



***Besleria macropoda* (Gesneriaceae): lectotypification, distribution, functional epiphyllly and discordant fruit morphology of a rare Costa Rican endemic**

ANDREAS BERGER¹, JOHN L. CLARK² & ANTON WEBER³

¹ Division of Systematic and Evolutionary Botany, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. andi.berger@univie.ac.at

² Science Department, The Lawrenceville School, 2500 Main Street, Lawrenceville, NJ 08648, USA. ilc@lawrenceville.org

³ Division of Structural and Functional Botany, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. anton.weber@univie.ac.at

Abstract

Besleria macropoda, a rare and poorly known gesneriad endemic to Costa Rica, was recently collected for the first time on the southern slopes of the Fila Costeña (Puntarenas Province, SE Costa Rica). The collection considerably widens the geographic distribution to the southeastern part of Costa Rica. Moreover, the following unique characters not previously addressed in the literature were observed and are documented here: (1) The elongate peduncles of the inflorescences are clamped in a channel formed by the sunken midrib of the leaf, rendering the flowers and fruits positioned in the center of the leaf blade. The epiphyllous appearance of the inflorescence on the leaf surface enhances contrasting colors that may aid the pollination and/or fruit dispersal. (2) The fruits split open irregularly, with the fleshy carpel lobes becoming reflexed. This fruit dehiscence deviates from the indehiscent berries that typically characterize *Besleria*. This results in displaying a globose head of red placental tissue covered by tiny, red seeds. A preliminary survey of *Besleria* fruits suggests that this peculiar fruit type is present in at least 15 species representing almost 8% of the genus. Fruit morphology of *Besleria* is therefore less uniform than previously recognized and the “indehiscent berry” can no longer serve as a distinctive generic character of *Besleria*, which necessitates consideration in floras and identification keys. In addition, a list of herbarium specimens, lectotypification, a distribution map, IUCN red list assessment and an amended key to diagnose *Besleria* relative to *Gasteranthus* are provided.

Introduction

The neotropical genus *Besleria* Linnaeus (1753b: 619) comprises an estimated number of 200+ species, with centers of diversity in the Andes of Colombia and Ecuador. It is the type genus of the monophyletic (but morphologically heterogeneous) tribe Beslerieae within the subfamily Gesnerioideae (Roalson & Clark 2006, Clark *et al.* 2010, Weber *et al.* 2013). A remarkable flower and fruit diversity is found within the Beslerieae which has led to confusion on the circumscription of some genera included therein. The genus *Besleria* was last revised by Morton (1939) who used an overly broad generic concept that included *Gasteranthus* Benth (1846: 233), which was later segregated from *Besleria* based on an improved understanding of fruit characters (Wiehler 1975, Skog & Kvist 2000). Subsequent generic circumscriptions within the tribe have been confirmed by phylogenetic studies (Smith 2000, Roalson & Clark 2006, Clark *et al.* 2010). Nevertheless, the genus is in need of a modern revision and much work remains to be done, especially concerning the circumscription of currently recognized species and the description of many new species.

The present paper refers to the rare species *Besleria macropoda* Donnell Smith (1898: 155–156), a population of which was recently discovered on the southern slopes of the Fila Costeña range (Puntarenas Province, SE Costa Rica). It is one of the least collected species of Gesneriaceae in Costa Rica and is considered to be endemic there (Kriebel 2006, 2010). The recent collection widens the known distribution range of the species considerably. Moreover, *in vivo* observations revealed two peculiar characters: (1) The peduncles are clamped in a channel formed by the sunken midrib of the leaf, resulting in a (functionally) epiphyllous position of the flowers and fruits (fig. 2). (2) The fruits rupture at maturity resulting in exposing the colorful placentae and seeds (figs. 2 C, 4 A, B). The contrasting colors are typical of the display fruits in the traditional tribe Episcieae (now Gesnerieae-Columneinae, Weber *et al.* 2013)

where somewhat fleshy capsules dehisce loculicidally at maturity. However, rupturing fruits deviate from typical (indehiscent) berries that are traditionally used for defining *Besleria* and for delimiting it against the related genus *Gasteranthus*. The taxonomic and biological implications of these findings are discussed in context with an evaluation of relevant literature. In addition, *B. macropodia* is lectotypified, and a list of herbarium specimens, a distribution map and an IUCN red list assessment are provided.

Material & methods

A population of *B. macropoda* was discovered on the southern slopes of the Fila Costeña range at the gorge of the Río Esquinas in the Punarentas Province, Costa Rica (voucher: *Berger & Etl 1443*, WU-0074954; for additional locality and collection details see “List of herbarium specimens” below) Observations and collections were made in the context of research activities of the Tropical Research Station La Gamba (University of Vienna).

A comprehensive physical and digital search of herbarium specimens and photographs was conducted to establish the geographical distribution of *B. macropoda* and to assess fruit diversity of other *Besleria* species. Specimens from the two major Costa Rican herbaria, CR (Museo Nacional de Costa Rica, San José) and INB (Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia), were examined. Furthermore, the following publicly accessible databases were searched for additional records: The Andes to Amazon Biodiversity Program (housed at BRIT: <http://atrium.andesamazon.org>), the Gesneriaceae Image Library (housed at UNA: <http://gesneriads.ua.edu>), the TROPICOS database (housed at MO: <http://tropicos.org>) and the digital herbaria BR, E, F, GH, MO, NY, PMA and US. All retrieved specimens are listed below and were sorted by country, provinces and then chronologically. The first author (A. B.) checked the identity of specimens at the herbaria CR and INB, specimens at UNA and US were determined by the second author (J.L.C.).

The program QGIS was used to create the distribution map of *B. macropoda*. For most collections, the geographic coordinates were available on the specimens. The remaining collections were georeferenced based on locality information and their estimated coordinates are given in square brackets. The “Gazetteer of Costa Rican Plant-Collecting Locales” was used for eight collections of *B. macropoda* (<http://mobot.org/mobot/costaricagazetteer/gazetteer.aspx>).

Specimens and field observations of *Besleria macropoda*

In total, 31 collections (>77 specimens when duplicates are included) of *B. macropoda* were located and their coordinates were used to create the distribution map (fig. 1). Images of functional epiphylls (fig. 2) and rupturing dehiscence (figs. 2 C, 4 A, B) are based on recent field expeditions and in vivo photographs of *Berger & Etl 1443*.

Besleria macropoda:—COSTA RICA. Alajuela: San Ramón, ca. Río San Lorenzo, camino a Colonia Palmareña, [10°15'N, 84°34'W], s.d., *Gómez-Laurito et al. 11128* (CR-117016); Near shore of Laguna Hule, 740 m, [10°18'N, 84°12'W], 6 August 1967, *Lent 1193* (CR-44468, NY, US-00992906); 13 km W of Fortuna on road to Arenal Dam near crossing of Río Tabacón, 500–550 m, 10°29'N, 84°43'W, 29 April 1983, *Liesner et al. 15229* (CR-99532, MO-946809, US-00580586); Reserva Biológica Monteverde, Río Peñas Blancas, alrededores de Quebrada Azufre, 700 m, 10°21'N, 84°42'W, 27 October 1987, *Haber & Bello 7672* (CR-138600, INB-0002916703, MO-946808, US-00580580). Cartago: Forêts de Tuis, 650 m, [09°51'N, 83°35'W], October 1897, *Tonduz 11358* (BR-0013349219, -226, CR-11358, GH-00375574, US-00078573, -574); Parque Nacional Barquilla, Sendero Principal, 300–400 m, 09°58'20"N, 83°27'10"W, 15 January 2001, *Mora & Rojas 1757* (CR-0231332 ex INB-0003161923, INB-0003161924, MO-1018897). Heredia: El Recreo, dans les bois humides [09°54'N, 83°41'W], July 1888, *Cooper* [“Pittier”] 572 (BR-0005107995, CR-572); Finca La Selva, 100 m, 10°25'53"N, 84°00'13"W, 6 July 1980, *Grayum 2953* (DUKE, MO-540176); Finca La Selva, 100 m, 10°25'53"N, 84°00'13"W, 19 July 1980, *Hammel 9241* (DUKE); Parque Nacional Braulio Carrillo, Estación El Ceibo, 500–546 m, 10°19'38"N, 84°04'40"W, 12 March 2003, *González 3084* (MO-2129844). Limón: Santa Clara, Río Destierro, 200 m, [10°08'N, 83°36'W], June 1899, *Pittier 13381* (UC, US-00078575); Siquirres, orilla del Río Pacuarito, 62 m, [10°06'14"N, 83°28'25"W], 25 October 1986, *Umaña Dodero 132* (CR-121131, -132); Parque Nacional Braulio Carrillo, Quebrada González, 500 m, 10°09'00"N, 83°55'48"W, 16 May 1988, *Chavarría & Umaña Dodero 129* (CR-130046, MO); Parque Nacional Braulio Carrillo, Río Sucio, 500 m, 10°09'00"N, 83°56'24"W, 21 June 1988, *Chavarría 174* (INB-0001514267, MO-946810); Along Quebrada Cañabral, from Río Barquilla to ca. 1.5 km upstream, 100–200 m, 10°02'N, 83°24'W, 8 September 1988, *Grayum et al. 8879* (CR-144464, INB-0002914474, MO-946807, SEL ex US-00318185, US-00738125); Las Brisas de Pacuarito, camino en Río Dantas y Río Barquilla, rumbo a Cerro Tigre, 350 m, 09°57'30"N, 83°26'10"W, 31 October 1995, *Herrera et al. 8632* (CR-223864); Siquirres,

