THE POLLINATION OF MARCGRAVIA: A CLASSICAL CASE OF ORNITHOPHILY?

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INTRODUCTION

Since the publication of Darwin's investigations upon the pollination of orchids, many biologists have tended to assume that flowers which are visited by insects and birds are pollinated by these animals, and that aberrant types of floral organization are adaptations to insure cross-pollination. Thus, the bizarre inflorescences of Marcgravia, with their curious pitcher-like nectaries, are assumed to facilitate cross-pollination by birds. In fact, this extraordinary genus is cited as one of the most striking illustrations of ornithophily.

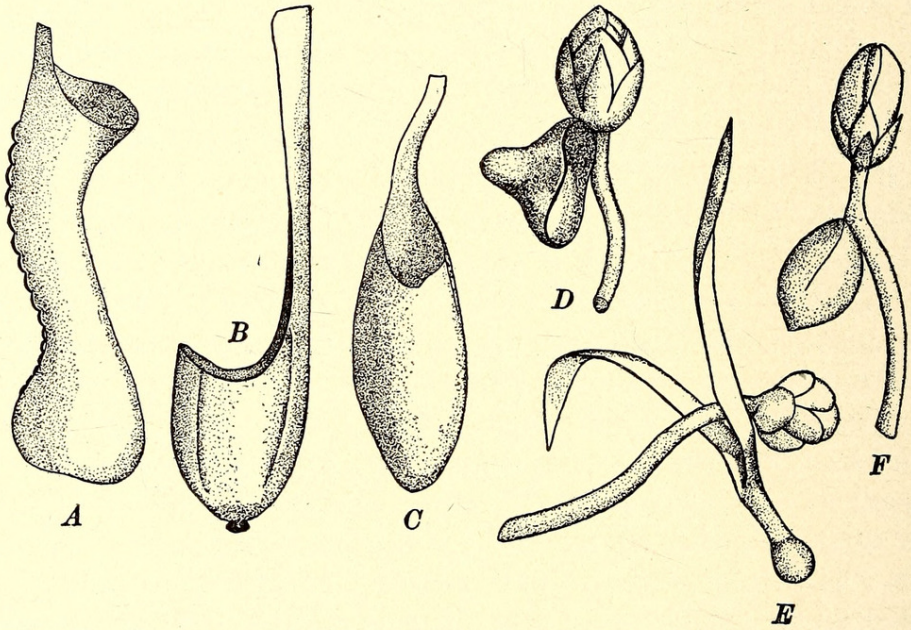

FIG. 1. Nectariferous appendages of Marcgraviaceae. *A. Marcgravia coriacea* Vahl. *B. M. picta* Willd. *C. Norantea guianensis* Aubl. *D. Souroubea pilophora* Wittm. *E. S. guianensis* Aubl. *F. Ruyschia sphaerodenia* Delp. After Wittmack.

While collecting along the banks of the Mazaruni and Cuyuni Rivers near the Tropical Station of the New York Zoölogical Society,[1] the writer encountered two species of Marcgravia. As much time as could conveniently be spared from other work was devoted to a study of the structure

[1] At Kartabo, British Guiana.

and pollination of these interesting plants. Before discussing the results of this investigation, however, it is essential to outline certain salient morphological features of the Marcgraviaceae.

Salient Features in the Morphology of the Marcgraviaceae

As shown by Jussieu (1809), Delpino (1869), Wittmack (1878), Szyszylowicz (1895), and others, the small neotropical family Marcgraviaceae is characterized by having nectariferous appendages which are closely associated with the flowers. These nectaries vary considerably in size, shape, and structure in different species and genera, and are significant in the classification of the various representatives of the family (text fig. 1). In the genera Caracasia and Ruyschia, they are small spherical or hemispherical organs which are attached to the pedicels of the flowers, as are the more or less deeply concaved and spurred nectaries of Souroubea. In Marcgravia, on the contrary, they are relatively large sac-shaped or galeate structures which are inserted upon the apex of the peduncle.

There has been considerable speculation concerning the origin and morphological significance of these nectariferous appendages. Are they metamorphosed bracteoles, abnormal pedicels, modified bracts, or appendages *sui generis?* Most recent students of the Marcgraviaceae have accepted Planchon and Triana's (1863) conclusion that they are evaginated bracts. It must be admitted that there is considerable evidence in favor of this view.

The leaves of the Marcgraviaceae are provided with hypophyllous excretory organs which vary considerably in size, number, and distribution in different representatives of the family. Two of these glands tend to be located at the base of the lamina, one on either side of the midrib. In small, rudimentary leaves, such as commonly occur near floral axes, these basal glands become proportionately accentuated as the lamina is reduced in area. Interesting transitions between rudimentary glandular leaves of this type and spoon-shaped, hooded, or sac-shaped nectaries occur in various Marcgraviaceae; and are particularly numerous and conspicuous in Norantea, *e.g.*, *N. anomala* H.B.K. and *N. brasiliensis* Choisy. In certain specimens, the nectariferous bracts at the base of the inflorescence resemble rudimentary leaves and are attached to the peduncle just below the points of insertion of the pedicels, but in the middle and upper portions of the racemes they become more and more deeply concaved or evaginated, and their petioles fuse with, and therefore appear to arise from, the pedicels of the flowers. The concave or inner surface of the nectariferous appendages is the morphological equivalent of the under surface of the leaves. The outlets or pores of the hypophyllous glands are located in this dorsal surface (Pl. XXIII, fig. 2) and, accordingly, discharge their sugary excretions into the concavities of the bracts (Pl. XXIV, fig. 9).

