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***Sipaneopsis* (Sipaneae, Ixoroideae): A unique flowering process in the family Rubiaceae and its taxonomic significance**

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Abstract

The process of anthesis of *Sipaneopsis* is unique within the Rubiaceae, and is here described and illustrated in detail for the first time. During the initial stage of anthesis the flowers are small, with the corolla lobes already open and erect before tube elongation, and the corolla lobe basal appendages are appressed against each other, forming a convex structure at the corolla mouth obstructing the entrance of visitors and pollinators. At the final stage of anthesis, the corolla lobes reflex and become perpendicular to the tube, and their basal appendages become erect, not touching each other, allowing visitors and pollinators to access the corolla tube and the nectar disk. *Neobertiera* and *Sipaneopsis* are unique within the tribe Sipaneae in having indehiscent dry fruits and recent molecular phylogenies positioned them as sister taxa. *Sipaneopsis* is distinguished from *Neobertiera* in having flowers consistently homostylous (vs. distylous or rarely tristylous in *Neobertiera*), stamens inserted at the middle of the corolla tube (vs. at variable positions), and five triangular appendages at the base of each corolla lobe (vs. corolla lobes thickened at base, without appendages). The differences in flower morphology and process of anthesis between the two genera (which most likely influence their different pollination syndromes) provide an important set of significant taxonomic and diagnostic characters that can be used to distinguish them.

Key Words: Guiana Shield, French Guiana, Guyana, Surinam, Brazil, South America, *Neobertiera*, taxonomy

Introduction

Members of the Sipaneae have either been included in the tribe Rondeletieae (Verdcourt 1958; Steyermark 1974; Delprete 1999) or treated as a separate tribe (Bremekamp 1934, Robbrecht 1988, 1993 1994) and positioned in subfamily Cinchonoideae, based on morphological characters. The molecular phylogenies of Rova *et al.* (2002) supported the Sipaneae as a separate tribe, and positioned it within the subfamily Ixoroideae instead. Delprete & Cortés-B. (2004), produced the first phylogenetic study focused on the Sipaneae, using *trnL-F* and ITS sequence data in which it was shown that the tribe and several of its genera are monophyletic. While continuing a taxonomic revision of the tribe, new observations were made on two genera unique within the tribe by having indehiscent, dry fruits, namely *Neobertiera* Wernham (1917: 169) and *Sipaneopsis* Steyermark (1967: 284), which, in the molecular phylogenies of Delprete & Cortés-B. (2004), were positioned as sister taxa. *Sipaneopsis* has been traditionally distinguished from *Neobertiera* by stamens inserted at about the middle of the corolla tube (vs. at variable positions in *Neobertiera*), five triangular appendages at the base of the corolla lobes (vs. corolla lobes thickened at the base, without appendages), and corolla lobes either imbricate or left-contorted in bud (vs. always left-contorted). However, the taxonomic significance of these appendages has previously been questioned. In addition, the two genera occupy different ecological niches, and have different geographical distributions. *Sipaneopsis*, as currently delimited (Kirkbride 1980; Delprete & Steyermark 2004; Delprete, 2015), is a genus of seven species endemic to white sand savannas, growing in sunny exposures (heliophilous), occurring mostly in the lowlands (although with a few collections from higher altitudes) of the Guiana Shield, ranging from Colombia, southern Venezuela to northern Brazil, North of the Amazon River. A few specimens collected in Guyana (Henkel *et al.* 1449, McDowell & Stobey 3853, and Mutchnick *et al.* 156) were incorrectly identified as *Sipaneopsis cururuensis* Kirkbride (1980: 113, figs. 19, 24); these specimens were recently re-identified as *Neobertiera pakaraimensis* Delprete (2015: 126, figs. 2, 5); therefore, *S. cururuensis* is the only species of the genus

known to occur south of the Amazon River, as it is only known by the type collection from the Upper Tapajos River Basin (Cururu River, Erereri [River, ca. 7°37'S, 57°37'W], based on *Egler & Raimundo 1265* [IAN, MG, US]). On the other hand, *Neobertiera*, as currently circumscribed (Delprete, 2015), is a genus of four species growing on lateritic or alluvial soils, in forest undercanopy (umbrophilous), often close to slowly running water courses, endemic to the Guianas, with one in Guyana, one in Guyana and Suriname, and two species apparently restricted to French Guiana.

As a result of a recent morphological analysis of the four species currently recognized in *Neobertiera*, Delprete (2015) discovered that all of them are distylous (rarely tristylous), while the flowers of *Sipaneopsis* are consistently homostylous. Field observations and a detail analysis of herbarium specimens revealed additional morphological characters of both taxa, and a newly reported process of anthesis in *Sipaneopsis*, which represent a set of significant characters that can be used to distinguish the two taxa.

