

THE REINSTATEMENT OF *HILAIRANTHUS* (ACANTHACEAE): A GENUS FROM NEOTROPICAL AND WESTERN-PALEOTROPICAL MANGROVES

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Abstract. On the basis of previously documented genetic evidence, which correlates with morphological traits and a well-defined biogeographic pattern of distribution, *Hilairanthus* Tiegh. is recognized and reinstated as a genus of mangrove segregated from *Avicennia* (Acanthaceae). The genus is lectotypified, and the following combinations are formally proposed for *Hilairanthus germinans*, *H. bicolor*, and *H. schaueriana*.

Keywords: *Avicennia*, Acanthaceae, mangroves, Neotropics, Paleotropics

Resumen. Con base en evidencia genética, correlacionada con caracteres morfológicos y un definido patrón de distribución biogeográfica, se reconoce y restaura *Hilairanthus* Tiegh., un género de mangle segregado de *Avicennia* (Acanthaceae). Se lectotipifica a *Hilairanthus* y además se proponen formalmente las siguientes combinaciones: *Hilairanthus germinans*, *H. bicolor* y *H. schaueriana*.

Palabras claves: *Avicennia*, Acanthaceae, manglares, Neotrópico, Paleotrópico

Avicennia L. (1753) is a well-known and widely distributed woody genus of Acanthaceae, found in mangroves, beaches, and salt marshes along tropical coastlines around the world (Bakhuizen, 1921; Moldenke, 1960; Duke, 1991; Daniel, 2016). The species of this genus, regarded as true mangroves, are characterized by the presence of subsuperficial cable roots bearing pencil-thick erect pneumatophores, decussate evergreen leaves, and water-dispersed fruits, adapted to settling in periodically inundated habitats with high levels of salinity (Tomlinson, 1986; Cornejo, 2014). On the basis of fossil records and molecular analysis, the calibrated basal position of *Avicennia* dates back 100 MYA; the genus began to diversify during the Eocene, 55 to 35 MYA; and the assumed range of divergence time of the main lineages has been estimated to be from 10 to 50 MYA (Tripp and McDade, 2014). Molecular phylogenetic studies based on chloroplast and nuclear sequences have revealed the presence of two monophyletic clades within the genus (Li et al., 2016): the Indo–Western Pacific (IWP) lineage and the Atlantic–Eastern Pacific (AEP) lineage. The IWP lineage comprises five species and three varieties grouped into three subclades: (1) *A. officinalis* L. and *A. integra* N.C. Duke; (2) *A. marina* var. *marina* (Forssk.) Vierh., *A. marina* var. *eucalyptifolia* (Zipp. ex Moldenke) N.C. Duke, and *A. marina* var. *australasica* (Walp.) Moldenke; and (3) *A. alba* Blume and *A. rumphiana* Hallier f. The AEP lineage is represented by the transoceanic *A. germinans* (L.) L., the Mesoamerican–Eastern Pacific *A. bicolor* Standl., and the western Atlantic and South American *A. schaueriana* Stapf & Leechm. ex Moldenke. These two clades, currently gathered under the same generic name, have well-defined and disjunct biogeographical patterns of distribution and are correlated with morphologically different floral structures (Table 1). Therefore, the diphyletic *Avicennia* s. l. nomenclature does not reflect natural taxonomic units. As the South Asian *A.*

officinalis is the nomenclatural type of the genus (Linnaeus, 1753; Moldenke, 1960), the molecular results suggest that the name *Avicennia* must be kept for the IWP clade. Consequently, a proper generic name must be found for the remaining species included in the sister AEP clade, which do not fit biogeographically or morphologically the IWP clade of *Avicennia* s. str. The aim of this article is to provide an accurate generic name that is useful taxonomically and for conservation and management of AEP black mangroves, which are currently threatened by turistic and aquacultural development throughout its geographical range. The choice to recognize the AEP *Avicennia* s. l. as a distinct taxon at generic rank is based not only on biogeographical disjunction correlated to morphological differences but on the fact that the AEP clade is the outer group of *Avicennia* s. str. (Li et al., 2016), and that each of the three IWP subclades is characterized by distinctive morphological floral characters. These characters include corolla aestivation, stigma position in relation to the anthers, length of style, and insertion of filaments (Tomlinson, 1986; Li et al., 2016), suggesting that further studies are needed for the IWP subclades and that those taxa may deserve subgeneric recognition. Moreover, the species of the IWP and AEP clades are geographically isolated, so given the great distances that separate them, at least at present, the possibility of exchanging genetic material by natural means does not exist.

