Observations on the Presence of Stomata in some Species of Cuscuta

T. G. YUNCKER, DePauw University

The evolutionary departure of phanerogamic plants from the way of normal autotrophic living and their development along the pathway leading to the nutritional status known as parasitism commonly involves a number of morphological changes and reductions associated with their new and more dependent way of life. The more noticeable of these changes involve the photosynthetic apparatus together with the development of haustoria which serve to attach the parasite to its host and to extract food from it. Leaves often become smaller. The chlorophyll is commonly reduced or completely lacking.

Comparisons among the large number of parasitic and saprophytic phanerogams show great differences in the amount of modification which has taken place. In the mistletoes, for example, the leaves and chlorophyll appear to be but slightly if at all reduced. In other plants, such as *Monotropa,* the reduction of the structures associated with the photosynthetic process is apparently complete.

Members of the genus *Cuscuta* are well known parasitic plants in which the leaves have been reduced to insignificant scale-like structures. They are often cited in textbooks as examples of "plants completely parasitic" because of the lack of roots, leaves, chlorophyll, and, consequently, the capacity to photosynthesize. An examination of the literature, however, shows there is, in fact, no agreement of opinion in regard to the amount of chlorophyll present, the presence or absence of stomata, or the ability of the plants to manufacture foods.

Sachs (6) says: "Like the mistletoe, so also are the species of *Cuscuta* parasitic on the aerial green shoots of woody plants: their parasitism is, however, complete, since they not only possess no roots fastening them into the soil, but they also completely lack chlorophyll, and are necessitated to take the whole of their nourishment from the host." Seifriz (7) makes the following statement: "The true parasite lacks chlorophyll and must therefore obtain all its nourishment from the host. One of the best known is the dodder, *Cuscuta.* It is a typical seed plant but lacks chlorophyll and roots, haustoria taking the place of the roots." Peirce (5) states: "After the comparatively small amount of food stored in their seeds is consumed the Cuscutas are absolutely dependent upon their hosts for food." A number of additional references might be quoted in which the statements are definitely made to the effect that species of *Cuscuta* do lack chlorophyll and thus are unable to photosynthesize.

This opinion, however, is not held by all writers. Strasburger (2), for example, states: "*Cuscuta europaea* may be cited as an example of a

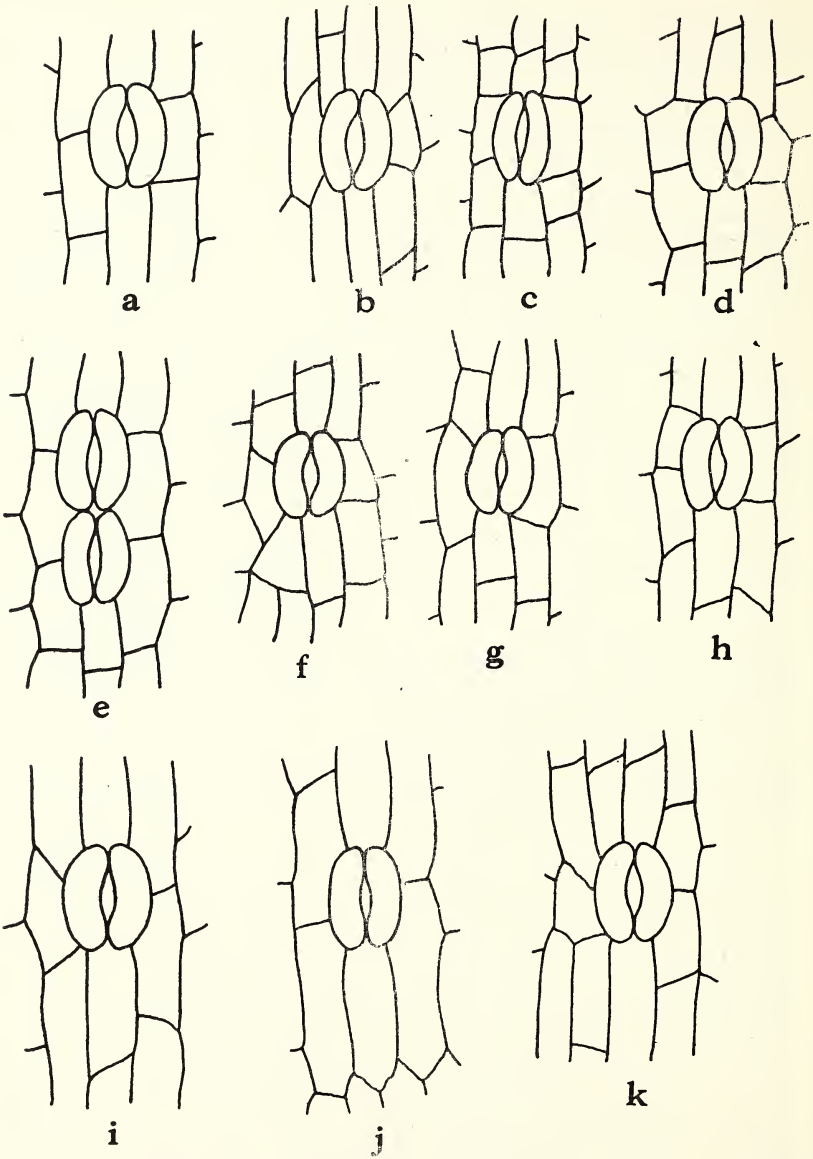
parasitic phanerogam. Although, owing to the possession of chlorophyll, it seems to some extent to resemble normally assimilating plants. . . ." Varrelman (9) says: "Dodder seed germinates and sends forth a green (protonema-like) filament. Its buds also are quite green, its fruits very green. Alcoholic and ether extracts would show that the fruits have as much chlorophyll as any other convolvulaceous plant, its buds nearly as much, its haustellate areas about half as much and other parts of the stem a little. Inasmuch as plants with little chlorophyll produce more carbohydrate per unit than those with much chlorophyll, it is quite likely that *Cuscuta* may be able to sustain itself on its own organic foods, as does mistletoe. *Cuscuta* and *Cassytha* are green plants, even though they are parasites. They do contain chlorophyll, both alpha and beta."

