

Revision of the
Genus *Psyllocarpus* (Rubiaceae)

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A B S T R A C T

Kirkbride, Joseph H., Jr. Revision of the Genus *Psyllocarpus* (Rubiaceae). *Smithsonian Contributions to Botany*, number 41, 32 pages, 41 figures, 8 plates, 1979.—*Psyllocarpus*, a member of the Rubiaceae tribe, Spermaceae, is separated from all other genera of the tribe by its capsule, which is strongly compressed parallel to the septum. Section *Amazonica* is found only in white-sands vegetation in the Amazon valley, and section *Psyllocarpus* is encountered only on savannas of the Planalto Central do Brasil. The two sections, of which *Amazonica* Kirkbride is described as new, are sharply delimited by their leaf structure, floral biology, number of calyx lobes, pollen morphology, and distribution. The history, morphology, and distribution of the genus are discussed. A key to the sections and species of *Psyllocarpus*, a taxonomic treatment of each taxon including nomenclature, synonymy, description, distribution and type, and an index to exsiccatae critically examined are given. Two species are described as new, *P. cururuensis* Kirkbride and *P. goiasensis* Kirkbride, and two species *P. campinorum* (Krause) Kirkbride and *P. psyllocarpoides* (Sucre) Kirkbride, are transferred into *Psyllocarpus*.

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Revision of the Genus *Psyllocarpus* (Rubiaceae)

Joseph H. Kirkbride, Jr.

Introduction

Psyllocarpus, a member of the Rubiaceae tribe Spermaceae, is separated from all other genera of the tribe by its capsule, which is strongly compressed parallel to the septum. It is found on savannas in the Planalto Central do Brasil and white-sands vegetation in the Amazon valley. It was described by von Martius and Zuccarini in 1824 from collections made by the former in 1818 and 1819. They undoubtedly intended *Psyllocarpus* and its four new species to be published in the first volume of their *Nova genera et species plantarum*, but a few months earlier they published in *Flora* the diagnostic phrases for the taxa *Psyllocarpus*. Under article 11 of the *International Code of Botanical Nomenclature* (1972), their publication in *Flora* has clear priority over their later one in the *Nova genera et species plantarum* and must be cited as the place of publication.

Subsequent authors (Sprengel, 1827; Schultes and Schultes, 1827; de Candolle, 1830; G. Don, 1834) followed von Martius and Zuccarini, and they often used their very phrases to describe *Psyllocarpus* and its four species. The only other revision of *Psyllocarpus* prior to this one was made by Schumann (1888) for *Flora brasiliensis*. He maintained three species in *Psyllocarpus* and transferred *P. thymbroides* to *Staëlia* following neotypification of that species. Considering the collections available to him at that time, he was correct in maintaining

three species in *Psyllocarpus*, but his key to those species is misleading and inaccurate for some characters.

In 1898, Schumann published two additional species of *Psyllocarpus* based upon collections sent to Berlin by Glaziou for identification. After Schumann, two more species of *Psyllocarpus* were incorrectly associated with other genera by Krause (1908) and Sucre (1971). Each of these species is found in the type of vegetation known as "campinas," which occur on podzolized sands in Amazonian Brazil. The enormous number of new collections made in this century, as compared to those available to Schumann, indicated the need to re-evaluate his work and to transfer into *Psyllocarpus* those species incorrectly assigned to other genera.

Psyllocarpus has traditionally been placed in tribe Spermaceae (de Candolle, 1830; G. Don, 1834; Hooker, 1873; Baillon, 1881; Schumann, 1888, 1891; Wernham, 1916; Hayden, 1968). Within the tribe, the genera are distinguished by the occurrence and the manner of fruit dehiscence. The opinion is again being actively presented that a number of genera of tribe Spermaceae should be merged (Hooker, 1873; Bremekamp, 1934; Verdcourt, 1975, 1976; F. R. Fosberg, pers. comm.) because the traditional generic delimitations do not, in the opinions of those cited above, divide the species into natural groups. The traditional generic divisions within tribe Spermaceae have been maintained by workers who have dealt principally with New World Rubiaceae (Schumann, 1888; Wernham, 1916; Standley, 1930, 1931a, 1931b, 1931c, 1936; Smith and Downs, 1956; Anderson, 1972;

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Steyermark, 1972, 1974). I believe that *Psyllocarpus* is a natural grouping of closely related species, and pending a worldwide revision of tribe Spermaceae that is beyond the scope of this study, I am maintaining them as the genus *Psyllocarpus*. In my opinion, it is most closely related to *Borreria* G.F.W. Meyer (sensu stricto) because of the manner of dehiscence of its fruits and its habit and foliar development as seen in section *Amazonica*.

ACKNOWLEDGMENT.—I am indebted to Drs. Rupert C. Barneby, Richard S. Cowan, Harold E. Robinson, and John J. Wurdack for their many helpful suggestions and reviews of the manuscript.

I am also grateful to the National Science Foundation for support of my field studies of section *Psyllocarpus* through a grant for improvement of doctoral dissertation research, GB-31978, and to the Fluid Research Fund of the Smithsonian Institution for supporting my studies of section *Amazonica*. I also want to thank the Universidade de Brasília, Brasília, D.F., Brasil, and the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil, for their co-operation and support. Access to herbaria was permitted and loans of specimens were made by numerous institutions, to whose directors I express my thanks.

Morphology

HABIT.—The habit of *Psyllocarpus* ranges from perennial herb to shrub, but the majority of species and individuals are subshrubs. Perennial herbs have been found in *P. laricoides* and *P. schwackei*. In both species these appear to be a fecund stage in young individuals that will, if unaffected by outside forces, continue to grow and become subshrubs. The subshrubs are robust plants that, except in the case of *P. schwackei*, develop woody stems four to six times greater in diameter than the new herbaceous ones. *Psyllocarpus schwackei* does not generally get as tall as other species, and it appears to die back to ground level much more frequently.

Well-developed brachyblasts are found on all species of *Psyllocarpus* except *P. campinorum* and *P. schwackei*, and it has not been possible to determine their presence or absence for *P. psyllocaepoides* since foliar structures are not known for this species. The brachyblasts are reduced axillary

branchlets with the form of their structures normal but reduced in size with the internodes the most strongly reduced. Consequently, the brachyblasts form fascicles of reduced leaves in the axils of the primary leaves. Rarely short branchlets will be found in the leaf axils in place of the brachyblasts from which they differ only by the increased length of their internodes.

The species of section *Amazonica*, *P. campinorum*, *P. cururuensis*, and *P. psyllocaepoides*, are usually taller than those of section *Psyllocarpus*. Also, so far as known from a very small sample, *P. campinorum* and *P. psyllocaepoides* are less frequently branched than *P. cururuensis* and the species of section *Psyllocarpus*. The habit of the members of section *Amazonica* is probably wand-like.

The species of section *Psyllocarpus* are usually of a lesser stature and more densely branched than those of section *Amazonica*. The branches of *P. laricoides*, *P. goiasensis*, and *P. asparagoides* are erect and strongly fastigiate so that the living plant has an obconical outline. When pressed and dried, it takes the form of many tightly compact, parallel branches. *Psyllocarpus phyllocephalus* has a distinct branching pattern: the main stem is erect and undivided until four or five cm long and then divides into numerous broadly spreading branches. These divide many times, further producing a spreading, flat top. When pressed and dried, specimens of *P. phyllocephalus* form a circle of tangled branches that seem to be divided numerous times. *Psyllocarpus schwackei* is also distinctive due to its short stature and slender stems and branches. It produces as many branches as other members of section *Psyllocarpus*, but they are shorter, thinner, and not further divided.

STIPULES.—The stipular structure of *Psyllocarpus* is typical of tribe Spermaceae. A membranous tissue or sheath connects the leaf base on each side of the stem forming a collar that completely surrounds the stem at each node. On the upper, free edge of the sheath are found three to eight setae, usually evenly spaced along the edge of the sheath between the leaf bases. Their length varies, the central one being the longest, the rest gradually shorter outward. The apex of each seta at the apical nodes is glandular and can be referred to as a colleter (Lersten, 1975). At the lower nodes, the colleters are missing from the setae thus indicating that their secretory function is in the early develop-

ment of the apex as has been suggested for other members of the Rubiaceae (Krause, 1909; Uphof, 1962; Horner and Lersten, 1968).

LEAVES.—The sections of *Psyllocarpus* are clearly separated by their foliar structures. The leaves of section *Amazonica* are dorsiventral (Figure 1) and appear grossly to be planar in form. From herbarium specimens, their orientation appears to be horizontal. In cross-sections of the leaves of *P. campinorum* and *P. cururuensis* (Figure 1), the structure of a typical dorsiventral leaf is seen. The epidermis are composed of a single layer of cells above and below. Stomata, as seen in cross-sections, are found on each face, although fewer on the adaxial one. The palisade parenchyma is a single layer of cells, elongated at right angles to the dorsal epidermis throughout, and more or less of uniform length. Immediately below it is the paraveinal mesophyll. This is a regular network of several-armed cells, lacking chlorophyll, one cell-layer thick, extending horizontally between the vascular bundles in the plane of the phloem (Fisher, 1967; Lackey, 1978). It has been reported from a number of unrelated families: Magnoliaceae (Pray, 1954), Cercidiphyllaceae (Chandrasekharam, 1972), Sapotaceae (H. E. Robinson, pers. comm.), Leguminosae (Debold, 1892; Fisher, 1967; Weston and Cass, 1973; Lackey, 1978), Sapindaceae (Radlkofer, 1890), Oxalidaceae (Dittmar, 1964), and Liliaceae (Pray, 1955). The spongy parenchyma fills the space between the paraveinal mesophyll and the ventral epidermis. Throughout both parenchyma layers there are en-

larged idioblasts containing either bundles of raphides or druses. The raphides occur in both types, but the druses are only encountered in the palisade layer. The large main vein is clearly evident in the center of the leaf and gives rise to smaller pinnate secondary veins.

Schumann (1888) described the leaves of section *Psyllocarpus* as "trigona" or "plana," and used these characters to identify the species of *Psyllocarpus*. In the living state, the leaves of section *Psyllocarpus* are actually terete (Figure 2). Sometimes on the abaxial side of the leaf there are two or three faint ridges or a slight flattening. When individuals of this section are dried, the leaves become angled an irregular number of times. The orientation of the leaves is close to vertical, which exposes the entire surface of the leaf to a more uniform intensity of sun light. In all species of the section, the epidermis in cross section is composed of a single layer of cells with stomata distributed all around the surface. The palisade parenchyma is composed of elongated cells, of more or less equal length, placed at right angles to the epidermis so as to form a continuous layer, the individual cells being arranged radially. The palisade parenchyma is composed of a single layer of cells in all species of section *Psyllocarpus* except *P. schwackei*, where it consists of two layers concentrically arranged. There is some spongy parenchyma, but it is much reduced in volume and sometimes completely absent. The leaves have one vein that occupies the long axis of the leaf blade. The bundle-sheath varies in thickness from a single

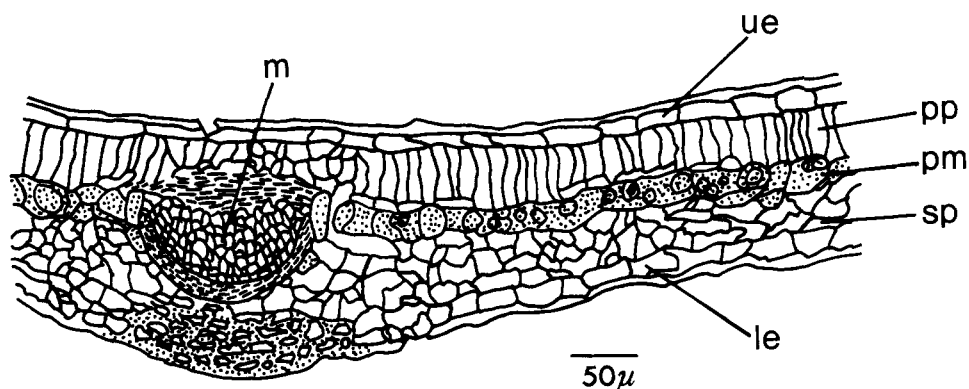


FIGURE 1.—Cross-section of portion of leaf blade of *Psyllocarpus campinorum* (Bahia 32) (ue = upper epidermis; le = lower epidermis; pp = palisade parenchyma; pm = paraveinal mesophyll; sp = spongy parenchyma; m = midrib).

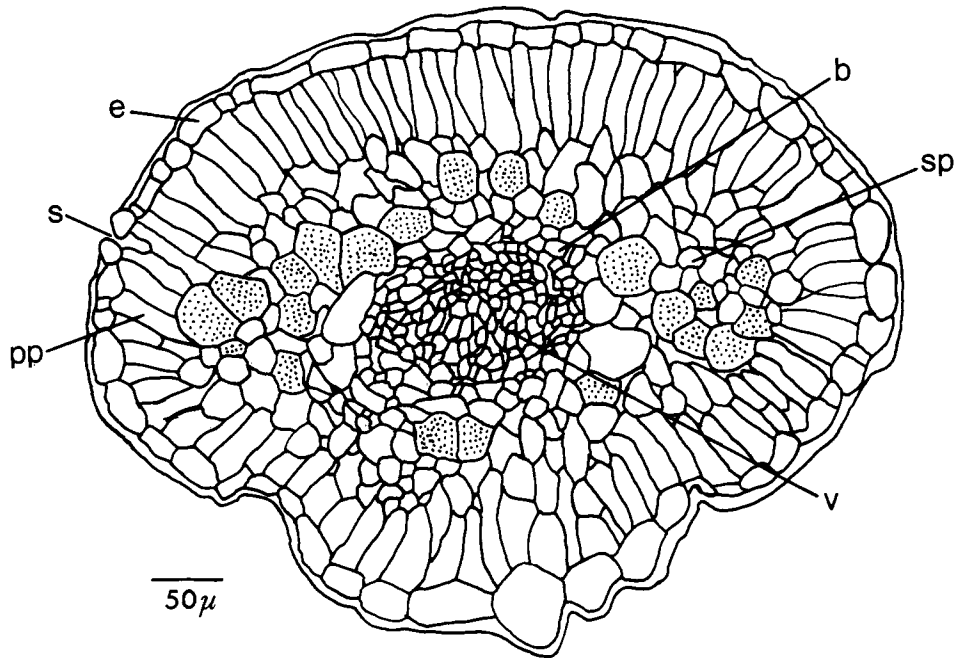


FIGURE 2.—Cross-section of leaf blade of *Psyllocarpus laricoides* (Anderson et al. 35761) (e = epidermis; pp = palisade parenchyma; sp = spongy parenchyma; v = vein; b = bundle-sheath; s = stoma).

layer of cells to many, occupying a great deal of space. Enlarged idioblasts with bundles of raphides are found in all species, and enlarged idioblasts with druses were also found in the closely related *P. asparagoides* and *P. phyllocephalus*.

INFLORESCENCES.—The inflorescence structures of *Psyllocarpus* are similar to those in the Labiatae, as described by Bentham (1835). Because of this striking similarity, Bentham's terminology for Labiate has been adopted here. The most common type of inflorescence encountered in *Psyllocarpus* is the verticillastrate raceme. It is an indeterminate inflorescence with pairs or rarely, in *P. laricoides*, whorls of three bracts, each subtending a cymule of 1 to 17 flowers. Each pair or whorl of bracts with their cymules is referred to as a verticillaster. In section *Amazonica*, the bracts are clearly differentiated from the leaves, and the flowers of each cymule range in number from 4 to 17. In the two species of section *Psyllocarpus* with verticillastrate racemes, *P. laricoides* and *P. goiasensis*, the bracts exhibit a gradual change distally in form from leaf-like to bract-like, the lowest being very similar to true leaves. In order

to maintain the distinction between the leaf and bract, Bentham's definition (1835) has been applied here, "that the (bracts) are always those situated at the base of a verticillaster." The cymules of the two species of section *Psyllocarpus* with verticillastrate racemes have one to four flowers.

