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THE IDENTITY OF TWO WATER-DISPERSED SPECIES OF HETEROPTERYS (MALPIGHIACEAE): H. LEONA AND H. PLATYPTERA

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ABSTRACT. A complex in *Heteropterys* composed of water-dispersed species was found to comprise two species, *H. leona* (Cav.) Exell and *H. platyptera* DC., differing most notably in their samaras. *Heteropterys leona* occurs mostly in Atlantic coastal regions, in the New World from Belize to northern Brazil, and in Africa from Senegal to Angola. The synonyms *H. reticulata* (Poir.) Nied. and *H. multiflora* (DC.) Hochr. commonly have been applied to the New World populations and the superfluous name *H. africana* to the Old World representatives. *Heteropterys platyptera*, also known by the synonym *H. longifolia* (Sw.) Nied., is restricted to the Lesser Antilles. The morphology, distribution, and extensive nomenclature are reviewed, and illustrations of the samaras are provided.

INTRODUCTION

The genus *Heteropterys* H. B. K. (Malpighiaceae) comprises well over 100 species found in the Neotropics, except *H. leona* (Cav.) Exell, which occurs also in West Africa. Cavanilles (1790) based his *Banisteria leona* on specimens from Sierra Leone and the New World, and suggested that it had perhaps been introduced to Africa ("fortasse ex America adsportata"). Subsequent authors considered, although hesitatingly, the American and African plants to belong to two separate species, and some also recognized a third species limited to the Lesser Antilles. Current floristic projects of Central and South America prompted a re-examination of this complex and its attendant tangled nomenclature. Two species are recognized here: *H. platyptera* DC. of the Lesser Antilles and *H. leona* (Cav.) Exell, comprising the African and remaining American elements.

MORPHOLOGICAL VARIATION AND DISTRIBUTION

Heteropterys is one of the wing-fruited genera of Malpighiaceae. The fruit is a schizocarp splitting into three samaras. Typically, each samara is composed of a nut bearing an elongated dorsal wing thickened along the lower (abaxial) margin. *Heteropterys platyptera* and *H. leona* grow in wet habitats, and their samaras are modified for dispersal by water. The locule is surrounded by abundant aerenchyma, which presumably allows the samara to float, and contains a seed much larger (ca. 1.5–2 × 1–1.5 cm) and thus heavier than in wind-dispersed species. In *H. platyptera* (Fig. 1) the elongate wing is retained, whereas in *H. leona* (Figs. 2, 3) the samara is flabellate and roughly as long as wide, somewhat similar to the samaras of *H. orinocensis* (H. B. K.) Adr. Juss., a riverine species common in the Orinoco and Amazon basins. As in many wing-fruited species of Malpighiaceae that have become adapted to water dispersal, the wing is variable in size and shape, and particularly

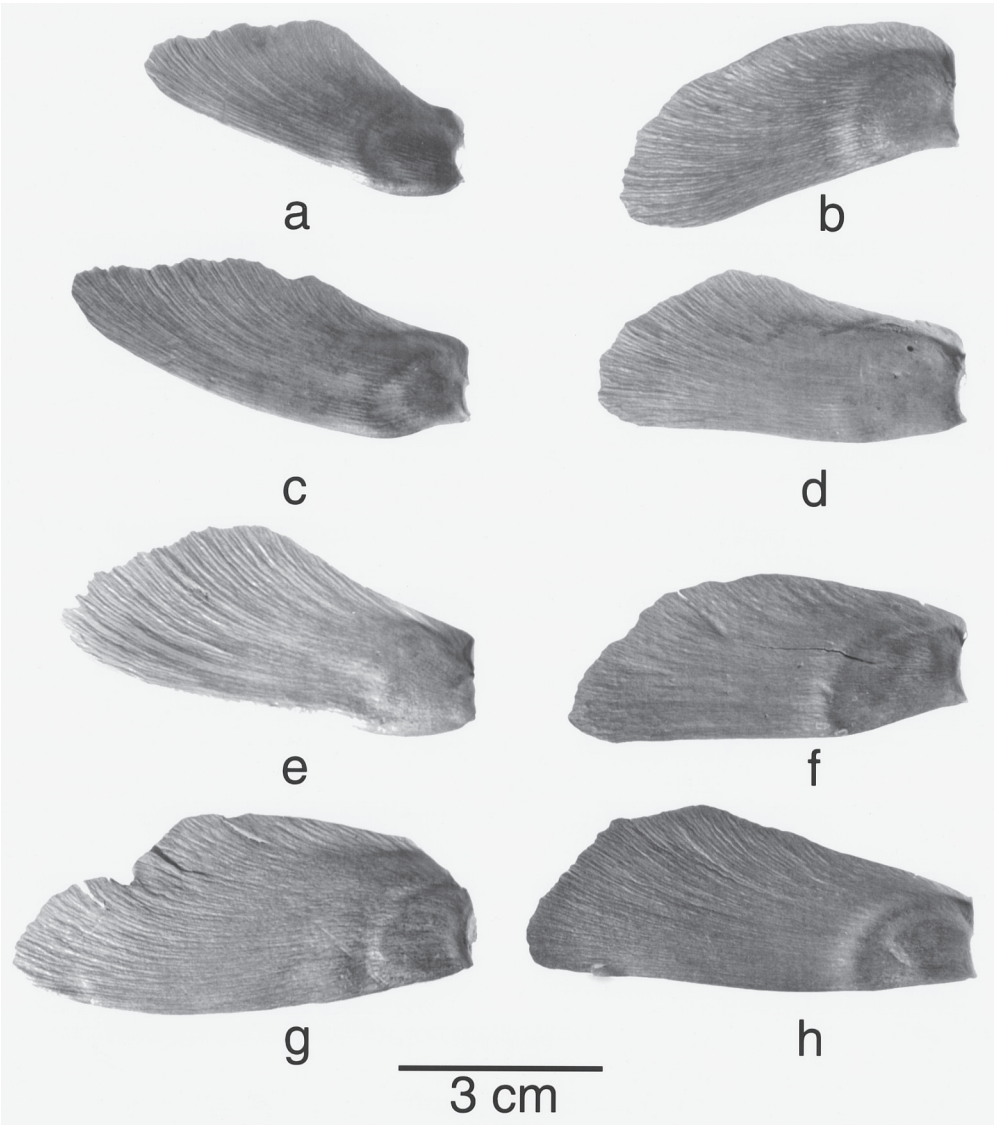

FIG. 1. Samaras of *Heteropterys platyptera* from the Lesser Antilles. a. St. Lucia (*Sturrock 530*, A). b. Martinique (*Stehlé & Stehlé 4802*, US). c. Guadeloupe (*Questel 5047*, US). d. Martinique (*Stehlé & Stehlé 6444*, US). e. St. Vincent (*Smith & Smith 1549*, US). f. Dominica (*Hodge 551*, GH). g. Dominica (*Fishlock 23a*, NY). h. Dominica (*Hill 25747*, NY).