Observations of different species of *Cuscuta* while living show a great deal of variation with respect to the amount of green color which they display. Some species are unquestionably green to a greater or lesser degree while others show little or no such coloration. It is evident that some species, perhaps the majority, do develop chlorophyll to some extent and consequently have the capacity to produce a part, at least, of their required food.

Kotschyev (3) states: "The pale green *Cuscuta Cephalanthi* and *Cuscuta europaea* liberate a small amount of oxygen in the light." This indicates that photosynthesis occurs in these species. Several species contain more green pigment than do these two and probably photosynthesize to a still greater extent. As far as is known the degree to which the various species of *Cuscuta* carry on photosynthesis has not been satisfactorily investigated by physiologists.

A great difference of opinion also exists relative to the presence or absence of stomata on the stems of *Cuscuta*. These structures are essential for the exchange of gases during the photosynthetic and respiratory processes and thus are intimately related to the question of photosynthesis.

Thomson (8) says: "The plant (*C. reflexa*) bears no leaves; its outer surface is covered by a distinct, though thin, cuticle; neither this species nor any other species of the Cuscutaceae is possessed of stomata," and "The presence of an uninterrupted cuticle over all its surface exposed to the air, and the total absence of stomata, render it extremely difficult for what chlorophyll there is in its tissues to obtain the necessary carbon dioxide for the photosynthesis of carbohydrate." Peirce (5) states of *C. americana*: "The epidermis, seldom if ever interrupted by stomata. . . ." DeBary (1) says: "in the stems of *Cuscuta* there is one stoma to many hundred epidermal cells." Mirande (4) in his excellent and comprehensive paper on the physiology and anatomy of *Cuscuta* states that in all of the large species the stomata form an important aerating apparatus. He found them on all parts of the stem but with the greatest abundance in the vicinity of the nodes, flowers, and floral axes. His report was limited almost entirely to those species having very large stems now included in the subgenus Monogyna. He found stomata abundant in *C. japonica* and *C. exaltata*, less abundant in *C. monogyna* and *C. Lehmanniana* and somewhat less yet in *C. lupuliformis*. He illustrates with camera lucida



Sketches illustrating stomata found on stems of species of Cuscuta. All enlarged approximately 400x.

a—C. reflexa; b—C. Lehmanniana; c—C. lupiliformis; d—C. japonica; e—C. monogyna; f—C. compacta; g—C. jalapensis; h—C. americana; i—C. campestris; j—C. Gronovii; k—C. Polygonorum.

sketches those which he found on *C. japonica* and also one on *C. chinensis*, a smaller stemmed species.

