

THE GENERA OF OROBANCHACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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OROBANCHACEAE Ventenat, Tabl. Règne Vég. 2: 292.

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(BROOMRAPE FAMILY)

Annual or perennial, root-parasitic, achlorophyllous herbs, often fleshy, with 1 to several flowering shoots arising from a more or less thickened base,² pubescent with glandular or sometimes also nonglandular hairs. Leaves reduced to scales, alternate, the upper passing imperceptibly into bracts. Inflorescence racemose or spicate, or flowers rarely solitary. Flowers perfect, zygomorphic, hypogynous, axillary to bracts, with or without bractlets, long-pedicelled to sessile. Calyx persistent, synsepalous, nearly actinomorphic to strongly zygomorphic, with 1–5 lobes or teeth. Corolla sympetalous, tubular, the limb mostly 2-lipped, the upper lip 2-lobed to entire, the lower usually 3-lobed. Androecium of 4 didynamous stamens inserted on the tube of the corolla and alternate with its lobes; filaments elongate to very short, included or exserted; anthers dorsifixed, with placentoids, 4-sporangiate, bilocular at maturity, the locules dehiscing lon-

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I am indebted to Dr. Wood for his careful review of the manuscript and for other aid always so unstintingly given; to Dr. B. L. Burtt for comments on parts of the manuscript; to Dr. Y. D. Tiagi for an English summary of his 1962 Russian paper on floral anatomy of certain Orobanchaceae and Scrophulariaceae and for permission to quote from this summary; and to the curators of the herbaria who responded to my request for data on and specimens of southeastern Orobanchaceae. The illustrations were made by Virginia Savage (FIGURE 1), and by Sydney B. Devore and Diane C. Johnson (FIGURE 2) from dissections by Dr. Wood. Specimens for the illustrations were collected for the Generic Flora of the Southeastern United States by Dr. Wood and Dr. K. A. Wilson, Mr. R. J. Eaton, and myself.

²I am aware of no acceptable (to me) morphological term to apply to the swollen base of the plant of *Epifagus* or *Orobanche* or to that — seemingly quite different — of *Conopholis*. For terms such as "tuber," "tubercle," and "gall," my enthusiasm knows bounds.

gitudinally; pollen triaperturate or rarely nonaperturate. Gynoecium syncarpous, the carpels 2 or rarely 3; stigma simple, variable, often capitate, crateriform, or bilamellate; style single, elongate, included or exerted; ovary usually unilocular, with 4 or rarely 5 or 6 [2 or 3] parietal placentae; ovules many, unitegmic, tenuinucellar, mostly anatropous; embryo sac development normal (*Polygonum* type); endosperm *ab initio* cellular, with terminal haustoria. Fruit a 2- or rarely 3-valved capsule, typically dehiscing anteroposteriorly, the valves usually lateral, each bearing 2 [1] placentae; seeds numerous, endospermous, with a minute undifferentiated embryo. TYPE GENUS: *Orobanche* L.

The Orobanchaceae comprise about 150 species in 17 genera (14 recognized by Beck-Mannagetta; three — *Mannagettaea*, *Necranthus*, and *Tienmuia* — described since). In the conterminous United States four genera occur; three of these, represented by four species, are found in the Southeast.

A majority of the genera and about 90 per cent of the species of Orobanchaceae are native to the Old World. *Conopholis*, *Epifagus*, and *Kopsiopsis* are confined to the New World; *Boschniakia* and *Orobanche* are native in both hemispheres. The family is primarily one of the North Temperate and warm zones. Only about 10 per cent of the species occur in the tropics; only one species reaches the arctic.

Orobanchaceae are one of only about a dozen families of angiosperms in which the parasitic habit is known. They are the largest family of holoparasitic flowering plants. The range of hosts is large, including both woody and, more commonly, herbaceous species; both gymnosperms (rarely) and angiosperms; monocots and dicots. Reports of Orobanchaceae on ferns require verification. Some Orobanchaceae are confined to a single host species or genus; at the other extreme, some parasitize many species and genera, especially Compositae, Labiatae, and Leguminosae.

One earlier worker (Wiesner) claimed to have detected chlorophyll in *Orobanche*, but modern studies, utilizing electron microscopy (Laudi; Laudi & Albertini) and chromatography (Baccarini & Melandri; cf. *Orobanche*) found this pigment to be completely lacking in *Orobanche* and *Lathraea*. There seems little doubt that Orobanchaceae are achlorophyllous.

It is generally assumed that seeds of Orobanchaceae germinate only in the presence of stimulants produced by roots of the host plant — a phenomenon of obvious advantage to the parasite. However, the need for host-stimulants has been demonstrated only in *Orobanche*; such work remains to be done with other orobanchaceous genera. In *Orobanche*, not one but a complex of substances is involved. Some of these have been characterized chemically, but their structure is undetermined. Production of the substances is most active in that region of the root apex where the cells are undergoing and completing their growth in length. The substances may diffuse into the soil for a distance in excess of 1 cm. It would appear that many *Orobanche* seeds within this zone of diffusion

are stimulated to germinate but are unable to form a parasitic attachment because their radicles usually do not exceed 2 mm. in length. The "axiom" that host-stimulants are always required for germination of *Orobanche* seeds was recently called into question by Krenner, who reported that *fresh* seeds of *O. cumana* germinated in plain water in fair numbers. After overwintering, however, the seeds germinated only in the presence of host root exudates.

The embryo of members of the Orobanchaceae is quite undifferentiated and may consist of as few as 45 cells. Its proximal end gives rise to the radicle. After germination of the seed and subsequent penetration of the host by the primary haustorium, the part of the seedling outside the host root enlarges to form the small, so-called "tubercle." At the apex of the "tubercle," which corresponds to the distal end of the embryo, is the plumule. From the proximal part of the "tubercle" secondary roots may arise. Continued enlargement of the "tubercle"—often incorporating tissues of the host, which are stimulated to abnormal growth—may result in a large, rather regularly shaped "tuber" (e.g., *Epifagus*) or in a large, misshapen "tuber" (e.g., the "gall" of *Boschniakia* and *Conopholis*). The "tubercle" in some species enlarges but little, the bulk of the subterranean part of the plant being secondary roots.

Parasitic haustoria in Orobanchaceae are of two kinds. The primary haustorium, terminal in origin, develops from direct transformation of the radicle after it reaches the host root. Secondary haustoria arise laterally from secondary roots of the parasite following contact of these roots with those of the host. Secondary roots do not always bear haustoria. There is no evidence of phloem in the haustoria, the vascular systems of host and parasite being connected by a slender strand of xylem that is sometimes irregular or even double (Kuijt). In *Orobanche*, many of the distal cells of the primary haustorium are said to be multinucleate.

The roots of *Orobanche* are exogenous, but "they are unmistakably roots" (Kuijt). In contrast, those of *Epifagus* are endogenous. *Conopholis* produces no roots.