Material and Methods

This study was based on examinations of individuals in their natural environment, herbarium specimens, samples preserved in 60% ethanol, and digital images. Field observations of *Sipaneopsis maguirei* Steyermark (1967: 287) were made in populations on white-sand savannas in southern Venezuela, State of Amazonas, near Minicia Nuevo village (*P.G. Delprete et al. 7451, 7452, 7453*). Field observations of *Neobertiera glomerata* Delprete (2015: 124) were made in populations of two localities in French Guiana, one in the forests of the coastal region, along the trail to Bagne des Annamites (*P.G. Delprete & G. Quenette 11860*) and the other in the forests of the Upper Oyapock River Basin, near Tampak village (*P.G. Delprete et al. 12310*). Herbarium specimens were studied either by visiting and/or through loans from BBS, BM, CAY, F, IAN, K, MG, MO, NY, P, U, UB, and US herbaria, and were examined using a dissecting microscope. Details about collection locality, collectors, and herbaria of deposit of specimens of *Neobertiera* and *Sipaneopsis* analyzed for this study are available in Appendix 1.

The process of anthesis in *Sipaneopsis*: a unique case within the Rubiaceae

The Rubiaceae is a family of more than 13,000 species (Govaerts 2017) and is extremely diverse in terms of habit, ecological adaptations, flowering strategies, fruit types, and seed dispersal. The corollas of this family are generally sympetalous (except *Dialypetalanthus* J.G. Kuhlmann (1925: 363), with free petals), with a tube ranging from a few mm long (e.g., species of *Spermacoce* Linnaeus (1753: 102) and *Galium* Linnaeus (1753: 105)) to 27 cm long (e.g., *Posoqueria* Aublet (1775: 133), *Osa* Aiello (1979: 115)). The common process of anthesis in Rubiaceae is that after the corolla tube is completely elongated, the lobes open and reflex outwards, allowing the access to pollinators (e.g., Baillon 1881; Delprete 2004, 2009; Endress 1996; Proctor & Yeo 1975; Richard 1830; Robbrecht 1988; Robbrecht & Puff 1986; Schumann 1891; Weberling 1977, 1992; Yeo 1993). However, in several genera with protogynous flowers (e.g., *Chimarrhis* Jacquin (1763: 61); see Delprete 1999), the style elongates while the corolla is still closed, pushing through the lobes and exposing the stigmatic branches, which become reflexed and receptive before the corolla opens.

After an exhaustive search of specialized literature (see references cited above) it was concluded that the process of anthesis of *Sipaneopsis* is unique within the Rubiaceae, and is here described and illustrated (Figures 1–3) for the first time. In Figures 1 and 2D is shown an inflorescence with flowers of *Sipaneopsis maguirei* in different developmental stages, and in Figures 2F–H are illustrated three flowers in successive flowering stages. In Figure 3 are depicted the successive stages of anthesis of the same flower, with details of the distal portion of the corolla tube and basal portion of the lobes, clearly illustrating the peculiar process of anthesis of this genus. The description of the process of anthesis and all these illustrations are of *S. maguirei* because field observations, herbarium and pickled specimens, and images were available; at the same time, detailed observations of herbarium specimens demonstrated that this flowering modality is present in all species of the genus (see Appendix 1). During the initial stage of anthesis the flowers are still very small; however, their corolla lobes are already open and erect (although not fully expanded) before tube elongation, while stamens and style are still short and non-functional (Figs. 3A, B); at this stage the triangular appendages present at the base of the corolla lobes are appressed against each other, forming a convex structure at the corolla mouth (Figs. 3A, B), obstructing the entrance of visitors and pollinators. During successive stages of anthesis, the corolla tube and lobes elongate, and the corolla lobes remain erect and the corolla lobe appendages are still appressed against each other (Figs. 3C–F), continuing to obstruct the entrance of visitors and pollinators. At the final stage of anthesis, the corolla lobes reflex and become perpendicular to the tube (corolla hypocrateriform), and the corolla lobe basal appendages

become erect, not touching each other anymore (Figs. 3G, H), and therefore allowing visitors and pollinators to access the corolla tube and nectar disk. In addition, flowers of *Sipaneopsis* are protandrous, which means that after the lobes have become perpendicular to the corolla tube, on the first day the anthers reach full maturity and dehisce, releasing pollen, while the stigmatic branches are still appressed to each other and not receptive (Fig. 3G); on the following day the anthers are no longer releasing pollen, the stigmatic branches spread apart and are reflexed, and the stigmatic surfaces are exposed and become receptive (not illustrated).

