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The identity of the long-overlooked *Ronabea morindoides* and *Patabea tenuiflora*, synonymous with a species of *Appunia* (Rubiaceae)

Piero G. Delprete, Charlotte M. Taylor & Timothy D. McDowell

Abstract

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The identity of *Ronabea morindoides* A. Rich. has long been unclear and is here investigated. Two sheets of original material corresponding to this name are deposited in the General Herbarium of the National Museum of Natural History of Paris (P), and represent a mixed collection; one part of this material corresponds better with the description of this taxon and is more unambiguously identifiable, and is here designated the lectotype. With this typification, *Ronabea morindoides* represents a species of *Appunia* Hook. f. The identity of *Patabea tenuiflora* DC. has also remained uncertain since its description and is here clarified by studying the holotype in the Candolle Herbarium (G-DC); this is an additional synonym of *R. morindoides*. Taxonomic review of this group in the Guianas also finds that *Ronabea morindoides* is an older name for *Appunia brachycalyx* (Bremek.) Steyerl. and *Appunia surinamensis* Bremek. (*Morindeae*). Therefore, the new combination *Appunia morindoides* (A. Rich.) Delprete, C.M. Taylor & T. McDowell is here published.

Keywords

RUBIACEAE – *Lasiantheae* – *Morindeae* – *Palicoureeae* – *Psychotriaceae* – *Appunia* – *Morinda* – *Patabea* – *Psychotria* – French Guiana – Surinam – New Combination

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Introduction

The identity of *Ronabea* Aubl. has been incompletely known until recently, due to diagnosis of this genus only by several common conditions in *Rubiaceae*, poor documentation of the species described in it, the occurrence of most of its described species in regions that are not well known floristically, and changing circumscriptions of the *Rubiaceae* genera and tribes that share the characters of *Ronabea*. The type of this genus, *R. latifolia* Aubl., has small white flowers with valvate corolla lobes and fleshy, drupaceous fruits with two plano-convex pyrenes, and was long included in *Psychotria* L. when that genus was broadly circumscribed (e.g., LEMÉE, 1954; STEYERMARK, 1972) or considered a closely related genus in the tribe *Psychotrieae* (BREMEKAMP, 1934a, 1934b). In recent years that broad circumscription of *Psychotria* was found to be polyphyletic (NEPOKROEFF et al., 1999; RAZAFIMANDIMBISON et al., 2014), and many of those species are now included in other genera of various tribes. The three core species of *Ronabea* are now treated as a genus in the tribe *Lasiantheae*, but the other seven species described in *Ronabea* are not closely related to those three. The identities of six of those other species has become clear in recent decades (see below), and here we clarify the identity of the seventh species.

Three clearly delimited Neotropical species that agree in their characters with the type of *Ronabea* were studied by TAYLOR (2004), who separated them from *Psychotria* based on their persistent, triangular, unlobed, interpetiolar stipules, axillary inflorescences, and oily rather than starchy endosperm. Before this, the identity of *Ronabea* was so broadly diagnosed that it included a heterogeneous group of both Neotropical and Paleotropical species, which are now treated in genera of several tribes. As the systematics of the *Rubiaceae* became better resolved with the application of molecular data, *Ronabea* s.str. was associated with genera that were then separated in *Morindeae*, such as *Morinda* L. and *Lasianthus* Jack. Further study then separated *Lasianthus* into a new tribe (BREMER & MANEN, 2000), and both morphological and molecular data (PIESSCHAERT et al., 2000; SMEDMARK et al., 2014) found *Ronabea*'s relationships there. Smedmark et al. found *Ronabea* most closely related to the African *Trichostachys* Hook. f. and *Saldinia* Bremek. of the Indian Ocean based on molecular data, and they found this clade sister to *Lasianthus*. These four genera today comprise the pantropical tribe *Lasiantheae* (SMEDMARK et al., 2014).

