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COMPARATIVE SYSTEMATIC ANATOMY

OF THE

PARASITE CASSYTHA (LAURACEAE)

by
Bobby Glenn Beaman

Dissertation submitted to the Faculty of the Graduate School
of the University of Maryland in partial fulfillment
of the requirements for the degree of
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1971

APPROVAL SHEET

Title of Thesis: Comparative Systematic Anatomy of the Parasite Cassytha (Lauraceae)

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ABSTRACT

Title of Thesis: Comparative Systematic Anatomy of the Parasite Cassytha (Lauraceae)

Bobby Glenn Beaman, Doctor of Philosophy, 1971

Thesis directed by: William L. Stern, Professor of Botany

Five species of Cassytha (Lauraceae)--C. ciliolata, C. filiformis, C. glabella, C. melantha, and C. pubescens, were investigated anatomically. Comparative studies were done on mature stems, stem tips, leaves, and both developing and mature haustoria. The mode of parasitism was studied on a variety of host plants ranging from herbaceous to woody. Based on these investigations, there is no anatomical justification for the removal of Cassytha from the Lauraceae into a separate, monogeneric family. To the contrary, there are many points of similarity between Cassytha and other Lauraceae. Direct comparisons of xylem anatomy between Cassytha and other laurels are not made because of the almost total predominance of only primary xylem in the former; however, some interesting points of similarity between the xylem of the two groups are noted. It is suggested that a comparison of the primary xylem of Cassytha and several autotrophic lauraceous genera might be profitable scientifically. The unusual type of secondary growth which occurs in conjunction with haustorial formation in Cassytha is related to the amount of xylem present in the host plants. Possible reasons for the apparent preference of the parasite for woody rather than herbaceous host plants are given. Anatomically, Cassytha is very homogenous.

Among the species studied, the only distinguishing anatomical features of possible taxonomic significance occur in C. glabella.

Haustoria were studied in terms of their origin, development, morphology, tissue components, mode of penetration into host, and connections to host tissues. Haustoria were found to consist of two distinct parts, an attachment cup and a penetration wedge, each arising endogenously from separate meristematic areas of the parasite stem. Morphology of the penetration wedge is variable, depending on the amount and arrangement of vascular tissue in the host plant. Only direct vessel element to vessel element connections between the haustoria and host are reported; however, the presence of sieve tubes in the phloem of haustoria in all species is confirmed.

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INTRODUCTION

Cassytha L. (Lauraceae) consists of perennial, herbaceous, vine-like plants which closely resemble Cuscuta (Convolvulaceae) in general morphology and parasitic habit. When growing in sunlight the small filiform stems vary in color from brick red to pale yellow. In shade the stems become deep green. The genus probably comprises between 11-20 species of subtropical and tropical distribution (Bentham 1870, Black 1948, Willis 1966). There is no comprehensive taxonomic treatment for Cassytha. The greatest number of species occurs in Australia and the Malay Archipelago (Hutchinson 1969); C. filiformis is the only pantropical species (Bentham 1870, Allen 1966), but C. ciliolata and one or two other species, although not truly pantropical, occur in both Africa and Australia (Meissner 1864, Kostermans 1957). Geographically these are among the most widespread species of Cassytha. Kuijt (1969) states that the genus is largely maritime in distribution occurring primarily along coastal strands, however, some species do extend into the Blue Mountains of Australia. C. filiformis is apparently more confined to coastal areas than any of the other species.

The taxonomic disposition of Cassytha has been controversial since the time of its original systematic description by Linnaeus in 1753. Some systematists have erected a monogeneric family, Cassythaceae, for these parasites while others have preferred to place them in some already established family to which they appeared closely related. With-

out exception, this latter group of taxonomists has placed Cassytha in the family Lauraceae. When so situated, it comprises the only herbaceous, parasitic member of that family. Among these botanists, however, there has been little agreement as to the exact rank or status Cassytha should occupy within the family. Accordingly, these plants have been given generic, tribal, and subfamilial ranking.

Cassytha was first described by Linnaeus (1753) as Cassyta. He recognized only a single species, Cassyta filiformis. According to Brown (1956), Cassyta is derived from the Greek kasytas or kadytas, a parasitic plant which Black (1948) said was presumed to be dodder.

Several eighteenth century contemporaries of Linnaeus also described and classified plants of the genus recognized by Linnaeus as Cassyta.[1] Adanson (1763) described this parasite and gave it the generic name Rombut. Rombut was placed in the family Garou which Adanson subdivided into two sections based on the length of the style or tube. Rombut was placed in Section I containing those plants which had short tubes. Likewise, these plants were also described by Forskål (1775), who applied the name Volutella to the genus. Volutella aphylla, the only species, was placed in the class Enneandria which also contained the genus Laurus. So far as I have been able to determine, this is the first implication of a relationship between Cassytha and other laurels. De Jussieu (1789) described Cassytha as an apetalous hermaphrodite with a superior ovary. He did not, however, place the parasite

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[1]A complete survey of the many names by which Cassytha has been called is presented in Kostermans's compendious "Bibliographia Lauracearum" (1964).

in a class or family but considered it among a special group of plants whose status was uncertain. Last among the contemporaries of Linnaeus to deal with the classification of Cassytha, was Joannis de Loureiro. In the system proposed by de Loureiro (1793) the generic name Calodium was applied to the parasite. Calodium was placed in the class Enneandria which was divided into two groups, Monogynia and Trigynia. The Monogynia comprised three genera: Calodium, Anacardium, and Laurus. Calodium was considered as a monotypic genus containing the single species C. cochinchinense.

In 1836 Rafinesque completely realigned the taxonomy of Cassytha. He disregarded any relationship between the parasite and the genus Laurus, considering the former to be a monocot! He used the name Rumputris and placed the genus in the family Olaxis of his class Mesogines. Although Rafinesque (1836) suggested a possible relationship between Rumputris and Viscum (Loranthaceae), he considered the nearest relative of the parasite to be Olax (Olacaceae). He stated that if Rumputris and Olax were not to be maintained in the same family, a separate family should be established for the parasite. He suggested using the name Casytides for such a family.

Endlicher (1836-1840) proposed a system of classification which paralleled that of Forskål and de Loureiro in reflecting a relationship between Cassytha and other laurels. Endlicher established the family Laurineae which he divided into 13 tribes. The last of these was the monogeneric tribe Cassyteae.

One of the most debated taxonomic treatments of Cassytha is that of Lindley (1830, 1853) in which he removed the parasite from the family Laurineae and placed it in a separate monogeneric family,

Cassythaceae. He placed this family in the order Daphnales which consisted of plants with monochlamydeous flowers, a solitary carpel, and seeds without endosperm. Other families included in the order are Thymelaeaceae, Proteaceae, and Lauraceae. According to Lindley (1853), the flower structure of the Cassythaceae and Lauraceae is almost identical. Despite this great degree of similarity, he maintained the "dodder-laurels" and laurels as separate families. This familial separation was based primarily on three taxonomic characters, the most important of which was the parasitic life form of "dodder-laurels." Such a life form, said Lindley, is found among no other members of the laurel family. Secondly, Cassytha has leaves which are reduced to colorless scales while true laurels have well-formed leaves. Finally, Cassytha produces fruits which are enclosed by a permanent and succulent calyx, while members of the Lauraceae produced "naked" fruits. Flower structure, therefore, constitutes the only common character known to be shared by the two groups. Consequently, Lindley suggested that Cassythaceae and Lauraceae be maintained as separate entities, at least until some "distinct connecting link" between the two groups is discovered, if such a link exists.

The system proposed by Lindley has encountered a great deal of criticism. One of the vigorous critics who opposed the separation of Cassytha from the Lauraceae was William Hooker. According to ~~Hooker~~ Gardner (1840), Lindley's primary motive for the creation of the family Cassythaceae was simply that it was "too violent a shock" to place a parasitic plant in the same family with some of our most "noble forest trees." Hooker considered the primary distinction between the two taxa, as stated by Lindley, to be the parasitic habit and he did not believe

that separation of major taxa based on habit alone could be justified. He thought that such a precedent would probably lead to the breakdown of many natural groups and the subsequent establishment of new orders which would be based on equally unjustifiable premises. Also, many existing taxa are composed of plants with equally heterogeneous habits but are nevertheless considered to be taxonomically sound. For these reasons, he considered the establishment of Cassythaceae as a separate entity from Lauraceae, to be both artificial and unjustifiable.

In the classification system of Bentham and Hooker (1870), the parasite Cassytha was returned to a position which also included woody, autotrophic lauraceous plants. These authors subdivided the family Laurineae into four tribes: Perseaceae, Litseaceae, Cassytheae, and Hernandieae. The tribe Cassytheae contained the single genus Cassytha with 15 recognized species.

The work of Lindley was again challenged by Bentham (1870) in his Australian flora where he stressed the similarity in flower structure between the laurels and Cassytha. In this work he placed Cassytha in the family Laurineae, apparently attaching more significance to similarities in floral structure than to the differences of habit. Bentham included three subfamilies in the family Laurineae: Laureae, Cassytheae, and Hernandieae. The subfamily Cassytheae comprised the single genus Cassytha with 11 species in Australia.

C. nodiflora Meissn.	C. filiformis L.
C. glabella R. Br.	C. melantha R. Br.
C. flava Nees	C. micrantha Meissn.
C. pubescens R. Br.	C. racemosa Nees
C. phaeolasia F. Muell.	C. pomiformis Nees

C. paniculata R. Br.

The work of Bentham was one of the first to give a listing of all the species then known to occur in the Australian area, and since Australia is considered to be the center of distribution of the genus, his list probably included most of the recognized species of the world at the time.

Meissner (1864) undertook a taxonomic revision of the laurels and produced a system which, like that of Bentham, was based primarily on floral structure. Meissner divided the laurels into three subfamilies, the Laurineae, Gynocarpeae, and Cassytheae. Each subfamily was divided into tribes which were numbered consecutively from one subfamily to the next. The first two subfamilies contained a total of five tirbes while the third contained the single tribe Cassytheae. This monogeneric tribe was subsequently divided into four taxa of subgeneric status, each of which comprised several species. A total of 29 species was recognized, four of which included one or more subspecies or varieties.

Capitate	Spicatae
1. C. capillaris Meissn.	15. C. melantha R. Br.
2. C. nodiflora Meissn.	16. C. robusta Meissn.
3. C. tasmanica Meissn.	17. C. pubescens R. Br.
4. C. flava Nees	C. p. var. fasciculata Meissn.
5. C. pomiformis Nees	18. C. rugulosa Meissn.
6. C. microcephala Meissn.	19. C. filiformis L.
7. C. dispar Schlechtd.	C. f. var. subpubescens R. Br.
8. C. casuarinae Nees	20. C. guineensis Schumann & Thonner
9. C. subcapitata Meissn.	C. g. var. livingstonii Meissn.
10. C. multiflora Nees	21. C. americana Nees

11. C. glabella R. Br.
12. C. capensis Meissn.
13. C. ciliolata Nees
14. C. coronata Nees
    C. a. var. puberula Meissn.
    C. a. var. brasiliensis Meissn.
    C. a. var. brachystachya Meissn.
22. C. micrantha Meissn.
23. C. paniculata R. Br.
24. C. remotiflora F. Muell.

Racemosa

25. C. muelleri Meissn.
26. C. racemosa Nees
27. C. ceratopoda Meissn.

Umbellatae

28. C. digitata Nees
29. C. umbellata Meissn.

Although many of the species recognized by Meissner are not considered valid today, the work does give one of the most extensive listings and descriptions of the various species of Cassytha.

A subdivision of the family Lauraceae was also undertaken by Mez (1889) who divided Lauraceae into two subfamilies, Laureae and Cassytheae, the latter group containing the single genus Cassytha. Pax (1891) expanded the system of Mez and others by dividing Lauraceae into two subfamilies, Persoideae and Lauroideae. Each subfamily was subsequently divided into a series of tribes. The genus Cassytha made up the last tribe of the Lauroideae and comprised approximately 15 species.

Wettstein (1935) and Rendle (1938) were among the early twentieth century taxonomists that classified Cassytha. Although both of these botanists considered Cassytha at the generic level, they did not list names of species.

In his "Flora of South Australia," Black (1948), followed other

systematists in placing Cassytha at the generic level in the laurel family. While he considered the genus as comprising approximately 20 species, only three of the most common species were described.

Kostermans (1957) revised the taxonomy of the Lauraceae and separated the family into the two subfamilies, Lauroideae and the monogeneric Cassythoideae. Kostermans's work was followed closely by Buchheim (1964) for the intrafamilial classification of the Lauraceae. The subfamily Cassythoideae is here listed with a single genus, Cassytha, composed of some 20 species. Thorne (1968) also placed Cassytha in the subfamily Cassythoideae but he did not list recognized species.

The most extensive recent studies on Cassytha are those of Sastri (1952, 1962, 1963) who has examined the floral anatomy and embryology, and considered the phylogeny of this and other lauraceous genera. After a detailed study of three species, C. filiformis, C. glabella, and C. pubescens, Sastri (1963) concluded that there was no justification for moving the parasite to a separate, monogeneric family. Cassytha does show some embryological features which are not found in other members of the Lauraceae. The most important of these are: 1. secretory type of anther tapetum, 2. formation of numerous embryo sacs in an ovule, 3. elongation of some embryo sacs beyond the nucellus, and 4. cellular endosperm (Sastri 1962). These differences, however, are not judged sufficient by Sastri to justify the removal of Cassytha from the Lauraceae because there are also many characters shared in common. For example, most genera of Lauraceae, including Cassytha, possess ethereal oil cells in all parts of the plant; acolpate pollen grains; a polygonum-type development of the embryo sac; thick-walled, unicellular epidermal trichomes; and anthers with valvular dehiscence

(Sastri 1962). Because of these, and other similarities, Sastri supports those systematists who include Cassytha as a subfamily or tribe in the family Lauraceae.