A review of the literature throughout the complex nomenclatural history shows that *Hilairanthus* Tiegh. (1898) is the only genus proposed as a segregate from *Avicennia* for the American and West African species. Morphological features, pattern of geographical distribution, and citation of species names assigned to the then-new genus perfectly match the AEP clade. In the original publication, *Hilairanthus* was described in French and without Latin; however, the genus fulfills the requirements

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Table 1. Morphological comparison of *Hilairanthus* Tiegh. and *Avicennia* L.

	<i>HILAIRANTHUS</i>	<i>AVICENNIA</i>
Flower buds	Often asymmetric, \pm curved upward, especially young ones	All symmetric and straight
Color of corollas	White or creamish white, yellow at inner throat	Full yellow to golden yellow or orange
Symmetry of corollas	Distinctly zygomorphic	Somewhat zygomorphic (in <i>A. officinalis</i>) and strictly actinomorphic
Corolla aestivation	Imbricate	Barely imbricate (in <i>A. officinalis</i>) to mostly valvate
Length of stamen filament	Didynamous, lower-inserted outer pair \pm longer than upper-inserted inner pair	\pm equal length
Insertion of stamen filament	Adnate only at inner base and mostly free from corolla tube	Inserted at mouth of corolla tube, connate, or adnate along full length of inner corolla tube (in <i>A. officinalis</i>)
Arrangement of stamen filament	Upper-inserted inner pair closer to central pistil, lower-inserted outer pair at maturity turning divergent from pistil	All equidistant or nearly so from all points of a square or pentagon and \pm equally placed around corolla tube mouth
Arrangement of anthers	Two on each side of pistil, all in a row or arc at upper half of corolla, \pm horizontal under upper corolla lobe	All equidistant or nearly so from all points of a square or pentagon and \pm equally placed on or over corolla tube mouth and around pistil
Distribution	Atlantic–East Pacific	Indo–West Pacific

of Art. 11, 38, and 39 of the ICN (Turland et al., 2018) and therefore, supported by the molecular, biogeographical, and morphological evidence, deserves to be recognized as valid. The genus was represented by *H. tomentosus* (Jacq.) Tiegh. and *H. nitidus* (Jacq.) Tiegh., without designation of a nomenclatural type. Both names previously published together by Jacquin (1760) under *Avicennia* were later

regarded as synonyms of the well-known and widespread black mangrove *A. germinans* (1764), which at that time was placed and remained in *Bontia* L. (since 1759). In this work, *Hilairanthus* is reinstated, a nomenclatural type is designated, and the corresponding new combinations in *Hilairanthus* are presented for the three species of the AEP clade.

TAXONOMY

Hilairanthus Tiegh., J. Bot. (Morot.) 12: 358. 1898. Fig. 1A–B.

Lectotype: *Hilairanthus nitidus* (Jacq.) Tiegh., J. Bot. (Morot.) 12: 358. 1898, designated here. = *Hilairanthus germinans* (L.) Cornejo, *comb. nov.*

Hilairanthus can be recognized by its zygomorphic white or creamish-white corollas, stamens didynamous, filament adnate at inner base of corolla tube, upper-inserted inner pair somewhat shorter and upright, close to central pistil, lower-inserted outer pair at maturity turning divergent from pistil, \pm longer than the inner pair, four anthers arranged into a row or arc at upper half of corolla under dorsal lobe and \pm horizontal to spike (vs. corollas yellow or golden-yellow to orange, filament of stamens of \pm equal length, all inserted or apparently inserted under the sinus between lobes and equally placed at the mouth of corolla tube, and anthers equidistant or nearly so from all points of a square or pentagon but never forming a row or arc). The white color of corollas as a distinct character has been noted by van Tieghem (1898) and Moldenke (1960: part

3). The distinctive zygomorphic corollas and arrangement of the stamens of *Hilairanthus*, most likely a result of coevolution, allow the more ample access at the lower part of corolla mouth that is preferred by entomophilous visitors and pollinators (Tomlinson, 1986; Cornejo, 2014).