Las Brisas de Pacuarito, Reserva Ecológica Río Dantas, 300 m, 09°59'35"N, 83°26'40"W, 7 November 1995, *Herrera 8730* (CR-223863, F-2228643); Las Brisas de Pacuarito, margen izquierda de Quebrada Jesús, camino a Cerro Tigre, 800 m, 09°56'40"N, 83°25'15"W, 22 March 1996, *Herrera & Valverde 8847* (CR-223865); Pococí, Parque Nacional Braulio Carrillo, cuenca del Sarapiquí, Guápiles, 2 km antes de la Estación Quebrada Gonzáles, 500 m, 10°09'20"N, 83°56'30"W, 25 January 1999, *Rodríguez et al. 4325* (CR-0248103 ex INB-0002843459, INB-0002843457); Siquirres, Parque Nacional Barbilla, cuenca del Matina, Sendero Valle Escondido, 400–500 m, 09°59'03"N, 83°28'25"W, 11 June 1999, *Mora 372* (CR-0248104 ex INB-0002834466, INB-0002834464, MO-2128239); Parque Nacional Barbilla, Sendero Cerro Azul, 300–400 m, 09°59'30"N, 83°22'40"W, 3 March 2000, *Mora & Rojas 851* (CR-0235291 ex INB-0003113776, INB-0003113776, MO-1016981); Colonia Puriscaleña, Sendero Quebrada Surubes, 300 m, 10°00'40"N, 83°23'00"W, 2 August 2000, *Rodríguez 6139* (INB-0003428414, MO-2494348). Puntarenas: Southern slopes of the Fila Costeña range, gorge at headwaters of Río Esquinas, vicinity of Virgen de Briceño, c. 600 m, 08°47'N, 83°10'W, 11 March 2013, *Berger & Etl 1443* (WU-0074954, and duplicates to be distributed to CR, MO, US). San José: Bord de la route à Carillo, 300 m, [10°09'N, 83°57'W], 12 May 1890, *Tonduz* ["Pittier"] 2495 (BR-0013349196, -202, CR-2495, CR-75711, US-00078576); Parque Nacional Braulio Carrillo, confluencia de los Ríos Sucio y Hondura, 500 m, [10°8'50"N, 83°56'52"W], 26 April 1981, *Gómez-Laurito 6565* (CR-81450), 6620 (2 sheets with nr. CR-81342); Parque Nacional Braulio Carrillo, union de los Ríos Sucio y Hondura, 600–700 m, 10°08'24"N, 83°56'24"W, 19 February 1983, *Chacón 390* (CR-92498, MO-159859, US-00992904); Parque Nacional Braulio Carrillo, cerca del Río Sucio, 10°09'24"N, 83°56'57"W, 17 January 1984, *Sánchez & Zamora 418* (CR-104176, MO-515038, US-00580593); Cerro Nara, 1000 m, 09°29'20"N, 84°00'40"W, 26 July 1995, *Chavarría & Solís 908* (INB-0001607522, US-00580560); Pérez Zeledón, Río Nuevo, El Brujo, 404 m, 09°28'46"N, 83°56'37"W, 6 February 2001, *Estrada et al. 2673* (CR-227923, MO-418789); Tarrazú, San Lorenzo Camino a Quebrada Arroyo, a 2 km del cruce a Cerro Nara, 305 m, 09°28'26"N, 84°01'40"W, 27 November 2008, *Estrada & Chacón 4412* (CR-257564); Cerro Nara, 09°29'03"N, 84°00'10"W, 5 March 2012, *Hammel 26160* (INB-0004311023).

Specimens and field observations of other *Besleria*

Beside *B. macropoda*, six further species were shown to have rupturing dehiscence. Furthermore, ten collections were found which, judging from morphology, belong to eight distinct but yet unidentified/undescribed species that may be identified/described in the future if sufficient material becomes available. For all of them, field observations, photographs, and/or notes on labels are mentioned to support the presence of rupturing dehiscence.

Besleria affinis C.V. Morton (1935: 75–76):—VENEZUELA. Barinas: along road from Barinitas to Apartaderos, 1000 m, [8°51'N, 70°34'W], 27 January 1965, *Breteler 4427* (MO-1496395).

Rupturing fruit dehiscence was indicated on the label of the above-mentioned specimen: "Wall of fruit inside yellowish-orange. Mass of seeds dark brownish-red."

B. montana Britton ex Rusby (1895: 240):—BOLIVIA. Cochabamba: Chaparé, near Comunidad Avispas, 400 m, 17°00'54"S, 65°33'06"W, 05 August 2002, *Clark & Rodriguez 6811* (BOLV, K, LPB, NY, SEL, US-00737506).

Field observations and image documentation from in vivo plants of *Clark & Rodriguez 6811* support the presence of rupturing dehiscence (photos: UNA; fig. 4 C).

B. pauciflora Rusby (1900: 31):—ECUADOR. Morona-Santiago: Cordillera Winchinkiaim, Tiwintza, 300–900 m, 03°03'43"S, 77°56'43"W, 14 August 2005, *Clark et al. 9280* (QCNE, US-00910109). PANAMA. Coclé: Antón, trail from El Valle de Antón to La Mesa, 08°38'N, 80°07'W, 21 May 1970, *Wilbur & Luteyn 11702* (DUKE, PMA-15463); Colón: Río Boquerón, 09°22'N, 79°34'W, 20 April 1974, *Dressler 4659* (PMA-15464); Donoso, 391 m, [08°30'N 80°24'W], s.d., *Clark & Martínez 12577* (PMA-96401, US).

Rupturing fruit dehiscence was noted on the specimens *Clark & Martínez 12577*: "Mature fruit a rupturing fleshy berry," *Dressler 4659*: "fruit pale green, irregular dehiscence, seeds red," and *Wilbur & Luteyn 11702*: "Fruit red at maturity from placentae." Field observations and image documentation from in vivo plants of *Clark et al. 9280* in Ecuador additionally supports the presence of rupturing dehiscence (fig. 4 F). In addition, an image showing rupturing dehiscence is found in Kriebel (2010).

B. pendula Klotzsch ex Hanstein (1865: 333):—VENEZUELA. Lara: Jiménez, Parque Nacional Yacambú, región de El Blanquito, 1660 m, [09°37'N, 69°35'W], 06 August 1970, *Steyermark et al. 103479* (MO-1496559, US-00079118, -123, VEN). Mérida: Justo Briseño, Quebrado El Molino near Las Cuadras, 1700–1850 m, 09°00'N, 70°56'W, 15 October 2002, *Clark & Yustiz 6866* (AAU, COL, E-00646681, K, MER, MO-1916925, NY, PORT, SEL, US-00662437, VEN). Trujillo: Boconó, La Laguna Negra, 1830 m, 09°18'00"N, 70°10'12"W, 19 October 2002, *Clark & Yustiz 6887* (E-00645632, NY, PORT, SEL, US-00662426, VEN).

Rupturing fruit dehiscence was noted on specimen *Steyermark et al. 103479* “fruit red-seeded with reflexed pale green valves.” Field observations and image documentation from in vivo plants of *Clark & Yustiz 6887* and *6866* (fig. 4 D) in two different populations in Venezuela support the presence of rupturing dehiscence.

B. sprucei Britton ex Rusby (1900: 31):—BOLIVIA. La Paz: Bautista Saavedra, Área Natural de Manejo Integrado Apolobamba, Paujeyuyo, 940 m, 15°02'12"S, 68°27'26"W, 14 November 2003, *Fuentes et al. 6135* (LPB, MO-2041038, US-00817983). PERU. Madre de Dios: Los Amigos Biological Station, 270 m, 12°34'12"S, 70°05'60"W, 22 October 2002, *Maceda 94* (MOL, USM); Los Amigos Biological Station, 260–290 m, 12°34'10"S, 70°05'60"W, 22 May 2010, *Clark et al. 11594* (MOL, US, USM).