Hutchinson (1964) has recently considered the standing of Cassytha at the familial and generic level. He placed Lauraceae in the order Laurales, where it is considered, not as a primitive family, but rather as a reduced apetalous family closely related to Monimiaceae, Austrobaileyaceae, and Trimeniaceae. Hutchinson (1964, 1969) divided Lauraceae into six tribes based on both habit and floral characteristics. The tribe Cassytheae, with a single genus comprising 15 species, is distinguished from the other tribes because of its herbaceous, parasitic habit.

The systematists who favored placing Cassytha in a separate, monogeneric family (Lindley 1853), or incorporating it into a family with certain other parasites (Rafinesque 1853), justified their separation on the parasitic habit of the genus. Most taxonomists, however, have considered habit as a weak character for separation at the familial level. These systematists have included Cassytha in the family Lauraceae, attaching more importance to similarities of flower structure between these two taxa than to differences in life form and nutrition.

The flowers of Cassytha are small and borne in indefinite inflorescences which are arranged in spikes, racemes, or heads. Individual flowers are regular, bisexual or "semi-dioecious" and may be sessile or pedicellate subtended by a minute, scale-like bract (Kostermans 1957). Two bracteoles occur immediately beneath the perianth. Each flower has six tepals, of which the outer three are smaller and re-

semble the bracts. There are nine fertile stamens with valvate anthers which are arranged in three rows of three stamens each. The outer two whorls are eglandular and have introrse anthers. The second row may be reduced to staminodes; however, this is a rare condition. In the third row, stamens have extrorse anthers and each is subtended by two gland-like staminodes. A fourth, inner whorl comprises only staminodes. The ovary is superior and contains a single pendulous, anatropous ovule; it bears a short style and capitate stigma. The fruit is drupaceous, indehiscent, and is encased in a succulent, enlarged and persistent calyx tube. The seeds possess a membranous testa. Cotyledons are thick, fleshy, and often unequal. Early in the development of the embryo, the cotyledons are distinct; however, in later stages the cotyledons are more or less consolidated and are not distinguishable as separate structures. Detailed descriptions of the genus may be seen in Baillon (1870), Bentham (1870), Black (1948), Kostermans (1957), and Hutchinson (1964).

Many of the floral characteristics of Cassytha are shared with other members of the Lauraceae. For example, Cassytha and other genera of Lauraceae are characterized by bisexual or unisexual flowers with several stamens; e. g., Cassytha has nine stamens, Umbellularia also has nine, and Laurus, the type genus, has 12 or more in the male flower (Kasapligil 1951, Hutchinson 1964). In these and other lauraceous genera, some of the staminal filaments are subtended by stipitate glands; have valvate anthers and staminodes. In various members of the Lauraceae, all the valvate anthers may be introrse or some introrse and some extrorse, as in Cassytha. In the tribe Crytocaryeae (sensu Hutchinson 1969) the mature fruit becomes enclosed in a per-

sistent floral tube, as does the fruit of Cassytha. Another common floral characteristic between Cassytha and Cryptocaryeae is the presence of a superior ovary containing a single, pendulous ovule.

Floral structure is used as the primary criterion for distinguishing among the various species of Cassytha. However, because of the great degree of similarity in floral structure among the species, the minuteness of the flowers, and because of little intraspecific variation, it is often difficult to differentiate among the species. Consequently, for these and other reasons, different names have often been assigned to the same plant.

Most anatomical work has been based on C. filiformis. Hackenberg (1899) described the mature stem of C. americana Nees (C. filiformis L.) as being devoid of medullary rays and having small furrows around the periphery of the xylem cylinder with bundles of soft bast being inserted in these furrows. Inside the xylem cylinder and external to the pith, are small groups of primary xylem. He attributed the formation of cavities in the phloem to a breakdown of phloem and pericycle cells. Also, Hackenberg described the presence of mucilage cells in the pith, cortex, and leaf, and of transversely placed stomata on the stem.

Although Mirande (1905) criticized Boewig (1904) for not detailing the early development of C. filiformis, nevertheless, she devoted a large portion of her paper to fruit and seed structure, seed germination, and seedling growth. In her description of the mature stem, Boewig described the presence of medullary rays and internal "patches" of phloem which extend into the pith. Pith cells were described as thin walled and non-protoplasmic. Boewig attributed the formation of

lacunae, internal to the patches of fibers in the cortex, to the degeneration of phloem cells. No mention was made of secondary growth. In describing the leaves, Boewig stated that each leaf is supplied by three veins and contained stomata in both the upper and lower epidermises. Stomata are described as ". . . transverse on the stems, small and of ordinary appearance." Boewig further stated that individual stomata are always separated by two cells.

Mirande (1905) was primarily concerned with seed germination and early development of C. filiformis during the time it was ". . . puisant dans le sol ses aliments au moyen de ses propres racines. . . ." (drawing its nutrients from the soil by means of its own roots). Mirande criticized the work of Hackenberg (1899) and Boewig (1904) for concerning themselves ". . . ne se sont occupés que de la tige adulte des Cassythes . . ." (only with the adult stems of Cassytha) at a time when the parasites are free of the soil and ". . . fixée sur une plante hospitalière" (attached to a host plant). Mirande first discussed the root system which comprises an ephemeral terminal root and four lateral roots that arise exogenously from ". . . bourgeons formateurs de ces racines" or root-forming buds. Then he described the formation of several buds side by side which form a common trunk of roots. Mirande discussed the formation of an easily recognizable endodermis in the mature stem which contains ". . . cellules en marteau . . ." or hammer-shaped cells as seen in longitudinal view. These cells divided to increase the length of the endodermal envelope. The endodermis, according to Mirande, also extended into the leaf. He also considered the formation of a pericycle which arose from small arcs of cells apparently sandwiched between the "hammer" cells of the endodermis. Internal

to the pericycle, small cavities are formed. Mirande speculated upon, but did not observe, the cellular origin of these cavities. Lastly, Mirande discussed the development of secondary tissue from "l'assise génératrice" (a generative layer) outside the xylem ring. He stated that the phloem bundles are greatly increased in size, often completely filling the lacunae. Internal to the generating layer radial bands of parenchyma cells are formed which ultimately change into vessels. This growth caused the formation of a vascular system which was ". . . très puissant avec predominance du bois sur le liber" (very strong with a predominance of wood over phloem). Secondary growth was reportedly greatest toward the outer side of the stem, opposite that portion of the parasite stem in contact with host plants.

Kienholz (1926) studied the stem anatomy of C. filiformis from Philippine beach vegetation. He described the stem as possessing a single layer of heavily cutinized epidermal cells covering a cortex, the outer one to two layers of which are free of chloroplasts while the inner layers constitute "chlorophyll-bearing" cells. Mucilage cells are scattered throughout the cortex and no definite endodermis is present. Phloem cavities result from the crushing and disintegration of protophloem. Protoxylem cells are visible as small strands of tissue extending into the pith. An indefinite layer of cambium separates the phloem from the xylem. Stomata are arranged in definite vertical rows and are oriented horizontally on the stem.

While a great deal of study has been devoted to stem anatomy, a relatively small amount of attention has been focused on haustorial origin and structure. Cartellieri (1928) investigated the haustorial structure of C. pubescens. He described a mature haustorium as having

vessel elements and parenchyma cells surrounded by a cambial layer, and also well-developed vessel elements external to the cambium. The vessels of the haustorium connect both with the vessels of the parasite stem and those of the host to form a continuous conducting tube. Cartellieri did not mention phloem as occurring in haustoria, and he described the primoridium of a haustorium to be three cells located between the epidermis and a deep-seated layer of starch-containing cells.

McLuckie (1924) examined haustoria in C. glabella, C. pubescens, and C. melantha. He described an endogenous origin for haustoria and showed them arising just outside the phloem in the parasite stem. He further stated that haustoria frequently branch before penetration of the host has been accomplished. According to McLuckie, phloem is entirely absent from haustoria in each of the three species studied, and, therefore, he postulated that members of the genus Cassytha are water parasites only. He mentioned the occurrence of lateral growths of haustoria which intrude into the cortex or phloem of the host plant, but he said that these occurred only on the haustoria of C. melantha.

Job Kuijt (1969) has presented an excellent review of pertinent anatomical and associated studies on Cassytha, as well as similar reports on other parasitic flowering plants. Besides discussions of the structure of fruit and seed, seed germination, and general anatomy, Kuijt has skillfully summarized the work of Mirande (1905), Boewig (1904), McLuckie (1924), and Sastri (1962) on Cassytha. He described haustorial structure and very clearly pointed out the conflicting facts and frequent lack of knowledge concerning these absorbing structures.

This study was originally undertaken with the hope of finding

anatomical characters of possible importance in separating the species of Cassytha and which might have been, at the same time, instructive in determining the taxonomic relationships of Cassytha. A review of the anatomical literature, however, raised many questions concerning the true anatomical structure of these parasites. Among the major anatomical studies on C. filiformis, e. g., the works of Boewig (1904), Mirande (1905), McLuckie (1924), and Kienholz (1926), many conflicting anatomical statements were noted. Also, it became apparent that most species of Cassytha, except for C. filiformis, have been largely ignored from an anatomical viewpoint. In light of these facts, a thorough, comparative anatomical study of C. filiformis and other Cassytha species was considered of critical importance before any studies on the natural history, physiology, comparative anatomical systematics, and host-parasite relationships could be made.

Another intriguing question which arose during this investigation concerned the distribution and host range of Cassytha. As stated previously, Cassytha is primarily a coastal genus, especially C. filiformis, which appears indiscriminately to parasitize a wide variety of host plants (Kuijt 1969). I have personally observed C. filiformis in southern Florida and on the Florida Keys parasitizing ferns, cycads, palms, mangroves, pines, and citrus species as well as a variety of small herbaceous to semiwoody annuals and perennials. Growth of the parasite, however, always appears to be much more luxuriant on large woody shrubs or trees than on small herbs or succulents.

Other authors, e. g., Boewig (1904) and McLuckie (1924), also observed the indiscriminate selection of host plants by Cassytha; however, they did not study the parasite on a wide range of these host

plants nor did they attempt to explain why it attains better growth on woody hosts than on herbaceous hosts. An objective of this project, therefore, has been to study the parasite on both herbaceous and woody hosts and to search for possible anatomical explanations for the differences in parasite growth attained on these two classes of host plants.

Because of discrepancies in the existing anatomical descriptions of C. filiformis and because of a lack of anatomical data on other species of Cassytha, this work was designed to present a basic set of facts comprising both new and revised data. These data are considered to be a necessary prelude to any other studies on Cassytha.

MATERIALS AND METHODS

In order to obtain the greatest possible number of different species of Cassytha from diverse areas, plant collections in the United States National Herbarium and pertinent literature were examined. Fluid-preserved specimens were received from the Forest Research Institute, Pretoria, South Africa; Dr. Winifred M. Curtis, Hobart, Tasmania; Mrs. J. C. Gee, Launcesten, Tasmania; and Dr. T. C. Chambers, Melbourne, Australia. I personally collected specimens of C. filiformis on Grassy Key and Big Pine Key, Florida, U. S. A.; these specimens bear Stern et al. collection numbers 2752 through 2759. Individual specimens selected for study, along with their collectors and localities, are listed in table 1. Three criteria were used to choose specimens for study: 1. representatives to reflect a range of species, 2. representatives to reflect a range of geographical areas, and 3. representatives to reflect a range of host plants, from herbaceous to woody.

Segments of mature parasite stems, stem tips, and host plant parts penetrated by haustoria, were dehydrated in tertiary butyl alcohol and embedded in paraffin following the method outlined by Johansen (1940). Serial transverse and longitudinal sections were cut on a rotary microtome at 10μ and 12μ, respectively, mounted on slides, stained with safranin, and counter-stained with fast green following standard microtechnical procedures. Stained sections were mounted in Canada balsam. Specimens, too hard to cut after embedding in paraffin, were softened

by soaking in a solution of Aerosol OT as outlined by Ayensu (1967). Where the parasite was growing on a woody host plant, small segments of host stem with the parasite attached, were frozen onto the stage of a sliding microtome. Sections of these were cut at 20μ, maintained in series, and stained with safranin and Heidenhain's iron-alum hematoxylin. An ethyl alcohol series was used for dehydration and mounting was done in Canada balsam.

In order to study phloem in the parasite, a special lacmoid-ferric chloride staining procedure, as outlined by Cheadle, Gifford, and Esau (1953), was used. Mounting was done with "XAM," a synthetic neutral resin produced by George T. Gurr, London.

Macerations were prepared using Jeffrey's fluid. After removal from the macerating fluid, the material was washed, dehydrated with tertiary butyl alcohol and stained with safranin. Small pieces of stained plant material were placed in a watch crystal containing a mixture of xylene and Canada balsam. These pieces of material were then gently teased apart with a glass rod and a few drops of the mixture placed on a microscope slide. Epidermal strips, which remained intact as the internal stem tissues were teased apart, were mounted separately and used to study the stomatal apparatus.

Ontogenetic studies on the development of primary phloem and primary xylem were carried out using transverse and longitudinal sections of stem tips, 10μ in thickness. Serial sections were cut from the apex of the apical meristem through the region of mature protophloem and protoxylem into the region of maturing metaphloem and metaxylem Individual stem tips were stained either by the lacmoid-ferric chloride method or with safranin and fast green. Determinations of distances

from the tip of the apical meristem to the maturation regions of protophloem and protoxylem were made by examining each individual section until these tissues appeared, and then counting the number of sections back to the tip of the stem. Ontogenetic data are based on studies of the stem tips of C. ciliolata, C. melantha, and C. pubescens, because better material was available for these species.

To study stems of the parasite, segments from five different plants of each species were sectioned transversely and longitudinally. These stem sections were chosen, inasmuch as possible, to reflect comparably aged material. Measurements of stem diameters and cuticle, cortex, and pith thicknesses were made on a compound microscope from transverse sections. Measurements were taken at two points on each of the five stem segments and from these 10 measurements, an average and a range were calculated for each species. Lengths of epidermal and pith cells were made from longitudinal sections. Ten measurements were taken for each species from which ranges were calculated.

