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SINKER STRUCTURE OF *PHORADENDRON CALIFORNICUM* (VISCACEAE) CONFOUNDS ITS PRESUMED CLOSE RELATIONSHIP TO OTHER ACATAPHYLLOUS SPECIES

RUDOLF SCHMID,[1] CLYDE L. CALVIN,[2] AND CAROL A. WILSON[2]

[1]*Department of Integrative Biology, University of California, Berkeley, California 94720-3140, USA (schmid@berkeley.edu);* [2]*Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711-3157, USA (clyde.calvin@cgu.edu; carol.wilson@cgu.edu)*

ABSTRACT

Phoradendron is the largest genus of New World mistletoes, with about 250 species in two subgenera, *Boreales* and *Aequatoriales*, corresponding, respectively, to northern acataphyllous and southern cataphyllous groups. The typically acataphyllous *P. californicum* of western North America is controversial because recent phylogenetic work has nested it in the southern cataphyllous clade. Seedling establishment, stem anatomy, and endophytic system structure of this species were studied. Seedling haustorial holdfasts have gland cavities, structures considered absent in the Viscaceae clade of Santalales. The stem epidermis has a thick cuticle, deeply sunken stomata, and branched multicellular trichomes. The stem has an outer cortex of palisade chlorenchyma and an inner cortex of large isodiametric parenchyma cells. The boundary area between the outer and inner cortex contains druses and an unusual ring of small xylic bundles lacking protoxylem fibers and phloem. Sinkers are of two types: uniseriate, with only parenchyma that often has thick-walled transfer cells at its interface with vessels of the host; and multiseriate, with parenchyma and vessel elements that often are in direct contact and share simple perforation plates with vessels of the host. Sinker morphology is also dimorphic in the cataphyllous *P. fragile* but only unimorphic (multiseriate) in the acataphyllous *P. juniperinum* and *P. serotinum.* The dimorphic sinker system of *P. californicum* may be functionally partitioned, whereas these functions are combined in the unimorphic sinkers of other acataphyllous species. Differences in sinker morphology may reflect evolutionary trends in *Phoradendron.* This study also supports the hypothesis that *P. californicum* is more closely aligned with the mainly tropical cataphyllous species of the genus.

Key words: haustorial system, mistletoe, *Phoradendron*, Santalales, seedling establishment, sinker structure, stem anatomy, Viscaceae clade.

INTRODUCTION

Phoradendron Nutt. is the largest genus of mistletoes in the New World. Kuijt (2003) recognized 234 species. Research based on DNA sequence data (Ashworth 2000*a*) indicates that species of the closely related genus *Dendrophthora* Eichler are nested in *Phoradendron.* Kuijt (1961) accepted 53 species of *Dendrophthora*; subsequent studies brought that number to 110 (Kuijt 2000). Were *Dendrophthora* merged into *Phoradendron*, a change supported by Ashworth's (2000*a*,*b*) work, the species total of *Phoradendron* would approach 350. The size of the genus, its wide distribution in the New World, and its recognition as a keystone ecological resource in forests and woodlands (Watson 2001) all contribute to the significance of *Phoradendron* in temperate and tropical ecosystems.

Two subgenera of *Phoradendron* have been recognized (Trelease 1916), *Boreales* and *Aequatoriales*, corresponding, respectively, to northern acataphyllous and southern cataphyllous groups (Wiens 1964; Kuijt 2003; Table 1). Cataphylls, not to be confused with prophylls, are small leaf-like or bract-like structures typically inserted in pairs near the base of the first internode of lateral shoots (for a detailed discussion of other cataphyll positions see Kuijt 1996, 2003).

This report focuses on the seedling establishment, stem anatomy, and endophytic-system structure of *Phoradendron californicum*, the California, desert, or mesquite mistletoe (Fig. 1). Ranging from southwestern Utah to southern Nevada, southeastern California, and Arizona, and southward in Mexico through Baja California, Sonora, and northern Sinaloa (Kuijt 2003: map p. 129, which omits Utah), the species parasitizes chiefly members of Fabaceae, especially *Prosopis* L. (Wiens 1964; Kuijt 2003). Berries of *P. californicum* ripen in late fall and early winter (Fig. 2) and are an important food source for birds, such as *Phainopepla nitens* Swainson (silky-flycatcher) in southern California (Cowles 1936; Heide-Jørgensen 2008: Fig. 162). Seeds are widely dispersed in areas where birds feed (Fig. 3) and often accumulate in large, multi-year masses below long-term perches (Tinnin et al. *1971*).

