Nomenclature and taxonomy of *Croton glabellus* L. (*Euphorbiaceae*), a widespread Caribbean species

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Abstract The application of the names *Croton glabellus*, *C. lucidus*, and *Phyllanthus glabellus* has been confusing since the earliest publications that used them. After a thorough review of these publications and corresponding herbarium specimens, we clarify the nomenclatural confusion surrounding these names and their taxonomy. We identify a new name, *Phyllanthus glabellus* Fawc. & Rendle, that was inadvertently made. We make the new combination *Croton glabellus* subsp. *polytrichus*, and we designate lectotypes for *Astrocasia tremula*, *Croton* subsect. *Astraeopsis*, *C. glandulifer*, *C. lucidus* var. *polytrichus*, and *C. spicatus*.

Keywords *Astrocasia tremula*; *Croton glabellus*; *Croton lucidus*; *Euphorbiaceae*; nomenclature; *Phyllanthus glabellus*; taxonomy

■ INTRODUCTION

Croton glabellus L., *C. lucidus* L., and *C. nitens* Sw. (*Euphorbiaceae*) are widely used names applied to certain widespread Caribbean species of *Croton*. A study of historical specimens and the literature reveals problems with the application of these names. The identity of *Croton glabellus* (Fig. 1A) has been unclear since it was first published by Linnaeus (1759a). The name *Croton lucidus* has been misapplied to the taxon we treat here as *C. glabellus*, and the name *C. glabellus* has been misapplied to *C. nitens* (Fig. 1B) and *C. schiedeanus* Schltdl., which are both members of the more distantly related *C.* sect. *Eluteria* Griseb. The true *C. lucidus* (Fig. 1C) is a member of *C.* sect. *Adenophylli* Griseb. The annotation "*Croton glabellum*" in Linnaeus's hand on the *Browne 7* (LINN 1140.3) specimen, which is *Astrocasia tremula* (Griseb.) G.L. Webster, has also entangled the name with *Astrocasia* B.L. Rob. & Millsp. (*Phyllanthaceae*). *Croton lucidus*, in the sense of what we now treat as *C. glabellus*, was treated as the type of *Croton* sect. *Astraeopsis* Baill. by Webster (1993), and this section was also recognized by Berry & al. (2005) and in subsequent molecular phylogenetic studies. Van Ee & al. (2011) transferred it as *Croton* (sect. *Barhamia* (Klotzsch) Baill.) subsect. *Astraeopsis* (Baill.) B.W. van Ee. Given the continued use of this name for a subdivison of *Croton*, we seek to clarify its type and correct application.

■ MATERIALS AND METHODS

We examined the original literature and nomenclatural types. We inspected specimens in person, specimen photographs available from JSTOR Plant Science (http://plants.jstor.org), and photographs available online directly from various herbaria. We examined specimens from: A, B, BM, C, F, G, G-BOIS, G-DC, GH, GOET, JE, K, LE, LINN, MA, MICH, MO, NY, P, P-JU, PH, S, TCD, and US.

■ HISTORY

Several of Browne's (1756) seven species of *Croton* have been applied differently by various authors (Table 1). There has been no single, clear, and consistent application of *C. glabellus* and *C. lucidus* (Govaerts & al., 2000), and our goal is to clarify their application according to their nomenclatural types (McNeill & al., 2006: Art. 7.1). Alternatively, to continue the usage of Fawcett & Rendle (1920), which is not consistent with the Linnaean types that they cited but possibly did not examine, it would be necessary to conserve *C. glabellus* and *C. lucidus* with different types, and this would displace the commonly used name *C. nitens*. To continue the usage of Adams (1972), it would be necessary to conserve *C. glabellus*, *C. lucidus*, and *C. eluteria* (L.) W. Wright with different types, *C. nitens* would be displaced, and the application of *C. eluteria* would change. To continue the usage of Webster (1993), it would be necessary to conserve *C. lucidus* with a different type, and *C. glabellus* would be displaced. Neither does rejecting any of these names provide an expedient solution because the problems lie with the changed applications of names, rather than with names blocking other names. For example, if *C. lucidus* were rejected and *C. glabellus* and *C. wilsonii* Griseb. were used instead for the two species that *C. lucidus* has been applied to, it would still be necessary to clarify the application of *C. glabellus* given that it would be a different usage relative to that of Fawcett & Rendle (1920). Rejecting *C. glabellus* would still require that *C. lucidus*

