



An updated description of *Parkia barnebyana* (Leguminosae: Caesalpinioideae, mimosoid clade) from Amazonian Venezuela and Brazil, and comparison with other species in sect. *Parkia* with erect capitula

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Summary. An updated description, including characters of the capitulum and fertile flowers, is provided for *Parkia barnebyana*. Originally recorded from southern Venezuela, this small canopy tree from igapó (blackwater flooded forest) is now also known by two collections from north-western Brazil. The capitula are yellow and held erect, with the fertile flowers uppermost; they are borne on short, robust, upright peduncles that arise from long compound inflorescence axes projecting directly above the crown. The structure and shape of the capitula place this species in pantropical sect. *Parkia* and its pod morphology suggests that it lies outside the largely Amazonian nitida-group; both conclusions are supported by a recent phylogenetic analysis. The indehiscent pods remain in the tree at maturity and most seeds are apparently removed by arboreal dispersers and vertebrate seed predators. Two other neotropical species in sect. *Parkia*, *P. cachimboensis* and *P. decussata*, are known to have erect, yellow or largely yellow capitula and in both, a well-developed fringe of staminodia projecting from the basal flowers is absent. Both these species are chiropterophilous and although we predict that *P. barnebyana* is also likely to be bat-pollinated, we have made no observations. A fourth neotropical species, *P. nana*, also with yellow flowers, is reported to have erect capitula but they do have staminodial fringes; its pollination has not been studied. Within sect. *Parkia*, erect capitula occur only in the Neotropics, probably because of the head-down position in which quite large generalist phyllostomid bats land on them to access nectar. Erect capitula appear to have evolved more than once within neotropical sect. *Parkia* and at least sometimes from ancestors with pendent capitula, but further phylogenetic data are needed to confirm this.

Key Words. Amazonia, bat-pollination, chiropterophily, clinanthium, Fabaceae, Mimosoideae, Phyllostomidae

Introduction

Parkia barnebyana H.C.Hopkins is a little known species with a restricted distribution. Its original description was based on two gatherings from a remote region of southern Venezuela but further collections now extend its occurrence in Venezuela and into north-western Brazil. When first described (Hopkins 2000), it was clearly distinct from other Latin American species in this genus even though the material was incomplete, consisting of leaves, compound inflorescence axes, the clinanthium (the structure at the centre of a capitulum on which the flowers are inserted, see below) and fruits. We have now seen flowering material and additional fruits and so we provide a more complete description. This includes some characters repeated from the protologue so that only a single description needs to be consulted, although the illustration from Hopkins (2000) is not reproduced. A key in Hopkins (2001) distinguished this species from those

that co-occur in southern Venezuela. The discussion compares *P. barnebyana* with three other neotropical species that are known or reported to have erect capitula, and examines their characteristics in relation to bat-pollination.

Material and Methods

The additional characters for *Parkia barnebyana* were taken from herbarium material at K and INPA, and from field notes. Flowers were rehydrated before examination. Barcodes have been added for types and one pod from the isotype at K is excluded as appears to belong to *P. multijuga* Benth. Images of herbarium collections, including types of several species, were viewed through the following online sites: Smithsonian National Museum of Natural History (US), Tropicos (MO), Field Museum (F) and Jstor Global Plants.

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Fig. 1. *Parkia barnebyana* (Redden et al. 3651, K). **A** three capitula in bud and one post-anthesis at the apex of a compound inflorescence; **B** successive segments of a compound inflorescence axis; **C** foliage and basal part of a compound inflorescence axis; **D** specimen label. Images **B** & **C** © The Trustees of the Royal Botanic Gardens, Kew.

The term “clinanthium”, defined by Little *et al.* (1983) as “the receptacle or torus of a Composite flower”, is used here for the swollen, often woody, clavate to ellipsoid structure at the end of the peduncle, at the centre of each capitulum. It bears the numerous flowers, which, after anthesis, develop into pods or leave rhomboidal scars when flowers abscise. Little *et al.* indicated that the word is based on the Greek for “a couch” plus “flower”. Although Beentje (2016) considered the word obscure and “receptacle” has sometimes been used for this structure in *Acacia* (e.g. Maslin 1972), this latter term is ambiguous because it could equally refer to a structure at the base of each individual flower.