The gynoecium of most Orobanchaceae (the "Orobanchaceae bicarpelatae" of Beck-Mannagetta), including those of southeastern United States, has traditionally been interpreted as consisting of two carpels, with each carpel bearing two placentae displaced from the margin toward the midline of the carpel. Accordingly, each of the resulting four placentae is the product of but one carpel. That *Orobanche* has *four* carpels was first suggested by B. Tiagi & Sankhla, then denied by Guédès in a reaffirmation of the traditional interpretation of the gynoecium, and finally defended and elaborated upon by Y. D. Tiagi. According to Tiagi, *Orobanche* has four carpels, two median and two lateral; each carpel bears a placenta along each margin. The marginal placentae of adjacent carpels are fused, and thus the ovary contains four placentae, each the product of two carpels. Dr. Tiagi interpreted in exactly the same way the gynoecium of *Conopholis*, FAA-preserved specimens of which I sent to him. The gynoecium of *Epifagus* is basically identical to that of *Conopholis* and

Orobanche and so would certainly be regarded by Tiagi as four carpellate also.

Two lines of gynoeceal evolution in the Orobanchaceae are recognized by Y. D. Tiagi. In one line, exemplified by *Boschniakia*, the number of carpels is reduced from four to two. In the other line, exemplified by *Aeginetia*, *Cistanche*, and *Orobanche*, all four carpels are retained, but the lateral ones are smaller and are devoid of midrib bundles. It is unfortunate that Tiagi's scheme does not account for those species of Orobanchaceae (the "Orobanchaceae tricarpellatae" of Beck-Mannagetta) that have six placentae. Are these six-carpellate?

The relationships of Orobanchaceae are controversial. Three points of view are held: the broomrapes are most closely related to the (1) Scrophulariaceae, (2) "Solanaceae and allied taxa" (Y. D. Tiagi), and (3) Gesneriaceae. Also questioned is the maintenance of Orobanchaceae as a separate family.

The majority of workers favors a close relationship between Orobanchaceae and Scrophulariaceae. Boeshore concluded that these taxa form a continuous morphological and physiological series "from non-parasitic through semi-parasitic Scrophulariaceae to the most degraded parasites of the family [e.g., *Striga orobanchoides*, *Harveya*, *Hyobanche*], and that these again show direct continuity with the still more degraded and condensedly parasitic types of Orobanchaceae" and that the Orobanchaceae and Scrophulariaceae, "alike logically and biologically . . . should be treated in continuous descending series from the highest to the most degraded genera."

After a study of the stomatal apparatus of various heterotrophic flowering plants, Linsbauer & Ziegenspeck concluded that *Orobanche* is the culmination of an evolutionary series beginning with nutrient-salt parasites, such as *Striga*, among the Scrophulariaceae-Gerardiaceae [Buchneraeae].

On embryological grounds, relationship between Orobanchaceae and Scrophulariaceae was first suggested by Schnarf. Several years later Glišić pointed out that the two families are so similar embryologically that they could well be united. More recently, B. Tiagi (1963) concluded, again on the basis of embryology, that the Orobanchaceae are "derived from the family Scrophulariaceae (Rhinanthoideae) through forms like *Striga orobanchoides*."

In anther structure, certain Orobanchaceae and certain parasitic Scrophulariaceae are similar in that one longitudinal half of the anther has become reduced or otherwise modified. Some of these genera were placed by Livera in his proposed family Aeginetiaceae, distinguished mainly by characteristics of the anthers: "Of the two anther cells [i.e., halves] one only is fertile, the other either wanting . . . or in the form of a spur. . . ." Kuijt suggested that, on the basis of anther evolution and "other evolutionary trends, there appear to be no serious objections to the possibility that *Christisonia*, and perhaps even *Aeginetia* [both of the Orobanchaceae], are derivatives of *Harveya* [Scrophulariaceae]. Should this conception be

valid, the familial status of Orobanchaceae would be further undermined." Nikiticheva found the similar development of microspores and pollen in Orobanchaceae and in certain parasitic Scrophulariaceae particularly striking.

Gynoecial differences are the traditional ones separating Orobanchaceae and Scrophulariaceae, the former having a unilocular ovary with parietal placentae, the latter, a bilocular ovary with axile placentae. Locule number is, however, not an infallible characteristic. Species of *Christisonia* (including *Campbellia*) of the Orobanchaceae may have either a unilocular or bilocular ovary; in at least one species the ovary is bilocular below and unilocular above. Among the Scrophulariaceae a few genera (*Dopatrium*, *Limosella*, *Micranthemum*) have unilocular or imperfectly bilocular ovaries. Members of *Lathraea*, a genus that has been shifted back and forth between Orobanchaceae and Scrophulariaceae, have unilocular ovaries. Arekal reported a tendency toward unilocularity in the distal portion of the ovary of the scrophulariaceous genera *Orthocarpus* and *Aureolaria* ("Gerardia") and concluded that a clear transition from the two-celled [two-locular] ovary of most Scrophulariaceae to the one-celled [one-locular] ovary of Orobanchaceae exists. Levyns found the ovary of *Hyobanche*, a genus of South African Scrophulariaceae, to be imperfectly bilocular, with axile placentation below and parietal above; considering that this "discovery . . . breaks down the principal character separating the families," she included Orobanchaceae in Scrophulariaceae. (The two families had been combined even earlier by Bellini and by Hallier.)

That placentation in Orobanchaceae and Scrophulariaceae is fundamentally different was recently questioned by Y. D. Tiagi, who concluded that in these families placentation is anatomically the same. In *Veronica longifolia* and other Scrophulariaceae studied by him, he found the placentae to be so close together as to appear united, thus making the ovary bilocular, but the placentae were only connivent, each having its own epidermis. In some flowers a gap could be seen between the placentae. Tiagi concluded that placentation in both Orobanchaceae and Scrophulariaceae is parietal.

According to Y. D. Tiagi, "the occurrence of a fundamentally tetracarpellary gynoecium in the family Orobanchaceae must rule out any suggestion of its origin from the Scrophulariaceae," which "have a uniformly bicarpellary gynoecium."³ The similarities between "Orobanchaceae and certain of the Scrophulariaceae can be more logically considered as examples of parallel evolution rather than indicative of relationships. Search for the ancestors of the Orobanchaceae may be better made among the Solanaceae and allied taxa where the multicarpellary condition of the gynoecium is quite often met with."

³ The Scrophulariaceae would perhaps be better characterized as "almost" uniformly bicarpellary. The South African genus *Bowkeria* apparently can be tricarpe-
pellary: Phillips (Gen. So. Afr. Fl. Pl. 669. 1951) describes the ovary as "2-3 cham-
bered" and the capsule as having "3 or 2" valves.

