

brous; keel 2.0–2.5 mm wide at the widest point, angle 108–118°, ciliated along the upper margin from the acumen to half the distance back; ovules 2–3; pods 10 mm long, 5 mm wide, silky-villous to woolly; seeds 2–3, 2.5 mm long, 2.0 mm wide, 1.0 mm thick, beige to tan color; flowers in mid-June; (fig. 3).

DISTRIBUTION: *Lupinus cusickii* subsp. *brachypodus* has been collected only in eastern Oregon in Grant, Harney, Malheur, and Umatilla counties (fig. 2). The plants are found primarily in arid, rocky stream beds and on mountain ridges. They do not occur in abundance, and they have been collected infrequently. Associated plants are predominantly *Artemisia* spp. and *Chrysothamnus* spp.

Subspecies *brachypodus* generally has capitate racemes like subsp. *cusickii*, but the flowers are larger, approaching the size and shape of those of *L. aridus*. The vegetative height and general stature of subsp. *brachypodus* resemble *L. caespitosus* var. *utahensis*, but *utahensis* usually has elongated, narrower racemes and smaller flowers than the former. The petioles of subsp. *brachypodus* are mainly basal, unlike the cauline leaves of *L. caespitosus* var. *utahensis*. Although the raceme diameter and flower size of subsp. *abortivus* approximate those of subsp. *brachypodus*, the former has elongated racemes that surpass the foliage by 1–5 cm, forming larger clumps with more filiform stems and petioles.

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FURTHER EVIDENCE FOR THE SYSTEMATIC POSITION OF PSITTACANTHUS SONORAE (LORANTHACEAE)

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The Mexican mistletoe *Psittacanthus sonorae* (S. Wats.) Kuijt has recently been transferred to *Psittacanthus* from *Phrygilanthus* on the basis of a single character (Kuijt, 1971). This character, the absence of endosperm in the mature seed, is in Loranthaceae unique to *Psittacanthus*, at least under the current circumscription of neotropical genera. I should like to further substantiate this taxonomic transfer by means of some observations on the fruit and seedling. These observations, furthermore, include a number of details in which *P. sonorae* differs from other known *Psittacanthus* species; some of these details seem to represent adaptations to the extremely xerophytic environment of the Sonoran Desert. A comparative basis has been provided by my two earlier articles on *Psittacanthus* (Kuijt, 1967 and 1970).