Phoradendron californicum occupies a unique position in the genus as its type species (Nuttall 1848). Its squamate leaf form, a character shared with 10–15 species, is unusual in *Phoradendron.* Ashworth's (2000*b*) research argues against a monophyletic acataphyllous lineage of *Phoradendron* because *P. californicum*, although generally lacking cataphylls, is nested in the cataphyllous group. Analyses of morphological characters (Wiens 1964; Kuijt 1996, 1997, 2003) have also questioned the validity of Trelease's (1916) two subgenera and stressed that *P. californicum* is a taxonomically problematic species in the genus.

The endophytic structure of only a few species of *Phoradendron* has been described, resulting in relatively thorough descriptions of the endophytic systems of two acataphyllous and a less detailed description for one cataphyllous species. Table 1 summarizes information on distribution, morphology, and anatomy of *P. californicum*, *P.*

Table 1. Comparison of leaf and sinker characters for four species of *Phoradendron* included in this study. Geographical distribution also given (Kuijt 2003).

Characters	Species			
	P. californicum Nutt.	*P. juniperinum* Engelm. ex A.Gray	*P. serotinum* (Raf.) M.C.Johnst.	*P. fragile* Urb.
Cataphylls	Absent[1]	Absent	Absent	Present
Leaves	Squamate	Squamate	Leafy	Squamate
Sinker type	Uni- & multiseriate	Multiseriate	Multiseriate	Uni- & multiseriate
Distribution	Southwestern USA & northwestern Mexico	Western USA & northern Mexico	Southern USA & northern Mexico	Central & southeastern Brazil

[1]Cataphylls in *P. californicum* often present (Kuijt 2003: p. 4, Fig. 66).

juniperinum, *P. serotinum*, and *P. fragile*. The anatomy of the endophytic system of the widespread acataphyllous *P. serotinum* has been studied intensively (Cannon 1901; York 1909; Bray 1910; Thoday 1957; Calvin 1967*b*), including the ultrastructure of cellular relationships between parasite and host (Fineran and Calvin 2000). To summarize, the endophytic system of *P. serotinum* is comprised of a system of longitudinally oriented bark strands with radially oriented sinkers that extend through the phloem of the host into its xylem. Each sinker has a cambial zone that functions in unison with that of its host. The sinkers when viewed in tangential sections through host wood are tall, multiseriate, and largely independent of host rays. Individual sinker cells may differentiate as either vessel elements or parenchyma. The parenchyma cells are of a specialized type, "flange-type parenchyma" (Fineran 1996). Flange cells at the parasite-host interface are exceedingly elaborate and, besides having lignified secondary wall thickenings in the form of flanges, have a labyrinth of wall ingrowths characteristic of transfer cells (Fineran and Calvin 2000: Fig. 10–15). Sinkers of the acataphyllous *P. juniperinum* are also tall and multiseriate when viewed tangentially in wood of its conifer host *Juniperus* L. (Calvin et al. 1991). Sinker cells of the parasite differentiate as vessel elements or parenchyma, but flange-type parenchyma or transfer cells as described for *P. serotinum* were not observed at the light microscopic level.

The preliminary report by Schmid and Lindemann (1979) is the only published work on the anatomy of the mature endophytic system of the acataphyllous *P. californicum*. They recognized its dimorphic nature: multiseriate sinkers consisting of vessel elements enclosed by parenchyma, and mostly uniseriate sinkers consisting of only thick-walled parenchyma.

Less is known about the endophytic system in the primarily tropical cataphyllous species of *Phoradendron* (Rizzini 1950; Thoday 1957). The squamate *P. fragile* from Brazil has both uniseriate and multiseriate sinkers (Rizzini 1950), as in *P. californicum*, but in contrast to the leafy *P. serotinum* and squamate *P. juniperinum*. The uniseriate sinkers of *P. fragile* consist entirely of parenchyma, and may or may not be associated with host rays, whereas the multiseriate sinkers contain both parenchyma cells and vessel elements.