The Orobanchaceae, because of their typically unilocular ovary, have been included by some authors (e.g., Baillon, Eichler, and Warming) as a parasitic offshoot of the Gesneriaceae. The idea of close relationship between these two families has been revived by Crété, who asserted that embryologically the Orobanchaceae and Scrophulariaceae do not have "direct affinities" but that the broomrapes are so closely related to the Gesneriaceae that they could well be united with them. The Orobanchaceae seem especially similar to Gesneriaceae in their accumulation of orobanchin, in their lack of aucubin-like glucosides, and in their high silicic acid content (Hegnauer).

The biology of most Orobanchaceae — their ecology, morphology, development, host relationships, longevity, pollination, dispersal, etc. — is not well known. Even such basic information as host plant is seldom determined and noted by collectors. Orobanchaceae, because of discoloration and brittleness, usually make rather unpleasing exsiccata. The discoloration, at least in *Orobanche*, has been attributed to the oxidation of orobanchoside, a glucoside.

Cleistogamy in the family appears to be a regular feature only in *Epifagus* although subterranean cleistogamous flowers have been reported in *Cistanche*. Peloric flowers are known to occur in *Orobanche*.

Orobanchaceae, especially *Aeginetia* and *Orobanche* but also *Christisonia*, are of economic importance primarily as parasites of various crop plants. A few species are used in folk medicine.

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KEY TO THE GENERA OF OROBANCHACEAE IN THE SOUTHEASTERN UNITED STATES

General characteristics: root parasites lacking chlorophyll; leaves scale-like, crowded to clearly alternate; flowers sympetalous, zygomorphic; stamens 4, epipetalous; ovary superior, 1-locular, with 4 parietal placentae, each bearing many anatropous ovules; fruit capsular; embryo minute, undifferentiated.

- A. Flowers in large part with calyptriform corollas, cleistogamous, sometimes a distal few tubular and chasmogamous. 1. *Epifagus*.
- A. Flowers all with tubular corollas, chasmogamous.
- B. Flowers bibracteolate; calyx split anteriorly, "spathaceous"; stamens exerted. 2. *Conopholis*.

- B. Flowers ebracteolate; calyx split anteroposteriorly or campanulate and 5-cleft to 5-parted; stamens included. 3. *Orobanche*.

1. *Epifagus* Nuttall, Gen. N. Am. Pl. 2: 60. 1818, nom. cons.⁴

Low, puberulent or glandular-puberulent, yellow, black-purple, purple-brown, yellow-brown, or brown, simple or branched annuals. Base of plant an enlarged "tuber" bearing leaf-scales and thick, short, coralloid, usually branched secondary roots. Stem with scattered, alternate leaf-scales. Inflorescence racemose, each flower bibracteolate, short pedicelled. Calyx obliquely broadly campanulate, nearly equally 5-toothed to 5-lobed. Cleistogamous flowers: usually fertile; corolla calyptriform, persistent for a time on the enlarging capsule, 4-lobed, the upper lobe internal, entire to slightly notched; stamens included, the filaments very short, the anthers at first free but becoming hard and firmly adnate to the stigma, anther halves somewhat divergent, mucronulate basally, those of adjacent stamens becoming connate; style declined anteriorly, very short, included; stigma capitate, slightly bilobed; style, stigma, corolla, and stamens deciduous as a unit. Chasmogamous flowers: usually sterile; corolla tubular, somewhat laterally compressed, usually slightly arcuate, often widening distally, soon deciduous, 4-lobed, the upper lobe internal, erect, rounded, entire or slightly notched, the lower lobes erect to somewhat spreading, acute; stamens included to slightly exserted, the filaments elongate, anthers free, anther halves somewhat divergent, mucronulate basally; style elongate, soon deciduous, usually exserted; stigma capitate, slightly bilobed. Capsule somewhat compressed laterally, thickest below the middle, more or less reniform in lateral view but with a truncate base, 2-valved or rarely 3-valved, dehiscing anteroposteriorly. Seeds minute, very numerous, narrowly ovoid to ellipsoid; testa finely reticulate. (*Leptamnium* Raf.) TYPE SPECIES: *E. americanus* Nutt., nom. illeg. = *E. virginiana* (L.) Bart. (*Orobanche virginiana* L.). (Name from Greek, *epi*, upon, and Latin, *fagus*, beech, in allusion to the host plant.) — BEECHDROPS, CANCER-ROOT.

A genus of one North American species. *Epifagus virginiana* (L.) Bart. (*Leptamnium virginianum* (L.) Raf.), beechdrops, ranges from Cape Breton and Prince Edward islands south to northern Florida and west to eastern Texas, Arkansas, southeastern Missouri, southern Illinois, Indiana, eastern Wisconsin, and the upper peninsula of Michigan. Isolated occurrences, separated from the main range by at least 550 miles, are in the highlands of Tamaulipas and Hidalgo. The ranges of beechdrops and its host trees, American beech (*Fagus grandifolia* var. *grandifolia*), and Mexican beech (*F. grandifolia* var. *mexicana*), are more or less identical, although beechdrops has not yet been found in Oklahoma or in Puebla.

Fagus grandifolia was not reported from Mexico until 1939; *Epifagus*, not until 1950. These species share, with a number of others, a charac-

⁴ Conservation superfluous; see Rickett & Stafleu, *Taxon* 9: 113. 1960.

