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Source: Willdenowia, 55(1) : 51-65

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.55.05>

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***Inga pectinata*, basionym of *Parkia pectinata*, from the Río Casiquiare, Venezuela, is synonymized with *Dimorphandra cuprea* (Leguminosae: Caesalpinioideae: Dimorphandreae)**

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Version of record first published online on 7 April 2025.

Abstract: The type material of *Inga pectinata* Humb. & Bonpl. ex Willd., which is the basionym of combinations in *Acacia*, *Mimosa* and *Parkia* (all Leguminosae: Caesalpinioideae: Mimoseae), is Bonpland & Humboldt 1167 (B-W, P-Bonpl.), collected near the Río Casiquiare in southern Venezuela in 1800. Both sheets are sterile, each consisting of a bipinnate leaf with disarticulated pinnae that bear small, sessile, narrowly oblong, opposite leaflets with reddish hairs on the abaxial surface. This material is not conspecific with *Spruce* 2727, the type of *P. panurensis* Benth. ex H. C. Hopkins from northwestern Amazonian Brazil, although Bentham erroneously placed the Spruce collection in *P. pectinata*. Despite a superficial similarity to *P. barnebyana* H. C. Hopkins, which has also been collected near the Río Casiquiare, Bonpland and Humboldt's collection is conspecific with *Dimorphandra cuprea* Sprague & Sandwith, in *D.* subg. *Pocillum* (Caesalpinioideae: Dimorphandreae). The combination *D. pectinata* (Humb. & Bonpl. ex Willd.) H. C. Hopkins & G. S. da Silva is published, an epitype with flowers is designated, and the names *D. cuprea* and *D. ferruginea* Ducke are put into its synonymy. Notes on the distribution and ecology of *D. pectinata* are accompanied by a list of specimens from Venezuela's Amazonas State.

Keywords: Amazonia, Caesalpinioideae, *Dimorphandra cuprea*, *Dimorphandra ferruginea*, *Dimorphandreae*, *Fabaceae*, *Inga pectinata*, lectotype, Leguminosae, nomenclature, Orinoco, *Parkia panurensis*, *Parkia pectinata*, synonymy, Río Casiquiare, Venezuela

Article history: Received 24 November 2023; peer-review completed 18 March 2024; received in revised form 18 September 2024; accepted for publication 20 September 2024.

Citation: Hopkins H. C. F. & Silva G. S. da 2025: *Inga pectinata*, basionym of *Parkia pectinata*, from the Río Casiquiare, Venezuela, is synonymized with *Dimorphandra cuprea* (Leguminosae: Caesalpinioideae: Dimorphandreae). – Willdenowia 55: 51–65. <https://doi.org/10.3372/wi.55.05>

Introduction

Inga pectinata Humb. & Bonpl. ex Willd. was published in 1806 in the 4th edition of *Species plantarum* (Willdenow 1806: 1026), based on a sterile collection, number 1167, made by Aimé Bonpland and Alexander von Humboldt near the Río Casiquiare in southern Venezuela. Bonpland and Humboldt were travelling in this region in May 1800, during their five-year expedition through the Spanish territories of South America (Botting 1973). Their route took them up the Río Casiquiare from near the settlement of San Carlos de Río Negro to the point where the Casiquiare branches from the Río Orinoco, close to Tamatama (Huber & Wurdack 1984: map 4; Huber 1995a: fig. 2–3). According to Stafleu & Cowan (1976, 1979; TL-2 1976–2009), the main part of the plant material from their travels in the Americas is located at P (P-Bonpl.), with a minor part extant in the Willdenow herbarium at B (B-W). Although the sheet at P (P00679369, image in the online database for P [Muséum national d'Histoire naturelle

2023+]) has an original, printed label for “Herbier Humboldt & Bonpland”, the plant collections from their expedition are now attributed to Bonpland, who was a botanist (e.g. Staufer & Staufer 2020). The sheet in B-W (B-W 19056 -01 0) (Fig. 1, 2) has the number 1167 but no collector's name, though the online image is labelled “Leg. A. J. A. Bonpland and F. W. H. A. v. Humboldt”. Both the B-W and P-Bonpl. sheets are sterile, each consisting of parts of a bipinnate leaf, including a single leaf rachis and several detached pinnae, each with numerous leaflets.

The leaves of the specimen from the Río Casiquiare do not resemble those of any species of *Inga* Mill. as it is now circumscribed. In trying to determine where this plant belonged taxonomically, the combinations *Mimosa pectinata* (Humb. & Bonpl. ex Willd.) Poir. (Poiret 1810) and *Acacia pectinata* (Humb. & Bonpl. ex Willd.) Kunth (1824) were published, with Candolle (1825) repeating Kunth's name in *Acacia* Mill., although with a question mark. Finally, Bentham (1875), in his magnum opus on the *Mimoseae* (sometimes referred to as *Mimosoideae* or

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Fig. 1. Type material of *Inga pectinata*, Bonpland & Humboldt 1167 from the Río Casiquiare, Venezuela (B-W 19056-01 0). – Image supplied by, and copyright of Botanischer Garten und Botanisches Museum (BGBM), Berlin.

Caesalpinioideae: mimosoid clade), made the combination *Parkia pectinata* (Humb. & Bonpl. ex Willd.) Benth., citing the previous combinations in *Inga*, *Mimosa* L. and *Acacia* in synonymy.

When reviewing the names of accepted species and their synonyms in the pantropical genus *Parkia* R. Br. (*Leguminosae*: *Caesalpinioideae*: *Mimoseae*) for the Legume Data Portal (2023+) via the World Checklist of Vascular Plants (2023+, WCV) in March 2023, the first author found that this and the related Plants of the World Online (2023+, POWO) listed *P. pectinata* as an accepted species with *P. panurensis* Benth. ex H. C. Hopkins given as a heterotypic synonym. However, the types of these two names clearly belong to different taxa, and Hopkins (1982) stated that the type of *Inga pectinata* did not appear to be a *Parkia* and was certainly not conspecific with the type of *P. panurensis*. The status of *P. panurensis* was changed to “accepted” in POWO and WCV in April 2023 but at the time of writing (June 2024), the distribution of *P. panurensis* is shown on a map in the Global Biodiversity Information Facility (2024+, GBIF) under the name *P. pectinata*. The aims of this paper are to unravel the past confusion between *P. pectinata* and *P. panurensis*, and to determine the identity of Willdenow’s *I. pectinata*.