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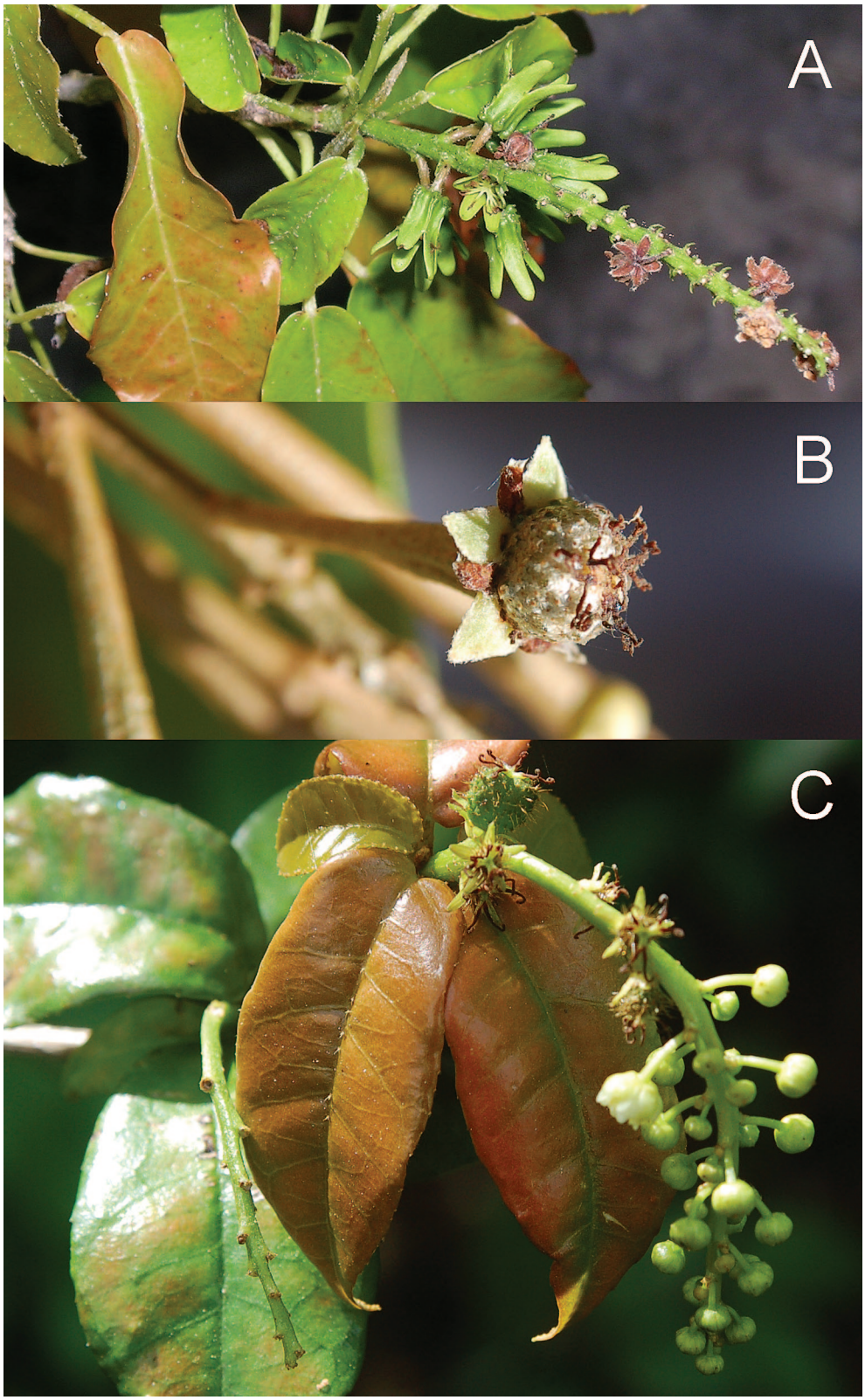