Vessel element lengths and widths were measured from macerations. Vessel element diameters were measured from outside wall to outside wall and vessel element length from tip to tip. A total of 45 random measurements for each character was taken and from these measurements, a range and an average were calculated for each species.

Four different types of preparations were employed in studying stomata because of their arrangement and orientation on the parasite stem: epidermal strips obtained from macerations, and transverse, longitudinal, and paradermal stem sections. Epidermal strips and paradermal sections were used to study the stomatal apparatus in surface view. Stomatal lengths were obtained by measuring 10 stomata of

each species, from tip to tip. An average and a range were then calculated for each. Because of the orientation of the stomatal apparatus on the parasite stem, it was studied in transverse and longitudinal view from longitudinal and transverse stem sections, respectively.

Haustoria were studied by making transverse serial sections through portions of host plant parts that had been penetrated by at least one haustorium. Sections were also made of parasite stems which had bent back on themselves, coiled around, and subsequently parasitized themselves. Ontogenic studies of haustoria were carried out using transverse and longitudinal sections of parasite stems in which there were young, developing haustoria.

In this study no specifically outlined set of anatomical characters was used for making observations. An attempt was made to examine, compare, and interpret as many characteristics as appeared necessary to explain the ontogeny and mature anatomy of the vegetative portions of Cassytha plants. Terms used in this paper are those which conform to current general usage, not special terms which conform to pre-determined guidelines. Because of the large degree of anatomical similarity among the species studied, a single anatomical description is presented. Exceptions to and variations from this general description are noted as and where they occur.

Table 1. Species of Cassytha examined.

Species	Host	Collector and number	Locality	Research reference number[c]
ciliolata Nees	Passerina vulgaris Thoday	Forest Research Institute, Pretoria	South Africa	101
filiformis L.	Conocarpus erectus L.	Stern, Beaman, Phipps, Rock, and Sweitzer 2756[b]	Grassy Key, Florida	119
filiformis L.	Croton linearis Jacq.	Stern, Beaman, Phipps, Rock, and Sweitzer 2752[b]	Big Pine Key, Florida	116
filiformis L.	Sesuvium portulacastrum L.	Stern, Beaman, Phipps, Rock, and Sweitzer 2759[b]	Grassy Key Florida	122
glabella R. Br.	Casuarina monilifera L. Johnson	Curtis G_4	Tasmania	111
glabella R. Br.[a]	Leptospermum myrsinoides Schlecht.	Chamb s s. n.	Australia	126

melantha R. Br.[a]	*Schinus molle* L.	Gee s. n.	Tasmania	124
pubescens R. Br.	*Leptospermum lanigerum* Sm.	Curtis P_2	Tasmania	109

[a] Suitable haustoria were not present for describing the mode of parasitism; however, specimens of the parasite stem were used in describing these species.

[b] Herbarium vouchers deposited in herbarium, Department of Botany, University of Maryland; MARY.

[c] Voucher material is not available for all specimens. Therefore, a separate research reference number was assigned to each specimen. A portion of each specimen is being maintained, under these reference numbers, as fluid-preserved material.

RESULTS

Mature Stem

The stems of Cassytha are circular to slightly oval in transverse section and bear small indentations or ribs in which the stomata are located (fig. 1). Among the five species of Cassytha studied, interspecific variations in stem diameter were found to be significant in some instances, while in others, intraspecific variations were as great as interspecific variations. The smallest stem diameter was found in C. ciliolata with a range of 540-680μ and an average of 620μ. C. glabella was only slightly larger, having a range of 688-837μ and an average of 728μ. The other three species possessed stems which were appreciably larger. Within this latter group, stems of C. pubescens were the narrowest having a diameter range of 930-1178μ and an average of 1042μ. C. filiformis was next with a range of 1011-1488μ and an average of 1257μ. Stems of C. melantha were widest and ranged from 1457-1885μ averaging 1591μ.

In all species of Cassytha the stems are covered by a relatively thick cuticle. The thinnest cuticle is that of C. pubescens which averages 2.9μ. In C. melantha the cuticle averages 6.3μ in thickness; it is 7.8μ in C. glabella and C. filiformis, and 8.7μ in C. ciliolata. In transverse section the cuticle is contoured, and distinct gulley-like depressions occur over the anticlinal walls of the epidermal cells except in C. glabella, where the outer periphery of the cuticle is level or bears only very slight indentations (figs. 10, 11). The cuticular

surface may be distinctly serrated as in C. ciliolata and C. pubescens, or smooth to very lightly serrated as in C. filiformis, C. glabella, and C. melantha.

The epidermis comprises a uniseriate layer of cells which are shield shaped, as viewed in transverse section (fig. 11). Epidermal cells are more or less uniform in size, having evenly thick cell walls, light staining cytoplasm, and prominent spherical nuclei (figs. 1, 2). In longitudinal section the epidermal cells are columnar, ranging from 65-91μ long in all species studied (fig. 12). They have circular to slightly fusiform nuclei. Anticlinal walls of epidermal cells are bowed leaving small gaps between the cells which are filled with cuticular material. Frequently, epidermal cells are partially or completely filled with an amorphous, anisotropic substance which, upon staining with safranin, becomes yellowish-red, to deep red, to brown (fig. 8). These cells are present in the epidermal layer of all five species and in longitudinal sections, they appear in rows approximately two to five cells in length.

Stomata are located in small ribs or indentations on the stem and are arranged in vertical rows with their long axes at right angles to the long axis of the stem (fig. 6). Individual stomata may abut one another or they may be separated, usually by one to four epidermal cells. The stomatal apparatus is paracytic (sensu Metcalfe and Chalk 1950), that is, there are one or more subsidiary cells on either side of the guard cells which are oriented parallel with the long axis of the pore and guard cells. In all five species, the stomatal apparatus consists of a pore, two guard cells, two accessory cells, and a sub-stomatal chamber which is irregular in size and shape. The two guard cells,

when viewed in transverse section (longitudinal section of the stem) are more or less circular with small horns near their upper surfaces (fig. 7). Guard cells are sunken, and the adjacent accessory cells are modified to overlap the guard cells on their outer surfaces. The accessory cells are also horned on their outer surfaces. In face view these horns create the impression of an extremely thick common cell wall between guard cells and accessory cells. Also, in this view, the guard cells are somewhat bow shaped with rounded, thickened end walls. A nominal amount of variation occurs in the length of the stomatal apparatus among various species. C. pubescens, C. glabella, and C. ciliolata are almost identical with averages of 48μ, 50μ, and 51μ, respectively. C. filiformis and C. melantha are only slightly larger with averages of 60μ and 63μ, respectively. In longitudinal section (transverse section of the stem) the guard cells are boat shaped and possess very elongate nuclei (figs. 8, 9). Chloroplasts are present in the guard and accessory cells.

Trichomes are present only on the mature stems of C. pubescens and C. melantha. In C. pubescens the trichomes are abundant, unicellular, and have one of two possible shapes: 1. small at the base, swollen through the central portion, and gradually tapering to a point giving the trichome a "feather" shape, and 2. small at the base and somewhat bulbous at the distal end (figs. 16, 17, 18). Both types may be either extended straight outward or appressed to the epidermis. Cell walls are thick, and a narrow lumen extends from the base to the tip of the trichome. The lumen frequently serves as a repository for the same type of amorphous, deep red staining material frequently found in other epidermal cells. Protoplasts are absent in mature

hairs.

In C. melantha the trichomes, which are scarce on mature stems, branch just above the base into two unequal parts. One branch is short, narrow, and closely appressed to the adjacent epidermal cell. The other branch has a narrow neck, becomes greatly expanded through its central portion, then tapers to a narrow point. These trichomes are unicellular, thick walled, and devoid of protoplasts on the mature stem (fig. 19).

Immediately beneath the epidermis is a parenchymatous cortex. Among the five species examined, variation in diameter of the cortex was large in some species and small or non-existent in others. In C. glabella the average cortical thickness was 119μ. In C. pubescens, C. ciliolata, and C. melantha, the average cortical thicknesses were 173μ, 176μ, and 205μ, respectively. The largest cortical diameter was measured in C. filiformis with an average width of 331μ. No significant variation occurred in cell numbers counted through the diameter of the cortex; in all species the cortex averaged seven or eight cells thick except for C. glabella where the average was five.

The outermost layer of cortex, immediately beneath the epidermis, forms a distinct hypodermal layer (figs. 1-5). The hypodermis is a continuous sheath of cells, interrupted only by the sub-stomatal chambers. Hypodermal cells are circular when viewed in transverse section and columnar when viewed in longitudinal section (figs. 1-5, 12). The cells are closely applied to one another and to the epidermal cells. They have uniformly thick cell walls and contain numerous chloroplasts.

The remainder of the cortex is a lacunous tissue of loosely arranged, parenchymatous cells among which are numerous, small, variably

shaped intercellular spaces. The cortex is distinctly dimorphic with the outer one to three cell layers, immediately beneath the hypodermis, comprising cells which are elongated at right angles to the main axis of the plant (fig. 5). These cells contain numerous chloroplasts and closely resemble cells of the palisade layer of a "typical" dicotyledonous leaf. Internal to each of the vertical rows of stomata, cells of this layer become even more loosely arranged, creating small, irregularly shaped sub-stomatal chambers. In these areas this layer closely resembles a "typical" spongy mesophyll tissue (fig. 6). The inner two to four layers of cortical cells are more or less isodiametric to slightly elongated parallel with the long axis of the stem. These cells are typically parenchymatous with thin walls and a light staining cytoplasm. Chloroplasts are also present in these cells but are not as numerous as in the outer layers (fig. 6). Raphide crystals are very common in the cortical cells and occasionally can also be found in cells of the epidermis. Secretory cells are commonly found in the cortex (figs. 1, 5). These cells are partially or completely filled with an amorphous, deep red to brown staining material. Lysigenous cavities are also formed in the cortex (figs. 2, 3). These cavities occur at irregular intervals throughout the cortex and are usually small but variable in size and shape. They result from the breakdown of from one to three adjacent cortical cells. The cavities do not have an epithelial lining and they appear to be devoid of contents.

The central portion of the stem is occupied by a parenchymatous pith (figs. 1-5). There is some variation in pith diameter among the species. For example, in C. pubescens, C. filiformis, and C. glabella, the pith is approximately the same size with average diameters of 149μ,

158μ, and 219μ, respectively. The pith is wider in C. ciliolata and C. melantha with average diameters of 349μ and 502μ, respectively. Pith cells are circular when viewed in transverse section and are highly variable in size. Numerous intercellular spaces occur among cells. Cell walls are thin, however, they may have small thickened areas which stain light pink with safranin, possibly indicating a small degree of lignification. When observed in longitudinal section, pith cells are columnar, usually ranging from 200-650μ in length. The thin cell walls possess simple pits. Nuclei are fusiform in shape and the cytoplasm is light staining (fig. 44). Secretory cells, identical to those described in the cortex, are also present in the pith.

The vascular tissues in Cassytha are positioned between the pith and cortex. Stelar arrangement is in the form of an ectophloic siphonostele which comprises a central cylinder of xylem surrounding the pith, and individual bundles of phloem implanted in the cortex immediately external to the xylem (figs. 1-5). Along its outer periphery, the xylem cylinder radiates outward into small arms. There is nominal inter- and intraspecific variation in the number of xylem arms.

Situated between the xylem arms are separate bundles of phloem, each of which comprises both protophloem and metaphloem (figs. 1-5). In C. ciliolata, C. filiformis, and C. glabella, the number of these larger bundles varies between five and eight for each species. In C. pubescens the range is from nine to ten, and in C. melantha, from 13-14. Opposite the tips of the xylem arms, and alternating with the larger phloem strands, are small phloic bundles composed entirely of protophloem fibers (fig. 1). These smaller bundles are consistently present, except in C. glabella, where they are conspicuously absent (fig. 4).

Ontogenetically, maturation of the phloem is centripetal. The first phloem cells to mature from the procambium are protophloem sieve elements. These cells, which mature toward the outer edge of the phloic procambium early in the ontogenetic development of the parasite stem, have thin walls and a light staining protoplast (fig. 14). The protoplast disappears as the sieve areas develop. These cells ultimately are crushed as other cells in the phloic procambium begin to differentiate into protophloem fibers. Remnants of sieve plates from protophloem sieve tube elements are commonly found among these fibers (fig. 23). Mature phloem fibers have very thick walls and are devoid of protoplasts (fig. 23). When viewed in longitudinal section they are extremely elongated (fiber lengths could not be measured because the fibers are easily broken both by sectioning and by maceration processes).

Internal to the protophloem fibers there is a lysigenous cavity which results from the breakdown of some of the phloic procambial cells (fig. 20). These cavities are highly variable in size and have a circular to oval shape in transverse section. Metaphloem matures to the inside of this cavity and consists of sieve elements and companion cells, parenchyma cells, and very occasional fibers (fig. 20). Sieve elements are circular to slightly oval in transverse section. Sieve plates are circular in outline and simple with numerous small perforations (fig. 20). Sieve areas also occur on the lateral walls of the sieve elements. These areas are circular to oval (fig. 21). In longitudinal section, it can be seen that these cells are sieve tube elements positioned one on top of another to form a continuous sieve tube (fig. 22). Companion cells are small and circular in outline when viewed in transverse section (fig. 20). In longitudinal view the companion cells appear as narrow, elongated, nucleated cells with a densely staining cytoplasm. Often, several companion cells will be associated with a single sieve tube

element. Fibers, when present in the metaphloem, are shorter but otherwise identical in appearance to the protophloem fibers. Phloem parenchyma cells are thin walled, nucleated, and more or less isodiametric in shape (fig. 20). Frequently these cells are secretory, becoming filled with the same type of material described in other secretory cells.