Field observations and image documentation from in vivo plants of *Fuentes et al. 6135* in Bolivia (photos: MO), *Maceda 94* in Peru (photos: BRIT) and *Clark et al. 11594* in Peru (fig. 4 G), support the presence of fruits with rupturing dehiscence.

B. variabilis C.V. Morton (1939: 435–436):—ECUADOR. Morona-Santiago: Near Logroño, 600 m, 02°37'S, 78°11'W, 17 June 1989, *Dorr et al. 6324* (MO, QCNE, US-00325018); road Patuca–Santiago, 782 m, 02°46'20"S, 78°14'55"W, 12 August 2005, *Clark et al. 9188* (QCNE, US-00910468); Tiwintza, road Patuca–Santiago, 350 m, 03°01'14"S, 78°03'03"W, 15 August 2005, *Clark et al. 9308* (QCNE, US-00910479). Napo: Talag, Comunidad Cando, North of Río Jatunyacu, 540 m, 01°04'S, 77°56'W, 20 December 2000, *Clark et al. 5629* (AAU, COL, MO-1984678, NY, QCA, QCNE, US-00661622).

Rupturing fruit dehiscence was noted on specimen *Dorr et al. 6324*: “Fruit dehiscing to expose the ovary and numerous, small purple seeds.” Field observations and image documentation from in vivo plants of *Clark et al. 5629*, *9188* and *9308* (fig. 4 M) in three different populations in Ecuador also show the presence of fruits with rupturing dehiscence.

***Besleria* sp. 1:**—BOLIVIA. Cochabamba: Chaparé, Parque Nacional Carrasco, 700 m, 17°06'14"S, 65°32'11"W, 04 August 2002, *Clark & Rodriguez 6797* (LPB, UNA, US-00662497). PERU. Cusco: Camanti, near Quincemil, 825 m, 13°12'33"S, 70°45'10"W, 12 May 2010, *Clark et al. 11372* (US, USM).

Field observations and image documentation from in vivo plants of *Clark & Rodriguez 6797* in Bolivia and *Clark et al. 11372* in Peru (fig. 4 K) show the presence of fruits with rupturing dehiscence.

***Besleria* sp. 2:**—PERU. Huánuco: Chinchao, San Pedro de Carpish, trail to Hacienda Patti, 1700–2400 m, 09°40'12"S, 76°04'48"W, 08 June 2003, *Clark et al. 8197* (SEL, UNA, US-00818218, USM).

Field observations and image documentation from in vivo plants of *Clark et al. 8197* show the presence of fruits with rupturing dehiscence (fig. 4 H).

***Besleria* sp. 3:**—ECUADOR. Zamora-Chinchipe: Chinchipe, road Zumba–Amaluza, 1800 m, 04°52'54"S, 79°10'16"W, 31 March 2005, *Clark et al. 8972* (LOJA, QCNE, US-00961763); Zamora, S of Zamora, 904 m, 04°05'08"S, 78°57'23"W, 04 June 2007, *Clark et al. 9998* (UNA-00068391, US-00961582).

Field observations and image documentation from in vivo plants of *Clark et al. 8972* and *9998* (fig. 4 O) show the presence of fruits with rupturing dehiscence.

***Besleria* sp. 4:**—PERU. Cusco: Camanti, SE of Quincemil, 800–1100, 13°19'06"S, 70°48'56"W, 16 May 2010, *Clark et al. 11461* (US, USM).

Field observations and image documentation from in vivo plants of *Clark et al. 11461* show the presence of fruits with rupturing dehiscence (fig. 4 N).

***Besleria* sp. 5:**—PERU. Cusco: Camanti, SE of Quincemil, 800–1100, 13°19'06"S, 70°48'56"W, 16 May 2010, *Clark et al. 11470* (US, USM).

Field observations and image documentation from in vivo plants of *Clark et al. 11470* show the presence of fruits with rupturing dehiscence (fig. 4 L).

***Besleria* sp. 6:**—PERU. Cusco: Camanti, SE of Quincemil, trail to mining camp at Rio Yanaurco, 840–900 m, 13°14'37"S, 70°48'45"W, 18 May 2010, *Clark et al. 11505* (US, USM).

Field observations and image documentation from in vivo plants of *Clark et al. 11505* show the presence of fruits with rupturing dehiscence (fig. 4 I).

***Besleria* sp. 7:**—PERU. Cusco: Paucartambo, on road Pilcopata–Huacaria, 500–600 m, 12°55'12"S, 71°25'12"W, 30 May 2010, *Clark et al. 11703* (MOL, US, USM).

Field observations and image documentation from in vivo plants of *Clark et al. 11703* show the presence of fruits with rupturing dehiscence (fig. 4 E).

***Besleria* sp. 8:**—PERU. San Martín: Rioja, Bosque Protección Alto Mayo, Trocha Kovachii, 1700–1800 m, 05°42'11"S, 77°44'20"W, 03 June 2010, *Clark et al. 11765* (US).

Field observations and image documentation from in vivo plants of *Clark et al. 11765* show the presence of fruits with rupturing dehiscence (fig. 4 J).

Results and discussion

Lectotypification

Besleria macropoda Donn. Sm. *Botanical Gazette* 25(3): 155–156. 1898.

Lectotype (designated here):—*Cooper* [“*Pittier*”] 572 (BR-0005107995; isoelectotype: CR-572). Syntypes:—*Tonduz* [“*Pittier*”] 2495 (BR-0013349196, -202, CR-2495, CR-75711, US-00078576); *Tonduz* 11358 (BR-0013349219, -226, CR-11358, GH-00375574, US-00078573, -574).

When publishing *B. macropoda*, Donnell Smith (1898) listed three collections in the protologue: *Pittier* 572, *Pittier* 2495 and *Tonduz* 11358. Upon this syntype collections, a possible lectotype must be selected. In the Gesneriaceae treatment in Standley’s *Flora of Costa Rica*, Morton (1938: 1153) cited only one exemplary collection for *Besleria macropoda*: “Damp woods, El Recreo, *Pittier* 572.” In his later revision of the entire genus, Morton (1939: 454) chose the same collection (intentionally?) as the lectotype by writing “Type. El Recreo, Costa Rica, *Pittier* 572.” Unfortunately, he did not cite or select a specific herbarium specimen as he did for other specimens and taxa in the same treatment. However, by including the term “type” this has to be considered a valid [first step] lectotypification according to the ICN (Melbourne Code, Art. 9.17).

The type specimens based on Donnell Smith names are usually deposited at the Smithsonian Institution’s National Museum of Natural History (US), to which he donated his private herbarium in 1905 (Coulter 1908). It must be noted that there are no known duplicates of the above-mentioned collection at US (J. Boggan, US; pers. comm.), indicating that the specimen was lost, misplaced, or sent out for exchange before Morton revised *Besleria* (Morton 1938, 1939).

From the two duplicates located by us, the specimen at CR bears a pre-printed “Herb. Instit. physico-geogr. nat. costaricensis” label that gives H. Pittier as collector, which is in accordance with the protologue. The specimen at BR includes the following pre-printed label “H. Pittier & Th. Durand / *Plantae costaricensis exsiccatae*”, with only the plant name written in. Above it is an additional smaller, hand-written label, which gives the collection number 572, locality, etc. and which indicates that the collection was made by J. J. Cooper, who also collected for J. Donnell Smith. In addition, J. Boggan verified that the collection number and label are in Cooper’s handwriting. Hence, we consider the handwritten label of the duplicate at BR as bearing the authentic information and the label of the duplicate at CR as an incomplete later transcript. We therefore refer to the collection as *Cooper* [“*Pittier*”] 572 and select the duplicate from BR as the [second step] lectotype. In addition, the specimen at BR includes more fertile material and is in better condition than the specimen at CR.

A similar case is found in one of the syntype collections that is referred to as *Pittier* 2495 in the protologue, but should be attributed to A. Tonduz as the collector. The duplicate at BR (#0013349196) includes a handwritten label that gives Tonduz as the collector. Concordantly, the duplicates at CR and US include preprinted labels with Pittier as the collector (i.e., Tonduz is not included on the preprinted label). We consider the information of the handwritten BR label as verification that Tonduz is the collector and therefore refer to the collection as *Tonduz* [“*Pittier*”] 2495.