Fig. 1. Flower details of *Croton* species. **A,** *Croton glabellus* L. subsp. *glabellus* showing pistillate flowers with reduplicate-valvate sepals that exceed the mature ovary, no petals, and glandular bracts subtending the staminate flowers; Cuba, *Van Ee 378* (WIS); **B,** *Croton nitens* Sw. showing pistillate flowers with petals and a lepidote ovary; Jamaica, *Van Ee & al. 774* (MICH); **C,** *Croton lucidus* L. showing pistillate flowers without petals, long, stellate trichomes on the ovary, and sepals that are much smaller than the mature ovary; Jamaica, *Van Ee & al. 776* (MICH).

be conserved with a different type than the one that Fawcett & Rendle (1920: 281) designated as its lectotype in order for it to continue to be used in the sense in which Fawcett & Rendle (1920), Adams (1972), and Webster (1993) used it.

Linnaeus first published *C. glabellus* in the 10th edition of his *Systema Naturae* (Linnaeus, 1759a: 1275–1276), for which he gave a diagnosis and cited a single reference ("Sloan. Jam. t. 174. f. 1."). This Sloane figure corresponds exactly to the specimen *Sloane 145* (Vol. 5: 111 in the Sloane Herbarium, BM), and the original of the illustration appears opposite the specimen in the bound volume. However, the labels on the *Sloane 144* (*C. nitens*) and *Sloane 145* (*C. glabellus*) specimens were transposed, as indicated in a note by J.E. Dandy, Keeper of Botany at the British Museum from 1956 to 1966. The label on *Sloane 144* reads "*Mali folio arbor, artemisiae odore, flore pentapetalo spicato*", while that on *Sloane 145* reads "*praecedentis varietas*". This makes even more sense considering that *Sloane 143*, with the label "*Mali folio arbor artemisiae odore & flore*", is an excellent example of *C. nitens*. In the descriptions of *C. glandulosus* L., *C. subtomentosus* L., *C. flavens* L., and *C. lucidus* L., Linnaeus (1759a) referred to four of Browne's (1756: 346–348) seven *Croton* species (*Croton* nos. 1–3 and 6, respectively). For *C. glabellus*, Linnaeus (1759a: 1275) referenced only Sloane, and not any of Browne's material. Consequently, Van Ee & Berry (2009) designated Sloane's (1725) tab. 174, fig. 1 the lectotype of *C. glabellus*, and *Sloane 145* (BM) the epitype. They also determined that the lectotype of *C. lucidus* corresponds to a species of *C.* sect. *Adenophylli* Griseb. endemic to Jamaica that Grisebach (1859) later named *C. wilsonii* Griseb. (Fig. 1C). The *Sloane 145* specimen clearly belongs to *C.* subsect. *Astraeopsis* rather than to *C.* sect. *Eluteria* Griseb.