Taxonomic Treatment

Parkia barnebyana H.C.Hopkins (2000: 133). Type: Venezuela, AM, Cucurital de Caname, upper Caño Caname, 3°38'N 67°08'W, 100 m, 11 Nov. 1992, lvs and fr., Berry & Melgueiro 5399 (holotype: MO [MO-04636357]; isotypes: K [K000504676, excl. fruit at upper RHS], P [P00135059], TFAV n.v.)

Small tree 7–9 m tall, branching low, crown wide. Twigs c. 1.2 cm diam. bearing short, simple hairs. Young stems, developing leaves, and rachises of leaves and pinnae densely hairy to velutinous, indumentum darkish red-brown on growing tips and paler, orange to straw-coloured on rachises of pinnae, hairs mostly 0.5–1 mm long. Leaves bipinnate, alternate, petiole and rachis up to 19 cm long, petiole with single or double, slightly raised elliptical gland on upper surface, c. 5 mm above base of pulvinus; rachis sometimes bearing small circular glands between bases of most distal pairs of pinnae. Pinnae in 19–21 pairs, opposite or subopposite, their rachises to 7 cm long, shorter in most proximal and distal pairs, sometimes rather irregular in length. Leaflets 35–40 pairs per pinna, opposite, oblong, largest per pinna 4–5×1–1.5 mm, apex rounded, base unequal, auriculate on proximal side, rounded on distal side; main nerve central throughout its length, straight at apex; secondary venation not distinct; indumentum of fairly sparse but very noticeable, straight, stiff, erect, white hairs on upper and lower surfaces and along margins, hairs to 0.5 mm long; upper surface of leaflets sometimes also covered by a white felty deposit. Compound inflorescence axes terminal, erect, to 1.12 m long in herbarium material (to 1.5 m *vide* field notes of Redden *et al.* 3651) by 8–10 mm diam., projecting vertically above crown, unbranched, covered in dense yellow-brown pubescence. Peduncles semi-erect to erect, to 20 per inflorescence axis, alternate, (0.6–)

1.5–5.5 cm long, covered in yellow-brown pubescence. Capitula in bud clavate, semi-erect to erect, brown, velutinous. Bracts subtending fertile flowers 10 mm long, spatulate, apical part to 3 mm wide, dark brown velutinous, slightly raised over flowers giving a ‘spiky’ surface to capitulum in bud just prior to anthesis. Capitula at anthesis yellow (*vide* field notes of Redden *et al.* 3651); apical part a rounded ball 3–3.5 cm diam., composed of fertile flowers on a swollen clinanthium; clinanthium immediately post anthesis c. 4 cm long with apical part ellipsoid, c. 1 cm diam., basal part terete, c. 4 mm diam., both parts with numerous rhomboidal floral scars. Fertile flowers (those examined functionally male): floral receptacle (formed by fused bases of calyx, corolla and androecium) not clearly distinct from the exterior; base of flower to tip of calyx lobes 7.5–8 mm, lobes 5 (2 large and 3 smaller), pubescent, triangular, the largest to 1 mm long and wide; base of flower to tip of corolla c. 9.5 mm, corolla 5-lobed at apex, lobes narrow, 2 mm long, then united below usually to the base or sometimes divided into segments proximally, before becoming adnate to the calyx; filaments 10, united with corolla and calyx for 2 mm at base, then connate above for c. 4 mm, then free for 9 mm, the final 2.5 mm of which projecting beyond the mouth of the corolla; anthers 1 mm long, each with a minute apical gland; ovary absent. Apparently a constricted zone of flowers (presumed to be nectar-secreting) below fertile ones; basal flowers unknown (only small floral bracts seen attached near base of clinanthium). Fruits 1 or several (–10) per clinanthium, ± planar, indehiscent, valves oblong in outline, 13–27×4–7 cm, somewhat rounded at the apex and narrowing abruptly at the base into a stipe 2–3.7 cm long; surface of valves minutely and sometimes densely rusty brown velutinous, hairs <0.1 mm long; pod wall scarcely corrugated over seeds, sub-woody or coriaceous, composed of several layers; sutures either ± equally developed or the anti-funicular one only slightly broader than the funicular one, somewhat thickened and rounded; interior of pod lacking mealy pulp; clinanthium in fruiting stage 4.2–6 cm long, apical part subspherical, 1–3 cm diam., basal part 2–3.5 cm long. Seeds 10–16 per pod. (Figs 1 and 2).