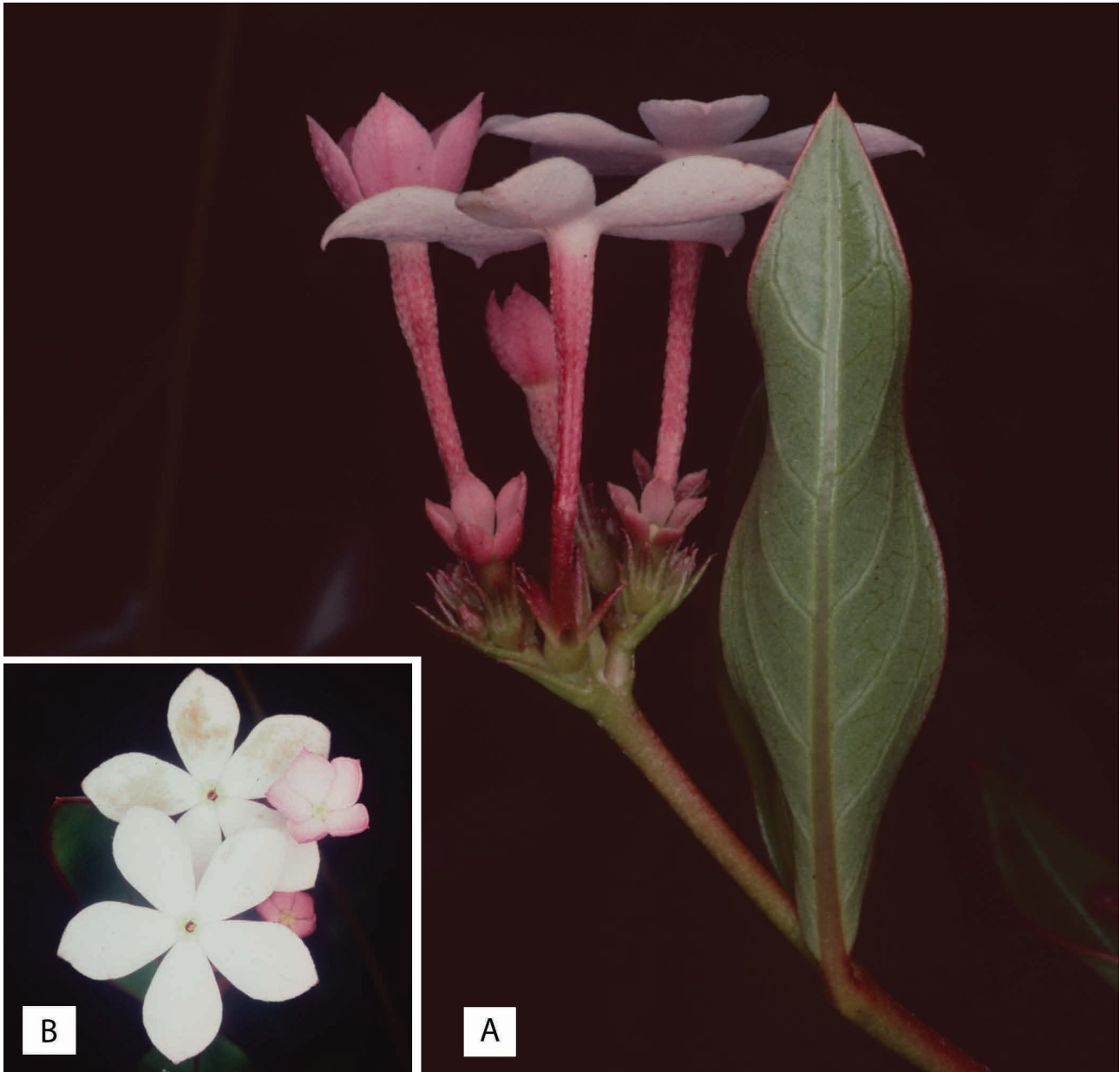


FIGURE 1. *Sipaneopsis maguirei*. Inflorescence with flowers at different stages of anthesis. **A.** Side view. **B.** View from top, showing young flowers (pink) with corolla lobe appendages obstructing the mouth, and fully developed flowers (white) with corolla mouth open. Photos by Piero G. Delprete.

