

**STUDIES OF NEOTROPICAL COMPOSITAE—XVII.
UNXIA CAMPHORATA (MILLERIEAE) ON WHITE SAND IN LORETO,
A NEW GENERIC RECORD FOR PERU**

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ABSTRACT

Unxia camphorata (Millerieae) is documented in white-sand savannas in Loreto, and represents a new generic record for Peru. Descriptions are given for the genus and species, the species is illustrated, and a map showing known Peruvian localities is provided.

The helianthoid genus *Unxia* L.f. (Compositae tribe Millerieae) is typified by herbaceous *U. camphorata* L.f. and contains two northern South America-centered species (Stuessy 1969; Pruski 1997, 2002; Pruski & Robinson 2018). *Unxia* was recognized by Candolle (1836), but treated as an infragenus of *Melampodium* L. by Bentham and Hooker (1873). Baker (1884) treated *Unxia* as *Melampodium* subg. *Unxia*, described subshrubby *M. suffruticosum* Baker from Spruce 3225 collected along the Rio Orinoco, and also provided the combination *M. camphoratum* (L.f.) Baker for the generitype. Badillo (1946) treated the subshrubby species as *Polymnia suffruticosa* (Baker) V.M. Badillo. *Polymnia suffruticosa* was recognized by Aristeguieta (1964: 401), whereas Aristeguieta (1964: 465) maintained *Melampodium camphoratum*, the two congeners thereby placed in different genera. These three genera, *Melampodium*, *Smallanthus* Mack. (most tropical members of *Polymnia* P. Kalm are now placed in *Smallanthus*), and *Unxia*, each now of tribe Millerieae (Panero 2007) and characterized by uniseriate-radiate capitula and functionally staminate central disk florets, the marginal pistillate rays forming fruits in a ring (Fig. 1). Pruski and Robinson (2018) keyed *Unxia* and *Smallanthus* as adjacent, and they gave *Smallanthus* as differing by its pinnately lobed to often pentagonal leaves, open capitulescences, and strongly dimorphic phyllaries. The fine revision by Stuessy (1969) treated *Unxia camphorata* and *U. suffruticosa* (Baker) Stuessy as the only two species of newly resurrected *Unxia* — the two species were treated earlier by Baker (1884) and Robinson (1901) as congeneric, but then under *Melampodium*.

In 1984, Julian Steyermark (pers. comm.) mentioned that he collected a new species of *Calea* L. in canyons along the Rio Orinoco in Amazonas, Venezuela. This collection, *Steyermark et al.* 130394 (NY), was determined (Pruski in sched. 1985) as subshrubby *U. suffruticosa*. This 1984 Steyermark collection and earlier Venezuelan material of *U. suffruticosa*, however, also matched subshrubby Brazilian *U. kubitzkii* H. Rob., described by Robinson (1980) as a third species of *Unxia*. In the *Flora of the Venezuelan Guayana*, Pruski (1997) reduced *U. kubitzkii* by treating it in synonymy with *U. suffruticosa*, thus returning to the two species concept of Stuessy (1969), a concept still followed.

Unxia has usually been recognized within tribe Heliantheae (Stuessy 1969, 1977; Robinson 1980, 1981; Bremer 1994; Pruski 1997), often aligned with *Galinsoga*, but now *Unxia* and *Galinsoga* are treated as members of tribe Millerieae (Panero 2007). *Unxia* was the only genus of Millerieae treated by Robinson (1981) in subtribe Neurolaeninae, which is now recognized as tribe Neurolaeneae and includes *Calea* (Panero 2007; Pruski & Robinson 2018; Pruski 2023). The generitype *U. camphorata* is occasional in distribution and known from scattered localities in French Guiana and northern Brazil, thence eastwards into Panama (Stuessy 1969; D'Arcy 1975; Pruski 1997,

2002; Pruski & Robinson 2018). *Unxia suffruticosum* was given by Stuessy (1969) as found only in Venezuela, but is now known from Venezuela and Brazil (Pruski 1997), where it is restricted to Amazonia and Guayana.

Here, herbaceous *Unxia camphorata* L.f. is documented in white-sand savannas in Loreto and represents a new generic record for Peru. *Unxia* has been anticipated in Peru because the plant is so widespread in northern South America — the Peru localities are between those just to the south in nearby Cruzeiro do Sul, Brazil, and those to the north in nearby Colombian Guayana. The genus is undocumented, however, in Ecuador (Robinson 2006), but it was cited by Stuessy (1969) as to be looked for in Ecuador. The Peruvian localities are the furthest known upriver Amazon River stations.

Dillon and Hensold (1993) did not record *Unxia camphorata* in Peru, and the only citation by them of the genus was their citation of *U. anemonifolia* Kunth in synonymy with a species of *Vasquezia* Phil (now *Villanova* Lag.). More recently, Dillon and Sagástegui (2001: 35) did not list *Unxia* as occurring in Peru. Pruski and Robinson (2018) gave the species as in Peru but did not voucher it, and they incorrectly cited the plant as in Bolivia. Descriptions adopted from Pruski (1997, 2002) and Pruski and Robinson (2018) are given here for the genus and species and follow the format of the Flora of Peru Compositae treatments of Jones (1980), Dillon (1980, 1981, 1982), Holmes and McDaniel (1982), Dillon and Sagástegui (1991), and Ferreyra (1995).



Figure 1. *Melampodium perfoliatum* (Cav.) Kunth, fruiting capitulum from above, showing a ring of 13 fruiting ray florets each held within subtending inner phyllaries and forming a conceptacle; the disk florets are functionally staminate, thus not forming fruits, and in this image the disks and paleae have fallen, leaving the broad flat center of the clinanthium naked. (Stuessy & Gardner 4485, MO).

UNXIA L.f., Suppl. Pl. 368. 1781 [1782]. **TYPE:** *Unxia camphorata* L.f.

Greenmania Hieron., *Pronacron* Cass.