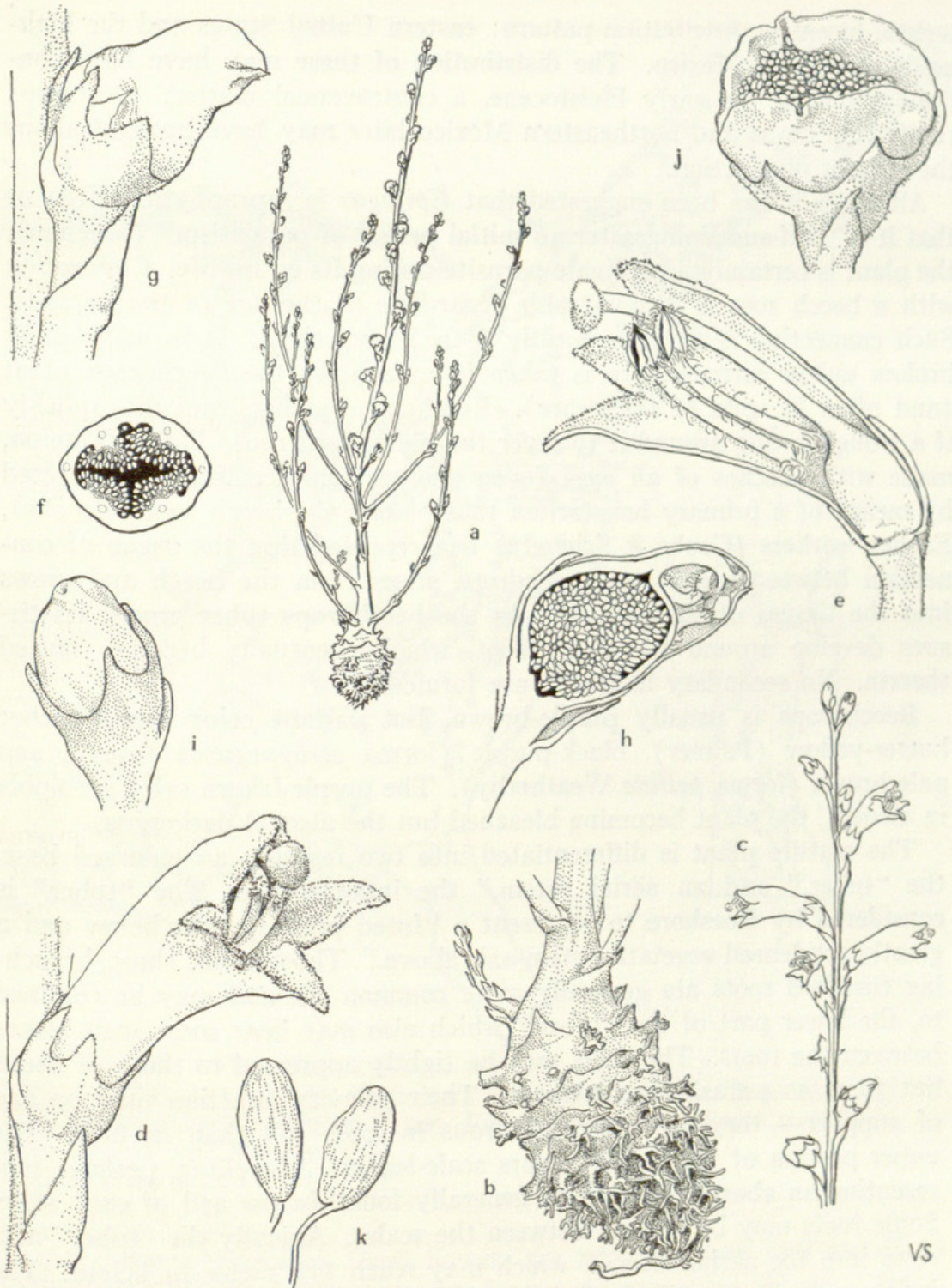


FIGURE 1. *Epifagus*. a-k, *E. virginiana*: a, plant with fruits, cleistogamous flowers, and buds, $\times 1/3$; b, base of plant, showing coralloid roots below, leaf-scales with buds or branches above — note portion of small root of *Fagus* to which plant is attached, $\times 1$; c, tip of flowering branch with chasmogamous flowers above and two cleistogamous ones below, the lowermost flower with partly developed fruit, the corolla already fallen, $\times 1$; d, chasmogamous flower, $\times 5$; e, same, with half of calyx and corolla and two stamens removed — note nectary at base of ovary on abaxial side, $\times 5$; f, diagrammatic cross section of ovary, showing placentation, $\times 10$; g, cleistogamous flower, the calyptriform corolla being pushed off by growth of ovary, $\times 5$; h, same, in vertical section — note developing seeds, $\times 5$; i, nearly mature fruit seen from abaxial side, $\times 5$; j, open capsule with seeds, abaxial side at left, $\times 5$; k, two seeds, $\times 40$.

teristic bicentric distribution pattern: eastern United States and the highlands of eastern Mexico. The distribution of these may have been continuous during the early Pleistocene, a controversial matter. Decreased rainfall in Texas and northeastern Mexico later may have brought about the present disjunction.

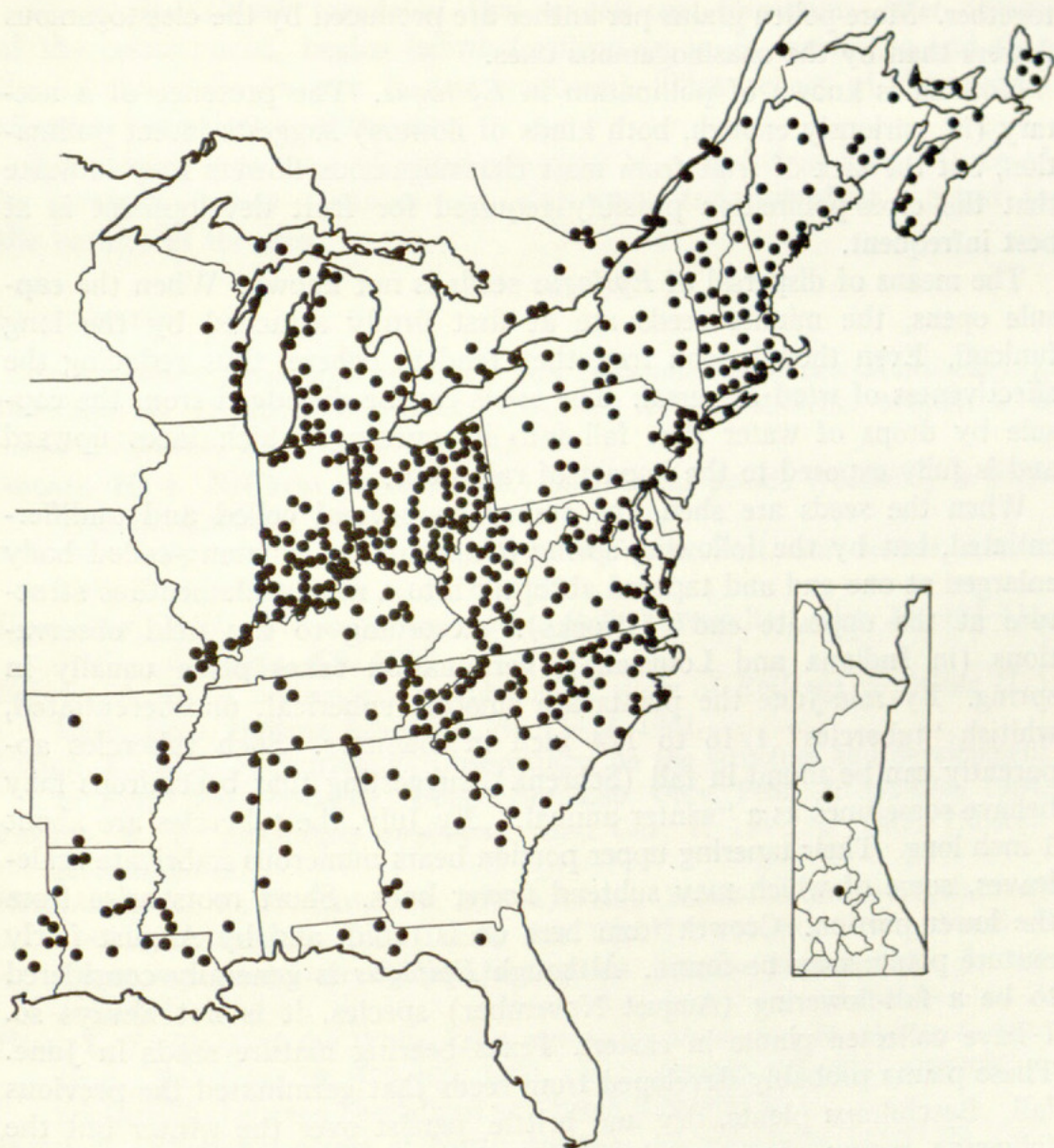
Although it has been suggested that *Epifagus* is saprophytic (Hill) or that it is "self-sustaining after an initial period of parasitism" (Meehan), the plant is certainly an obligate parasite during its entire life. Connection with a beech root is demonstrable regardless of the age of the parasite. Such connection is to roots mostly 1 to 3 mm. thick. It is most easily broken unless extreme care is taken in excavating the beechdrops plant (and often in spite of such care). Beechdrops withers and dies quickly if a trough is dug around it to sever the parasitized root. Parasitic union, made with beeches of all ages (even one-year-old seedlings), is effected by means of a primary haustorium that pierces the beech root (Brooks). Earlier workers (Cooke & Schively) had reported that the organ of connection between beech and beechdrops arises from the beech and grows into the tissues of the parasite. As the beechdrops tuber grows, its tissues develop around the beech root, which eventually becomes buried therein. No secondary haustoria are formed.