DISTRIBUTION. Southern Venezuela and north-west Amazonian Brazil (Map 1).

ADDITIONAL MATERIAL SEEN. VENEZUELA. Amazonas: Dept. Atabapo, Cucurital de Caname, southern bank of middle part of Caño Caname 3°40'N 67°22'W, 100 m, 30 April–1 May 1979, lvs and fr., Davidse *et al.* 16992 (MO×2, NY×2; also MY, MYF, VEN, all n.v., paratypes); Rio Baria, 1°25'30"N 66°27'17"W, 89 m,



Fig. 2. *Parkia barnebyana* in NW Brazil. **A** crown of a tree in centre of photo; **B** crown with erect compound inflorescence axes projecting above it; **C** foliage and axes of compound inflorescences (LHS); **D** foliage and old pods with seeds missing. Voucher: M. J. G. Hopkins 1902 (INPA). PHOTOS: M. J. G. HOPKINS.

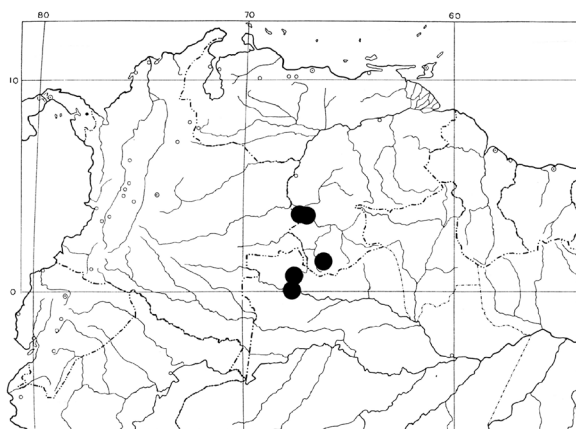
9 Feb. 2005, lvs and fl., Redden *et al.* 3651 (K, US).

BRAZIL. Amazonas: São Gabriel da Cachoeira, Boca do Rio Içana, margem esquerda do Rio Içana, lago atrás da comunidade Jauacanã, 0°33'51"N 67°24'05"W, 82 m, 29 June 2009, lvs & fr., M. J. G. Hopkins *et al.* 1902 (INPA); São Gabriel da Cachoeira, Rio Uaupés, 0°06'17"S 67°25'42"W, lvs & fr., 20 April 2009, L. A. G. de Souza & A. Cortês 17_09 (INPA).

ECOLOGY. *Parkia barnebyana* grows in riverine forest along blackwater streams and in flooded forest (igapó).

Discussion

When originally described from fruiting material, it was not clear to which section of the genus *Parkia* *barnebyana* belonged (Hopkins 2000). However, the shape of the capitula in bud and at anthesis, and the arrangement of flowers within a single capitulum in Redden *et al.* 3651 indicate that it belongs to pantropical sect. *Parkia* and this was confirmed in a phylogenetic analysis (Oliveira *et al.* 2021b). In this section, each capitulum consists of three principal types of flower



Map 1. Distribution of *Parkia barnebyana* in Venezuela and Brazil.

in a fixed arrangement: at the apex is a large ball of fertile flowers (hermaphroditic, or functionally male with the gynoecium reduced or absent, or a mixture of both male and hermaphroditic); below this is a constricted ring or cylinder of comparatively short, thick, nectar-secreting flowers; and at the base is a variable number of rows of sterile, staminodial flowers (Hopkins 1984, 1986, 1998). In most neotropical species with pendent capitula, the basal staminodial flowers are relatively numerous and their filaments project quite far beyond the mouth of the corolla; at anthesis they form a fringe that overhangs the nectar flowers. In contrast, species with erect capitula usually have few or fewer staminodial flowers and the fringe is often less well-developed or absent (see below). Capitula in bud are clavate in sect. *Parkia*, resembling a traditional light bulb in shape. In the remaining sections of the genus, the capitula in bud are spherical in sect. *Sphaeroparkia* and oblate or occasionally somewhat turbinate in sect. *Platyparkia*. The functional types of flowers and their arrangement also differ in these two groups.