Comparison of flower morphology and process of anthesis in *Neobertiera* and *Sipaneopsis* and their taxonomic significance

Neobertiera and *Sipaneopsis* are unique within tribe Sipaneeae in having indehiscent, dry fruits, while the remaining genera of the tribe have septicidal or loculicidal capsules. In the molecular phylogenies of Delprete & Cortés-B. (2004) these genera were found to be sister taxa on a strongly supported clade. However, these molecular phylogenies only included a small portion of Sipaneeae taxa, and these two genera were represented by only one species each. Therefore, more species need to be added to the analysis to test the monophyly of all the genera in the tribe and to further clarify their evolutionary relationships. In addition, all the species of *Neobertiera* are protandrous, meaning that on the first day of anthesis the anthers open and release pollen, and the stigmatic branches are appressed to each other and not

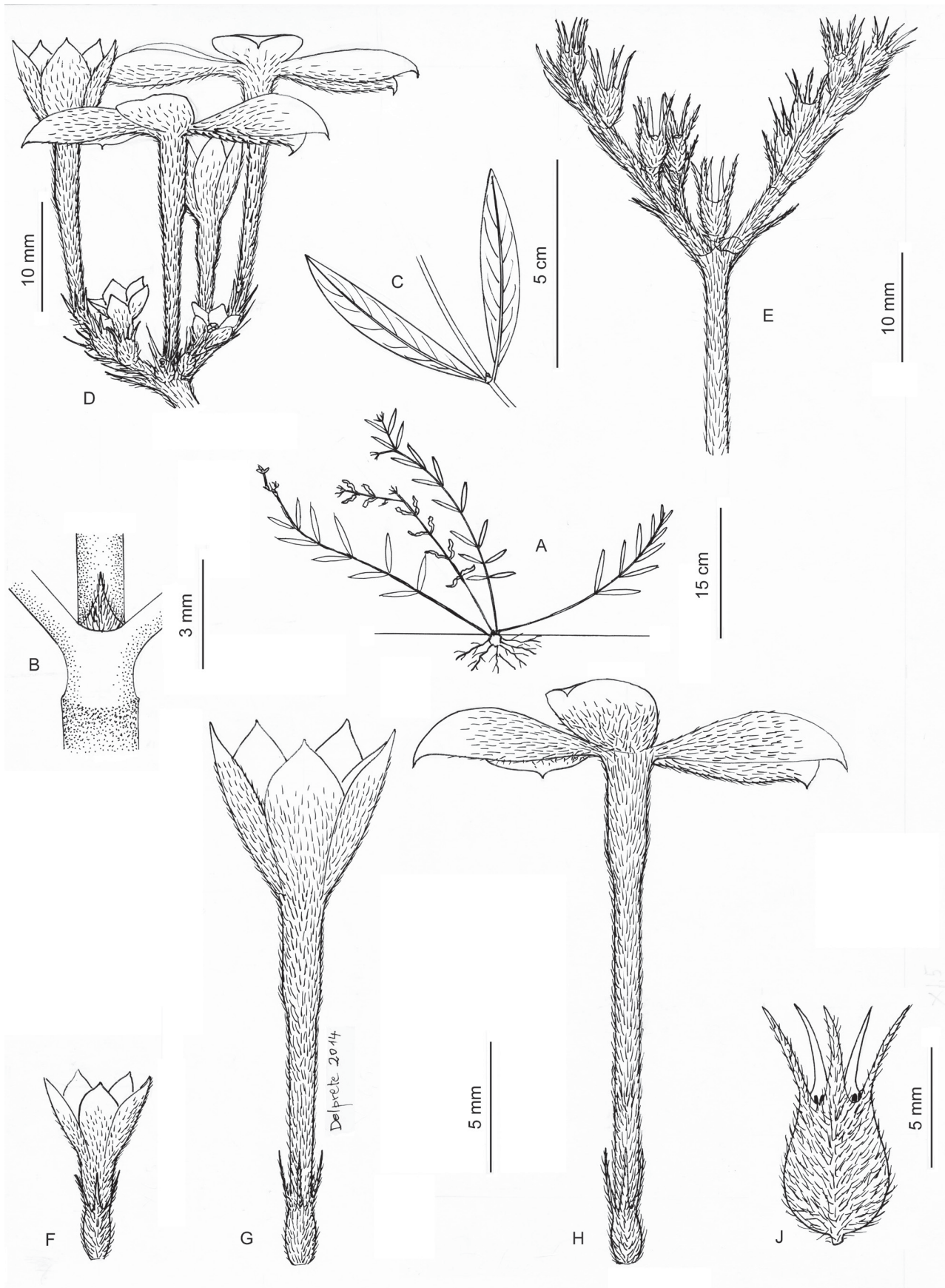


FIGURE 2. *Sipaneopsis maguirei*. **A.** Habit. **B.** Node with stipule. **C.** Portion of a stem with a leaf pair. **D.** Inflorescence with flowers in different developmental stages. **E.** Infructescence with fully expanded branches. **F.** Flower at initial stage of anthesis. **G.** Flower at intermediate stage of anthesis. **H.** Flower at final stage of anthesis. **J.** Fruit. Drawn by Piero G. Delprete from P.G. Delprete, A.C. Araujo & L. Alvarez 7452.