The three remaining species of *Psyllocarpus* exhibit two types of inflorescences: (1) capitate (*P. asparagoides* and *P. phyllocephalus*) and (2) solitary flowers in each leaf-axil at a few terminal nodes. (*P. schwackei*). The capitula are very tightly packed heads of 6 to 24 flowers. Paired bracts subtending one to three (rarely four) flowers are present within each head and are connected at base by a membranous tissue similar to that which connects the bases of bracts of the verticillasters and of the stipules. The capitula are therefore tightly packed concentric rings of sheathing tissues, bracts, and flowers.

Psyllocarpus schwackei has only solitary flowers, each subtended by a setiferous bract. The solitary flowers occur always in opposed pairs at a few of the terminal nodes.

FLOWERS.—As is typical for family Rubiaceae, the flowers of *Psyllocarpus* have an inferior ovary, an actinomorphic, gamopetalous corolla, and epicorollar stamens; as is less usual a tetramerous corolla and bilocular ovary. The species of section *Amazonica* are heterostylous, and those of section *Psyllocarpus* homostylous.

The hypanthium is turbinate, bearing a persistent calyx of either two (section *Psyllocarpus*) or four (section *Amazonica*) lobes. The bases of the lobes are either joined by a low membrane or completely free. Between the calyx-lobes, on the edge of the calyx-tube or along the distal edge of the hypanthium, there are usually one to eight setae of varying lengths, which resemble those of the stipules. Very rarely these setae are lacking. The hypanthium has in each of its two locules one ovule peltately fastened to its funiculus that arises from the center of the septum separating the locules.

The corolla is small, blue or white, and salverform or very rarely funnelform. The corolla-lobes are always much shorter than the tube and valvate. In heterostylous section *Amazonica*, the pin flowers have short filaments that separate from the corolla tube above the middle and below the apex so that the anthers are included, and the thrum flowers have long filaments that separate from the apex of the tube so that the anthers are exerted. In homostylous section *Psyllocarpus*, the short filaments separate from the tube wall below the middle so that the anthers are always included.

The style varies in length, with distinct and much longer stigmatic lobes in section *Amazonica*. In pin flowers with exerted stigmatic lobes, the styles are two to three times longer than in thrum flowers with included stigmatic lobes. The style in section *Psyllocarpus* is always short and one-eighth to one-quarter as long as the corolla tube. The stigma frequently is weakly bilobate, but sometimes it is capitate or distinctly lobed. As a consequence of the relative sizes, the anthers in section *Psyllocarpus* are always positioned slightly above the stigma.

The pollens of the two sections are very distinct. The species of section *Amazonica* have significantly larger grains (Figures 3, 5, 7) and are oblate-spheroidal with short spinules distributed evenly over the perforate sexine (Figures 4, 6, 8). In section *Psyllocarpus*, the grains are smaller and prolate-spheroidal (Figures 9, 11, 13, 15, 17) with short

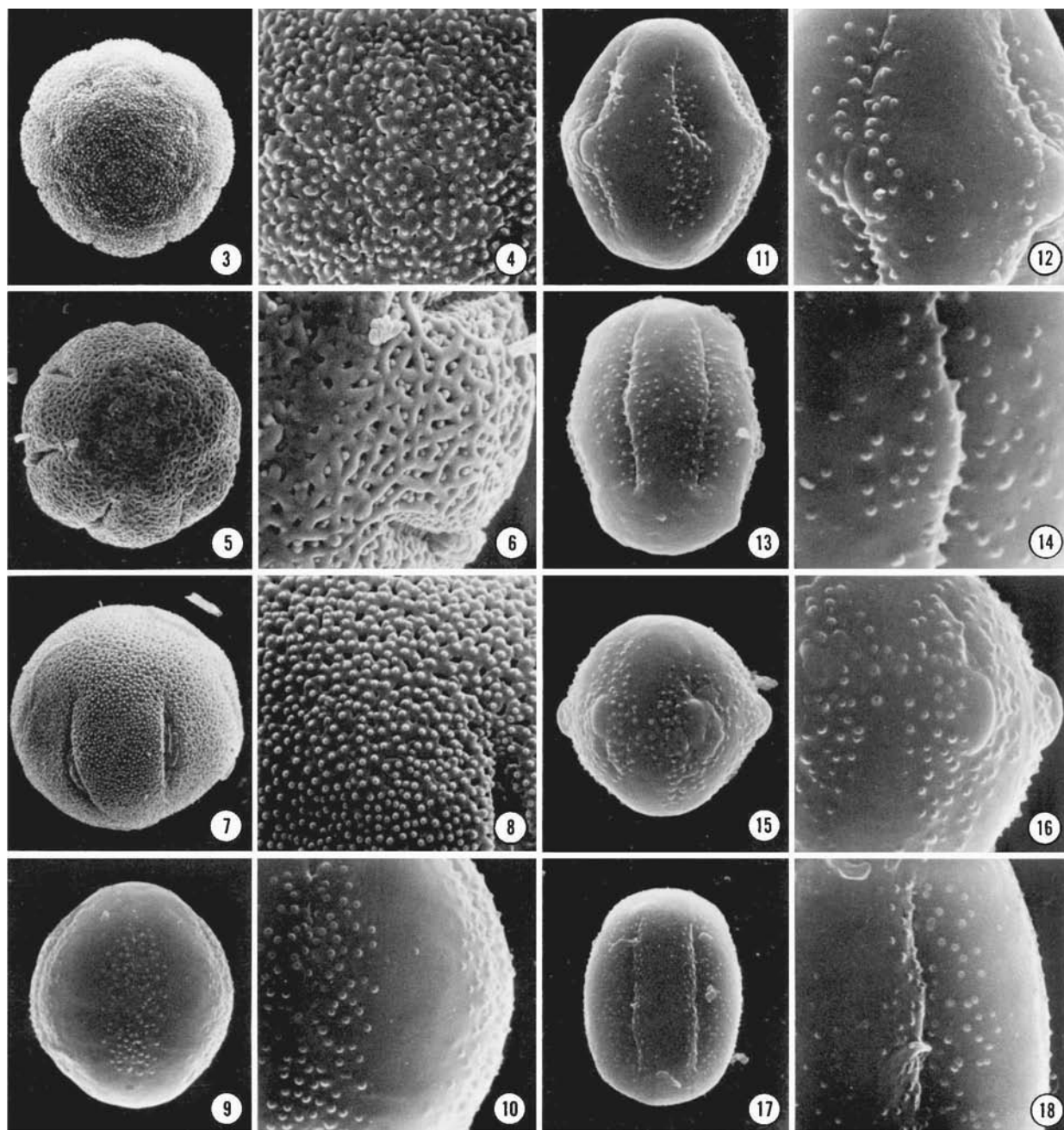
spinules occurring along the edges of the colpi in a nonrandom pattern over the smooth and non-perforate sexine (Figures 10, 12, 14, 16, 18).

FRUITS.—The fruits of *Psyllocarpus* are capsules strongly compressed parallel to the septum. They dehisce from the apex downwards, the lines of dehiscence following the junction of the septum with the wall of the capsule on each side. Each unbroken valve of the capsule reflexes outwards, leaving the complete septum erect in the center. The fruits were measured at the stage just prior to dehiscence, and the planar shape, length, and width of their outline determined as well as the thickness of their compressed dimension.

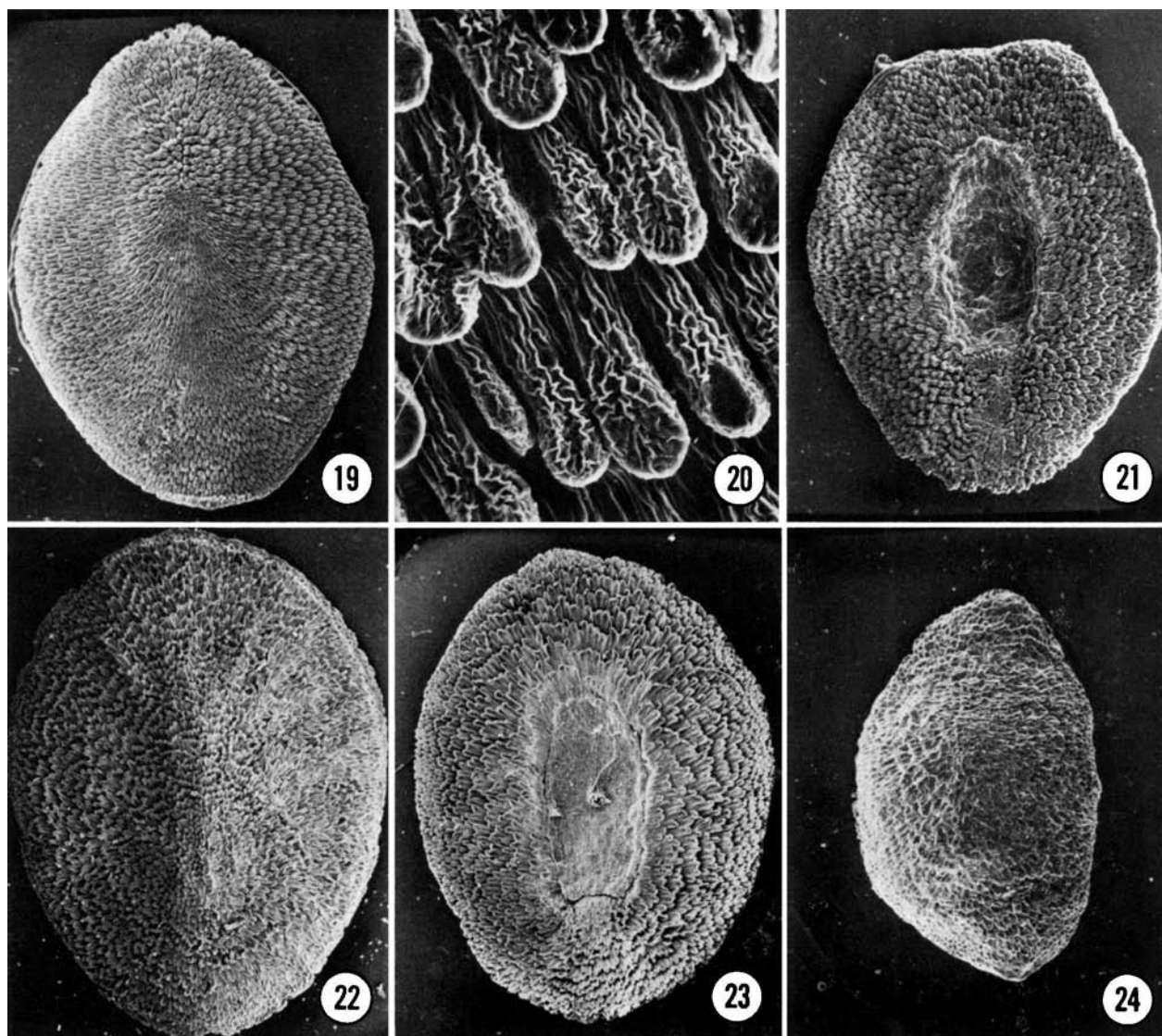
The seeds of *Psyllocarpus* are strongly compressed and were measured in the same manner as the intact fruits. They are shed from the fruit after it dehisces. There is a tendency towards development of a narrow, irregular wing by an extension of the testa around the edge of the seed (Figure 19, 22, 25, 27, 31, 33, 37, 39). The abaxial surface of the seeds is rugulose. The surface sculpturing of the rugae on the seeds of section *Amazonica* is similar for all three species (Figure 20), but the rugae of each species of section *Psyllocarpus* have a distinct pattern of surface sculpturing (Figure 26, 29, 32, 35, 38). The strophiole is on the adaxial side of the seed. Based upon data from two species, the strophiole of *Psyllocarpus* was described as "reduced to a single, round central spot" (Hayden, 1968). This description is very apt for all species of *Psyllocarpus* (Figure 21, 23, 27, 33, 39) except *P. goiasensis* (Figure 30) and *P. phyllocephalus* (Figure 36). In these two species, length and width of the strophioles are sufficiently different so that the strophioles become oblong to linear.

Distribution

The genus *Psyllocarpus* is found only within the confines of modern-day Brazil. Its distribution parallels its subgeneric classification. Section *Amazonica* is now known from the extreme eastern end of Amazonas, the western end of Rondônia and the southwestern corner of Pará in the Amazon valley (Figure 40). The herbarium label data indicate that the three species of section *Amazonica* grow only in "campina" vegetation. This is a form of low, woody vegetation found on podzolized white-sand soils. Campinas have a low species di-



FIGURES 3-18.—*Psyllocarpus* pollen, SEM. *Psyllocarpus campinorum*: 3, polar view, $\times 1350$; 4, surface, $\times 3750$ (3, 4, *Silva 4346*). *Psyllocarpus cururuensis*: 5, Polar view, $\times 1250$; 6, surface, $\times 3750$ (5, 6, *Anderson et al. 10779*). *Psyllocarpus psyllocarpoides*: 7, equatorial view, $\times 1200$; 8, surface, $\times 3750$ (7, 8, *Frões 25262*). *Psyllocarpus laricoides*: 9, equatorial view, $\times 2500$; 10, surface, $\times 5000$ (9, 10, *Anderson et al. 35750*). *Psyllocarpus goiasensis*: 11, equatorial view, $\times 2500$; 12, surface, $\times 5000$ (11, 12, *Anderson et al. 7161*). *Psyllocarpus asparagoides*: 13, equatorial view, $\times 2550$; 14, surface, $\times 7500$ (13, 14, *Irwin et al. 22247*). *Psyllocarpus phyllocephalus*: 15, equatorial view, $\times 2500$; 16, surface, $\times 5000$ (15, 16, *Irwin et al. 34434*). *Psyllocarpus schwackei*: 17, equatorial view; $\times 2000$; 18, surface, $\times 5150$ (17, 18, *Duarte 11381*)