Herbs or subshrubs to 2.5 m tall; stems branched, spreading, subterete, pilose to subglabrous, not stipitate-glandular, trichomes often as long as or longer than stem diam. **Leaves** simple, opposite, decussate, sessile to short-petiolate; blade linear-lanceolate to ovate, not lobed, chartaceous, 3–5-veined from near base, adaxial surface subglabrous to pilose, abaxial surface subglabrous to densely pilose, sparsely punctate-glandular, nearly smooth to abaxial surface conspicuously reticulate. **Capitulescence** a leafy compact terminal cyme with 1–5 subsessile to short-pedunculate capitula. **Capitula** radiate or sometimes indistinctly so, 8–30-flowered; involucre campanulate to hemispherical; phyllaries 6–18, moderately dimorphic, imbricate, subequal to somewhat graduate with the outer typically more than half as long as the inner, 2–3-seriate, greatly spreading only post-fruit, elliptic to obovate, at least the inner pluristriate; outer series 2 or 4, opposite or opposite-decussate, subherbaceous to thinly so, appressed or ascending, flat, pubescent to pilose; innermost phyllaries navicular-plicate, scarious-chartaceous, often yellowish; clinanthium convex to short-conical, paleate to often irregularly so in the outer disk florets, sometimes all disk florets appearing epaleate; paleae linear-lanceolate to lanceolate-pyriform or sometimes rudimentary and squamulose, not conduplicate, scarious, brittle, deciduous individually or sometimes persistent but greatly spreading or reflexed. **Ray florets** pistillate, 3–7(–9), 1-seriate; corolla attached to center of ovary apex, yellow, tube glandular or pilose to infrequently glabrous, tube and limb subequal or limb somewhat longer than tube, limb ovate (ours) to oblong, evenly thin-nerved, abaxially glandular, apex rounded to shallowly 3-lobed; style branches with stigmatic surfaces 2-banded with paired stigmatic lines. **Disk florets** epappose, functionally staminate, 5–20; corolla small, funnellform, 5-lobed, yellow to yellow-orange, glandular (glands readily collapse in EtOH) or sometimes seemingly glabrous, rarely pilose, throat usually with resin ducts single along veins, lobes triangular-lanceolate, shorter than the throat, erect; anthers yellow to black; ovary sterile, style undivided. **Ray cypselae** epappose, obovoid, moderately compressed, black, striatulate, smooth or sometimes sublenticellate, never tuberculate, glabrous, annulus sometimes raised. $x = 16$ (Turner and King 1962; Jansen et al. 1984: 18).

UNXIA CAMPHORATA L.f., Suppl. Pl. 368. 1781 [1782]; see also Linnaeus, Pl. Surinam. 14. 1775, invalid; see also Linnaeus (1785): Linnaeus, Amoen. Acad., Schreb. ed. 8: 262. 1785 which gave the species as "110. Unxia 105. *camphorata*." *Melampodium camphoratum* (L.f.) Baker, in Martius, Fl. Bras. 6(3): 161. 1884. In Linnaeus (1775), "*Unxia* was given no separate generic description and *U. camphorata* [of L.] is therefore invalid" (Jarvis 2007: 907): the genus and the species are to be attributed to Linnaeus f. (1781); *Plantae Surinamenses* was written by Jacob Alm, a student of Linnaeus; Stafleu and Cowan (1981: 110, item 4848) gave Dahlberg as the source material studied for *Plantae Surinamenses*. See also Pruski (1996: 414) for typology of the species [*Tilesia baccata* (L.) Pruski] that on the same page in *Plantae Surinamenses* (Linnaeus 1775, 1785) follows *Unxia camphorata*, and Pruski (1999) for discussion of the typification of *Gurania lobata* (L.) Pruski (Linnaeus 1775: 15; Linnaeus 1785: 263) Cucurbitaceae, each of which are based similarly on only Dahlberg materials (see also Jarvis 2007; Moraes 2012; Stafleu and Cowan 1981). **TYPE: SURINAM.** Locis arenosis, 1754–1755, *Dahlberg s.n. (105)* (lectotype sheet, as holotype in Stuessy 1969: LINN-1010.1, as IDC microfiche 177 69.III.2; possible authentic material UPS-Thunberg 19489). *Dahlberg s.n.* was the material cited in the protologue, and LINN-1010.1 was presumably the sole sheet seen by Linnaeus and Linnaeus f., who apparently did not have access to early Rolander material from Surinam. Figures 2–9.

