) flowers that are coriaceous (leathery). The outer surfaces of the flowers of the shrubby species appear waxy because they are covered with resin deposits (Fig. 3 and back cover). A selection of campanulate corollas with resin deposits is featured in Figure 3. Another character of many *Gesneria* flowers is the presence of fimbriations along the margins of the corolla lobes (Figs. 3B, F, and H).

Rhytidophyllum flowers

The flowers of *Rhytidophyllum* are mostly campanulate (bell-shaped), with tubes that are greenish-yellow or yellow suffused with purple splotches (Fig. 4). Another useful feature for recognizing *Rhytidophyllum* is that abundant populations often grow in full sunlight along secondary roads (Fig. 1A). It is relatively easy to observe *Rhytidophyllum* on a fast-moving bus where clumps of populations of 30-50 individuals are common. The stems are stout and erect, and the leaves are covered with viscous (sticky) hairs. Unlike the ephemeral flowers of many *Gesneria*, the flowers of *Rhytidophyllum* are usually persistent and easily observed above tufts of terminally clustered leaves.

Rhytidophyllum that are terrestrial shrubs can be more than two meters tall (Fig. 1A).

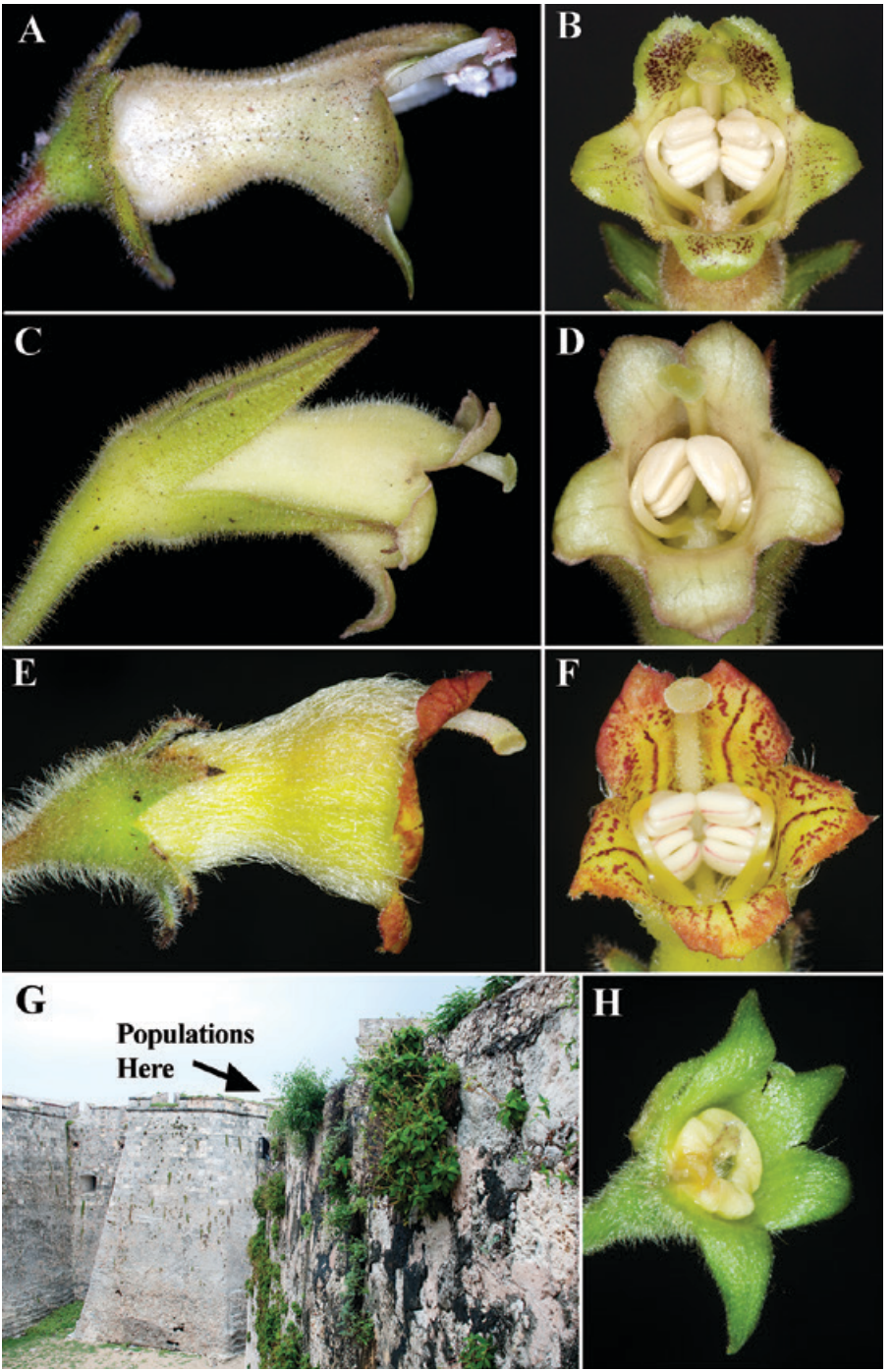

Figure 4. *Rhytidophyllum* flowers. **A** and **B.** *Rhytidophyllum crenulatum*. **C** and **D.** *Rhytidophyllum rhodocalyx*. **E** and **F.** *Rhytidophyllum auriculatum*. **G.** Walls of Morro Castle, entrance of Havana Bay, Cuba where *Rhytidophyllum crenulatum* grows in abundant populations. **H.** Annular nectary of *Rhytidophyllum exsertum*.