Material and methods

All material cited has been seen either in the herbarium (BM, F, INPA, K, MO, NY, P, RB, US) and/or as an image online, unless marked “n.v.” (not seen), and the barcode, QR-code (U) or accession number (VEN) is given, when known, in the section on Taxonomy and in Appendix 1. Images were seen online via GBIF (2024+), Herbario Virtual Austral Americano (2024+, also accessed as the Neotropical Plant Portal 2024+), JACQ (2023+), JSTOR Global Plants (2000–2024), Re flora Virtual Herbarium (2024+), *speciesLink* (2024+), as well as through the virtual herbaria of some individual institutions, including B (Herbarium Berolinense 2000+) and U (Naturalis Bioportal 2024+), or sent to us in response to specific requests (HBG, MO, NY, PORT, VEN). For types only, we distinguish between sheets seen in the herbarium and those seen



Fig. 2. Details enlarged from Fig. 1. – A: adaxial surface of leaflets; B: notes attached to specimen; C: notes on a separate sheet in the same folder (B -W 19056 -00 0); D: leaflets from P00679369, abaxial surface showing ferruginous indumentum. – Images supplied by, and copyright of: (A–C) Botanischer Garten und Botanisches Museum (BGBM), Berlin; (D) Muséum national d’Histoire naturelle, Paris.

as images, and, when referring to type material, “image!” means that we have seen an image only, but it is the specimen, not the image, that we are citing or designating as the type. Herbarium abbreviations follow Index herbariorum (Thiers 2024+). The following abbreviations are used when referring to collections: fl. = flowers; fr. = fruit; imm. = immature; lv. = leaves; R. = Río or River; st. = sterile.

To compare the type of *Inga pectinata* with taxa that have similar leaves, we scored vegetative characters for two species of *Parkia* (*P. panurensis*, *P. barnebyana* H. C. Hopkins) and several of *Dimorphandra* Schott (*Caesalpinioideae*: *Dimorphandreae*), supplemented by data from the literature. This included the most recent accounts for both genera (Hopkins 1986; Silva 1986; Silva & Tavares 1995; Silva 2019; Hopkins & al. 2023) and the protologues of some taxa.

When choosing an epitype for *Inga pectinata*, we considered leaf characters, collection locality, reproductive state, and the existence of several duplicates, including at least one in a Venezuelan herbarium.

Results and Discussion

Characters of *Inga pectinata*

The online images of Bonpland & Humboldt 1167 from B-W and P-Bonpl. show that each leaf rachis bore c. 17



Fig. 3. Holotype of *Parkia panurensis*, Spruce 2727, from Rio Uaupés, Brazil (K000504617). – Image supplied by the Royal Botanic Gardens, Kew, and copyright of the Trustees.

pairs of opposite to subopposite pinnae. Each pinna has numerous strictly opposite, sessile, narrowly oblong leaflets (length to width ratio 5:1) (Fig. 2A), whose adjacent margins are contiguous. The leaflets each have a small, rounded auricle on the proximal side at the base and the midvein is centrally placed, parallel to the lateral margins and straight toward the rounded, micro-mucronulate leaflet apex. The point of attachment to the secondary rachis is \pm centrally placed along the bottom margin. When the specimen in P-Bonpl. was viewed with a binocular microscope, no extra-floral nectary was found on the adaxial surface of the petiole, the midvein of each leaflet was strongly prominent on the abaxial surface, and the leaflet margins were revolute. The secondary venation was not visible on either surface due to the thickness of the cuticle. The brief description of *Inga pectinata* by Willdenow (Fig. 2C), attached to sheet B - W 19056 -00 0 in the same folder as the herbarium specimen, mentioned ferruginous pubescence, and the published description (Willdenow 1806: 1026) noted this was present on the petiole and underside of the leaflets and that the leaflet margins were ciliate. This indumentum is not easily seen in the online scans, but in the herbarium, short, adpressed ferruginous hairs, neither densely nor sparsely arranged, are visible on the abaxial surface of the leaflets (Fig. 2D).

The confusion of *Inga pectinata* and *Parkia panurensis*

Before making the combination *Parkia pectinata*, Benthams could have seen Bonpland and Humboldt's collection of *Inga pectinata* either in Berlin or Paris because he visited both at various times prior to 1875 (e.g. in 1867, fide Jackson 1906). However, his diaries in the archives at the Royal Botanic Gardens, Kew (e.g. GEB/2/18 diary for 1866–1874, accessed 18 July 2023) record everyday events and do not discuss specimens, and the nine volumes of his notes on *Leguminosae* (GEB/4/1–GEB/4/9) cover the *Papilionoideae* and *Caesalpinioideae* in their traditional sense, and not the *Mimoseae* or *Mimosoideae* (Index in GEB/4/9, accessed 18 July 2023). His extensive archives of correspondence and other personal papers were not consulted. No fragment of *Bonpland & Humboldt 1167* was located at K in 2023, and no further duplicates are currently recorded in online databases such as JSTOR Global Plants (2000–2024) and JACQ (2023+).