Several other species described in *Ronabea* do not correspond to either *Ronabea* or *Psychotria* in our modern taxonomy. The circumscription of *Ronabea* was markedly expanded by RICHARD (1830: 503), who included here species related to *Psychotria* but separated from that genus based on their abaxially smooth pyrenes. This pyrene form, however, is a common condition in many genera of *Rubiaceae*, and has not yet been shown to be consistent within lineages. Thus, the species

with this character are a heterogeneous group, so Richard's *Ronabea* does not correspond to any of our modern genera. The identities of the Paleotropical species named in *Ronabea*, from southeastern Asia and New Zealand, have been clarified by regional studies to belong to *Canthium* Lam. (*Vanguerieae*) (e.g., MERRILL, 1905) and *Coprosma* J.R. Forst. & G. Forst. (*Anthospermeae*) (e.g., ALLAN, 1961; CONNOR & EDGAR, 1987). The other Neotropical species correspond variously to two genera of *Palicoureeae*, *Palicourea* Aubl. (e.g., *Palicourea didymocarpus* (A. Rich.) Griseb.; TAYLOR, 2014; DELPRETE & KIRKBRIDE, 2016), and *Notopleura* (Benth.) Bremek. (TAYLOR, 2004), except for one name, *Ronabea morindoides* A. Rich. Its identity has never been clear.

The Identity of *Ronabea morindoides*

In the protologue of *Ronabea morindoides*, RICHARD (1830) described this plant as having “floribus minimis in capitula pisiformia pedunculata plura terminalia congestis” [flowers very small, congested in several pedunculate, pea-shaped, terminal capitula]. The distinctive characters in the protologue, according to our taxonomy, are the terminal inflorescences with relatively small flowers in pedunculate heads and “pea-shaped” fruits, together with Richard's diagnostic genus character of abaxially smooth pyrenes. In the description of *R. morindoides*, he also noted that the seeds are “externè et inequaliter rimoso-cerebriformibus [“cerebrose” or rugulose]”, and this contrasts with the smooth “nutlets” or pyrenes that Richard used to diagnose the genus, so he clearly regarded these as distinct structures. His characterization of these seeds appears to describe ruminated endosperm, which is found in occasional species of various genera of *Rubiaceae*, in various tribes, and has been found by recent authors to vary within species and among the species of well-supported lineages in several genera (e.g., TAYLOR, 2020).

Two specimens deposited in P correspond with original material of *Ronabea morindoides*, and these are a mixed collection with two different *Rubiaceae* species. Both of these specimens have old inflorescences from which the corollas have recently fallen, and one or more mature fruits. These inflorescences are borne at the stem apex and have 5 to 15 flowers that are subsessile in subcapitate, pedunculate groups, and one or a few mature fruits are also present on each specimen. These two specimens correspond to two different species, belonging to different genera, in today's taxonomy. Both of these species have the petiolate leaves, bilocular ovaries, small white corollas with valvate lobes, and drupaceous fruits with abaxially convex and smooth pyrenes that Richard used to diagnose his *Ronabea*. One species in the type material has solitary terminal inflorescences, and the other species has variously solitary to grouped, terminal and leaf-opposed inflorescences. The two species represented in the type material also differ

in their ovary arrangements: one has bilocular ovaries with two ovules, which develop into fruits with two plano-convex pyrenes (*Eumachia* DC.), while the other has bilocular ovaries with septate locules and four ovules, which commonly develop into fruits with four quarter-spherical pyrenes (*Appunia* Hook. f.). However, in *Appunia* the four ovules might not develop into four pyrenes, so some of the fruits might have only two or three pyrenes with the residual, undeveloped ovule(s) still present. The description in the protologue applies fairly well to both of the species represented in the type material, so it appears to have been based on this mixed collection that was not fully studied. In particular, the fruits of both of the species in the type material were probably not dissected by Richard.

One of these sheets, [P00837123], has two branches with solitary, terminal, capitate inflorescences and two labels. One label is handwritten, and bears the heading in red ink in A. Richard's hand: "L. Cl. Richard. Herbarium Guyanensis Antillanum" followed by "Psychotria ? morindoides. capitula pedunculata; floribus sessilibus congestis. – Guy." The other label, which is affixed with a red "ISOTYPE" tag, has the printed text "HERB. MUS. PARIS. Louis Claude Richard. Herbarium Guyanensi-Antillanum" and "Ronabea morindoides Richard" handwritten in black ballpoint pen. The specimens mounted on this first sheet all correspond in our taxonomy to *Eumachia guianensis* (Bremek.) Delprete & J.H. Kirkbr. (DELPRETE & KIRKBRIDE, 2015; RAZAFIMANDIMBISON et al., 2014; TAYLOR et al., 2017). This species has bilocular ovaries that are not septate and fruits with two pyrenes, so these branches appear to correspond to the protologue description of the fruits.