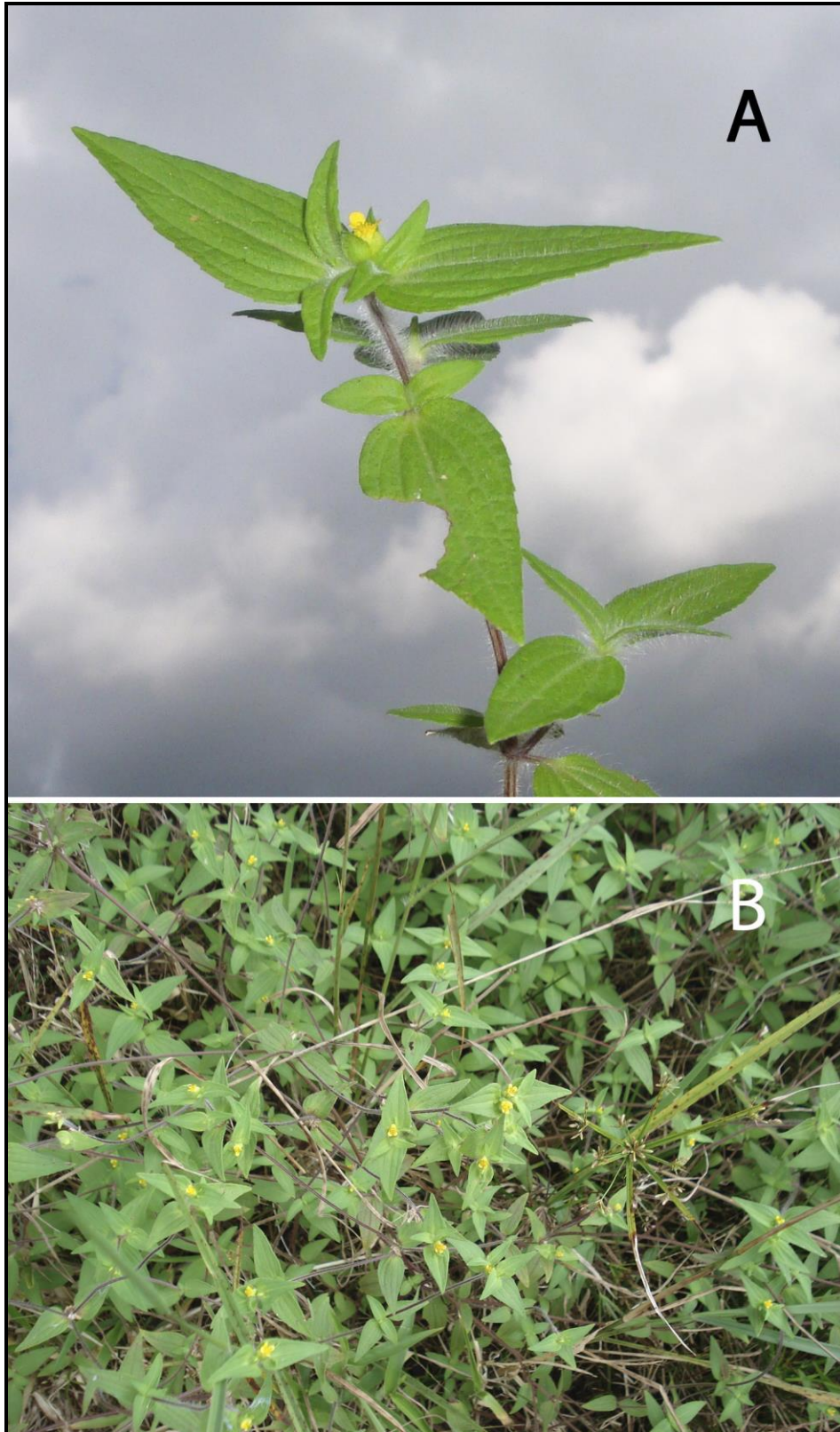


Figure 2. *Unxia camphorata* L.f. in Loreto, Peru. A. Distal portion of stem showing decussate leaves and a subsessile capitulum. B. Representative habitat, here a grassy white-sand savanna in Amazonia. (A Pruski et al. 4626, B Pruski et al. 4348).

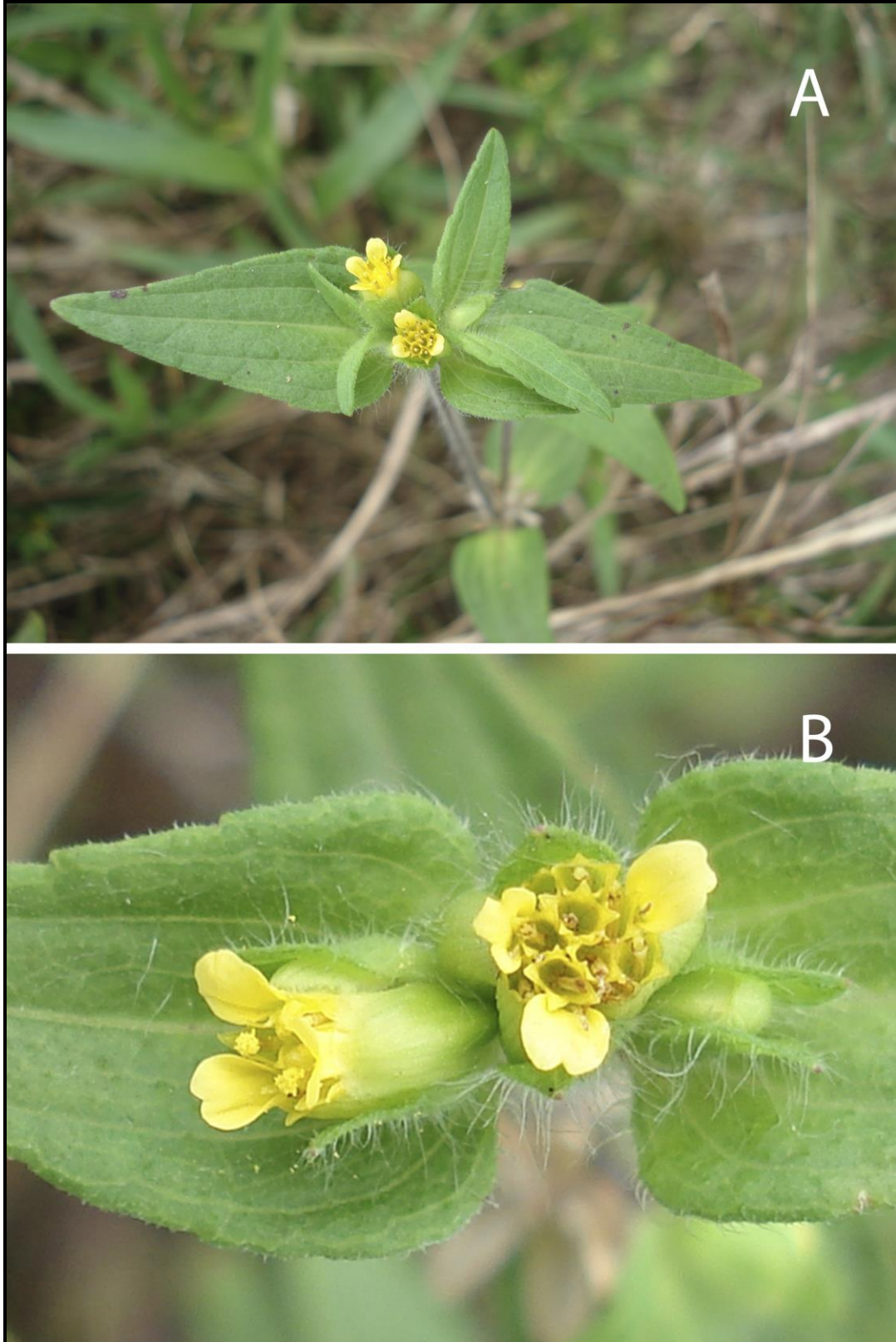


Figure 3. Flowering capitula of *Unxia camphorata* L.f. in Loreto, Peru, showing stem apices each 1–3-capitulate, pilose indument, and short-yellow-rayed subsessile capitula with functionally staminate disk florets. (A–B Pruski et al. 4348).



Figure 4. Habit of *Unxia camphorata* L.f., showing opposite-leaved herbaceous stems and subsessile capitula. A. Line drawing. B. Pressed field collection. (A reproduced from Pruski 1997: 384, fig. 330, drawn by Bruno Manara from *Westra* 47322; B Pruski *et al.* 4626, unmounted duplicate).

Unxia hirsuta Rich., Actes Soc. Hist. Nat. Paris 1: 112 (as page "105"). 1792. **TYPE: FRENCH GUIANA.** Cayenne, 1792, *LeBlond* 346 (holotype: G). Pruski (1998) cited no further LeBlond material, and the name seems to have been described upon a unicate holotype. Stuessy (1969) incorrectly cited "holotype: P; isotype G" but Pruski (1998) noted that the original set of collections used by Richard are in G.

Pronacron ramosissimum Cass. in F. Cuvier (ed.), Dict. Sci. Nat. (ed. 2) 43: 370. 1826. **TYPE: FRENCH GUIANA.** "Dans la Guiane francoise," 1817–1822, *Poiteau s.n.* (holotype: K-Herb. Gay).

Unxia digyna Steetz in Seemann, J. Bot. Voy. Herald. 154. 1854. *Melampodium digynum* (Steetz) Benth. & Hook. f. ex B.D. Jacks., Index Kew 1: 188. 1895. **TYPE: PANAMA.** Ad rios [illegible], Nov 1846, *Seemann* 46 (holotype: BM; isotypes: K-Hooker, MEL, fragment in US).