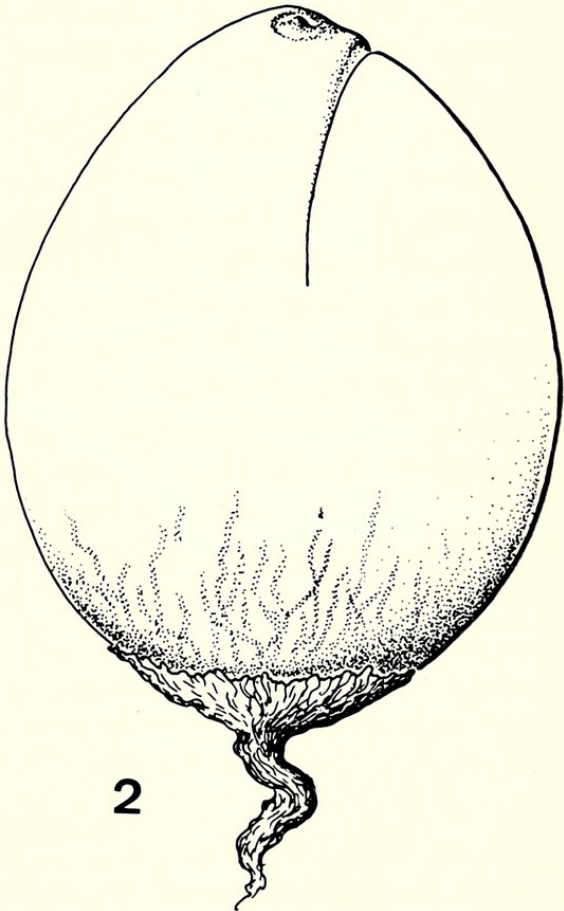
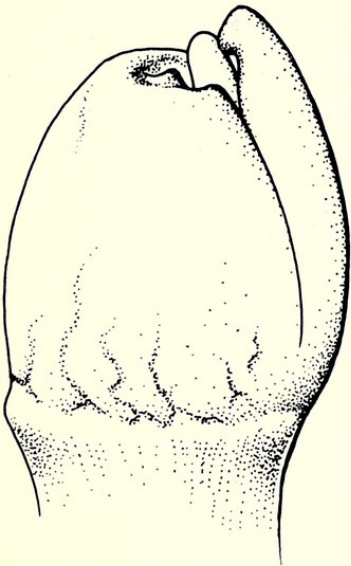
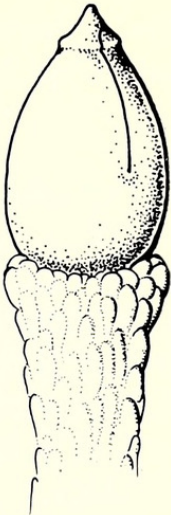
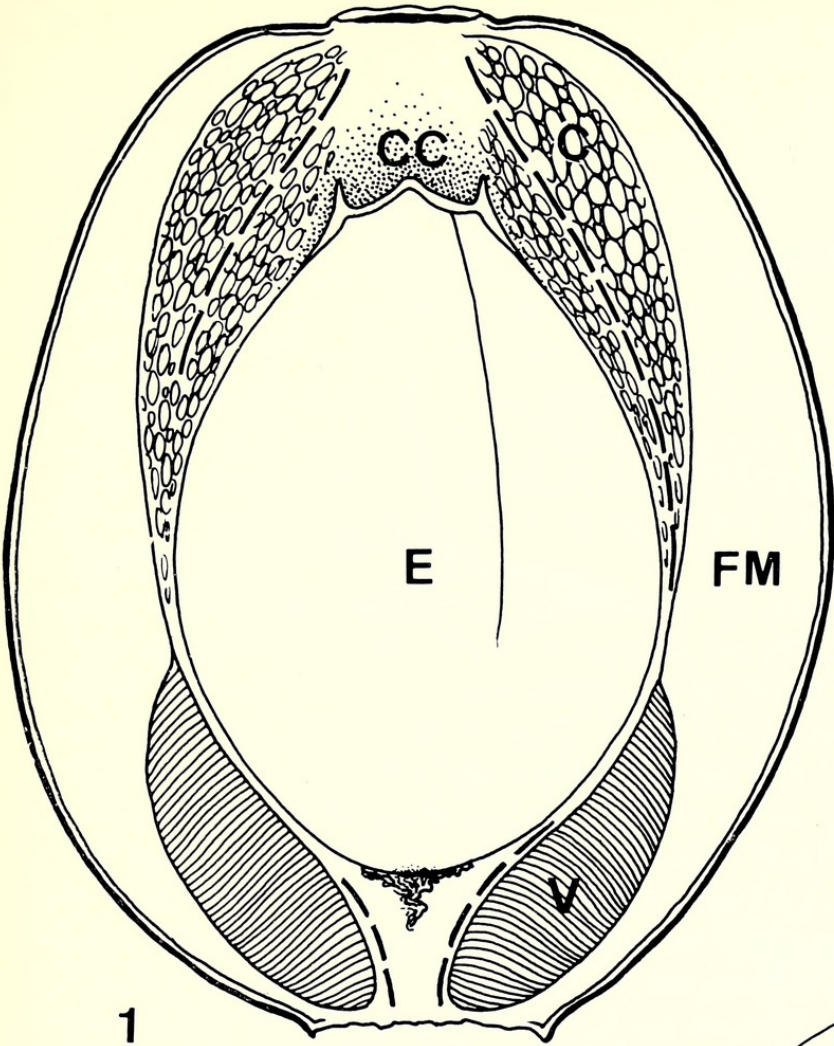
The materials for this study were gathered by Dr. P. D. Warrington and me about 5 km north-west of Bahia de los Angeles, Baja California, 8 Jan 1968. All individuals seen were parasitic on *Bursera*, the plants here described growing on *B. microphylla* A. Gray.