Benthams (1875: 362, 662) treated *Parkia pectinata* as species number 13 in this genus under *P. sect. Paryphosphaera* Benth., providing a brief description, and the name was listed in the index to species; there is no key to species in this work. He did not cite any specimens for *P. pectinata* but mentioned characters of the peduncles, fruits and leaves, stating that the leaflets were sub-sigmoid-falcate; indumentum was not mentioned. Because *Bonpland & Humboldt 1167* is sterile, the fruit and peduncle characters must have been taken from a different collection, and presumably the peduncle and receptacle



Fig. 4. Details enlarged from Fig. 3. – A: enlargement of leaflets, adaxial surface; B: notes attached to specimen; C: Benthams erroneous identification as *P. pectinata*, probably written by D. Oliver. – Images supplied by the Royal Botanic Gardens, Kew, and copyright of the Trustees.

at its apex in this other material were in keeping with a biglobose capitulum in order to merit its inclusion in *P. sect. Paryphosphaera*. The shape of the leaflets must also have been taken from other material because those of *Bonpland & Humboldt 1167* are narrowly oblong, not sub-sigmoid-falcate.

Toward the end of his account in 1875, Benthams listed mimosoid legumes collected by various botanical explorers, including Richard Spruce. *Spruce 2727* (Fig. 3, 4) was cited as "*Parkia panurensis*" (Benthams 1875: 645), which was a nomen nudum at the time because no description was given by Benthams there or elsewhere. This name was included in neither his generic account of *Parkia* in this work nor in the index to species. The Spruce material was collected near Panuré on the Rio Uaupés in northwestern Amazonian Brazil, southwest of the Rio Casiquiare.

In his treatment of the *Mimoseae* in Martius's *Flora brasiliensis* published the following year, Benthams (1876: 264 [key] & 266 [species account]) gave a longer description of *Parkia pectinata* that included characters of the leaves, capitula, flowers and fruits, and he described the petiole as "ferrugineo-puberulo v. glabrato". In particular, he mentioned in the key that the capitula

were biglobose and the staminodia were red. Again, this description is based on specimens additional to the Bonpland and Humboldt material, and this time *Spruce 2727* was cited. Both sheets of this collection at K have “*Parkia pectinata* Benth. *Mimoseae* 362” written on them in ink (Fig. 4C), almost certainly by Daniel Oliver (see JSTOR Global Plants [2000–2024] for documents in his hand). He worked at Kew in various capacities between 1858 and 1890, starting as an assistant and later becoming librarian and keeper of the herbarium (Anon 1916). The sheets also have “*Parkia* [or *P.*] *panurensis*” written on them in pencil, possibly in Bentham’s hand. In 1876, Bentham was now clearly treating his undescribed “*P. panurensis*” as belonging to the same species as Willdenow’s *Inga pectinata*, although the resemblance is not close. While the opposite leaflets of both species have parallel lateral margins with a small auricle at the base on the proximal side and the midvein is central and parallel to the margins, in *Bonpland & Humboldt 1167* this vein is straight at the rounded, micro-mucronulate leaflet apex, whereas in *Spruce 2727* the leaflets are somewhat sigmoid with the midvein curving distally toward a more pointed apex (Fig. 4A). Furthermore, the leaflets of *Bonpland & Humboldt 1167* have reddish indumentum on the abaxial surface, whereas those of *Spruce 2727* are glabrous. *Parkia panurensis* is compared with *Bonpland & Humboldt 1167* in Table 1.

Following Bentham’s accounts of the *Mimoseae*, material that matched *Spruce 2727* became known as *Parkia pectinata* until the genus was being revised for *Flora neotropica* (Hopkins 1986), when it was realized that *Bonpland & Humboldt 1167* (seen as a black and white image) and *Spruce 2727* (seen at K and elsewhere) were not conspecific, and material of the latter, a relatively common tree in central and western Amazonia, had no valid name. Bentham’s epithet *panurensis* was taken up for a new species with the Spruce collection as the type (Hopkins 1982). Since then, the name *P. panurensis* has become established in herbaria and in the literature on molecular biology, ecology and phylogeny (e.g. Luettmann & al. 2010; Heymann & al. 2012, 2022; Bialozyt & al. 2014; Arellano-P. & al. 2019; Cavada & al. 2020; Oliveira & al. 2021), as well as in regional checklists (e.g. Hokche & al. 2008 for Venezuela; Bernal & al. 2015 for Colombia).

However, it was not clear in the 1980s to what taxon the Bonpland and Humboldt collection belonged because it did not match any material of *Parkia* known at the time and, being sterile, it was not even certain that it was correctly placed in this genus. Although deciding that *Inga pectinata* and *P. panurensis* were distinct, Hopkins (1986) did not specifically exclude *P. pectinata* from the genus, nor did she treat it as a doubtful species, but merely mentioned it in synonymy under *P. panurensis* (“*Parkia pectinata* auct. (non Benth.) [...]”) and stated that *P. panurensis* had previously been confused with *I. pectinata*.

Comparison of *Bonpland & Humboldt 1167* with *Parkia* and *Dimorphandra*

Among the characters described above for *Inga pectinata*, bipinnate leaves with opposite, oblong to narrowly oblong, sessile leaflets with a centrally placed midvein, a central basal attachment to the secondary rachis, and an auricle on the proximal side at the base are features commonly seen in species of *Parkia* and, as far as we are aware, this precise combination of characters is not found in any other genus of *Mimoseae* in Amazonia. When reviewing images of *Bonpland & Humboldt 1167* and Willdenow’s (1806) description, the shape of the leaflets, their relatively large number per pinna, and mention of ferruginous indumentum suggested a resemblance to *P. barnebyana* H. C. Hopkins. This species was described from two collections made at Cucurital de Caname on the upper Caño Caname, in Amazonas State, Venezuela (Hopkins 2000) and has since been collected from localities near the Río Casiquiare. The Bonpland and Humboldt collection was not compared with specimens of *P. barnebyana* in 2000 but comparison of images in 2023 with the type of the latter (Berry & Melgueiro 5399, K) and with Redden 5399 (K) initially suggested that *P. barnebyana* and the type of *I. pectinata* might be conspecific. However, after seeing the sheet of *Bonpland & Humboldt 1167* at P, it was clear that they differ in several significant features.