Beechdrops is usually purple-brown, but variant color forms occur; butter-yellow (Palmer), black-purple (forma *atropurpurea* Pease), and pale brown (forma *pallida* Weatherby). The purple-brown color is soluble in alcohol, the plant becoming bleached but the alcohol darkening.

The mature plant is differentiated into two regions: an enlarged base, the "tuber," and an aërial "stem," the inflorescence. The "tuber" is considered by Boeshore to represent a "fused primary root below and a greatly condensed vegetative stem-axis above." The curious, short, branching coralloid roots are generally more common on, and may be confined to, the lower part of the "tuber," which also may bear some scale-leaves between the roots. The roots may be tightly appressed to those of beech but form no parasitic attachment. Their primary function may be one of support—they are more numerous in loose soil than in firm. The upper portion of the "tuber" bears scale-leaves. A swelling, perhaps representing an abortive branch, is generally found in the axil of each scale. Some roots may be present between the scales. Apically the "tuber" narrows into the aërial "stem," which may reach 1/2 meter in height. The inflorescence is usually branched but may be simple. All branches are axillary to scale-leaves. Some additional branches may arise from the apex of the "tuber."

Stomata are abundant and widespread on the aërial parts, even including the style. The rapid wilting of beechdrops after it is severed from the host root is probably due largely to excessive transpiration through the numerous stomata.

Cleistogamous flowers are the first to appear and are usually more numerous than chasmogamous ones. They may even develop underground. Some plants, or even whole colonies, may bear no chasmogamous



MAP 1. Documented distribution of *Epifagus virginiana*. Inset shows north-eastern Mexico and southern Texas. For distribution of *Fagus grandifolia* see Jour. Arnold Arb. 52: 169. 1971.

flowers. When produced, these flowers are proterogynous and are distal on the branches that have been producing cleistogamous flowers. Above the chasmogamous flowers one to several cleistogamous flowers usually occur. The two types of flowers are often connected by some of intermediate morphology. Cleistogamous flowers generally are followed by good fruits, and chasmogamous flowers are not, but exceptions occur.

In young cleistogamous flowers the anthers are free from each other and from the stigma. Later, but still in early bud, the anthers become firmly connate to each other and adnate to the stigma. The adnation apparently is caused, at least in part, by the many pollen tubes that grow through the anther wall into the stigma, binding these structures

together. More pollen grains per anther are produced by the cleistogamous flowers than by the chasmogamous ones.

Nothing is known of pollination in *Epifagus*. The presence of a nectary (in, curiously enough, both kinds of flowers) suggests insect pollination, but the lack of fruit from most chasmogamous flowers may indicate that the cross-pollination possibly required for fruit development is at best infrequent.

The means of dispersal of *Epifagus* seeds is not known. When the capsule opens, the minute seeds are at first firmly attached by the long funiculi. Even though soon free, they tend to cohere, thus reducing the effectiveness of wind dispersal. The seeds can be dislodged from the capsule by drops of water that fall into its opening, which faces upward and is fully exposed to the impact of raindrops.

When the seeds are shed, the embryo is several celled and undifferentiated, but by the following spring it appears as a "many-celled body enlarged at one end and tapered abruptly into a nearly filamentous structure at the opposite end" (Brooks). According to my field observations (in Indiana and Louisiana), germination takes place usually in spring. By mid-June the plants are smooth, spherical, undifferentiated, whitish "tubercles" $1/16$ to $1/4$ inch in diameter. Such tubercles apparently can be found in fall (Schrenk), suggesting that beechdrops may behave sometimes as a "winter annual." By July, the tubercles are about 1 inch long. Their tapering upper portion bears numerous imbricate scale-leaves, some of which may subtend flower buds. Short roots arise from the lower portion. Growth from here on is rapid, and by August fairly mature plants may be found. Although *Epifagus* is generally considered to be a fall-flowering (August–November) species, it is not always so. I have collected plants in eastern Texas bearing mature seeds in June. These plants probably developed from seeds that germinated the previous fall. Beechdrops plants, dry and brittle, persist over the winter but the following spring show no sign of life, their tuberous bases being in various stages of decay. There seems little doubt that *Epifagus* is an annual plant.

The vascular system is a dictyostele, consisting of usually bicollateral vascular bundles, with the phloem exceeding the xylem in extent. In the inflorescence the bundles are regularly arranged in a ring, but in the tuber they show "a most confused and irregular arrangement, running in all directions and planes apparently" (Cooke & Schively). However, Brooks noted, in the tuber, that the phloem "follows a very irregular branching pattern" but "the xylem masses . . . are arranged in a ring." The bast fibers are greatly developed in the inflorescence, giving it its stiff and elastic nature. Brooks found no evidence of a cambium in *Epifagus*.

The roots, called "grapplers" by Fergus, have neither root caps nor endodermis. The cortical parenchyma cells closest to their small central vascular bundle have greatly thickened cell walls; it is these cells that account largely for the stiffness and rigidity of the roots.

Cooke & Schively reported that endosperm formation, after fusion of the polar nuclei, begins before fertilization in *E. virginiana* and that the second male gamete is non-functional. This report of "precocious albumen" requires confirmation.

Beechdrops was once of some notoriety as a medicinal herb. Three of its common names — cancer-root, clap-wort, and flux-plant — attest to the variety of its uses.