Maturation of the primary xylem is endarch. In C. ciliolata, C. filiformis, and C. glabella, there are usually three to four small "patches" of protoxylem. In C. melantha and C. pubescens there are seven to nine. These small patches of protoxylem are arranged at irregular intervals around the periphery of the pith and usually consist of from one to eight tracheary cells (figs. 1-5). Cells comprising the small groups of protoxylem are vessel elements which have annular or spiral secondary cell wall thickenings. Metaxylem differentiates externally to the protoxylem. The first metaxylem cells to mature are large diameter vessel elements. These cells form a more or less continuous ring just outside the protoxylem. Interspersed among these large vessel elements and continuing outward to form the remainder of the primary xylem cylinder, are smaller diameter metaxylem cells consisting of vessel elements and metaxylem parenchyma. Fibers and other imperforate tracheary elements are absent.

Large diameter metaxylem vessel elements may be solitary, surrounded by smaller vessel elements or parenchyma cells, or in clusters of two to three cells. Pores in these large metaxylem vessel elements are angular and considerably wider in diameter than pores in the remainder of the primary xylem cylinder. Average vessel element diameters are 41μ, 47μ, 61μ, 67μ, and 70μ, respectively, for C. ciliolata, C. glabella,

C. pubescens, C. melantha, and C. filiformis. The range for all five species is from 18-99μ. Ranges for individual species are given in table 2.

Pits in lateral walls of large diameter metaxylem vessel elements are large, distinctly circular bordered, and have a conspicuous torus. The arrangement of pits in the vessel wall is alternate. Smaller metaxylem vessel elements have uniseriate or biseriate rows of circular bordered pits in lateral walls. When biseriate rows are present, they alternate along the length of the cell (fig. 44). A few vessel elements have only one or two circular bordered pits at either end of the cell, adjacent to the perforation plates. The remainder of the cell body has only simple to very slightly bordered vessel to parenchyma pits.

Vessel element end walls may be truncated at both ends or truncated at one end and gradually tapering to a rounded tip at the other end (fig. 43). Average lengths of vessel elements vary from 332μ in C. ciliolata to 935μ in C. melantha. Vessel element length in C. filiformis, C. glabella, and C. pubescens, falls between these two extremes with averages of 436μ, 491μ, and 527μ, respectively. Over all five species, vessel element length ranges from 190-1562μ. Ranges for individual species are shown in table 2. Perforations are all simple and in a given vessel element both may be terminal in position, or one may be terminal and the other sub-terminal. Rarely are both subterminal.

Vessel to parenchyma pitting may be simple or partially bordered on the vessel side and simple on the parenchyma side. Parenchyma pits are simple, enlarged and oval to rectangular in shape.

Secondary vascular tissues may be produced in the parasite stem

itself, but this is always associated with the production of haustoria. A lateral meristem arises from a single layer of small undifferentiated procambial cells located between the primary phloem and primary xylem and from a single layer of parenchyma cells immediately external to the primary xylem cylinder between it and the primary phloem bundles (fig. 24). This meristem usually does not form a continuous cylinder but extends only about half way around the parasite stem; however, in some cases it may develop into a continuous cylinder. Periclinal divisions of the meristem cells usually start in the area between the primary vascular tissues immediately beneath the metaphloem producing secondary phloem to the exterior. Secondary vessel elements and axial xylem parenchyma cells which form in radial rows are produced to the inside (fig. 25). This frequently causes a crushing of some metaphloem and pith cells and gives the impression of arms of secondary xylem radiating outward from the primary xylem cylinder internal to the area of the phloem bundles. Next, parenchymatous xylem mother cells, produced by the portion of the meristem which is between two phloem bundles, begin to mature into secondary vessel elements and axial xylem parenchyma. These vessel elements are oriented both axially, that is, with their long axes parallel to that of the parasite stem, and also horizontally. The horizontal vessel elements in this tissue are oriented so that their long axes are at right angles to those of the radial rows of vessel elements produced just internal to the phloem bundles. These elements, therefore, make lateral connections between the radial rows of tracheary elements. Secondary cell wall thickenings may be helical, transitional to reticulate, or provided with distinct circular bordered pits. Very little, if any, secondary phloem is produced to the

external side of the meristem in this area.

Development of this meristematic layer is associated with penetration of haustoria into a host plant. Penetration of a haustorium into an adjacent parasite stem can also stimulate formation of this meristematic layer in the "host" stem. Serial sections of the parasite stem above the level of a developing or incipient haustorium show no such meristematic layer or any of its derived tissues (fig. 24). Sections of the same stem, below the haustorium, show this secondary tissue gradually tapering out at the same time that the meristematic activity of the cells ceases (figs. 25, 26).

Table 2. Size of vessel elements in Cassytha (μ).

Species	Vessel element width		Vessel element length	
	Average	Range	Average	Range
ciliolata	41	26-65	332	190-530
glabella	47	19-87	491	316-725
pubescens	61	25-99	527	341-992
melantha	67	18-99	935	428-1562
filiformis	70	25-70	436	187-795

Haustoria

Origin.--Haustoria of Cassytha can conveniently be divided into two parts: 1. an attachment cup which appears to function in joining parasite and host, and 2. a penetration wedge which actually enters the host tissue.

The first evidence of haustorial formation occurs when epidermal and cortical cells of the parasite stem, in the area where the individual haustorium will be formed, dedifferentiate and assume mitotic activity (fig. 27). Divisions in the epidermal cells are largely transverse and anticlinal. Divisions in the cortex, usually restricted to the two or three layers immediately beneath the epidermis, occur in both anticlinal and periclinal planes. These divisions cause the stem to bulge outwards. This bulge is rectangular in outline when viewed in longitudinal section, with its long axis at right angles to the long axis of the stem. On the contrary, externally it is circular in outline with a flattened distal end. The outermost cells in this flattened distal end continue to divide, increasing the surface area and gradually causing the protuberance to develop into a more or less saucer-shaped structure. At the same time, divisions also continue in the two or three layers of cortical cells just under the surface. These divisions cut off parenchymatous cells internally and increase the length of the attachment cup (fig. 28). Cell divisions may occur throughout the attachment cup; however, the most intensive area of cell division is at the tip next to the host plant. Once the attachment cup contacts the host plant, cells of the distal epidermal layer cease their meri-

stematic activity. These cells enlarge greatly, become tumid, and develop a densely staining protoplast (fig. 35). Eventually, the cells in this layer which are immediately external and adjacent to the developing penetration wedge, will break down and lose their integrity as a tissue.

Concommitant with the formation of the attachment cup, the penetration wedge also begins to form. The innermost layer of cortical cells, located between two phloem bundles, and the metaphloem parenchyma cells, dedifferentiate and begin to divide by periclinal divisions. This activity produces an internal "apical" meristem, much like that which forms a branch root, which continues to undergo both periclinal and anticlinal cell divisions at its apex (fig. 28). This apical growth causes the penetration wedge to push through the tissues of the attachment cup, crushing cells in its path as new cells are cut off and left behind. Eventually, the penetration wedge will grow completely through the attachment cup and into the host plant.

Tissues.--The outermost tissue layer of the haustorium consists of a uniseriate epidermis. This epidermis is derived from, and is a continuation of, the epidermis of the parasite stem. Cells of the former tissue are identical to those of the latter, both have the same type of cuticle, stomata, and secretory cells. Species bearing trichomes as part of the mature epidermis, have the same type of trichomes in the haustorial epidermis. Likewise, the parenchymatous cortical tissues in the attachment cup are similar to the cortical tissues in the parasite stem from which they were derived. Cells contain chloroplasts, oval to spindle-shaped nuclei, and frequently, raphide crystals. Both a hypo-

dermis and secretory cells are also present.

Vascular tissues of the haustorium develop within the penetration wedge. Maturation of the primary xylem begins within the parasite stem next to the central xylem cylinder, e. g., acropetal maturation. Connections are formed between vessel elements in the parasite stem and those developing in the haustorium. Maturation of primary xylem then proceeds outward toward the distal end of the haustorium. In the portion of the penetration wedge encased in the attachment cup, a massive central core of tracheary elements is produced. These elements are short, narrow, and usually have helical, transitional to reticulate thickened secondary cell walls. They are arranged both vertically and horizontally and also parallel with and at right angles to the long axis of the haustorium forming a reticulum of tracheary tissues. The central tracheary core gradually tapers distally into five or six vessels. These extend out to the very tip of the penetration wedge and make vessel element to vessel element connections with the host (fig. 32). Individual vessel elements of the haustorium in this region usually have spiral, and sometimes annular or helical, secondary cell wall thickenings (fig. 38). Circular bordered pits are occasionally observed in combination with the helical, transitional to reticulate elements near the tip of the haustorium.

In C. glabella, near the proximal end of the haustorium a system of vessel elements is produced which radiates outward into the attachment cup but around and peripheral to the central core of tracheary elements. This system forms an arc of vessel elements which surrounds the central core and which almost joins the central core at the place of emergence of the penetration wedge from the attachment cup. These

arcs, two to four cells wide, comprise vessel elements with loosely spiraled thickenings in the secondary cell walls (figs. 35, 36).

Phloem, in the haustoria, comprises sieve elements, companion cells, and phloem parenchyma. Maturation of phloem begins near the proximal end of the individual haustorium, where it connects with sieve elements in the parasite stem, and proceeds distally (fig. 29). Sieve tube elements in the haustoria are connected to form sieve tubes, and the sieve tissue is usually one to two cells wide (fig. 30). Sieve tube elements of the haustoria are identical to those in the parasite stem.

Mode of Parasitism

Cassytha filiformis.--Host: Sesuvium portulacastrum L. (Aizoaceae). These are succulent halophytes which grow in coastal sand dunes and on shores from North Carolina to Florida and in the West Indies, Central America, and Mexico. Our specimen was collected on Grassy Key, Florida. Field notes indicate that the parasite weakens the host and kills it rapidly, thus resulting in early death to the parasite as well. Penetration was observed on the host stem.

When the attachment cup of the haustorium contacts the host stem, cells in the layer next to the host cease their meristematic activity and become greatly elongated parallel with the long axis of the haustorium. The penetration wedge then grows through the attachment cup and penetrates the host epidermis. It continues to grow, pushing through the cortex of the host stem. Frequently, in this region, the penetration wedge will branch, both parts growing to the host vascular cylinder (figs. 39, 40). Behind this growing tip, vascular elements are maturing in the haustorium (fig. 40). Near the host phloem, the tip of the penetration wedge will branch, one part growing to the phloem and the second part growing through the phloem and into the xylem, usually through a medullary ray (fig. 39). Once the host vascular tissue has been penetrated, cell division in the growing tip of the penetration wedge stops. Maturation of vessel elements proceeds to the distal tip of the penetration wedge where direct vessel element to vessel element connections are made between the haustorium of the parasite and the host plant (fig. 39). Thus, continuous communication is established

between the xylem of the parasite and that of the host, via the haustorium. Maturation of haustorial phloem also appears to proceed toward the phloem of the host. In only one case was a developing haustorial sieve element observed which appeared to be in direct contact with the host phloem.

Host: Croton linearis Jacq. (Euphorbiaceae). These are small shrubs, usually 1-2 m tall, which grow in the pinelands of peninsular Florida, the Florida Keys, and tropical America. Our specimen was collected on Big Pine Key. Penetration was observed on the host stem.

The haustorial penetration wedge grows into the periderm of the host stem. In the region of the cork parenchyma, the haustorium frequently branches, either on one or both sides. These branches grow into the phloem of the host. Cells in these branches appear to be parenchymatous; however, they are elongate, have fusiform nuclei, and are highly vacuolated (fig. 41). While no distinct sieve elements were observed in the haustorium, the parenchymatous cells just described probably comprise immature sieve tissue.

The central portion of the penetration wedge grows into the xylem cylinder of the host, usually to a depth of 550-600μ. Following penetration of the host xylem, tracheary elements mature in this portion of the haustorium and connect with vessel elements of the host (fig. 42). Vessel elements in the haustorium never connect with any cells of the host xylem other than vessel elements. Usually there are two to five vessels extending through this portion of the haustorium, each connecting with a different vessel element in the host. The part of the haustorium actually embedded in the host is cylindrical in shape in longi-

tudinal view. It tapers from about 350μ in diameter at its point of entry into the periderm to about 90μ at its distal tip.

Host: Conocarpus erectus L. (Combretaceae). These are coastal shrubs or trees occurring on muddy or sandy shores in peninsular Florida, the Florida Keys, the West Indies, Central America, and tropical South America. Our specimen was collected on Grassy Key, Florida. Field notes indicate a good growth of the parasite on these host plants. Penetration was observed on the leaf.

Haustoria almost invariably contact the leaf immediately over a vein. This may be the large, arcuate mid-vein or one of the smaller secondary veins (fig. 38). The penetration wedge grows through the upper epidermis and parenchymatous tissue to reach the vascular tissue of the mid-vein. Growth of the haustorium continues, pushing the penetration wedge through layers of phloem fibers, other phloem cells, and ultimately into the xylem (fig. 38). Maturation of vessel elements proceeds through the penetration wedge to the tip where vessel element to vessel element contacts are secured between the haustorium of the parasite and the host xylem. Inside the leaf, the penetration wedge frequently branches, thereby making connections with two or more leaf veins.

Sieve tubes are clearly present in the haustoria. Clear connection can be seen between the sieve elements of the haustoria and those in the parasite stem (fig. 30). Companion cells are also present in the haustoria. The sieve tubes are located on either side of the xylem. Sieve elements of the haustoria are identical to those in the parasite stem.

Haustoria frequently become attached to and penetrate the petiole as well as the leaf blade. Penetration and vascular connection with the central vein of the petiole are identical to these phenomena in the leaf blade. Within the petiole, an individual haustorium frequently branches making connections with more than one vascular bundle.

Cassytha ciliolata.--Host: Passerina vulgaris Thoday. (Thymelaeaceae). These plants are shrubs or shrublets occurring largely in South Africa and southern Rhodesia. Our specimen was obtained from South Africa, where, according to the sender, it is frequently heavily parasitized by C. ciliolata. Penetration was observed on the stem.