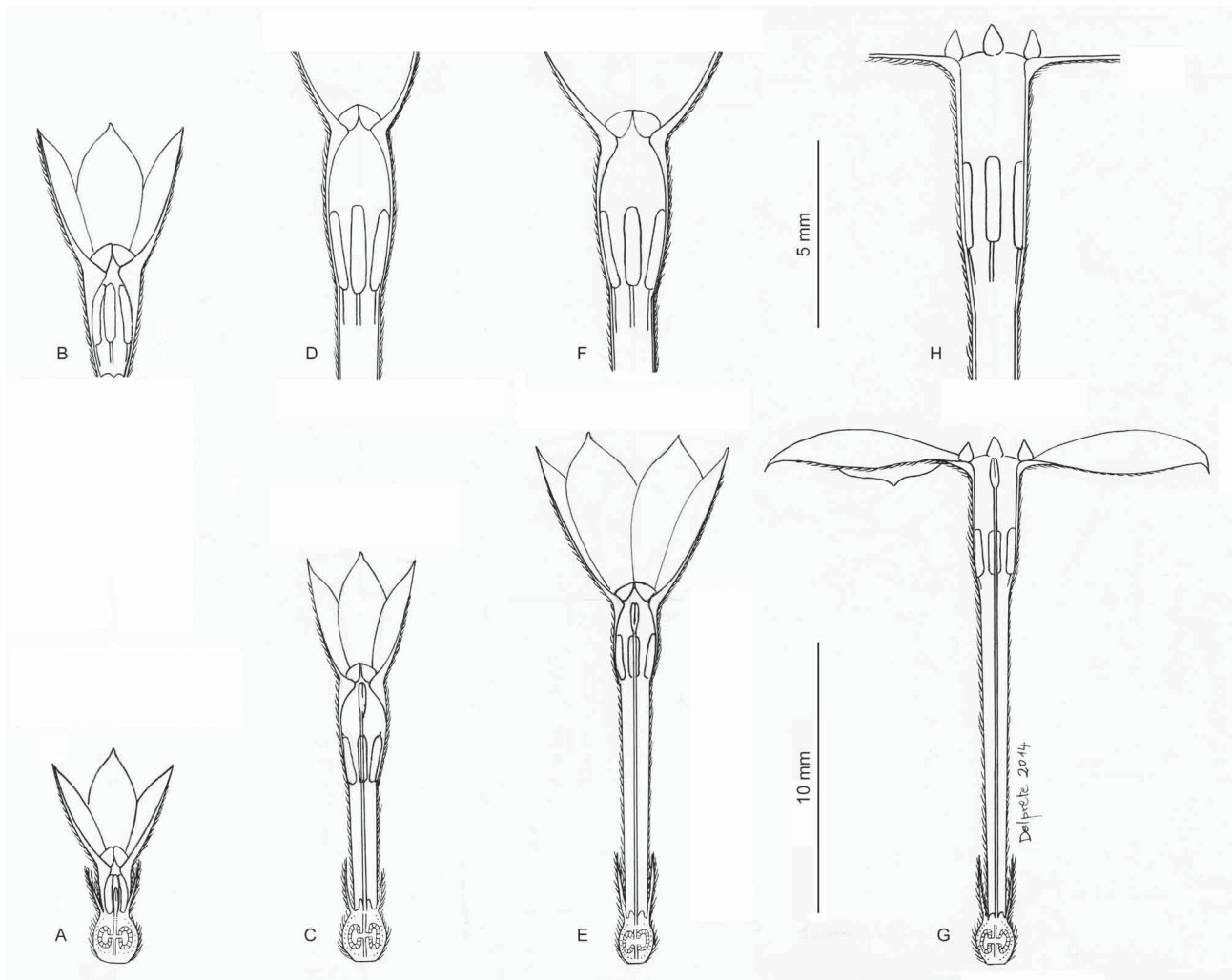


FIGURE 3. *Sipaneopsis maguirei*. **A, B.** Flower at initial stage of anthesis, with corolla-lobe basal appendages appressed against each other. **C, D.** Longitudinal section of flower at intermediate stage of anthesis. **C.** Longitudinal section. **D.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages appressed against each other. **E, F.** Longitudinal section of flower at successive intermediate stage of anthesis. **E.** Longitudinal section, with tube and lobes further elongated. **F.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages appressed against each other. **G, H.** Longitudinal section of flower at final stage of anthesis, with mature anthers and style branches not receptive (still appressed to each other), allowing visitors and pollinators to access the corolla tube and nectar disk. **G.** Longitudinal section of flower, with lobes spreading perpendicularly to the tube, and erect appendages not touching each other. **H.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages not touching each other. Drawn by Piero G. Delprete based on field observations, photographs and pickled flowers (voucher *P.G. Delprete, A.C. Araujo & L. Alvarez 7452*).