Whereas the leaves of *Bonpland & Humboldt 1167* have some characteristics that are common though not universal in *Parkia*, these features also occur in some members of the rather distantly related genus *Dimorphandra*. That the name *D. megacarpa* Rolfe is a synonym of the Amazonian tree *P. multijuga* Benth. is further evidence of a superficial similarity between some members of these two genera.

Containing some 26 species, *Dimorphandra* is paraphyletic and currently divided into three subgenera (Silva 1986; Silva 2019; Silva & Simon 2024). Its bipinnate leaves exhibit a variety of leaflet shapes, but the taxa with small, oblong, sessile, opposite leaflets, similar to those of *Bonpland & Humboldt 1167*, all belong to *D.* subg. *Pocillum* Tul. This group is monophyletic (Rocha & al. 2024) and comprised of about ten largely or exclusively Amazonian species, several of which occur in southern Venezuela and the adjacent part of northwestern Brazil (Silva 1986; Silva 2019).

Fertile material of *Parkia* and *Dimorphandra* subg. *Pocillum* is unlikely to be confused because of marked differences in the flowers, inflorescences and fruits, and whereas some species in both have leaflets that are similar in outline, their leaves differ in at least two significant respects. Firstly, in *Dimorphandra*, the petiole lacks an extrafloral nectary (Silva & Simon 2024), which is always present in *Parkia* (Hopkins & al. 2024) and is sometimes double (e.g. in *P. barnebyana*). Secondly, their patterns of secondary venation differ. In *D.* subg. *Pocillum*, the secondary venation is pinnate with

Table 1. Comparison of leaf characters and distribution of Bonpland & Humboldt 1167, *Parkia panurensis*, *P. barnebyana*, and seven species of *Dimorphandra* subg. *Pocillum*. – Data for *Parkia* species from (1) Hopkins (1986) and (2) Hopkins & al. (2023); data for *Dimorphandra* species from Silva (1986) and Silva (2019); see also (3) Sandwith (1932), (4) Ducke (1935) and (5) Ducke (1915); (6) *D. macrostachya* includes all three subspecies (numbers in parentheses refer to superscript numbers after taxon names).

	petiolar gland?	number of pairs of pinnae/leaf	number of pairs of leaflets/pinna	leaflet dimensions (mm)	leaflet shape	indumentum on abaxial surface of leaflets	known from S Venezuela and/or NW Brazil?
<i>Bonpland & Humboldt 1167</i>	no	17	44–53 (60 fide Willdenow)	8–9 × 1.5	narrowly oblong	adpressed ferruginous pubescence	yes
<i>Parkia panurensis</i> ¹	single	6–16	28–41	7–13 × 1.5–3	sigmoid	glabrous	yes
<i>P. barnebyana</i> ²	double	19–21	35–40	4–5 × 1–1.5	oblong	hairs on older leaflets ± erect, white, sparse (very young leaves golden-ferruginous)	yes
<i>Dimorphandra campinaranum</i>	no	5–7(–9)	20–30(–37)	10–15 × 2–3(–4)	narrowly oblong, slightly obovoid	reddish pubescence with some erect black hairs	no
<i>D. coccinea</i>	no	10–15(–17)	20–25	5–10 × 2–4	narrowly oblong	yellow pubescence on midvein	no
<i>D. cuprea</i> subsp. <i>cuprea</i> ³	no	9–12	20–40	5–12 × 1–2	narrowly oblong	dense reddish-ferruginous or coppery pubescence	yes
<i>D. cuprea</i> subsp. <i>ferruginea</i> ⁴	no	13–22(–25)	30–54	4–5 × 1–1.5	narrowly oblong	dense yellow to ferruginous villous	yes
<i>D. cuprea</i> subsp. <i>velutina</i> ⁵	no	13–21	21–48	10–18 × 2–4.5	narrowly oblong	adpressed yellowish silky hairs to ferruginous velutinous	no
<i>D. gigantea</i>	no	18–27	30–40(–50)	3–5(–7) × 1–2	narrowly oblong, slightly falcate	subglabrous	yes
<i>D. macrostachya</i> ⁶	no	5–12(–25)	20–30(–35)	10–30 × 2–6	narrowly oblong	glabrous to golden pubescence	yes
<i>D. pennigera</i>	no	13–15(–18)	30–35(–40)	20–40 × 4–6	narrowly oblong	sparse ferruginous to shiny yellow, glabrescent	yes
<i>D. urubuensis</i>	no	8–14(–16)	20–30(–38)	5–10 × 1–2	very narrowly oblong to slightly falcate	ferruginous strigose, pilose on midvein	yes

the veinlets equidistant from one another and perpendicular to the midvein, especially in species with small leaflets, or sometimes at a more acute angle in those with larger leaflets, and craspedodromous or almost so in both (Silva 1986: fig. 2). In Amazonian *Parkia* species with oblong or narrowly oblong, rather than linear, leaflets, the venation is palmate-pinnate with one or more veins additional to the midvein arising at or near the leaflet's attachment point (Hopkins 1986: fig. 18; Silva 2015: fig. 1–10; Gobo 2018: fig. 2E–F). Secondary veins arise along the length of the midvein at an acute angle and are more widely spaced toward the base of each leaflet than distally. These secondary veins are arcuate and looping, usually forming an intramarginal vein which is often clearly visible, especially in species with larger leaflets. The exact pattern is not identical in all taxa according to Silva (2015), but her description for *P. barnebyana* made clear that its venation is similar to that of several other Amazonian species of *Parkia* with oblong leaflets. However, secondary and higher-order venation are not always easily visible in herbarium material of species with small leaflets in either *Parkia* or *Dimorphandra*.