Extension of known distribution of *Besleria macropoda*

The distribution of *B. macropoda* is shown in fig. 1 and is based on coordinates from 31 collections. Previously, the species was only known from the Cordillera de Tilaran, and the northeastern slopes of the Cordillera Central and the Cordillera de Talamanca mountain ranges as well as from the Cerro Nara area on the Pacific slope of Costa Rica (Kriebel 2006). The new locality from the Fila Costeña range (indicated by a triangle in fig. 1) is less than 30 km from the Panamanian border and significantly widens the range of the species southeastwards. Although *B. macropoda* is considered endemic to Costa Rica, it would not be surprising to find populations that extend its range into Panama.

Conservation and IUCN Red List category

Besleria macropoda is endemic to Costa Rica and partly occurs in areas that are not formally protected (e.g., the Fila Costeña range) and are threatened by habitat destruction through logging. Most of the currently known populations

are located in two formally protected areas located on the northeastern slopes of the Central and Talamanca Mountain ranges near the Caribbean Coast. These areas are protected by Costa Rica's Ministry of the Environment and Energy (MINAE) and constitute part of the Sistema Nacional de Áreas de Conservación (SINAC). The Barbilla and the Braulio Carrillo National Parks combined protect more than 55,000 hectares. A third population is located in the La Selva Biological Station, which is a protected area that is owned and operated by the Organization for Tropical Studies (OTS). In addition, La Selva also constitutes part of the Central Volcanic Conservation Area that is administered by the SINAC. According to the IUCN Red List (IUCN 2001) criteria for estimated geographic range, area of occupancy and population size (B1 and B2), *B. macropoda* should be listed in category VU (Vulnerable).

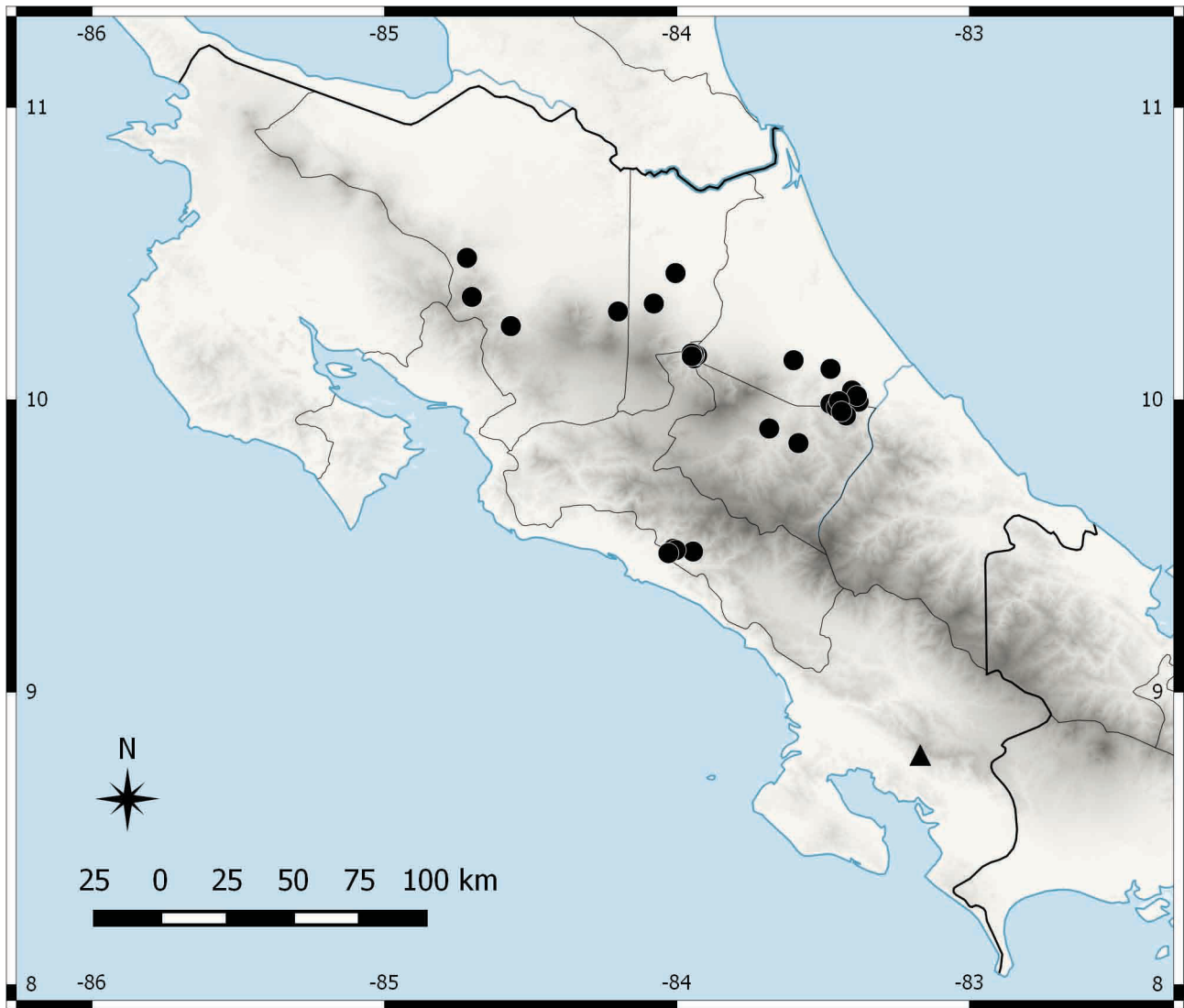


FIGURE 1. Distribution of the Costa Rican endemic *Besleria macropoda*. The map is based on 31 previous collections (circles) and the recent collection (11 March 2013) *Berger & Etl 1443* from the Fila Costeña range, Puntarenas Province (triangle).

Epiphyllous inflorescence position

The flowers and fruits of *B. macropoda* appear to arise directly from the center of the leaf blade (fig. 2), much like the epiphyllous flowers of *Helwingia* Willdenow (1806: 716–717; Helwingiaceae) and some other angiosperm taxa of various families (see below). However, closer inspection shows that the peduncle is not adnate to the midrib of the leaf. It is principally free, but clamped over its entire length in a channel formed by the sunken midrib of the leaf blade. In addition, the basalmost part of the peduncle is somewhat hidden from view by the wrinkled leaf base. We refer to this phenomenon as “functional epiphyllous” because there is no adnation to the leaf blade.