so in *H. leona*. In that species the samara may be nearly semicircular in outline, or the wing may extend well below the nut or even nearly encircle it; the wing is usually somewhat longer than wide but sometimes almost as wide as long.

In the New World, *H. leona* is widely distributed along the Atlantic Coast from Belize to northern Brazil (Pará), but also in Pacific Colombia (Chocó, Valle). Niedenzu (1903, 1928) also reported it (as *H. reticulata*) from the Brazilian state of Amazonas, but the collection cited (*Poeppig 2645*, G!) proved to be *H. prancei* W. R. Anderson (W. R. Anderson, pers. comm.). *Heteropterys leona* occurs on Trinidad and has been recorded three times from Jamaica, where it is rare (Adams 1972).

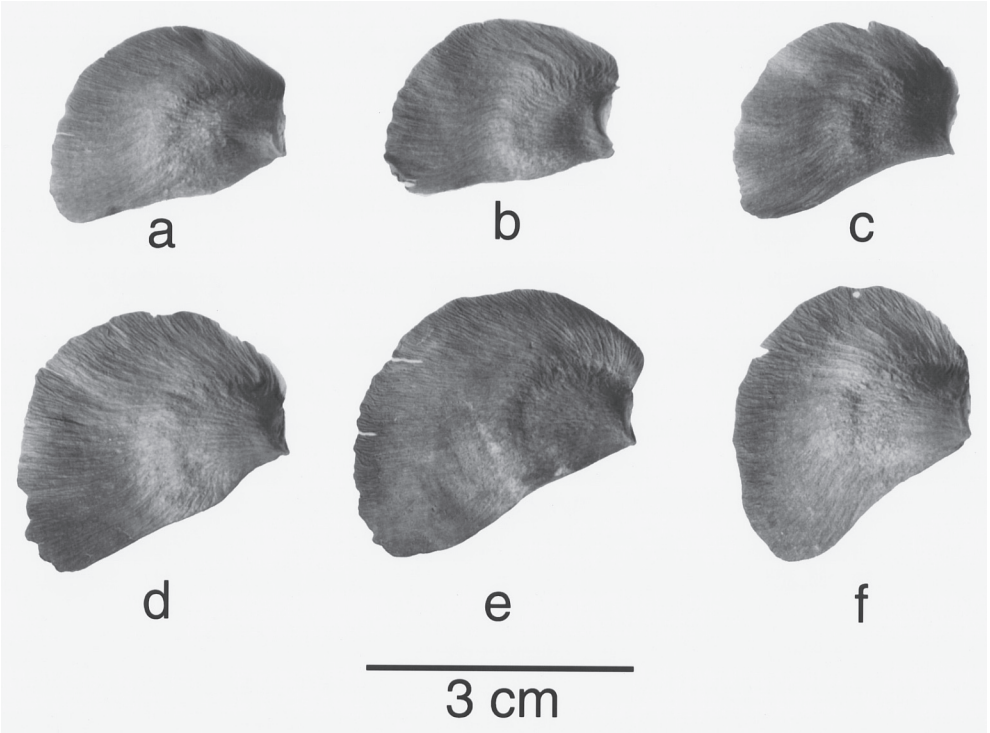

FIG. 2. Samaras of *Heteropterys leona* from Africa. a. Liberia (*Adam 21349*, MO). b. Equatorial Guinea (*Carvalho 3425*, MO). c. Gabon (*Reitsma 2467*, NY). d. Nigeria (*Okafor & Latilo FHI57277*, MO). e. Cameroon (*Zenker 1107*, MO). f. Cameroon (*Thomas 2159*, MO).

Although most collections are from coastal areas, *H. leona* has on occasion also been found inland (e.g., in Guyana near Dadanawa on the Rupununi River, *de la Cruz 1414, 1462*). In West Africa, it occurs in coastal regions from Senegal to Angola. A similar disjunction is also known for *Stigmaphyllon bannisterioides* (L.) C. Anderson [synonyms: *Stigmaphyllon ovatum* (Cav.) Nied.; *Brachypterys ovata* (Cav.) Small], a species of seashores, beaches, mangrove swamps, and salt marshes (C. Anderson 1997). In the New World *S. bannisterioides* occurs along the Atlantic Coast from southern Mexico (Veracruz) to northern Brazil (Maranhão) and in the West Indies, in the Old World in coastal areas of Guinea Bissau, Guinea, and Sierra Leone.

The populations of *H. leona* show quantitative differences in size of leaves and aspects of floral structure but few qualitative differences; none are correlated with geographic range. The variation is greater among the American populations than the African ones, but no characters separate the African specimens from the American ones, and they cannot be maintained as separate species. Differences include the nature of the abaxial epidermis, shape of petals, presence/absence of anther pubescence, presence/absence of a dorsal claw at style apex, and size and shape of samara. Also, the flowers vary somewhat in size, but all the parts then vary proportionally. The cells of the abaxial epidermis may be somewhat convex, giving a blistered appearance, or extended into prominent papillae to 0.03 mm long and easily discerned at low magnification. The papillate condition may lend a whitish sheen to the leaf surface, which was already noted by Jussieu (1843). All