The other sheet at P [P00837122] (Fig. 1) has three branches, corresponding to two different species. On the upper portion of the sheet is a short branch with two leaves (labeled A in Fig. 1), which also corresponds to *Eumachia guianensis*. On the lower portion of the sheet are a large branch with numerous large leaves and inflorescences and a short branch with one leaf (labeled B and C in Fig. 1); both of these have inflorescences that are grouped at the stem apices, and correspond in our current taxonomy to *Appunia brachycalyx* (Bremek.) Steyerl. (McDowell, in prep.). This second sheet has three labels. The uppermost handwritten label on the lower left says, in Richard's hand, "Ronabea morindoides Nob." in black ink and "scripsit A. Richard" in red ink, and has a red "TYPE" tag placed immediately above it. The lower handwritten label on the lower left says, also in Richard's hand, "Herbarium Richard" in red ink and "Psychotria ? morindoides. – Guy." in black ink. And, the label on the lower right corner has only the printed text "HERB. MUS. PARIS. Louis Claude Richard. Herbarium Guyanensi-Antillanum". The two lower branches of this specimen, the *A. brachycalyx* material, appear to have a fasciculate group of terminal peduncles, which actually are several solitary, leaf-opposed inflorescences borne on several closely grouped nodes at the stem apex. This

appearance of several pedunculate heads in a terminal inflorescence is consistent with Richard's protologue description of the inflorescence arrangement.

As noted, the characters that Richard used to diagnose *Ronabea* are not unique to this genus, and most or all of them also agree with both *Eumachia* and *Appunia*. Also as noted, the protologue description of *R. morindoides* appears to be based on this mixed collection and does not fully describe or disagree with either specimen. We here conclude that in terms of the observations Richard made of these plants, the protologue description of *R. morindoides* more closely matches the lower branches on the second, *Appunia* specimen because it has, in our interpretation, the "several terminal capitula" described in the protologue. Descriptions by Richard of other *Rubiaceae* species with solitary terminal inflorescences specify that condition, that the peduncles are solitary, so his protologue here is not a completely accurate description of the consistently solitary inflorescences of the other, *Eumachia* specimen, either. Richard's descriptions are, on the whole, very precise, as seen in the distinction here between pyrenes and seeds. In this case, however, Richard clearly did not carefully examine all the fruits in his material, because the fruits of the *Appunia* material do not agree with the genus description or the other specimen branches in having two pyrenes. Therefore, we conclude that the two lower branches of specimen [P00837122], labeled B and C in Fig. 1, better correspond to the protologue description, and we here designate them as the lectotype of *R. morindoides*. Accordingly, we here make the corresponding new combination in *Appunia* based on the oldest name for this species.

The Identity of *Patabea tenuiflora*

Another genus that has at times included a heterogeneous group of species according to our current systematic understanding is *Patabea* Aubl., and the identities of some of its names have also been unclear. As to the identity of the genus, AUBLET (1775) described *Patabea* with a single species, *P. coccinea* Aubl., based on material that he collected in French Guiana. SANDWITH (1937, 1949, 1963) and STEYERMARK (1967) treated *P. coccinea* as a synonym of *Ixora davisii* Sandwith, a decision with which we concur (the epithet "*coccinea*" was previously used for *Ixora coccinea* L. so Aublet's name cannot be transferred to *Ixora*). More details about the taxonomic history and lectotypification of *P. coccinea* are available in DELPRETE (2015).