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2. *Conopholis* Wallroth, Orobanches Generis Diaskeue 78. 1825.

Low, glabrous to glandular-pubescent, cream, yellow-brown, or brown, simple or very rarely branched perennials. Base of plant an enlarged irregular "tuber" ("gall") covered with thick porous bark; secondary roots lacking. Stem densely covered with imbricate leaf-scales below, these becoming scattered and alternate above. Inflorescence racemose, each flower with [1] 2 bractlets [or none], short- to long-pedicelled. Calyx tubular, split anteriorly ("spathaceous"), 2- or 4-5-toothed or -lobed. Corolla tubular, frequently arcuate, persistent for a time on the enlarging capsule, 2-lipped, the upper lip external, erect, rounded, notched or rarely 3- or 4-lobed, the lower lip erect to spreading, 3-lobed or rarely 1- or 2-lobed, the lobes rounded to acute. Stamens exserted; anthers free, anther halves somewhat divergent, mucronulate basally. Style elongate, persistent or deciduous, included or exserted; stigma capitate, slightly depressed centrally to horizontally furrowed. Capsule ovoid to ellipsoid, dehiscing irregularly or anteroposteriorly. Seeds small, numerous, triangular, quadrangular, or rhomboidal; testa smooth, marked with darker lines forming a reticulum. TYPE SPECIES: *C. americana* (L.) Wallr. (*Orobanche americana* L.). (Name from Greek, *conos*, cone, and *pholis*, scale, the appearance of the plant suggesting a pine cone — especially to those who have never seen a pine cone.) — SQUAW ROOT.

A North American genus of two allopatric species. *Conopholis americana*, $2n = 40 \pm 2$, squaw-root, ranges from Nova Scotia to Upper Michigan and Wisconsin south to northern Florida. The similar *C. alpina* Liebm., ranging from Arizona and New Mexico south to Panama, is distinguished from *C. americana* by the greater length-width ratio of its leaf-scales and bracts, by its denser and thicker inflorescence, and by its style being usually deciduous from the fruit. Haynes, the recent monographer of *Conopholis*, recognized two varieties of *C. alpina* — var. *alpina* and var. *mexicana* (Gray ex Watson) Haynes — distinguished by range, texture of leaf-scales, and vestiture. *Conopholis americana* and *C. alpina* are so closely related that they could well be considered conspecific. However, Haynes preferred to treat the eastern and western populations as two species because of their reproductive isolation, their morphological

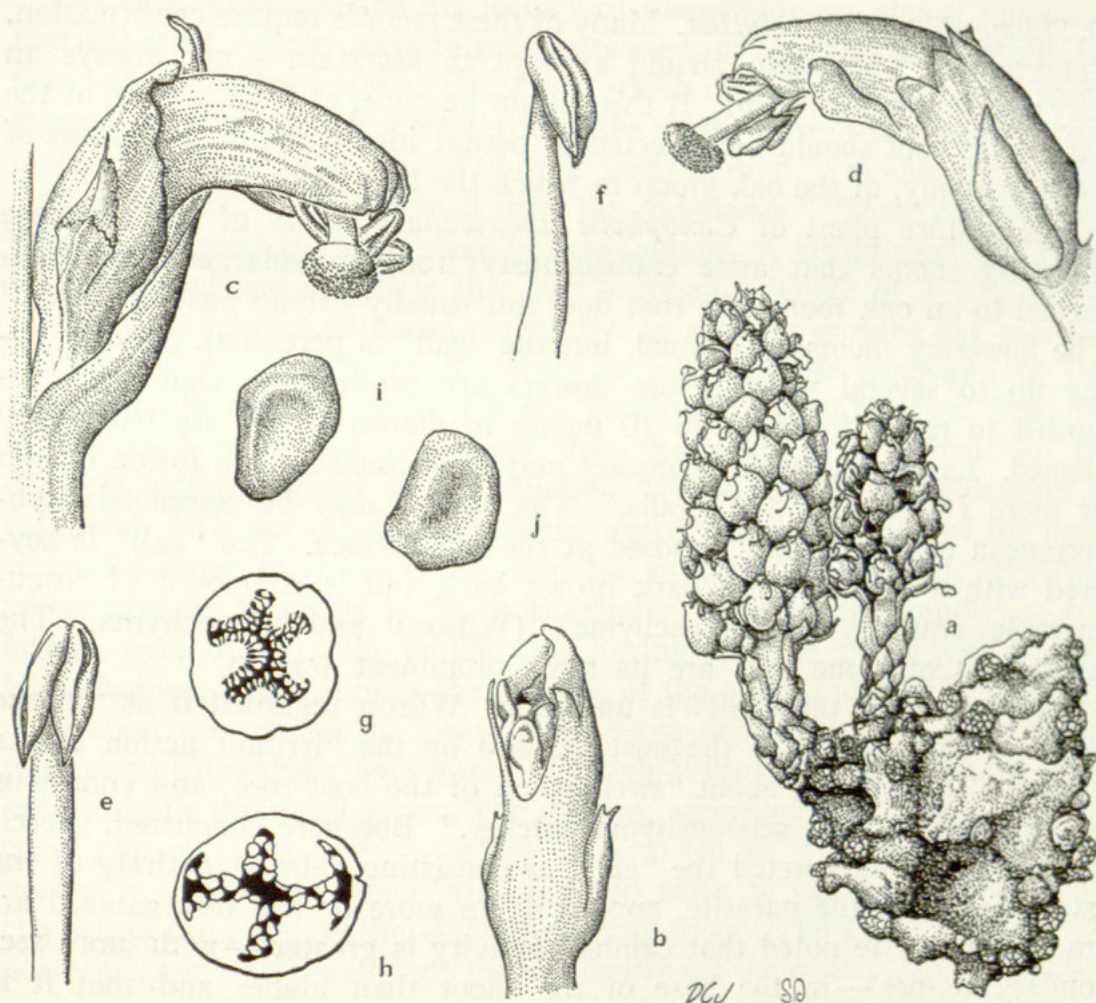


FIGURE 2. *Conopholis*. a-j, *C. americana*: a, fruiting plant detached from root of *Quercus rubra*, which was to right — note scaly buds on "tuber," $\times 1/2$; b, bud, from below to show calyx with two bractlets and aestivation of petals, $\times 4$; c, d, lateral views of two flowers, $\times 4$; e, f, two stamens, $\times 8$; g, diagrammatic cross section of ovary with five placentae, $\times 6$; h, diagrammatic cross section of fruit with four placentae, $\times 2$; i, j, two seeds, $\times 12$.

distinctness, and their apparent host specificity. So far as is known, the two taxa approach no closer than about 800 miles to each other. The oaks available as hosts for the two species differ. Only *Quercus Muehlenbergii* and *Q. virginiana*, neither known to be parasitized by *Conopholis*, occur sympatrically with both species of the genus. Whether one species of *Conopholis* could parasitize the hosts of the other is not known.