FRUIT

The mature fruit is nearly spherical and about 7 mm in diameter. It is shiny and smooth, and dark purple or black. A longitudinal section reveals the main details of its complex inner structure (fig. 1). The outer tissues, including the fleshy part of the mesocarp layer, slip off with remarkable ease. The proximal region of the fruit includes a very thick and rigid layer of large, hyaline cells that are light brown. This tissue is referred to as the *capsule* for reasons that will become clear below. The axial region, however, is occupied by a strong, persisting "collenchymatous cup" that seems to function as a barrier or receptacle to the descending embryo (and, in other genera, endosperm; Maheshwari et al., 1957). Six vascular bundles can be traced through the middle of the capsular tissue and around the embryo to the scars of the petals. As will be seen below, the capsule functionally is comparable to the testa. Morphologically, however, it represents the endocarp; as in other Loranthaceae, a true testa is absent. Distally, a funnel-shaped mass of viscid tissue adheres tightly to the seed. Its cells are greatly elongated in a radial direction, and are of a clear, blue-green color. The viscid tissue probably should be counted with the mesocarp, as is indicated by a comparison with another species, *P. schiedeanus* (Cham. & Schlecht.) Blume (Kuijt, 1967).

The central portion of the fruit is occupied by a single, ovate, fleshy embryo (fig. 2). The cotyledons make up about half of its bulk. Most embryos have two cotyledons, but some with three may also be found. Furthermore, even in those with two cotyledons much variation in cotyledon size occurs; one cotyledon is often two or three times as large as its mate (fig. 3). The apex of the larger of the two is pressed tightly into the collenchymatous cup and consequently bears the latter's nipple-like imprint. A colorless, thin tissue invests the very base of the embryo and is attached to it (fig. 2). It is the compressed remnant of the massive suspensor that characterizes the embryogeny of *Psittacanthus* (Kuijt, 1967). In a fruit that is about half mature this remarkable suspensor can still be seen as a stout, translucent stalk made up of very large cells

FIGS. 1-4. 1. Longitudinal section of mature fruit, the scar of the peduncle being above. $\times 13$. C. Capsule, the broken lines representing vascular bundles. CC. Collenchymatous cup. E. Embryo, with suspensor remnant basally attached. FM, Fleshy mesocarp. V. Viscin. 2. Mature, dicotyledonous embryo and suspensor remnant, dissected from a ripe fruit. $\times 13$. 3. Top of a young seedling, the capsule removed, showing a young leaf pushing aside the smaller (right) of two very unequal cotyledons. $\times 6.5$. 4. Young dicotyledonous embryo and upper portion of suspensor dissected from a semi-mature fruit. $\times 13$.



(fig. 4), pressing the embryo against the collenchymatous cup. Subsequently the expanding embryo compresses and obliterates the suspensor. The embryo lacks green coloration, and is light cream-colored throughout except for series of red-pigmented epidermal cells at the base (fig. 2).