Among other differences between the leaflets of these two genera, the midvein is often impressed on the adaxial surface and strongly prominent abaxially in *Dimorphandra* subg. *Pocillum*, and the leaflet margins are commonly revolute, whereas in *Parkia* the midvein is not impressed adaxially, at most only weakly prominent abaxially, and the margins are not revolute except when due to



Fig. 5. Lectotype of *Dimorphandra cuprea*, Jenman 1030, from Kaieteur Savannah, Potaro River, Guyana (K000555310). – Image supplied by the Royal Botanic Gardens, Kew, and copyright of the Trustees.

poor drying conditions. In species of *D.* subg. *Pocillum* with small leaflets, the cuticle is generally thick on both leaflet surfaces, largely or entirely obscuring the secondary venation, whereas in *Parkia* leaflets of similar size, the cuticle is somewhat thinner, though the secondary venation is not always clearly visible.

The leaf characters of *Bonpland & Humboldt 1167* are compared with those of *Parkia barnebyana* and the species of *Dimorphandra* subg. *Pocillum* that have oblong or narrowly oblong leaflets in Table 1, and it is clear that the type of *Inga pectinata* belongs to *D.* subg. *Pocillum*, not *Parkia*. No gland is visible on the petiole of *Bonpland & Humboldt 1167* at P, although part of the petiole is slightly obscured by the paper loop attaching it to the mounting sheet. Several additional characters confirm this placement (midvein of each leaflet strongly prominent abaxially; leaflet margins revolute; cuticle thick on both surfaces, entirely obscuring the secondary venation). Because not all species of *Parkia* have glabrous leaflets and leaf rachises, the presence of hairs in *Bonpland & Humboldt 1167* does not preclude it from belonging to this genus.

Based on our observations and the data in Table 1, we conclude that *Bonpland & Humboldt 1167* closely resembles *Dimorphandra cuprea* Sprague & Sandwith. Silva (1986) said this species was easily recognized by the reddish-ferruginous indumentum on various parts, including the abaxial surface of the leaflets, and it is known to occur in Amazonas State in southern Venezuela (Silva & Tavares 1998), close where the type of *Inga pectinata* was collected. The *Bonpland & Humboldt* material matches *D. cuprea* in its indumentum, the size and number of the leaflets, including the sizes of the proximal and distal leaflets in any pinna, the size of the pinnae, and leaflet spacing within pinnae, especially if subsp. *ferruginea* (Ducke) M. F. da Silva and subsp. *cuprea* are combined (see below).

According to Silva (1986) and Silva (2019), other species of *Dimorphandra* subg. *Pocillum* that have small, oblong leaflets include: *D. campinaranum* Ducke, which has many fewer pairs of pinnae and larger leaflets than *Bonpland & Humboldt 1167*; *D. coccinea* Ducke, but that species has leaflets pale on the abaxial surface with yellow indumentum on the midvein; *D. gigantea* Ducke, in which the leaflets are mucronulate but smaller and glabrous adaxially; *D. macrostachya* Benth., whose leaflets are larger than in *Humboldt & Bonpland 1167* and either glabrous or golden pubescent abaxially; *D. pennigera* Tul., which also has larger leaflets with sparse, shiny yellow to ferruginous hairs on the abaxial surface, becoming glabrous; and *D. urubuensis* Ducke, whose type has very narrow, strongly recurved leaflets. In both *D. macrostachya* and *D. pennigera*, the pinnate secondary venation is readily visible because the cuticle on the abaxial surface is not sufficiently thick to obscure it. None of these species is a close match to *Bonpland & Humboldt 1167*.

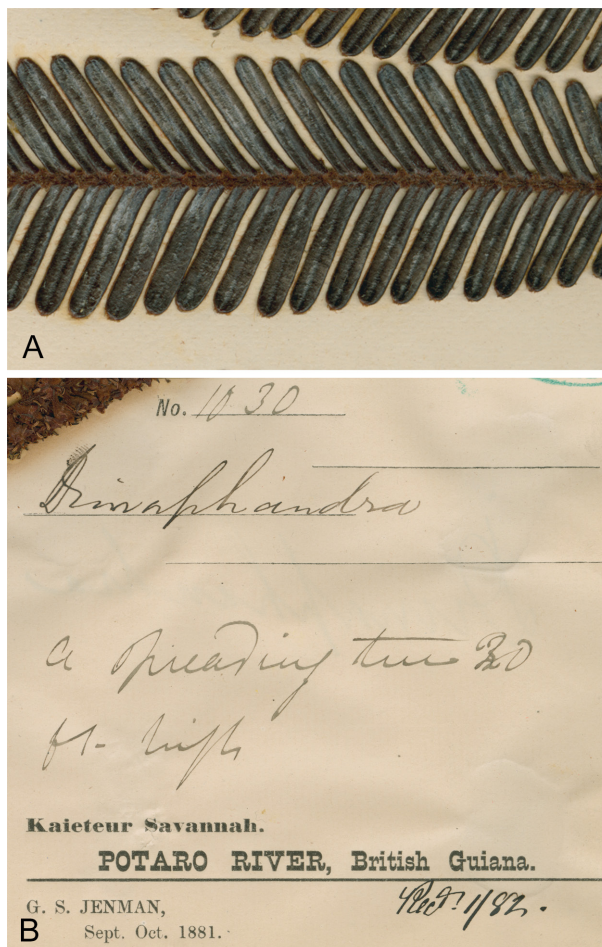


Fig. 6. Details enlarged from Fig. 5. – A: enlargement of leaflets, adaxial surface; B: specimen label. – Images supplied by the Royal Botanic Gardens, Kew, and copyright of the Trustees.