We report on the structure of the endophytic system of the acataphyllous, squamate *P. californicum*, especially its sinkers, and make comparisons to the acataphyllous, squamate *P. juniperinum*, the acataphyllous, leafy *P. serotinum*, and the cataphyllous, squamate *P. fragile* (Table 1). We also report on the anatomy of seedling establishment and the aerial shoot of *P. californicum*. Currently, there is only limited information of seedling establishment (Kuijt 1989; Ruhland and Calvin 2001) and stem anatomy (Calvin 1967*a*; Ashworth and Dos Santos 1997) in *Phoradendron*.

MATERIALS AND METHODS

This study is based on collections of *P. californicum* parasitic on *Prosopis glandulosa* var. *torreyana* (L.D.Benson) M.C.Johnst. from three California locations: (1) north of Kelso, San Bernardino Co., 23 Jan 1976, *Schmid 1976-1* (UC); (2) south of Indio, Riverside Co., 15 Apr 1967, *Calvin 1967-3* (RSA); and (3) near Palm Springs, Riverside Co., 13 May 1992, *Calvin 1992-1* (RSA). Collected materials ranged from early seedling establishment where the berry was still present to mature infections. All materials were fixed in formalin-propionic acid-alcohol (FPA) in the field. To facilitate sectioning of the parasite-host complex, we collected host shoots of the smallest possible diameter.

Materials were embedded in paraffin. Modifications to standard techniques included softening by: (1) immersion in a solution of glycerol-Aerosol OT-water (10 : 1 : 90) (Schmid 1972) before wax infiltration; (2) soaking tissue-exposed ends of wax blocks overnight or longer in water containing a drop or two of detergent (Calvin 1967*a*). Other methods of softening tissue, such as Burkart's (1966) triethylene-glycol technique, proved unsuccessful. After fixing sections to slides with Haupt's adhesive, Schmid and Calvin used a different technique: (1) before staining with safranin-fast green, Schmid removed tannins from some slides by bleaching them with Stockwell's solution, which also removes crystals (Schmid 1972, 1977). (2) In contrast, Calvin stained slides with either safranin-fast green or tannic acid-ferric chloride-lacmoid without prior removal of tannins (Calvin 1967*a*). We captured images (Fig. 1–27) on Kodachrome 35 mm film and/or Panatomic-X 4 × 5″ sheet film (Eastman Kodak Company, Rochester, New York), which were digitized for the photographic plates.

This study uses a comparative anatomical approach, comparing (1) the endophytic system of *P. californicum* to *P. fragile* based on information from Rizzini (1950) and (2) the stem and endophytic system of *P. californicum* to *P. juniperinum* and *P. serotinum* based on information from the literature (Cannon 1901; York 1909; Bray 1910; Thoday 1957) and from Calvin and Wilson's collection of microscope slides housed at RSA.

Terminology

The fruit of *Phoradendron* is often called a "pseudoberry" because the ovary lacks true ovules. In the same sense, the seed is not a true seed as it is not a matured ovule. Likewise, the first emergence at germination is root-like in position and structure but lacks a root cap. Although we acknowledge these evolutionary specializations, for brevity and convenience we use the terms berry, seed, and radicle to describe, respectively, the fruit, seed, and first root of *P. californicum*. For haustorial terminology see Kuijt (1977: especially pp. 109–115, 2003: p. 495), Bhandari and Mukerji (1993), and Heide-Jørgensen (2008).

RESULTS

Seedling Establishment

Seed of *P. californicum* germinates immediately after deposition, with the elongating radicle growing parallel to the surface of the stem of the host, *Prosopis glandulosa* var. *torreyana* (Fig. 4). Normally, each seed of the parasite contains a single mature embryo, but two mature embryos may occur in a seed, and then two radicles emerge (Fig. 5: unlabeled arrows). In a few weeks, the radicle turns toward the host surface and flattens to form a circular haustorial disk, the holdfast (Fig. 4). The upper side of the holdfast has a thick cuticle (Fig. 6), while the lower side conforms to the contour of the stem of the host and is covered with densely protoplasmic, papilla-like epithelial cells (Fig. 6–7). These cells appear glandular and frequently form a new cell plate that is laid down perpendicular to the long axis of the cell (Fig. 7: unlabeled arrow). The disc contains a prominent layer of collapsed cells at its flanks and a large, centrally located gland cavity (Fig. 6–7). From near the center of the disk, a wedge-shaped mass of parasitic tissue, the primary haustorium, penetrates the bark of the host (Fig. 8) to initiate the endophytic system.