CANDOLLE (1830: 537–538) expanded the delimitation of *Patabea* with two additional species, *P. alba* Kunth [= *Palicourea justicifolia* (Rudge) Delprete & J.H. Kirkbr.; DELPRETE & KIRKBRIDE, 2016], and *P. tenuiflora* DC., of unclear identity. CANDOLLE (1830: 538) described the latter as having "foliis oblongis utriusque acutis membranaceis, stipulis lanceolato-linearibus 4 basi connatis, capitulis aliis sessilibus aliis pedunculatis,



Fig. 1. – Type material of *Ronabea morindoides* A. Rich. **A.** *Eumachia guianensis* (Bremek.) Delprete & J.H. Kirkbr.; **B–C.** Lectotype of *Ronabea morindoides* A. Rich. (\equiv *Appunia morindoides* (A. Rich.) Delprete, C.M. Taylor & T. McDowell). [P00837122; © Muséum national d'Histoire naturelle, Paris]

fauce cor. nudâ, lobis linearibus tubo gracili, limbo calycis truncato [...] Folia 5–6 poll. longa, 1 ½ lata” [the leaves oblong, 5–6 inches long, 1.5 inches wide, membranaceous, acute at the apex; stipules lanceolate-linear, connate at the base; inflorescence capitate, sessile or pedunculate; calyx truncate; corolla glabrous at the mouth, with a narrow tube and linear lobes]. The fruit was unknown to him, as he only had a flowering specimen. In the original publication, he also noted that it was collected by Patris in French Guiana. After its description the identity of *P. tenuiflora* remained unclear, and this name was not even cited by specialists working later on the *Rubiaceae* of the Guiana Shield (e.g., Bremekamp, Standley, Steyermark). The single specimen of *P. tenuiflora* at G-DC [G00667064] (Fig. 2), is apparently the only original material corresponding to this name. It has two labels handwritten by A.P. de Candolle, “*Patabea tenuiflora* DC.” and “*rubiacées, Cayenne*”. Candolle wrote “Cayenne” on the labels of all the specimens collected by Patris in French Guiana, although they were actually collected in several different localities (CANDOLLE, 2004: 191; CHAÏA, 1975). This specimen has a third handwritten label, probably written by Patris, with the text “N° 28, diar. 7^{bris} 1785, Tetrandia monogynia, did. descrip. e delineatam”. The portion “N° 28, diar. 7^{bris} 1785” alludes to Patris’s unpublished travel diary and the date of September 1785. This specimen in Candolle’s own herbarium, [G00667064] and annotated by him, was collected in French Guiana by Patris in September 1785 and is the holotype of *P. tenuiflora*. This plant corresponds entirely with the protologue description of this species. The single branch has the stem minutely puberulent to glabrate and leaf-opposed inflorescences. It has four pedunculate, shortly branched inflorescences at the lower node, and a subsessile, capitate inflorescence at the terminal node. The corolla lobes have abaxial corniform appendages, which are clearly visible in the flower buds of the specimen. This plant also agrees in our taxonomy with *Appunia brachycalyx*, and represent an additional synonym for it. The two newly discovered names for *A. brachycalyx*, *P. tenuiflora* and *R. morindoides*, were published in the same volume of Candolle’s *Prodromus* (CANDOLLE, 1830) so they have priority over names currently being used and have equal nomenclatural priority with each other. However, the binomial *Appunia tenuiflora* (Benth.) Jacks. & Hook. f. (JACKSON & HOOKER, 1893: 166) has already been published for a different species, so the name *Ronabea morindoides* and its new combination *Appunia morindoides* are the names to be used.

The circumscription of *Appunia morindoides*

The type of *Ronabea morindoides* agrees with specimens that have been included in *Appunia brachycalyx*, but that species is circumscribed differently here than by previous authors. *Appunia brachycalyx* and *A. surinamensis* (Bremek.) Steyermark.

have not been studied in detail since Bremekamp’s descriptions of them. STEYERMARK’S (1967) review of these names was part of a general survey for species such as these that were not found in his flora area, not a detailed evaluation, and his later treatment (STEYERMARK, 1972) was only a list of the species occurring in the Guiana Shield that he transferred to *Morinda*. *Appunia* has recently been treated as a monophyletic group distinct from *Morinda* based on molecular phylogenies (RAZAFIMANDIMBISON et al., 2009) and recognizable by its flowers free (i.e., ovaries not fused) and congested, style lobes club-shaped, and fruits simple and free; while *Morinda* can be distinguished by its flowers basally or completely fused, style obtuse and capitate or shortly bifid, and syncarpous fruits (RAZAFIMANDIMBISON et al., 2009).