Taxonomy of *Dimorphandra cuprea*

Dimorphandra cuprea was said by Silva (1986) to comprise three subspecies: subsp. *cuprea*, which is a small to medium-sized tree; subsp. *ferruginea*, also a smallish tree but its type has denser ferruginous indumentum and smaller leaflets than the type of *D. cuprea*; and subsp. *velutina* (Ducke) M. F. da Silva, which is a larger tree that occurs only in eastern Amazonia. The name *D. cuprea* was published in 1932, and the basionyms of the two non-nominate subspecies, *D. velutina* Ducke and *D. ferruginea* Ducke, were published in 1915 and 1935 respectively (Ducke 1915, 1935; Sandwith 1932). This means that *velutina* was in fact the oldest epithet at specific rank for Silva's concept of a variable, widespread taxon and had priority over *cuprea*. However, we consider that *Inga pectinata* is conspecific with *D. cuprea*, and so *D. pectinata* (Humb. & Bonpl. ex Willd.) H. C. Hopkins & G. S. da Silva becomes the correct name for this plant. Floral characters are significant for species delimitation in *D.* subg. *Pocillum* and, because *Bonpland & Humboldt 1167* is sterile and fragmentary, it could be ambiguous. We therefore designate a flowering specimen from south-

ern Amazonas State, Venezuela as an epitype to support the application of the name *D. pectinata* (Turland & al. 2018: Art. 9.9). Furthermore, recent research by G. S. da Silva suggests that *D. ferruginea* should be a synonym of *D. cuprea* at specific rank, rather than being treated as a subspecies, and *D. velutina* should be reinstated as distinct from *D. cuprea*. For these reasons, new combinations are not made here for M. F. da Silva's subspecies. The rationale behind these decisions will be presented in detail elsewhere (G. S. da Silva in prep.).

Distribution and ecology

Distribution maps in Silva (1986) and Silva (2019), plus additional herbarium records, show that *Dimorphandra cuprea* (excluding subsp. *velutina*) has been collected in western and central Amazonia, in Brazil, Colombia, Peru and Venezuela, in the upper to middle Orinoco drainage in Venezuela and Colombia, and in Guyana, in the Essequibo catchment. Specimens in Venezuela's Amazonas State are from the west and the south (Appendix 1) and several are from close to where Bonpland & Humboldt found it along the Río Casiquiare. This channel, some 355 km long, originates as a bifurcation of the Orinoco and flows south, then southwest, through a largely flat landscape of low elevation (c. 100 m a.s.l.), with a few small, scattered inselbergs (Huber 1995b). Just above San Carlos de Río Negro, it joins the south-flowing Río Guainía to form the Río Negro, which continues southward into Brazil. The Casiquiare is an example of ongoing river capture and when the process is complete, it will expand the Amazon basin northward, diverting more of the Orinoco headwaters (Stokes & al. 2018).

Within the Orinoco drainage in Amazonas State, this species has been collected near Ríos Atabapo, Autana and Temi, including at Yavita on the Río Temi. In the Amazonian catchment, localities include the settlement of Maroa on the Río Guainía, and Caño Pimichín, which flows into the Guainía near Maroa. Other specimens are from major southern tributaries of the Casiquiare. These include Río Pasimoni and its side channel Río Baria, which has its headwaters in and around Sierra de la Neblina, close to the border with Brazil. Caño Chimoni is a tributary of Río Siapa, another major tributary of the Casiquiare, and the eastern slopes of Cerro Aracamuni drain into the upper Siapa. Maps showing watercourses and other features can be found in Huber & Wurdack (1984) and accompanying Huber (1995b).

Silva (1986) reported that *Dimorphandra cuprea*, excluding subsp. *velutina*, occurs in savanna on sandy soils, in "caatinga úmida" on the sandy and rocky margins of rivers, and in wet, riparian forest. Caatinga úmida was referred to as "Rio Negro caatinga" by Huber (1995c) and as "Amazonian caatinga" by Grande & al. (2023), to distinguish it from the Caatinga of northeastern Brazil. It is characterized by large stands of small to medium-sized, sclerophyllous trees with small, open crowns and

is found on white-sand soils of low nutrient content with a fluctuating water table that sometimes results in surface flooding. The field notes of some specimens from Amazonas State, Venezuela, mention "bana", which Huber (1995c) described as small patches of shrubby vegetation growing on white sand, referred to simply as scrub by Grande & al. (2023). Although many of the tributaries of the Casiquiare and other watercourses in this region are blackwater (Huber 1995b), the Río Siapa is reported to be whitewater (Hamilton Rice 1921). Elevations for specimens from Amazonas State range from 89–140 m with the exceptions of Huber & Medina 5926 (c. 750 m) and Fernández & al. 6014 (1500 m), which are both from rather different habitats.

Conclusions

More than two centuries after its collection, and forty years since the first suggestion that it was misplaced in *Parkia*, the type of *Inga pectinata* is recognized as belonging to *Dimorphandra* subg. *Pocillum*. The similarity between Bonpland & Humboldt 1167 and *P. barnebyana* is an example of superficial convergence in leaf morphology in two species that have been collected in the same region of Venezuela, where they grow in similar habitats. Although the leaves of some species of *Parkia* and *D.* subg. *Pocillum* could perhaps be confused in digital images, they are unlikely to be mistaken for one another when viewed side by side using a binocular microscope. This highlights the continuing importance of seeing original material in the herbarium when making taxonomic decisions, rather than only as images online, despite the enormous benefits for taxonomic research of having access to digital images.

Taxonomy

1. *Dimorphandra pectinata* (Humb. & Bonpl. ex Willd.) H. C. Hopkins & G. S. da Silva, **comb. nov.** = *Inga pectinata* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 1026. 1806 = *Mimosa pectinata* (Humb. & Bonpl. ex Willd.) Poir., Encycl., Suppl. 1: 48. 1810 = *Acacia pectinata* (Humb. & Bonpl. ex Willd.) Kunth, Nov. Gen. Sp. 6: 282. 1824 = *Parkia pectinata* (Humb. & Bonpl. ex Willd.) Benth. in Trans. Linn. Soc. London 30: 362. 1875. – Protologue: "*Humboldt et Bonpland* [...] *Habitat in America meridionali ad fluvium Cassiquiare*". – Lectotype (designated by Seigler & al. 2024: 177): [Venezuela, Amazonas State], Río Casiquiare, [May 1800] (st.), Bonpland & Humboldt 1167 (P-Bonpl. [P00679369]!; isolectotype: B-W [B -W 19056 -01 0] image!). – **Epitype (designated here)** by G. S. da Silva: Venezuela, R. Pasimoni, a altura de Pueblo Viejo, sabana arbustiva con arbolitos de arena blanca o semi blanca, 10–22 Feb 1989 (fl.), B. Stergios, K. Kubitzki, G. Aymard & E. Meiqueiro 13327

(NY [NY04954987]! with drawing of fl. attached to sheet; isoeptype: PORT image!).