GERMINATION

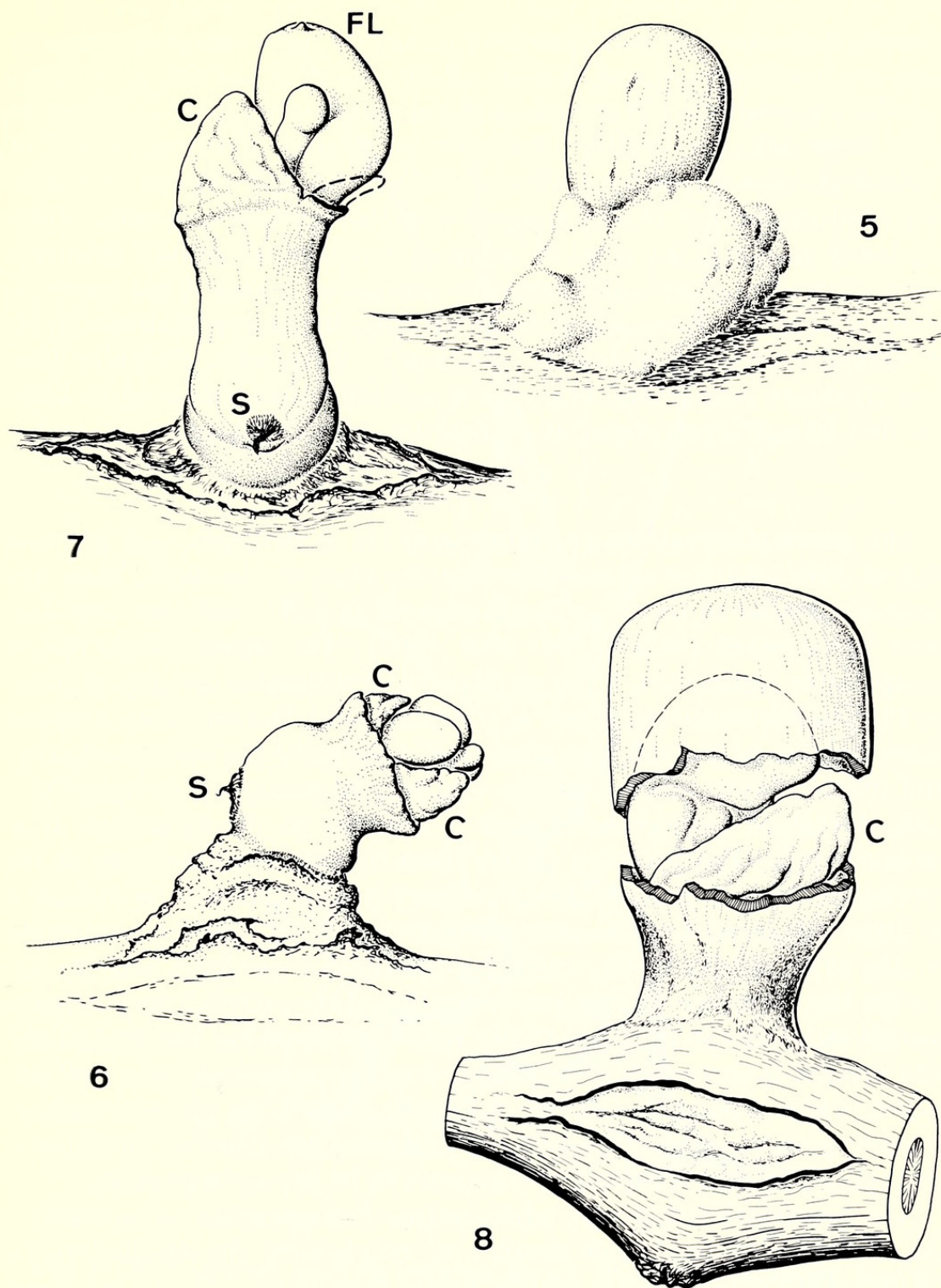
The seed adheres to the host twig in such a way that the radicular pole is nearest the host surface, a position probably due to the presence of viscid tissue at that end. The most common position of a germinating seed is thus with the cotyledonary end tilted obliquely upward (figs. 5 and 6). The associated capsular layer and the viscid tissue now dry up and apparently seal off the seedling from the air. The former tissue persists as a rigid capsule, the latter as a much more elastic, sleeve-like envelope.

The cotyledons do not, as in other *Psittacanthus* species, spread immediately. In fact, they do not spread at all in the normal sense of the word, but are forced apart by the young leaves much later. The haustorium apparently forms very early. That it originates from the lower flanks of the embryo and not from its apex is clearly demonstrated in established seedlings, where one can always observe the suspensor scar or remnant that has been pushed to the side (S in figs. 6, 7, and 9). A small, smooth haustorial cushion develops just external to the host (fig. 7). In older seedlings irregular, globular swellings lower down indicate the growth of the haustorium, which, as in other species of the genus, can become very massive. *Bursera* twigs, where attacked by *P. sonora* seedlings, often exude gum copiously, in extreme cases investing the base of the seedling completely (fig. 5). A comparison of the mature embryo and established seedlings shows that the lower half of the embryo elongates somewhat during haustorial formation, but also that it becomes thinner (cf. figs. 2 and 7).

When the seedling is securely established the cotyledons, which until now have been tightly appressed to each other, are forced apart by one to several young leaves (figs. 2, 6, 7). The cotyledons at this stage are wrinkled and obviously shrunken. As their color is now a dull, light brown they may no longer contain living tissues. The zone where hypocotyl and cotyledons meet does not shrink as much as the tissues above and below, and thus often stands out as an elevated collar (fig. 6).