Trees or shrubs. Secondary subsuperficial cable roots with many pneumatophores, those narrow, pencil-thick, erect to 50 cm high, lenticellate. *Leaves* decussate; blade simple, entire, petiolate. *Stipules* absent. *Inflorescences* terminal and axillary, in dense panicles or spikes. *Flowers* sessile. *Calyx* dialysepalous, sepals 5, persistent in fruit. *Corolla* white to creamish-white, zygomorphic, gamopetalous, forming a tube at basal third to half, the lobes 4(–5), free (2 fused at dorsal lobe). *Stamens* 4, didynamous, the filaments alternipetalous at base, mostly free, adnate at inner base of corolla tube, the upper-inserted inner pair upright closer to central pistil and somewhat shorter, the lower-inserted outer pair farther from pistil and at maturity turning divergent, the 4 anthers arranged into a row or arc at upper half of corolla under dorsal lobe and \pm horizontal to spike, longitudinally

dehiscent, initially white, turning black at maturity. *Ovary* 1, superior; style 1, white; stigma bifid, the lobes shortly linear. *Fruit* asymmetric, laterally compressed, dehiscent in 2 valves after falling in water, the epicarp nearly smooth to usually rugose; *seed* 1, without testa, cotyledons 2, thick, folded, the outer cotyledon enclosing the inner, the radicle white, densely pilose.

Distribution: a genus found along both coasts of the American continent—on the eastern Pacific coast from western Mexico to northwestern Peru (Piura) and the Galapagos Islands, and on the Atlantic coast from southern North America (southeastern United States and Mexico), Bermuda, West Indies, and Central America to South America (to southern Brazil and Uruguay)—and in tropical Western Africa (van Tieghem, 1898; Moldenke, 1960).

1. *Hilairanthus germinans* (L.) Cornejo, *comb. nov.* Fig. 1A–B.

Basionym: *Bontia germinans* L., *Syst. Nat.* ed. 10 (2): 1122. 1759. TYPE: JAMAICA. *P. Browne s.n.* (Lectotype, designated by Stearn, 1958: LINN-813.2).

Homotypic synonym: *Avicennia germinans* (L.) L., *Sp. Pl.* ed. 3 (2): 891. 1764, *syn. nov.*

Heterotypic synonyms: *Avicennia nitida* Jacq., *Enum. Syst. Pl.* 25. 1760. TYPE: WEST INDIES. Without date, *N. Jacquin s.n.* (Lectotype, designated by Moldenke, 1960: BM-992851).

Avicennia officinalis var. *nitida* (Jacq.) Kuntze, *Revis. Gen. Pl.* 2: 502. 1891.

Hilairanthus nitidus (Jacq.) Tiegh., *J. Bot. (Morot)* 12: 358. 1898.

Avicennia tomentosa Jacq., *Enum. Syst. Pl.* 25. 1760. TYPE: WEST INDIES. Without date, *N. Jacquin s.n.* (Lectotype, designated by Moldenke, 1960: BM-992852).

Hilairanthus tomentosus (Jacq.) Tiegh., *J. Bot. (Morot)* 12: 358. 1898.

Avicennia tomentosa Jacq. var. *cumanensis* Kunth, *Nov. Gen. Sp.* 2: 229 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: VENEZUELA. Cumana: “Crescit ad litora maris Cumanensis,” *A. Bonpland* 68 (Lectotype: B, not found).

Avicennia tomentosa Jacq. var. *campechensis* Kunth, *Nov. Gen. Sp.* 2: 229 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: MEXICO. Campeche: “Crescit prope Campeche Mexicanorum,” *A. Bonpland s.n.* (Lectotype, designated here: P-00670135; Isolectotype: P-00689943).

Avicennia tomentosa Jacq. var. *guayaquilensis* Kunth, *Nov. Gen. Sp.* 2: 230 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: ECUADOR. Guayas: Guayaquil, “Crescit prope Guayaquil Quitensium,” *A. Bonpland s.n.* (Lectotype, designated here: P-00670136; Isolectotypes: P-00689945, P-00689946, P-00689947).

Avicennia africana P. Beauv., *Fl. Oware* 1: 80. 1806. TYPE: Oware et Benin, *A.M.F. Palisot de Beauvois s.n.* (Lectotype, designated here: G-00023640; Isolectotype: G-00023641).