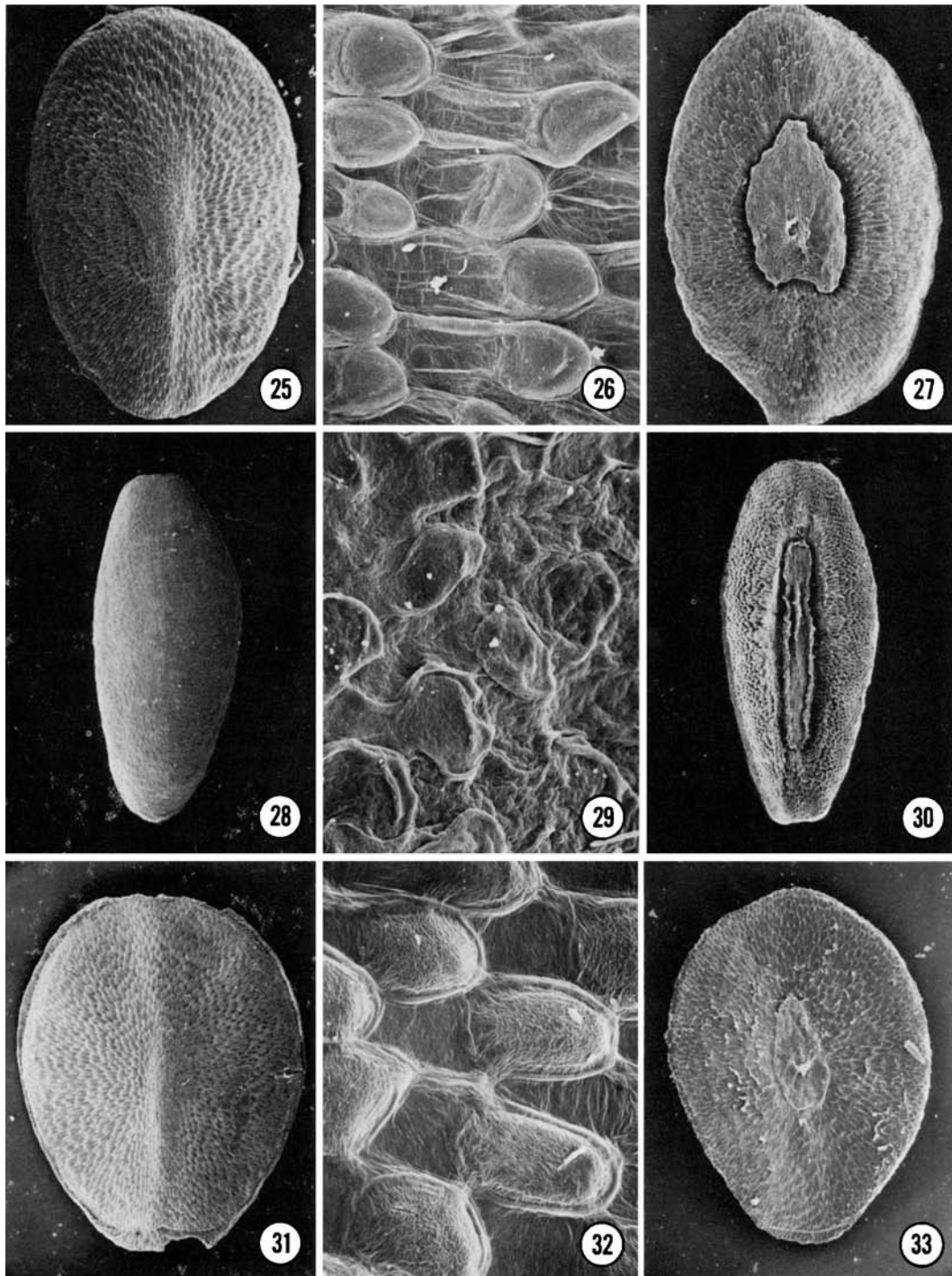


FIGURES 19–24.—Section *Amazonica* seeds, SEM. *Psyllocarpus campinorum*: 19, abaxial view, $\times 20$; 20, abaxial surface, $\times 270$; 21, adaxial view, $\times 22$ (19, 20, 21, *Bahia 32*). *Psyllocarpus cururuensis*: 22, abaxial view, $\times 20$; 23, adaxial view, $\times 19$ (22, 23, *Anderson et al. 10779*). *Psyllocarpus psyllocarpoides*: 24, abaxial view, $\times 22$ (24, *Fróes 25262*).

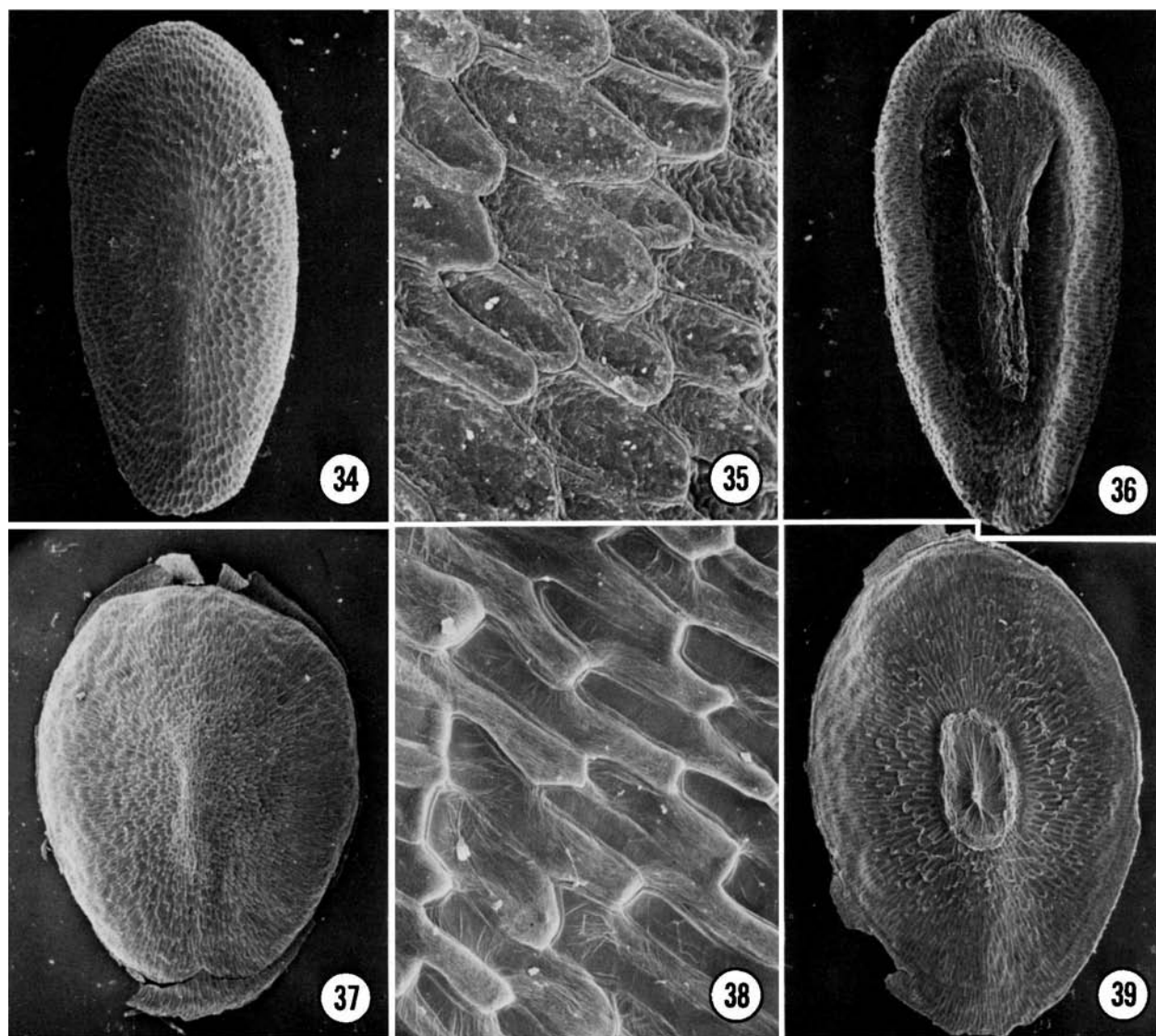
versity, and their flora contains a number of endemic species (Lisbôa, 1975). Judging from the number of herbarium collections, the species of section *Amazonica* are not common.

Section *Psyllocarpus* is known from the Distrito Federal, Goiás, Bahia, and Minas Gerais in southeastern Brazil (Figure 41). The distribution of the species falls into two groups: two species, *P. goiasensis* and *P. phyllocephalus*, which are not closely

related, are found on the system of chapadas that extends from Rios Tocantins and Paranã to the north and to the Rios Corumbá and São Marcos to the south, approximately centered on the Distrito Federal. *Psyllocarpus goiasensis* is found on its higher northern end, where occur a larger concentration of sand-based soils that are probably lithosols. *Psyllocarpus phyllocephalus* is found mainly on the lower center and southern end of



FIGURES 25-33. Section *Psyllocarpus* seeds, SEM. *Psyllocarpus laricoides*: 25, abaxial view, $\times 25$; 26, abaxial surface, $\times 340$; 27, adaxial view, $\times 25$ (25, 26, 27, *Mexia 5755*). *Psyllocarpus goiasensis*: 28, abaxial view, $\times 14$; 29, abaxial surface, $\times 340$; 30, adaxial view, $\times 14$ (28, 29, 30, *Irwin et al. 15531*). *Psyllocarpus asparagoides*: 31, abaxial view, $\times 23$; 32, abaxial surface, $\times 480$; 33, adaxial view, $\times 23$ (31, 32, 33, *Irwin et al. 21998*).



FIGURES 34–39.—Section *Psyllocarpus* seeds, SEM. *Psyllocarpus phyllocephalus*: 34, abaxial view, $\times 34$; 35, abaxial surface, $\times 360$; 36, adaxial view, $\times 35$ (34, 35, 36, Pires et al. 9143). *Psyllocarpus schwackei*: 37 abaxial view, $\times 22$; 38, abaxial surface, $\times 360$; 39, adaxial view, $\times 30$ (37, 38, 39, Macedo 2960).

the system. From my observations and the herbarium data, it seems to grow on soils that are regosols and latosols.

Three species of section *Psyllocarpus*, *P. laricoides*, *P. asparagoides*, and *P. schwackei*, are found on the series of highlands that run up through Minas Gerais and Bahia. This series of mountains and chapadas forms the eastern watershed of the Rio

São Francisco and separates the bulk of the savanna vegetation referred to as "cerrado," sensu lato, from the coastal forests. *Psyllocarpus laricoides* and *P. asparagoides* are generally distributed throughout this region and frequently encountered. From my experience in the southern portions of this area and the herbarium label data, these two species are found on the thin quartzite lithosols that in this

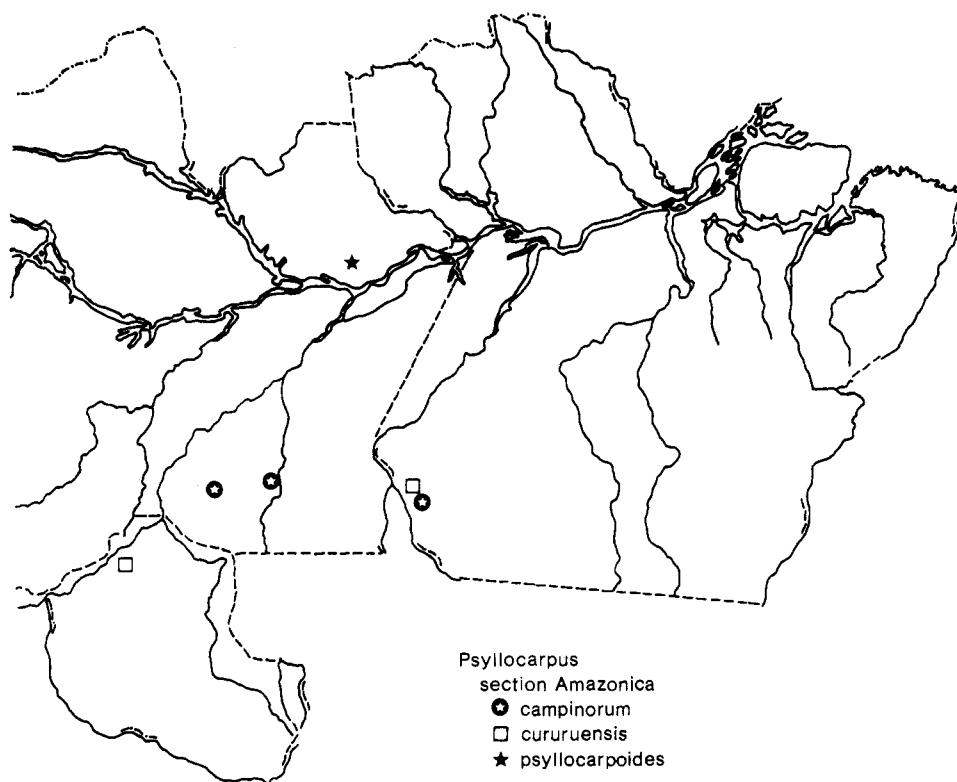


FIGURE 40.—Known distribution of section *Amazonica* in Amazonas, Pará, and Rondônia, Brazil.

region typically support 'campos rupestres' (Eiten, 1972, 1978), and *P. laricoides* is also encountered on regosols and latosols at the eastern side of the valley of the Rio São Francisco. *Psyllocarpus schwackei* is a narrow endemic that was described from Serra do Cipó and was known only from there for many years. I have examined it in the type locality, where it is also found in 'campos rupestres' over quartzite lithosols. Mello Barreto made two collections (nos. 1935 and 1939) of this species and labelled them as coming from Santa Luzia, which is near Belo Horizonte, in a much lower area with regosols and latosols typical of "cerrado" vegetation, *sensu lato*. It must be assumed that there is some edaphically suitable habitat near Santa Luzia in which *P. schwackei* can flourish.

It has been independently suggested by Kirkbride based upon *Declieuxia* (1976) and by Harley based upon *Eriope* (1976) that Pleistocene climatic changes have been an important factor in speciation in southeastern Brazil. These climatic changes have

caused cyclical range expansions and contractions of the species in this area. In section *Psyllocarpus*, there are two vicariant pairs of species, *P. laricoides-goiasensis* and *P. asparagoides-phyллоcephalus*, as indicated by their inflorescence forms and the presence or absence of druses. One member of each vicariant pair of species is found on either side of the drainage of the Rio São Francisco at higher elevation. The most parsimonious explanation would be that in a period of broader ranges, the ancestral populations of each species pair were in contact or continuous across the basin of the Rio São Francisco and that in a period of smaller ranges the populations were separated, giving impetus to their speciation through natural selection and genetic drift. It is also possible that the populations were established on each side of the basin of the Rio São Francisco by long range dispersal, but this seems less likely because the distribution of the seeds of *Psyllocarpus* is probably by gravity with only minor assistance by the wind.

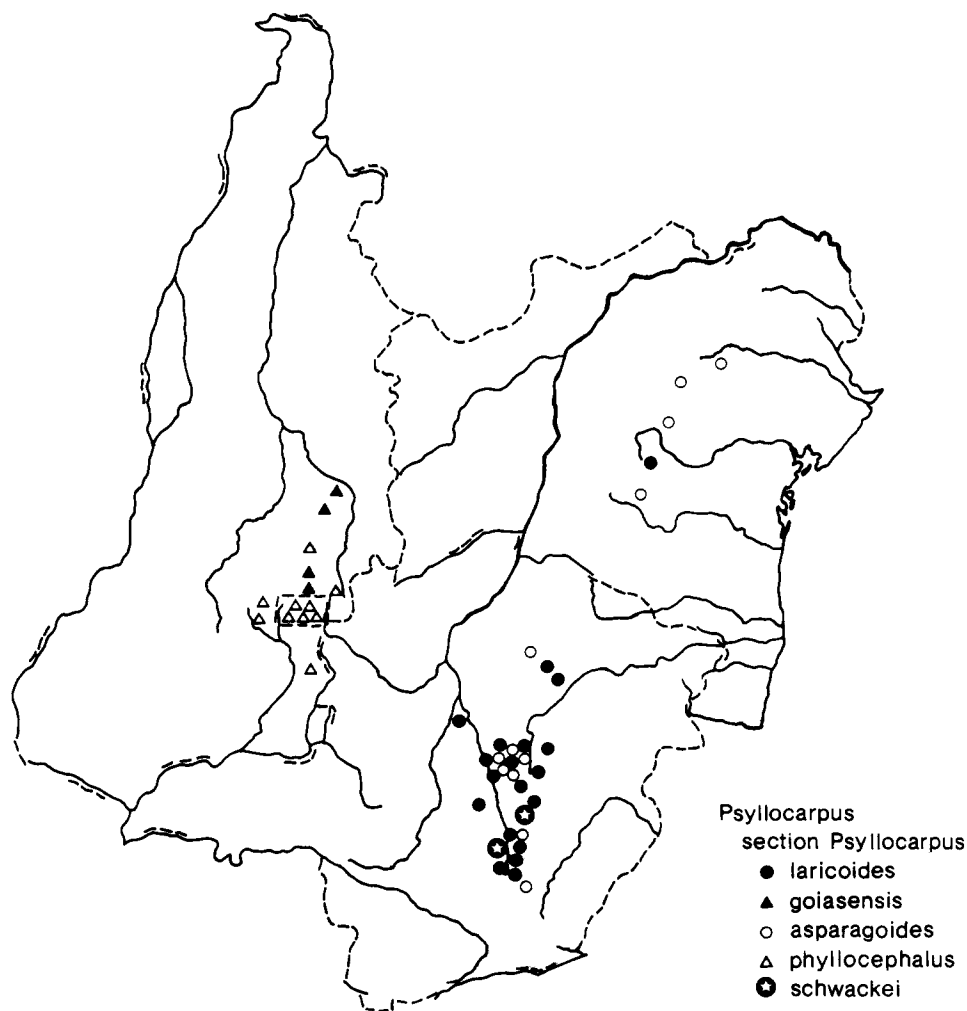


FIGURE 41.—Known distribution of section *Psyllocarpus* in the Distrito Federal, Goiás, Bahia, and Minas Gerais, Brazil.