In the more or less elongated, usually erect, racemes of Ruyschia,

Caracasia, Souroubea, and Norantea, there is a nectariferous bract for every flower; whereas in the pendent, more or less compacted, umbelliform racemes of Marcgravia, the nectaries are segregated at, and apparently

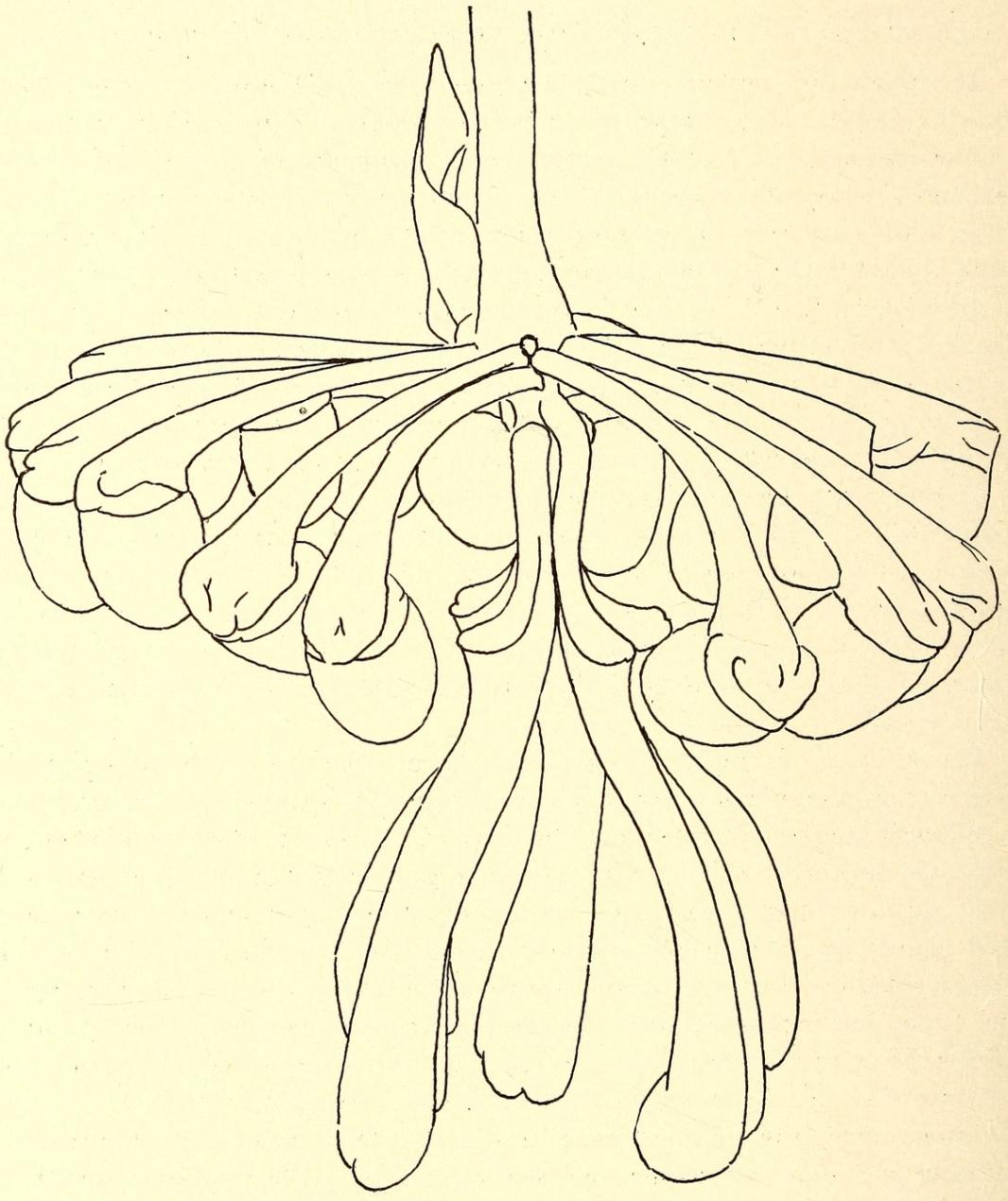

FIG. 2. *Marcgravia cuyuniensis* spec. nov. Mature inflorescence. One fertile pedicel removed from in front to show attachment of nectaries. From a field sketch by Miss Anna H. Taylor. × 1/1.

arise from, the terminal portion of the peduncle, which usually is devoid of fertile pedicels (text figs. 2, 4). These nectariferous bracts are not exact morphological equivalents of those which occur in the other genera, for they bear rudimentary flower buds at their apices (text figs. 3, 5). That the nectaries of Marcgravia are not abnormal pedicels, as maintained

by Seemann (1870), but are compound structures resulting from the fusion of a nectariferous bract and a sterile pedicel, is indicated, not only by their external morphology, but also by their internal anatomy. The fused pedicel shows as an embossed rib and terminates in a rudimentary flower bud, which occasionally develops into a normal flower (text figs. 3, 5). The fertile pedicels commonly are provided with corky excrescences. The outer surfaces of the adnate sterile pedicels are also conspicuously verrucose. Furthermore, as shown in figure 6, Plate XXIV, there are two distinct systems of fibro-vascular bundles in the nectaries, one belonging to the sterile pedicel and the other to the adnate bract.