Avicennia floridana Raf., *Atlantic J.* 1:148. 1832. TYPE: Not designated (no specimens cited).

Avicennia oblongifolia Chapm., *Fl. South. U.S.* 310. 1860. TYPE: U.S.A. Florida: Monroe County, Oct, Key West (fide protologue); specimens would be in the Chapman herbarium at NY, but not found (Daniel, 2016).

Avicennia floridana Gand., *Bull. Soc. Bot. France* 65: 64. 1918, *homon. illegit.* TYPE: U.S.A. Florida: Lee County, Fort Meyers, *A. Hitchcock* 270 (see discussion in Daniel, 2016).

Avicennia tonduzii Moldenke, *Phytologia* 1: 273. 1938. TYPE: COSTA RICA. Puntarenas: Punta Mala [ca. 09°03'54.48"N, 083°39'04.84"W], zone littorale du Pacifique, Mar 1892, *A. Tonduz* 6776 (Holotype: BR, fragment of holotype at NY; Isotypes: BM, M, MICH, US).

Habitat and distribution: southern North America (southeastern USA and Mexico), West Indies, Central America, and South America (Colombia, Ecuador [including the Galapagos islands]), and Peru on the Pacific coast; Venezuela, French Guiana, Guyana, Suriname, and Brazil on the Atlantic coast. Habitats include beaches, mangrove swamps, and salt marshes, at elevations at or near sea level (Moldenke, 1960; Cornejo, 2014; Daniel, 2016).

2. *Hilairanthus bicolor* (Standl.) Cornejo, *comb. nov.*

Basionym: *Avicennia bicolor* Standl., *J. Wash. Acad. Sci.* 13(15): 354. 1923. TYPE: PANAMA. Coclé. Aguadulce, along the outskirts of the tidal belt, 08°14'30"N 080°32'30"W, 5 Dec 2011 (fl), *H. Pittier* 4968 (Holotype: US-715142; Isotypes: BM-992849, F-636788, K-573632, NY-337274, P, US-715141).

Habitat and distribution: Pacific coast of southern Mexico (Chiapas) to southern Panama; in beaches, mangrove swamps, and salt marshes, at elevations at or near sea level (Moldenke, 1960; Cornejo, 2014; Daniel, 2016).

3. *Hilairanthus schaueriana* (Stapf & Leechm. ex Moldenke) Cornejo, *comb. nov.*

Basionym: *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, *Lilloa* 4: 336. 1939.

Heterotypic synonyms: *Avicennia nitida* var. *trinitensis* Moldenke, *Phytologia* 1: 96. 1934. TYPE: TRINIDAD AND TOBAGO. Caroni swamp, 29 May 1932 (fl), *R. L. Brooks* 12656 (Holotype: NY-337279), *syn. nov.*

Avicennia schaueriana f. *glabrescens* Moldenke, *Phytologia* 34: 485. 1976. TYPE: TRINIDAD AND TOBAGO. Caroni swamp, 9 May 1932 (fl), *R. C. Marshall* 12651 (Holotype: NY-337281), *syn. nov.*

Avicennia schaueriana f. *candicans* Moldenke, *Phytologia* 35: 13. 1976. TYPE: BRAZIL. Rio de Janeiro, Manguinhos, 16 Sep 1948 (fl), *A. L. Moldenke & H. L. Moldenke* 19606 (Holotype: NY-337280), *syn. nov.*

Habitat and distribution: Atlantic coast of Brazil to Uruguay, in mangrove swamps, at elevations at or near sea level (Moldenke, 1960; Tomlinson, 1986).