Following contact between the haustorium and host stem, a small, wedge-shaped penetration structure grows through the attachment cup and into the periderm of the host. This structure measures two to three cells in diameter at its distal tip as it enters into the host tissues. The penetration wedge grows through the tissues of the periderm into the xylem cylinder. At this point, the haustorial tip branches out into a foot-shaped structure partially growing around the xylem cylinder to become wedged between the secondary phloem and the secondary xylem (fig. 34). Actual penetration into the secondary xylem cylinder does not appear to occur, at least not in the material available. Vessel elements then mature in this portion of the haustorium and connect with vessel elements at the periphery of the host xylem cylinder (fig. 34). Although there is a massive central core of tracheary elements in the portion of the penetration wedge encased in the attachment cup, only two to four continuous vessel connections are secured between the haustorium and the host.

Sieve elements are present in the haustorium. Although no direct sieve element to sieve element connections have been observed between the haustorium and host phloem, some cells in the penetration wedge are at least in contact with the host phloem. These cells are elongate, parenchymatous cells with fusiform nuclei. Frequently they appear to have sieve areas in their lateral walls and are probably incipient sieve elements.

Cassytha pubescens.--Host: Leptospermum lanigerum Sm. (Myrtaceae). These plants are shrubs commonly found throughout Australia and Tasmania in heath tracts on sandy soils. Our specimen was from Tasmania. Penetration was observed on the stem.

As the attachment cup contacts the host stem it partially surrounds that stem. The epidermis of the host in the area of penetration is broken down and the penetration wedge grows into the host stem and through the cortex. Mitotic figures can be seen in the penetration wedge until contact with the host vascular tissues is made (fig. 31). There is a band of non-lignified fibers measuring approximately 65-75μ in diameter surrounding the vascular tissue of the host. As the penetration portion of the haustorium reaches this band of fibers it frequently branches dichotomously, and both branches grow through the cortex just outside of these fibers, before actual penetration through the fibers and into the host xylem is accomplished (fig. 31). Eventually some of the fibers are crushed and the tip of the penetration wedge grows through the phloem and into the xylem. Vessels of the haustorium then mature in this portion and connect with the vessel elements of the host.

Sieve elements occur in the haustoria, located just external to the xylem. These cells are thin walled and parenchymatous in appearance and often contain some cytoplasm. Sieve areas occur both in the end and lateral walls of the cell. Sieve elements were observed, at least in one instance, to be in contact with the host phloem. Continuous sieve tube connection from the host phloem through the haustorium, to the parasite phloem, has not been observed.

Cassytha glabella.--Host: Casuarinaceae. These are trees adventive in coastal areas of southern Florida and the Florida Keys, and native around the shores of the Indian Ocean eastward to Australia. Our specimen was Casuarina monilifera L. Johnson from Australia. Penetration was observed on the jointed branches.

The penetration portion of the haustorium invariably grows into one of the deep furrows of the host stem and penetrates the epidermis at the bottom of the furrow. Beneath the epidermis of the host, there is a small band of cortical parenchyma cells subtended by a band of fibers. The penetration wedge may grow directly through these fibers, or it may bend, grow through the parenchyma tissue for a short distance and then through the fibers (fig. 37). In either situation the haustorium ultimately reaches the host xylem. Frequently, it grows entirely through the xylem cylinder and pith to reach one of the leaf traces opposite the point of entry of the haustorium into the host stem. Vessel elements mature in that part of the haustorium embedded in the host stem (fig. 37). There they connect with vessel elements of the host to form two to five continuous vessels reaching from the host to the parasite, through the haustorium.

In the general region of the host phloem, the penetration portion of the haustorium branches. Branches grow to the host phloem. Cells which contact the host phloem are thin walled, parenchymatous, and frequently nucleated (fig. 37). These are probably undifferentiated sieve elements. Mature sieve elements are present in older parts of the haustorium which are identical to sieve elements in the parasite stem. Companion cells are absent.

Cassytha melantha.--Host: Self-parasitism. Collections of this species did not provide suitable material to demonstrate parasitism by mature haustoria on the host specimen. In the specimen received, however, there were numerous examples of self-parasitism in which a stem of the parasite had doubled back on itself and subsequently produced haustoria which penetrated the "host" stem. This type of self-parasitism is common in all species.

After contact between the haustorium and "host" stem, the penetration portion of the haustorium grows out of the attachment cup and into the host. Growth continues, pushing the penetration wedge through the cortex, between two of the large phloem bundles and into the xylem cylinder. At this point, its tip fans out so that a part grows to the metaphloem in the large phloem bundles on either side (fig. 33). Vessel element to vessel element connections between the haustorium and "host" are secured forming continuous vessels from one to the other.

Direct sieve element to sieve element connections between the "host" and parasite have not been observed. Phloem is present in the haustorium, located just external to the xylem, and comprises sieve elements, companion cells, and phloem parenchyma (fig. 33). Cells of

the haustorium which grow to the phloem of the "host" portion of the stem are identical to those described in the haustoria of other species of Cassytha.

Stem Tip

The stem tip of Cassytha has a tunica-corpus organization. The single layer of tunica cells is characterized by anticlinal cell divisions. Beneath the tunica is an outer layer of corpus cells, much resembling a second layer of tunica, but characterized by both anticlinal and periclinal cell divisions. Below this there is a small mass of corpus cells characterized by cell divisions which occur in all planes. A detailed description of the shoot apex of C. filiformis is given by Cutter (1955).

In transverse section three distinct histogenic regions can be seen in the stem tips of various species of Cassytha. These are protoderm, ground meristem, and procambium.

Protoderm.--Protoderm consists of the outer layer of cells covering the immature stem. It gives rise to the uniseriate epidermis, both on the mature stem and leaves. Cells of this region appear slightly rectangular in surface view; they are closely fitted together, have large nuclei, and densely staining cytoplasm (fig. 13). Individual cells undergo frequent anticlinal divisions. Protoderm cells frequently mature as trichomes which begin to develop at about 250μ below the stem tip (fig. 15). Trichomes are numerous around the stem tips of all species, except C. glabella where they are absent. Trichomes are less prevalent, or absent, on older parts of the stem. The first evidence of trichome formation is the development of a bulge in the outer periclinal wall of a protoderm cell (fig. 15). The bulge continues to en-

large, frequently with the nucleus moving out into the enlarging protuberance. Gradually this bulge begins to assume the shape of the mature trichome. Complete, intact trichomes are difficult to find as they are frequently broken, probably by the growth habit of the parasite or by embedding and sectioning procedures. They are extremely long, however, measuring up to 450μ in length.

Ground meristem.--The ground meristem gives rise to the cortex and pith of the stem and to the mesophyll of the leaf. It becomes distinguishable as a definite histogenic region 80-100μ below the stem tip. Up to this point all cells in the stem tip look alike; small and meristematic with densely staining cytoplasm and large nuclei. Cells of the ground meristem gradually enlarge and appear to become highly vacuolated with the nucleus becoming conspicuously smaller in relation to the size of the cell (fig. 13). That segment of the ground meristem which will develop into pith becomes distinctive first, followed shortly by that portion which will ultimately develop into cortex and hypodermis.

Procambium.--The procambium, which develops into the primary vascular tissues, first appears as "patches" of small, densely cytoplasmic cells embedded in the ground meristem (fig. 13). Xylary and phloic procambial cells are located in distinct bundles separated from one another by two to three layers of ground meristem cells (fig. 13). There are more bundles of phloic than of xylary procambial tissue. The phloic procambial strands are alternately large and small. Increases in the amount of phloic and xylary procambial tissue occur as a result of both periclinal and anticlinal divisions of their respective cells. These

divisions continue to occur well after the first primary phloem and primary xylem cells have matured from the procambium.

The first protophloem cells mature from the phloic procambium at between 120-150 μ below the stem tip. The first phloem cells which mature to the outside of the procambial strand are sieve elements (fig. 14). These sieve elements eventually are crushed, however, as fibers with thick nacreous walls begin to mature from surrounding phloic procambial cells. Internal to these first phloem cells, one or two of the procambial cells begin to enlarge greatly (fig. 14). As they continue to expand, their nuclei disappear and ultimately their cell walls break down resulting in the formation of a lysigenous cavity. Metaphloem matures internal to this lysigenous cavity.

Protoxylem begins to mature at between 340-350 μ below the stem tip. The protoxylem matures from the innermost portions of the xylary procambium and comprises small groups of two to five protoxylem vessel elements scattered around the periphery of the pith (fig. 13). Maturation of the primary xylem is endarch with the metaxylem maturing external to the protoxylem. The first metaxylem cells to mature are large vessel elements. Interspersed among these are the other metaxylem cells composed of narrower vessel elements and parenchyma cells.

Leaves

Leaves are produced alternately. They occur only near the growing tip of the stem, extending down about 4000μ, and below this point they are absent. Leaves remain in a position parallel with the long axis of the stem. The short, parenchymatous petiole is attached submarginally to the inner (adaxial) surface of the blade. When viewed in transverse section, the leaf blade is shaped somewhat like a flattened triangle (fig. 45). The blade consists of an outer or abaxial surface and an inner or adaxial surface. The abaxial surface is covered by a uniseriate epidermis comprising cells which are irregularly circular when observed in transverse section and slightly rectangular in longitudinal view. This epidermis is covered by a thick cuticle. Stomata are present, arranged in longitudinal rows, and are identical to those on the parasite stem. Epidermal cells may be modified as trichomes or secretory cells. The adaxial surface is also covered by a uniseriate layer of epidermal cells. These cells are smaller in size and more regular in shape than cells of the abaxial epidermal layer. They are rectangular in transverse section and columnar in longitudinal section. The cuticle is extremely thin. No stomata or trichomes are present in the adaxial epidermal layer.

The mesophyll is homogenous, that is, there is no distinction between a palisade and spongy layer, and comprises chlorenchyma cells which are highly variable in size. Small intercellular spaces occur among the cells. Small groups of one to three cells in the mesophyll gradually become greatly enlarged and ultimately break down leaving

large cavities of irregular size and shape (fig. 45). Secretory cells and raphide-bearing cells are frequently found in the mesophyll.

Conductive tissue in the leaf blade consists solely of a central vein of primary xylem tracheary elements which passes through the center to the tip of the leaf, thus dissecting the blade into non-vascularized halves. This central vein originates from a single vascular trace departing from one of the protoxylem bundles in the stem (fig. 46). The trace passes through the short, parenchymatous petiole and into the leaf blade. Vessel elements in the leaf are short and mostly have spiral or helical, transitional to reticulate secondary cell walls. Some elements with circular bordered pits may also occur in the leaf.

Phloem, which arises as a small trace from one of the protophloem bundles in the stem, comprises only three to four protophloem fibers located abaxially to the primary xylem (fig. 46). The phloem cells do not extend all the way to the tip of the leaf.

In the axils of the leaves there are small lateral buds which are identical in cellular constitution to the apical meristem of the stem tip (fig. 46). These buds give rise to lateral branches of the stem.

DISCUSSION

The distribution of Cassytha, especially C. filiformis, is reflective of the distribution of the Lauraceae in general in that both are found primarily in the tropics and sub-tropics. Lauraceous genera occupy diverse habitats in both hemispheres with approximately equal numbers of genera in tropical America and tropical Asia (Kostermans 1957, Hutchinson 1964). However, of the 31 genera accepted by Kostermans, only seven are considered to be pantropical in distribution. Interestingly, both Cassytha and Cryptocarya, which have remarkably similar floral structures, comprise two of the seven pantropical genera.

When one considers that most of the species of Cassytha are narrowly distributed geographically, that is, most of the species are tropical and occur in Australia and the Malay Archipelago, it is probably not too surprising that their anatomical characters are strikingly homogenous. Indeed, according to Metcalfe and Chalk (1950) and Hutchinson (1964), the entire laurel family is a remarkably homogenous group, both in general anatomy and floral morphology. The various genera are often separated on the basis of "quite trivial characters" (Hutchinson, 1964). Stern (1954) states that intrageneric xylem anatomical differences are frequently greater than intergeneric xylem anatomical differences. In the face of this, it is surprising, at least to me, that no appreciable anatomical differences exist between C. filiformis, which is ubiquitous in the tropical and subtropical regions

of the world, and those species which are confined to infinitely smaller geographical regions. In those regions where C. filiformis does occur, it often appears to be restricted to maritime habitats, a fact which led Wiens (1962) to postulate that Cassytha fruits could be disseminated by oceans. This still, of course, does not provide an answer to why C. filiformis has achieved such a broad geographical distribution, whereas other species of Cassytha, occupying the same habitat, are restricted in range.

The vegetative anatomy of the Lauraceae has been summarized by Metcalfe and Chalk (1950) and also by Stern (1954). Anatomically there are many points of similarity between Cassytha and other lauraceous genera. On the basis of this study, there is certainly no anatomical justification for the separation of Cassytha into a separate, monogeneric family as proposed by Lindley (1853). I would concur with those taxonomists, i. e., Kostermans (1957) and Thorne (1968), who ascribe to these parasites a subfamilial status.

Stem

The stem anatomy of Cassytha, especially of C. filiformis has been studied by several investigators including Schmidt (1902), Boewig (1904), Mirande (1905), and Kienholz (1926). These works have been summarized both by Solereder (1908) and Metcalfe and Chalk (1950). As mentioned previously, however, certain discrepancies exist among the observations and descriptions of these various investigators.

In taxonomic descriptions of Cassytha, stem sizes are frequently given as a distinguishing characteristic among the species (Meissner 1864, Black 1948). For this reason, measurements of stem diameters

were made. The five species measured fell into two groups. C. ciliolata and C. glabella were found to be small stem species, while C. pubescens, C. filiformis, and C. melantha have appreciably larger stem diameters. These data concur with the taxonomic descriptions given by Black in which he listed C. glabella, C. pubescens, and C. melantha, in that order, in reference to increasing stem thickness.

Almost every investigator who has studied Cassytha records the presence of a relatively thick, furrowed cuticle. However, no comparative cuticular measurements among various species have been reported. Such measurements were made here and from these data only C. pubescens was found to be distinctive, having a considerably thinner cuticle than that of the other four species studied. Also, the outer periphery of the cuticle was studied closely. In C. ciliolata and C. pubescens this outer edge was found to be distinctly serrated while in C. filiformis, C. glabella, and C. melantha, it was found to be only slightly serrated to smooth.