In his *Plantarum Jamaicensium Pugillus*, Linnaeus (1759b) treated 127 species (+ 2 species in the appendix), of which nos. 110–114 ('100–114') on pp. 27–28 account for five of Browne's seven species of *Croton* (nos. 1–3 and 6–7). For the Jamaican species no. 110 ('100'), Linnaeus (1759b: 27) assigned the name *C. glabellus* and referred to Browne's (1756: 348) *Croton* number seven, cited as "Brown. Jam. 348" (LINN 1140.3). This 1759b description differs from the earlier one (Linnaeus, 1759a: 1275) by including mention of the glaucous underside of the leaves and the long-pedunculate fruits. More significantly, it lacks a reference to the Sloane figure that was cited in the earlier publication (Linnaeus, 1759a). Later that same year, Linnaeus (1759c: 21) published a catalogue of Jamaican plants in which he listed the same five *Croton* species as in his 1759b publication. For *C. glabellus*, he referred to both Browne (1756: 348) and to Elmgren (cited as "E. 110.", which corresponds to Linnaeus, 1759b). These last two publications were subsequently reproduced by Linnaeus in 1760 (vol. 5, diss. 96: 383 and vol. 5, diss. 97: 409). For convenience, the 1760 (p. 409) version is used in the rest of this article. A picture of *Browne 7* (Herb. Linn. no. 1140.3), which is *Astrocasia tremula*, was reproduced in Jarvis (2007: 56). At S-LINN there are two specimens of *A. tremula*, IDC 390.19 and IDC 391.1, both labeled as *C. glabellus*, and the latter is attributed to P. Browne. Both of these appear to be duplicates of *Browne 7* (LINN 1140.3).

Table 1. The changing names applied to Browne's (1756) seven species of *Croton* and *C. glabellus* L. In 1760 Linnaeus changed his application of *Croton glabellus* relative to when it was first published, and in 1763 he referenced a mixture of elements for *C. glabellus* pertaining to both *C. nitens* Sw. and *Astrocasia tremula* (Griseb.) G.L. Webster.

Browne (1756)	Linnaeus (1759a)	Linnaeus (1760)	Linnaeus (1763)	Fawcett & Rendle (1920)	Adams (1972)	Webster (1993)	Jarvis (2007)	Van Ee & Berry (2009)	Current concept
1. The small trichotomous *Croton*	*Croton glandulosus* sp. nov.	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus*	*Croton glandulosus* L.
2. The small sea-side Balsam	*Croton subtomentosus* sp. nov.	*Croton humilis*	*Croton humilis*	*Croton humilis*	*Croton humilis*	*Croton humilis*	*Croton humilis*	*Croton humilis*	*Croton humilis* L.
3. The yellow Balsam	*Croton flavens* sp. nov.	*Croton flavens*	*Croton flavens*	*Croton flavens*	*Croton flavens*	*Croton flavens*	*Croton flavens*	*Croton flavens*	*Croton flavens* L.
4. The sea-side Balsam	[not referenced]	*Clutia eluteria*	*Croton glabellus*	*Croton glabellus*	*Croton eluteria*	*Croton nitens*	[not treated]	*Croton nitens*	*Croton nitens* Sw.
5. Wild Rosemary	[not referenced]	*Clutia cascarilla*	*Croton cascarilla*	*Croton linearis*	*Croton linearis*	*Croton cascarilla*	*Croton cascarilla*	*Croton cascarilla*	*Croton linearis* Jacq.
6. The smooth erect *Croton*	*Croton lucidus* sp. nov.	*Croton lucidus*	*Croton lucidus*	*Croton wilsonii*	*Croton wilsonii*	*Croton wilsonii*	*Croton lucidus*	*Croton lucidus*	*Croton lucidus* L.
7. The larger *Croton*, with roundish leaves	[not referenced]	*Croton glabellus*	*Croton glabellus*	*Phyllanthus glabellus*	*Astrocasia tremula*	[not treated]	*Phyllanthus glabellus*	[not treated]	*Astrocasia tremula* (Griseb.) G.L. Webster
[not included]	*Croton glabellus* sp. nov.	[changed application]	[mixed application]	*Croton lucidus*	*Croton lucidus*	*Croton lucidus*	*Phyllanthus glabellus*	*Croton glabellus*	*Croton glabellus* L.