Psyllocarpus Martius ex Martius & Zuccarini

Psyllocarpus Martius ex Martius & Zuccarini, *Flora* 7(1), suppl. (4):130, 25 Apr – 7 Jul 1824; *Nov. Gen. Sp. Pl.* 1:44, Oct 1824. [Not *Psyllocarpus* Pohl ex de Candolle, *Prodr.* 4:479, 1830 (published in synonymy)].

Diodoia Pohl ex Weldon, *Flora* 8(12):183, 1825 [invalid publication].

DESCRIPTION.—Shrubs, subshrubs, or rarely perennial herbs, erect with a single, erect main stem, the secondary and tertiary stems, when present, either erect and sometimes fastigate giving rise to an obconical habit, or spreading (*P. phyllocephalus*) and giving rise to a flat-topped habit, the stems quadrate to terete with 4 wings or ridges, often very

narrow (section *Psyllocarpus*), the bark glabrous to puberulent, splitting and peeling from the larger, older stems, many tissues with raphides.

Stipular sheaths uniting the leaf bases to form a collar about the stem, the edge of the sheaths each bearing 3–8 fimbriate appendages, the appendages narrowly triangular to subulate-linear, at apex narrowly acute and glandular, the central appendage longest, the lateral ones decreasing gradually towards each leaf base.

Leaves opposite or sometimes ternate, sessile, the blade either terete with the apex narrowly conical or planar and narrowly to very narrowly elliptic with the apex narrowly acute, sometimes subtending

axillary brachyblasts or short branchlets with 1–10 pairs of reduced, fasciculate leaves.

Inflorescences verticillastrate racemes or indeterminate capitula terminal and pedunculate or reduced to solitary flowers in a few distal leaf axils.

Flowers heterostylous or homostylous, pedunculate or sessile, subtended by few or numerous setae or by a setiferous bracteole; hypanthium turbinate, glabrous or puberulous above the middle or with puberulous stripes subtending the calyx lobes, biloculate with a discoid placenta peltately attached to the center of the septum and bearing one peltately attached ovule; calyx 4- or 2-lobate, when 2-lobate 1 lobe above each locule, the calyx-lobes triangular to narrowly triangular, narrowly acute, glabrous to glabrate and sometimes sparsely ciliate, sometimes joined at base into a tube, each charged with (0–)1–8 setae evenly spaced on the rim of the calyx-tube or of the hypanthium between the calyx lobes, the setae narrowly triangular, at apex narrowly acute and glandular, all equal or slightly unequal in length or rarely half as long as others; corolla white or blue, salverform to very rarely funnellform, the tube externally glabrous or variously pubescent, and internally on the upper $\frac{1}{2}$ – $\frac{2}{3}$ sericeous to sparsely sericeous and glabrate below, the lobes ovate or elliptic, narrowly to broadly acute, externally glabrous or variously pubescent, internally glabrous or papillate and sometimes apiculate at the apex; exerted stamens (in heterostylous species) separating from the tube

at the apex, included stamens (in homostylous species) separating below the middle or (in heterostylous species) at various heights, the filaments glabrous, the anthers with the filament attachment below the middle, dorsifixed or rarely versatile, oblong to narrowly oblong, glabrous, the pollen grains oblate- or prolate-spheroidal, 5- to 8-colporate, in polar diameter 15–42 μm and equatorial diameter 15–45 μm , the sexine perforate and finely and evenly spinulose or nonperforate with spinules along each side of the colpi; style terete, glabrous, the stigma deeply to weakly bilobate to rarely capitate, the lobes minutely papillate or scabrous or glabrous.

Fruit a pedicellate capsule crowned by persistent calyx-lobes, elliptic to circular or obovate to broadly obovate in outline, glabrous or sometimes puberulous above the middle to varying heights, strongly compressed parallel to the septum, dehiscent from the apex downwards along the edge of the septum, the valves both free and spreading, the septum entire and erect; seeds shed from the capsule after dehiscence, elliptic to rarely broadly elliptic in outline, strongly compressed, weakly and irregularly winged, colliculate to verruculose, adaxially concave, abaxially convex, glabrous, the striophiole narrowly to broadly elliptic or linear to narrowly oblong and the ends obtuse to truncate or (*P. asparagoides*) the base sagittate and the lobes spreading, broadly acute.

Key to the Sections and Species of *Psyllocarpus*

1. Leaves strongly planar, the blade 1.5–10 mm wide (leaves of *P. psyllocarpoides* unknown); flowers heterostylous, the calyx 4-lobate, the stamens separating from the corolla tube wall above the middle, the pollen grains oblate-spheroidal, in polar diam 33–42 μm and in equatorial diam 33–45 μm , the sexine perforate and finely and evenly spinulose, the stigma deeply bilobate; Amazonas, Pará and RondôniaSection *Amazonica*
2. Bracts of inflorescence ovate to narrowly ovate, 1.8–2.6 mm long; calyx lobes 0.5–1.4 mm long; fruit 3.8–4.8 \times 3.2–3.8 mm.
 3. Leaf blade 6–13 mm wide; without brachyblasts; bracts 3.7–10 mm wide, subtending 13–17 flowers; drainages of the Rios Marmelos and Aripuanã, Amazonas, and Rio Cururú, Pará1. *P. campinorum*
 3. Leaf blade 1.5–2.8 mm wide; brachyblasts with 1–3 pairs of small leaves; bracts 0.6–3 mm wide, subtending 4–7 flowers; drainage of the Rio Cururú, Pará, and near Pôrto Velho, Rondônia2. *P. cururuensis*
2. Bracts of inflorescence linear, 3.5–4.7 mm long; calyx lobes 1.8–2 mm long; fruit ca. 3.2 \times 1.9 mm; drainage of the Rio Urubú, Amazonas3. *P. psyllocarpoides*
1. Leaves terete or, vary rarely (in *P. laricoides*), slightly flattened, the blade 0.1–0.5(-1) mm in diam; flowers homostylous, the calyx 2-lobate, the stamens separating from the corolla tube wall well below its middle, the pollen grains prolate-spheroidal, polar diam 15–24 μm and in equatorial diam 15–21 μm , the sexine nonperforate and spinulose along each side of the

- colpi, the stigma weakly bilobate to rarely (in *P. schwackei*) capitate; Minas Gerais, Bahia, and GoiásSection *Psyllocarpus*
4. Leaf axils with brachyblasts or short branchlets; inflorescences multi-flowered verticillate racemes or capitula of 6-77 flowers.
5. Inflorescences verticillate racemes.
6. Hypanthium glabrous; calyx tube 0.1-0.5 mm long; fruit glabrous; strophiole elliptic to broadly elliptic; Serra do Espinhaço, Minas Gerais, and Serra do Sincorá, Bahia4. *P. laricoides*
6. Hypanthium with the upper 1/2 puberulous and lower 1/2 glabrous; calyx tube 0; fruit with the upper 1/3 sparsely puberulous and lower 2/3 glabrous; strophiole narrowly oblong; eastern half of the central region of Goiás5. *P. goiasensis*
5. Inflorescence capitate.
7. Habit erect and slightly spreading, the branches appearing fastigiate when pressed; calyx lobes 1.2-2 mm long; corolla tube 1.1-1.5 mm long; strophiole elliptic to narrowly elliptic, at base sagittate with the lobes spreading, broadly acute; Serra do Espinhaço, Minas Gerais, and Chapada Diamantina, Bahia6. *P. asparagoides*
7. Habit spreading and flat topped, the branches radially spreading and tangled when pressed; calyx lobes 2.2-3.6 mm long; corolla tube 2.2-2.6 mm long; strophiole linear to narrowly oblong, at base obtuse to truncate; Distrito Federal and eastern half of the central region of Goiás7. *P. phyllocephalus*
4. Most leaf axils without brachyblasts or pairs of smaller leaves; flowers solitary in a few distal leaf axils; Serra do Cipó and Santa Luzia near Belo Horizonte, Minas Gerais8. *P. schwackei*

Amazonica, new section

DIAGNOSIS.—A sect. *Psyllocarpo* foliis valde compressis lamina 1.5-10 mm lata (*Psyllocarpi psyllocarpoidis* foliis ignotis), floribui heterostylis calyce quadrilobo, staminibus e corollini tubi parieti supra medium secedentibus, pollinis granis oblatis sphaeroideis diametro polari 33-42 μm, diametro equatoriali 33-45 μm, sexinio perforato subtiliter aequaliter spinuloso, stigmatate profunde bilobato differt. Sect. *Amazonicae* plantae in Brasiliae Amazonarum Rondoniae Paraeque civitatibus tantum crescut.

DESCRIPTION.—Shrub or subshrub, the stems quadrangular or older, larger ones terete, the wings well-developed.

Leaves (unknown for *P. psyllocarpoides*) opposite, the blade planar, narrowly to very narrowly elliptic, narrowly acute at apex, acute at base, with or without brachyblasts or short branchlets in the axils.

Inflorescences verticillate racemes, terminal, pedunculate, with opposite decussate bracts, each pair joined at base by a sheath.

Flowers heterostylous, pedicellate, the terete pedicels subtended by a few setae; calyx lobes 4, joined at base to form a tube, the rim of the tube bearing between the lobes 1-3 evenly spaced setae; corolla white, the tube externally glabrous; exerted sta-

mens separating from corolla tube wall at the mouth, the included ones above the middle, the anthers versatile or dorsifixed, the pollen grains oblate-spheroidal, 6- to 8-colporate, in polar diameter 33-42 μm and in equatorial diameter 33-45 μm, the sexine perforate and finely and evenly spinulose; stigma deeply bilobate, the lobes glabrous, scabrous or papillate; strophiole elliptic to narrowly so with the ends obtuse to subtruncate.

TYPE.—*Psyllocarpus cururuensis*, new species.

DISTRIBUTION.—Known only from "campina" vegetation presumably in extreme eastern Amazonas and the southeastern corner of Pará (Figure 40).

DISCUSSION.—Section *Amazonica* is well separated from section *Psyllocarpus* by its laminar leaf blades, heterostylous flowers with quadrilobate calyx, and larger, more highly sculptured pollen grains. It is probably the less specialized of the two sections since its vegetative structures more closely resemble those of closely related *Borreria* G.F.W. Meyer.

1. *Psyllocarpus campinorum* (Krause), new combination

PLATE 1

Borreria campinorum Krause, Verh. Bot. Vereins Prov. Brandenburg, 50(2):118, 1908. [Type: *Ule 6102* (lectotype HBG; isotype K), Mar 1902, "Campina an den Cachoeiras des Marmelos," Amazonas, Brazil.]

DESCRIPTION.—Shrub 50–100 cm tall, the stems and branches quadrangular with wings 0.2–0.4 mm wide, glabrous to sparsely puberulous between the wings, the internodes 14–60 mm long, 1–3 mm in diameter.

Stipular sheath 1.5–2.8 mm long, 2.4–4.2 mm wide at top, glabrous, bearing 3–7 setae, narrowly triangular, narrowly acute, $0.4\text{--}4.4 \times 0.2\text{--}0.8$ mm with the central seta longer than the lateral ones, glabrous.

Leaves including blade $24\text{--}68 \times 6\text{--}13$ mm, glabrous, with stomata on the abaxial surface, without axillary brachyblasts or short branchlets.

Inflorescences 20–40 cm long, 1–4.5 cm in diameter, 150–600-flowered, with 6–22 pairs of bracts, each bract subtending 13–17 flowers with a few setae at the base of each flower, the bracts ovate to narrowly ovate, narrowly long-acuminate or narrowly acute, $6.5\text{--}26 \times 3.7\text{--}10$ mm, glabrous, the peduncle quadrangular with wings 0.2–0.4 mm wide, glabrous to sparsely puberulous.

Pedicel 0.1–0.3 mm long; hypanthium 0.8–1 mm tall, 0.6–0.8 mm in diameter, glabrous or glabrate to sparsely puberulous on upper $\frac{1}{2}$; calyx tube 0.2–0.4 mm high, the rim of the tube bearing 1–3 evenly spaced setae between the lobes, the setae $0.1\text{--}0.3 \times \text{ca. } 0.05$ mm, glabrous or glabrate, the calyx lobes $0.6\text{--}1.3 \times 0.2\text{--}0.6$ mm; corolla-tube 2–2.7 mm long, ca. 0.6 mm in diameter at base, its orifice 0.8–1.0 mm in diameter, the lobes ovate, $1.5\text{--}1.9 \times 0.8\text{--}1.3$ mm, externally glabrous; filaments of exerted stamens ca. 1 mm long, of included ones ca. 0.2 mm long, the anthers dorsifixed, 1.1–1.8 mm long; style 1.2–1.4 or ca. 3.8 mm long, ca. 0.04 mm in diameter, the stigma 0.3–0.6 mm long, the lobes glabrous.

Fruit in outline broadly elliptic to circular or broadly obovate, $3.8\text{--}4.4 \times 3.3\text{--}3.8$ mm, 1.5–1.8 mm thick, glabrate to sparsely puberulous above the middle and glabrous below, the seed $2.7\text{--}3.2 \times 2.2\text{--}2.4$ mm, ca. 0.4 mm thick, the strophiole $1\text{--}1.4 \times 0.6\text{--}0.8$ mm.

DISTRIBUTION.—Known with certainty from the campinas along the Rio Marmelos and along the Rio Aripuanã near the Transamazonian Highway, Amazonas, and from sandy areas along the Rio Cururú, Pará (Figure 40).

DISCUSSION.—This species differs from other members of section *Amazonica* by its wider leaves and

inflorescence bracts, lack of brachyblasts, and large number of flowers.

2. *Psyllocarpus cururuensis*, new species

PLATE 2

DIAGNOSIS.—A *P. campinorum* foliorum laminiis 1.5–2.8 mm latis, brachyblastis e foliorum minorum paribus 1–3 compositis; inflorescentiarum bracteis 0.6–1.6 mm latis 4–7 flores subtendentibus et a *P. psyllocarpoide* inflorescentiarum bracteis anguste ovatis 1.8–7.7 mm longis, fructibus $4\text{--}4.8 \times 3.2\text{--}3.6$ mm differt.

DESCRIPTION.—Shrub or subshrub to 50 cm tall, the stems and branches quadrangular becoming terete with age, with wings 0.1–0.2 mm wide, puberulous to sparsely puberulose or glabrous between the wings, and the internodes 13–28 mm long, 1–4.2 mm in diameter.

Stipular sheath 0.4–0.5(–2) mm long, 1.2–2.4 mm wide at the top, puberulous, bearing 5 setae evenly spaced, the setae narrowly triangular to subulate-linear, $0.6\text{--}5 \times 0.2\text{--}0.4$ mm, narrowly acute and glandular, glabrous, the longest in the center and gradually decreasing in length on each side.