The epidermis of each species is uniseriate and comprises cells which are shield shaped when viewed in transverse section and columnar in longitudinal section. While lengths of epidermal cells within a given species may vary slightly, no significant overall interspecific variation was observed. Some epidermal cells may become modified as secretory cells which, in longitudinal view, frequently appear in short rows of vertically elongated cells. As pointed out later, there are certain analogies that can be drawn between the stems of Cassytha and "typical" dicotyledonous leaves. In view of these analogies, it is interesting to point out that leaves of many lauraceous genera contain secretory cells, usually in the palisade or spongy layer. In the genus

Umbellularia, however, secretory cells have also been reported in the lower epidermis of the leaf (Metcalfe and Chalk). In C. pubescens and C. melantha mature epidermal cells may also be modified as trichomes which are unicellular and thick walled, as in other members of the Lauraceae (Metcalfe and Chalk).

According to Metcalfe and Chalk, two types of secretory cells occur in the Lauraceae. Oil cells are usually spherical in shape and have yellowish contents. Mucilage cells are similar in shape to oil cells but are distinguishable from the former because of their contents. In Cassytha the secretory cells, which occur throughout the stem and leaf, are of the mucilage type and contain deep staining, amorphous deposits.

The stomata of C. filiformis were first completely described by Schmidt (1902) and later by Boewig. McLuckie (1924) and Kienholz also described the stomata of C. filiformis. All these investigators noted the peculiar arrangement of stomata in longitudinal rows, oriented at right angles to the long axis of the stem. As in other members of the Lauraceae, the stomata of Cassytha are of the paracytic type.

Boewig stated that stomata are always separated by two cells, a conclusion which is not borne out by my study. Rather, I observed that individual stomatal apparatuses could immediately abut one another or they could be separated by usually one to four epidermal cells.

Neither Boewig nor McLuckie mentioned the occurrence of horns on the guard cells. In transverse view of the stomatal apparatus, however, both guard and accessory cells can be observed to possess small horns which are slightly curved toward the stoma. These horns are covered by cuticular material, thus creating the impression of separate cuticu-

lar ridges. In face view the horn of the accessory cell appears as a small ridge which projects over the thickened common wall between the accessory cell and the narrow, bow-shaped guard cell. In this view also, the end of the guard cells taper to slightly rounded points with thickened walls.

In all the species considered in this study, the outermost single layer of cortical tissue comprises a hypodermis which forms a continuous band of cells beneath the epidermis interrupted only by the substomatal chambers. Contrary to the statements of Kienholz, chloroplasts are occasionally found in the hypodermal cells. Exclusive of the hypodermis, the remainder of the cortex is a distinctly dimorphic tissue. Kienholz observed that the layers of cortical cells beneath the hypodermis were elongated at right angles to the stem axis and contained numerous chloroplasts, thus closely resembling palisade mesophyll cells. He did not observe, however, that internal to these there are two to three layers of parenchymatous cells which appear circular in transverse section and which also contain chloroplasts. This dimorphism imparts a very leaf-like appearance to the cortex which is particularly obvious beneath the longitudinal rows of stomata, where the outer, "palisade-layers" are very loosely arranged and numerous large intercellular spaces are present. Such a cortex-leaf analogy becomes especially interesting when one also considers the presence of a distinct hypodermis. According to Metcalfe and Chalk, a hypodermis is present beneath the adaxial leaf surface of various lauraceous genera including species of Beilschmiedia, Cryptocarya, Endiandra, Endlicheria, Litsea, Nectandra, Ocotea, Persea, and others.

One of the most intriguing speculations about the stem anatomy of

Cassytha concerns the presence or absence of a morphologically distinct endodermis. Boewig made no mention of an endodermis. Mirande described, in great detail, an endodermis in the stem of C. filiformis. Later, both McLuckie and Kienholz, stated that no definite endodermis was present. Kuijt (1969) points out that this is a question still to be answered. An endodermis, which conforms to the definition of Esau (1965) as a layer of tissue surrounding the vascular cylinder and being characterized either by distinctive wall markings or by the accumulation of more abundant starch deposits than in the surrounding cortical cells, is absent. Cortical cells, including the hypodermis, all contain chloroplasts and are distinguishable from one another only in the ways already mentioned. Both secretory cells and lysigenous cavities are found in the cortex which is generally a lacunose tissue.

In each species the central portion of the stem is occupied by a parenchymatous pith. Pith cells, contrary to the statement of Boewig, are living cells with distinct nuclei. I could not verify the observation of Kienholz that pith cells contained an abundance of stored food. Small amounts of starch were occasionally observed in the pith but never in great abundance.

The vascular tissues in the stem of Cassytha, except for the endarch development of primary xylem, are similar in appearance to the primary vascular tissues in roots of many dicotyledonous plants.

In roots the phloem occurs as discrete strands situated near the periphery of the vascular cylinder and beneath the pericycle. Xylem may be in discrete strands which alternate with the phloem or in the form of a fluted cylinder (Esau). In Cassytha the primary xylem cylinder is polyarch, radiating into small arms along its outer periphery.

Nestled between these xylem arms are small bundles of primary phloem separated from the xylem by a single layer of undifferentiated procambium. Off the tips of the xylem arms, between the large phloem bundles are small groups of thick-walled fibrous elements, except in C. glabella where they are absent. The number of arms to the xylem cylinder and the number of phloem bundles vary with the size of the stem, C. pubescens and C. glabella having slightly more than the other species.

In both the small bundles off the tips of the xylem arms and over the outer periphery of the phloem cavities, the fibers which develop are phloic in origin. According to Esau (1965, 1969), the procambial origin of these types of fibers has been reported in several families; however, she does not specifically mention the Lauraceae. These fibers form a pericycle which is a part of the ground tissue of the stele located between the phloem and cortex (Esau 1960). The pericyclic fibers of Cassytha are primary phloem fibers which develop from the individual patches of phloic procambium. The pericycle of Cassytha is frequently interrupted by cortical parenchyma cells. Boewig stated that the "hard bast" was developed from the phloem; however, she also said that as the fibers were forming, the "true phloem" disintegrated and its function was replaced by patches of phloem internal to the xylem cylinder. Mirande correctly discounted this; however, he said the pericycle was formed from special cells sandwiched between the "hammer-cells" of the endodermis. This is also incorrect. As stated above, the pericyclic fibers are phloic in origin. McLuckie, Kienholz, and Cutter (1955), who studied the shoot apex of C. filiformis in detail, did not mention the origin of these pericyclic fibers.

In each large phloem bundle, beneath the protophloem fibers, a lysigenous cavity develops. Mirande attributed the formation of these cavities to large cells in the developing phloem. Boewig and later, Kienholz, attributed the formation of these cavities to a crushing or disintegration of the protophloem. Cutter recognized the occurrence of large cells in the procambial material and quoted Mirande in presuming that these cells break down to form lysigenous cavities. This study has shown that one or two cells, slightly internal to the first developing protophloem cells, begin to enlarge greatly and to develop conspicuously enlarged nuclei. The nuclei, along with the cell walls, eventually break down producing these large, lysigenous cavities.

Maturation of the primary xylem is endarch, each species having small groups of protoxylem cells scattered around the periphery of the pith. The number of protoxylem strands varies with the size of the stem; generally, the larger stemmed species having more strands than the smaller stemmed species. All the investigators cited for their work on the stem anatomy of Cassytha have described the large metaxylem vessel elements with distinct circular bordered pits which mature just external to the protoxylem strands. No evidence has been found, however, that these botanists prepared macerations of xylem tissue in order to study the metaxylem cells forming the remainder of the primary xylem cylinder.

In describing the xylem of Cassytha, Boewig reported the presence of a continuous cylinder of wood which comprised large and small pitted vessel elements with circular bordered pits in their end walls, and frequently containing tyloses. She also reported "faintly present" medullary rays in older stems. A few vessel elements, with a single

tapered end wall, do have circular bordered pits in the tip of such walls. Tyloses and medullary rays, however, were not observed in this study. McLuckie stated that the xylem was composed of a few large pitted vessels, numerous xylem parenchyma cells, and wood fibers. Kienholz simply stated that the xylem comprised large, pitted vessels and smaller elements. Macerations of stem tissue, however, showed some of these findings to be erroneous. The primary xylem cylinder is composed entirely of protoxylem and metaxylem vessel elements of variable sizes and of xylem parenchyma cells. Fibers and other imperforate tracheary elements are absent.

Stern studied the secondary xylem anatomy of several lauraceous genera. Although valid comparisons cannot be made between primary and secondary xylem, there are several analogies between the xylem of Cassytha and other members of Lauraceae. In Lauraceae, perforation plates are simple to scalariform, pores are angular to circular--tending to angularity, pit borders are round to elliptical, and intervascular pitting is usually alternate. In Cassytha, perforation plates are exclusively simple, pores are angular, pit borders are round, and intervascular pitting is alternate. The bordered pits of Cassytha have distinct tori. While valid comparisons can be made only between the xylem of Cassytha and the primary xylem of other laurels, these analogies at least show that Cassytha, anatomically, is not drastically unlike its lauraceous relatives.

The occurrence of tori is rare, but not unknown, among Angiosperms (Esau 1965). Since tori have a presumed regulatory function in the passage of water through bordered pits, their occurrence in a parasitic plant is intriguing. Possibly these structures function to regulate

water flow in the parasite depending upon the water conditions in the host plant. For example, if the water supply of the host plant becomes critically low could these tori plug up the vessel elements in the parasite stem to prevent a reverse flow of water from the parasite, through the haustoria, to the host!

Mirande first mentioned the occurrence of secondary growth in C. filiformis. Kienholz also discussed the presence of a cambium and the production of secondary tissue. According to Mirande, this type of growth occurs mainly at the nodes and on the outer side of the parasite stem, i. e., the side which is not in contact with the host plant. Indeed, a type of lateral meristem does develop from the undifferentiated procambial strands which produces radial files of secondary xylem cells to the inside and a small amount of secondary phloem to the outside, beneath the metaphloem. Also the single row of cells between the phloem bundles and immediately external to the primary xylem cylinder, divides periclinally producing cells to the inside which mature into xylem tracheary elements. This kind of growth, however, does not appear to be related to nodes, rather to the production of haustoria, and it does not occur all along the length of the parasite stem. Further, the amount of such tissues which is produced appears to be directly related to the amount of xylem present in the host plant. When the host plant is herbaceous or only slightly woody, the amount of secondary growth in the parasite is small, or completely absent. If the host plant has a considerable amount of secondary xylem, the amount of secondary tissue produced in the parasite is appreciably larger. From this, it appears that secondary growth in Cassytha forms a mechanical buttress which strengthens the parasite stem at the point

where haustoria are produced and subsequently penetrate woody host plants. Also, secondary growth in this region increases the amount of conductive tissue in the parasite at the point where materials from the host are entering the parasite stem.

Haustoria

In his book, Kuijt pointed out the great lack of information on the haustorial structure of Cassytha. The only important works on Cassytha haustoria are those of McLuckie and Cartellieri (1928). Because of this lack of information, a discussion of the haustorium is presented here with reference to these authors being made only on important points of disagreement.

Several similarities exist between the haustoria of Cassytha and the adventitious roots of "typical" dicots. These prompt one to conjecture if the haustoria themselves are a type of adventitious root. First, both structures have the same function, that is, to attach the plant to a substrate and to absorb water and other essential substances from that substrate. Secondly, their origin is similar, both arising endogenously in stems. Adventitious root primordia are initiated near the periphery of the vascular cylinder or even deeper, near the vascular cambium (Esau 1965). The primordium that forms the penetration portion of a haustorium arises from dedifferentiated parenchyma cells immediately external to the primary xylem cylinder. In both adventitious roots and haustoria an apical meristem is formed. Cell divisions in this apical meristem cause these structures to grow through the peripheral tissues of the stem and ultimately, to break through the epidermis and grow into their respective substrates. Because of these

similarities, I believe the haustoria comprise a specialized adventitious root system which utilizes other plants, rather than soil, as a substrate.

Each haustorium consists of two distinct parts, each arising from different meristematic areas, not from a common primordium as indicated by Cartellieri. The attachment cup arises from radial and transverse cell divisions in the epidermis and the outer two to three layers of cortical cells. Coincident with the development of the attachment cup, tangential divisions begin to occur in the single row of cells immediately external to the primary xylem and between two phloem bundles, and also in metaphloem parenchyma cells; not, as stated by McLuckie, from cells external to the pericyclic fibers. These divisions produce the penetration wedge.

McLuckie stated that haustoria frequently branched before actually penetrating the host tissues. However, my observations indicate that although such branching occurred, it was by no means common.

Cartellieri noted that surrounding this central mass of xylem in the haustoria of Cassytha pubescens there are approximately two to six layers of undifferentiated procambial cells, several layers of elongated parenchyma cells, and vessel elements external to these parenchyma cells. In C. glabella, an arc of small vessel elements, two to four cells in width, is produced around the periphery of this central core, and remains separated from it by several layers of parenchyma tissue. This appears to be a distinctive feature of C. glabella as it is always present. However, these vessel elements were not observed in C. pubescens or any of the other species.

McLuckie stated that phloem was absent from haustoria. Sieve

tube elements, however, are present in haustoria, maturing externally to the xylem tissue. Sieve tube elements are joined together to form sieve tubes which are clearly connected with the phloem in the parasite stem. Companion cells are also present.

The central mass of xylem cells gradually tapers, and usually only about two to six continuous xylem vessels mature in the portion of the penetration wedge embedded in the host plant. These vessels connect with vessels in the host plant forming continuous vessels from parasite to host via the haustoria. There appears to be definite selectivity in the formation of connections between vessel elements of the host and parasite. Xylem association between host and haustorium was always a vessel element to vessel element connection. Vessel elements in the haustorium were never connected with any tracheary elements of the host other than vessel elements. The exact mechanism by which vessel elements in the haustorium joins with vessel elements in the host has never been observed. As Kuijt points out, this is another area in which our knowledge is incomplete and which needs to be studied.