We conclude that Linnaeus changed his application of *C. glabellus* from the species represented by *Sloane 145* in Linnaeus (1759a: 1275) to that represented by *Browne 7* in Linnaeus (1760: 409). We therefore interpret the later use as a misapplied name. Fawcett & Rendle (1919: 65) treated the original *C. glabellus* of Linnaeus (1759a) as a synonym of *C. lucidus* L., and they then transferred the 1760-use of the name to *Phyllanthus*, publishing *Phyllanthus glabellus* Fawc. & Rendle as what they described as a "comb. nov." They indicated that *C. glabellus*, as treated by Linnaeus (1763), included a mixture of heterogeneous elements. Although their intent was to base *P. glabellus* on "*C. glabellus* L. (1760: 409)", they in effect published *P. glabellus* as a new species for what they overtly cited as "*C. glabellus* sensu L. (1760), non L. (1759a)". Furthermore, Fawcett & Rendle considered "*C. glabellus* L. (1760)" and *P. tremulus* Griseb. (1859) to be conspecific, and they treated the latter as a heterotypic synonym of their *P. glabellus*. Since "*C. glabellus* L. (1760)" does not formally exist, and since Fawcett & Rendle referred to an 1859-name as a synonym, *P. glabellus* Fawc. & Rendle was superfluous and illegitimate when published (McNeill & al., 2006: Art. 52.1). However, it is not automatically typified under Art. 7.5 by the type of *P. tremulus*, because, by their adoption of the epithet '*glabellus*' from "*C. glabellum* L. Amoen. v. 409 (1760)" as a "comb. nov.", they definitely indicated a different type (cf. Art. 7, Ex. 5).

In his treatment of West Indian *Phyllanthus*, Webster (1958: 208) transferred *P. tremulus* to *Astrocasia*, as *A. tremula* (Griseb.) G.L. Webster, and synonymized *P. glabellus* sensu Fawc. & Rendle under *A. tremula*, correctly giving priority to Grisebach's (1859: 34) name. Although Fawcett & Rendle (1919) had explicitly recognized two distinct *C. glabellus* species of Linnaeus (1759a vs. 1760), Webster (1958) stated that he did not consider it admissible to do so, and made it clear that he considered the name "*Phyllanthus glabellus* (L.) Fawc. & Rendle" as being linked back to Linnaeus's first (1759a) use of the epithet.

Jarvis (2007: 461) listed "*P. glabellus* (L.) Fawc. & Rendle" as the accepted name of *C. glabellus* L. (1759a), which is not what Fawcett & Rendle (1919: 65) intended. An added complication to the interpretation of Linnaeus's use of *C. glabellus* is that he later (1763) used the name again and referred to his earlier work ("Amoen. Acad. 5. p. 409." [1760]), to Browne's (1756) *Croton* number seven ("Brown. Jam. 348."), to Sloane ("Sloan. jam. 139. hist. 2. 30. t. 174. f. 3, 4." [1725]), and to John Ray ("Raj. dendr. 91" [1704]). Fawcett & Rendle interpreted Linnaeus's (1763: 1425) citation of Sloane's figs. 3 and 4 as an error for fig. 2, which corresponds to *Croton nitens* Sw. (Fig. 1B; Van Ee & Berry, 2009). We concur with Fawcett & Rendle that Linnaeus's (1763) treatment includes a mixture of heterogeneous elements, namely, "*P. Browne 7* (LINN 1140.3)" and "Sloane (1725) tabula 174 figs. 3 and 4" are in conflict with each other. The treatment of Webster (1958) supports this interpretation.

Baillon (1858: 362–363) provided a very detailed description of *Croton* sect. *Astraeopsis*, at the end of which he cited "*A. Hookeriana* † (Coll. Hook. herb. Mus.)." The dagger (†) was used in this publication to indicate species names used for the first time. Webster (1993) indicated that the type of *Croton* sect. *Astraeopsis* was "*C. hookerianus* Baill." Our interpretation of article 32 of the *International Code of Botanical Nomenclature* (McNeill & al., 2006) is that this listing of "*A. Hookeriana*" is a nomen nudum because it does not meet the conditions for valid publication as a species given that it is not accompanied by a description, diagnosis, or figure. Given this, "*Croton hookerianus*" cannot be the type of *Croton* sect. *Astraeopsis*, which necessitates the naming of a lectotype for the section.