Greenmania boladorensis Hieron., Bot. Jahrb. Syst. 28: 597. 1901. **TYPE: COLOMBIA.** In monte Bolador, Aug 1888, *Sonntag* 51 (holotype: B†, Macbride neg. 15169; isotype: a fragment of the holotype in US). Figure 5A.

Greenmania ulei Hieron., Verh. Bot. Vereins Prov. Brandenburg 48: 203. 1907. **TYPE: BRAZIL. Amazonas.** Manaus, Jul 1900, *Ule* 5146 (holotype: B†, Macbride neg. 15170; isotypes: HBG, K, branchlet fragment in US). Figures 5B, 7.

Herbs 0.1–0.6 m tall; stems single from base, thin, strongly divaricate-branched throughout, branching opposite proximally, branching distally appearing dichotomous with lateral branches quickly overtopping terminal remnant capitulescence of central branch, brownish to reddish-brown, paucicostate-sulcate, long white-pilose to sometimes sparsely so, internodes (0.5–)4–16 cm long, at mid-stem usually much longer than decussate leaves, distal 2–3 nodes sometimes closely spaced, trichomes to 3.5 mm long. **Leaves** opposite; blade 1.5–5(–8) × 0.3–1.7(–2.7) cm, linear-lanceolate to lanceolate-ovate, laterally spreading, arching basal pair or two of lateral veins reaching to near apex, long-pilose to sparsely so with trichomes to ca. 1 mm long, adaxial surface with veins slightly impressed, abaxial surface also sparsely punctate-glandular, base rounded or obtuse to sometimes cuneate, margins subentire to serrulate, apex acute to acuminate; petiole 0.1–0.5(–0.8) cm long. **Capitulescence** subsessile, 1–3-capitulate, about half as long as the subtending laterally spreading leaves; peduncles 1–6(–10) mm long, pilose to densely so. **Capitula** short-radiate, mostly paleate, 3.5–6 mm long, globose, 8–15-flowered; involucre 3–7 mm diam.; phyllaries 6–10; outer green-subherbaceous phyllaries 2–6 × 1–2.5 mm, lanceolate to elliptic, sometime slightly spreading, thinly subherbaceous, indistinctly 5–9-striate, hirtellous to more commonly white-pilose, ciliate; inner scarious-chartaceous phyllaries 3.5–5 × 1.5–3 mm, oblong to obovate, obviously ca. 11+-striate, hirsute to glabrous, apex rounded; clinanthium to ca. 0.6 × 0.6 mm diam., indistinctly and irregularly paleate to basically epaleate; paleae of outer disk florets few, (0.2–)1–2 mm long, linear-lanceolate or sometimes merely squamulose, the inner disk florets typically appearing epaleate. **Ray florets** pistillate, 3–5, shortly exserted and ascending to slightly spreading; corolla yellow, tube 0.4–1 mm long, usually sparsely glandular, limb (1–)1.3–2.2 mm long, ovate, 3(–5)-nerved, lobes (when present) < 0.1 mm long. **Disk florets** epappose, functionally staminate, 5–10; corolla yellowish, 2.2–3.2 mm long, glandular, infrequently glabrous or very rarely weakly pilose, tube 0.7–1.2 mm long, lobes 0.5–0.9 mm long; ovary to ca. 1 mm long. **Ray cypselae** epappose, 2–2.8 × ca. 2 mm, a gradually raised annulus sometimes present, to ca. 0.2 mm long. $2n = 32$.

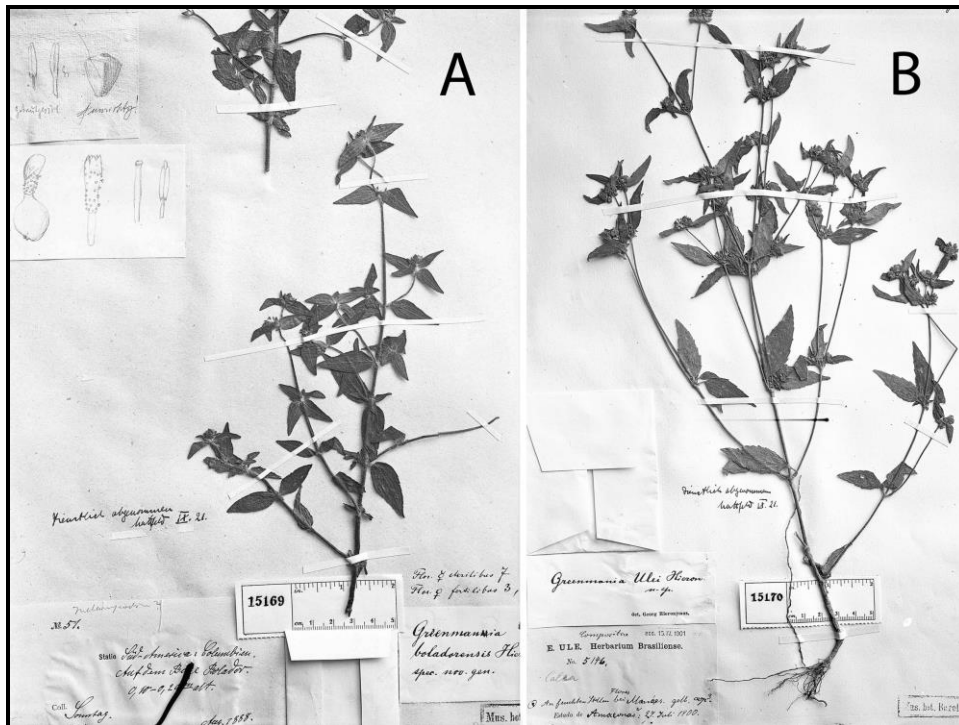


Figure 5. Photographs of the destroyed Berlin holotypes of the two species of *Greenmania* Hieron., each now treated in synonymy with *Unxia camphorata* L.f. A. *Greenmania boladorensis* Hieron., the type of the new genus *Greenmania* Hieron., described by Hieronymus (1901) at about the time future-MO curator Jesse Greenman was a student of Adolf Engler in Berlin. B. *Greenmania ulei* Hieron., described by Hieronymus (1907). (A *Sonntag 51*, B†, from Colombia, Macbride negative 15169; B *Ule 5146*, B†, from Brazil, Macbride negative 15170).