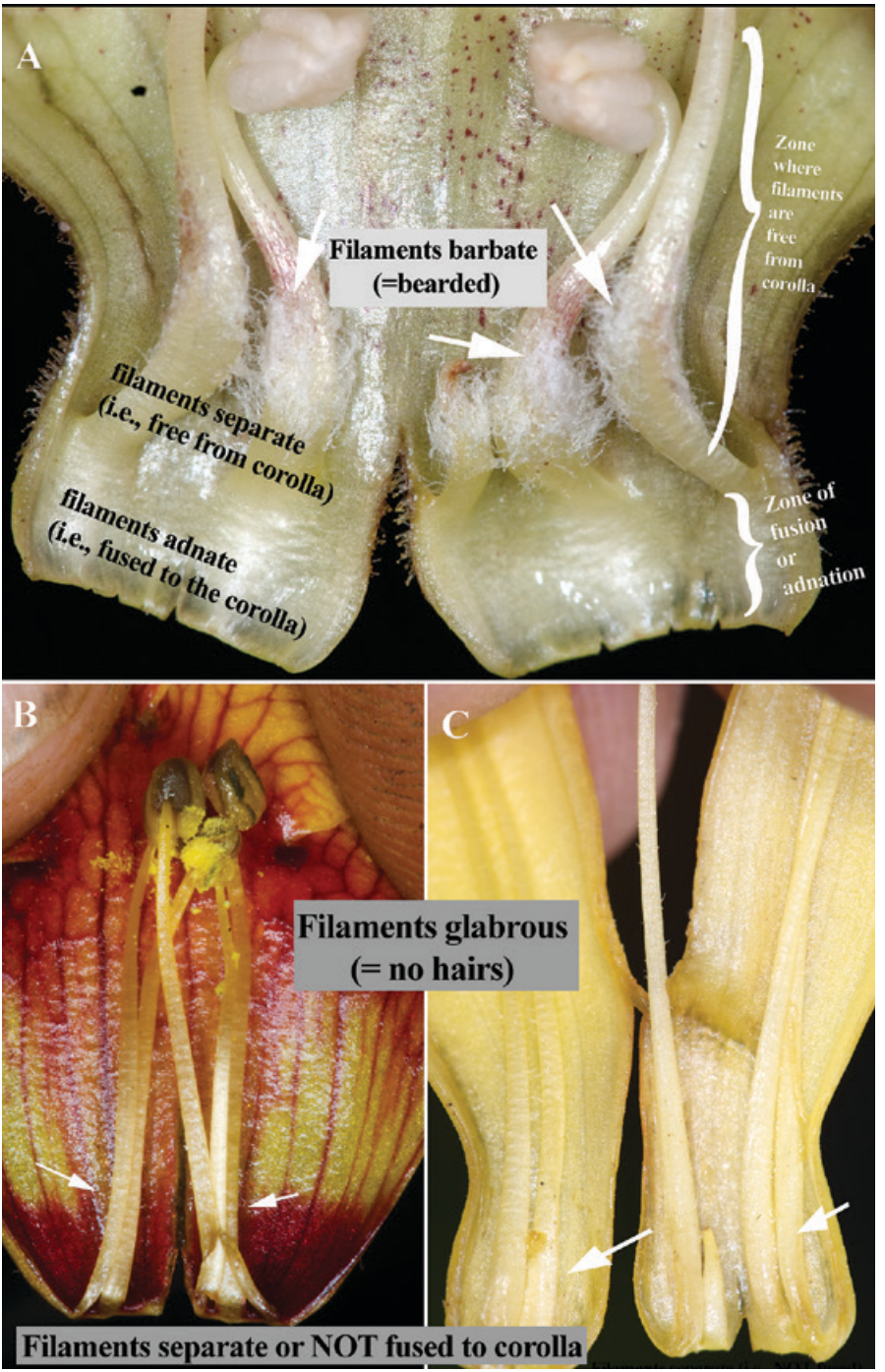

Figure 5. Filament character for *Rhytidophyllum* and *Gesneria*. **A.** *Rhytidophyllum crenulatum* featuring filaments adnate to the corolla tube with barbate hairs (indicated with arrows). **B** and **C.** *Gesneria depressa* (B) and *Gesneria salicifolia* (C) featuring filaments separate from the corolla tube and glabrous filaments (indicated with arrows).

Lithophytes (rock dwellers) represent a habit that is different from the more common terrestrial shrubs. Rock dwellers are smaller (usually less than 60 cm tall) than their terrestrial relatives. One of my favorite rock-dwellers and most readily observed species is *Rhytidophyllum crenulatum* that covers the walls of the Morro Castle near the entrance to Havana Bay in Havana, Cuba (Fig. 4G). A selection of *Rhytidophyllum* flowers is featured in Figure 4.

Characteristics differentiating *Gesneria* and *Rhytidophyllum*

Molecular phylogenetic studies (Martén-Rodríguez et al., 2010; Watson 2015; Joly et al., 2017) have mostly supported a sister-group relationship of *Gesneria* and *Rhytidophyllum*, but taxon sampling is limited and statistical support is low. A more comprehensive taxon sampling to evaluate *Gesneria* and *Rhytidophyllum* is an ongoing collaborative project by several botanists (e.g., Joly, Clark, and Martèn-Rodriguez.) Several morphological characters reflect a separation. The most useful character to differentiate *Gesneria* and *Rhytidophyllum* is the presence or absence of fusion of filaments to the corolla tube (Fig. 5). The term *connation* is used to describe similar parts