Clearly defined connections between the phloem of host and haustorium were not observed; however, in one or two instances, haustorial cells which appeared to be sieve elements were seen in direct contact with the host phloem. No clear cut sieve tube from parasite, through haustorium, to host was found. Kuijt mentions the possibility of a phloem gap between the haustoria and host; however, I do not subscribe to this idea. These connections do exist and will probably be revealed through more critical studies.

The mode of haustorial penetration is the same in each species of Cassytha: that is, contact of the attachment cup of the haustorium

with the host plant is followed by growth of the penetration wedge through the attachment cup into the host plant where it reaches the vascular cylinder. The penetration wedge, in all species, branches either on one or both sides as it is growing through the cortical region of the host. Branches of the penetration wedge grow into the host phloem, while the central portion grows into the host xylem. McLuckie confined such branching only to the haustoria of C. melantha. In some species of Cassytha these branches are large and very conspicuous while in others they are small, inconspicuous, and appear as only one or two cells which curve toward the host phloem. The size of these branches, however, is probably related to the proximity of the host phloem to the haustorium and is not a species characteristic.

Most observers have stated that Cassytha appears to grow best on woody plants. For this reason, C. filiformis was sectioned and studied on Sesuvium portulacastrum in an attempt to find the reasons for its poor growth on a herbaceous plant. The cortex, of older stems of this host, is extremely thick and succulent while younger stems have proportionally smaller cortical regions. It was found that when the cortical region was less than approximately 850μ in diameter, haustoria were able to grow through the cortex to reach the vascular cylinder. When the cortical region was appreciably thicker, however, the haustoria never grew all the way down to the host vascular tissues. This would seem to indicate that the individual haustorium is not capable of indefinite growth and since many herbaceous plants have thick cortical regions, this may account for the poor growth of the parasite on such hosts. Also, as pointed out earlier, the parasite itself tends to develop a more extensive xylem system when growing on a woody host

plant. Possibly the soft stems of herbaceous plants do not provide the stimulus for developing extensive secondary tissues in Cassytha.

Lastly, McLuckie described the morphological structure of the haustorial penetration wedge. While this structure is usually wedge shaped and slightly rounded at the tip when the host plants are woody, the shape is plastic and in the same species of Cassytha, it changes from one host plant to another. Particular haustorial shapes are not characteristic of individual species, as suggested by McLuckie. The tip may dichotomize or become foot-shaped when it contacts the vascular cylinder of a host, or if this cylinder is small, the penetration wedge may grow entirely through the vascular tissue with the tip becoming somewhat flared.

Stem Tip

The stem tip of C. filiformis has been studied both by Boewig and Cutter. I can concur with most of the observations of these authors, except where special differences are noted below.

The stem tip is surrounded by a uniseriate layer of protoderm cells which are frequently modified as trichomes except in C. glabella. As pointed out by Boewig, the procambial material is divided into separate phloic and xylary precursors separated by two to three layers of ground meristem. She asserted, however, that these precursors always differentiated into four protoxylem strands and 12 protophloem strands. I did not find this consistency to exist for all species. The number of procambial strands varies, smaller-stemmed species having fewer than larger-stemmed species as reflected by the number of phloem bundles and protoxylem strands in the mature parasite stem.

Protophloem sieve elements develop before protoxylem vessel elements. They develop toward the outer part of the phloic procambium; however, they become crushed as the protophloem fibers begin to develop. In longitudinal section, the crushed remains of sieve plates, originally associated with conducting cells of the protophloem, are occasionally found among these protophloem fibers. Beneath the protophloem sieve elements are one or two cells which become greatly enlarged and ultimately develop into lysigenous cavities.

Stomata are present only in the abaxial epidermal layer, contrary to the statement by Boewig that these structures are present in both epidermal layers. Boewig also indicated that stomata were scattered in the epidermal surfaces of the leaves and that each leaf was supplied by three veins. However, in section, the stomata are definitely oriented in longitudinal rows, and are identical in form and distribution to those present on the parasite stem. Furthermore, leaves are dissected only by a single, central vascular bundle.

SUMMARY AND CONCLUSIONS

Anatomical studies of five species of Cassytha from widely separated geographical locations indicate that the group is remarkably homogeneous. Each species possesses a moderate to thick, furrowed cuticle, uniseriate epidermal layer, paracytic stomatal apparatus, distinct hypodermis, dimorphic cortex, and a polyarc protoxylem cylinder surrounding a parenchymatous pith. The primary xylem of all species comprises: 1. vessel elements with mostly terminal, simple perforation plates, and alternately arranged circular bordered intervascular pits with distinct tori, and 2. lignified xylem parenchyma cells. Phloem, which is arranged in large bundles nestled between the primary xylem arcs, comprises protophloem fibers and metaphloem sieve tube elements, companion cells, parenchyma cells, and occasional fibers. Adjacent to the tips of the xylem arms are small patches composed only of protophloem fibers. Secretory cells are found in the epidermis, cortex, pith, and very occasionally in the phloem parenchyma.

Haustoria are analogous to adventitious roots in origin, structure, and function. Each haustorium consists of two parts, each arising endogenously from separate meristems. Morphology of the haustorial penetration wedge is variable, depending upon the amount and arrangement of vascular tissue in the host plant. Vessel elements in the haustorium always connect to vessel elements in the host plant. Sieve tubes are also present in the haustorium, but no direct sieve tube to sieve tube connection between parasite and host was observed.

Stem tips have a tunica-corpus organization. A single layer of tunica cells is subtended by a mass of corpus cells. Phloic and xylary procambial material is arranged in separate procambial strands separated by ground meristem cells. The number of phloic procambial strands is greater than the number of xylary procambial strands. Ontogenetically, protophloem begins to mature before protoxylem.

Leaves are alternately arranged, greatly reduced, and triangular in shape when viewed in transverse section. In position, the long axis of the leaf remains parallel to the stem. Mesophyll cells are homogeceous and contain few chloroplasts. Cells in the adaxial epidermal layer may be modified as trichomes.

Anatomical evidence, combined with similarities of floral structure, and the embryological evidence presented by Sastri, form a syndrome of characters which shows a definite relationship between Cassytha and other laurels. Among these anatomical characters are the ubiquitous presence of secretory cells, paracytic stomata, a hypodermis in the "leaf-like" cortical region of the stem, simple perforation plates, alternate intervascular pitting, distinct circular bordered intervascular pits, the presence of raphide crystals in non-lignified tissues, the occurrence of an interrupted ring of pericyclic fibers, and the presence of unicellular, thick-walled trichomes in some species. Because of the great difference in life form between Cassytha and other laurels, I support the views of Kostermans, Thorne, and others in placing the parasite in a separate subfamily within the Lauraceae but not in a different family as has been recommended by other taxonomists.

Among the five species studied, few anatomical characters of taxonomic significance were found. C. ciliolata and C. melantha appeared

to be distinctive because of their stem diameters. In the former, stem diameter was appreciably smaller than in the other species and in the latter it was appreciably larger. This distinction, however, may well be proven invalid when further species are examined. C. pubescens and C. melantha are distinctive because of the occurrence of trichomes on the mature stem. The most distinctive species anatomically was C. glabella where the absence of small patches of phloem fibers adjacent to the tips of the xylem arms and the presence of vessel elements in an arc external to the central core of primary xylem in the haustorium, are unique features.

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Figure 1. Cassytha ciliolata. Stem, cross-section, illustrating cuticle, epidermis, and hypodermis (arrow). 250X.

Figure 2. Cassytha melantha. Stem, cross-section, illustrating cortex, sub-stomatal cavity (upper arrow), and lysigenous cavity in the cortex (lower arrow). 250X.

Figure 3. Cassytha pubescens. Stem, cross-section, illustrating protophloem fibers (arrow) and underlying protophloem lysigenous cavity. 250X.

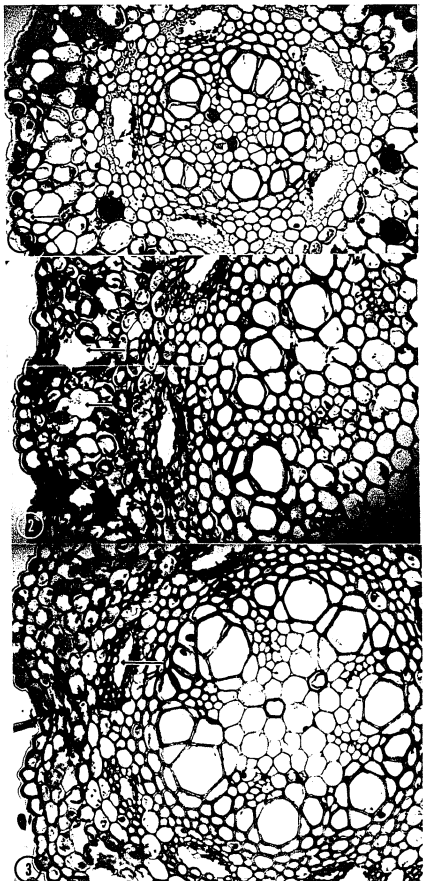


Figure 4. Cassytha glabella. Stem, cross-section, illustrating metaxylem vessel elements (upper arrow), and metaphloem (lower arrow). 250X.

Figure 5. Cassytha filiformis. Stem, cross-section, illustrating secretory cells (upper arrow), and protoxylem strand (lower arrow). 1000X.

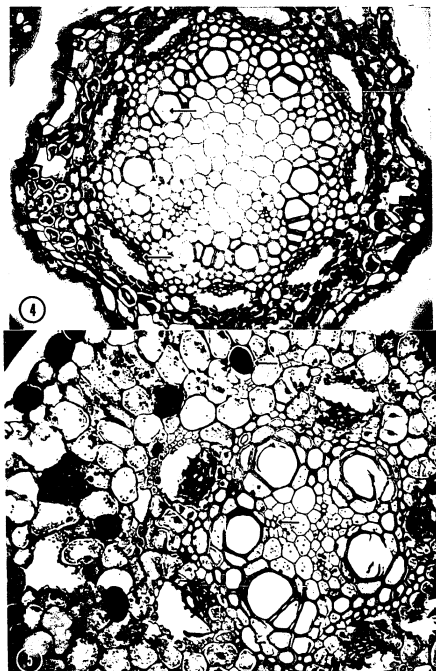


Figure 6. Cassytha melantha. Stomatal apparatuses, cross-section (longitudinal section of parasite stem), illustrating a vertical row of stomata (arrow), and underlying dimorphic cortex. 310X.

Figure 7. Cassytha melantha. Stomatal apparatuses, cross-section (longitudinal section of parasite stem), illustrating sunken guard cells (arrow), and adjacent horned accessory cells. 1000X.

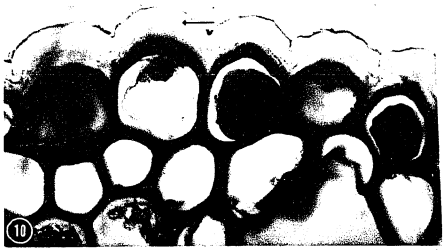
Figure 8. Cassytha glabella. Stomatal apparatuses, from cross-section of stem, illustrating longitudinal section of guard cell (arrow). 1250X.

Figure 9. Cassytha pubescens. Stomatal apparatus, from cross-section of stem, illustrating horned guard cell (arrow), and underlying sub-stomatal chamber. 1250X.

Figure 10. Cassytha ciliolata. Stem, cross-section, illustrating a thick furrowed cuticle (arrow). 1250X.

Figure 11. Cassytha glabella. Stem, cross-section, illustrating a non-furrowed cuticle and epidermal cells which appear shield-shaped in section (arrow). 1250X.

Figure 12. Cassytha pubescens. Stem, longitudinal section, illustrating palisade-like nature of cortex beneath stomatal apparatuses (arrow). 310X.



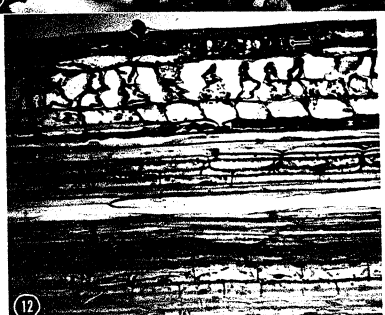


Figure 13. Cassytha pubescens. Stem tip, cross-section, illustrating separate xylary (upper arrow) and phloic (lower arrow) procambial strands. 310X.

Figure 14. Cassytha pubescens. Stem tip, cross-section, illustrating first phloem cells (arrow) and underlying enlarging cells which ultimately break down leaving lacunae. 1250X.

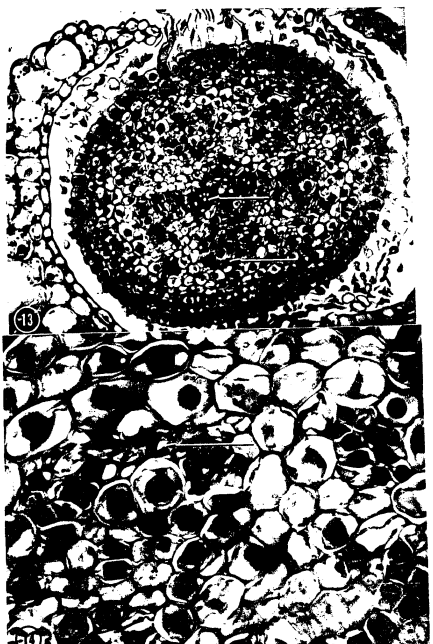


Figure 15. Cassytha pubescens. Stem tip, cross-section, illustrating developing trichomes. 1000X.

Figure 16. Cassytha pubescens. Stem, longitudinal section, illustrating a developing trichome. 1250X.

Figure 17. Cassytha pubescens. Stem, longitudinal section, illustrating a mature trichome. 1250X.