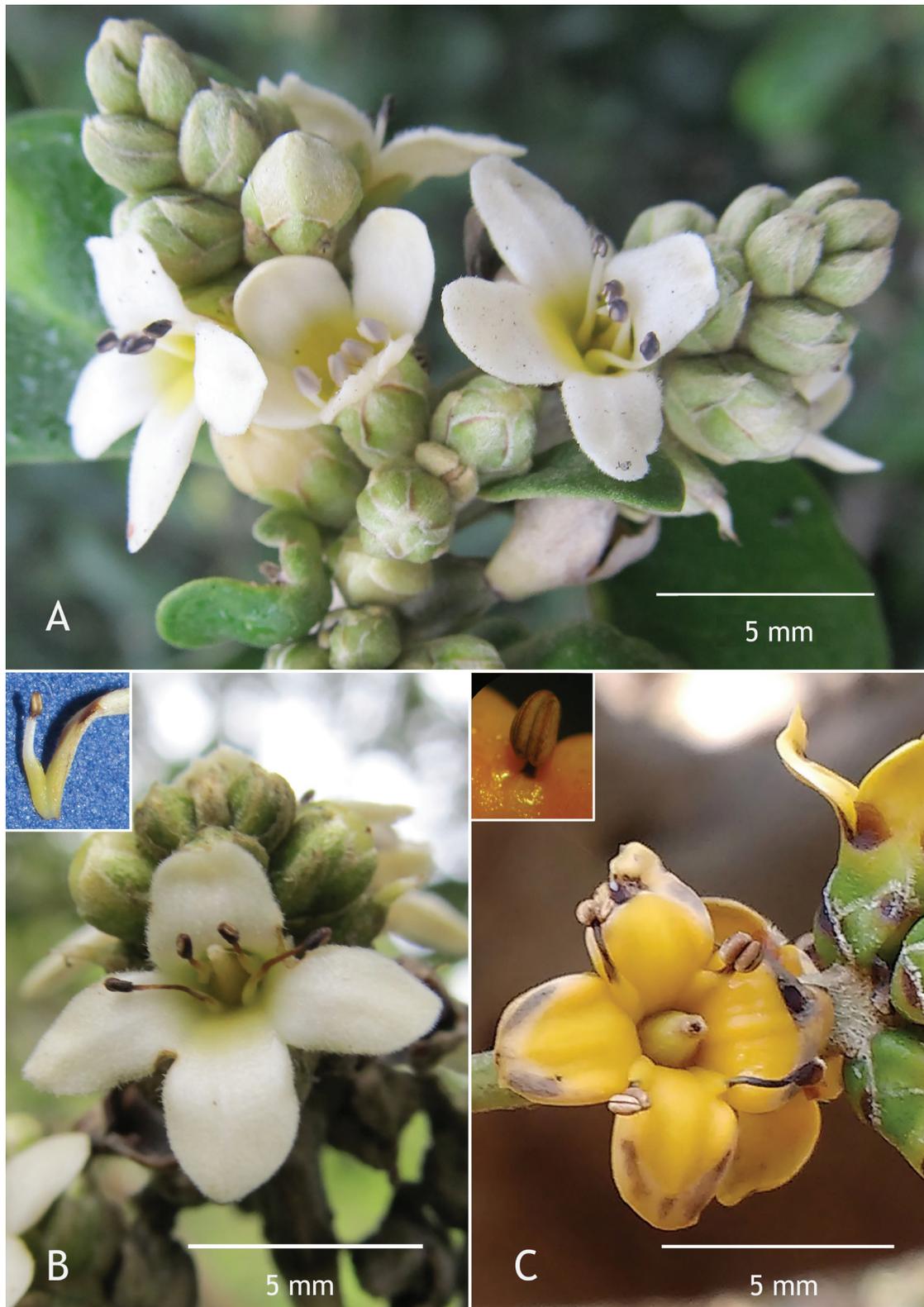


FIGURE 1. **A–B.** *Hilairanthus germinans* (L.) Cornejo. **A**, three dense spikes bearing open flowers, note the \pm horizontal one-row arrangement of anthers; **B**, flower, adaxial view, note the zygomorphic white corolla, stamens mostly free from corolla tube, and the filament adnate at inner base of corolla tube (upper left square). **C.** *Avicennia officinalis* L. and *A. marina* (Forssk.) Vierh. **C**, flower, adaxial view, note the mostly actinomorphic pale orange corollas, stamens arranged from all points of a square and \pm equally placed around corolla tube mouth, the filaments adnate along full length of inner corolla tube and apparently inserted under sinus at the mouth of corolla (*A. officinalis*) or the filament inserted at the mouth of corolla tube (*A. marina*, upper left square). **C.** *A. officinalis* courtesy of Mandar Datar and *A. marina* courtesy of Sajid Sheikh, both from Maharashtra, India.

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