Anatomy of the Endophytic System

The primary haustorium (Fig. 8) grows centripetally toward the vascular cambium of the host, where it establishes a position in the cambial cylinder. Concomitantly, the part of the primary haustorium in the living bark of the host forms lateral outgrowths, termed bark strands, that grow chiefly longitudinally in the host stem. At intervals, bark strands produce lateral emergences, termed sinkers, which, like the primary haustorium, extend to, and become incorporated into the cambial cylinder of the host. Once established, the vascular cambia of mistletoe and host function in unison, as reported for other mistletoe taxa (Calvin 1967*b*, for *P. serotinum*; Sallé 1979, for *Viscum album* L.).

Figure 9 shows small portions of two sinkers at their junction with a bark strand; note that each sinker contacts a phloem ray of the host. Similar sinkers are evident in tangential sections through secondary phloem of the host; in Fig. 10 the centrally located sinker is uniseriate and three cells high. This sinker, like the two sinkers seen to the right in Fig. 10, is associated with a host ray. The phloic sinker cells are larger in tangential diameter and have larger nuclei than the ray cells of the host. The primary cell walls of the phloic sinker cells often are slightly thicker than those of host ray cells, but at the light microscopic level they appear to lack the secondary wall features commonly associated with transfer cells.

Uniseriate sinkers are prominent in infected wood because most sinker cells have only non-lignified primary walls, whereas the surrounding cells of the host have lignified walls that stain red with safranin. In Fig. 11, the three sinkers at the left are associated with a tall host ray, whereas the two sinkers to the right are independent of host rays. As in the phloem, in the xylem a given ray often appears to contain more than one sinker. All sinker cells have large nuclei and moderately dense cytoplasm. Note that sinkers, independent of their affiliation with host rays, have a spatial orientation like that of host rays. Thus, the sinkers shown in Fig. 11 are uniseriate and one to three cells tall, whereas the host rays shown are either uniseriate or biseriate and are considerably taller than the tallest sinkers. None of the sinkers shown in Fig. 11 contact a host vessel. Uniseriate sinker cells are generally alive at maturity, but necrotic sinker cells occasionally occur: in Fig. 12 the two cells nearest the end of the sinker (actually its beginning in the host xylem) lack contents, and the end cell has a prominently thickened secondary wall on the side closest to the large-diameter vessel of the host (Fig. 12: unlabeled arrow). The darkly stained host tissue at the end of the sinker suggests a traumatic wound response by the host when the sinker first arrived and established its position in the cambial cylinder.

In contrast to the thin-walled sinkers seen in Fig. 11, the uniseriate sinkers adjoining host vessels commonly have cell walls with significant modifications. The two sinkers cells shown in Fig. 13 have thick walls where they contact the large host vessel but thin walls elsewhere. Note also in Fig. 13 the striking difference in cell diameter and nuclear size and density between cells of the sinker and host ray. In two of the host ray cells, nucleoli are clearly visible (Fig. 13). In Fig. 14, three sinker cells have uniformly thin walls, but a fourth sinker cell has a prominently thickened wall where it contacts the vessel element of the host. This cell appears to bulge into the vessel element, thus increasing its area of surface contact with the host. Sinker cells that interface with host vessels have differential wall thickenings (Fig. 13–14) that strikingly resemble in position and appearance the vessel-interface parenchyma cells observed in *P. serotinum* (Calvin 1967*b*: Fig. 42–43; Fineran and Calvin 2000: Fig. 3–4, 6), where these cells contain a labyrinth of secondary wall ingrowths characteristic of transfer cells (Fineran and Calvin 2000: Fig. 10–15). However, in *P. serotinum* the wall ingrowths occur in cells with lignified secondary wall thickenings in the form of flanges. The comparable cells in *P. californicum* (Fig. 13–14), although interpreted to be transfer cells, lack the lignified secondary wall thickenings in the form of flanges; that is, they are not "flange-type parenchyma cells," as are present in *P. serotinum*.