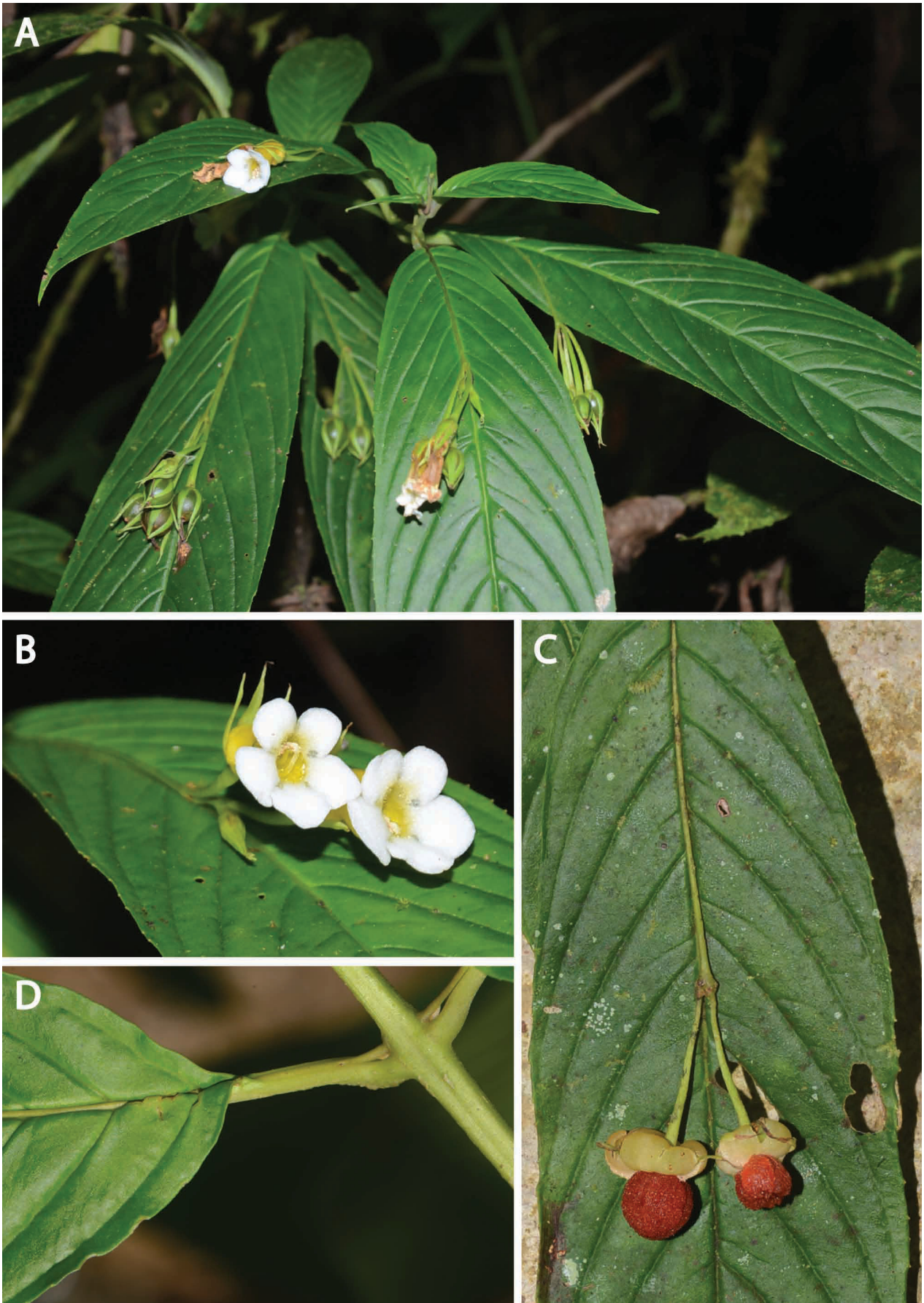


FIGURE 2. *Besleria macropoda*, epiphyllous position of flowers and fruits. **A.** Shoot. **B.** Inflorescence with open flowers. **C.** Infructescence showing fruits with split and reflexed carpel walls exposing red placentae and seeds. **D.** Sulcate petiole and leaf base clasping the peduncle above the sunken midrib. (Photos by A. Berger; voucher: *Berger & Etl 1443.*)

This conspicuous condition of epiphyllly in *B. macropoda* has never been addressed in the literature, including the original description of the species by Donnell Smith (1898) and the last revision of the genus by Morton (1939). This may be explained by the fact that the epiphyllous position is obvious only in the living plants. It is likely that the clamped peduncle is released as a result of force applied during collecting, pressing, drying, and processing of specimens. If it is not carefully noted in the field, the information is hardly conserved in herbarium specimens. Nevertheless, of all collections studied, we were able to find the following three specimens for which the collectors provided detailed information on the position of the inflorescence on the label: (1) *Sánchez & Zamora 418*: “los pedicelos sobre el nervio central de la hoja.” (2) *Grayum et al. 8879*: “Infls. axillary, the peduncle appearing fused to the midrib of the leaf (as in *Phyllonoma*), arching upward apically, the fl(s.) thus emerging from center of adaxial surface of leaf. Peduncle actually free to the stem, closely appressed to the petiole and embraced and hidden from view by laminar tissue in the proximal 1–2 cm of the leaf midrib.” (3) *Chavarría & Solís 908*: “Inflorescencia con pedúnculo que se coloca sobre la vena central de la hoja.” These notes and additional photographs in Kriebel (2006: 87) demonstrate that the observed “functional epiphyllly” is a consistent, but frequently overlooked character of *B. macropoda*.

Besides *B. macropoda*, three further species were found to have somewhat similar but less pronounced epiphyllous inflorescences and might represent transitional cases: *B. comosa* C.V. Morton (1939: 441–442; *Clark et al. 9931* US-00910342), *B. aff. comosa* (*Clark 6431* US-00818109, *6429* US-00818108 and *9976* US-00910353) and *B. reticulata* Fritsch (1934: 969–970; *Clark 8181* US-00818214). These species have a somewhat folded lamina base that channels the peduncle towards the upper side of the leaf blade, but all lack a sunken midrib that finally clamps the peduncle to the lamina as in *B. macropoda*. Further fieldwork may reveal other cases of “functional epiphyllly” within (and outside) the genus *Besleria*.

As already mentioned above, the present condition of *B. macropoda* does not represent epiphyllly in the traditional sense (i.e., “congenital” displacement of an axillary shoot to its subtending leaf). The phenomenon of “true” epiphyllly was reviewed by Dickinson (1978). Prominent examples include *Bougainvillea* Comm. ex Jussieu (1789: 91; Nyctaginaceae), *Helwingia* (Helwingiaceae), *Mocquerysia* Hua (1893: 259–260) and *Phyllobotryon* Müller Argoviensis (1864: 534; both Salicaceae), *Phyllonoma* Willd. ex Roemer & Schultes (1820: xx, 210; Phyllonomaceae), *Polycardia* Jussieu (1789: 377; Celastraceae), *Ruthiella* Steenis (1965: 127–128; Campanulaceae) and *Tilia* Linnaeus (1753a: 514; Malvaceae). Ontogenetic investigations have been carried out in *Helwingia* and *Phyllonoma* (Dickinson & Sattler 1974, 1975, Weber, 2003). *Phyllonoma* (in which the epiphyllous inflorescences emerge near the leaf tip) has been emphasized to represent a case of non-axillary, phyllogenous formation of inflorescences (Dickinson & Sattler 1975). However, the ontogenetic studies of Weber (2003) have shown that the inflorescences of *Phyllonoma* are of axillary origin and just represent an extreme case of the situation found in *Helwingia*.

“True” epiphyllly also occurs in Gesneriaceae. In some species of *Monophyllaea* Brown (1839: 121; subf. Didymocarpoideae, tribe Epithemateae) the inflorescences are located at the base and along the midrib of a solitary and subtending leaf (Burt 1978, Dickinson 1978, Weber 2004). In a number of species of the genus *Microchirita* (C.B. Clark) Y.Z. Wang in Wang *et al.* (2011: 59–60; subf. Didymocarpoideae, tribe Trichosporeae), the serial rows of axillary flowers (in fact representing series of two-flowered partial inflorescences) are displaced onto the petiole of the subtending leaf. The individual flowers are arranged in a way that the open flowers develop next to the leaf blade, pushing the postanthetic flowers towards the stem (Wood 1974, Weber 1975, sub *Chirita* sect. *Microchirita*).

In contrast, the axillary inflorescences of *B. macropoda* are not displaced onto the subtending leaf, but the peduncle is simply clamped in a channel formed by the sunken midrib (fig. 2). In terms of function, the result is the same (see below). Examples of similar functionally epiphyllous inflorescences include species of the temperate genus *Lonicera* Linnaeus (1753a: 173–175; Caprifoliaceae) such as *L. alpigena* Linnaeus (1753a: 174) and *L. nigra* Linnaeus (1753a: 173) and species of neotropical Orchidaceae subtribe Pleurothallidinae, including the speciose genera *Lepanthes* Swartz (1799: 85–86) and *Pleurothallis* R. Br. in Aiton (1813: 211). A similar, but morphologically completely different type of functional epiphyllly is found in *Ruscus* Linnaeus (1753b: 1041) and allies (Asparagaceae). Here the inflorescences are placed on phylloclades (flattened leaf-like shoots) that emerge from the axils of tiny bracts.

Ecological aspects of epiphyllly

For epiphyllous flowers, some relationships between spatial configuration, pollination and fruit dispersal were discussed by Dickinson (1978). In addition, Anderson (1976) suggested that in *Tilia* the bract fused to the inflorescence axis might advertise the presence of flowers to pollinators. Weber (1975) suggested that the epiphyllous position of the flowers of *Microchirita* enhances their visibility to potential pollinators. Flowers are presented to the pollinators

on a showy “platter-like” leaf where the flower color contrasts against a green leaf. A similar effect may occur in the Orchidaceae-Pleurothallidinae, in which small flies may alight on the leaf and rush to the flower(s). However, to date, no experimental confirmation of this idea is available. Epiphyllly may also play a role in the dispersal of fruits and/or seeds. In *Bougainvillea* and *Tilia* the bract is fused to the stalk of a dry, nut-like fruit and serves as a wing that aids in wind dispersal. No information is available on the dispersal of epiphyllous zoochorous fruits, but it may be hypothesised that the contrast between the green leaf and the colored fruit facilitates its localization by frugivores. This may be particularly important for plants growing in diverse and heterogeneous environments such as the understory of a rainforest, which is the typical habitat of most *Besleria* species.