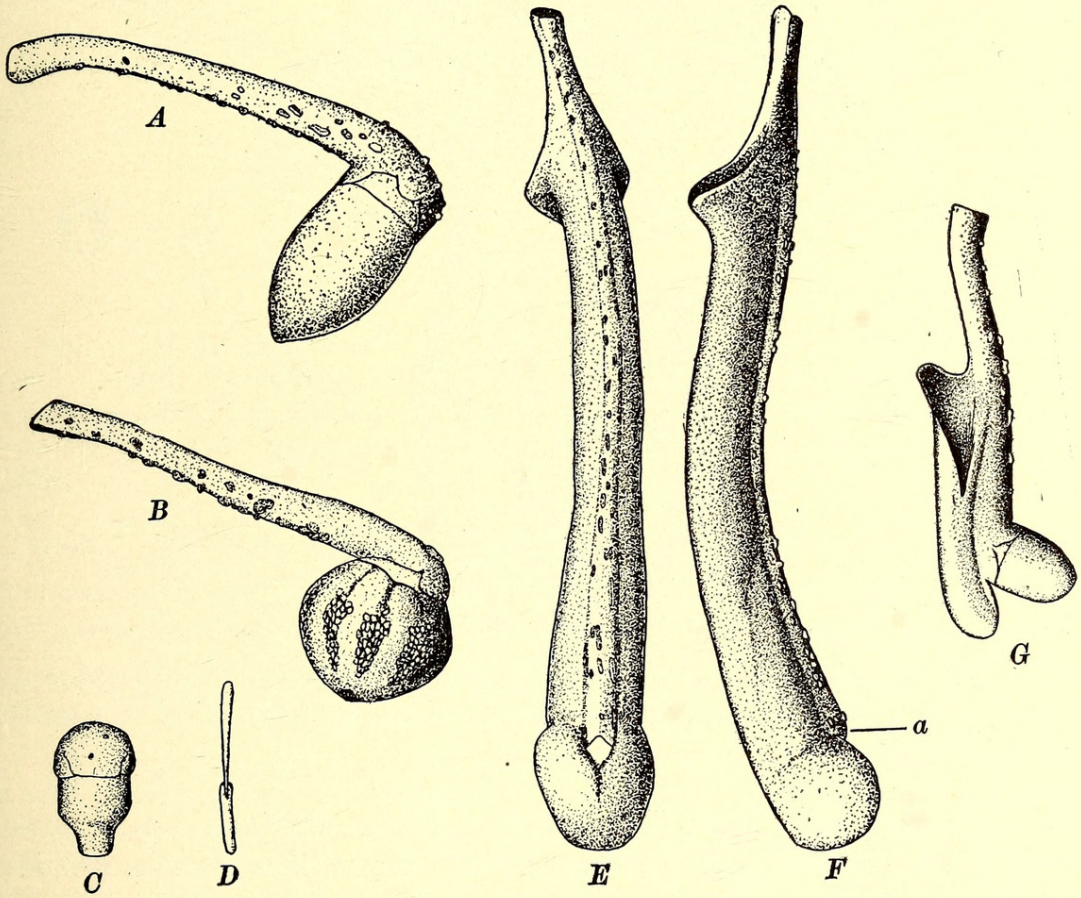

FIG. 3. *Marcgravia cuyuniensis* spec. nov. *A*. Pedicel and flower bud. *B*. Pedicel and fruit. *C*. Pistil. *D*. Stamen. *E*, *F*. Nectariferous appendages; (*a*) rudimentary flower bud at apex of adnate pedicel. *G*. Abnormal appendage, showing adnate flowering pedicel. × 1/1. Drawn from material preserved in formalin-alcohol by Miss Grace Griffin.

Although there are traces of cohesion of floral members in Ruyschia, Souroubea, and Norantea, the flowers of Marcgravia are characterized by having calyptriform corollas. The petals are fused into a tough, leathery capsule or thalamus which entirely encloses the pistil and stamens (text fig. 4). This capsule does not split longitudinally at the time of "flowering," but becomes detached at its attenuated base. Delpino (1869) divided the genus Marcgravia into two subgenera: Orthothalamium, having the

capsules in line with projections of the pedicels, and Plagiothalamium, having them turned downwards at right angles to the pedicels.

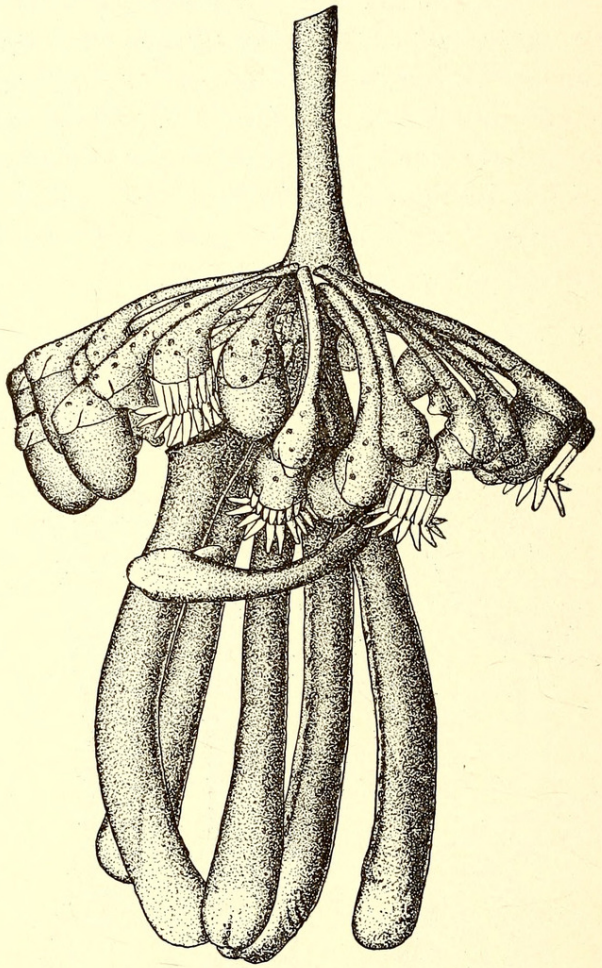

FIG. 4. *Marcgravia purpurea* spec. nov. Mature inflorescence. Four calyptriform corollas removed to show stamens. × 1/1. Drawn from material preserved in formalin-alcohol by Miss Grace Griffin.

It is evident, accordingly, in viewing the Marcgraviaceae as a whole, that there are certain distinct and closely correlated lines of morphological specialization which reach their climax in Plagiothalamium. In this subgenus the racemes are compacted into pendulous umbels, the large, highly modified nectariferous bracts are terminally segregated and are adnate to sterile pedicels, the corolla is fused into a deciduous capsule or thalamus, and the flower buds are bent downwards at right angles to the pedicels.

SIGNIFICANCE OF FLORAL MORPHOLOGY OF MARCGRAVIACEAE

Delpino (1869), who devoted considerable attention to the Marcgraviaceae, believed that the nectariferous bracts function as attracting organs in connection with the cross-pollination of the protandrous flowers; the small nectaries providing food for insects, and the larger and more complex

nectariferous appendages of Souroubea, Marcgravia, and certain species of Norantea supplying a delectable beverage for birds.