The emerging young leaves push against the inside of the rigid capsule that surmounts the seedling until the capsule separates by means of an irregular, transverse tear from the viscid "sleeve" below (fig. 8). Further elongation of the leaves completely lifts off the capsule and causes it to be dropped. Thus the cotyledons are exposed only when they are no longer functional as storage organs, and at a time when haustorial establishment is already secure.

The leaves that push off the capsule are not, however, morphologically the first foliar organs of the plumule. In all germinating seedlings a



FIGS. 5-8. 5. Seedling in natural position, its base enveloped by host gum. $\times 5$. 6. Dicotyledonous seedling with capsule and viscin removed. $\times 6$. C. Cotyledons, between which the expanding leaves. S. Suspensor remnant, pushed aside by the expanding haustorial organ below. 7. The same seedling as that in Figure 8, seen from the opposite side, with capsule and viscin removed. The broken line indicates one small cotyledon which had apparently aborted. $\times 7.5$. C. Cotyledon. FL. Foliage leaf. S. Suspensor remnant, below which the smooth haustorial cushion. 8. Young seedling in which one foliage leaf is in the process of pushing up and rupturing the capsule. The sleeve of viscin tissue is below the line of rupture. The swelling of the host branch shows the haustorium to be fully established. $\times 7.5$. C. Cotyledon.

zone of various numbers of extremely reduced leaves separates the cotyledons from the youngest expanded leaves. In some seedlings these organs are few or are reduced to such a degree as to be scarcely discernible. In others a small central prominence and surrounding leaf cushion is set apart from adjacent, similar organs. In the clearest instances such a leaf cushion is surmounted by a minute, awl-shaped leaf (fig. 9). An uninterrupted gradient of these reduced leaves may be observed when studying many seedlings. In any one seedling, however, an abrupt transition exists between reduced and normally expanded leaves. That even the smallest of these organs are, morphologically, leaves is confirmed by the occasional emergence of lateral branches in their axils. An older plant may therefore have lateral branches in positions that appear to be below the first foliage leaves, especially when the main axis has been injured.

DISCUSSION

The above observations on embryogeny, fruit structure, and germination of *Psittacanthus sonora* demonstrate that, in the main, these features are similar to those in the other species of *Psittacanthus* that have been investigated (Kuijt, 1967 and 1970). The mature fruit has no recognizable endosperm. The proembryo and suspensor develop conjointly, the proembryonic cell group at one time being no more than a minute distal portion of the massive suspensor. Gradually the embryo enlarges and differentiates, and eventually crushes the suspensor completely. A fully developed embryo bears only a remnant of the suspensor at its radicular pole. The presence of this tissue remnant implies that, in this precise locality, no truly terminal primary haustorium can be formed as in other advanced Lorantheae. The haustorium, therefore, originates on the lower flanks of the radicular end of the seedling, and in time pushes the suspensor scar or remnant aside. This extraordinary developmental sequence, so far known only from *Psittacanthus* but conceivably also present in some other South American Lorantheae, may well provide a firmer systematic foundation for the genus than the mere absence of endosperm associated with it. At any rate, the generic allocation of this species to *Psittacanthus* now appears to be beyond question.

Another feature that may characterize *Psittacanthus* as a whole is the variation in form and number of cotyledons. As detailed earlier (Kuijt, 1967), the species of this genus may have as many as eleven cotyledons. In one instance (*P. allenii* Woods. & Schery) what appears to be a single species is characterized by two flat cotyledons in one area of Costa Rica, and by numerous prismatic cotyledons in a different area of the same country (Kuijt, 1970). In *P. sonora* a certain amount of variation also occurs, but even more interesting is its loss of photosynthetic function.