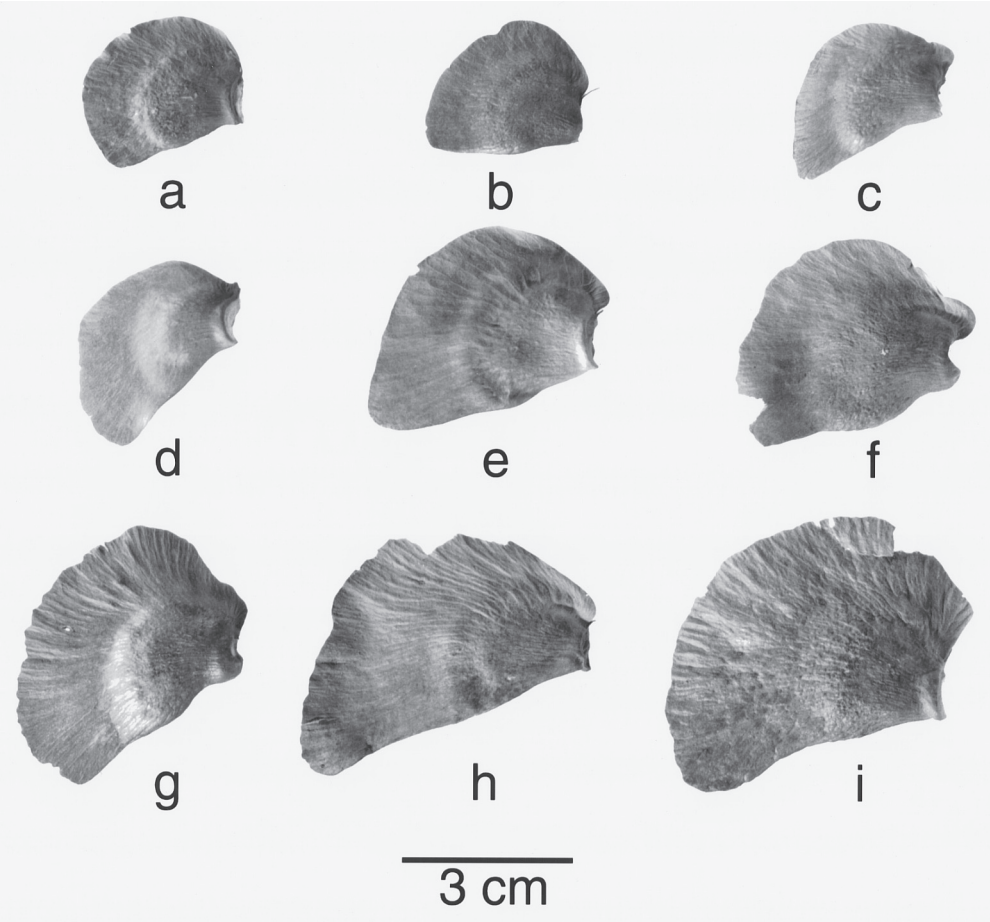

FIG. 3. Samaras of *Heteropterys leona* from the New World. a. Brazil (*Maguire et al. 47120*, NY). b. French Guiana (*Cremers & Hoff 11239*, US). c. Nicaragua (*Moreno & Sandino 12141*, MO). d. Honduras (*Vargas et al. 355*, NY). e. Guyana (*Gillespie 1203*, MICH). f. Colombia (*Albert de Escobar 3245*, NY). g. Jamaica (*Britton 1484*, NY). h. Colombia (*Cuatrecasas 15936*, US). i. Guyana (*Fanshawe 531*, NY).

specimens seen from Africa, Venezuela (and Trinidad), and French Guiana have the leaves abaxially papillate. Those from Central America, Colombia, and Suriname are either papillate or blistered. None of the collections seen from Jamaica, Guyana, and Brazil are papillate. The limb of the petals varies from broadly triangular to orbicular; in specimens from Central America and Brazil only orbicular limbs are present, but the condition is so variable elsewhere that the absence of the triangular shape may only indicate an inadequate sample. The anthers are glabrous in all African specimens examined. They commonly bear apical and basal tufts of hairs in plants from the New World, but the hairs may also be very few (and then difficult to see) or absent. The styles bear the stigma on the apex at the adaxial angle, a placement traditionally called an "internal" stigma. The apex is drawn out abaxially into a dorsiventrally flattened claw (up to 0.6 mm long) but sometimes only into a spur as short as 0.1 mm. In African specimens, the stylar claws measure (0.1–) 0.2–0.4 mm long. In the American samples, the claws in general are ca. 0.2–0.3 mm long and in larger flowers reach 0.4–0.6 mm, but

flowers with styles extended only into a short spur occur occasionally. The longest claws (0.55–0.6 mm) were seen in flowers from the Guianas and Brazil, whereas in samples from Central America the claws did not exceed 0.3 mm.

As already noted above, there is much variation in the size and shape of the samara's wing in *H. leona*, but the greater diversity is found in the New World (compare Fig. 2 with Fig. 3). When contrasting samaras, care must be taken to assure that they are mature or nearly so. From fruiting specimens in various stages of maturity, it is evident that the wing increases first in length. Thus, young samaras of *H. leona* show an elongated wing, whereas the mature ones exhibit the flabellate condition. Samaras from African material are generally small and semicircular (ca. 3–3.5 × 2–2.5 cm; Fig. 2) and are comparable to those seen from Central America, French Guiana, and Brazil (Fig. 3a–d). None of the collections seen from Costa Rica and Panama have mature samaras; immature samaras have the wing somewhat longer than wide, but again this may only indicate that the wing is not fully expanded, as in fruiting collections from other areas. The larger samaras (up to ca. 6 × 4 cm) with a more elaborate wing are found only in the New World (Fig. 3e–i). The samara of the fruiting collection from Jamaica (Fig. 3g) is most similar to those from Guyana (Fig. 3e, i); however, no fruiting collections from Venezuela and Trinidad were available for study.

The plants from Africa, the American mainland, Jamaica, and Trinidad are here recognized as representatives of one somewhat variable species, *H. leona*. Specimens from the Lesser Antilles differ in two distinct characters and one subtler aspect, and are here retained as a separate species, *H. platyptera*. The samaras of *H. platyptera* (Fig. 1) have a large elongated wing, always more than twice as long as wide (ca. 6–7 × 2.5–3 cm). In addition, the bracts are eglandular; in *H. leona* the bracts bear 1–5 minute glands on each margin. *Heteropterys platyptera* also differs in the apical ornamentation of the styles. Commonly the anterior style is dorsally rounded or bears a very short spur (0.05–0.1 mm), whereas the posterior styles lack an apical spur. Sometimes all styles are apically dorsally rounded, and sometimes all are spurred. Very rarely is the spur up to 0.2 mm long. *Heteropterys platyptera* and *H. leona* grow in similar wet habitats, but *H. platyptera* has not been reported from mangroves.