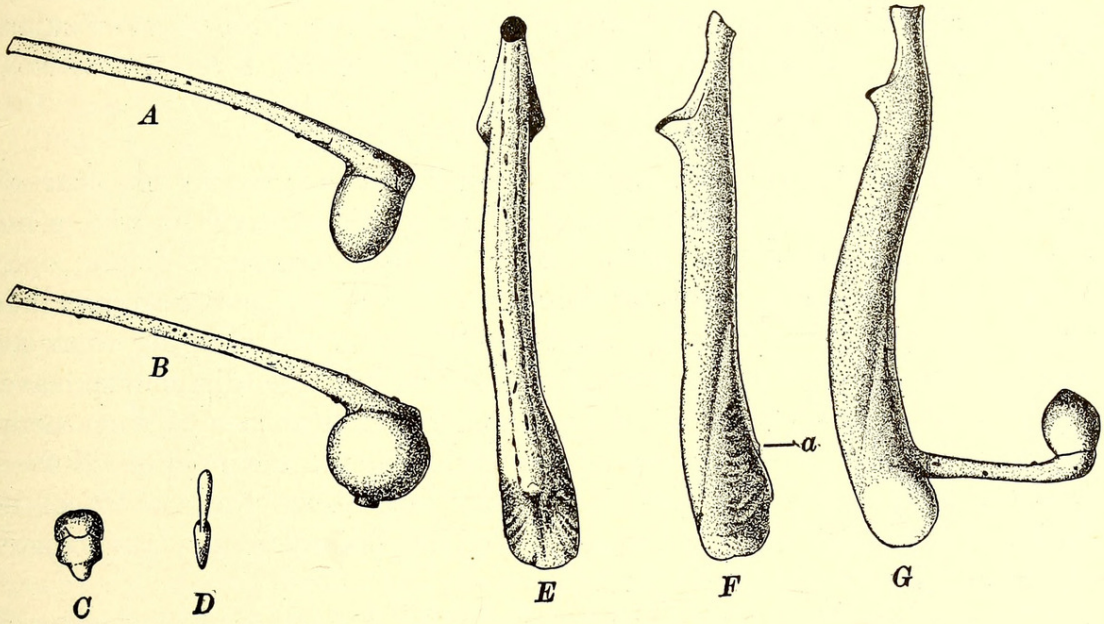

FIG. 5. *Marcgravia purpurea* spec. nov. *A*. Pedicel and flower bud. *B*. Pedicel and fruit. *C*. Pistil. *D*. Stamen. *E*, *F*. Nectariferous appendages; (*a*) rudimentary flower bud at apex of adnate pedicel. *G*. Abnormal appendage, showing elongated pedicel and flower bud. × 1/1. Drawn from material preserved in formalin-alcohol by Miss Grace Griffin.

Belt (1874) was the first, however, to offer any concrete suggestion concerning the significance of the morphological peculiarities of the highly specialized inflorescences of Marcgravia. The following paragraph, quoted from his highly entertaining book, "The Naturalist in Nicaragua," summarizes his hypothesis:

> Higher up the valley more trees were left standing and amongst these small flocks of other birds might often be found, one green with red head (*Calliste laviniae* Cass.); another shining green, with black head (*Chlorophanes guatemalensis*); and a third, beautiful black, blue and yellow, with a yellow head (*Calliste larvata* Du Bus.). These and many others were certain to be found where the climbing *Marcgravia nepenthoides* expanded its curious flowers. The flowers of this lofty climber are disposed in a circle, hanging downwards, like an inverted candelabrum. From the center of the circle of flowers is suspended a number of pitcher-like vessels which, when the flowers expand, in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds, including the species I have mentioned and many kinds of humming-birds. The flowers are so disposed with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another. A second species of Marcgravia, that I found in the woods around Santo Domingo, has the pitchers placed close to the pedicels of the flowers, so that the birds must approach them from above; and in this species the flowers are turned upwards, and the pollen is brushed off by the breast of the birds.

Belt's generalization, that the inflorescences of Marcgravia are adapta-

tions to insure cross-pollination by birds, is so plausible and appears to afford a satisfactory explanation for so many closely coördinated phenomena that it is not surprising that it should have been accepted without question by Hermann Müller (1873), Schimper (1898),[2] and others; particularly in view of the fact that the Marcgraviaceae are stated to be protandrous.

Descriptive and Taxonomic

The two species of Marcgravia growing in the vicinity of the Kartabo laboratory are characterized, as are other representatives of the genus, by having two distinct types of branches: (1) sterile runners (plagiotropic), and (2) pendulous fertile shoots (orthotropic) which bear terminal inflorescences. The former are provided with numerous clasping roots and small distichous leaves, whereas the latter have large distichous leaves. The plants scramble over the trunks and lower branches of trees which line the banks of the larger water courses. They are not lofty climbers, rarely rising more than fifteen or twenty feet above the surface of the rivers. Indeed, at high water certain of the inflorescences and clusters of fruit are completely submerged.

The two species may readily be distinguished, even at a considerable distance, by conspicuous differences in color and habit of growth. In one species, which was designated in the field as *A*, the fertile shoots are relatively infrequent, relatively long, and bear dark green leaves which are so oriented that their upper surfaces are clearly visible (Pl. XXIII, figs. 1, 3). In the other species, *B*, the flower-bearing shoots are more numerous, shorter, and have yellowish-green leaves that are nearly horizontal and are considerably folded dorsally (fig. 4). Upon closer inspection the broadly oblong-elliptical leaves of species *A* are found to be strongly petiolate and to be inserted upon a zigzaged axis (fig. 1), whereas those of species *B*, which are smaller and narrower, are nearly sessile and are borne on a straight shoot. Furthermore, the yellowish or brownish-green inflorescences of the latter species are attached close to the last leaf, whereas in the former species the dark, greenish-purple inflorescences form the terminus of a long, straight, terete peduncle.[3] As shown in text figures 2–5, the flower buds, fruits, pedicels, and nectaries of species *B* are larger and stouter than homologous members of the inflorescences of species *A*. The vines of the former bear inflorescences and fruits in various stages of maturity, whereas the fertile shoots of species *A*, at any given time, are all in equivalent stages of differentiation. In other words, species *B* flowers continuously, but species *A* exhibits a marked floral periodicity.