receptive; on the second day the anthers are no longer releasing pollen, while the stigmatic branches spread apart, are reflexed, and become receptive (pers. obs.). Additional features that can be useful to differentiate *Neobertiera* from *Sipaneopsis* are that in the former the corolla lobes are opened and reflexed only after the corolla tube is completely elongate (as in the rest of the family), while in the latter the lobes are already open (although not fully expanded) before corolla tube elongation, and its peculiar flowering process, which is described above. The differences in flower morphology and process of anthesis between the two genera (which most likely influence their different pollination syndromes) provide a significant set of taxonomic and diagnostic characters that can be used to distinguish them.

The taxonomic significance of the corolla lobe basal appendages of *Sipaneopsis* has sometimes been questioned (e.g., Delprete & Cortés-B. 2004), and became even more dubious when this genus was retrieved as sister taxon with *Neobertiera* in the molecular phylogenies of Delprete & Cortés-B. (2004). However, the corolla lobe appendages of *Sipaneopsis* are here confirmed to represent an important taxonomic and diagnostic character, when associated with the unique process of anthesis of this genus. Observations of pickled specimens using the dissecting microscope revealed that the lobe appendages consist of a triangular structure of the same nature as the corolla lobes (i.e., parenchymatic tissue),

covered by dense tufts of thick hairs, forming tough triangular units. The evolutionary advantage of the peculiar flower morphology and process of anthesis of *Sipaneopsis* remains poorly understood. It was observed only in populations of *S. maguirei* in southern Venezuela, and no observations focusing on potential pollinators were made, therefore, its pollination syndrome remains to be studied. Considering that *Sipaneopsis* is a genus restricted to white-sand savannas located in remote localities of the Amazon basin, this kind of studies are difficult to do. Nevertheless, future trips to these localities are planned, and the unique pollination syndrome of this genus will hopefully be comprehended.

Acknowledgments

I would like to thank Gwenaël Quenette and Juliana Costa da Silva, who helped during field observations, producing digital images, and processing herbarium and pickled specimens of *Neobertiera* from a population growing along the trail to the Bagne des Annamites, French Guiana. Funds for field work in French Guiana, during which I had the occasion to study an additional population of *Neobertiera* in the surroundings of the Camopi village, upper Oyapock River basin, were provided by the LABEX CEBA (Laboratory of Excellence—Center for the Study of Biodiversity in Amazonia; grant managed by the Agence Nationale de la Recherche, ANR-10-LABX-0025); during this expedition, I was accompanied by Guillaume Odonne (CNRS), Damien Davy (CNRS), and Sophie Gonzalez (CAY), who are here acknowledged for help during field work. I also wish to thank Ana Claudia Araujo (K) and Luis Álvarez (TFAV), who helped during field observations and processing herbarium and pickled specimens of *Sipaneopsis maguirei* from a population growing in white-sand savannas in the municipality of San Fernando de Atabapo, State of Amazonas, Venezuela. I am also grateful to the directors and curators of BM, BRG, CAY, COL, F, IAN, L, K, MG, MO, NY, P, RB, U, UB, US and VEN herbaria, for loans of material and/or for providing working space during my visits. Finally, I wish to express my gratitude to the anonymous reviewers and the Associate Editor for their useful comments and valuable corrections.

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Appendix 1. Selected herbarium specimens of *Neobertiera* and *Sipaneopsis* analyzed for this study.

Neobertiera micrantha Delprete (2015: 123): **French Guiana:** Commune de Camopi, Upper Oyapock River Basin, Roche Touatou, S slope of Mont Touatou, 2°57'N, 52°32'W, 120 m, 22 May 1995 (fl, fr), *G. Cremers & J.J. de Granville 14097* (CAY, MO, NY, P, U, US, type).