Neotropical species in sect. Parkia with erect capitula. Many, though not all, species of *Parkia* have their capitula held outside the crown, free of the foliage, and within sect. *Parkia*, all the paleotropical species have pendent capitula, as do the majority of neotropical ones. Capitula in which the apical ball of fertile flowers is held uppermost are known only in the Neotropics and *P. barnebyana* is the third species that definitely has its capitula oriented this way, the others being *P. cachimboensis* H.C.Hopkins and *P. decussata* Ducke (Hopkins 1984, 1986) (Table 1); a fourth, *P. nana* D.A.Neill, is also reported to have erect capitula.

Erect capitula in sect. *Parkia* are borne on semi-erect to erect peduncles, which themselves arise from

an erect, usually unbranched, compound inflorescence axis that projects above the foliage. Because the various axes are upright and must support capitula and later pods, they are often more robust than in species with pendent capitula; this is especially true in *P. barnebyana* and *P. decussata* which both have quite thick, woody pods. The compound inflorescence axes in *P. cachimboensis* are shorter than in *P. barnebyana*, in which they are said to reach 1.5 m. The only species known to have even longer erect axes is *P. igneiflora* Ducke but its peduncles and capitula are pendent.

Occasionally some of the basal sterile flowers in *Parkia cachimboensis* have a few straight, projecting staminodes that may form a very sparse fringe, whereas in *P. decussata* the filaments in the basal flowers are not or scarcely exerted (Fig. 3; Oliveira *et al.* 2021b: fig. 1E). *Parkia barnebyana* appears to have a few rows of small basal sterile flowers, as judged from the floral bracts persisting on a clinanthium, but we have not seen this species at anthesis in the field so we cannot be certain that these flowers lack projecting staminodes, although the size of the flowers supports this assumption. In contrast to *P. cachimboensis* and *P. decussata*, *P. nana* has numerous staminodial flowers that form a well-developed fringe (Neill 2009: fig. 1; images of Vasquez *et al.* 26063, type, USM & MO), similar to that in the neotropical species of sect. *Parkia* that have pendent capitula.

Phylogenetic relationships. The majority of neotropical species in sect. *Parkia* belong to the largely Amazonian nitida-group (Luckow & Hopkins 1995: figs 35 – 36), which appears to be a recently derived and rapidly radiating assemblage whose members share a particular feature of their pods: the suture opposite the funicle attachments (anti-funicular, i.e. the abaxial suture, see Eichler 1878) is slightly broader than the opposite, adaxial, funicular suture and flattened in the same plane as the valves (Luckow & Hopkins 1995: fig. 15). This anti-funicular suture is also sometimes a different colour from the valves, especially in immature pods. Most (all?) members of this group also share characters of the clinanthium and bud capitula. They form a subclade within a slightly larger neotropical clade in the analysis of Oliveira *et al.* (2021b: fig. 2, nitida-group not marked but comprises *P. decussata* to *P. reticulata* Ducke in Clade 3). In the analyses by Luckow & Hopkins (1995) and Oliveira *et al.* (2021b), and also based on its pod morphology, *P. cachimboensis* falls outside this subclade whereas *P. decussata* lies within it. *Parkia barnebyana* is sister to the nitida-group in Oliveira *et al.* (2021b) and its pods have sutures that are equally or almost equally developed along both margins and the abaxial one is slightly thickened and rounded, rather than flattened. *Parkia nana* was not included in Oliveira's study and we have seen no herbarium material

Table 1. Comparison of *Parkia barnebyana* with five other neotropical species in sect. *Parkia*. *Parkia decussata*, *P. igneiflora* and *P. discolor* all belong to the nitida-group and *P. nana* probably does also. Data for *P. nana* are taken from Neill (2009 & pers. comm. 2022), Alverson et al. 2001 and Tropicos (online), except for *P. barnebyana*, data for other species are from Hopkins (1986) except where indicated.