Niedenzu (1928) cited a record from Puerto Rico for *H. longifolia* var. *borealis* [=*H. platyptera*] based on a specimen by an unknown collector in the Ventenat Herbarium (G!); this collection is *H. leona*. Although it is possible that it represents a rare introduction, it is much more likely that the locality is in error. Aside from determinations by Adrien de Jussieu, the label bears only the words "Porto Rico" and "herb. Ventenat" by an unknown hand. No other Puerto Rican collections of this showy species are known, nor is it listed in floristic accounts of the island (e.g., Urban 1905–1911; Stahl 1936; Liogier & Martorell 1982).

CHROMOSOME NUMBER

Only one chromosome report has been published for the complex here examined, a count of 2n=20 from root tips of unvouchered African material (Mangenot & Mangenot 1962). W. R. Anderson (1993) noted that subfamily Malpighioideae, which includes *Heteropterys*, is characterized by chromosome numbers based on n=10; his reports in the same article of counts in other species of *Heteropterys* are all n=10.

NOMENCLATURE AND TYPIFICATION

Owing to a tortuous taxonomic and nomenclatural history, a diversity of names has been applied throughout the floristic literature to the two species here discussed. Jussieu (1840, 1843) recognized the African component of *H. leona* as his *H. africana* and all American collections as *H. platyptera.* Niedenzu (1903, 1928) also used the name *H. africana* but recognized two New World species; he referred the Central and South American specimens to *H. reticulata* and the Lesser Antillean material to *H. longifolia*. Later authors, aware that *H. africana, H. reticulata,* and *H. longifolia* are illegitimate names, applied the names *H. leona, H. multiflora*, and *H. platyptera*, respectively. Additional synonyms, which did not gain widespread use, are listed below in the synonymies for each species.

The earliest name for the species here recognized as *H. leona* is *Banisteria leona*, published by Cavanilles in 1790. Cavanilles cited a Smeathman gathering in Thouin's herbarium and unspecified American collections in the Jussieu herbarium. The Smeathman sheet consists of a flowering shoot of *H. leona*, a fragment apparently taken from a Smeathman specimen at BM, and a mounted packet containing samaras of *Acridocarpus* Guill. & Perr. The flowering branch has associated with it a strip of paper bearing "Banisteria leona. Cav. Diss." in Cavanilles's hand and is here designated the lectotype. This Smeathman sheet is now at MPU; Peter A. Schäfer, Conservateur des Herbiers, generously provided detailed information about the discordant elements and the annotations associated with them.

Candolle (1824), in the treatment of the Malpighiaceae for his *Prodromus*, recognized that Cavanilles's name applied to a mixed gathering and restricted the name *Banisteria leona* to the flowering material of the Smeathman collection by excluding the samaras. Adrien de Jussieu (1843), the first monographer of the Malpighiaceae, moved *Banisteria leona* from the diverse assemblage that constituted the genus *Banisteria* into *Heteropterys*; however, he applied his own and superfluous name *Heteropterys africana*. He, too, excluded the fruits on the Smeathman sheet from the type of *Heteropterys africana* [=*Banisteria leona*]; these samaras constitute the holotype of *Acridocarpus cavanillesii* Adr. Juss. Both parts of the Smeathman collection bear Jussieu's annotations: attached to the flowering shoot a strip of paper with "Heteropterys africana. Ad. Juss." and on the packet his inscription "Acridocarpus Cavanillesii. Ad. Juss." Hooker (1849) published an additional name, *Heteropterys jussieui*, based on Don and Vogel specimens with larger-winged samaras than what Hooker considered typical for "*H. africana*," though these proved to be encompassed by the morphological variation of *H. leona.* Later authors, including Niedenzu (1903, 1912, 1928), followed Jussieu until Exell (1944) published the combination *Heteropterys leona*, the correct name for the species in *Heteropterys*.

Poiret (1816) published the earliest name for the American mainland element, *Malpighia reticulata*, for a Martin collection from Cayenne. Candolle did not see Poiret's type and in his *Prodromus* (1824) mistakenly assigned it to *Byrsonima*. As already noted, he, too, limited *Banisteria leona* to African material; he assigned the American representatives to his new species *Banisteria multiflora*, based on a Patris specimen, also from Cayenne, but noted the great similarity to *B. leona* ("valde accedit B. leonam"). Niedenzu (1903) corrected Candolle by publishing the combination *Heteropterys reticulata*, but that name was already occupied by the earlier *Heteropterys reticulata* Griseb. (1858). Hochreutiner (1910) used the next available epithet and formed the combination *Heteropterys multiflora*.

The names *H. reticulata* and *H. multiflora* are found throughout the floristic literature for the American representatives of *H. leona* and here are considered synonyms of *H. leona*.

Swartz published *Banisteria longifolia*, the earliest name for the Lesser Antillean species, with a brief diagnosis in his *Prodromus* (1788). He provided a more detailed description in volume 1 of his *Flora Indiae occidentalis* (1797), in which he noted that he saw only fruits but no floral parts, except the calyx. Types of names published by Swartz are often not readily traced, and original material for *B. longifolia* had been not been located until now. Niedenzu (1903) cited an Isert collection of 1787 from Martinique (C!) as probable type material ("*Banisteria longifolia*, specimen originarium, ut videtur"), but this is a flowering specimen, and there is no evidence that Swartz saw it. The Swartz Herbarium at S includes two sheets of a Swartz gathering from Guadeloupe that constitute the type collection. One sheet, here designated the lectotype, consists of a branch bearing two leaves and several inflorescences in immature fruit. On the back the sheet is annotated at the top in pencil by Swartz as "Banisteria longifolia. Guadel."; Swartz's note was partially overwritten in ink by Casstroem, who also repeated the same information at the base of the sheet. A second sheet at S bears fragments of this collection, a partial leaf and, in a mounted packet, pieces of the inflorescence; this sheet also has Swartz's penciled annotation "Banisteria longifolia" (attested by Wikstroem's note "Swartz scripsit"). Roger Lundin, Curator of the Regnellian Herbarium, kindly searched for this collection, and provided interpretation and attribution of the handwritings.