In transverse and radial sections through host wood, uniseriate sinkers of *P. californicum* typically appear orderly as neatly arranged files of radially elongate cells joined end-to-end (Fig. 15–16). However, in the radial section through host wood shown in Fig. 17, the sinkers—when viewed in different tangential sections—appear as either two or three separate sinkers. In Fig. 17, at the right, the middle and upper sinker rows merge in response to a declining tier of cambial derivatives, whereas at the left, the middle and lower sinker

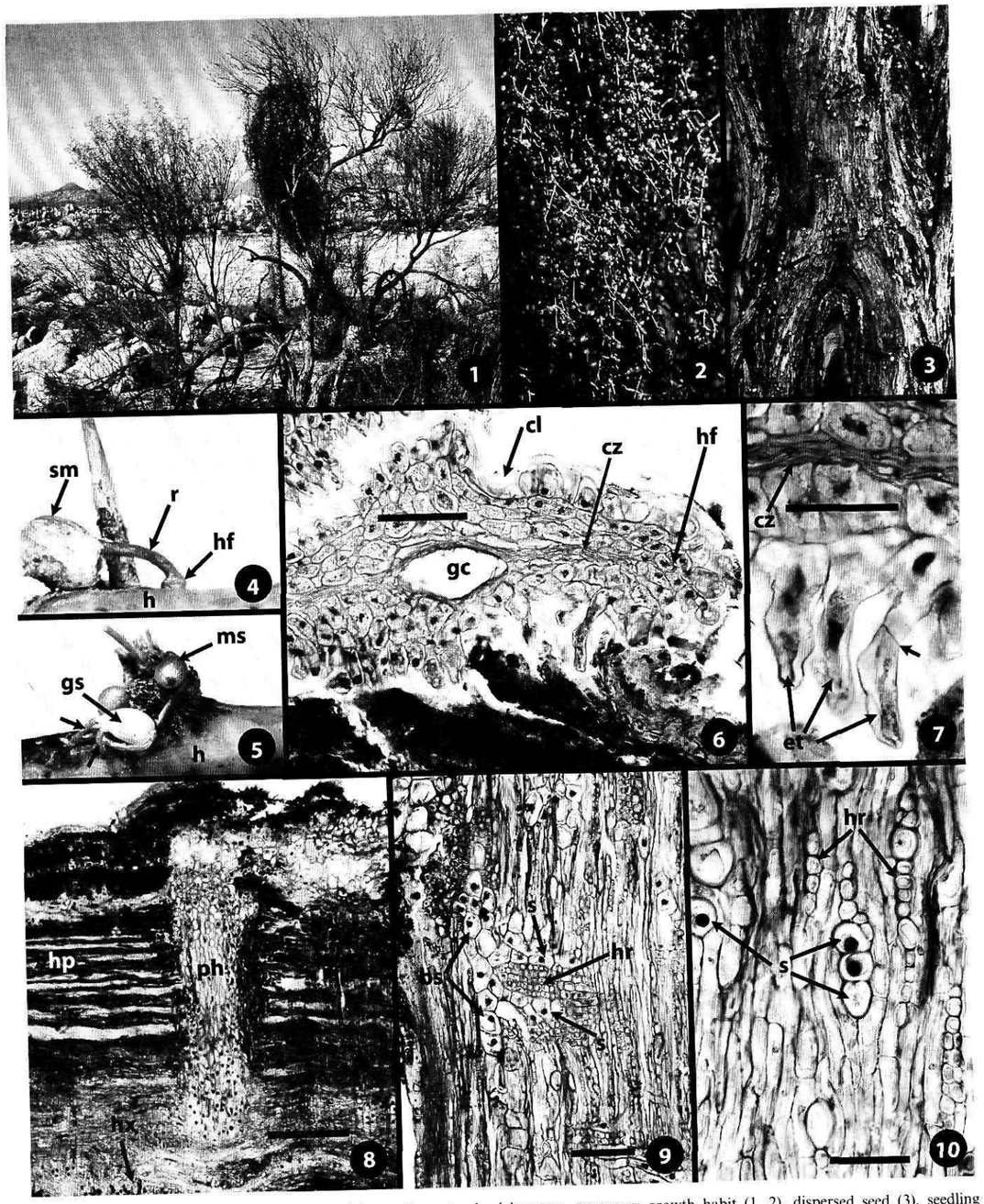

Fig. 1–10. *Phoradendron californicum* parasitic on *Prosopis glandulosa* var. *torreyana*: growth habit (1, 2), dispersed seed (3), seedling establishment (4–7), and haustorial structure (8–10).—1–3. Mistletoe parasitic on host in La Virgen boulder area, Baja California, Mexico (photos by R. Schmid, 14 Feb 1976).—1. Pendulous growth of large plant.—2. Pistillate plant in full fruit.—3. Bird-dispersed seed (arrows) on tree trunk.—4–5. Seedlings.—4. Elongate radicle, *r*, extending from seed mass, *sm*; note prominent holdfast, *hf*, now in close proximity to host branch surface, *h*.—5. Seed with two emergent radicles (unlabeled arrows); the mistletoe seed, *ms*, at upper right was deposited more recently on host.—6–7. Sections through adhesive holdfast.—6. Holdfast with thick cuticular layer, *cl*, collapsed zone of cells, *cz*, and centrally located gland

rows separate near what appears to be the juncture of two vessel elements of the host. In some cases, uniseriate sinkers also multiply locally (Fig. 18), usually in conjunction with larger host vessels. This sinker, if viewed sequentially through tangential sections, would appear as one, two, or three cells high over a relatively short distance. In most cases, sinkers are associated with typical rays of its host, *Prosopis glandulosa*. However, occasionally the host has large ray-like structures containing two to many separate sinkers (Fig. 19).