■ CONCLUSIONS

Our treatment here seeks to establish the usage of *C. glabellus* and *C. lucidus* according to their Linnaean types. How this concept differs from historical and more recent treatments, which are not consistent with each other, is summarized in Table 1.

Croton glabellus (Fig. 1A) is a widely distributed species in the Caribbean. It is found on the Bahamas, Cayman Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Turks and Caicos, the Yucatan Peninsula of Mexico, and in Belize. It grows on limestone, primarily near sea-level, but it has also been recorded at elevations up to 900 m in Jamaica. We recognize two allopatric subspecies that are differentiated by the size of their leaves and the pigmentation of their trichomes more so than by their pubescence, which Urban (1899) originally used to distinguish the taxa but that we find can be variable in both.

■ NOMENCLATURAL SUMMARY

Croton (sect. ***Barhamia*** (Klotzsch) Baill.) subsect. ***Astraeopsis*** (Baill.) B.W. van Ee in Taxon 60: 817. 2011 ≡ *Croton* sect. *Astraeopsis* Baill., Étude Euphorb.: 362. 1858 – Lectotype (designated here): *Croton glabellus* L.

Croton glabellus L., Syst. Nat., ed. 10, 2: 1275. 7 Jun 1759 – Lectotype (designated by Van Ee & Berry in Syst. Bot. 34: 136. 2009): H. Sloane, Voy. Jamaica 2: tab. 174, fig. 1. 1725; Epitype (designated by Van Ee & Berry in Syst. Bot. 34: 136. 2009): Jamaica. *H. Sloane 145* (BM).

Key to the subspecies of *Croton glabellus*

1. Trichomes not dark-pigmented; leaves 6–11 × 2–5 cm; Cayman Islands, Cuba, Jamaica, Yucatan Peninsula, Belize ..... ***Croton glabellus*** subsp. ***glabellus***
1. Few to many trichomes dark-pigmented; leaves 2–5 × (0.5–) 1.5–2.0 cm; Puerto Rico, Hispaniola, Bahamas, Turks and Caicos..... ***Croton glabellus*** subsp. ***polytrichus***

Croton glabellus subsp. ***glabellus***

= *Croton spicatus* P.J. Bergius in Philos. Trans. 58: 132. 1768 – Lectotype (designated here): Jamaica. *H. Sloane 145*, Herb. Sloanei 145, volume 5: 111 (BM [589199]).

= *Croton fruticosus* Mill., Gard. Dict., ed. 8: 6. 1768 ≡ *Croton pallens* Sw. in Prodr.: 100. 1788, nom. superfl. et illeg. – Lectotype (designated by Van Ee & Berry in Syst. Bot. 34: 136): Jamaica. 1730, *W. Houstoun s.n.* (BM [947374]). 2009.

= *Croton lucidus* var. *pubigerus* Griseb., Fl. Brit. W.I.: 40. 1859 – Isotypes: Jamaica. *W. Purdie s.n* (A, TCD [7613], TCD [7614]).

= *Croton avenius* Vahl ex E.F. Geiseler, Croton. Monogr.: 11. 1807 – Type: "Habitat in America." Herb. Vaillant (presumably at P [not seen]), Herb Musei (presumably at C [not seen]).

= *Croton glandulifer* Vahl ex E.F. Geiseler, Croton. Monogr.: 37(–38). 1807 ≡ *Croton lucidus* var. *glandulifer* (Vahl ex E.F. Geiseler) Griseb. in Fl. Brit. W.I.: 40. 1859 – Lectotype (designated here): Herb. Jussieui Catal. No. 16367 (P-JU).

= *Croton campechianus* Standl. in Publ. Carnegie Inst. Wash. 461: 66. 1935 – Holotype: Mexico. Campeche, Dzibalchen, 21 March 1932, *C.L. Lundell 1398* (F [655124]; iso-: GH [47088], MICH [1104789]).

– "*Croton hookerianus*" Baill., Étude Euphorb.: 363. 1858 ('*A. Hookeriana*'), nom. nud.