Appunia brachycalyx and *A. surinamensis* were first described by BREMEKAMP (1934a) in his newly separated genus *Bellynckxia* Bremek. That genus was distinguished by leaf-opposed inflorescences derived in the terminal position, subtended by one leaf, or subtended by three leaves forming a false whorl due to the undeveloped final internode. These inflorescences may appear axillary due to the reiteration of an axillary branch present at the node just below the inflorescence (Fig. 3). Subsequent authors included *Bellynckxia* species in *Morinda* (STEYERMARK, 1972; TAYLOR & STEYERMARK, 2004) or *Appunia* (STEYERMARK, 1967; LORENCE, 2012). Bremekamp’s *B. brachycalyx* and *B. surinamensis* were each described on the basis of a single collection. He distinguished them by several floral and vegetative characters: in *B. brachycalyx* a calyx tube 0.2 mm long (vs. 1–2 mm long in *B. surinamensis*), four (vs. five) corolla lobes, the presence of one or two sessile flowers at the base of the peduncle(s) of the subcapitate inflorescences (vs. sessile flowers absent in *B. surinamensis*), shorter petioles and leaf blades similar in size (petioles to 2 cm long and blades 12–18 × 3.2–5.5 cm in *B. brachycalyx* vs. petioles 3–5 mm long and blades 11–15 × 3.5–4 cm in *B. surinamensis*), and usually puberulent stems and leaf undersides (vs. glabrous in *B. surinamensis*).

The examination of additional specimens of both of Bremekamp’s species for the *Flora of the Guianas* project (McDowell, in prep.; Delprete, pers. obs.) has shown that all the characters used to separate these species are either variable within the individual species or continuous between them. The sessile flowers at the peduncle bases are not present on the majority of the specimens otherwise assigned to *A. brachycalyx*; some specimens that otherwise agree with *A. brachycalyx* have 5-merous corollas; leaf size variation between Bremekamp’s two species is now documented to be continuous; and there is variation in the development of the stem and leaf pubescence, from pubescent to glabrous, in plants that otherwise agree with *A. surinamensis*. Variation in traits such as flower merosity and pubescence is not unusual within species of *Appunia*, so distinguishing species by these characters is problematic; for