that are fused (e.g., the fusion of petals to form a corolla tube as in most members of the Gesneriaceae). The term *adnation* is used to describe the fusion of dissimilar parts, such as the fusion of filaments to the corolla tube. The character that defines *Rhytidophyllum* is the presence of filaments that are adnate for 2-5 mm to the base of the corolla tube (Fig. 5A). The character that defines *Gesneria* is free filaments or complete lack of fusion (i.e., absence of adnate filaments to the corolla tube) (Figs. 5B & C). Fig. 5A features an open flower of *Rhytidophyllum crenulatum* where you can observe a zone of adnation for 2-3 mm near the base of the corolla and a zone where the filaments are free from the corolla tube. These two regions (i.e., separate filaments that are above the zone of adnation) are indicated on both sides of an opened corolla tube (Fig. 5A). In contrast, the filaments in *Gesneria* are free or separate from the entire length of the filaments (Figs. 5B and C) and therefore have no zone of adnation.

Another character that is useful for differentiating *Rhytidophyllum* is clusters of barbate (bearded) hairs at the base of the filaments and immediately above the zone of adnation. In *Gesneria*, the base of the filaments is glabrous (without hairs). Barbate clusters of hairs are indicated with white arrows (Fig. 5A) or lack thereof (Figs. 5B and C).

Images of *Rhytidophyllum* featuring adnate filaments to the corolla tube and barbate trichomes are featured in Figure 5A. Images of *Gesneria* featuring free filaments that are glabrous are featured in Figures 5B and C.