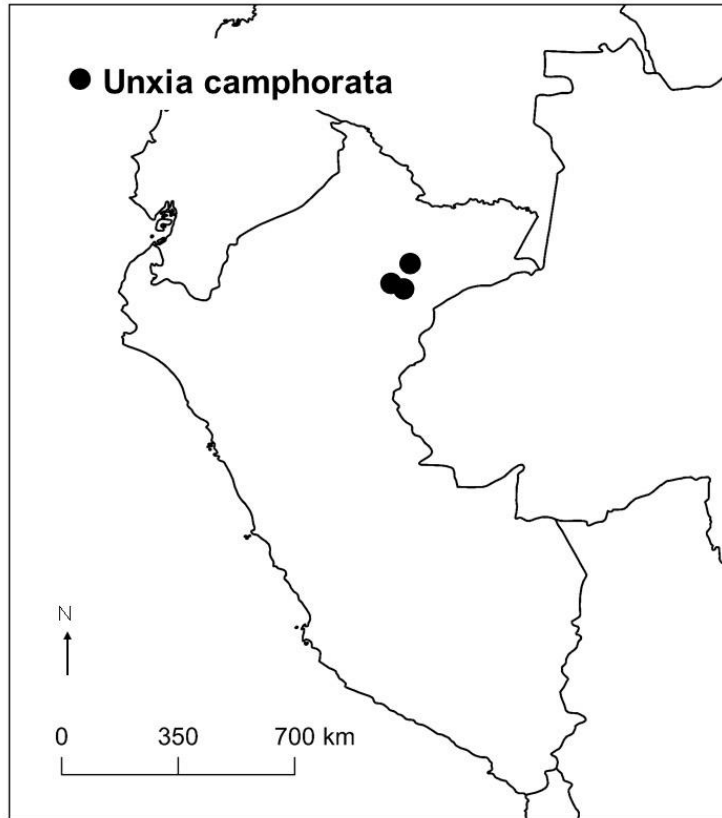


Figure 6. Distribution of *Unxia camphorata* L.f. in Peru.

Vouchers for the new Peruvian record of *Unxia camphorata*. (Fig. 6.). **PERU. Loreto.** Maynas, dry grassy white-sand (arena blanca) savanna 400 meters SW of Fundo UNAP forest regeneration field station buildings, SSW of Iquitos, km 31.5 carretera Iquitos–Nauta, 4° 00' 22" S, 73° 26' 24" W, 140 m, 25 Jun 2008, *Pruski, Ortiz & Amasifuen 4348* (AMAZ, HOXA, MO, USM; HOXA and USM are numbered incorrectly as 3448), same locality, 29 Dec 2011, *Pruski, Ortiz & Rios 4626* (IIAP-Iquitos, MO, US); Requena, white-sand (arena blanca) tierra firme along road bordering wet chamizal (= campina or caatinga scrub) in Jenaro Herrera-IIAP reserve, ca. 1.5 km E of herbarium building, ca. 4 km E of Rio Ucayali at Jenaro Herrera, 4° 54' 05" S, 73° 38' 20" W, 125 m, 2 Jan 2012, *Pruski, Ortiz & Dávila 4635* (F, HH, IIAP-Iquitos, MO, USM); Nauta, Reserva Nacional Pacaya-Samiria, Quebrada Pucate, 4° 44' 57" S, 73° 51' 56" W, 128 m, 6 Nov 2008, *Vásquez et al. 34589* (MO).

Representative extra-Peruvian specimens. BRAZIL. Acre. Cruzeiro do Sul, basin of Rio Juruá, BR-307 near intersection with Ramal Pentecostes, 12 Dec 2000, *Daly et al. 10654* (INPA, MO, NY, US). **Amapá.** Rio Jari, white sandy soil, 14 Jul 1961, *Egler & Irwin 45923* (NY, US; this is cited chromosome studies "anomalous count" voucher of Turner and King 1962); Rio Araguari, downriver from Porto Platón, 21 Sep 1961, *Pires et al. 51142* (NY); Aldeia, 15 Mar 1982, *Rabelo & Nonato 1577* (HAMAB, ULM); Rio Oiapoque, along Estrada de Cricu, about 2 km SE of Clevelandia, 2 Aug 1960, *Westra 47322* (K, NY, U, US). **Amazonas.** Across river from Maués, 20 Apr 1974, *Campbell et al. P22001* (K, MO, NY, S, US); Municipio de Borba, acima de Terra Preta, campina do rio Surubim, afluyente do rio Abacaxis, 4 Jul 1983, *Cid 4041* (K, MO, NY, US); Maués, rio Parauari, proximo Agua Mineral, 14 Jul 1983, *Cid 4128* (K, MO, NY, RB, US); Rio Abacaxis, across from Axinim, 8 Jul 1983, *Hill et al. 12990* (K, MG, MO, NY, RB, UB, US); Alto Amazonas, Ega (now Tefé), 1819–1820, *Martius s.n.* (M); Mun. de Manaus, Suframa, Rodovia BR 174, km 64,