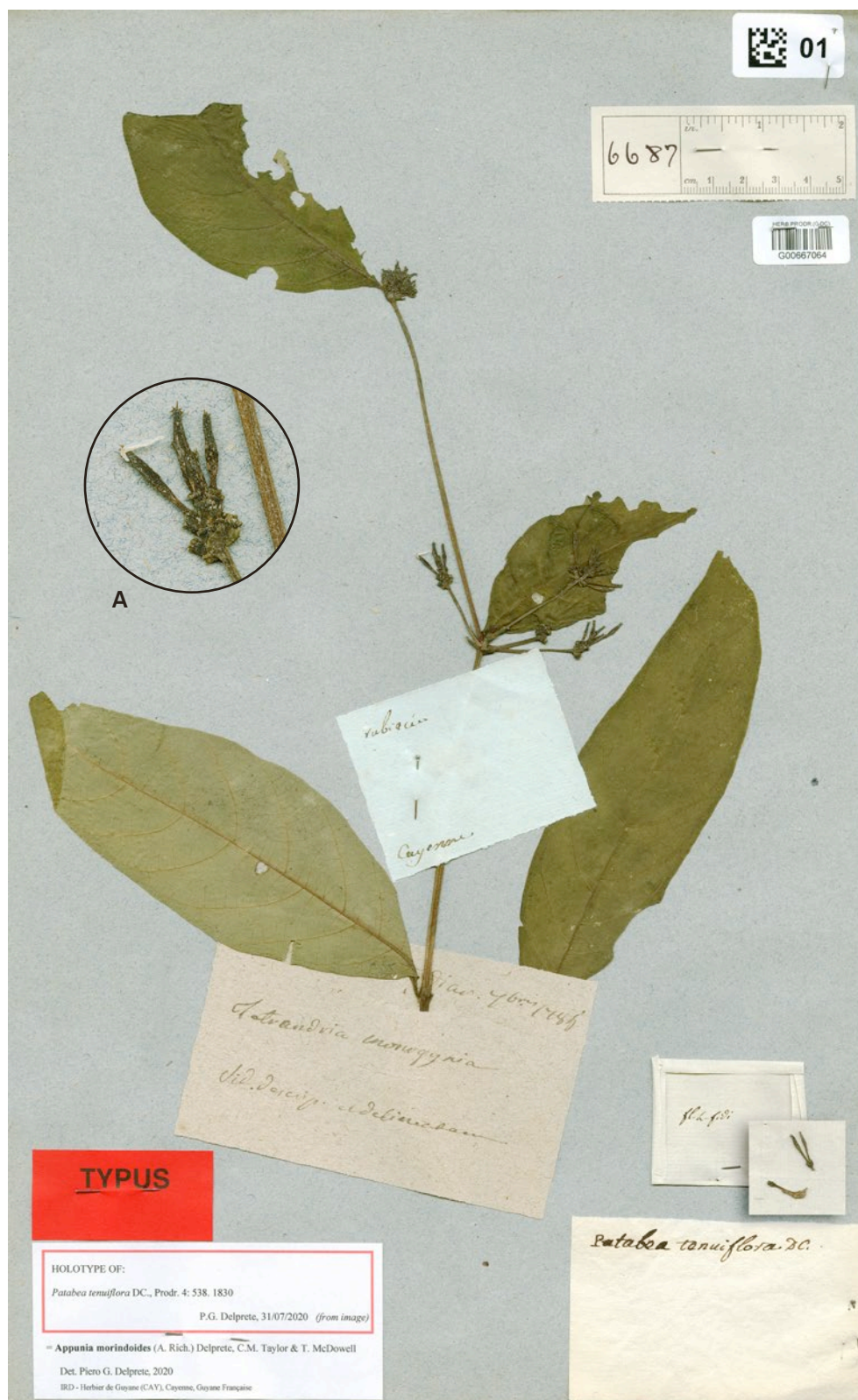


Fig. 2. – Holotype of *Patabea tenuiflora* DC. A. Detail of flower buds with abaxial corniform appendages.
[G–DC: G00667064]



Fig. 3. – *Appunia morindoides* (A. Rich.) Delprete, C.M. Taylor & T. McDowell. **A.** Branchlet with inflorescence; **B.** Stem closeup, showing distalmost nodes with stipules; **C.** Inflorescence with flower buds, being visited by small ants; **D.** Inflorescence with most corollas fallen off, showing calyx limbs and disks; **E.** Open flower (note corolla lobes with apical appendices, both galeate adaxial appendages and abaxial corniform appendages); **F.** Infructescence with ripe fruits. [**A–C, E:** trail to Savane-Roche Corail, Kourou, French Guiana; **D:** trail Grand Boeuf Mort, Saül, French Guiana; **F:** Montagne des Singes, French Guiana] [Photos: Hervé Galliffet]

example, in *A. debilis*, corollas may be 4-, 5- or 6-lobed, and in *A. tenuiflora* the stems and leaves are puberulent or glabrous.

BREMEKAMP (1934a, 1934b) also noted a difference in stamen insertion, style length, and shape of style lobes between his two new species of *Bellynckxia*, with the stamens inserted in the distal portion of the corolla tube and capitate style lobes in *B. surinamensis*, in contrast to the stamens inserted in the basal portion of the corolla tube and linear-spathulate style lobes in *B. brachycalyx*. These traits have been difficult to verify in herbarium specimens, but the differences he reported between these species are in any case consistent with differences between the morphs of distylous flowers, as known in other species of *Appunia*. In this genus, long-styled flowers have stamens inserted at the basal portion of corolla tube and the stigmatic lobes subcapitate, while short-styled flowers have stamens inserted at the distal portion of the corolla tube and the stigmatic lobes more elongated. Hence, we conclude that the type of *B. surinamensis* is a short-styled form, and the type of *B. brachycalyx* is a long-styled form of *Appunia morindoides* (see below).

Taxonomy

Appunia morindoides (A. Rich.) Delprete, C.M. Taylor & T. McDowell, **comb. nov.** (Fig. 3).

- = *Ronabea morindoides* A. Rich. in DC., Prodr. 4: 504. 1830. = *Psychotria morindoides* (A. Rich.) Lemée, Fl. Guyane Franç. 3: 564. 1954 [nom. illeg., non Hutch. 1916].