Leaves including blade $19.7\text{--}38 \times 1.5\text{--}2.8$ mm, glabrous or muricate above, glabrous beneath, with stomata on both surfaces, subtending axillary brachyblasts or short branchlets with 1–3 pairs of smaller leaves.

Inflorescences 2.5–20 cm long, 1–2.5 cm in diameter, 80–340-flowered, with 6–28 pairs of bracts, each bract subtending 4–7 flowers and some setae surrounding each flower, the bracts narrowly ovate, at apex mucronate, $1.8\text{--}22 \times 0.6\text{--}3$ mm, decreasing gradually in size from the lower primary to the uppermost ones, glabrous or weakly scabrous above, glabrous below, the sheath ca. 0.2 mm long, glabrous, the peduncle terete, 8–18 mm long, sparsely puberulous or glabrous.

Pedicel ca. 0.2 mm long; hypanthium 0.4–0.8 mm tall, 0.5–0.9 mm in diameter, glabrous; calyx tube 0.2–0.4 mm high, its rim bearing 0, 1, or 2 evenly spaced setae between the lobes the setae $0.05\text{--}0.2 \times \text{ca. } 0.05$ mm, glabrous, the lobes $0.5\text{--}1.4 \times 0.2\text{--}0.5$ mm; corolla-tube 1.9–2.4 mm long, 0.6–1 mm in diameter at base, its orifice 1.2–1.8 mm in diameter, the lobes ovate, $1.6\text{--}2.8 \times 1\text{--}1.2$ mm, externally glabrous; filaments of exerted stamens ca.

1.3 mm long, of included ones ca. 0.4 mm long, the anthers 0.8–1.1 mm long, the exerted ones versatile, the included ones dorsifixed; style ca. 1.5 or 3.2–4.2 mm long, 0.04–0.08 mm in diameter, the stigma 0.5–1 mm long, included stigma with scabrous lobes and exerted stigma with papillate lobes.

Fruit elliptic in outline, 4–4.8 × 3.2–3.6 mm, ca. 1.2 mm thick, glabrous, the pedicel 0.2–0.4 mm long, glabrous, the seed 3.2–3.4 × ca. 2.4 mm, ca. 0.1 mm thick, its strophiole ca. 1.6 × 0.8 mm.

TYPE.—*Anderson, da Fonseca, Reis dos Santos and Souza 10779* (holotype IAN; isotypes NY, US), 11 February 1974, region of village of Pratati, ca. 8° S, 57°5' W. 6–8 km S of village, Pará Brazil.

DISTRIBUTION.—Known from sandy habitats, possibly with campina vegetation, along the Rio Cururu, Pará, and near Pôrto Velho, Rondônia (Figure 40).

DISCUSSION.—*Psyllocarpus cururuensis* is separated from *P. campinorum* by narrower leaves and inflorescence bracts, presence of brachyblasts, and fewer flowers. It is distinguished from *P. psyllocarpoides* by its shorter, ovate inflorescence bracts, shorter calyx lobes, and larger fruits.

3. *Psyllocarpus psyllocarpoides* (Sucre), new combination

PLATE 3

Staëlia psyllocarpoides Sucre, Rodriguésia 26(38):255, 1971.
[Type: *Fróes 25262* (holotype IAN), 17 Sep 1949, Rio Urubú, Amazonas, Brazil.]

DESCRIPTION.—Subshrub 30–35 cm tall, the stem leafless at and following anthesis or indistinguishable from axis of the inflorescence.

Inflorescences 15–18 cm long, 5–9 cm in diameter, 90–300 flowered, with 11–22 pairs of bracts, each bract subtending 4–7 flowers, the bracts linear, with the apex narrowly acute, 35–47 × 3–4 mm, glabrous, the sheath 2–3 mm long, puberulous to sparsely puberulous.

Pedicels 0.1–0.2 mm long; hypanthium ca. 1 mm tall, ca. 0.6 mm in diameter, glabrous; calyx tube ca. 0.2 mm high, its rim bearing 1 or 2 evenly spaced setae between the lobes, the setae ca. 0.15 × 0.04 mm, glabrous and sometimes sparsely ciliate, the lobes 1.8–2 × 0.4–0.6; corolla-tube (fide Sucre, 1971) 1.5 mm long, the lobes narrowly triangular;

anthers (fide Sucre, 1971) 0.3 mm long; stigmatic lobes (fide Sucre, 1971) papillate.

Fruit elliptic in outline, ca. 3.2 mm × 1.9 mm, ca. 1.9 mm thick, glabrous, the pedicel ca. 0.2 mm long, glabrous, the seed 2.4–2.9 × 1.4–2 mm, ca. 0.4 mm thick, the strophiole 1–1.6 × 0.5–0.7 mm.

DISTRIBUTION.—Known only from the type locality, campinarana vegetation near the Rio Urubú, Amazonas (Figure 41).

DISCUSSION.—This is easily separated from the other members of section *Amazonica* by its longer, linear inflorescence bracts, longer calyx lobes and smaller fruit.

Section *Psyllocarpus*

DESCRIPTION.—Shrub, subshrub, or perennial herb, the stems terete or quadrangular to weakly quadrangular sometimes with ridges or small wings.

Leaves opposite or sometimes ternate, the blade terete with apex conical to very rarely (in *P. laricoides*) planar and linear with apex narrowly acute, subtending axillary brachyblasts or short branchlets with 2–10 pairs of smaller leaves or very rarely (in *P. schwackei*) with 1 or 2 pairs of smaller axillary leaves.

Inflorescences terminal verticillate racemes or capitulate or (in *P. schwackei*) solitary flowers in a few distal leaf axils.

Flowers homostylous, sessile or pedicellate, subtended by setae or 1 or 2 setiferous bracteoles, the pedicel terete and glabrous when present; calyx lobes 2, free or joined at base to form a tube, the rim of the calyx tube or of the hypanthium bearing 0–8 evenly spaced setae between the lobes; corolla blue or white, the tube externally glabrous or variously pubescent; stamens included, the filaments separating from corolla tube wall well below the middle, the anthers dorsifixed, the pollen grains prolate-spheroidal, 5- to 7-colporate, in polar diameter 15–24 μm and in equatorial diameter 15–21 μm, the sexine nonperforate with spinules along each side of the colpi; stigma weakly bilobate to rarely (in *P. schwackei*) capitate, minutely papillate; strophiole narrowly to broadly elliptic or linear to narrowly oblong with the ends obtuse to truncate, or (*P. asparagoides*) sagittate at base with the lobes spreading, broadly acute.

TYPE.—*Psyllocarpus laricoides* Martius ex Martius & Zuccarini (Lectotype).

DISTRIBUTION.—Known from the chapadão and its extensions west of the basin of the Rio São Francisco in Distrito Federal and Goiás, and from the upper and western slopes of the Serra do Espinhaço, Minas Gerais, and of Chapada Diamantina, Bahia, east of the basin of the Rio São Francisco (Figure 41).

DISCUSSION.—Section *Psyllocarpus* is readily distinguished from section *Amazonica* by its ericoid foliage or needle-like, terete leaves, homostylous flowers with bilobate calyx, and smaller, less sculptured pollen grains.

4. *Psyllocarpus laricoides* Martius ex Martius & Zuccarini

PLATE 4

Psyllocarpus laricoides Martius ex Martius & Zuccarini, Flora 7(1), suppl. (4):131, 25 Apr – 7 Jul 1824; Nov. Gen. Sp. Pl. 1:45, pl. 28, Oct 1824. [Type: *Martius s.n.* (lectotype M, plant farthest left on the herbarium sheet; presumed isotype M), 1818, “habitat sumo Brasiliae monte Itambé,” Minas Gerais, Brazil.]

Psyllocarpus ericoides Martius & Zuccarini, Flora 7(1) suppl. (4):131, 25 Apr – 7 Jul 1824; Nov. Gen. Sp. Pl. 1:45, pl. 28, Oct 1824. [Type: *Martius 1295* (holotype M; presumed isotype M), 1818, “habitat in campis ad Bandeirinha, propr Tijuco,” Minas Gerais, Brazil.]

Psyllocarpus laricoides var. *β densifolius* Martius & Zuccarini, Nov. Gen. Sp. Pl. 1:46, Oct 1824. [Type: *Martius s.n.* (holotype M, plant farthest right on the herbarium sheet), 1818, “habitat sumo Brasiliae monte Itambé,” Minas Gerais, Brazil.]

Psyllocarpus laricinus Sprengel, Caroli Linnaei, Syst. veg., 16th edition, 4(2):39, 1827 [superfluous name].

Psyllocarpus laricoides var. *γ longicornu* Schumann, Mart. Fl. bras. 6(6):33, 1888. [Type: *Pohl 1317(851)* (lectotype W; isotypes K, W), 1820, Ouro fino, Minas Gerais, Brazil.]

DESCRIPTION.—Shrub, subshrub, or perennial herb 22–120 cm tall, obconical in outline, the stems and branches erect and fastigiate to slightly spreading, moderately to sparsely branched, quadrangular to weakly quadrangular and terete with age, with narrow wings 0.05–1 mm wide, puberulous to sparsely puberulous or glabrous, the bark thin, splitting and peeling from the older stems and branches, the internodes 3–28 mm long, 0.4–5.4 mm in diameter.

Stipular sheath 0.6–1.4 mm long, (0.9–)1.4–2 mm wide at the top, puberulous to glabrate or glabrous, bearing 4–6 setae evenly spaced, these narrowly triangular to linear-subulate, narrowly acute, (0.2–)0.3–1.4 × 0.04–0.28(–0.4) mm, all equal in length or

with some half as long as other, scabrous or glabrous and ciliate to minutely ciliate.

Leaves opposite or ternate, the leaf blades (4–)5–16(–21) mm long, 0.2–1 mm in diameter or wide, scabrous to glabrate or glabrous, subtending axillary brachyblasts with 2–7 pairs of leaves forming dense fascicles.

Inflorescences verticillastrate racemes, terminal, pedunculate, 2.1–8.5 cm long, 0.8–1.2 cm in diameter, 8–48-flowered, with opposite and decussate or rarely ternate bracts in 4–13 pairs or whorls, with a sheath joining the bases or each pair or trio of bracts, each bract subtending 1 or sometimes 2 flowers, the bracts decreasing upward gradually, narrowly oblong to linear, narrowly acute, 1.2–7.3 × 0.3–0.8 mm, scabrous to glabrate or glabrous, the sheath gradually decreasing in length from the lowermost to the uppermost, 0.6–1 mm long, puberulous to glabrate or glabrous, the peduncle terete, 1.4–19 mm long, puberulous to sparsely puberulous or glabrous.

Pedicels 0.1–0.4 mm long, subtended by 1 or 2 setiferous bracts 0.2–0.4 mm long or by numerous setae; hypanthium 0.8–1.4 mm tall, 0.8–1.4 mm in diameter, glabrous; calyx lobes 1–2.8 × 0.2–0.8 mm, joined at base to form a tube 0.1–0.5 mm high, glabrous, its rim bearing 3–7 evenly spaced setae between the lobes, the setae 0.1–0.8 × 0.01–0.2 mm, glabrous and minutely ciliate; corolla blue, the tube (2.4–)2.9–6.7 mm long, 0.7–1.2 mm in diameter at base, the orifice 1.2–2 mm in diameter, externally scabrous or glabrous, the lobes ovate to broadly so or elliptic to very broadly elliptic, 1.2–3.2 × 0.8–2.2 mm, externally glabrous or scabrous, internally papillate to minutely papillate; filaments 0.2–0.4 mm long, the anthers 0.9–1.3 mm long; style 0.3–0.7 mm long, 0.1–0.3 mm in diameter, the stigma weakly bilobate, 0.2–0.3 mm tall, 0.2–0.4 mm in diameter.

Fruit elliptic to broadly elliptic in outline, 2.8–4.4 × 1.8–3.2 mm, 1–1.6 mm thick, glabrous, the pedicels 0.2–0.6 mm long, glabrous, the seed 2.6–3.6 × 1.7–2.6 mm, ca. 0.1 mm thick, its strophiole elliptic to broadly elliptic, obtuse at both ends, 0.9–2 × 0.4–1.1 mm.

DISTRIBUTION.—Known from the higher regions of Serra do Espinhaço, Minas Gerais, and of Serra do Sincorá, Bahia.

DISCUSSION.—*Psyllocarpus laricoides* is most closely related to *P. goiasensis*, from which it is set apart

by its glabrous hypanthium and fruit and by the presence of a calyx tube. These are vicarious species whose ranges are separated by the lower portions of the basin of the Rio São Francisco. From my own field experiences with *P. laricoides* and the data in the herbaria, this species appears to be found in the vegetation referred to by Eiten (1972) as "campos rupestres" that are characteristically formed on thin lithosols of quartz sand.

5. *Psyllocarpus goiasensis*, new species

PLATE 5

DIAGNOSIS.—A *P. laricoide* hypanthiis fructibusque supra medium puberulis infra medium glabris, calycisque tubo nullo differt.

DESCRIPTION.—Subshrub 31–63 cm tall, stem and branches erect and slightly spreading, moderately branched, terete to subquadrangular with ridges or small wings 0.05–1 mm wide, puberulous, the bark thin, splitting, and peeling from the older stems and branches, the internodes 4–21(–24) mm long, 0.5–3.7 mm in diameter.

Stipular sheath (0.6–)0.8–1 mm long, 1.2–1.6 mm wide at the top, puberulous, bearing 5–8 setae evenly spaced, these narrowly triangular, narrowly acute, 0.6–2 × 0.1–0.3 mm, all equal in length or with some half as long as others, scabrous.

Leaves opposite, the leaf blade (5.5–)7.3–12.5 mm long, 0.2–0.3 mm in diameter, scabrous, subtending axillary brachyblasts with 4–9 pairs of smaller leaves forming dense fascicles.

Inflorescences verticillastrate racemes, terminal, pedunculate, 1.5–6.5 cm long, 0.8–1.7 cm in diameter, 16–77-flowered, with opposite and decussate bracts in 5–11 pairs and a sheath joining the bases of each pair of bracts, each bract subtending 2–4 flowers surrounded by setae, the bracts decreasing upward gradually in size, linear, narrowly acute, 2.8–5.2 × 0.3–0.5 mm, scabrous, the sheath upward gradually decreasing in length 0.4–1.4 mm long, puberulous to sparsely puberulous, the peduncle terete, (2–)5–17 mm long, puberulous.

Flowers sessile, the hypanthium 1.6–1.7 mm tall, 1–1.2 mm in diameter, with the upper ½ puberulous and the lower ½ glabrous or glabrate; calyx lobes 2.4–3 × 0.7–2 mm; 4–8 setae evenly spaced along the apical rim of the hypanthium between them, the setae 0.2–1.4 × 0.04–0.24 mm, glabrous and

minutely ciliate; corolla blue or white, the tube 3.6–4.6 mm long, externally glabrate to sparsely puberulous, ca. 0.8 mm in diameter at base, the orifice 1–1.2 mm in diameter, the lobes ovate to broadly ovate, 1.8–2 × 1.2–1.3 mm, externally glabrous, internally minutely papillate, tipped with an apicule ca. 0.1 mm long; filaments 0.2–0.3 mm long, the anthers 0.8–1 mm long; style 0.4–0.6 mm long, ca. 0.1 mm in diameter, the stigma bilobate, 0.1–0.2 mm tall, ca. 0.2 mm in diameter.

Fruit elliptic in outline, 3.4–4(–4.8) × 2.3–2.4(–3) mm, 1.4–1.7 mm thick, the upper ⅓ sparsely puberulous and the lower ⅔ glabrous, the seed 2.2–4.3 × 0.8–2.7 mm, 0.04–0.28 mm thick, the strophiole narrowly oblong 1.6–2.4 × 0.3–0.5 mm, its ends truncate.