then 23 km east, 29 Jan 1992, *Nee 42375* (MO, NY, US); Lago Tefé, mouth of Rio Bauana, 13 Dec 1982, *Plowman et al. 12557* (K, NY, RB, US); Ega (now Tefé), 1831, *Poeppig Addenda 124* (W); Manaus, SW corner of Reserva Ducke, sandy area in full sun, 11 Sep 1987, *Pruski et al. 3212* (F, INPA, K, LSU, MG, NY, RB, TEX, UB, UC, US); Manaus, 20 Aug 1928, *Tate 30* (NY); Manaus, Jul 1900, *Ule 5146* (B†, HBG, K, branchlet fragment in US figure 7; type of synonymous *Greenmania ulei* Hieron.); Across Rio Maués from town of Maués, 22 Jul 1983, *Zarucchi et al. 3141* (K, MG, MO, NY, RB, US). **Mato Grosso.** Cachoeirinha do Rio Peixoto, 24 Apr 1997, *Souza et al. 15592* (K). **Pará.** Belém, 19 Oct 1942, *Archer 7698* (K, NY, US); Carape, 1829–1830, *Burchell 9825* (K, NY, P); Belém, 12 Jul 1935, *Drouet 2055* (F, GH, MO, NY, S, UC); Cachoeira do Curuá, north of Serra do Cachimbo, 20 Feb 1977, *Kirkbride & Lleras 2944* (K, MO, US); Santarém, 1819–1820, *Martius s.n.* (M); Belém, 20 May 1968, *Philcox 5053* (MO); Almeirim, Estação Ecológica do Jari-SEMA, 24 Jun 1987, *Pires & Silva 1701* (K, MG, MO, NY); Marabá, Serra dos Carajás, N-4, próximo a transição para a mata, 19 Mar 1984, *Silva et al. 1879* (NY); Itaituba, km-63 da estrada Itaituba–Jacarecanga, P.N. Tapajós, 12 Nov 1978, *Silva & Rosario 3688* (NY, US); Para, July-Aug 1849, *Spruce 200* (K, W as *s.n.*); Bank of Rio Xingu, Altimira, Oct 1943, *Swallen 6911* (US); Belém, 25 Jul 1987, *Tsugaru & Sano B-472* (MO, NY); Camp. Lucia, aranosis, 1849–1855, *Wullschlägel 294* (NY, W), same data, *Wullschlägel 295* [Pl. Berlyn 54] (K, NY, W-2). **Rondônia.** Itapuã do Oeste, Floresta Nacional do Jamari, Pedra Grande, 21 Apr 2015, *Medeiros et al. 1660* (MO). **Roraima.** Igarapé Água Boa, rio Mucajaí between Pratinha and rio Apiaú, sandy high savanna at river bank, 22 Jan 1967, *Prance et al. 4009* (K, N Y, S, US). The material seen from Ceará labeled as *Unxia camphorata* is misdetermined. **COLOMBIA. Amazonas.** Puerto Santander, trocha a La Chorrera [this locality is along the Rio Caquetá near Araracuara and the border with Caquetá], 14 Aug 1986, *Battjes 801* (COAH). **Antioquia.** Puerto Berrio, 1 Dec 1931, *Archer 1458* (US). **Boyacá.** Vía Santa María al Alto La Burra, 750–800 m, 4 Oct 2007, *Fernández-Alonso et al. 25802* (COL). **Caquetá.** San Vicente del Caguán, sabanas del Yará, 210 m, 29 Aug 2016, *Cárdenas et al. 46771* (COAH); Montañita, reserva Las Dalias, 369 m, 31 May 2013, *Trujillo 2753* (COAH, HUAZ). **Guainía** (sometimes as Vaupés on labels). Región de San Felipe a orillas del río Guainía, 250 m, 21 Nov 1948, *Araque Molina & Barkley 18Va015* (COL, US); Inirida, resguardo indígena Almidón-Ceiba, cercanías La Ceiba (this is very near the Río Orinoco at San Fernando de Atabapo, Venezuela), 80–90 m, 19 Oct 1998, *Prieto et al. 761* (COL, MO); Vicinity of San Felipe, ca. 600 ft, 6 Nov 1952, *Schultes et al. 18293* (NY, US). **Guaviare.** Mun. San José del Guaviare, Serranía de La Lindosa, 315 m, 25 Oct 2016, *Barona et al. 4284* (COAH); Mun. San José del Guaviare, Serranía de la Lindosa, 300–450 m, 5 Aug 2007, *Cárdenas et al. 20823* (COAH). **Meta.** Llanos de Cumaral, *André 1120* (GH); Mun. S. Juan Arama, SW de la Sierra de la Macarena, Estación La Curia, 580–600 m, 23 Sep 1987, *Fuertes et al. 344* (COL, MA, MO, US); Parque la Macarena, por el camino que conduce del río Guayabero al caño cristales, 400 m, 1 Aug 2000, *López et al. 6728* (COAH); Villavicencio, 450 m, 26–31 Aug 1917, *Pennell 1402* (NY, US). **Vaupés.** Mun. de Mitú, comunidad Cerrito Verde, 200 m, 19 Jun 2024, *Barona et al. 7841* (COAH); Río Pirá - Paraná, comunidad Piedra Ñi, 200 m, 3 Apr 2009, *Betancur & Cardenas 14069* (COAH, COL); Mitú, entre la comunidad Mitú Cachivera y el cerro Guacamaya, suelo arenas blancas, 180–370 m, 24 Sep 2007, *Cárdenas et al. 21092* (COAH); Río Vaupés, a Mitú, bassin de l'Amazone, 320 m, 7–8 Nov 1952, *Humbert & Fernandez 27238* (P, US); Mun. de Mitú, Villa Fátima, 282 m, 22 Jun 2024, *J. Velez et al. 8802* (COAH). **Vichada** (These two localities are along the Rio Negro just north of Puerto Ayacucho, Venezuela). Puerto Carreño, corregimiento de Santa Rita, loma granítica, 150 m, 13 Dec 1993, *Cortés et al. 1184* (COL); Puerto Carreño, 23–24 Oct 1938, *Cuatrecasas & Barriga 4069* (COL, US). **Without Dept.** In monte Bolador, Aug 1888, *Sonntag 51* (B†, fragment in US; type of synonymous *Greenmania boladorensis*; there is a Cerro El Volador in Antioquia near Medellín). **Without Dept., seemingly near border of Bolivar, Cesar, and Magdalena.** Rincon Hondo, Magdalena valley, 18 Aug 1924, *Allen 425* (F, MO); La Jagua, Magdalena valley, dry exposed savana, 5 Sep 1924, *Allen 573* (MO). **FRENCH GUIANA.** Vicinity of Cayenne, 13 Jun 1921, *Broadway 486* (NY, US); 10 km from St. Laurent, white-sand savanna, 20 Dec 1954, *Cowan 38947* (MO, NY, US); Route de Belizon-R.N. 2, 1 Jun