Neobertiera glomerata Delprete (2015: 124): **French Guiana:** Commune de Montsinery, Route D-5, trail to Bagne des Annamites, ca. 1 km from Route D-5, 4°50'03"N, 52°31'02"W, 10 m, 18 April 2012 (fl), *P.G. Delprete & G. Quenette 11860* (CAY, K, L, MG, MO, NY, P, RB, US, type); loc. cit., 4°50'03"N, 52°31'02"W, 10 m, 19 February 2014 (fl buds), *P.G. Delprete & J.C. da Silva 12293* (CAY, NY, U); Commune de Camopi, near Tampak village, base of Montagne Couronné, 3°10'03"N, 52°32'16"W, 100 m, 25 February 2014 (fl buds), *P.G. Delprete, G. Odonne, D. Davy & S. Gonzalez 12310* (CAY, K, MG, NY, P, US); Route Nationale 2, P.K. 58, 4°35'N, 52°20'W, margin of forest trail, 25 March 1986 (fl), *C. Feuillet 3635* (CAY, MO, P); Montagne Maripa, Route Nationale 2, P.K. 75, 10 May 1979 (fl, fr), *J.J. de Granville 2888* (CAY, U, UB); Commune de Montsinery, along trail between D-5 and Bagne des Annamites, 8 June 2008 (fl), *J.J. de Granville & M. Rome 17592* (CAY, K, MO, P, NY, US).

Neobertiera pakaraimensis Delprete (2015: 126): **Guyana:** Potaro-Siparuni Region, Pakaraima Mountains, Mount Wokomung, across slope to SW 0.5 km from headwaters of Wusupubar Creek, 5°03'N, 59°53'W, 9751125 m, 17 February 1993 (fl), *T.W. Henkel, M. Chin & W. Ryan 1449* (BBS, CAY [2 sheets], MO, U, US, type); Kuyuni-Mazaruni Region, Eping River, 6°00'N, 60°10'W, 120 m, 6 February 1991 (fl), *T.McDowell & A. Stobey 3853* (BRG, CAY, MO, US); Potaro-Siparuni Region, Pakaraima Mountains, upper Ireng watershed, Sukabi River, E branch to Kukunang Falls, 5°07'N, 59°57'W, 720 m, 21 October 1994 (fl), *P. Mutchnick, T.W. Henkel & R. Williams 156* (MO, US).

Neobertiera gracilis Wernham (1917: 169): **Guyana:** Macouria River, November 1886 (fl), *G. S. Jenman 2388* (BM, K, type); Rockstone, June 1904 (fl, fr), *Bartlett A.B. 8547* (K, L); Moraballi Creek, Essequibo River, 3 October 1938 (fl–fr), *Forest Department of British Guiana F120 (Record N. 2729)* (K [2 sheets]); Potaro River, Amatuk Mountain, 1–2 April 1958 (fl, fr), *V. Graham 193* (K); Potaro River, Garraway Stream, 25 April 1944 (fl, fr), *B. Maguire & D.B. Fanshawe 22964* (F, MO, NY, U, US); Potaro River, below Kaieteur, September–October 1881, *G.S. Jenman 945* (K); Demerara River, March 1898 (fl), *G.S. Jenman 7338* (K); Potaro-Siparuni Region, from camp on Elizabeth Creek, ca. 1 km along rd to NE and along creek, 5°18'N, 59°05'W, 120 m, 16 October 1990 (fl, fr), *T. McDowell & D. Goupal 3571* (MO, US); Essequibo River, Moraballi Creek, near Bartica, near sea level, 14 September 1929 (fl), *N.Y. Sandwith 256* (K, NY, U); Basin of Essequibo River, Head Falls, 67°N, 20 September 1937 (fl), *A.C. Smith 2106* (F, NY, U, US); ca. 83 miles, Bartica–Potaro rd., Amatuk Fall, 26 August 1933 (fl, fr), *T.G. Tutin 602* (BM, K, US). **Suriname:** Wilhelmina Geberte, forested lower slopes of Frederik Top, 3.5 km SSE of Juliana Top, 3°36'41"N, 56°30'34"W, 500 m, 20 August 1963 (fr), *H.S. Irwin, G.T. Prance, T.R. Soderstrom & N. Holmgren 54918* (MO, NY, U); Wilhelmina Mountains, top 1059, SE of Julianatop, 900 m, 24 July 1963 (fl), *J.P. Schultz & J.G. Wessels Boer s.n. (LBB 10223)* (BBS [2 sheets], MO, U); Wilhelmina Mountains, nameless top SE of camp km 14 in line to Lucie River, 700 m, 24 July 1963 (fl), *J.P. Schultz s.n. (LBB 10471)* (BBS, K, NY, U).

Sipaneopsis cururuensis Kirkbride (1980: 113): **Brazil.** Pará: Upper Tapajós River Basin, Cururu River, Erereri [River, ca. 7°37'S, 57°37'W], 8 February 1960 (fl, fr), *W.A. Egler & Raimundo 1265* (IAN, MG, US, type).