Croton glabellus subsp. ***polytrichus*** (Urb.) B.W. van Ee, **comb. et stat. nov.** ≡ *Croton lucidus* var. *polytrichus* Urb. in Symb. Antill. 1: 335. 1899 – Lectotype (designated here): Puerto Rico, 2 July 1886, *P. Sintenis 3672* (GH [277420]; iso-: A [277418], G-BOIS (2 duplicates), GOET [003354], MO [1905453], NY [83357]); Syntypes: Puerto Rico, prope Peñuelas in montibus calcareis ad Tallaboa poniente, 16 July 1886, *P. Sintenis 4827* (JE [879]), *P. Sintenis 5002* [not seen].

= *Croton portoricensis* Vahl ex E.F. Geiseler, Croton. Monogr.: 43(–44). 1807 – Type: Puerto Rico. Herb. Desfontaines (presumably at P [not seen]).

= *Croton bahamensis* Ham., Prodr. Pl. Ind. Occid.: 55. 1825 – Holotype: Bahamas. Herb. Desvaux (P [P00633402]).

= *Croton hjalmarsonii* Griseb., Fl. Brit. W.I.: 40. 1859 ≡ *Oxydectes hjalmarsonii* (Griseb.) Kuntze in Revis. Gen. Pl. 2: 612. 1891 – Holotype: Turks and Caicos. Turk Islands, *J.A. Hjalmarson s.n.* (GOET [003353]; iso-: K [185950]).

= *Croton sublucidus* Müll. Arg. in Linnaea 34: 128. 1865 – Holotype: Dominican Republic. *C.J. Mayerhoff s.n.* (B, presumed destroyed).

= *Croton acuminatus* Sessé & Moc., Fl. Mexic., ed. 2: 223. 1894, nom. illeg. non Lamarck (1786) ≡ *Croton sesseianus* P.T. Li in Guihaia 14: 131. 1994 – Lectotype (designated by Nelson in Anales Jard. Bot. Madrid 55: 395. 1997): *M. Sessé y Lacasta 4588*, CNHM neg. 43515 (MA [602084]).

Croton sect. ***Adenophylli*** Griseb., Fl. Brit. W.I.: 40. 1859 ('*Adenophyllum*') – Type: *C. adenophyllus* Bertero ex Spreng.

Croton lucidus L., Syst. Nat., ed. 10, 2: 1275. 07 Jun 1759 – Lectotype (designated by Fawcett & Rendle in Fl. Jamaica 4: 281. 1920): Jamaica. *P. Browne 6* (LINN 1140.12).

= *Croton wilsonii* Griseb., Fl. Brit. W.I.: 40. 1859 – Lectotype (designated by Van Ee & Berry in Syst. Bot. 34: 137. 2009): Jamaica. Feb 1824, *W. Purdie s.n.* (K [185984]; iso-: K [185982], TCD [7615]).

Astrocasia tremula (Griseb.) G.L. Webster in J. Arnold Arbor. 39: 208. 1958 ≡ *Phyllanthus tremulus* Griseb., Fl. Brit. W.I.: 34. 1859 – Lectotype (second-step, designated here): Jamaica. Hills above the ferry, Aug 1843, *W. Purdie s.n.* (K [573152 (specimen on right of sheet)]; iso-: K [573151], K [573153]), first-step lectotype designated by Webster in Syst. Bot. 17: 319. 1992; Syntype: Jamaica. *H.R. Wullschlägel 1320* (GOET [001394]).

= *Astrocasia phyllanthoides* B.L. Rob. & Millspaugh in Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1905 – Holotype: Mexico. Yucatán, Mérida, 14 Mar 1903, *C. Seler & E.G. Seler 3943* (GH [00106203]; iso-: F).

= *Phyllanthus glabellus* Fawc. & Rendle in J. Bot. 57: 68. 1919, nom. superfl. & illeg. (*Croton glabellus* sensu L. in Pl. Jamaic. Pug.: 27. 18 Nov 1759 et Amoen. Acad. 5: 409. Sep 1760, non L. 7 Jun 1759).

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