[2] Schimper, in quoting the above passage from Belt, substitutes *Marcgravia umbellata* for *Marcgravia nepenthoides*. He also figures the inflorescence of the former instead of the latter species.

[3] During the earlier stages in the development of the flowering shoots of species *A*, the peduncle may be provided with numerous small glandular leaves. Most of these more or less rudimentary leaves drop off before the inflorescences attain any considerable size.

Concerning the identity of these Marcgravias, it may be stated at once that they both belong in Delpino's subgenus, Plagiothalamium. Furthermore, the prolongation of the peduncle beyond the points of attachment of the pedicels in species *B* indicates clearly that this species should be referred to Wittmack's subsection Dolichoracheae, just as the absence of this extension in species *A* leads to its inclusion in his Brachyracheae.

The leaves and inflorescences of Marcgravias vary considerably, particularly in different stages of their ontogeny, and are difficult to season for herbarium purposes. Many of the descriptions of species in the literature appear to be based upon the study of somewhat fragmentary material; not infrequently of immature leaves or inflorescences. Such facts as these, coupled with the difficulty of securing access to the widely scattered type specimens, makes the determination of species a somewhat difficult and unsatisfactory undertaking.

Species *B* appears to be closely allied to *M. coriacea* Vahl and *M. acuminata* Miguel, but differs from these species in certain of its floral and foliar characters, particularly in having filaments which are not basally connate. Species *A* resembles *M. parviflora* Rich. var. *pedunculosa* (Triana and Planchon) Wittm., but has large nectaries which are longer than the pedicels of the flowers. In view of the abundance of both living and dried material at my disposal, it seems wiser to describe these plants as new species, rather than to refer them to any of the above-named species. Furthermore, it is desirable to make detailed and fairly comprehensive descriptions, since there appears to be some doubt as to which characters are of greatest specific significance in these sections of Marcgravia.

Marcgravia (Dolichoracheae) **cuyuniensis** spec. nov.

Folia ramorum floralium breviter petiolata, oblongo-elliptica, coriacea, ex glandulis marginalibus depressis numerosis subcrenulata, apice acuminata, basi acuta vel subrotundata; in sicco haud nitentia, supra punctata, venis patentibus; glandulis hypophyllis saepissime duobus, ad basim costae mediae; nervo crasso subtus prominente, supra basim versus profunde sulcato; petiolis crassis antice canaliculatis. Racemus umbelliformis, pendulus, submultiflorus, breviter pedunculatus. Bracteae 3–6, elongatae, tubuloso-cucullatae, crassae, clavatae, deciduae, sub ore rotundato plus minusve constrictae. Pedicelli 16–24, crassi, tuberculato-verrucosi. Corolla coriacea, ovoidea vel conico-ovoidea. Stamina ± 46, *filamentis basi non connatis*, antheris rubellis. Ovarium 9- — 11-loculare. Fructus magnus, globosus, rubidus, plus minusve tuberculato-verrucosus, stigmate mammiformi coronatus. Semina sanguinea nitentia

Scandent epiphytic shrub. Plagiotropic shoots quadrangular, bearing small coriaceous leaves and short clasping roots. The former oval, oval-oblong, or oblong, distichous, conspicuously glandular at the base. The latter aggregated in clusters, more or less completely sheltered by the leaves. Orthotropic fertile shoots numerous, short, stout, usually terete and pendulous, sparsely linear-verrucose. Leaves distichous, coriaceous, somewhat conduplicate dorsally, elliptical-oblong, acuminate, acute, retuse,

or subcordate at the base, 10–16 cm. long, 3.5–4.5 cm. broad, glabrous, glossy, yellowish green with midrib and principal veins outlined in yellow; when dry, dull, scabrous, punctate above, veins more or less prominent and embossed; petiole 3–5 mm. long, canaliculate above, subtending a long, shallow groove in the stem; two basal glands large, conspicuous; glandular marginal depressions numerous, making the leaves distinctly subcrenulate. Umbelliform racemes yellowish or brownish green, pendulous. Pedicels stout, horizontal or curved downwards at the time of flowering, 4.5–5.5 cm. long, covered with large, conspicuous, corky excrescences. Calyptriform corolla thick, coriaceous, ovoid or ovoid-conical, 1.3–1.8 cm. long, 1.0–1.2 cm. diameter. Stamens numerous, free; filaments cream-colored, 8–11 mm. long, tapering, stout and more or less quadrangular at the base; anthers reddish or pink at maturity, lanceolate, 5–7 mm. long. Ovary slightly obovoid, ± 7 mm. diameter, 9- to 11-locular, abruptly conical above, terminating in a short, blunt style, ± 3 mm. long. Fruit large, globose, ± 2.0 cm. diameter, crowned by the slightly elevated hemispherical stigmatic surface; at maturity reddish, scabrous or banded-verrucose. Seeds glistening, blood-red. Nectaries elongated, 5.5–8.0 cm., considerably swollen at the apex, tapering towards the base; orifice surrounded by a protruding rim or lip; petiole ± 15 mm. long; fused pedicel showing as a slightly embossed, verrucose rib; flower bud rudimentary, depressed.

Banks of the Cuyuni River near Kartabo, British Guiana. Bailey nos. 128, 177, 178, and 193, deposited in the Gray Herbarium of Harvard University.

Marcgravia (Brachyracheae) **purpurea** spec. nov.

Folia ramorum floralium pro genere longe petiolata, elliptica vel oblongo-elliptica, coriacea, basi acuta, apice acuminata vel attenuato-acuminata; in sicco membranacea, supra punctata, venis secundariis patentibus; nervo crasso supra sulcata, petiolis crassis antice canaliculatis; glandulis hypophyllis inconspicuis, duobus, ad basim costae mediae; glandulis marginalibus depressis paucis. Racemus umbelliformis, multiflorus, purpureus, longius pedunculatus. Bracteae 4.7, elongatae, tubuloso-cucullatae, *pedicellis longiores*, clavatae, deciduae. Pedicelli 24–42, graciles, pauce tuberculato-verruculosi, prophyllis a calyce discretis. Corolla conico-ovoidea, purpurea. Stamina ± 16, libera; antheris rubellis. Ovarium turbinato-globosum in stigma productum, 7--8-loculare. Fructus parvus, globosus, stigmate apiculo coronatus.