Persoon (1805) also published a name for the Lesser Antillean species, *Banisteria macrocarpa*, based on a Terrason specimen from Martinique in the Jussieu herbarium. In his *Prodromus* Candolle (1824) described a fruiting specimen from Guadeloupe as *Heteropterys platyptera*, unaware that the earlier names *Banisteria longifolia* Sw. and *Banisteria macrocarpa* Pers. applied to his new species. Jussieu (1843) recognized the synonymy but chose to use Candolle's name, the earliest in *Heteropterys*. It should be noted that Jussieu considered *Banisteria multiflora* DC. a synonym of *H. platyptera;* since these names were published simultaneously, Jussieu's choice must be followed. Niedenzu (1903) made the combination *Heteropterys longifolia* but again created a later homonym, for *Heteropterys longifolia* H. B. K. (1822). He should have proposed a combination based on Persoon's name, but that is now occupied by *Heteropterys macrocarpa* (Nied.) Kralik (1908). The earliest legitimate name for the Lesser Antillean species in *Heteropterys* is *Heteropterys platyptera.*

TAXONOMY

Heteropterys leona (Cav.) Exell, Cat. S. Tomé 123. 1944. *Banisteria leona* Cav., Diss. 9: 424. 1790. *Heteropterys africana* Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 276. 1840, nomen superfl. *Heteropterys africana* var. *borealis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 55. 1903, nomen superfl. *Heteropterys africana* var. *borealis* f. *nigritiana* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 55. 1903, nomen superfl.—TYPE: SIERRA LEONE, *Smeathman s.n.*, the flowering branch only (lectotype, here designated: MPU; isolectotype: BM!). [The samaras contained in the packet on the sheet at MPU constitute the holotype of *Acridocarpus cavanillesii* Adr. Juss.]

Malpighia reticulata Poir., Encycl. méth. Bot. Suppl. 4: 8. 1816. *Byrsonima reticulata* (Poir.) DC., Prodr. 1: 581. 1824, non *Byrsonima reticulata* Griseb., 1849. *Heteropterys reticulata* (Poir.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 54. 1903, non *Heteropterys reticulata* Griseb. in Mart., 1858. *Banisteria reticulata* (Poir.) C. B. Rob. in Small, N. Amer. Fl. 25(2): 138. 1910.—TYPE: FRENCH GUIANA. Cayenne, *Martin s.n.* (holotype: FI, photo: MICH!; isotype: P-JU 11628+B, photo and microfiche: MICH!).

Banisteria multiflora DC., Prodr. 1: 589. 1824, non *Banisteria multiflora* Adr. Juss., 1840. *Heteropterys multiflora* (DC.) Hochr., Bull. New York. Bot. Gard. 6: 277. 1910.—TYPE: FRENCH GUIANA. Cayenne, *Patris s.n.* (holotype: G-DC, photos: GH! MICH!, microfiche: MICH!; isotype: G!).

Banisteria magnoliifolia Desv. ex Hamilton, Prodr. Ind. occ. 40. 1825.—TYPE: "Herb. Prof. Desv. Guyana" (holotype: not located).

Heteropterys jussieui Hook. f., Niger Flora 246. 1849.—TYPE: SIERRA LEONE, *Don s.n.* (lectotype, here designated: BM!, fragment of lectotype: K!).

Heteropterys africana var. *borealis* f. *senegalensis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 55. 1903.—TYPE: [GUINEA]. "Senegambié. Croit dans les partis supérieurs du rio Nuñez et du rio Pongos," *Heudelot 892* (holotype: B, destroyed; isotypes: G! K! P-JU; microfiche of P-JU isotype: MICH!).

Heteropterys africana var. *australis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 55. 1903.—TYPE: CAMEROON. Bipindi, 1896, *Zenker 1107* (lectotype, here designated: MO!; isolectotypes: G! K!).

Figs. 2, 3.

Liana, scandent or climbing shrub to 10 m, sometimes a shrub to 6 m, or rarely a small tree. Lamina of the larger leaves 10–37.5 cm long, 3.5–19.7 cm wide, coriaceous, oblong, elliptical, lanceolate, ovate, or oblanceolate, apex short- to long-acuminate or rarely caudate, base rounded to subcordate, adaxially sparsely sericeous when young, soon glabrous or with a few hairs retained on and near the costa, abaxially sparsely sericeous or sometimes glabrate or rarely glabrous, the hairs 0.1–0.3 (–0.5) mm long, the abaxial epidermis minutely blistered or papillate (always papillate in African specimens), the papillae up to 0.03 mm long, with scattered small impressed glands near the margin abaxially; petioles 0.5–1.8 cm long; stipules minute and caducous, 0.2–0.3 mm long, or absent (?). Inflorescence a panicle of pseudoracemes (5–) 6–18 (–30) cm long, usually only 2 (or sometimes 4) opposing flowers of a pseudoraceme fully open at one time. During anthesis peduncles 1.5–5 (–6) mm long, pedicels (1–) 2–6.5 mm long, peduncles (0.3–) 0.5–1.4 (–2) times as long as pedicels; peduncles and pedicels thickening/elongating as the fruits mature. Bracts 3–9 mm long, 1.5–4 (–5) mm wide, narrowly elliptical, elliptical, lanceolate, or ovate, with 1–5 tiny glands along each margin; bracteoles 2.3–5 (–6.5) mm long, 1.5–2.5 (–3.5) mm wide, elliptical to sometimes suborbicular, eglandular. Calyx of 4 biglandular lateral sepals and 1 eglandular anterior sepal; sepals 2.5–4 mm long, recurved to revolute, the lateral ones exceeding the glands by ca. 1 mm. Petals 5, yellow or pale yellow, the limbs triangular to triangular-orbicular to orbicular with the margin erose or erose-fimbriate and the base truncate or sometimes cordate; posterior petal: claw 2.7–3.5 (–4.5) mm long, limb 3.5–4.5 (–6.5) mm long, 3.5–4.5 (–5.5) mm wide; lateral petals: claw 2.2–3 (–4) mm long, limb 4–6 (–7) mm long, 4–6.5 (–7) mm wide. Filaments (2–) 2.5–4.5 mm long,