It may well be that the cotyledonary variation in *Psittacanthus* stands in some relation to its remarkable embryogeny or to the disappearance of the endosperm. It is as if the conjoint suspensor-embryo development,

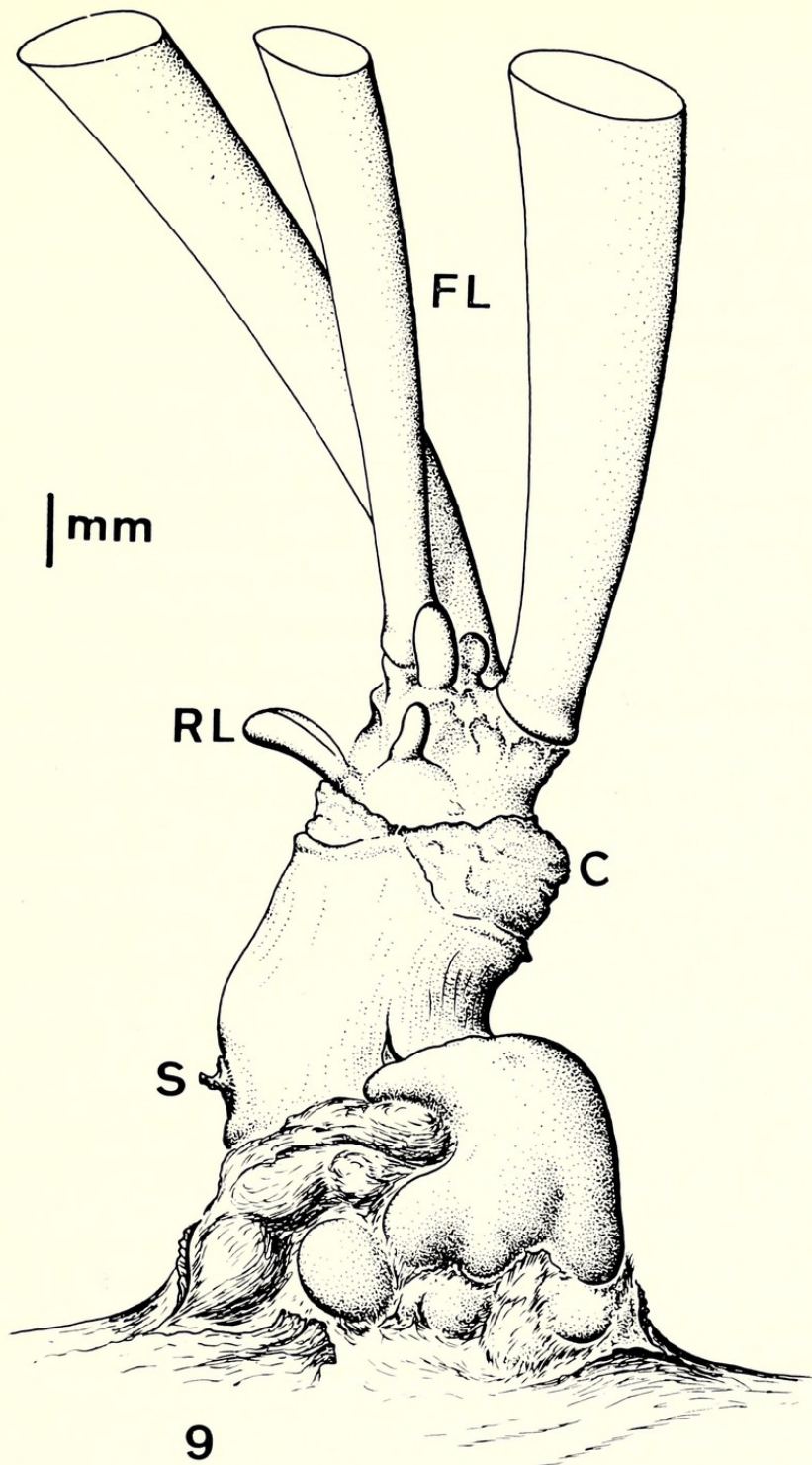


FIG. 9. Older seedling, showing irregular growth of haustorium below. C. Cotyledon. FL. Expanding foliage leaves. RL. Rudimentary leaves. S. Suspensor remnant.

or the loss of the endosperm, has somehow weakened the morphogenetic control over cotyledon number and shape. It is interesting to find, in this context, that cotyledon number in at least some normally dicotyledonous plants is amenable to a certain amount of experimental manipulation (Haccius and Reinholz, 1953).