Scandent epiphytic shrub. Plagiotropic shoots quadrangular, bearing small subcoriaceous or membranous leaves and short clasping roots. The former oblong or oblong-oval, distichous, glandular at the base. The latter aggregated in clusters, sheltered by the leaves. Orthotropic, fertile shoots long, bilaterally compressed, flexuous, terminating in a straight, terete peduncle, 15–30 cm. long. Leaves distichous, coriaceous, elliptical or oblong-elliptical, acuminate or attenuate-acuminate, acute at the base, glossy, dark green, 12–19 cm. long, 5–8 cm. broad; when dry, membranaceous with conspicuously embossed veins and veinlets, punctate above; petiole 1.0–1.5 cm. long, deeply canaliculate above; basal glands inconspicuous; marginal glandular depressions widely spaced. Leaves of peduncle 1–6, more or less rudimentary and early deciduous, conspicu-

ously glandular, broadly elliptical or obovate, 5.5–8.5 cm. long, 3.5–5.5 cm. broad, or small oblong or ovate, 2.5–4.0 cm. long, 1.5–2.5 cm. broad. Umbelliform racemes dark greenish purple, pendulous. Pedicels numerous, slender, 3.5–4.0 cm. long, regularly and evenly distributed, straight and nearly horizontal or curved downwards at time of flowering; corky excrescences few, inconspicuous; bracteoles widely separated from the calyx. Calyptriform corolla ovoid or ovoid-conical, thin, coriaceous, 8–11 mm. long, 7–9 mm. diameter. Stamens non-coherent; filaments stout, short, ± 5 mm., quadrangular, abruptly tapering above; anthers broadly lanceolate, reddish, ± 5 mm. long. Ovary turbinate-obovoid, ± 3.5 mm. diameter, abruptly tapering into a short, blunt style, 2.5 mm. long. Fruit small, globose, ± 10 mm. diameter, reddish, scabrous; style and stigma conspicuously protuberant. Nectaries elongated, 5.5–6.5 cm. long, bilaterally compressed, swollen at the apex, tapering towards the base, orifice surrounded by a slightly protruding rim or lip; petiole ± 7 mm. long; fused pedicel showing as a slightly embossed, verrucose rib; flower bud rudimentary, depressed or protuberant.

Banks of the Mazaruni and Cuyuni Rivers near Kartabo, British Guiana. Bailey nos. 136, 179, 192, 195, deposited in the Gray Herbarium of Harvard University.

Pollination of M. cuyuniensis and M. purpurea

(1)

I first was led to question the accuracy of Belt's generalization concerning the pollination of Marcgravia by a detailed study of the arrangement of the nectaries and flower buds in *M. cuyuniensis* and *M. purpurea*. In these species, as in *M. umbellata* L. and most representatives of the Brachyracheae, the pitchers are placed close to the pedicels of the flowers (text figs. 2, 4). Therefore, according to Belt's hypothesis, birds would have to visit these inflorescences from *above*, but the flower buds and flowers are not turned *upwards*.

During my stay at Kartabo, I did not succeed in finding birds in the vicinity of the inflorescences of *M. cuyuniensis*, although many of the nectaries contained a sweetish liquid. Dr. and Mrs. Alfred Emerson and Miss Anna H. Taylor were more fortunate in the case of *M. purpurea*, which flowered after my return to the United States. A humming bird was seen to hover *above* an inflorescence and to sip nectar from one of the pitchers. The following observations of Miss Bryant (1905) are also significant in this connection. She states concerning *M. umbellata* L. (?):

> The plant is common here climbing to the summit of the forest trees, and is frequently visited by humming birds. The bird settles on the *top* of the flowers (inflorescences) and inserts its long curved beak into the pitchers below.

Such observations as these suggested, of course, that the highly specialized inflorescences of these Marcgravias are not efficient mechanisms for insuring cross-pollination by birds.

(2)

During several weeks spent in exploring the banks of the Cuyuni River, I was considerably puzzled by the fact that, although the vines of *M. cuyuniensis* bore flower buds and fruits in various stages of maturity, there appeared to be none that was actually in flower. A more intensive search led to the finding of numerous inflorescences from which the calyptriform corollas had recently fallen, but still no flowering pedicels were in evidence. Finally, an inflorescence was encountered, one evening, which had shed only three of its numerous protecting capsules. Early the next morning nine more were missing, which demonstrated conclusively that the plant had flowered at night. At 11 P.M. the next night five of the remaining buds were found to be in "flower," with their pink stamens still attached at the base of the pistil. It seemed to be highly improbable, therefore, that *M. cuyuniensis* is cross-pollinated by birds, Trochilidae, Coerebidae, or Tanagridae.

(3)

The question suggested itself, accordingly, are the flowers cross-pollinated by moths, bats, or other night-flying animals? In order to throw some light upon this point, several inflorescences were entirely enclosed in specially prepared cloth bags, and several others were divested of their nectariferous appendages. These inflorescences subsequently flowered and produced fruits. But how could the flowers form fruits if the Marcgraviaceae are protandrous, as maintained by Delpino and others? Obviously there were three possibilities to be considered in this connection: (*a*) that the flowers were cross-pollinated by small insects which worked their way into the bags through small openings; (*b*) that the fruits were abnormal and did not contain viable seeds; and (*c*) that the flowers were self-fertile. The first supposition did not appear to be a particularly reasonable one, since certain of the inflorescences (both of the bagged and unbagged specimens) were without their hypothetical attracting organs, *i.e.*, nectaries. Furthermore, when certain of the inflorescences were in flower, there were no other flowering vines within a radius of several miles.[4]

A detailed study of numerous inflorescences at different stages of maturity revealed the fact that dehiscence occurs within the calyptriform corolla. The stamens are so arranged (Pl. XXIV, fig. 7) that the stigma is coated with a thick layer of viscous pollen before the protecting capsule falls off. This layer of pollen persists, and may be found adhering to the stigmatic surface on old fruits. Stamens examined just after the corollas have dropped are found to be more or less completely devoid