unequal, those opposite the posterior petal and the anterior-lateral petals usually the shortest, anthers 0.8–1.1 mm long, with apical and basal tufts of hairs or the hairs very sparse, sometimes glabrous (always glabrous in African specimens). Anterior style (2.3–) 2.6–4.5 (–5.2) mm long, posterior styles 2.6–5 (–5.5) mm long, all with the apex dorsally extended, commonly with a dorsiventrally flattened claw (0.1–) 0.3–0.5 (–0.6) mm long or sometimes only spurred. Samaras 3–6 cm long, 2–4 cm wide, ca. 1–1.5 times as long as wide, with a flabellate dorsal wing, the wing extending or not below the nut, the locule embedded in aerenchyma; embryo 1.3–2.3 cm long, 1–1.5 cm wide, ovoid, the cotyledons straight or rarely slightly folded. Chromosome number: 2n = 20 (Mangenot & Mangenot 1962).

Phenology. Collected in flower and fruit throughout the year.

Distribution. In the Old World in coastal West Africa, from Senegal to Angola; in the New World mostly in the Atlantic coastal regions from Belize to northernmost Brazil (Amapá, Pará), or sometimes also farther inland, also in Colombia (Chocó, Valle); rare in Jamaica (3 records); one doubtful report from Puerto Rico; in riverine vegetation, swamps, wet and flooded forest, rainforest, wet areas of beaches, mangroves, and at edges of lagoons; sea level to 200 (–450) m.

Representative Specimens. **Senegal.** Basse-Casamance, Etomé, *Vanden Berghen 7831* (MO). **Guinea.** Timbo, *Boué 71* (G, NY). **São Tomé e Príncipe.** Porto Allegre, *Chevalier 14197* (K). **Sierra Leone.** Near Njala, *Deighton 1753* (BM, K, MO); Boujema near Njala, *Deighton 4635* (K); Goderich, *Deighton 4752* (K); Waterloo, *Lane-Poole 266* (K). **Liberia.** Robertsfield, *Adam 21349* (MO); Sino Co., Greenville, *Baldwin 11556* (K, MO, NY); 3 mi NE of Suacoco, Gbarnga, *Daniel & Barker 209* (MO); near Haindi, 40 km N of Kakata, *Leeuwenberg & Voorhoeve 4972* (K, MO); Monrovia, *Massey 77* (NY). **Ivory Coast.** Along Ebrie Lagoon near ORSTOM, W of Abidjan, *de Wilde 624b* (K); Adiopodoumé, 05°20'N, 04°09'W, *Geerling & Bokdam 337* (MO); near Canal d'Assini, E of Grand Bassam, *Oldeman 148* (K, MO); near Bonoua, 15 km NE of Grand Bassam, *Versteegh & de Outer 634* (MO). **Ghana.** Asuboni River, near Ankoma, *Hall & Agyakwa GC39670* (MO); Princes, *Akpabla 7798* (K). **Nigeria.** Cross River: Oban Dist., *Talbot & Talbot s.n.* (BM, K).—Lagos: swamp forest S of Lagos University campus, *Hossain 1441* (MO); Lagos, *Miller 160* (K).—Ondo: Dist. Ondo, Agbabu, *Okafor & Latilo FHI57277* (K, MO).—Rivers: Dist. Nembe, between Nembe and Brass, *Gbile & Daramola 54/80* (MO). **Cameroon.** Littoral province, Wouri district, Dibamba River bridge on road from Douala to Yaondé, 03°59.98'N, 09°50.68'E, *Davis 99-5* (MICH); bank of Nyong River, ca. 65 km SSW of Eséka, *de Wilde 2746b* (K, MO); right bank of Lobé River, 8 km S of Kribi, *Leeuwenberg 5562* (MO); 22 km SW of Douala, right bank of Dibamba River, *Leeuwenberg 6447* (K, MO); Buea-Douala, bank of Mana (Ndian) River, 04°55'N, 08°50'E, *Thomas 2159* (MO); Dept. Fako, Bakingili, 04°04'N, 09°02'E, *Thompson 1329* (K, MICH, MO, NY). **Equatorial Guinea.** Bioco, Malabo–Luba, Km 33, camino del patio María Isabel, *Carvalho 2986* (K, MO); Bioco, Ela Nguema, barrio de Santa Cruz, *Carvalho 3425* (K, MO), *3415* (BM, G). **Gabon.** Moka Creek, E of Mondah river, 00°39'N, 09°28'E, *Bos et al. 10809* (K, MO); environs de Egolani, sur le lac Oghémoné, *Chevalier 26456* (K); Libreville, *Klaine 3338* (K); Prov. Woleu-Ntem, descente sur le Ntem à partir de Evela, 02°03'N, 12°15'E, *Louis 2906* (MO); Xalibé, 00°33'N, 09°22'E, *Reitsma 2467* (NY); Lopé Reserve, Ogoove, 00°15'N, 11°40'E, *White 1226* (MO). **Angola.** Sumba, Peco, *Gossweiler 9120* (BM, K, US).

Puerto Rico. [?; doubtful record] unknown collector, Herb. Ventenat (G). **Jamaica.** St. Elizabeth: Lacovia and vicinity, border of Black River, *Britton 1484* (NY); banks of Black River, Lacovia, *Harris 9753* (BM, K, NY); Black River, Lacovia to Elam, *Harris 9850* (BM, K). **Trinidad.** Pt. Coco near Irois, *Broadway 8477* (K, NY).