TYPE.—*Irwin, Harley, and Smith 33082* (holotype UB; isotypes NY, US), 24 March 1971 ca 10 km N of Alto Paraíso, Goiás, Brazil.

DISTRIBUTION.—Known from the Chapada dos Veadeiros and Serra Geral do Paranã as far south as Formosa, east-central Goiás (Figure 41).

DISCUSSION.—This species is most closely related to *P. laricoides*, from which it is separated by the hypanthium puberulous above the middle, the absence of a calyx tube, and the fruit with the upper third sparsely puberulous. As was pointed out earlier, this species forms with *P. laricoides* a vicarious pair whose ranges are separated by the lower basin of the Rio São Francisco. The Chapada dos Veadeiros has many areas in its higher reaches that have soils composed of quartz sands that are probably lithosols. The scanty herbarium data would indicate that *P. goiasensis* is found on this type of soil as is *P. laricoides* in the Serra do Espinhaço.

6. *Psyllocarpus asparagoides* Martius ex Martius & Zuccarini

PLATE 6

Psyllocarpus asparagoides Martius ex Martius & Zuccarini, *Flora* 7(1), suppl. (4):131, 25 Apr – 7 Jul 1824; *Nov. Gen. Sp. Pl.* 1:46, Oct 1824. [Type: *Martius s.n.* (holotype M; presumed isotype M), 1818, "habitat in campis altis termini Minarum Novarum prope Piedade," Minas Gerais, Brazil.]

DESCRIPTION.—Subshrub 15–65 cm tall, the stems and branches erect and slightly spreading, terete, sometimes with ridge ca. 0.05 mm high, puberulous

to sparsely puberulous on older stems, the bark thin, reddish, splitting, deciduous from older stems, the internodes 3–35(–65) mm long, 0.3–3 mm in diameter.

Stipular sheath 0.5–0.8 mm long, 0.6–2.4 mm wide at top, glabrous to puberulous, bearing 3–8 setae evenly spaced, these narrowly triangular to subulate-linear, narrowly acute, $0.1\text{--}0.8 \times 0.03\text{--}0.15$ mm, all equal in length or sometimes with shorter ones $\frac{1}{4}\text{--}\frac{1}{2}$ as long as the others, glabrous to minutely sparsely scabrous.

Leaves opposite, the blade 8–19 mm long, 0.15–0.3 mm in diameter, glabrous, with 3 faint parallel ridges running from base to apex on the abaxial side, subtending axillary brachyblasts with (3–)4–10 pairs of shorter leaves forming dense fascicles.

Inflorescences capitulate, terminal, pedunculate, 5–15 mm in diameter, 16-flowered, with 4 decussate pairs of bracts, each pair joined by sheaths to form concentric rings within the inflorescence, glabrous to sparsely puberulous, each bract subtending 2 (very rarely 3 or 4) flowers surrounded by numerous setae, the primary bracts linear to narrowly oblong, narrowly acute, $3\text{--}6.7 \times 0.3\text{--}0.5$ mm, with sheath 0.8–2.2 mm long, the secondary ones narrowly oblong, narrowly acute, $2\text{--}4.4 \times 0.4\text{--}0.5$ mm, with sheath 0.8–1.2 mm long, the tertiary ones narrowly oblong, narrowly acute, $1.2\text{--}2.3 \times 0.2\text{--}0.4$ mm, with sheath 0.4–0.8 mm long, the quaternary ones narrowly triangular, narrowly acute, $0.4\text{--}1.3 \times 0.1\text{--}0.2$ mm with sheath 0.2–0.4 mm long, the peduncle terete, (0.3–)1.8–4.8 cm long, glabrous to sparsely puberulous.

Pedicels 0.1–0.2 mm long; hypanthium 1–1.2 mm tall, 0.7–0.9 mm in diameter, glabrous; calyx lobes $1.2\text{--}2 \times 0.3\text{--}0.9$ mm, with 0–5 setae evenly spaced along the rim of the hypanthium between the lobes, the setae $0.1\text{--}0.2 \times 0.04\text{--}0.08$ mm, glabrous; corolla white, the tube 1.1–1.5 mm long, externally granulate, the orifice 0.9–1.2 mm in diameter, 0.5–0.9 mm in diameter at base, the lobes broadly to very broadly ovate, $0.7\text{--}1.5 \times 0.6\text{--}1.2$ mm, externally granulate, internally papillate; filaments 0.1–0.2 mm long, the anthers 0.4–0.6 mm long; style 0.2–0.4 mm long, ca. 0.1 mm in diameter, the stigma weakly bilobate, 0.1–0.2 mm tall, ca. 0.2 mm in diameter.

Fruit obovate to broadly obovate in outline, $3\text{--}3.7 \times 2.2\text{--}3$ mm, 0.8–1.3 mm thick, glabrous, the pedicel 0.3–0.5 mm long, glabrous, the seed $2.7\text{--}3.4 \times 1.8\text{--}2.8$ mm, ca. 0.2 mm thick, its strophiole

elliptic to narrowly elliptic, the apex obtuse, the base sagittate with spreading, broadly acute lobes $0.6\text{--}0.9 \times 0.3\text{--}0.4$ mm.

DISTRIBUTION.—Known from higher elevations of the Serra do Espinhaço, Minas Gerais, and of the Chapada Diamantina, Bahia (Figure 41).

DISCUSSION.—*Psyllocarpus asparagoides* is most closely related to *P. phyllocephalus*, from which it can be distinguished by its erect, fastigiata habit and shorter calyx lobes and corolla tube. The degree of similarity and therefore probable kinship between *P. asparagoides* and *P. phyllocephalus* is not nearly as close as that between *P. laricoides* and *P. goiasensis*, but they are also a pair of vicarious species with similar distributions again separated by the lower drainage of the Rio São Francisco.

7. *Psyllocarpus phyllocephalus* Schumann

PLATE 7

Psyllocarpus phyllocephalus Schumann, Bot. Jahrb. Syst. 25(3), suppl. (60):17, 19 Jul 1898. [Type: *Glaziou 21504* (lectotype P; isotypes BR, C, G, K, LE, S), "entre Paranauá et le Rio Torte," Distrito Federal, Brazil.]

DESCRIPTION.—Subshrub 12–50 cm tall, flat-topped, the stem erect, terete with ridges ca. 0.05 mm high, puberulous to sparsely puberulous, diffusely and extensively branched at the apex, the branches terete, puberulous, the bark thin, splitting, deciduous from the older portions of the stem and branches, the internodes 4.2–8.3 mm long, 0.3–2.7 mm in diameter.

Stipular sheath 0.8–1.2 mm long, 0.8–1.6 mm wide at top, puberulous to sparsely puberulous, bearing 3–6 setae evenly spaced, these narrowly triangular to subulate-linear, narrowly acute and glandular at apex, $0.3\text{--}1.2 \times 0.08\text{--}0.1$ mm, all equal in length or occasionally some ca. $\frac{1}{2}$ as long as the rest, glabrous to sparsely puberulous.

Leaves opposite or ternate, the left blade 4.5–10 mm long, ca. 0.2 mm in diameter, weakly scabrous, with a narrow, flat, abaxial face running from the base to the apex, subtending axillary brachyblasts with (3–)4–8 pairs of smaller leaves forming dense fascicles.

Inflorescences capitulate, terminal, sessile or pedunculate, 5–17 mm in diameter, 6–24-flowered, with 3–7 sets of opposite and decussate or rarely ternate bracts, each pair or trio joined by sheaths to

form concentric rings within the inflorescences, each bract subtending 1–3 flowers surrounded by numerous setae, the bracts decreasing upward gradually in size, linear, narrowly acute, 3.3–8.3 × 0.2–0.4 mm, glabrous or scabrous, the sheath gradually decreasing upward in length, 0.6–1.5 mm long, glabrous to sparsely puberulous, the peduncle if present terete, 1.5–9 mm long, puberulous to sparsely so.

Flowers sessile, the hypanthium 0.8–1.2 mm tall, 0.6–1.1 mm in diameter, glabrous or with a puberulous stripe subtending each calyx lobe or with the upper $\frac{1}{3}$ glabrate; calyx lobes 2.2–6 × 0.4–0.6 mm, with 3–5 setae evenly spaced along the rim of the hypanthium between them, the setae 0.3–0.8 × 0.04–0.16 mm, sparsely puberulous; corolla blue or white, the tube externally puberulous or scabrous, 2.2–2.6 mm long, 0.4–0.7 mm in diameter at base, the orifice 0.5–1 mm in diameter, the lobes ovate to narrowly ovate, 0.8–1.2 × 0.4–0.7 mm, externally puberulous to scabrous, internally papillate, apiculate at apex; filaments 0.1–0.3 mm long, the anthers 0.4–0.5 mm long; style 0.2–0.5 mm long, ca. 0.1 mm in diameter, the stigma weakly bilobate, 0.2–0.3 mm tall, 0.1–0.3 mm in diameter,

Fruit obovate in outline, 2.2–2.9 × 1.2–2 mm, 1.1–1.5 mm thick, glabrous or upper $\frac{1}{3}$ sparsely puberulous, the seed 1.7–2.2 × 0.9–1.6 mm, 0.2–0.3 mm thick, the strophiole linear to narrowly oblong, 0.7–1.4 × 0.1–0.3 mm, its ends obtuse to subtruncate.

DISTRIBUTION.—Frequent in the Distrito Federal and known from the Serra dos Cristais, the vicinity of the Serra dos Pirineus and the southernmost flanks of the Chapada dos Veadeiros in east-central and southeastern Goiás (Figure 41).

DISCUSSION.—This species is related to *P. asparagoides*, from which it is separated by its spreading, frequently branched, flat-topped habit that appears as a circular, tangled mass when dried for the herbarium and by the longer calyx lobes and corolla tube (see page 17).

8. *Psyllocarpus schwackei* Schumann

PLATE 8

Psyllocarpus schwackei Schumann, Bot. Jahrb. Syst. 25(3), suppl. (60):18, 19 Jul 1898. [Type: Anderson, Stieber, and Kirkbride 36254 (neotype US; isotypes NY, UB), 18 Feb 1972, Serra do Cipó, elev. ca. 1125 m, Minas Gerais, Brazil.]

DESCRIPTION.—Subshrubs or perennial herbs 15–60 cm tall, the stems and branches erect and slightly spreading, terete, rarely with faint ridges ca. 0.02 mm high, glabrous, the internodes (4)7–25(27) mm long, 0.1–3.3 mm in diameter.

Stipular sheathes 0.6–1 mm long, 0.5–1.5 mm wide at top, glabrous, bearing 3–5 setae evenly spaced, these narrowly triangular, narrowly acute, 0.2–1 × 0.04–0.2 mm, all equal in length or sometimes the central one or ones up to twice as long as the lateral ones, glabrous or sometimes sparsely and minutely ciliate.

Leaves opposite, sometimes subtending 1 or rarely 2 pairs of smaller axillary leaves, the leaf blade 8–24 mm long, 0.2–0.5 mm in diameter, glabrous.

Inflorescences of solitary flowers in a few distal leaf axils.

Pedicels 0.2–0.5 mm long, subtended by a setiferous bracteole 0.7–1 mm long, the setae $\frac{1}{3}$ – $\frac{1}{2}$ as long as the bracteole; hypanthium 0.8–1.3 mm tall, 0.8–1.3 mm in diameter, glabrous; calyx lobes 1–1.8 × 0.3–0.6 mm, joined at base to form a tube 0.15–0.25 mm high, glabrous, the rim of the tube bearing 3–6 setae between the lobes, the setae 0.2–0.6 × 0.1–0.2 mm, sparsely and minutely ciliate but facially glabrous; corolla blue, externally minutely and densely papillate, the tube 3.8–6.1 mm long, 0.7–1.1 mm in diameter at base, the orifice 1.2–1.8 mm in diameter, the lobes elliptic to broadly elliptic, 1.6–3.7 × 1–2.2 mm, externally minutely and densely papillate, internally glabrous, tipped with a setae standing at right angles to its surface; filaments 0.2–0.5 mm long, the anthers 0.9–1.3 mm long; style 0.1–0.6 mm long, 0.08–0.25 mm in diameter, the stigma capitate to weakly bilobate, ca. 0.2 mm tall, 0.1–0.3 mm in diameter.

Fruit elliptic in outline, 2.7–4.4 × 1.8–2.7 mm, 0.7–1.1 mm thick, glabrous, the pedicel 0.4–0.8 mm long, glabrous, the seed 1.5–2.5 × 1–1.6 mm, ca. 0.1 mm thick, the strophiole elliptic, ca. 0.7 × 0.4–0.5 mm, its end obtuse.

DISTRIBUTION.—Known from Serra do Cipó in the Serra do Espinhaço and from Santa Luzia near Belo Horizonte on the wester slope of the Serra do Espinhaço, Minas Gerais (Figure 41).

DISCUSSION.—In his publication of *P. schwackei* (1898), Schumann cited the following collection, “in Brasiliae civitate Minas Geraes, locis arenosis in Serra do Cipo: Schwacke n, 8089, floret Aprili.” The

specimen studied by Schumann at Berlin was destroyed in the Second World War, and I have been unable to locate any duplicates of this collection. In the Field Museum of Natural History type photograph series, there is a photograph of the specimen that existed in Berlin prior to the war, negative number 896. Based upon the description, the photograph of the Berlin specimen, and my experience at the type locality, Serra do Cipó, I have selected my topotypical collection, *Anderson, Stieber, and Kirkbride 36254*, as neotype.

Psyllocarpus schwackei is easily separated from the other species of section *Psyllocarpus* by its lack of brachyblasts and only rare occurrence of 1 or infrequently two pairs of smaller leaves in leaf axils and an inflorescence structure of only a few solitary flowers in some distal leaf axils. The relationships of *P. schwackei* are very difficult to assess because of its reduction in these characters. In view of its lack of capitular inflorescence development, it would seem to be related to the species pair *P. laricoides-goiasensis*, but not closely.

Excluded Species

Psyllocarpus thymbroides Martius ex Martius & Zuccarini

Psyllocarpus thymbroides Martius ex Martius & Zuccarini, *Flora* 7(1), suppl. (4):131, 25 Apr – 7 Jul 1824; *Nov. Gen. Sp. Pl.* 1:46, Oct 1824. [= *Staëlia thymbroides* (Martius

ex Martius & Zuccarini) Schumann, *Mart. Fl. bras.* 6(6):77, 1888.]

DISCUSSION.—Martius and Zuccarini described *Psyllocarpus thymbroides* from a collection made by Martius “in campis montosis ad montium tractum Serra do Gran Mogol adamantibus divitem, Provinciae Mina Geraës” in July of 1818. They gave a diagnostic phrase of one sentence, one line of general description, the collection locality and time of flowering, but omitted those characteristics of the fruit that are essential for determining the generic affinity. I have not been able to locate any specimens of the collection upon which they based their species.

Schumann in the *Flora brasiliensis* (1888) transferred the epithet to *Staëlia*, citing, however, in place of the type collection, *Martius s.n.* (in alpinis ad Rio das Contas, Bahia, Brasil) and *Blanchet 3605* (in Serra da Jacobina, Bahia, Brasil). Apparently, he too was unable to locate the type collection. Schumann’s extensive description matches the scanty protologue in all particulars except that it fails to mention fasciculate leaves, but the collections that he cited do exhibit this character. In my opinion, Schumann neotypified *Psyllocarpus thymbroides* by the citation of the above neosyntypes and transferred it to *Staëlia* based upon this typification.

I have examined Schumann’s neosyntypes, and they are both members of the genus *Staëlia*. They show what may be significant differences from each other that may necessitate their specific or subspecific segregation. I now have underway a revision of the genus *Staëlia* that will resolve this question.