Note — The original material of *Inga pectinata* consists of two similar sheets, each comprising most of a single bipinnate leaf and with a label giving the locality and collection number, and both sheets accord with Willdenow's description. The sheet in P-Bonpl. is currently filed under Kunth's name, *Acacia pectinata*, and Kunth would have seen the material in Paris when working with Bonpland and Humboldt (Stafleu & Cowan 1979; TL-2 1976–2009). Although the epithet *pectinata* must have originated with Humboldt and Bonpland, the protologue of *I. pectinata* was published by Willdenow and the sheet in B-W has his descriptive notes attached to an accompanying sheet (B -W 19056 -00 0) and so was certainly studied by him. In addition to the images online, both sheets can be seen in IDC microfiches (no. 6209 for P-Bonpl., fiche no. 154/11 [IDC 1988] and no. 7440 for B-W, catalogue number 19056 [IDC 1972]). An epitype is designated for the reason specified under "Taxonomy of *Dimorphandra cuprea*" above. The leaflets of the epitype are similar in size to those in the original material, especially when comparing the pinnae at the base and central part of the leaves, but the ferruginous indumentum on their abaxial surfaces appears to be somewhat denser.

= *Dimorphandra cuprea* Sprague & Sandwith in Bull. Misc. Inform. Kew 1932: 402. 1932. – Protologue: "BRITISH GUIANA. Kaieteur Savannah, Potaro River, Sept.-Oct. 1881, Jenman 1030". – Lectotype (designated by Silva 1986: 91): [Guyana], Kaieteur Savannah, Potaro River, Sep–Oct 1881 (fl.), G. S. Jenman 1030 (K [K000555310]!; isoelectotype: K [K000555311]!).

Note — Silva (1986) stated that one sheet at K was the holotype (Fig. 5, 6) and the other was an isotype and she labelled the specimens accordingly; her use of these terms is treated as an error to be corrected to lectotype and isoelectotype respectively (Turland & al. 2018: Art. 9.10).

= *Dimorphandra ferruginea* Ducke in J. Wash. Acad. Sci. 25: 197. 1935 = *Dimorphandra cuprea* subsp. *ferruginea* (Ducke) M. F. da Silva, Fl. Neotrop. Monogr. 44: 94. 1986. – Protologue: "Ad ripas saxosas et arenosas fluminis Curicuriary, Rio Negro superioris affluentis (civ. Amazonas), 26-12-1931 flor., leg. A. Ducke, H. J. B. R. no. 23,969". – Lectotype (designated by Silva 1986: 94): [Brazil], AM, upper Rio Negro, Rio Curicuriary, 26 Dec 1931 (fl.), A. Ducke HJBR 23969 (RB [RB00539569]!; isoelectotypes: INPA [INPA95497]!, K [K000555309]!, P [P03090008]!, S [herbarium no. S-R-8674] image!, U [U.0003275] image!, US [US00001048]!).

Note — Silva (1986) stated that the holotype and one of the isotypes were at RB. However, only a single sheet, which was labelled by her as the holotype, was shown from RB in the Re flora Virtual Herbarium (2024+) in April 2024. Her use of the term holotype

is treated as an error to be corrected to lectotype (Turland & al. 2018: Art. 9.10).

2. *Parkia panurensis* Benth. ex H. C. Hopkins in Brittonia 34: 347. 1982. – Holotype: Brazil, [Amazonas], Rio Uaupés, [nr Panuré], Feb 1853 (lv., fl. & imm. fr.), R. Spruce 2727 (K [K000504617]!; possible isotypes, or else paratypes: BM [BM000952313]!, BR [BR000000520273] image!, K [K000504618]!, P [P02436133, P02777904]!, W [herbarium no. 110500] image!).

Note — Hopkins (1982) stated that the holotype at K and had both flowers and immature fruits, with the date February 1853. Although there are two sheets of Spruce 2727 at K, only the one now with the barcode K000504617 has both reproductive stages plus this date, and so the holotype designation is unambiguous and lectotypification is not required. The handwritten label on the holotype states: "2727 In ripis fluv. Uaupés. Feb/53. (Specms brought me from a tree said to grow in gapó [sic]. Sterile stamens palish red, fertile dull yellow. *Parkia*" and the sheet has a stamp for Herbarium Benthamianum with the date 1854. The second sheet, K000504618, is stamped Herbarium Hookerianum 1867, it has leaves and flowers, the locality "Prope Panuré ad Rio Uaupés" and the date "Oct. 1852–Jan. 1853". This locality and date range are indicated on the other sheets cited above as possible isotypes. They are all sufficiently similar that they could belong to a single gathering, but it is not possible to be certain, nor can we be sure whether the holotype and these other sheets also comprise a single gathering. If Spruce was using 2727 as a species number, rather than a collection number, the sheets additional to the holotype could be paratypes, rather than isotypes. According to Rolfe (1896), the type of *Vanilla sprucei* Rolfe also has the collection number Spruce 2727.

– "*Parkia panurensis*" Benth. in Trans. Linn. Soc. London 30: 645. 1875, nom. nud., designation not validly published (Turland & al. 2018: Art. 38.1).

– "*Parkia pectinata*" auct., non Benth. in Trans. Linn. Soc. London 30: 362. 1875 & in Martius, Fl. Bras. 15(2): 267. 1876, pro parte quoad Spruce 2727.

Author contributions

H.C.F.H. initiated the study and wrote the first draft. G.S.S. contributed data and ideas. The authors collaborated to produce the final version, which both have approved.