Although small percentages of polycotyledonous seedlings occur in a great variety of normally dicotyledonous plants (Haccius, 1955), the

number of species for which polycotyledony is the rule is exceedingly small. *Bruguiera* (Rhizophoraceae) is characterized by four cotyledons, and the number ranges from two to eight in *Persoonia* (Proteaceae), as reported by Goebel (1932). A few species of *Navarretia* (Polemoniaceae) normally have either three or four cotyledons (Brand, 1907). Finally, in several New Zealand species of *Pittosporum* (Pittosporaceae) three or four cotyledons are usual (Stebbins, 1972). As this sort of information is difficult to recover from the scientific literature I may well have overlooked other instances. It would be interesting to know if any unusual features in the embryogeny are associated with polycotyledony in the species listed, comparable to those of *Psittacanthus*.

The formation of rudimentary leaves as first foliar organs above the cotyledons has also been mentioned and illustrated for *P. allenii* (Kuijt, 1970). In the latter species, however, the rudimentary leaves are very few and difficult to discern, and transitional leaf-forms do not seem to occur. Their greater number and prominence in *P. sonora* is perhaps related to the time-lag in plumular differentiation as mentioned below.

In spite of the above-mentioned structural correspondence between *P. sonora* and its fellow species, there are also some significant differences. First of all, *P. sonora* may be the only *Psittacanthus* species in which the cotyledons do not spread immediately and are not photosynthetically active. Secondly, compared with the fruit of *P. schiedeana* (Kuijt, 1970), the *P. sonora* fruit has a viscid zone that is histologically very distinct from the fleshy part of the fruit wall, their contact zone being a separation layer. Thirdly, the inner fruit wall is strongly developed in *P. sonora*, particularly at the cotyledonary end of the embryo, and dries into a hard shell or capsule surrounding that part of the seedling. Finally, the development and expansion of normal foliage leaves appears to lag far behind haustorial establishment. The reduced leaves mentioned earlier may indicate a degree of meristematic activity of the plumular apex during haustorial formation. There is little question that the presence of the protective capsule, aided by the viscin tissue and perhaps even the gum exudates from the host, is of great ecological advantage during the early phases of germination. The delayed foliar expansion extends the duration of this adaptive feature by keeping the capsule intact until the haustorial connection is fully functional.

SUMMARY

The structure of the fruit and seedling of the Mexican mistletoe *Psittacanthus sonora* (S. Wats.) Kuijt (Loranthaceae) confirms its generic position. Differences from other species of *Psittacanthus* are to be found in the non-chlorophyllous cotyledons, which do not expand normally, and particularly in the capsule-like differentiation of the endocarp, providing extended protection for the young seedling. The first expanding foliage leaves rupture the base of the capsule at a time that the haustorium is fully established.

ACKNOWLEDGMENTS

The financial support of the National Research Council of Canada, and the use of a vehicle supplied by Dr. Reid Moran of San Diego are gratefully acknowledged.

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MORPHOLOGY, FLAVONOID CHEMISTRY, AND
CHROMOSOME NUMBER OF THE
CHENOPODIUM NEOMEXICANUM COMPLEX

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The genus *Chenopodium* is generally recognized as very difficult taxonomically. Often it is almost impossible to circumscribe species with certainty because no sharp morphological discontinuities appear to exist in particular groups or complexes of plants. This paper represents the first of a series that will be devoted to the systematics of western North American species of *Chenopodium*. The investigations will utilize flavonoid chemistry, field studies of natural populations, micromorphology, chromosome numbers, and morphology.

This report is concerned with the results of a study of a group of triangular-leaved, attached-pericarp chenopods that are restricted to Arizona, New Mexico, Texas, and northern Mexico, here referred to as the *Chenopodium neomexicanum* complex. They occur typically in disturbed, weedy roadside habitats in mountains above 1650 m elevation. Individuals apparently are not common; collections in herbaria are few, and I have had some difficulty in locating plants in the field.

Chenopodium neomexicanum was described by Standley (1916) in



Kuijt, Job. 1973. "FURTHER EVIDENCE FOR THE SYSTEMATIC POSITION OF PSITTACANTHUS SONORAE (LORANTHACEAE)." *Madroño; a West American journal of botany* 22, 177–185.

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