1988, *Cremers 10043* (MO, NY, P, US); Laussat, bassin de la Basse-Mana, 15 Apr 1989, *Cremers & Hoff 10634* (MO, NY, P, US); Montagne de Kaw, 251 m, 7 Mar 2011, *Croat & Ferry 102770* (MO, NY); Along road from St. Georges to Saut Maripa, 40 m, 28 Aug 2011, *Croat 103337* (MO, NO); Tumuc-Humac, granitique, 550 m, 6 Aug 1972, *de Granville 1128* (P, US); Haut Camopi, Mont Belvédère, savane roche, 250 m, 21 Nov 1984, *de Granville 6918* (CAY, MO); "Guiane," 1836, *Leprieur s.n.* (P); Cayenne, 1792, *LeBlond 346* (holotype: G; type of synonymous *Unxia hirsuta* fide Pruski 1998); Mataroni River, Savanne de Virginie, inselberg, 4 May 2001, *Mori et al. 25277* (NY); Dans la Guiane francoise, 1817–1822, *Poiteau s.n.* (holotype: K-herb. Gay; type of synonymous *Pronacron ramosissimum*); Montagne des Chevaux, 26 Jul 2007, *Tostain 735* (MO, US). **GUYANA.** Cuyuni-Mazaruni, Karowtipu Mt., 1000 m, 21 Apr 1987, *Boom & Gopaul 7582* (NY, US); Demerara-Mahaica, Ceiba Biological Center, Madewini, low forest on pure white-sand, 27–30 m, 8 Jan 2011, *Croat 101619* (K, MO, NO, TEX); Upper Rupununi River, near Dadanawa, 24–29 Jul 1922, *de la Cruz 1698* (F, MO, NY, US); Pomeroon District, Mora landing, Moruka River, 21–23 Aug 1922, *de la Cruz 1826* (F, MO, NY, US); Kangaruma, 25–27 Jun 1921, *Gleason 202* (NY, US); Rockstone, 13–30 Jul 1921, *Gleason 510* (NY, US); Demerara-Mahaica, Santa Mission, 0–200 m, 9 Nov 1992, *Görts-van Rijn et al. 456* (MO, U, US); Demerara-Mahaica Region, 16 mi S of Georgetown, savannas on white-sand, 1–50 m, 7 Dec 1986, *Pipoly et al. 9138* (MO, NY, US); Savannas of the Rupununi (as Rupunoony), 1837, *Rob. H. Schomburgk Ser. 1, 380* (BM, F, NY, US, W); sin. loc., 1841, *Rob. H. Schomburgk Ser. 2, 60* (NY, US, W); Bassin of the Essequibo River, Kurupukari, 3 Oct 1937, *A.C. Smith 2175* (F, NY, US); Demerara-Mahaica, Ceiba Reserve, 22 Feb 2004, *Torke et al. 288* (MO, NY). **PANAMA.** Canal Zone, sabanas along drowned Rio Azote Caballo, 66–70 m, 7 Dec 1934, *Dodge et al. 16839* (MO); Hills northeast of Hacienda La Joya, 50–300 m, 9 Dec 1934, *Dodge et al. 16878* (MO); Canal Zone, near Goofy Lake, Cerro Azul, 24 Aug 1960, *Ebinger 985* (MO); 2–3 miles S of Goofy Lake, rd. to Cerro Jefe, 2000–2200 ft, 10 Dec 1966, *Lewis et al. 277* (GH, MO, UC, US); "About Panama," ad rios [illegible], Nov 1846, *Seemann 46* (BM, K-Hooker, MEL, fragment in US; type of synonymous *Unxia digyna*); Canal Zone, Corozal, 0–25 m, Dec 1923, *Standley 27385* (US). **SURINAM.** Near Scotelberg, 1934, *Archer 2653* (US); Sipaliwini, along road from Zanderij to Apoera, 64 m, 17 Feb 2011, *Croat & Ferry 102347* (BM, MO, NY); Habitat in Surinami locis arenosis, 1754–1755, *Dahlberg s.n. (?105)* (LINN-1010.1; lectotype of *Unxia camphorata*); Prope Post Oranjewoud, s.d., *Focke 681* (U); Talouakem, Inselberg, Monts Tumuc-Humac, 700 m, 31 Jul 1993, *de Granville et al. 11926* (US); In campis arenosis prope stationem Victoriam, Dec 1843, *Kappler 1399* (MO); Sectie O, 3 Aug 1920, *Pulle 148* (MO, U); prope Paramaribo, 1754–1755, *Rolander 25* (SBT-Bergius); Sipaliwini, Kayserberg Airstrip savanna, 235 m, 4 Jun 2003, *Rosario 1871* (K, MG, MO, U); sin. loc., s.d., *Tullekan s.n.* (MO); Nature Reserve Brinckheuvel-Sabanpasi, 1 Sep 1967, *Wildschut & Teunissen 11554* (US). **VENEZUELA.** **Amazonas.** Vicinity of Puerto Ayacucho, below 100 m, 22 Nov 1984, *Croat 59242* (MO, NY); San Carlos Rio Negro, 100 m, 28–29 Jan 1930, *Holt & Gehriger 311* (NY, US); NW edge of San Carlos de Río Negro, 120 m, 10 Apr 1979, *Liesner 6469* (MO, NY); Crystalline laja, 1–1.5 km E of Puerto Ayacucho, 100–120 m, 7 Nov 1953, *Maguire et al. 36062* (NY, US); Grand rapids of the Orinoco, 15 km south of Puerto Ayacucho, 100–120 m, 9 Nov 1953, *Maguire et al. 36087* (F, MO, NY); Ayers, Orinoco, 1839, *Schomburgk s.n.* (US); Piedra Guachapita, 2 km arriba da Solano en el bajo Casiquiare, 26 Nov 1984, *Stergios & Aymard 7326* (MO, NY); Río Pasimoni, entre la boca y Piedra Arapacoa, 175 m, 20–30 Oct 1986, *Stergios et al. 9520* (MO, NY); Laja margin along Cano Cupaven, Rio Orinoco opposite mouth of Rio Atabapo, 125–150 m, 5 Jun 1959, *Wurdack & Adderley 42802* (NY, S, US); Caño Caname, Rio Atabapo, 5 km below Guarinum, 125–140 m, 8 Jun 1959, *Wurdack & Adderley 42867* (F, NY, US). **Bolivar.** Distrito Cedeño, vicinity of Panare village of Corozal, granitic slopes, 370 m, 16 Oct 1985, *Boom & Grillo 6398* (MO, NY); Vicinity of Icabarú, white sand soil, 600 m, 25 Jul 1982, *Croat 54129* (MO, NY); W del río Cuchivero, 220 m, Nov 1988, *Fernández 232* (NY, PORT); 43 km S of Los Pijiguaos, 100 m, 4 Nov 1985, *Holst & van der Werff 2601* (MO); Independencia along Río Pauji, 800–900 m, 13 Nov 1985, *Liesner 20030* (MO); Sierra de Lema, 50 km SE de El Dorado, 300 m, 1 Sep 1961, *Steyermark 89678* (NY, US); Suroeste de Icabarú, savanna,

450 m, 17 Dec 1978, *Steyermark et al. 117715* (MO); Savanna, 261 km SW of Caicara del Orinoco, 100 m, 5 Sep 1985, *Steyermark et al. 131405* (MO); Rio Pargueni, N of river mouth, 90–100 m, 11 Dec 1955, *Wurdack & Monachino 39807* (F, NY, US). **Yaracuy**. Gravel road 5.2 km east of Salom, 780–790 m, 4 Aug 1982, *Croat 54587* (MO). *Unxia camphorata* has also been recorded for Cojedes, Mérida, Miranda, Portuguesa, and Táchira.