While genera other than *Quercus* have been reported to be hosts for *Conopholis*, in all cases where the parasitized root has been traced to its origin, it has been found to belong to an oak. Boeshore and Percival indicated the hosts to be members of the red oak group (*Quercus* subg. *ERYTHROBALANUS*), but Doak reported that *Q. bicolor*, one of the white oaks (subg. *QUERCUS*), was parasitized. According to literature and herbarium label data, *C. americana* parasitizes members of both oak groups, including *Q. alba*, *Q. bicolor*, *Q. borealis* (= *Q. rubra*), *Q. falcata*, *Q. hemispherica* (= *Q. × laurifolia*), *Q. marilandica*, *Q. nigra*, *Q. petraea* (in the Botanical Garden at Copenhagen; see B. Tiagi, 1965), *Q. rubra*,

Q. Shumardii, and *Q. velutina*. Many of these records require confirmation. Collectors of *Conopholis* should attempt to ascertain—not always an easy task—the host plant. If this cannot be done, at least a piece of the parasitized root should be collected to permit identification, by means of wood anatomy, of the oak group to which the host belongs.

The mature plant of *Conopholis americana* consists of one or more flowering shoots that arise endogenously from an enlarged “gall” attached to an oak root. The root does not usually extend past the “gall.” The flowering shoots are annual, but the “gall” is perennial, perhaps living up to several years before flowers are produced. “Galls” are recorded to range from 0.5 to 10 inches in diameter and are irregularly shaped. Large conglomerate masses may be formed by the fusion of two or more (to at least 18) “galls.” The “galls” may be completely subterranean or be partially exposed at the soil surface. The “gall” is covered with a thick, porous dark brown bark and is composed of “innumerable granules of sclerenchyma” (Wilson) and parenchyma. The aggregates of stone cells are its most prominent feature.

The nature of the “gall” is uncertain. Wilson regarded it as “in the main, a modification of the host” caused by the “irritant action of the parasite” that brings about “swelling up of the host root, and enormous multiplication of its sclerenchyma patches.” Boeshore concurred. Percival, however, interpreted the “gall” as consisting “almost entirely of the stem tissues of the parasite, apparently in more or less disorganized arrangement.” He noted that cambial activity is greater—with more secondary tissues—in the base of the shoot than higher and that it is greater yet in the “gall.” In the “gall” there is a pronounced increase in the amount of secondary tissue, resulting from “a very active cambium which is sufficient to explain the excessive hypertrophy.” The vascular bundles can be traced directly from the shoot through the “gall” to their junction with the xylem of the host root.

Wilson noted stomata on the epidermis of the shoot but none on the leaves. The stomata were apparently vestigial and the guard cells functionless, the stomata being either open or closed (Percival). Boeshore found some misshapen and poorly developed stomata on the outer surface of the upper leaves. The leaves are devoid of palisade tissue.

Little is known concerning pollination in *Conopholis*. Haynes observed a bumblebee visiting a flower of *C. americana* in Georgia. He reported only one additional pollination record, based on herbarium label data, for the genus: bumblebees on *C. alpina* var. *alpina* in Tamaulipas. Evidence that *Conopholis* may, at least occasionally, be self-pollinated in the bud was found by Haynes: a slide of pollen from dehiscent anthers from a bud of an alcohol-preserved plant of *C. americana* showed that about one-half of the pollen grains had already germinated.

The seeds of *Conopholis* are large and few relative to those of other Orobanchaceae. Their highly diversified shapes develop as a result of pressure exerted by the enlarging ovules. Double ovules and seeds are frequent. Nothing is known of seed dispersal in the genus.

The early stages in the life history of *Conopholis* are almost unknown. Percival tried various ways to germinate seeds of *C. americana*, both in the field and in the laboratory. His study, which involved about 22,000 seeds, showed negative results except where the seeds were in proximity to oak roots. The embryos of several of these seeds showed "a modification of cell content and absorption of food from the endosperm." These changes may have represented the first stage in germination. A single seed was found to have developed a radicle that had attained a length of 3 mm. before it came into contact with and penetrated an actively growing oak root tip.

The vascular system of the shoot is a dictyostele composed of two (Boeshore, Wilson) or three (Chatin, Percival) rings of bundles. That the inner ring is much less prominent than the others may account for the different interpretations of ring number. Wilson described the bundles as collateral, with the xylem and phloem inverted in the bundles of the inner ring; Boeshore interpreted the bundles as being bicollateral. Percival, whose account probably is the most reliable, regarded the bundles as collateral, with those of the middle ring having inverted xylem and phloem. He identified a cambium in the bundles of the outer and middle rings.

Percival was unable to locate sieve tubes and companion cells in the phloem of *Conopholis americana*, although Wilson had reported the presence of both these cell types. The phloem, according to Percival, is made up of phloem parenchyma — which he regarded as "apparently quite useless as a conductive tissue, the more so since it was often completely crushed in the basal section of the flowering shoot. The xylem vessels were numerous and well developed; they evidently are the main pathways for the conduction of food and water from the host." Percival considered it logical to assume that any *Conopholis* cells could obtain dissolved foods from contiguous cells of the host because of the difference in sap concentration reported by Doak.

An interesting reaction of the host root to *C. americana* is the gradual infiltration of tannin into the root tissues adjacent to the tissues of the parasite. The older a "gall" becomes, the more completely the vascular tissues of the host are infiltrated and plugged until, at length, the "gall" dies and disintegrates, leaving an oak root well protected by tannous deposits against attack by decay-producing organisms.

So far as is known, *Conopholis* is of no economic importance. An extract of the whole plant of *C. americana* is said to possess insecticidal properties.

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3. **Orobanche** Linnaeus, *Sp. Pl.* 2: 632. 1753; *Gen. Pl.* ed. 5. 281. 1754.

Low, glandular-pubescent to nearly glabrous, yellowish to tan, sometimes reddish- or bluish-tinged, simple or branched annuals or perennials. Base of plant slender to enlarged; secondary roots present. Stem covered with imbricate leaf-scales below, these becoming scattered and alternate above. Inflorescence racemose or spicate or rarely of a single flower, each flower ebracteolate [or bibracteolate], sessile to long pedicelled. Calyx campanulate and [4-]5-toothed to [4-]5-parted, or split anteroposteriorly into 2 lateral segments, these entire to 2-lobed. Corolla tubular, more or less arcuate, often marcescent, the lobes subequal to strongly unequal, the limb obscurely to strongly 2-lipped, the upper lip external or internal, notched or 2-lobed, the lower 3-lobed, the lobes rounded. Stamens included; anthers free, anther halves parallel to somewhat divergent, mucronulate basally. Style elongate, usually persistent, included or exserted; stigma variable, commonly crateriform, bilamellate, or 2-lobed. Capsule ovoid to ellipsoid, dehiscing anteroposteriorly, the valves sometimes remaining attached at their tips. Seeds minute, numerous, cylindric, ovoid, or ellipsoid; testa finely reticulate. (Including *Aphyllon* Torr. & Gray in Gray, *Myzorrhiza* Phil., and *Thalesia* Raf.) LECTOTYPE SPECIES: *O. major* L.; see Britton & Brown, *Illus. Fl. No. U. S.* ed. 2. 3: 234. 1913. (Name from Greek, *orobos*, vetch, and *anchein*, to strangle, in allusion to the plants' parasitic habits. — BROOMRAPE.