[4] The specimens of *M. cuyuniensis* occurred at infrequent intervals along the widely separated banks of the Cuyuni River, so that there were only a comparatively limited number of individuals in the vicinity of Kartabo. All these plants were carefully located and visited every morning and evening. By observing the deciduous corollas it was possible to determine what vines had flowered during a particular period.

of pollen and rapidly to become deciduous. As shown in figure 10, the multilocular ovary contains a large number of ovules, only a portion of which produce embryos (figs. 5, 8). The remaining ovules, presumably the unfertilized portion, undergo a curious metamorphosis or process of enlargement. Their outer integument becomes greatly thickened by radial elongation of its constituent cells, which contain a reddish or amber-colored, amorphous substance (fig. 8). The proportion of these aborted ovules varied considerably in different fruits, but was no higher in the bagged specimens than in those which were unprotected. In fact, the former frequently contained more embryos or viable seeds than the latter. In other words, *M. cuyuniensis*, instead of being protandrous and cross-pollinated, appears to be self-pollinated and practically cleistogamous.

(4)

The objection may be raised at this point that, in dealing with *M. cuyuniensis*, I was concerned with an abnormal or aberrant representative of the genus Marcgravia, and that the typical, day-flowering species are protandrous and cross-pollinated by birds. *Marcgravia purpurea*, which belongs in an entirely different section of the genus, flowers during the daytime, and therefore may be considered to be significant in this connection. Although I was obliged to leave the Kartabo Station before this species flowered, Miss Anna H. Taylor and Dr. and Mrs. Alfred Emerson very kindly consented to watch for the flowering season, and were able to make a number of important observations. I have already referred to the fact that "a humming bird, believed to be the species *Topaza pella* or the long-tailed, crimson Topaz, visited a flower in bloom and sucked nectar from the nectary." However, the bird did not approach the inflorescence from *below*, but "hovered from the *top*, dipping its slightly curved or straight bill of medium length into the nectary for a short distance." In *M. purpurea*, as in *M. cuyuniensis*, dehiscence occurs within the calyptriform corolla, and at the time when the capsule falls the stigma is already coated with a thick layer of pollen. Furthermore, the stamens show a pronounced tendency to wither, and to drop off with the deciduous capsules. Dr. Emerson states:

> The caps split at the base and work slowly off. When they fall, they often carry a large number of stamens with them. In a few cases, when the caps were about halfway off, we could see that many of the stamens had withered at the base and would very likely fall with the cap. The pistil is covered with pollen at the time that the cap falls.

Evidently the day-flowering *M. purpurea* is self-pollinated like the night-flowering *M. cuyuniensis*.

Discussion

Such facts as these raise the question whether the Marcgraviaceae are protandrous and whether their curious nectariferous appendages are adap-

tations to insure cross-pollination. Although the inflorescences of certain Marcgraviaceae are known to be visited at times by insects and birds, there is no reliable evidence to indicate that these animals actually are concerned in the pollination of the flowers. Statements to the effect that certain species are entomophilous or ornithophilous are based upon purely teleological inferences, rather than upon detailed field observations and carefully planned experimental controls. Furthermore, the prevailing view that the Marcgraviaceae are protandrous may be traced back to Delpino (1869), whose conclusions appear to have been derived, not from the study of living plants, but from the examination of herbarium material and from Martius' figures of certain species of Ruyschia and Norantea.

It is essential, therefore, that various species of Norantea, Ruyschia, Souroubea, and Marcgravia be critically studied in order to determine (1) whether any of the Marcgraviaceae are protandrous, and (2) whether the insects and birds which visit the nectaries actually are concerned in cross-pollinating the flowers.

Delpino (1874), Belt (1874), Kerner (1876), and certain of their contemporaries were of the opinion that extra-floral nectaries are adaptations for attracting insects or other animals. The theories of these investigators have been severely criticized, if not actually demolished, by Rettig (1904), von Üxküll-Güldenbrandt (1907), von Ihering (1907), and others, and it must be admitted that biologists are still as ignorant as they were in the days of Linné concerning the true function of the extra-floral nectaries and the so-called food-bodies of plants. Therefore, it is to be emphasized, in conclusion, that the hypophyllous glands and nectariferous appendages of the Marcgraviaceae, and extra-floral nectaries and "food-bodies" in general, deserve to be studied intensively along physiological lines.

Conclusions

1. Although the inflorescences of Marcgraviaceae are visited at times by insects and birds, there is no reliable evidence to indicate that these animals actually are concerned in the pollination of the flowers.

2. The highly specialized inflorescences of *Marcgravia umbellata* L., *M. cuyuniensis* spec. nov., *M. purpurea* spec. nov., and of similar species do not appear to be efficient mechanisms for insuring cross-pollination by humming birds. The pedicels and nectaries are so arranged that birds tend to approach the inflorescences from *above* and, therefore, do not become coated with pollen which subsequently is rubbed off on the pistils of other flowers.

3. The flowers of the only two species of Marcgravia, *M. cuyuniensis* and *M. purpurea*, which have been studied in detail in the field, appear to be self-fertile or autogamous, instead of being protandrous and cross-pollinated by birds.

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DESCRIPTION OF PLATES

Plate XXIII

Fig. 1. *Marcgravia purpurea* spec. nov. Foliage and immature inflorescences. Photograph by John Tee-Van. × 5/22.

Fig. 2. *M. cuyuniensis* spec. nov. Section of leaf, showing outlet of hypophyllous gland. × 30.

Fig. 3. *M. purpurea*. General habit of growth. Photograph by John Tee-Van. × 1/30.

FIG. 4. *M. cuyuniensis.* General habit of growth and bagged inflorescences. Photograph by John Tee-Van. × 1/26.

PLATE XXIV

FIG. 5. Same. Section of seed showing embryo. × 42.

FIG. 6. Same. Transverse section of nectariferous appendage, showing two fibrovascular systems. × 30.

FIG. 7. *M. purpurea.* Transverse section of flower bud. × 8.