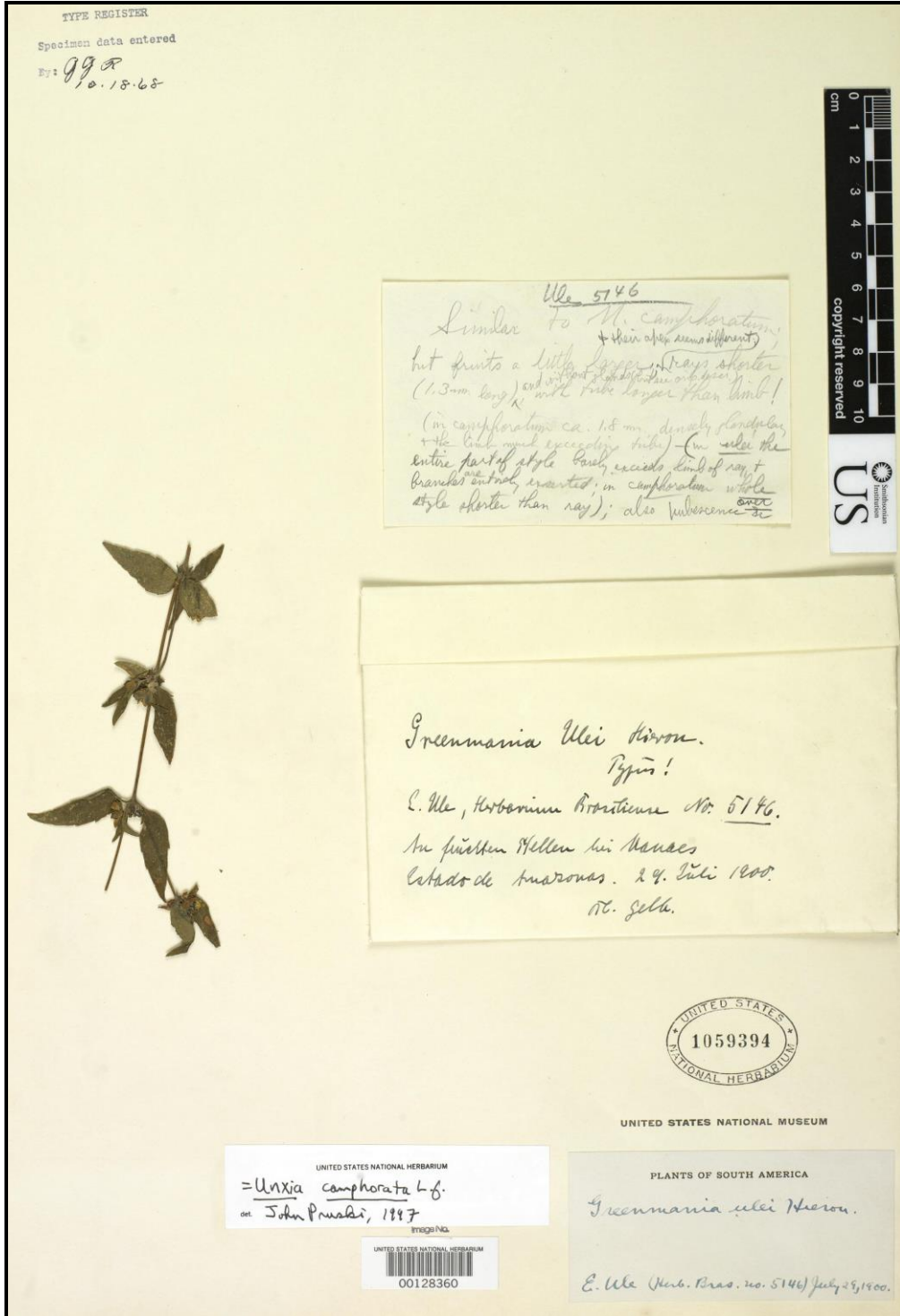


Figure 7. Isotype of synonymous *Greenmania ullei* Hieron. (= *Unxia camphorata* L.f.) (*Ule 5146*, US).



Figure 8. Flowering (upper) and budding (center bottom) capitula of *Unxia camphorata* L.f. in Loreto, Peru, lateral view showing white-pilose outer phyllaries. (Pruski *et al.* 4635, photograph by Rosa Ortiz).



Figure 9. Mid-stem node of *Unxia camphorata* L.f. in Loreto, Peru, showing white-pilose stems with trichomes longer than the stems are wide, opposite plinerved leaves, a few reflexed phyllaries of a post-fruiting capitulum in image center, and a dichotomous pair of elongate axillary-lateral branches overtopping the terminal (that seems axillary) subsessile capitulum (Pruski *et al.* 4348).

Distribution and ecology. *Unxia camphorata* flowers year-round and has been collected from sea level to about 900(–1200) meters elevation in a variety of habitats including in sandy savannas and on granite lajas. *Unxia camphorata* seems best known from relatively low elevational material flowering mostly from November to January. Much information of such habitats has been provided by, e.g., Adeney et al. (2016), Anderson (1981), Chrostowski and Denevan (1970), Daly et al. (2016), Devecchi et al. (2020), García-Villacorta et al. (2016), Gröger and Huber (2007), Huber (1982, 1995), Keel and Prance (1979), Macedo and Prance (1978), Pires and Prance (1985), Prance (1996), Prance and Schubart (1978), and Sarthou and Villiers (1998). *Unxia camphorata* is widespread from Panama to northern South America (Brazil, Colombia, French Guiana, Guyana, Peru, Surinam, and Venezuela, but not known in either Ecuador or Bolivia). The species has not been found in Central America northwest of Panama, nor has it been reported in the West Indies. The collections cited herein document *Unxia camphorata* in Peru (Fig. 6), where it represents a new generic record for the country.

The cut stems and crushed leaves of *Unxia camphorata* have a strong camphor-like odor, and preparations from the plant are widely used medicinally in Amazonia and Guayana (Pruski 1997, 1998). Some genera misdetermined as *Unxia* of tribe Millerieae in herbaria and databases include *Blainvillea* Cass., *Eleutheranthera* Poit., *Riencourtia* Cass., and *Synedrella* Gaertn. Although *Unxia camphorata* is Amazonian-centered and has functionally staminate disk florets, by its delicate stems, somewhat similar leaf shape, and long internodes it recalls widespread pantropical mostly bisexual-disked tuberculate-fruited *Eleutheranthera ruderalis* (Sw.) Sch. Bip. *Blainvillea*, *Riencourtia*, and *Synedrella* are coarser genera of Heliantheae subtr. Ecliptinae (*Eleutheranthera* is also placed in subtr. Ecliptinae) and these genera of Ecliptinae are distinguished from *Unxia* by having fibers associated with the five primary nerves of their disk corolla throats (Pruski and Robinson 2018). Moreover, Amazonian and Guayanan materials of *Riencourtia*, although having functionally staminate disk florets, differ by herbage with mostly stiff trichomes. *Unxia camphorata* recalls widespread neotropical *Jaegeria hirta* (Lag.) Less. and in overall aspect-gestalt recalls the epappose form of Andean *Galinsoga unxioides* Griseb., but these two further genera of Millerieae differ from *Unxia* by bisexual disk florets.

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