Sipaneopsis foldatsii Steyermark (1967: 288): **Venezuela:** Amazonas: Santa Cruz, Río Atabapo, mouth of Río Atacavi, 4 September 1960 (fl, fr), *E. Foldats 3678* (VEN, holotype); loc. cit., 4 October 1960 (fl, fr), *E. Foldats 3692* (VEN); loc. cit., 9 October 1960 (fl, fr), *E. Foldats 3830* (VEN).

Sipaneopsis huberi Steyermark (1984: 37). **Venezuela:** Amazonas: Depto. Río Negro, granitic dome, left margin of Río Siapa medio, ca. 15 km E of Punta N of Cerro Aracamuni, 1°41'N, 65°41'W, 350 m, 6 February 1981 (fl, fr), *O. Huber & E. Medina 5786* (MO, NY, U, US, VEN, type); Depto. Río Negro, hilly savanna in central portion of plateau of Serranía del Vinilla, ca. 20 km SW of Mavaca, 2°26'N, 65°20'W, 420 m, 13 June 1981 (fl, fr), *O. Huber 6192* (COL, VEN).

Sipaneopsis maguirei Steyermark (1967: 287): **Venezuela** [“Colombia”]: Amazonas: Río Atabapo, between San Fernando de Atabapo and Caño Temi, Cacagual Savanna, 135 m, 13 September 1957 (fl, fr), *B. Maguire, J.J. Wurdack*

& *W.M. Keith 41438* (NY, type); Depto. Atabapo, SE bank of the middle part of Caño Yagua at Cucurbital de Yagua, 3°36'N, 66°34'W, 120 m, 8 May 1979 (fl), *G. Davidse, O. Huber & S.S. Tillett 17391* (MO, US); Mun. San Fernando de Atabapo, Comunidad Indígena de Minicia Nuevo, 3°55'N, 67°26'W, 120 m, 7 January 2001 (fl, imm fr), *P.G. Delprete, A.C. Araujo & L. Alvarez 7451* (CAY, NY, TFAV, VEN); loc. cit., *P.G. Delprete, A.C. Araujo & L. Alvarez 7452* (CAY, MO, NY, TFAV, VEN); loc. cit., *P.G. Delprete, A.C. Araujo & L. Alvarez 7453* (CAY, MG, TFAV, VEN); Río Orinoco, Savanna N. 3 at NW base of Cerro Yapacana, 130 m, 1 January 1951 (fl), *B. Maguire, R.S. Cowan & J.J. Wurdack 30549* (NY, US); Río Guainía, Sabana El Venado, on L bank of Caño Pimichín, 120140 m, 23 November 1963 (fl), *B. Maguire, J.J. Wurdack & G. Bunting 36353* (NY); Río Guainía, Sabana El Venado, on L bank of Caño Pimichín, 140 m, 14 April 1953 (fl), *B. Maguire & J.J. Wurdack 35564* (NY).

Sipaneopsis morichensis Steyermark (1967: 286): **Venezuela:** Amazonas: Cerro Moriche, Río Ventuari, 800 m, 14 January 1951 (fl), *B. Maguire, R.S. Cowan & J.J. Wurdack 30878* (NY MICH MO, NY, VEN, type); Cerro Moriche, frequent in E slope, 300800 m, 13 January 1951 (fl), *B. Maguire, R.S. Cowan & J.J. Wurdack 30868* (NY, US, VEN).

Sipaneopsis pacimoniensis Steyermark (1967: 289): **Venezuela:** Amazonas: Infrequent in savanna on R bank of Río Pacimoni, 50 km above mouth, 100140 m, 7 February 1954 (fl), *B. Maguire, J.J. Wurdack & G. Bunting 37570* (NY, type).

Sipaneopsis rupicola (R. Spruce ex K. Schumann in K. Schumann 1889: 222) Steyermark (1967: 285): **Colombia:** Vaupes: Cerro de Chiribiquete, near margin of Río Macaya, 17 January 1944 (fl), *G. Gutiérrez & R.E. Schultes 654* (US); Mitú and vicinity, lower Río Kubiyú, 1 July 1976 (fl), *J.L. Zarucchi & M.J. Balick 1796* (US). **Venezuela:** Amazonas: “ad flumina Casiquiare, Vasiva et Pacimoni,” s.d. [1853-1854] (fl), *R. Spruce 3392* (BR, C, E, G, GH, L, LD, NY, RB, type); Guainía, Caño San Miguel, near mouth of Caño Ichana, 127 m, 26 March 1942 (fl), *Ll. Williams 14897* (US); Caño San Miguel, between Limoncito and Caño Ikebenie (ca. 70 river km from mouth), 120–130 m, 29 June 1959 (fl, fr) *J.J. Wurdack & L.S. Adderley 43253* (UB).