Convergent evolution and the presence of red flowers in *Gesneria and Rhytidophyllum*

One difference between the generic concept presented here and those of Skog (2012) is a complex of three red-flowered species that are more recently (Clark et al., 2019; 2020) recognized as belonging to *Rhytidophyllum*. It is important to note that Morton (1957a; 1957b) and early publications by Skog (1976) are congruent with the generic concepts presented here. Ideas on generic concepts have changed, and phylogenetic or evolutionary trees are an essential method for accepting or rejecting classifications based on relationships. In the example presented here, the presence of red flowers is not a shared derived character, and it does not suggest a close relationship – especially in gesneriads that share the same geographic range.

These three species (*Rhytidophyllum earlei*, *R. lomense*, and *R. rupincola*) are often misplaced by horticulturists as members of *Gesneria* because of their red tubular corollas. In contrast, these three species have red tubular flowers but also have features that are typical in *Rhytidophyllum*. The filaments of *Rhytidophyllum earlei, R. lomense*, and *R. rupincola* are adnate to the corolla tube with clusters of barbate hairs at base of filaments.

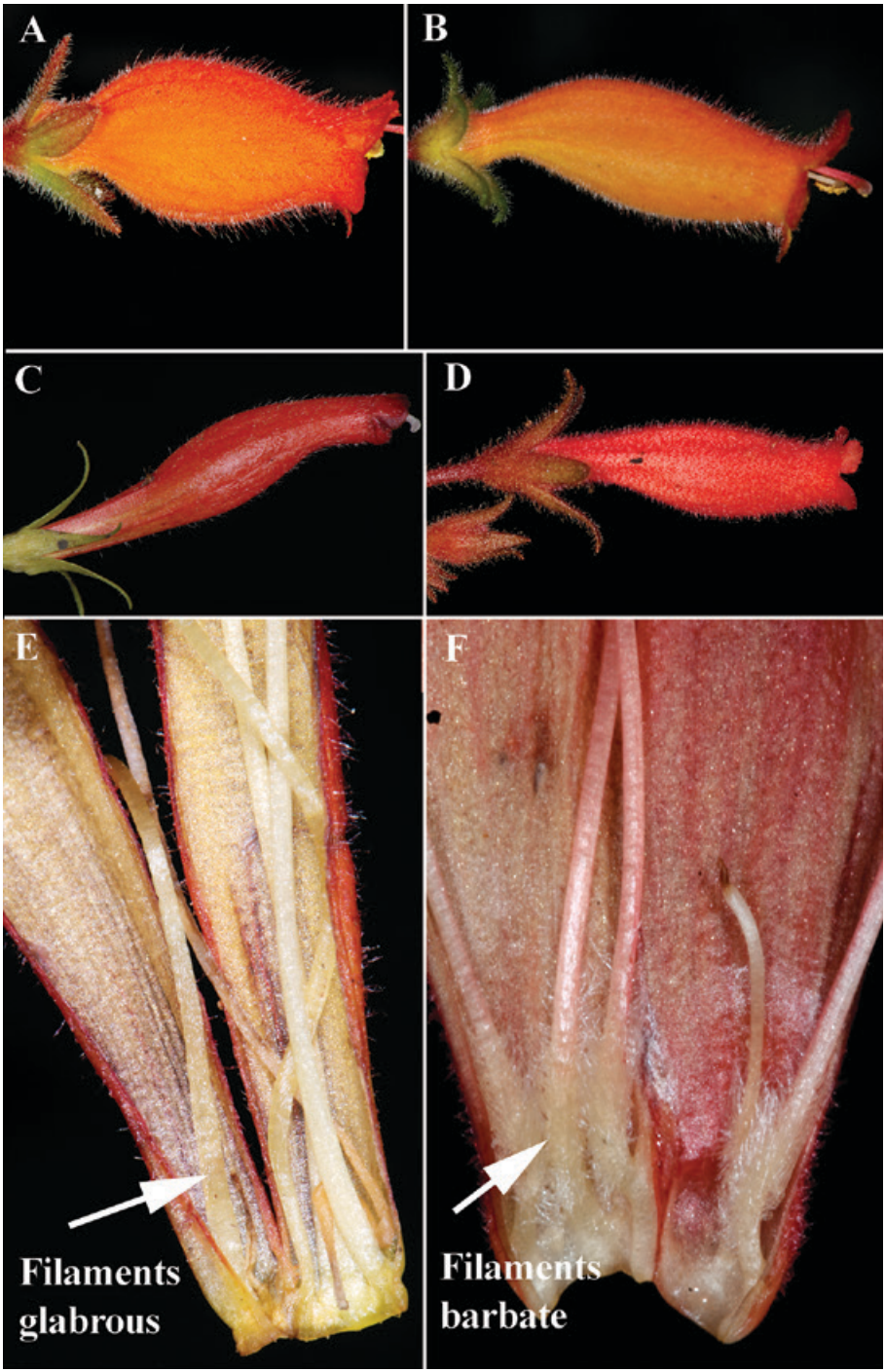

Figure 6. Tubular red flowers in *Gesneria* (C and E) and *Rhytidophyllum* (A, B, D and F). **A.** *Rhytidophyllum lomense*. **B.** *Rhytidophyllum earlei*. **C.** *Gesneria libanensis*. **D** and **F.** *Rhytidophyllum rupincola*. **E.** *Gesneria libanensis*.

Thus, the flowers are red (not typical in *Rhytidophyllum*), but the filaments are barbate above the zone of adnation to the corolla tube (typical in *Rhytidophyllum*). Photographs and descriptions provided here explain this remarkable example of convergent evolution, and how this has resulted in the back-and-forth of their generic placement as members of *Rhytidophyllum* and *Gesneria*. These three species were the basis for the discrepancy between recognizing one large genus (sensu Wiehler, 1983) versus two distinct genera (sensu Skog, 1976). A recent dissertation explored these discrepancies in more detail (Watson 2015), and provided here is a simplified summary.

It is important to note that phylogenetic analyses provide an objective framework for evaluating generic concepts. Previous traditional concepts are likely to depend on a single character with multiple origins (e.g., convergent evolution). It is challenging to define any group by a single morphological feature without evaluating its evolutionary history. For example, not all columneas have berries (e.g., *Columnea dielsii* has a fleshy capsule). Not all drymonias have poricidal anther dehiscence (e.g., there are multiple reversals to longitudinal slits as outlined in Clark et al., 2015). A single character will not readily define the diversification and evolution of *Gesneria* and *Rhytidophyllum*. When these genera are evaluated in a phylogenetic context, red tubular flowers are likely convergent. Their presence in *Gesneria* and *Rhytidophyllum* is explained by multiple origins or convergent evolution.