Lectotypus (designated here): FRENCH GUIANA: *sine loco*, s.d. [1781–1785], L.C.M. Richard s.n. (P [P00837122, excl. the small branch at the top of the sheet] image!) (Fig. 1, branches labeled B and C).

- = *Patabea tenuiflora* DC., Prodr. 4: 538. 1830. = *Cephaelis tenuiflora* (DC.) D. Dietr., Syn. Pl. 1: 774. 1839. = *Ixora tenuiflora* (DC.) Lemée, Fl. Guyane Franç. 3: 536. 1954 [non *Appunia tenuiflora* (Benth.) Jacks. & Hook. f. 1893], **syn. nov.** **Holotypus:** FRENCH GUIANA: “Cayenne”, IX.1785, *Patris s.n.* (G-DC [G00667064]!) (Fig. 2).
- = *Bellynckxia brachycalyx* Bremek. in Recueil Trav. Bot. Néerl. 31: 277. 1934. = *Appunia brachycalyx* (Bremek.) Steyererm. in Mem. New York Bot. Gard. 17: 359. 1967. = *Morinda brachycalyx* (Bremek.) Steyererm. in Mem. New York Bot. Gard. 23: 385. 1972, **syn. nov.** **Holotypus:** SURINAME: Emma Range, 15.III.1922, *Gonggrijp & Stael* 5679 (U [U0006082]!).
- = *Bellynckxia surinamensis* Bremek. in Rec. Trav. Bot. Neerl. 31: 276. 1934. = *Appunia surinamensis* (Bremek.) Steyererm. in Mem. New York Bot. Gard. 17: 359. 1967. = *Morinda surinamensis* (Bremek.) Steyererm. in

Mem. New York Bot. Gard. 23: 386. 1972, **syn. nov.** **Holotypus:** SURINAME: Para, II–IV.1844, *Kappler* 1453 (U [U0006085]!; iso-: MO-124295!, P [P04579957]!, S-S05-1569!).

Habitat and Distribution. – This species is mostly found in the Guianas, northeastern South America, in primary and secondary moist forests, on lateritic and brown sand soils, at 50–700 m elevation. It is also known by a few collections in Amazonian Brazil, in the states of Amapá, Pará, Mato Grosso, and Acre.

Notes. – A full description, habitat, and range of this species will be presented in the forthcoming *Appunia* treatment (McDowell, in prep.) of the *Flora of the Guianas Rubiaceae* (Delprete et al., in prep.). Selected additional information about *Ronabea* and *Appunia* is available in the RUBIACEAE PROJECT (2020).

Appunia morindoides is recognized by its inflorescences that are leaf-opposed, which develop on distal nodes with one opposed leaf, or with three leaves forming a false whorl due to the extremely reduced final internode (Fig. 3A). The inflorescences may also appear to be axillary (Fig. 3A), due to reiteration of the corresponding axillary branch of the same node, and are often present at alternate nodes, resulting in branches with 2–6(–10) peduncles present at the distal nodes. Each peduncle bears a head of (2–)5–9(–12) flowers, and may have one (occasionally two) sessile or subsessile flower at the base (Fig. 3C–D). Sessile flowers at the base of the peduncle may also rarely occur in *A. tenuiflora* (Benth.) Jacks. & Hook. f. and other *Appunia* species occurring in the Guianas.

The stipules of *Appunia morindoides* are 2–7(–10) mm long, usually longer than in most other species of the genus, puberulent, and entire (Fig. 3B) or bifid at apex. Its leaf blades are often relatively large, (5–)10–15(–30) × (1.5–)3–7(–10) cm, and membranaceous to chartaceous (Fig. 3A), while blades are usually smaller, and papyraceous to subcoriaceous in most other species of the genus. *Appunia morindoides* is similar to *A. calycina* (Benth.) Sandwith, but the latter can easily be differentiated by its conspicuously larger calyx, which is funnelliform to broadly cupular with the free portion of the tube 3–6 mm long and the 5 rounded lobes about 2 mm long; also its calyx is pubescent outside with sparse, stiff hairs (vs. a very short calyx tube, 0.2 mm long that is entire or sometimes denticulate and minutely puberulent or glabrous outside in *A. morindoides*). In *A. calycina* the funnelliform calyx continues to expand after anthesis and forms a conspicuous crown above the fruit, which is lacking in *A. morindoides*.

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