	<i>P. barnebyana</i>	<i>P. cachimboensis</i>	<i>P. decussata</i>	<i>P. nana</i>	<i>P. igneiflora</i>	<i>P. discolor</i>
maximum height of tree (m)	9	5	40	4	18	15
compound inflorescence axes	erect, far projecting	erect, shortly projecting	erect, projecting	erect, shortly projecting	erect, far projecting	horizontal to semi-erect, projecting
maximum length of compound inflorescence axes	1.5 m	50 cm (Zappi 1985, K)	1 m	25 cm (based on images of types at MO and USM)	up to 5 m	1 m+
orientation of peduncles	semi-erect to erect	semi-erect to erect	semi-erect to erect	semi-erect?	pendent	pendent
orientation of capitula	erect	erect	erect	erect?	pendent	pendent
colour of capitula	yellow	yellow	yellow with red flowers at base	yellow	reddish-purple, or brownish-pink, or orange and yellow	reddish-purple or pinkish
width of ball of fertile flowers (cm)	3 – 3.5	4	3.5 – 5	2 – 2.5	3 – 3.5	2 – 2.6
projecting staminalodes in basal flowers?	?	sometimes a few	none	many, forming a fringe	many, forming a fringe	many, forming a fringe
pollinators	not known	phyllostomid bats (Hopkins 1984)	phyllostomid bats (Hopkins 1984)	not known	phyllostomid bats (Hopkins 1984)	phyllostomid bats (Vogel 1968)
Pods	indehiscent, velutinous	dehiscent, velutinous	indehiscent, velutinous	indehiscent, velutinous	indehiscent, glabrous (to subglabrous?)	indehiscent, glabrous
habitat	riparian, seasonally flooded blackwater forest (igapó)	rocky savanna/ cerrado rupestre	lowland rain forest	sub-Andean dwarf forest on oligotrophic sandstone mesas or ridges (“Andean tepuis”) (600 –) 900 – 1450 m	campinarana	riparian, seasonally flooded blackwater forest (igapó)
distribution	S Venezuela – NW Brazil	Brazil: Para (Serra do Cachimbo) and northern Mato Grosso (Cristalinos and elsewhere) (Pessoa et al. 2021; Zappi et al. 2011)	Amazonian Brazil and French Guiana (rarely in Suriname and Amazonian Colombia) (fide GBIF, online)	Peru: Amazonas and Loreto Regions	west & central Amazonian Brazil, southern Guyana and Venezuela, Amazonian Colombia, Ecuador and Peru (fide GBIF, online)	primarily in Amazonian Brazil, esp. along Rio Negro



Fig. 3. *Parkia cachimboensis*: **A** crown of a small tree with erect inflorescences; **B** semi-erect capitulum at anthesis with a few staminodia projecting from the basal flowers plus a capitulum in bud. *Parkia decussata*: **C** crown of a large tree with erect compound inflorescences protruding above it, capitula at anthesis and in bud, plus a few clinanthia with old pods; **D** erect capitulum at anthesis, the basal flowers without projecting staminodia. PHOTOS: M. J. G. HOPKINS & H. C. F. HOPKINS.

but a photograph by Robin Foster (Field Museum website, Plant identification tools) shows that the pods have unequally developed sutures that are differently coloured from the valves and so this species appears to be another member of the nitida-group. Neill (2009) also considered this species was close to *P. nitida* Miq.

That these four species do not form a clade within sect. *Parkia* could suggest that erect capitula have

evolved more than once in the Neotropics or that the common ancestor of the nitida-group had erect capitula. However, resolution amongst members of the subclade was absent or poor in both the morphological and phylogenetic analyses mentioned above and *P. decussata* was not recovered as sister to the other members of the group. Further phylogenetic data are required to resolve the question of how many times erect capitula have evolved.