Single character systems that define genera have been supplanted and supplemented by phylogenetics. The use of evaluating characters in the context of evolution provides a more objective and robust system for classification. For example, bats and birds fly, but the presence of flight is not because they share a recent common ancestor. Likewise, it is crucial to understand morphological features in the Gesneriaceae in the context of evolutionary relationships.

The red tubular flowers of *Rhytidophyllum lomense* (Fig. 6A), *R. earlei* (Fig. 6B), and *R. rupincola* (Fig. 6D and F) look like the red tubular flowers of *Gesneria libanensis* (Fig. 6C and E). The similar shapes and colors are independently derived, and that is best explained in the context of an evolutionary tree (Martén-Rodríguez et al., 2010; Watson 2015; Joly et al., 2017). The presence of red flowers in this example is convergent in *Gesneria* and *Rhytidophyllum*. That is why it is crucial to evaluate the filament character when determining their proper generic placement. The red-flowered species of *Rhytidophyllum* (e.g., *R. lomense*, *R. earlei*, and *R. rupincola*) retain the filament characteristics of other *Rhytidophyllum* such as adnation to the corolla tube and barbate hairs above the zone of adnation (Fig. 6F). Even though these three species of *Rhytidophyllum* have red tubular flowers that appear like *Gesneria libanensis* (Fig. 6C), they share a more recent common ancestor with members of *Rhytidophyllum.*

Recommendation

If Caribbean gesneriads pique your interest, then I encourage you to read Skog (1976), where historical literature, nomenclature, taxonomy, species descriptions, and pollination biology are covered for *Gesneria* and *Rhytidophyllum*. Likewise, recent literature has transformed current concepts on the pollination and diversification of Caribbean gesneriads (cf., Martén-Rodríguez & Fenster 2008, 2010; Martén-Rodríguez et al. 2010, 2015; Lambert et al. 2017; Alexandre et al. 2018; Joly et al. 2018). Hopefully, some of the shrubby species that are typical in the Caribbean and rarely found in cultivation may soon be available. Most importantly, I hope that the forests that harbor these remarkable gesneriads are preserved and maintained in perpetuity for current and future generations.

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