No positive statement has been found in the literature relative to the presence of stomata on any American species with the exception of the one made by Peirce that on *C. americana* they are seldom if ever present. Last autumn (1942) seeds of three Indiana species common in Putnam County (*C. campestris* Yuncker, *C. Gronovii* Willdenow, *C. Polygonorum* Engelmann) were collected. They were planted in the greenhouse where they grew well on a variety of hosts and flowered. When matured, the stems were examined for stomata which were found to be present in each of the species.

Although they are infrequent, inconspicuous, and easily overlooked, there is at least one stoma to each several hundred epidermal cells. The shape and arrangement of the stomata found in these three species agree with Mirande's description of those of the larger stemmed species. They are rounded-oval with their long axis parallel with that of the stem. Neither the guard cells nor the surrounding cells showed any concentration of color nor was there any noticeable elevation at the site of the stomata, as is characteristic of some of the other species. They were not found to be more numerous in the vicinity of the nodes, haustoria, inflorescences, or floral parts. In *C. Polygonorum* (originally named *C. chlorocarpa* by Engelmann) the developing capsule is often definitely green. One would suspect, therefore, that stomata might be present on the fruit, but none were found.

The stems of herbarium specimens of several species were examined for stomata after having been softened by boiling. This method, however, did not prove very successful. With the exception of species with comparatively large stems, it was impossible to properly prepare the epidermis for microscopical examination. Stomata have been found, however, in every species in which it has been possible to make a proper examination of the material available. It is believed that they are probably present on the stems of all species.

The following list includes, in addition to the three living species already discussed, those in which it was possible to prepare herbarium material for examination.

Cuscuta reflexa Roxburgh (*fig. a*). It is difficult to understand why Thomson did not find stomata on the stems of this common Asiatic species. They are not as abundant or as conspicuous as are those on some of the other species. However, they were present on all of the stems examined and usually situated on slight papillate elevations of the epidermis. Only dry herbarium material was available for study and it is possible that they are less conspicuous on living stems, though the contrary would seem more probable.

Cuscuta Lehmanniana Bunge (*fig. b*). Stomata were more numerous in this species than in any of the others examined. Mirande found them to be less abundant in this species than with *C. japonica* and *C. exaltata* but I found the contrary to be true. About 50 were counted in a centimeter of stem length. They are very easily observed because the stomatal

area is strongly reddened and slightly dome-shaped with the stomata at the tops of the elevations.

Cuscuta lupuliformis Krocker (*fig. c*). The stomata are situated on low, reddish, papillate elevations. Twenty to 30 were counted in one centimeter of the stem but in the vicinity of haustoria as many as 50 were found in a comparable area.

Cuscuta japonica Choisy (*fig. d*). Mirande found stomata more abundant on stems of this species than any other. In the herbarium material examined I found up to 25 in a centimeter of stem length with a somewhat greater number in the haustorial areas. The stomata are situated on slightly raised and reddened areas which renders them conspicuous and easily seen.

Cuscuta monogyna Vahl (*fig. e*). In the several specimens examined of this species the stomata were very conspicuous because the guard cells exhibited a bright yellow pigment which was in strong contrast with the adjacent non-pigmented cells. Whether this yellow pigment is characteristic and present in living material is not known. The number of stomata varied considerably with usually 5 to 15 present in a centimeter of stem length. Two stomata were seen adjacent to each other, a condition observed only this once.

Cuscuta exaltata Engelmann. The stomata in this species, which were found to be fewer than for *C. Lehmanniana*, are located on slight elevations, the cells of which exhibit a brown color.

Cuscuta compacta Jussieu (*fig. f*). A few pieces of stem of this American species were examined. The stomata were found to be present though infrequent and inconspicuous. Living material might reveal them to be more abundant.

Cuscuta jalapensis Schlechtendal (*fig. g*). In this Mexican species a small number of scattered stomata on slightly raised areas were found.

Cuscuta americana Linnaeus (*fig. h*). Peirce stated that this species had few if any stomata. The writer found them to be present though infrequent, inconspicuous and indistinct.

Cuscuta campestris Yuncker (*fig. i*), *C. Gronovii* Willdenow (*fig. j*), and *C. Polygonorum* Engelmann (*fig. k*) are discussed above.

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