Chiropterophily, erect capitula, staminodial fringes and floral colour. The size, shape, colour and structure of the capitula in *Parkia barnebyana* are all typical of the bat-pollinated species in sect. *Parkia* from the Neotropics although we have no observations to confirm chiropterophily in this case. Both *P. cachimboensis* and *P. decussata* are known to be pollinated by quite large generalist phyllostomids (Hopkins 1984), including the widespread *Phyllostomus discolor* Wagner, 1843, and a prediction of bat-pollination in *P. barnebyana* is not unreasonable.

The bats that are effective pollinators in the species of sect. *Parkia* studied so far in both the Neo- and Paleotropics land, rather than hover, to take nectar (Baker & Harris 1957; Grünmeier 1990; Hopkins 1984, 1998). Bats that usually hover at flowers are morphologically more specialised for nectarivory, and while they do visit some species of *Parkia*, they are much less likely to become dusted with pollen and so are largely nectar-thieves. In the Neotropics, the phyllostomid bats that are the major pollinators of both pendent and erect chiropterophilous capitula land head-downwards to obtain nectar and in the case of erect capitula, they grab hold of the apical ball of fertile flowers to reach the nectar below them. This contrasts with the situation in the Paleotropics where the capitula are always pendent and the pteropodid bats that visit typically land head upwards, again grabbing the fertile flowers to access the nectar (Grünmeier 1990: fig. 5; Hopkins 1998: fig. 11; Oliveira *et al.* 2021a: fig. 1H). Erect capitula would be maladapted for bat-pollination in the Paleotropics without considerable modification because a bat's mouth would not be adjacent to the nectar-flowers when it landed.

In the neotropical species of sect. *Parkia* with pendent capitula, the well-developed staminodial fringe acts as a landing platform for bats (Hopkins 1984, 1998), though we do not exclude the possibility of other functions (protection of nectar from thieves and/or rain, dissemination of scent). The fact that *P. cachimboensis* and *P. decussata* have little or no fringe is consistent with the idea that acting as a landing platform is a primary function of the staminodes in the Neotropics. It is possible that the erect capitula of *P. cachimboensis* could have evolved from an ancestor with pendent ones and the fringe has been largely but not always entirely lost when the capitula switched to being erect. However, the idea of a landing platform would not explain the presence of a fringe in *P. nana* nor in some paleotropical taxa with pendent capitula, such as *P. bicolor* A.Chev. from Africa and *P. speciosa* Hassk. from South East Asia. However, well-developed fringes are present only in some species in the Paleotropics, where the range in capitular shape, though not size, is greater than in the Neotropics.

The situation in *Parkia nana* is intriguing. The capitula are typical in size, shape and structure to those of species in sect. *Parkia* that are known to be chiropterophilous. They appear to be erect (D. Neill pers. comm. 2022; R. Foster pers. comm. 2022) but the staminodial fringe would not be well-placed as a landing platform for quite large bats and could point to some other function, or maybe *P. nana* has only recently evolved from a species with pendent capitula and has not yet lost its projecting staminodes. Alternatively, it might not be pollinated by bats, or not by ones that land head-downwards to feed. Clearly field observations are needed to confirm the orientation of the capitula and show how they function in relation to their pollinators.

So far, *Parkia nana* has been recorded from five localities in Peru between 600 and 1450 m (GBIF online; Tropicos online) where it occurs in dwarf forest on oligotrophic sandstone mesas or ridges known as Andean tepuis (Alverson *et al.* 2001; D. Neill pers. comm. 2022). Only one other neotropical species in sect. *Parkia* has been collected regularly above 600 m, *P. nitida*, which is primarily found in lowland Amazonia but occurs up to 1400–1500 m in Colombia, Ecuador and Bolivia, 850 m in Peru and 1200 m in Venezuela and Guyana (Tropicos online). In a study at low elevation near Manaus (Hopkins 1984), its principal pollinator was *Phyllostomus discolor* but the presence of this tree to c. 1500 m suggests that suitable generalist pollinating bats are likely to be present at these altitudes and could thus also be available to *P. nana*. Alverson *et al.* (2001) recorded more than 20 species of Phyllostomidae though their survey area included low elevations as well as the higher locality for *P. nana*.