The largest genus of Orobanchaceae, with about 100 species, a majority (about 90 species of sects. *OROBANCHE* and *TRIONYCHON*) native to Eurasia and Africa, especially the Mediterranean region, about 10 species (sects. *EUANOPLON* and *MYZORRHIZA*) American. Several Old World species are widely distributed weeds. Each of the four sections of *Orobanche* has been accorded generic status by various workers; Beck-Mannagetta's inclusive interpretation of the genus is almost universally accepted today. In the southeastern United States, *Orobanche* is represented by one native and one introduced species, which belong to different sections.

Section *EUANOPLON* (Endl. ex Walp.) Thieret⁵ (§ *Aphyllon* (Torr. & Gray) G. Beck and § *Gymnocaulis* Nutt.), with two species, is characterized by its long-pedicelled, ebracteolate flowers and by its campanulate, subregular, 5-cleft to 5-parted calyx. It is represented in the southeastern United States by *O. uniflora* L. var. *uniflora* (*Aphyllon uniflorum* (L.) Torr. & Gray in Gray; *Thalesia uniflora* (L.) Raf.), $2n = 36, 72$ (in a diploid-parthenogenetic form). The species ranges, in several too confluent varieties, over much of extreme southern Canada (including Newfoundland) and the conterminous United States but is not yet recorded from Manitoba, Saskatchewan, South Dakota, Arizona, New Mexico, and Louisiana. Its habitats include moist to dry deciduous or mixed woods, stream banks, rocky glades, and grassy roadsides; it has been recorded as parasitic on *Artemisia*, *Aster*, *Coreopsis*, *Lithophragma*, *Potentilla*, *Quercus*, *Sedum*, *Solidago*, and *Tellima*.

According to Smith, the roots of *Orobanche uniflora* (rarely present on herbarium specimens) are thick and fleshy and branch freely. He distinguished two kinds of roots: those forming parasitic connections, and the "soil roots," which do not. The soil roots seem functionless in absorption, probably serving as supporting organs. Neither kind of root possesses root hairs or root cap. The vascular tissues are disposed in a diarch or, less often, a triarch arrangement. The phloem exceeds the xylem in extent. Sieve tubes seem to be absent.

The vascular system of the stem is a dictyostele composed of a ring of collateral bundles, with the phloem better developed than the xylem. Sieve tubes are lacking; the phloem consists of "elongated elements with granular contents, which are sometimes nucleated." The xylem consists of "tracheae." Smith could not, with assurance, identify a cambium. He concluded further that the xylem has no conductive function but serves solely to support and strengthen the plant.

Achey recognized two species in sect. *EUANOPLON*, *Orobanche uniflora* and *O. fasciculata* Nutt. Usually rather easily distinguished, the two seem connected by occasional specimens of intermediate morphology. *Orobanche fasciculata* var. *subulata* Goodman, described from Oklahoma, is not easily placed in either species, at least on the basis of herbarium material. A biosystematic study of sect. *EUANOPLON* is a desideratum.

Section *OROBANCHE* (§ *Ospreolen* Wallr.), with about 60 species, is the

⁵ *Orobanche* sect. *Euanoplon* (Endl. ex Walp.) Thieret, comb. nov. *Anoplanthus* sect. *Euanoplon* Endl. ex Walp., Repertorium 3: 480. 1844.

largest section of the genus. It is characterized by its sessile or nearly sessile, ebracteolate flowers and by its calyx, deeply cleft anteroposteriorly into two lateral segments, each of which is entire to two-lobed. It is represented in southeastern United States by an introduced Mediterranean species, *O. minor* Sm., $2n = 38$, collected from several counties in Florida and North Carolina, where it is recorded as parasitizing *Crotalaria*, *Nicotiana*, *Petunia*, and *Trifolium*. Beck-Mannagetta lists many additional host species. *Orobanche minor* has been alleged to be toxic to cattle and goats.

Some work (Holdsworth & Nutman) indicates that *Orobanche minor* does not initiate flowers unless the host has reached the flowering condition. To what extent other broomrapes follow this pattern is not known, although flowering in "several strains" of *Orobanche* occurs on hosts that are in purely vegetative condition (Kribben).

An additional section, *TRIONYCHON* Wallr., characterized by its bibracteolate flowers and its mostly 4-lobed calyx, is represented in the United States by the introduced *O. ramosa* L., $2n = 24$, a Eurasian species that has been collected on *Cannabis* in Kentucky and that may yet be found in the Southeast.

The flowers of *Orobanche* are homogamous or, more rarely, proterogynous. They may or may not secrete nectar. Pollination in some species is by insects, especially Hymenoptera. In other species, the flowers appear to be self-pollinated. The seeds are distributed mainly by wind and by rain wash. They have been shown to pass unharmed through the digestive tract of cattle but subsequently to be rendered inviable during fermentation of the feces.

Chromosome counts are available for members of all four sections of *Orobanche*: *EUANOPLON*, $2n = 36, 72$ (one species); *MYZORRHIZA*, $2n = 24$ (one species); *OROBANCHE*, $2n = 38$ (12 species) or $38, 40$ (one species); and *TRIONYCHON*, $2n = 24$ (three species). Gardé suggested that six is the basic number for the genus and that those species having 38 chromosomes are heteroploids, $6n + 2$.

As angiospermous parasites of agricultural plants, various species of *Orobanche* rank in importance with the witchweeds (*Striga* and *Alectra*, of the Scrophulariaceae) and the dodders (*Cuscuta*, of the Convolvulaceae). Various methods are used to control *Orobanche*. Weeding is effective for infestations of limited extent if it is carried out over the several weeks that broomrape shoots may appear. "Catch crops," plants that serve as hosts for the parasite, may be sown and then, before the parasite has produced mature seeds, be plowed under. "Trap crops," plants that do not serve as hosts but do stimulate the germination of *Orobanche* seeds, have been used with some success. Control with chemicals has shown promise, especially certain hormone-type sprays and soil fumigation with methyl bromide. Biological control with phytophagous insects or parasitic fungi has been suggested. The breeding of *Orobanche*-resistant strains of crop plants is under investigation, especially in *Helianthus*.

Successful use of an extract of *Orobanche crenata* to treat kidney stones has been reported (Ibrahim).

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