Literature Cited

- Anderson, W. R.
1972. A Monograph of the Genus *Crusea* (Rubiaceae). *Memoirs of the New York Botanical Garden*, 22(4): 1-128.
- Baillon, H.
1881. Rubiaceae. In *The Natural History of Plants*, 7:257-503. London: L. Reeve & Co.
- Bentham, G.
1835. Inflorescence Structure of the Labiatae. In *Labiatarum genera et species*, pages xvi-xix. London: James Ridway & Sons.
- Bremekamp, C.E.B.
1934. Notes on the Rubiaceae of Surinam. *Recueil des travaux botaniques néerlandais*, 31(1-2):248-308.
- Candolle, A. P., de
1830. *Psyllocarpus*. In *Prodromus systematis naturalis regni vegetabilis*, 4:570-571. Paris: Fortin, Masson et Socies.
- Chandrasekharam, A.
1972. Spongy Mesophyll Remains in Fossil Leaf Compressions. *Science*, 177(4046):354-356.
- Debold, R.
1892. Beiträge zur anatomischen Charakteristik der Phaseolen. 77 pages. Doctoral dissertation, Ludwig-Maximilian-Universität, München.
- Dittmer, H. J.
1964. *Phylogeny and Form in the Plant Kingdom*. 642 pages. New York: Van Nostrand.
- Don, G.
1834. *Psyllocarpus*. In *A General History of the Dichlamydeous Plants*, 3:629-630. London: J. G. & Rivington et al.
- Eiten, G.
1972. The Cerrado Vegetation of Brazil. *Botanical Review*, 38(2):201-341.
1978. Delimitation of the Cerrado Concept. *Vegetatio: Acta geobotanica*, 36(3):169-178.
- Fisher, D. B.
1967. An Unusual Layer of Cells in the Mesophyll of the Soybean Leaf. *Botanical Gazette*, 128:215-218.
- Harley, R. M.
1976. A Review of *Eriope* and *Eriopidion* (Labiatae). *Hooker's Icones Plantarum*, 38(3):1-107.
- Hayden, M. V.
1968. Systematic Morphological Study of New World Rubiaceous Seeds: (Rubiaceae sensu Bremekamp). 95 pages. Doctoral dissertation, Saint Louis University.
- Hooker, J. D.
1873. Rubiaceae. In G. Bentham and J. D. Hooker, *Genera Plantarum* 2(1):7-151.
- Horner, H. T., and N. R. Lersten
1968. Development, Structure and Function of Secretory Trichomes in *Psychotria bacteriophila* (Rubiaceae). *American Journal of Botany*, 55(9):1089-1099.
- Kirkbride, J. H., Jr.
1976. A Revision of the Genus *Declieuxia* (Rubiaceae). *Memoirs of the New York Botanical Garden*, 28(4): 1-87.
- Krause, K.
1908. Rubiaceae. In E. Ule, III, Beiträge zur Flora der Hylaea nach den Sammlungen von Ule's Amazonas-Expedition. *Verhandlungen des Botanischen Vereines der Provinz Brandenburg*, 50(2):97-119.
1909. Über harzsecernierende Drüsen an den Nebenblättern von Rubiaceen. *Berichte der Deutschen Botanischen Gesellschaft*, 27:446-452.
- Lackey, J. A.
1978. Leaflet Anatomy of Phaseoleae (Leguminosae: Papilionoideae) and Its Relation to Taxonomy. *Botanical Gazette*. 139(4):436-446.
- Lersten, N. R.
1975. Colleter Types in Rubiaceae, Especially in Relation to the Bacterial Leaf Nodule Symbiosis. *Botanical Journal of the Linnean Society*, 71(4):311-319.
- Lisbôa, P. L.
1975. Estudo sobre a vegetação das campinas Amazônicas, II: Observações gerais e revisão bibliográfica sobre as campinas amazônicas de areia branca. *Acta Amazônica*, 5 (3):211-233.
- Martius, C.F.P., von, and J. G. Zuccarini
1824a. *Psyllocarpus*. In Ankündigung der Fortsetzung eines Werkes über brasilianische Pflanzen. *Flora* 7(1), supplement (4):130-131. [Published between 25 April and 7 July 1824.]
1824b. *Psyllocarpus*. In *Nova genera et species plantarum* 1:44-46, pl. 28. München: Typis Lindaueri. [Published in October 1824.]
- Pray, T. R.
1954. Foliar Venation of Angiosperms, I: Mature Venation of *Liriodendron*. *American Journal of Botany*, 41 (8):663-670.
1955. Foliar Venation of Angiosperms, I: Pattern and Histology of the Venation of *Hosta*. *American Journal of Botany*, 42(7):611-618.

- Radlkofer, L.
1890. Ueber die Gliederung der Familie der Sapindaceen. *Sitzungsberichte der mathematisch-physikalischen Classe der k. b. Akademie der Wissenschaften zu München*, 20(1, 2):105-379.
- Schultes, J. A. and J. H. Schultes
1827. *Psyllocarpus*. In *Mantissa in volumen (secundum, tertium) systematis vegetabilium*, 3:14, 211-213. Stuttgart: J. G. Cotta.
- Schumann, K.
1888. Tribus VIII: Spermaceae Kth. In Rubiaceae, Tribus VII-XIX, in C.E.P. von Martius, *Flora brasiliensis* 6(6):5-102.
1891. Rubiaceae. In A. Engler and K. Prantl, *Die Natürlichen Pflanzenfamilien*, 4(4):1-156.
1898. Rubiaceae. In I. Urban, editor, *Plantae novae americanae imprimis Glaziovianae*, II. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 25(3), suppl. (60):17, 18.
- Smith, L. B., and R. J. Downs
1956. Resumo preliminar des Rubiaceas de Santa Catarina. *Sellowia*, 7, 8(7):13-86.
- Sprengel, K.P.J.
1827. *Psyllocarpus*. In *Caroli Linnaei . . . Systema vegetabilium*, 16th edition, 4(2):38-39. Göttingen: Libraria Dieterichiana.
- Standley, P. C.
1930. The Rubiaceae of Colombia. *Publications of the Field Columbian Museum, Botanical Series*, 7(1): 3-175.
1931a. The Rubiaceae of Ecuador. *Publications of the Field Columbian Museum, Botanical Series*, 7(2): 179-251.
1931b. The Rubiaceae of Bolivia. *Publications of the Field Columbian Museum, Botanical Series*, 7(3):255-339.
- 1931c. The Rubiaceae of Venezuela. *Publications of the Field Columbian Museum, Botanical Series*, 7(4): 343-485.
1936. Rubiaceae. In J. F. MacBride, *Flora of Peru. Field Museum of Natural History, Botanical Series*, 13(6):3-261.
- Steyermark, J. A.
1972. Tribe Spermaceae. In B. Maguire, et al., *Botany of the Guayana Highland, Part IX. Memoirs of the New York Botanical Garden*, 23:777-832.
1974. Tribu XVIII. Spermaceae. In T. Lasser, *Flora de Venezuela*, 9(3):1834-1978.
- Sucre, D.
1971. Estudo das Rubiaceae Brasileiras, III: Cinco novas espécies da Tribo Spermaceae. *Rodriguésia*, 26(38): 253-260.
- Uphoff, J.C.T.
1962. Plant Hairs. In W. Zimmermann and P. G. Ozenda, editors, *Encyclopedia of Plant Anatomy*, IV(5): 292 pages. Berlin: Gebrüder Borntraeger.
- Verdcourt, B.
1975. Studies in the Rubiaceae, 1: Rubioideae for the "Flora of Tropical East Africa." *Kew Bulletin*, 30(2):247-326.
1976. Rubiaceae, 1. In R. M. Polhill, *Flora of Tropical East Africa*. 414 pages. London: the Whitefriars Press Ltd.
- Welden, F. L., von
1825. II, Correspondenz. *Flora*, 8(12):182-190.
- Wernham, H. F.
1916. Tropical American Rubiaceae, VII. *Journal of Botany, British and Foreign*, 54:322-334.
- Weston, G. D., and D. D. Cass
1973. Observations on the Development of the Paraveinal Mesophyll of Soybean Leaves. *Botanical Gazette*, 134:232-235.

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(Numbers in parentheses refer to species treated in this paper)

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- Anderson, W. R., S. G. da Fonseca, R. Reis dos Santos, and R. Souza 10779 (2); 10918 (1)
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- Barreto, M. 1128, and A. C. Brade 14736 (8)
- Barreto, M. 1130, and A. C. Brade 14737 (4)
- Barreto, M., and A. P. Viégas 6349 (4)
- Blanchet, J. S. 2534 (6); 3332 (6); *s.n.* (6)
- Brade, A. C. 13448 (4); 13838 (6); 13839 (4); 13847 (4); 13988 (4)
- Bunbury, C.J.F. *s.n.* (4)
- Campos, R. F. *s.n.* (4)
- Castellanos, A. 25970 (6)
- Casaretto, G. 2713 (4)
- Claussen, P. 5 (4); 64 (4); 162 (4); 182 (4); 183 (*pro parte*) (4); 264 (4); 336 (4); 603 (4); *s.n.* (4)
- Damazio, L. 234 (4); 1647 (4); *s.n.* (4)
- Dawson, E. Y. 14169 (5)
- Duarte, A. P. 2113 (4); 2595 (4); 2655 (8); 2730 (4); 8528 (4); 9697 (8); 11381 (8); 11580 (4)
- Duarte, A. P., and G. Barroso 7931 (4)
- Duarte, A. P. 9199, and E. Pereira 10109 (6)
- Egler, W. A. 1238 (2)
- Eiten, G., and L. T. Eiten 6707 (4); 6799 (8)
- Fróes, R. L. 25262 (3)
- Gardner, G. 4735 (4); 4736 (4); 4737 (4)
- Glaziou, A.F.M. 8470 (4); 14930 (6); 14931 (4); 14932 (4); 17641 (4); 19428 (7); 19429 (7); 19430 (6); 19431 (4); 19432 (4); 19432a (4); 19540 (8); 20350 (4); 21504 (7)
- Gounelle 41 (4)
- Harley, R. M., S. A. Renvoize, C. M. Erskine, C. A. Brighton, and R. Pinheiro 15055 (6); 15355 (6)
- Hatschbach, G., W. R. Anderson, R. Barneby, and B. Gates 36224 (7); 36340 (5); 36410 (5); 36475 (6)
- Hatschbach, G., and P. Pelanda 27900 (6); 28001 (4)
- Hatschbach, G., L. B. Smith, and E. Ayensu 29059 (4)
- Herlinger, E. P. 10683 (7); 11451 (5); 13078 (7); *s.n.* (7)
- Herlinger, E. P., and A. Castellanos 22080 (8); 22204 (4)
- Hoehne, F. C. 4914 (4); 4937 (4)
- Irwin, H. S., W. R. Anderson, M. Stieber, and E. Y.-T. Lee 34434 (7)
- Irwin, H. S., S. F. da Fonseca, R. Souza, R. Reis dos Santos, and J. Ramos 26662 (7); 27090 (4); 27490 (4); 27643 (6); 27724 (4); 28097 (4); 28313 (4); 28316 (6); 28493 (6)
- Irwin, H. S., J. W. Grear, Jr., R. Souza, and R. Reis dos Santos 12221 (7); 12870 (5); 13445 (7); 13656 (7)
- Irwin, H. S., R. M. Harley, and E. Onishi 28875 (4); 28967 (4); 29135 (4); 29254 (4); 29634 (4); 30430 (4)
- Irwin, H. S., R. M. Harley, and G. L. Smith 30890 (6); 32482 (6); 33082 (5)
- Irwin, H. S., H. Maxwell, and D. C. Wasshausen 18633 (7); 19449 (7); 19888 (4); 19976 (8); 20642 (4); 20659 (4)
- Irwin, H. S., R. Reis dos Santos, R. Souza, and S. F. da Fonseca 21850 (4); 21998 (6); 22085 (4); 22247 (6); 22352 (4); 22359 (4); 22597 (4); 22720 (4); 23118 (6); 23466 (4); 23572 (4); 24745 (5)
- Irwin, H. S., and T. R. Soderstrom 5143 (7); 5655 (7)
- Irwin, H. S., R. Souza, J. W. Grear, Jr., and R. Reis dos Santos 15531 (5)
- Irwin, H. S., R. Souza, and R. Reis dos Santos 8214 (7); 8993 (7); 10678 (7)
- Kuhlmann, J. G. *s.n.* (4)
- Langsdorff, G. H. *s.n.* (4)
- Lanstyak, L. *s.n.* (4)
- Lima, A. 58–2957 (7)
- Lund, P. W. *s.n.* (4)
- Macedo, A. 2067 (4); 2827 (4); 2960 (8)
- Magalhães, M. 1281 (4); 1785 (4); 2364 (4); 2586 (4); 16909 (4); 17981 (4)
- Markgraf, F. 3406, M. Barreto 12011 and A. C. Brade (4)
- Martius, K.F.P. von 998 (4); 1295 (4); *s.n.* (4); *s.n.* (6)
- Mexia, Y. 5755 (4)
- Mota, C. D., and L. Coêlho 209 (2)

- Oliveira, J. E. de *s.n.* (8)
- Palacios, Balegno, and Cuezco 3976 (4)
- Pereira, E. 1566 (6); 7385 (7); 8892 (8); 9070 (7)
- Pereira, E. 2526, and G. Pabst 3362 (4)
- Pereira, E. 2834, and G. Pabst 3670 (4)
- Philcox, D., and E. Onishi 4815 (7)
- Pires, J. M., N. T. Silva, and R. Souza 9143 (7)
- Pohl, J. E. 1317(851) (4); 3445 (4); 3477 (4); *s.n.* (4)
- Prance, G. T., and N. T. Silva 58197 (5)
- Ramariz, D. 0309 (4)
- Reinhardt, J. T. *s.n.* (4)
- Riedel, L. 39 (4); 376 (4); 1238 (6); 1335 (4); 1385 (4); 1884 (4); 2884 (4); *s.n.* (6)
- Saint-Hilaire, A. de *BI* 835 (4); *BI* 989 (4); *BI* 1157 (4); *s.n.* (4)
- Silva, N. T. 4346 (1)
- Sampião, A. J. de 6828 (4)
- Santos, G. *s.n.* (4)
- Schwacke, C.A.W. *s.n.* (4)
- Segadas-Vianna, F. 6044 (4)
- Segadas-Vianna, F., and J. Lorêdo 1081 (4)
- Sellow, F. 1167 (4); *s.n.* (4)
- Smith, L. B. *A-20* (7); 15040 (7)
- Sucre, D. 279 (7)
- Ule, E. 2576 (4); 6102 (1)
- Vauthier 230 (4); 231 (4); 233 (8); 570 (4); *s.n.* (4)
- Vidal, J. *II* 5981(953) (4); *II* 6038(953) (4); *IV* 1172 (4); *s.n.* (4)
- Warming, E. *s.n.* (4)
- Weddell, H. A. 1738 (4); *s.n.* (4)
- Williams, L. O., and V. Assis 6977 (4); 7918 (4); 8150 (4)



PLATE 1.—Lectotype of *Psyllocarpus campinorum* with an insert showing a verticillaster (*Ule* 6101. HBG).



PLATE 2.—Holotype of *Psyllocarpus cururuensis* with an insert showing the distal portion of an inflorescence (Anderson et al. 10779, IAN).



PLATE 3.—Holotype of *Psyllocarpus psyllocarpoides* with an insert showing a verticillaster with a dehiscent fruit (Fröes 25262, IAN).