FIG. 8. *M. cuyuniensis.* Section of fruit, showing seeds (light) and abnormal ovules (dark). × 26.

FIG. 9. Same. Transverse section of nectariferous appendage, showing outlets from glandular tissue and rudimentary flower bud. × 9.

FIG. 10. Same. Transverse section of flower bud, showing parietal placentation. × 6.

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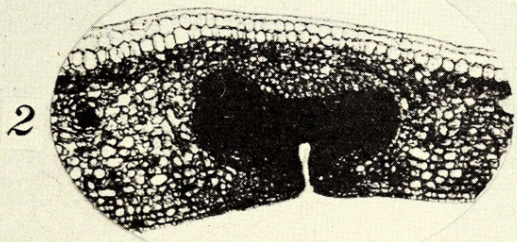

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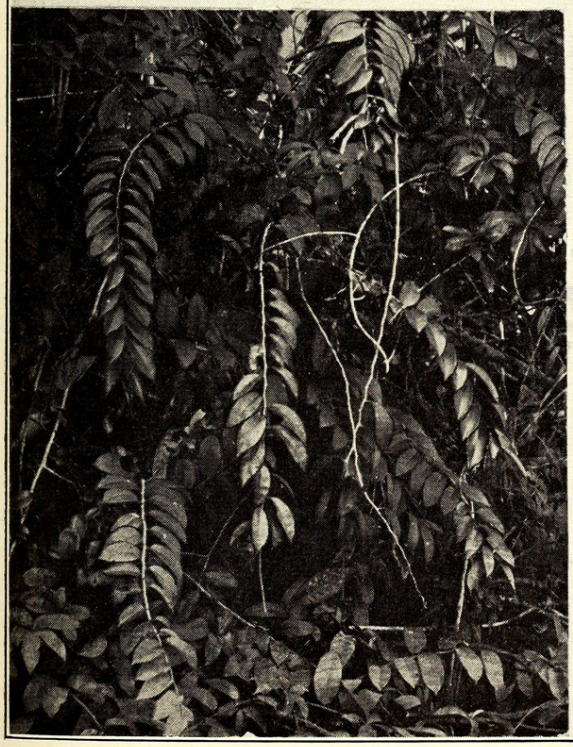

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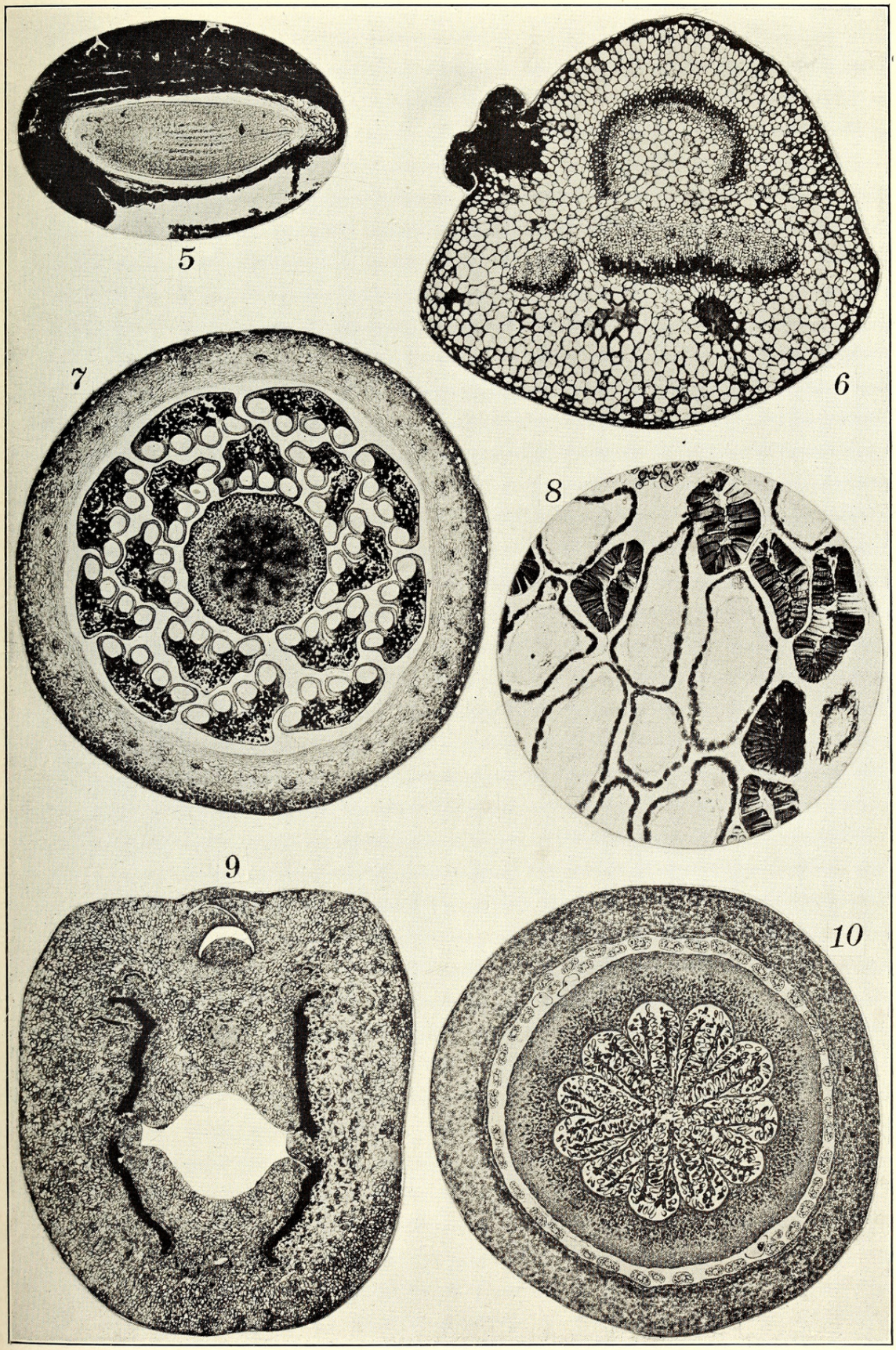

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