Acknowledgements

We are indebted to Luciano Paganucci de Queiroz (HUEFS) and his field assistant, whose name we do not know, for their insights into the differences in leaf morphology between *Parkia* and *Dimorphandra*. We thank

the curators who kindly responded to our requests for images and/or information about collections: Matthias Schultz (HBG), Mike Blomberg and Colin Robinson (MO), Amy Weiss (NY), Santos Miguel Niño (PORT) and Neida Avendaño (VEN). We also thank Juraj Paule for assistance regarding the image of *Bonpland & Humboldt 1167* in B, which is reproduced with the permission of the herbarium at the Botanischer Garten und Botanisches Museum, Berlin; Odile Poncy regarding the image of this collection in P, which is reproduced with thanks to the Muséum national d'Histoire naturelle, Paris; and Laura Pearce and Alison Moore regarding images of specimens in K that are reproduced with the permission of the Trustees of the Royal Botanic Gardens, Kew. H.C.F.H. is also grateful to Corrine Sarthou for help at P, and to Odile Poncy for her kind hospitality; the staff of the Library and Archives at Kew, especially Kiri Ross-Jones and Alice Nelson, for help with the Bentham archives; Jacek Wajer (BM) for help identifying handwriting; Ian Turner (K) for some nomenclatural advice; and Mike Hopkins (INPA) for information about collections of *Parkia* and references relating to *P. panurensis*. Finally we thank Gwilym Lewis (K) and Luciano Paganucci de Queiroz for their comments on an earlier version of this paper.

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Appendix 1. Additional collections of *Dimorphandra pectinata* (syn. *D. cuprea*) from Amazonas State, Venezuela, in alphabetical order of collector.

VENEZUELA: AMAZONAS STATE: 1–4 km S of Yavita, 02°52'–54'N, 67°26'–27'W, 110 m, forest on white sand, along roadside and edge of bana, 27 Nov 1995 (fl.), *Berry & al.* 5693 (MO-1780482, VEN291277); W of Laguna de Uquirá, W side of lower R. Temi (black-water river), 6 km (direct air distance) S of mouth of R. Temi, 03°11'42"N, 67°23'54"W, forest, 6 March 1996 (fr. + galls), *Berry & al.* 6023 (MO-1780479, NY04954994); Caño Pimichin, entre Pimichin y la desembocadura [02°51'37"N, 67°32'08"W], 128 m, en bosque en las margenes inundadas del caño, 6–19 July 1969 (fl.), *Bunting & al.* 4073 (U.1248416); Atures, Caño Piedra, 115 km al SE de Pto. Ayacucho, 04°54'N, 66°54'W, 1500 m, lomas graníticas, Sep 1989 (st.), *Fernández & al.* 6014 (NY04954995, PORT); Atures, al norte del medio R. Autana, transecto desde la margen derecha de caño “Cabeza de Manteco”, a 3–4 km de la boca, 04°51'N, 67°32'W, 90–100 m, sabana de arena blanca, matorral denso, bosque medio ralo inundable hasta arenisca, 12 Nov (or 11 Dec) 1984 (fl.), *Guanchez & Melgueiro* 3568 (NY04954993); al W del medio R. Temi, a unos 5 km al río, 02°57'N, 67°29'W, 100 m, pequeña sabanita, en el ecotono entre sabana y bosque, 24 Feb 1979 (fr.), *Huber* 3411 (K002899147, NY04954996, VEN175326); bajo R. Pasimoni, en la margen derecha (E), a unos 3 km al E del río, 01°38'N, 66°32'W, 125 m, pequeña sabana, 9 Feb 1981 (fr.), *Huber & Medina* 5891 (INPA136809, K002899144, NY04954990, NY04954991, US00226984, US00226985); Macizo

[Massif] Aracamuni, en la vertiente oriental, 01°32'N, 65°48'W, c. 750 m, roca abierta y bosque bajo denso, 10 Feb 1981 (fl.), *Huber & Medina* 5926 (INPA136811, K00289945, K002899146, NY03196768, NY04954989, U.1248417, US00224959, VEN169308); Yavita, in nicht überschwemmbarer Savanna auf weissen Sand, 21 Oct 1991 (fl. & fr.), *Kubitzki & Feuerer* 91-12 (HBG ×2); R. Atabapo, on white sand savanna, 18 Oct 1950 (fl.), *Maguire & al.* 29284-A (NY04954985); R. Guainía, 1 km E of Maroa, 120–140 m, in sabanita, 25 Nov 1953 (fl.), *Maguire & al.* 36401 (F [cat. no. 1450608], NY04954983, P03090017, RB00141715, VEN40882); R. Pacimoni, right bank, 50 km above mouth, 100–140 m, at edge of savanna, 7 Feb 1954 (fr.), *Maguire & al.* 37602 (BM, NY04954984); R. Pasimoni, 01°28'40.7"N, 66°33'12.5"W, 96 m, gallery forest, blackwater, white and brown sand mixed, 28 Jan 2005 (fr.), *Redden & al.* 3379 (US00974463); R. Baria, 01°25'30.1"N, 66°27'16.8"W, 89 m, gallery forest, blackwater, 9 Feb 2005 (fl.), *Redden & al.* 3642 (K002899143, PORT, US00999212, VEN245174; + GUYN, TFAV, both n.v.); Caño Chimoni, 8 vueltas arriba de la boca del caño, 02°02'N, 66°24'W, 200 m, sabana natural, 20 Sep 1986 (fl.), *Stergios & al.* 9455 (INPA159175, MO-1780486, PORT); Caño Chimoni, sabana arbustiva de arena blanca (bana), 22 Feb 1989 (fr.), *Stergios & al.* 13308 (HBG ×2, NY04954986, PORT, US00815130); Camino de Yavita, 128 m, en los sitios claros o entre árboles pequeñas y arbustos en terreno arenoso a lo largo de camino, 23 Jan 1942 (old fl. & fr.), *Williams* 13938 (NY04954992, RB00141748, US00226980, US00229601; + GH, W fide Silva [1986], both n.v.).

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Open-access online edition bioone.org/journals/willdenowia



Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2023 Journal Impact Factor 1.8

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

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