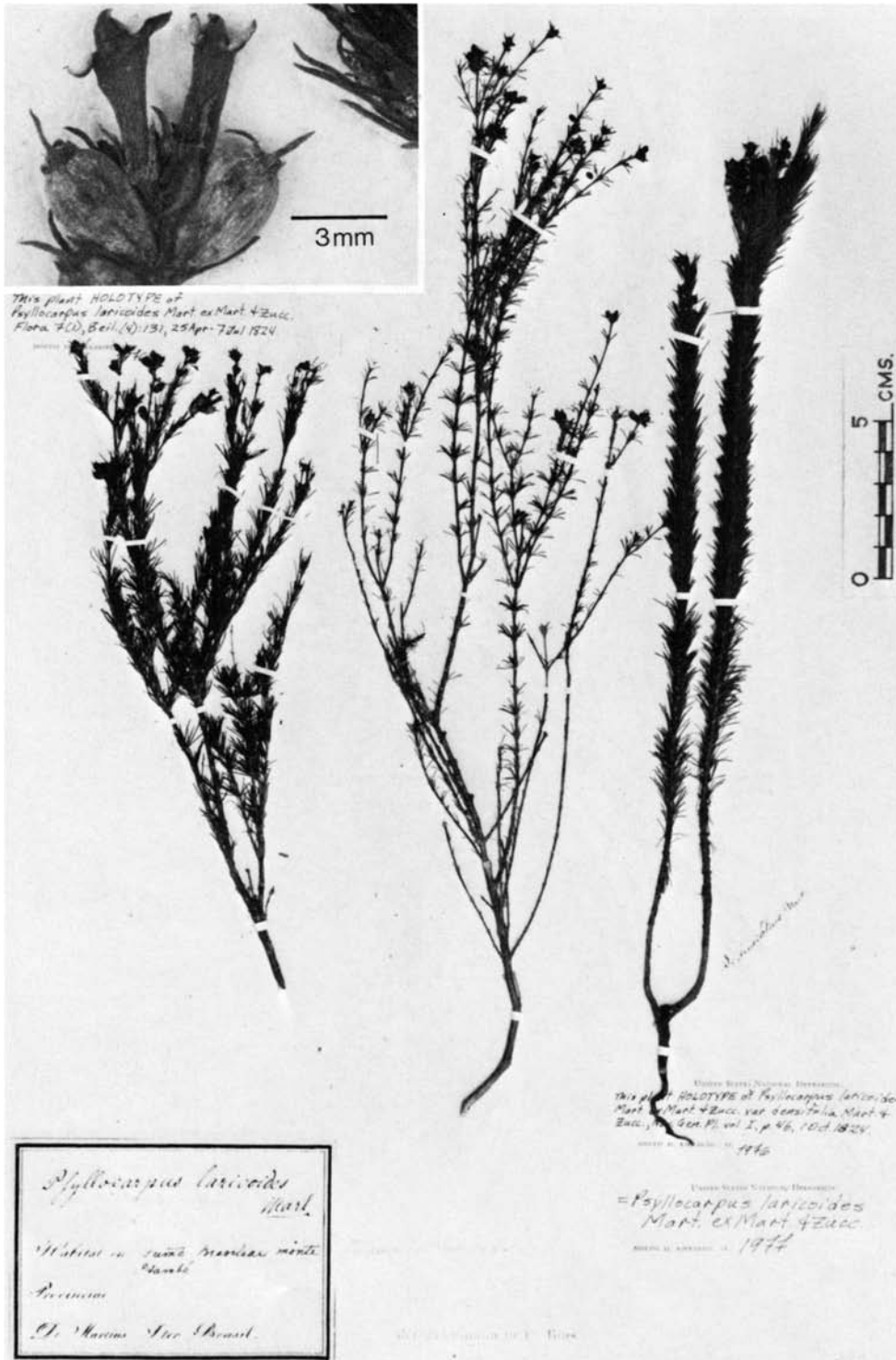


PLATE 4.—Lectotype of *Psyllocarpus laricoides*, farthest left, and holotype of *P. laricoides* var. *densifolius*, farthest right, with an insert showing the distal portion of an infructescence of *P. laricoides* with late flowers (Martius s.n., M).

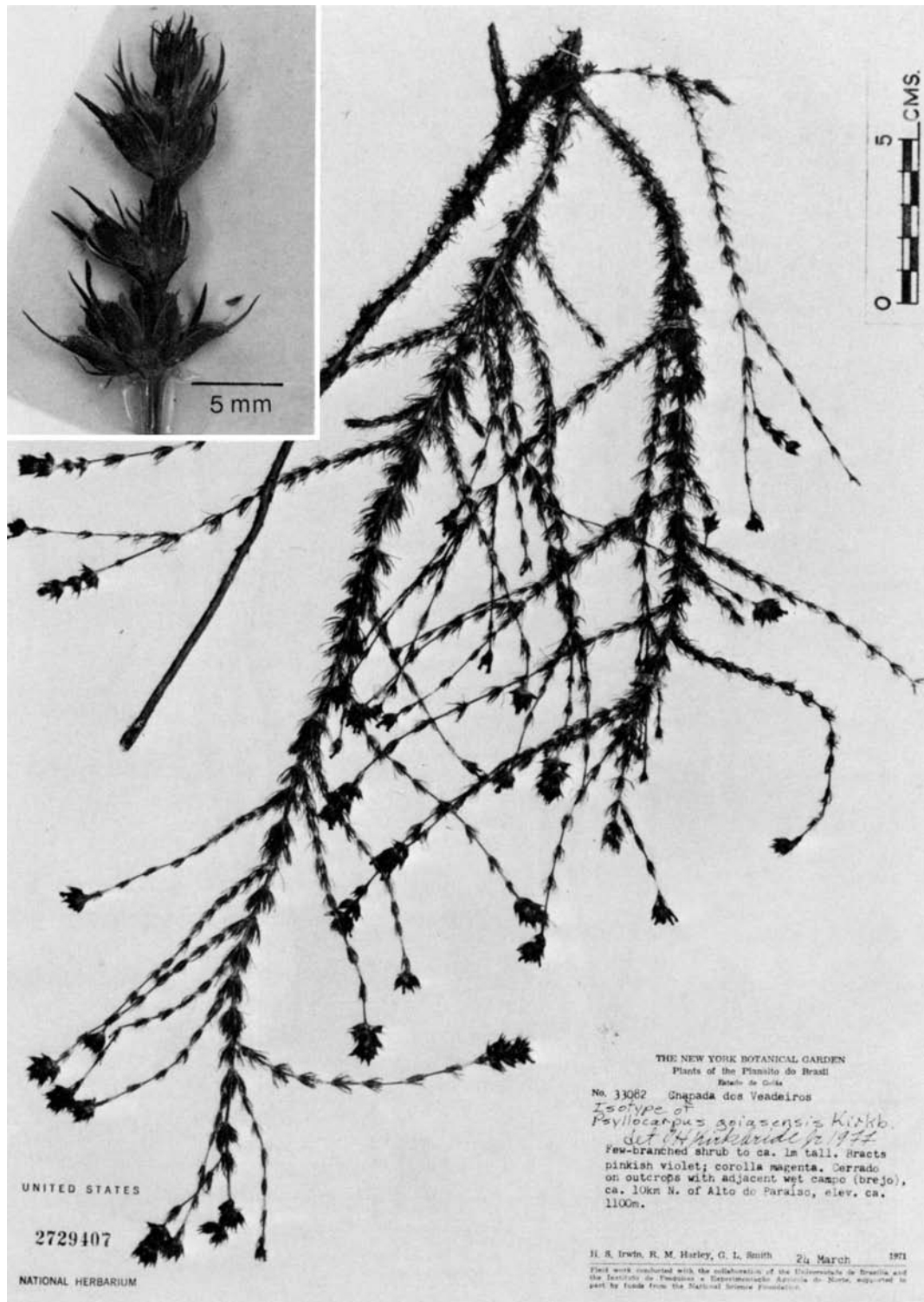


PLATE 5.—Isotype of *Psyllocarpus goiasensis* with an insert showing an infructescence (Irwin et al. 33082, US).



PLATE 6.—Lectotype of *Psyllocarpus asparagoides* with an insert showing an infructescence (Martius s.n., M).

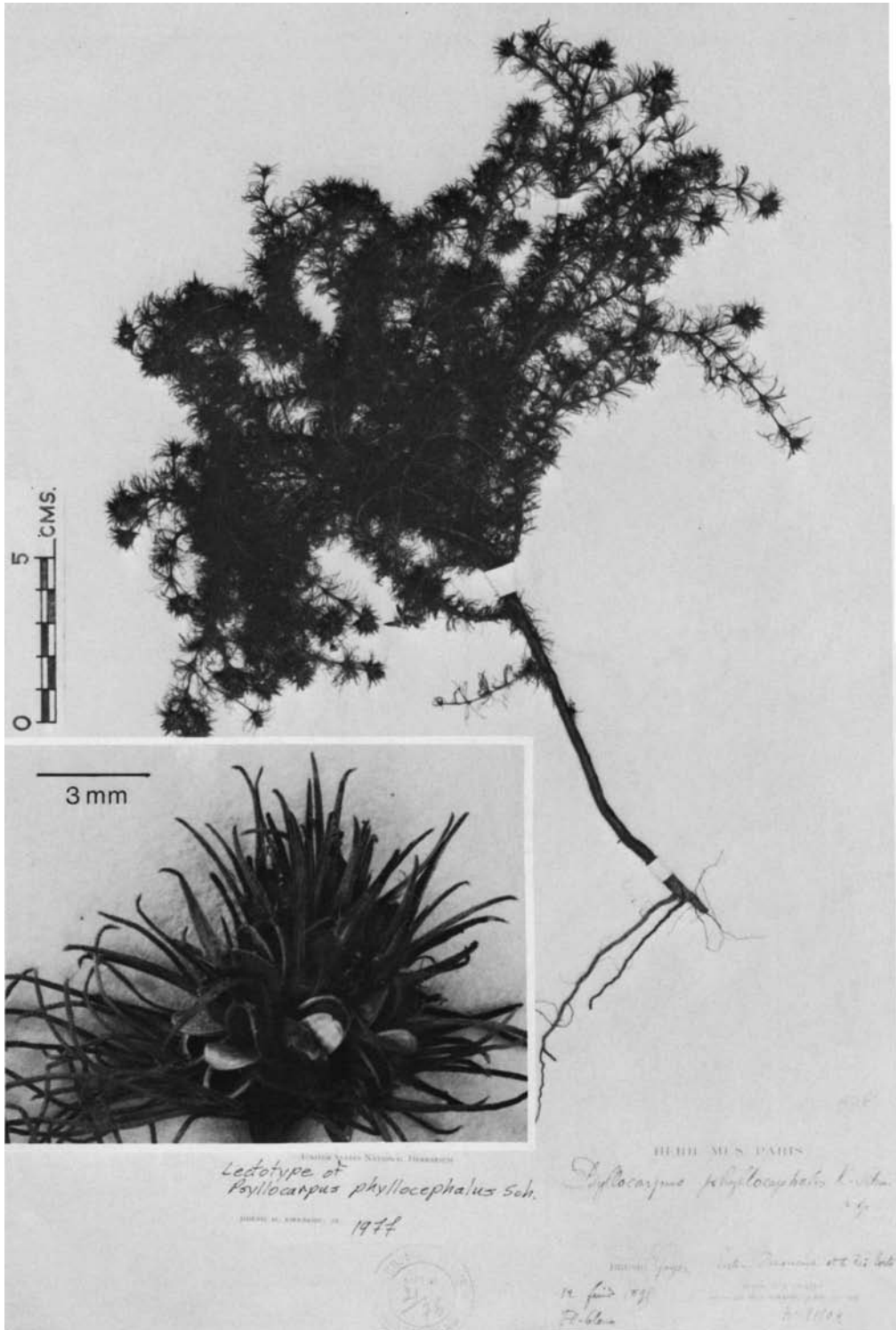


PLATE 7.—Lectotype of *Psyllocarpus phyllocephalus* with an insert showing an infructescence (Glaziou 21504, P).

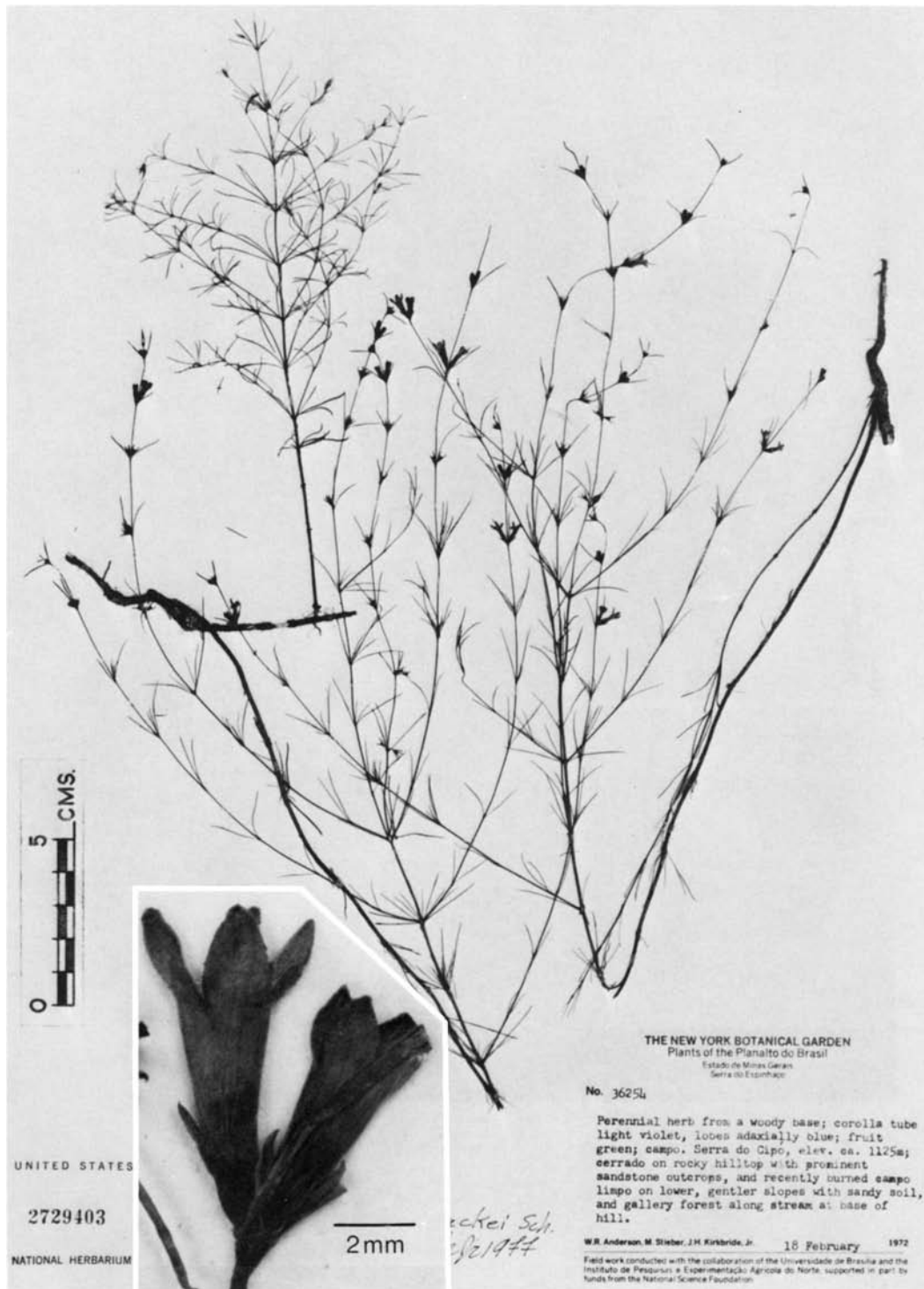


PLATE 8.—Neotype of *Psyllocarpus schwackei* with an insert showing two flowers (Anderson et al. 36254, US).