Parkia decussata and *P. barnebyana* are large and medium-sized canopy trees respectively in lowland forests, whereas *P. cachimboensis* is a small tree or shrub restricted to low-growing cerrado rupestre or rocky savanna (Pessoa *et al.* 2021; previously called Amazonian caatinga [Anderson 1981] or white sand campina [Lleras & Kirkbride 1978]) on the largely quartzite Serra do Cachimbo and other localities at the southern margin of the Amazon basin (e.g. Zappi *et al.* 2011). It is perhaps not surprising that it has erect capitula because relatively large phyllostomids, including *Phyllostomus discolor*, are unlikely to forage as close to the ground as some smaller hovering bats because they are less manoeuvrable and in low-growing vegetation erect capitula may be more accessible to them than pendent ones.

All four species known or suspected of having erect capitula have yellow or predominantly yellow flowers. Capitular colour is more variable amongst the neotropical species of sect. *Parkia* than in the Paleotropics, where all the species in Africa have red or orange capitula (or

rarely partially yellow) and those in the Indo-Pacific and Madagascar have yellow ones, sometimes with a whitish fringe (Hopkins 1998). In the Neotropics, the majority of taxa in sect. *Parkia* have yellow capitula (10 out of 14, again sometimes with a white fringe), red or reddish capitula are found in three, and two, including *P. decussata*, have capitula composed of both red and yellow flowers. (In *P. igneiflora* Ducke as currently circumscribed, flowers can be either reddish or yellow-orange [Ducke 1949] so it is counted here twice.)

Hopkins (1984) argued that floral colour in the Neotropics was loosely correlated with the position of capitula relative to the tree crown, so that the reflective capitula would be more visible to bats either against the sky if red and borne on far-projecting axes, or against foliage if yellow and borne on shorter axes, but with its long, projecting inflorescence axes, *P. barnebyana* does not fit this pattern. It would be interesting to know what the eyes of generalist phyllostomids see when visiting *Parkia* capitula, in addition to what the bat detects through its sonar and sense of smell, to help explain why the capitula are usually brightly coloured, rather than being bright white or dull purplish-brown, which are more typical of chiropterophilous flowers. The question of what flower-visiting bats see is now being addressed in some other neotropical groups that are pollinated by more specialised nectarivores (e.g. Domingos-Melo *et al.* 2021 and refs therein).

Fruits and dispersal. The pods of *Parkia barnebyana* are indehiscent, woody and velutinous, at least when young. Although a clinanthium can bear 1 – 10 pods, usually only one or a few per clinanthium reach maturity and only a minority of capitula per compound inflorescence axis produce pods, which is not unexpected since some capitula appear to be composed only of male fertile flowers.

After fruiting, some or most pods remain in the tree (Fig. 2B, D). Old pods cut down from the crown had their seeds missing, presumably removed by arboreal frugivores which probably include monkeys and parrots, though the latter are more likely to be seed predators than dispersal agents. The damage to the valves in Fig. 2D resembles that seen in some other neotropical species of *Parkia* (Hopkins & Hopkins 1983: fig. 2). The field notes of the type, *Berry & Melgueiro* 5399, mention that old pods were found on the ground and the specimen at MO shows damage to the valves but it is not known whether the seeds were removed before or after the fruits fell.

The only species in neotropical sect. *Parkia* besides *P. barnebyana* that regularly occurs in blackwater riverine and inundated forest is *P. discolor* Spruce ex Benth., which is found principally along the Rio Negro. Its pods fall at maturity and are water-dispersed (Hopkins & Hopkins 1983) but hydrochory is unlikely in *P. barnebyana* because its fruits do not fall readily.

The pods of both *Parkia nana* and *P. decussata* are densely velutinous, as are those of *P. cachimboensis* but in the latter, the valves dehisce when ripe, making it unique in sect. *Parkia*. We have no information about seed dispersal in *P. nana* and *P. cachimboensis* but damage to pods in *P. decussata* resembles that in *P. barnebyana*, again suggesting arboreal frugivores are involved.

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Declarations

Conflicts of interest The authors have no conflicts of interest regarding this paper.

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