It is probable that in *B. macropoda*, the epiphyllous position of both the flower and the fruit is of functional relevance (cf., fig. 2). The limbs of the flowers are white and contrast well with a green background. Likewise, the open fruits are red and contrast well with their complementary green color.

Fruit morphology of *Besleria*

Fruits of *Besleria* species, including the generic type *B. lutea* Linnaeus (1753b: 619; fig. 3 A), are known as globose or ovoid fleshy berries with colorful white, orange or red pericarp (fig. 3). However, fruits of *B. macropoda* are in strong contrast to such “true” (indehiscent) berries: They split open irregularly, in the manner of a thin-walled capsule. The pericarp is pale greenish-white and, after rupturing, become coiled above a globose interior of the fruit which consists of red placental tissue and glistening red seeds covering the surface (figs. 2 C, 4 A, B). The fruits, though being small (ca. 10 mm in diam.), are visually distinctive from a distance of several meters. Visibility is enhanced as the fruits lie on the middle of the subtending leaf (fig. 2).

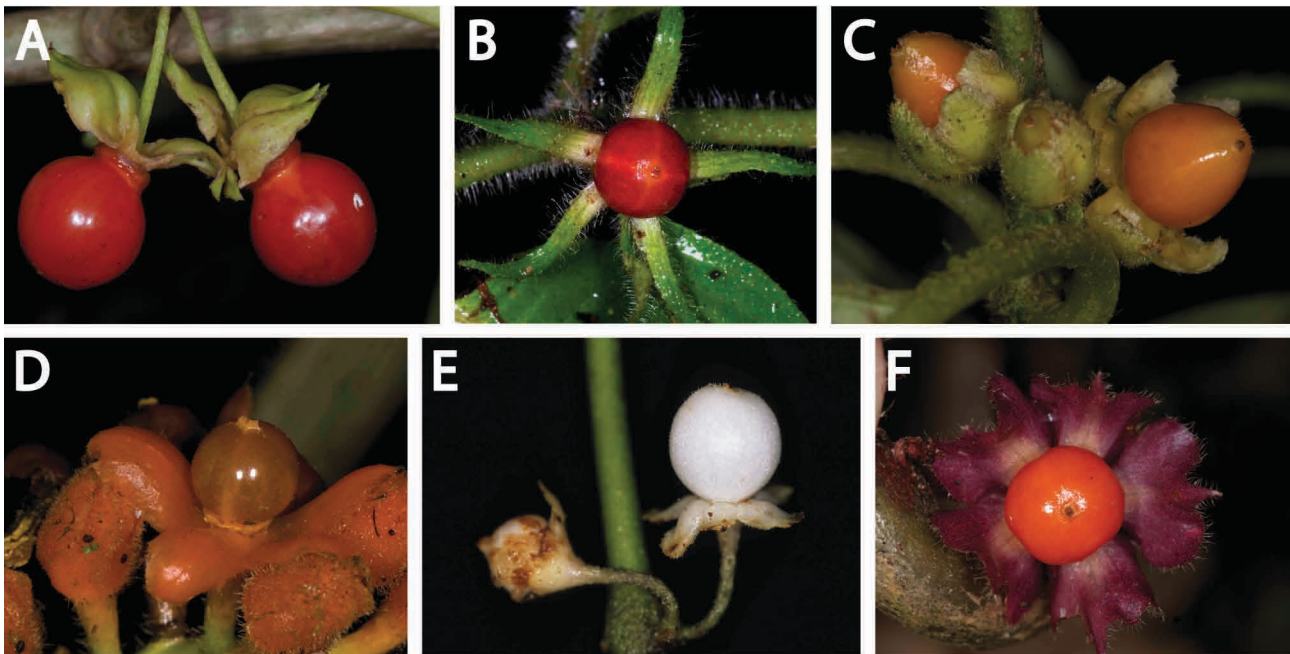


FIGURE 3. Examples of *Besleria* species with indehiscent (non-rupturing) fruits, note variation in orientation, coloration and contrasting effect of the calyx lobes. **A.** *B. lutea* (Clark 10541). **B.** *B. comosa* (Clark et al. 9931). **C.** *Besleria* sp. (Clark 11685). **D.** *Besleria* sp. (Clark 10815). **E.** *B. solanoides* (Clark 8583). **F.** *Besleria* sp. (Clark 11355).

It is important to note that *B. macropoda* is not the only species of *Besleria* exhibiting this type of fruit dehiscence. Wiehler (1983: 44–45) was the first to note inconsistencies in fruit morphology in *Besleria* and reported that the fruits of *B. affinis*, *B. pauciflora* and *B. pendula* deviate from typical berries in that they “peel either irregularly, or loculicidally and septicidally, with the bright-colored thin carpel walls reflexed or coiled above the hanging remainder of the fruit consisting of attractively colored placental tissue and seeds.” More recently, Roalson & Clark (2006: 264) observed “some instances where the berries rupture, thereby the fruit wall dehisces irregularly or unevenly,” but did not give further details on the identity of the species observed.

In addition to *B. macropoda* and the three species cited by Wiehler (1983), another eleven species were found to have rupturing dehiscence by the evaluation of *in vivo* images posted in the Andes to Amazon Biodiversity Program,

the Gesneriaceae Image Library, and the TROPICOS database (see Materials and Methods). Representative examples are given in fig. 4. The full (but still provisional) list includes the following species: *B. affinis*, *B. macropoda*, *B. montana*, *B. pauciflora*, *B. pendula*, *B. sprucei*, *B. variabilis* and ten collections which, judging from morphology, belong to eight taxa that may represent distinct but yet undescribed/unidentified species. In conclusion, more than 15 *Besleria* species are presently known to have fruits with rupturing dehiscence, which is almost 8% of the estimated number of species in the genus. This study strongly supports that fruit morphology in *Besleria* is less uniform than previously reported.



FIGURE 4. Examples of *Besleria* species with dehiscent fruits. Note differences in the mode of rupturing and coloration of carpel lobes, placentae and seeds. **A, B.** *B. macropoda* (Berger & Etl 1443), placentae apparently removed by a frugivore in **B**. **C.** *B. montana* (Clark 6811). **D.** *B. pendula* (Clark 6887). **E.** *Besleria* sp. 7 (Clark 11703). **F.** *B. pauciflora* (Clark 9280). **G.** *B. sprucei* (Clark 11594). **H.** *Besleria* sp. 2 (Clark 8197). **I.** *Besleria* sp. 6 (Clark 11505). **J.** *Besleria* sp. 8 (Clark 11765). **K.** *Besleria* sp. 1 (Clark 11372). **L.** *Besleria* sp. 5 (Clark 11470). **M.** *B. variabilis* (Clark 9308). **N.** *Besleria* sp. 4 (Clark 11461). **O.** *Besleria* sp. 3 (Clark 9998). Photos **A** and **B** by A. Berger, all others by J. L. Clark.

It should be noted that the terms “peeling/rupturing berries” as used by Wiehler (1983) or Roalson & Clark (2006) are self-contradictory from a strictly morphological point of view: by definition, berries are indehiscent fruits, while

the terms legume, follicle (both unilocarpellate) and capsule (bi- or plurilocarpellate) are tied to dehiscent fruits. However, there is preliminary evidence from ITS sequence data that two species with rupturing dehiscence, *B. pendula* and *B. variabilis*, are nested at different positions within the bulk of species having typical (indehiscent) berries (Roalson & Clark 2006). This suggests that the rupturing dehiscence is phylogenetically informative and derived (apomorphy) from true or indehiscent berries (plesiomorphy). Therefore, the terms peeling or rupturing berry may be justified in *Besleria*. This statement needs confirmation through additional phylogenetic analysis based on increased taxon sampling of species with rupturing and non-rupturing dehiscence.

Putative function of fruit rupture

The peeling/rupturing dehiscence of the mentioned *Besleria* species is an underreported fruit character in the Gesneriaceae and other angiosperms. An overall survey on display fruits will be presented in a forthcoming paper. Although their mode of dehiscence is different, their putative function is certainly the same as in the better known display fruits of *Alloplectus* Martius (1829: 53–57), *Drymonia* Martius (1829: 57–59), *Glossoloma* Hanstein (1854: 191, 208–209) and *Nematanthus* Schrader (1821: 718–719). Here the capsular fruits open loculicidally by two valves exposing the seeds in a conspicuous manner (Wiehler 1983: fig. 63, Weber 2004: fig. 17 D, E, G–K, Clark *et al.* 2006: fig. 6 F–H, Clark *et al.* 2012: figs. 1 I, 7 A, B).