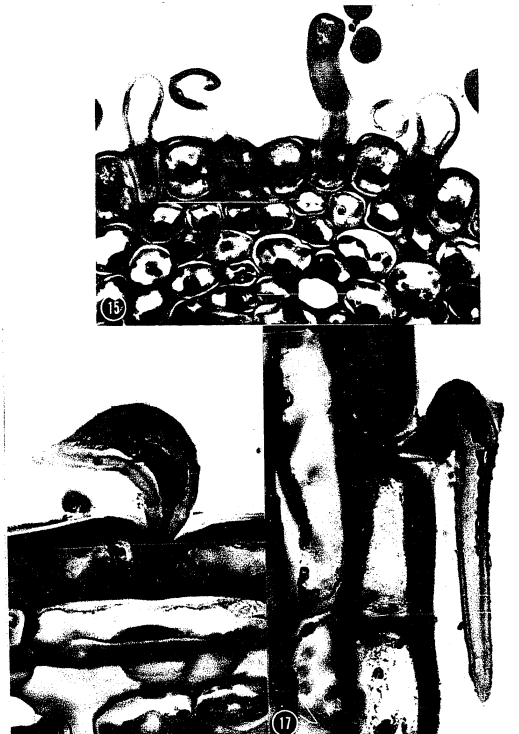


Figure 18. Cassytha pubescens. Stem, cross-section, illustrating rounded type of trichome (arrow). 1500X.

Figure 19. Cassytha melantha. Stem, longitudinal section, illustrating a branched trichome (arrow). 1000X.

Figure 20. Cassytha pubescens. Stem, cross-section, illustrating sieve plate (upper arrow), and companion cells (lower arrow). 1250X.

Figure 21. Cassytha ciliolata. Stem, longitudinal section, illustrating sieve tube element with lateral sieve areas (arrow). 1375X.

Figure 22. Cassytha pubescens. Stem, longitudinal section, illustrating slime plug (arrow) between two sieve tube elements. 310X.

Figure 23. Cassytha ciliolata. Stem, longitudinal section, illustrating a crushed sieve plate (arrow) among the protophloem fibers. 1500X.

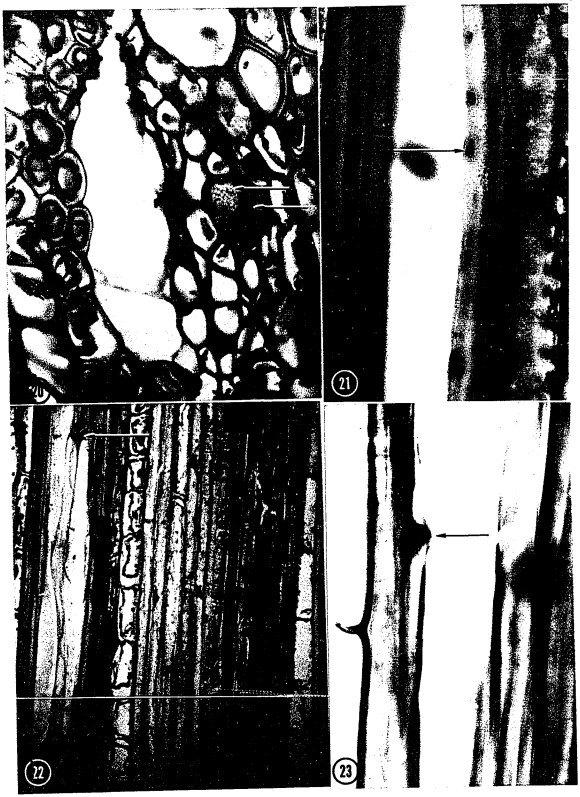


Figure 24. Cassytha pubescens. Stem, cross-section, illustrating tissues immediately above the area of haustorial formation. Note the layer of dividing cells (arrow) between the xylem and phloem. 250X.

Figure 25. Cassytha pubescens. Stem, cross-section, illustrating secondary growth in area of haustorial formation. Note radial rows of vessel elements (arrow). 250X.

Figure 26. Cassytha pubescens. Stem, cross-section, below the area of haustorial formation. Note reduced amount of secondary growth as compared with figure 25. 250X.

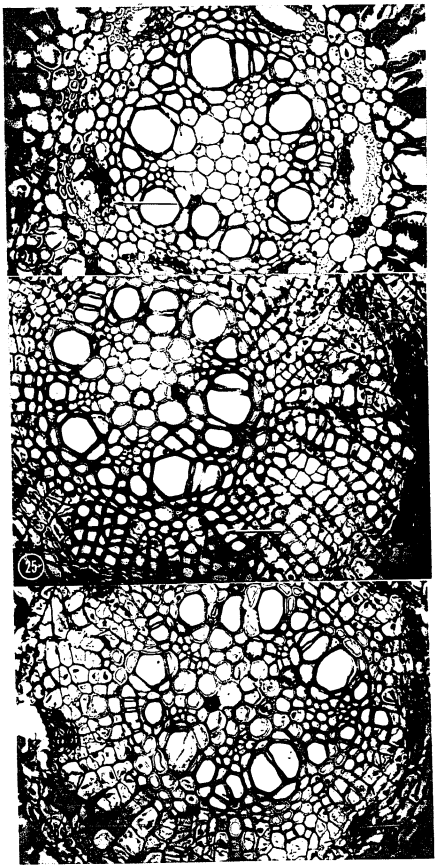


Figure 27. Cassytha pubescens. Stem, longitudinal section, illustrating cell divisions in epidermis (upper arrow) and cortex (lower arrow) to form attachment cup. 250X.

Figure 28. Cassytha pubescens. Haustorium, longitudinal section, illustrating apical meristem of penetration wedge (arrow). 250X.

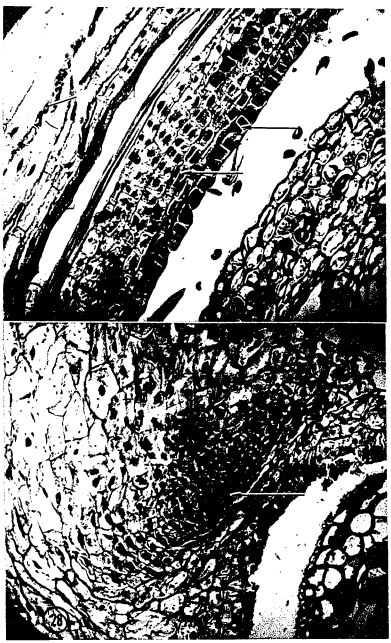


Figure 29. Cassytha filiformis. Haustorium, longitudinal section, illustrating phloem connections between haustorium and parasite stem (arrow). 310X.

Figure 30. Cassytha pubescens. Haustorium, longitudinal section, illustrating immature phloem cells in haustorium (lower arrow) emerging from phloem in parasite stem (upper arrow). 1250X.

Figure 31. Cassytha pubescens. Haustorial penetration of Leptospermum lanigerum (cross-section of Leptospermum stem). Note branching of the haustorium (arrow). 250X.

Figure 32. Cassytha pubescens. Self-parasitism, longitudinal section of haustorium, illustrating vessel element to vessel element connection between haustorium and host (lower arrow). Also note bending of haustorial tip into phloem of host (upper arrow). 250X.

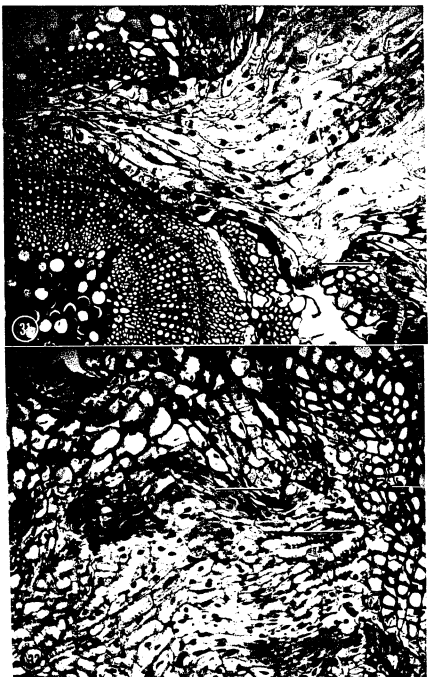


Figure 33. Cassytha melantha. Self-parasitism, longitudinal section of haustorium. Note branching of haustorium into phloem of host (arrow). 250X.

Figure 34. Cassytha ciliolata. Haustorial penetration of Passerina vulgaris (cross-section of Passerina stem). Note vessel element to vessel element connection between haustorium and host (arrow). 340X.

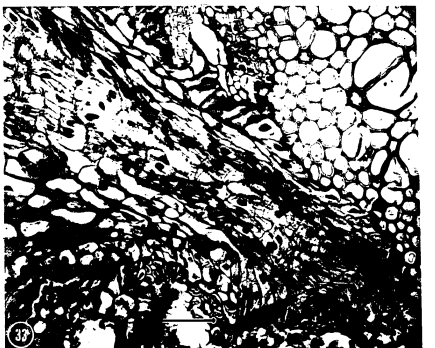


Figure 35. Cassytha glabella. Haustorium, longitudinal section, illustrating arc of vessel elements (upper arrow) external to penetration wedge (lower arrow). 250X.

Figure 36. Cassytha glabella. Haustorium, longitudinal section, illustrating xylem connections between the haustorium and parasite stem (upper arrow). Also note central mass of vessel elements in the penetration wedge (lower arrow). 250X.

Figure 37. Cassytha glabella. Haustorial penetration of Casuarina monilifera (cross-section of Casuarina stem). Note haustorial growth through the central vascular cylinder of host (arrow). 250X.

Figure 38. Cassytha filiformis. Haustorial penetration of Conocarpus erectus (cross-section of Conocarpus leaf). Note penetration of haustorial tip to host vessel elements (arrow). 250X.

Figure 39. Cassytha filiformis. Haustorial penetration of Sesuvium portulacastrum (cross-section of Sesuvium stem) illustrating successful haustorial attachment to vessel elements of the host (arrow). 250X.

Figure 40. Cassytha filiformis. Haustorial penetration of Sesuvium portulacastrum (cross-section of Sesuvium stem) illustrating unsuccessful haustorial attachment. Also note branching of haustorium (arrow). 250X.

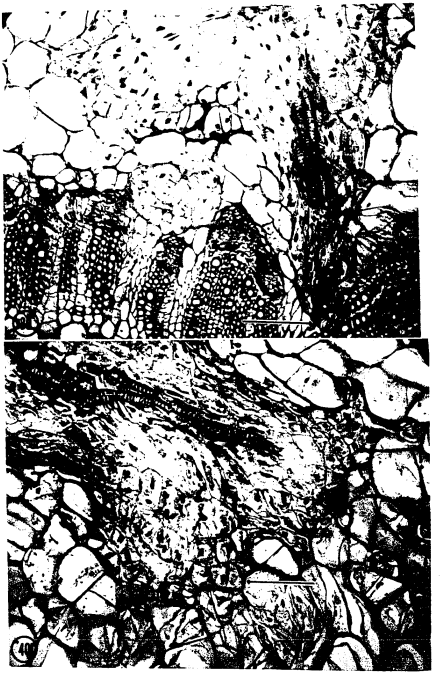


Figure 41. Cassytha filiformis. Haustorial penetration of Croton linearis (cross-section of Croton stem) illustrating branching of haustorium toward phloem of host (arrow). 250X.

Figure 42. Cassytha filiformis. Haustorial penetration of Croton linearis (cross-section of Croton stem) illustrating vessel element to vessel element connection between haustorium and host (arrow). 250X.

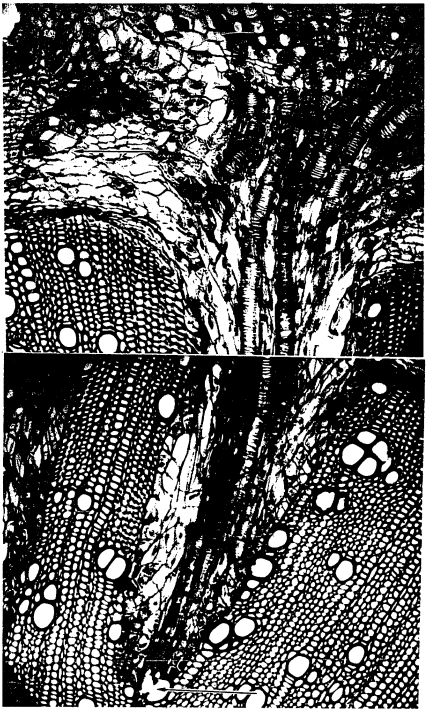


Figure 43. Cassytha pubescens. Maceration, illustrating vessel element with truncate and tapered end walls. Also note the simple vessel to parenchyma pits. 375X.

Figure 44. Cassytha pubescens. Stem, longitudinal section. illustrating vessel elements with circular bordered pits. 375X.

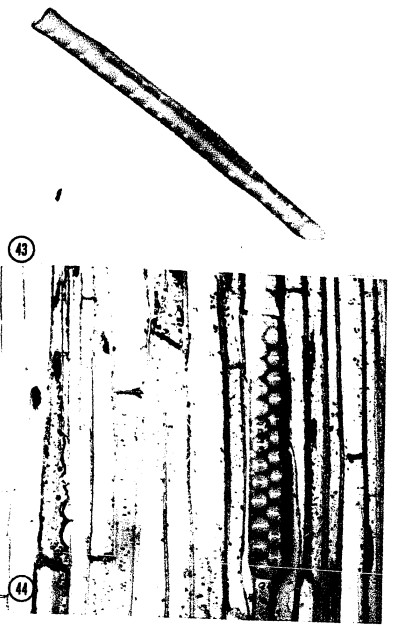


Figure 45. Cassytha pubescens. Leaf, cross-section, illustrating a lysigenous cavity in the mesophyll (upper arrow) and mid-vein (lower arrow). 310X.

Figure 46. Cassytha pubescens. Leaf, longitudinal section, illustrating submarginal attachment of leaf to stem, lateral bud (upper arrow), and vascular traces into leaf (lower arrow). 310X.

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