Guatemala. Izabal: near Puerto Barrios, *Standley 73169* (US). **Belize.** Toledo: Rio Sarstoon, Belize-Guatemala border, 5 mi inland, *Dwyer 14874* (MICH, MO); Rio Grande, *Gentle 4681* (MICH, MO). **Honduras.** Atlántida: Triunfo, near Tela, *Standley 53779* (A, US).—Colón: Laguna Guaimoreto, 4.5 mi NE of Trujillo on old rd to Castilla, 15°57'30"N, 85°54'30"W, *Saunders 916* (NY).—Gracias a Dios: Barra Plátano, 15°53'N, 84°42'W, *Fryxell 2836* (BM, MICH, NY); vicinity of Puerto Lempira, *Proctor 38925* (BM); Klauban, W de Brus, *Vargas et al. 355* (NY). **Nicaragua.** Zelaya: Bluefields, *Long 210* (F); Monkey Point, 11°36'N, 83°39'W, *Moreno & Sandino 12141* (MO); between Lamblaya and Laguna Kauropura, *Vincelli 673* (MICH). **Costa Rica.** Limón: CantónTalamanca, P. N. Cahuita, cerca de la Punta Cahuita, 09°44'N, 82°49'W, *Morales 4936* (CR); Parque Tortuguero, 600 m al SE de

Tortuguero sobre el Río, 10°31'N, 83°30'W, *Robles 1430* (MICH, MO). **Panama.** Bocas del Toro: Laguna de Chiriquí, Nuri, 15 km W de Punta Cricamola, 08°55'N, 81°49'W, *Foster 14633* (F); vicinity of Chiriquí Lagoon, Old Bank Island, *von Wedel 2027* (GH, MO, US).—San Blas: trail to village of Cangandí, 09°24'N, 79°24'W, *de Nevers et al. 7427* (MICH, MO); along rd between Mandinga and Cangandí, *Duke 14724* (MO, US).

Colombia. Chocó: along Río Truando between Riosucio and Esperanza, *Duke 9132* (NY); hoya del Río San Juan, Río Fujiadó, afluente del Río San Juan, 04°36'N, 76°54'W, *Forero et al. 4794* (MO); area of Baudó, ca. 13 km upstream from estuary, *Fuchs & Zanella 21748* (G, MO, NY); Mpio. Quibdó, carretera Quibdó–Yuto, Río Cabi, *García Cossio 70* (MO); Río El Salto, tributary of Río Suruco, 9 km W of Andagoya, *Lellinger & de la Sota 440* (US); Istmo de San Pablo, *Triana 388* (G, K, NY).—Valle: Mpio. Buenaventura, Corr. Bocas del Tigre, quebrada Mondoyá, *Cuadros V. 943* (MO); Río Yurumanguí, *Cuatrecasas 15899, 15936* (US). **Venezuela.** Delta Amacuro: Winiquina, *Gines 5011, 1015* (NY); Río Cuyubiní, upstream from Casa Cuyubiní, *Steyermark 87498* (MICH, MO, NY, US); Depto. Antonia Díaz, Caño Joba–Suburu, W of Caño Guayo and E of Caño Sacupana, 09°00'W, 61°00'W, *Steyermark et al. 115137* (MICH, MO). **Guyana.** Mt. Everard, *de la Cruz 1327* (NY, US); Upper Rupununi River, near Dadanawa, 02°45'N, *de la Cruz 1414, 1462* (MO, NY, US); vicinity of Wismar, Demerara River, 06°N, *de la Cruz 2422* (MO, NY); Kaieteur Falls, Potaro River, *de la Cruz 4491* (MO, NY, US); Mabura Hill area, just before bridge to base camp at Ekuk, *Ek & Nathan 1140* (MICH); Kamuni Creek, Groete Creek, Essequibo River, *Fanshawe 531* (NY); Pomeroon-Supenaam Region, Pomeroon River between Charity and Araplako River, 07°23'N, 58°36'W, *Gillespie 1203* (MICH, US); vicinity of Kartabo Station, junction of Mazaruni and Cuyuni Rivers, *Graham 272* (NY, US); Region Upper Demerara-Berbice, Essequibo River, 2–4 km from Bartica, 06°25'N, 58°35'W, *Henkel 1747* (MICH, US); Region Essequibo Islands-West Demerara, Groete River, *Henkel 2757* (MICH, NY, US); Region Barina-Waini, Upper Sebai River, 8 km from Sebai village, 07°51'N, 59°17'W, *Hoffman 660* (MICH, NY, US). **Suriname.** Without locality, *Hostmann 531, 895, 1030* (K); vicinity of Paramaribo, *Kramer & Hekking 2540* (NY); along Kabo Creek, Tibiti savanne, *Lanjouw & Lindeman 1917* (K, NY); along bank of Wayombo River, *Lindeman 6261* (US); Wilhelmina Gebergte, Zuid River, between Kayser airstrip and confluence of Lucie River, *Maguire et al. 54020* (NY, US). **French Guiana.** Vicinity of Cayenne, *Broadway 937* (K, NY); Crique Iracoumpapy, *Cremers & Hoff 11239* (US); route de Saint Elie avant d'arriver au village, *de Granville B.5121* (MICH); Km 19, piste de St. Elie, *Prévost 588* (MICH, NY); Mana, *Mélinon 57* (MICH); Karouany, *Sagot 93* (G, K); Godebert, *Wachenheim 120* (K, US). **Brazil.** Amapá: Rio Oiapoque, near Santo Antonio, 03°53'N, 51°48'W, *Maguire et al. 47120* (K, NY, US).—Pará: north woods of I.A.N., Belém, *Archer 8305* (NY); Rio Guamá, *Fróes 20434* (K); estrada Belém–Mosqueiro, *Silva 59708* (K, MICH, NY, US); Ilha do Marajó, Rio Anajás, ca. 2 km downstream from the city of Anajás, *Sobel et al. 4795* (K, MICH, NY).

Heteropterys platyptera DC., Prodr. 1: 592. 1824.—Type: Guadeloupe, *Krauss s.n.* (holotype: G-DC, photo and microfiche: MICH!).

Banisteria longifolia Sw., Prodr. 75. 1788. *Heteropterys longifolia* (Sw.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 53. 1903, non *Heteropterys longifolia* H. B. K., 1822 ["1821"]. *Heteropterys longifolia* var. *martinicensis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 54. 1903, nom. superfl. *Heteropterys platyptera* var. *martinicensis* (Nied.) J. F. Macbride, Candollea 6: 12. 1934, nom. superfl.—Type: Guadeloupe. *Swartz s.n.* (lectotype, here designated: S, the sheet bearing the branchlet with leaves and inflorescences; isolectotype: S, the sheet bearing a partial leaf and packet containing fragments of inflorescences; photocopies of lectotype and isolectotype: MICH!).