Display capsules and their contrasting color effects are assumed to attract seed dispersing animals in *Drymonia* and related genera (Wiehler 1983, Weber 2004, Clark *et al.* 2006, 2012). For the fleshy and irregularly dehiscent capsules of *Solenophora calycosa* Donnell Smith (1898: 152), Weber & Weissenhofer (2007) suggested that the contrast provided by the fruit wall (orange) and the placentae plus seeds (deep red) is attractive to birds and/or small mammals. Similarly, the rupturing fruits of the above-mentioned *Besleria* are certainly to be considered as display fruits: the red or black color of the placentae and seeds makes a striking contrast against the reflexed or coiling fruit wall. By contrast, in species with non-rupturing berries, a visibility enhancing effect is often provided by conspicuously colored calyx lobes (fig. 3), which are never found in species showing rupturing dehiscence (fig. 4).

Generic delimitation in the Beslerieae, particularly between *Besleria* and *Gasteranthus*

For a long time, knowledge of the genera of the tribe Beslerieae suffered from poor information on fruit morphology, which is indeed difficult to ascertain from herbarium specimens (Wiehler 1983). In the meantime, field studies and studies of cultivated material have added important data on fruit morphology of many taxa and molecular phylogenetic studies have been carried out, which provide a framework for analysis of this data (Smith 2000). The most recent and comprehensive phylogenetic study of the tribe Beslerieae are that of Roalson & Clark (2006) and Clark *et al.* (2010). The authors demonstrated that both the (morphologically heterogeneous) tribe and the genera included therein are monophyletic and that *Besleria* forms the crown group. *Besleria* was last monographed by Morton (1939), who recognized 141 species in four sections and 18 subsections. Two of the four sections, which Morton (1939) based essentially on corolla and calyx characters, have been segregated from *Besleria* and now constitute the genus *Gasteranthus* (Wiehler 1975). This segregation was adopted in all recent monographs and floras (Skog & Kvist 2000, Weber 2004, Weber *et al.* 2013, Kriebel 2006, 2010) and confirmed by molecular systematic studies (Smith 2000, Roalson & Clark 2006, Clark *et al.* 2010). According to Roalson & Clark (2006), *Gasteranthus* is sister to a clade containing *Cremosperma* Benth (1846: 234) + *Besleria* and many of Morton's subsections of *Besleria* proved para- or polyphyletic and are no longer taxonomically relevant.

At present, *Besleria* is thought to comprise more than 200 species and is, after *Columnnea* Linnaeus (1753b: 638–939) with ca. 300 species, the second-largest genus of New World Gesneriaceae (Wiehler 1983, Burt & Wiehler 1995, Weber 2004, Weber *et al.* 2013). *Gasteranthus* was originally described by Benth (1846), but later included in *Besleria*. Wiehler's re-establishment was mainly based on fruit morphology: *Gasteranthus* has fleshy capsules which split open by two valves that are sometimes secondarily dehiscent and appear four-valved. In contrast, *Besleria* has (indehiscent) berries. This character has often been used as a differential character between the two genera in identification keys of floras and taxonomic treatments. The recognition and documentation of "rupturing dehiscence" in some species of *Besleria* precludes them from being called berries and hampers correct identification of the genus. Hence, in Tab. 1 we present an amended compilation of characters (based on Wiehler 1975, 1983, Skog & Kvist 2000, Smith 2000, and Kriebel 2006, 2010) which separate *Besleria* from *Gasteranthus*. The distinction of the two genera is expanded here in the following key.

1. Underside of leaves without clustered stomates (“stomata islands”); corolla red, orange or yellow, rarely white, mostly tubular or narrowly funnelform; nectary perfectly annular in the majority of species; fruits indehiscent or irregularly dehiscent (“rupturing”) by more than two valves..... *Besleria*
- Underside of leaves with clustered stomates (“stomata islands”) that usually appear as white or pale spots visible with the naked eye; corolla red, orange, yellow or pink, strongly urceolate-ventricose, with contracted entrance, narrow limb and protruding pouch; or corolla whitish or cream-colored, funnelform to campanulate, or urceolate, with wide entrance and broad limb and prominent spur; nectary never perfectly annular, either reduced to a dorsal gland or semi-annular to annular with a dorsal swelling; fruits laterally compressed fleshy or semi-fleshy capsules that split loculicidally with two reflexed valves, sometimes splitting loculicidally plus septicidally into four valves..... *Gasteranthus*

TABLE 1. Differentiating characters for *Besleria* and *Gasteranthus*.

	<i>Besleria</i>	<i>Gasteranthus</i>
Stomata	Irregularly scattered	Clustered on underside of leaf (“stomata islands”)
Spur	Usually absent, sometimes short, or reduced to a saccus or gibbosity at the corolla base	Usually conspicuous, long in euglossophilous and shorter in ornitophilous species
Nectary	Annular in most species	Not annular, either reduced to a dorsal gland or semi-annular to annular with a dorsal swelling
Fruits	Fleshy, globose, indehiscent berries or dehiscent through irregular rupturing	Semi-fleshy to dry capsules, laterally compressed, bivalved, sometimes secondarily four-valved

Conclusions

The recent collection of *Besleria macropoda* widens the known distribution considerably and highlights two unique characters not previously addressed. The inflorescences/infructescences are functionally epiphyllous possibly aiding in pollination and/or fruit dispersal. Fruit dehiscence deviates from indehiscent berries that typically characterize *Besleria*: the fruits appear ruptured and split open irregularly, with the fleshy carpel lobes becoming reflexed. This results in displaying a globose head of red placental tissue embedded with tiny, red seeds. In addition to *B. macropoda*, this specific fruit type was found in 14 other species of the genus. Fruit morphology of *Besleria* is thus less uniform than previously understood, and the “indehiscent berry” can no longer serve as a distinctive generic character of *Besleria*, which necessitates consideration in generic keys such as in regional floras. However, further fieldwork is necessary to fully understand the distribution, phylogenetic context, and functional implications of this particular fruit type and fruit dehiscence.

Acknowledgements

We thank the Field Station La Gamba and its staff for providing convenient research facilities, particularly Werner Huber and Anton Weissenhofer (Department of Botany and Biodiversity Research, University of Vienna, Austria) for arranging research and export permits for Costa Rica. We thank Florian Etl for his companionship during field expeditions. Much gratitude is due to Astrid and Werner Klar for hospitality in their Finca in Virgen de Briceño where *Besleria macropoda* was studied and collected. Additionally, their efforts to conserve the endangered primary forests in the Fila Costeña range are gratefully acknowledged. Christian Gilli is thanked for comments on the manuscript and for proof-reading. John K. Boggan (Smithsonian Institution’s National Museum of Natural History—Department of Botany) is thanked for providing insights on type specimens at US based on names published by John Donnell Smith.

Literature

- Aiton, W.T. (1813) *Hortus Kewensis* 2nd ed., 5. London, 568 pp.
- Anderson, G.J. (1976) The pollination biology of *Tilia*. *American Journal of Botany* 63 (9): 1203–1212.

<http://dx.doi.org/10.2307/2441737>

- Bentham, G. (1846) Gesneriaceae. In: *Plantae Hartwegianae*. W. Pamplin, London, pp. 228–236.
- Brown, R. (1839) *On Cyrtandreae*. In: Bennett, J.J. & Brown, R. (Aut.) *Plantae Javanicae Rariores*, 2. London, pp. 105–122.
- Burt, B.L. & Wiehler, H. (1995) Classification of the family Gesneriaceae. *Gesneriana* 1: 1–4.
- Burt, B.L. (1978) Studies in the Gesneriaceae of the Old World. XLV. A preliminary revision of *Monophyllaea*. *Notes from the Royal Botanic Garden, Edinburgh* 37 (1): 1–59.
- Clark, J.L., Funke, M.M., Duffy, A.M. & Smith, J.F. (2012) Phylogeny of a Neotropical clade in the Gesneriaceae: More tales of convergent evolution. *International Journal of Plant Sciences* 173 (8): 894–916.
<http://dx.doi.org/10.1086/667229>
- Clark, J.L., Neill, D.A., Gruhn, J.A., Weber, A. & Katan, T. (2010) *Shuaria* (Gesneriaceae), an arborescent new genus from the Cordillera del Cóndor and Amazonian Ecuador. *Systematic Botany* 35 (3): 662–674.
<http://dx.doi.org/10.1600/036364410792495917>
- Clark, J.L., Herendeen, P.S., Skog, L.E. & Zimmer, E.A. (2006) Phylogenetic relationships and generic boundaries in the Episcieae (Gesneriaceae) inferred from nuclear, chloroplast, and morphological data. *Taxon* 55 (2): 313–336.
<http://dx.doi.org/10.2307/25065580>
- Coulter, J.M. (1908) Library of John Donnell Smith. *Botanical Gazette* 46 (4): 310.
<http://dx.doi.org/10.1086/329729>
- Dickinson, T.A. & Sattler, R. (1974) Development of the epiphyllous inflorescence of *Phyllonoma integerrima* (Turcz.) Loes.: implications for comparative morphology. *Botanical Journal of the Linnean Society* 69 (1): 1–13.
<http://dx.doi.org/10.1111/j.1095-8339.1974.tb01609.x>
- Dickinson, T.A. & Sattler, R. (1975) Development of the epiphyllous inflorescence of *Helwingia japonica* (Helwingiaceae). *American Journal of Botany* 62 (9): 962–973.
<http://dx.doi.org/10.2307/2441641>
- Dickinson, T.A. (1978) Epiphyllous in Angiosperms. *Botanical Review* 44 (2): 181–232.
<http://dx.doi.org/10.1007/BF02919079>
- Donnell Smith, J. (1898) Undescribed plants from Guatemala and other Central American republics. XX. *Botanical Gazette* 25 (3): 145–157.
<http://dx.doi.org/10.1086/327650>
- Fritsch, K. (1934) Zur Kenntnis der Gattung *Besleria*. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 11: 961–977.
<http://dx.doi.org/10.2307/3994602>
- Hanstein, J.L.E.R. von (1854) Die Gesneraceen des königlichen Herbariums und der Gärten zu Berlin, nebst Beobachtungen über die Familie im Ganzen. *Linnaea* 26 (2): 145–217.
- Hanstein, J.L.E.R. von (1865) Die Gesneraceen des K. Herbariums und der Gärten zu Berlin, nebst monographischer Uebersicht der Familie im Ganzen. II. Abschnitt. Gattungen und Arten. Drittes Stück. Die Eugesnereen, Rhytidophylleen und Beslerieen. *Linnaea* 34 (3): 305–462.
- Hua, H. (1893) *Mocquerysia*. Nouveau genre a fleurs épiphyllous de l'Afrique tropicale occidentale. *Journal de Botanique* 8 (13–14): 257–260.
- IUCN (2001) *IUCN Red List Categories and Criteria*, Version 3.1. Prepared by the IUCN Species Survival Commission. ii. Gland, Switzerland and Cambridge: International Union for Conservation of Nature and Natural Resources, pp. 1–30.
- Jussieu, A.L. de (1789) *Genera plantarum*. Apud viduam Herissant et Theophilum Barrois, Paris, pp. 1–498.
<http://dx.doi.org/10.5962/bhl.title.284>
- Kriebel, R. (2006) *Gesneriaceas de Costa Rica = Gesneriads of Costa Rica*. Santo Domingo de Heredia, Instituto Nacional de Biodiversidad, 372 pp.
- Kriebel, R. (2010) Gesneriaceae. In: Hammel, B.E., Grayum, M.H., Herrera, C. & Zamora, N. (Eds.) *Manual de Plantas de Costa Rica. Volume 5. Monographs in Systematic Botany from the Missouri Botanical Garden* 119, pp. 844–930.
- Linnaeus, C. von (1753a) *Species plantarum*, 1. Laurentii Salvii, Stockholm, [i–xii], 1–560 pp.
<http://dx.doi.org/10.5962/bhl.title.669>
- Linnaeus, C. von (1753b) *Species plantarum*, 2. Laurentii Salvii, Stockholm, [i], 561–1200 pp.
<http://dx.doi.org/10.5962/bhl.title.669>
- Martius, C.P.F. von (1829) *Nova genera et species plantarum*, 3(1). Typis C. Lindaueri, München, 1–80.
- Morton, C.V. (1935) The genus *Besleria* in Venezuela. *Proceedings of the Biological Society of Washington* 48 (19): 73–76.
- Morton, C.V. (1938) Gesneriaceae. In: Standley, P.C. (Ed.) *Flora of Costa Rica. Publications of the Field Museum of Natural History Botanical series* 18(4): 1137–1616.
- Morton, C.V. (1939) A revision of *Besleria*. *Contributions from the United States National Herbarium* 26 (9): 395–474.

- Müller Argoviensis, J. (1864) Neue Euphorbiaceen des Herbarium Hooker in Kew, auszugsweise vorläufig mitgeteilt aus dem Manuskript für De Candolle's Prodrum. *Flora* 47 (34): 529–540.
- Roalson, E.H. & Clark, J.L. (2006) Phylogenetic patterns of diversification in the Beslerieae (Gesneriaceae). In: Sharma, A.K. & Sharma, A. (Eds.) *Plant genome: biodiversity and evolution, Phanerogams 1C*. Science Publishers, Inc., Enfield, New Hampshire, pp. 251–268.
- Rusby, H.H. (1895) On the collections of Mr. Miguel Bang in Bolivia.—Part II. *Memoirs of the Torrey Botanical Club* 4 (3): 203–274.
- Rusby, H.H. (1900) An Enumeration of the Plants collected by Dr. H. H. Rusby in South America, 1885–1886, XXVIII. *Bulletin of the Torrey Botanical Club* 27 (1): 22–31.
<http://dx.doi.org/10.2307/2477739>
- Schrader, H.A. (1821) *Göttingische gelehrte Anzeigen* 1821 (2): 705–719.
- Schultes, J.A. (1820) *Systema vegetabilium ed. 15 bis*, 6. Sumtibus J. G. Cottae, Stuttgart, [i]–lxx, pp. [1]–852.
<http://dx.doi.org/10.5962/bhl.title.825>
- Skog, L.E. & Kvist, L.P. (2000) Revision of *Gasteranthus* (Gesneriaceae). *Systematic Botany Monographs* 59: 1–118.
<http://dx.doi.org/10.2307/25027883>
- Smith, J.F. (2000) A phylogenetic analysis of tribes Beslerieae and Napeantheae (Gesneriaceae) and evolution of fruit types: parsimony and maximum likelihood analyses of ndhF sequences. *Systematic Botany* 25 (1): 72–81.
<http://dx.doi.org/10.2307/2666674>
- Steenis, C.G.G.J. van (1965) *Ruthiella*, a new generic name for *Phyllocharis* Diels, 1917, non Fée, 1824 (Campanulaceae). *Blumea* 13: 127–128.
- Swartz, O. (1799) Dianome Epidendri generis Linn. *Nova Acta Regiae Societatis Scientiarum Upsaliensis 2nd ser.* 6: 61–88.
- Wang, Y.-Z., Mao, R.-B., Liu, Y., Li, J.-M., Dong, Y., Li, Z.-Y. & Smith, J.F. (2011) Phylogenetic reconstruction of *Chirita* and allies (Gesneriaceae) with taxonomic treatments. *Journal of Systematics and Evolution* 49 (1): 50–64.
<http://dx.doi.org/10.1111/j.1759-6831.2010.00113.x>
- Weber, A. & Weissenhofer, A. (2007) *Solenophora*: a little known genus of Central American Gesneriaceae. *Gesneriads* 57 (3): 12–19.
- Weber, A. (1975) The cristate inflorescence of *Chirita* sect. *Microchirita* (Gesneriaceae). *Notes from the Royal Botanic Garden, Edinburgh* 34 (2): 221–230.
- Weber, A. (2003) What is morphology and why is it time for its renaissance in plant systematics? *Regnum Vegetabile* 141: 3–32.
- Weber, A. (2004) Gesneriaceae. In: Kubitzki, K. & Kadereit, J. (Eds.) *The families and genera of vascular plants. Vol. 7. Dicotyledons. Lamiales (except Acanthaceae including Avicenniaceae)*. Springer, Berlin/Heidelberg, pp. 63–158.
http://dx.doi.org/10.1007/978-3-642-18617-2_8
- Weber, A., Clark, J.L. & Möller, M. (2013) A new formal classification of Gesneriaceae. *Selbyana* 31 (2): 68–94.
- Wiehler, H. (1975) *Besleria* L. and the re-establishment of *Gasteranthus* Benth. (Gesneriaceae). *Selbyana* 1 (2): 150–156.
- Wiehler, H. (1983) A synopsis of the neotropical Gesneriaceae. *Selbyana* 6 (1–4): 1–249.
- Willdenow, C.L. von (1806) *Species plantarum, Editio quarta*, 4(2). G. C. Nauk, Berlin, pp. [631]–1157.
- Wood, D. (1974) A revision of *Chirita* (Gesneriaceae). *Notes from the Royal Botanic Garden, Edinburgh* 33 (1): 123–205.