Banisteria macrocarpa Pers., Syn. pl. 1: 507. 1805, non *Heteropterys macrocarpa* (Nied.) Kralik, 1908.—Type: Martinique, 1792, *Terrasson 31* (holotype: P-JU 11628+C, photo: A!, microfiche: MICH!).

Banisteria macradena β *guadalupensis* DC., Prodr. 1: 590. 1824.—Type: Guadeloupe, *Bertero s.n.* (holotype: G-DC, photo and microfiche: MICH!).

Banisteria pubiflora DC., Prodr. 1: 591. 1824. *Heteropterys pubiflora* (DC.) Bello, Anales Soc. Esp. Hist. Nat. 10: 245. 1881.—Type: Guadeloupe,

L'Herminier s.n. (lectotype, here designated: G-DC, photo and microfiche: MICH!).

Heteropterys longifolia var. *borealis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 53. 1903. *Heteropterys platyptera* var. *borealis* (Nied.) J. F. Macbride, Candollea 6: 12. 1934.—TYPE: DOMINICA. *Imray 405* (lectotype, designated by W. R. Anderson, 1988: GH!).

Fig. 1.

Liana, scandent or climbing shrub to 10 m, sometimes a shrub to 5 m, or rarely a small tree. Lamina of the larger leaves 8–33 cm long, 3.5–15 cm wide, coriaceous, oblong, elliptical, lanceolate, or ovate, apex (long-) acuminate to caudate, base rounded to subcordate, adaxially sparsely sericeous when young, soon glabrous or with a few hairs retained on and near the costa, abaxially sparsely sericeous to glabrate or glabrous, the hairs 0.1–0.3 mm long, the abaxial epidermis minutely blistered but epapillate, with scattered small impressed glands near the margin abaxially; petioles 0.8–1.7 cm long; stipules minute and caducous, 0.2–0.3 mm long, or absent (?). Inflorescence a panicle of pseudoracemes (5–) 6–22 cm long, usually only 2 (or sometimes 4) opposing flowers of a pseudoraceme fully open at one time. During anthesis peduncles 1.5–4.6 (–6) mm long, pedicels 1.7–4.5 mm long, peduncles 0.6–1.2 (–2) times as long as pedicels; peduncles and pedicels thickening/elongating as the fruits mature. Bracts 3–4.5 mm long, 2–3 (–4) mm wide, narrowly elliptical to ovate, eglandular; bracteoles 2.4–3.8 (–5) mm long, 1.5–2.5 mm wide, elliptical to ovate, eglandular. Calyx of 4 biglandular lateral sepals and 1 eglandular anterior sepal; sepals 3–3.3 mm long, recurved to revolute, the lateral ones exceeding the glands by ca. 1 mm. Petals 5, yellow or pale yellow, the limbs triangular to triangular-orbicular with the margin erose or erose-fimbriate and the base truncate; claw of posterior petal 3–3.3 mm long, claw of lateral petals 2.5–3 mm long; limb of all petals 4–4.6 mm long, 4–4.8 mm wide. Filaments 2.2–3.5 mm long, unequal, those opposite the posterior petal and the anterior-lateral petals usually the shortest, anthers 0.8–1 mm long, mostly with apical and basal tufts of hairs, or the hairs very sparse or sometimes absent. Anterior style 2.6–3.2 mm long, posterior styles 3.1–3.5 mm long, all with the apex dorsally blunt or with a tiny spur up to 0.1 (–0.2) mm long. Samara with an elongate dorsal wing 5.8–7 cm long, 2.5–2.7 cm wide, 2.2–2.8 times as long as wide, never extending below the nut, the locule embedded in aerenchyma; embryo 1.4–1.8 cm long, 1–1.2 cm wide, ovoid, the cotyledons straight or rarely slightly folded. Chromosome number unknown.

Phenology. Collected in flower and fruit from December through August.

Distribution. Lesser Antilles (Guadeloupe, Dominica, Martinique, St. Lucia, and St. Vincent); mostly in wet and flooded areas: in rain forest, swamps, and along riverbanks, also in drier sites: in forests, woodlands, ravines, and disturbed areas; sea level to 400 (–580) m.

REPRESENTATIVE SPECIMENS. **Guadeloupe.** BASSE TERRE: Barè-Mahault, *Questel 741* (MICH, US); Vernou, Grand Rivière, *Questel 5047* (US); Sofaia, Rivière Salée, *Sastre 2746* (A, MO); near Duclos, Petit Bourg, *A. C. Smith 10358* (A, K, NY, US). **Dominica.** Between Point Lolo and Pont Cassé, NW of Moren Trois Pitons, *Ernst 1289* (GH, MICH, US); W of Rosalie, ca. 1–2 mi on rd to Castle Bruce Junction and Pont Cassé, *Ernst 1352* (US); without locality, *Fishlock 23a* (NY, US); old trail from Petite Savane to Point Mulatre, 15°15'N, 61°16'W, *Hill 25747* (GH, NY); Sylvania Estate, *Hodge 551* (GH, NY, US); Wet Area Experimental Station near D'Eau Gommier, *Nicolson 4180* (BM, MICH, US). **Martinique.** Champ Flore area, *Howard & Howard 18845* (A, BM, NY, US);

without locality, 1787, *Isert s.n.* (C); hauteurs du Diamant, *Stehlé & Stehlé 4790* (US); plateau militaire, hauteurs de Case-Pilote, Bois de la Démarche, *Stehlé & Stehlé 4802* (US); St. Joseph, Petite Rivière, *Stehlé & Stehlé 6444* (US); Balata à Tivoli, *Stehlé & Stehlé 6888* (MICH, US). **St. Lucia.** Anse la Raye, *Beard 1055* (GH, MO, US); Le Toc to Cul de Sac Bay, *Howard 11368* (A, BM, MICH, NY); between Quilesse and Morne Troumasse, *Howard 11649* (A, BM, MICH, NY); Morne, *Sturrock 530* (A). **St. Vincent.** Along Chateaubelaire River, *Morton 5237* (BM, GH, US); without locality, *H. H. Smith & G. W. Smith 1549* (BM, GH, K, NY, US).

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