Although most sinkers observed in *Phoradendron californicum* are uniseriate, a few large multiseriate sinkers also occur in infected stems (Fig. 20). The multiseriate sinker in Fig. 20 contacts a large host vessel, which on its other side contacts many uniseriate sinkers. Thus, both multiseriate and uniseriate sinkers may parasitize a vessel simultaneously. At their margins, multiseriate sinkers often narrow gradually to a single cell (Fig. 20). Multiseriate sinkers, in contrast to the uniseriate sinkers, contain abundant tracheary elements besides thin-walled parenchyma (Fig. 20–21). The tracheary elements are vessel elements with simple perforation plates and alternate intervascular pitting (Fig. 21). The coarse tertiary spiral-wall thickenings illustrated by Ashworth and Dos Santos (1997) for vessel elements in the wood of *P. californicum* are also observed in tracheary elements of its sinkers (Fig. 21) and bark strands (Fig. 23). Multiseriate sinkers often directly contact large-diameter vessels of the host (Fig. 20, 22) and connect via shared simple perforation plates between mistletoe and host (Fig. 22). Significantly, the interface parenchyma cells of the multiseriate sinkers (Fig. 20) generally lack the prominent secondary wall thickenings present in some interface parenchyma cells of uniseriate sinkers (Fig. 13–14). Druse crystals were not observed in parenchyma of sinkers, but occur, often abundantly, in parenchyma of older bark strands (Fig. 23). Druses reportedly are rare in axial parenchyma cells of wood of *P. californicum* (Ashworth and Dos Santos 1997). Differences in crystal type, druses in the mistletoe versus solitary prismatic crystals in its *Prosopis* host (Fig. 12, 16), are a useful marker to determine identity of cells and tissues of parasite and host.

Anatomy of the Aerial Stem

Figure 24 shows a stem of *P. californicum* with some secondary growth. A thick cuticular layer covers the epidermal cells (Fig. 24–25), which had initiated development of a cuticular epithelium, the unusual secondary protective covering replacing the epidermis and characteristic of the Viscaceae clade of Santalales (Wilson and Calvin 2003). The stomata are markedly sunken and are oriented transversely (Fig. 25). Substomatal chambers are small (Fig. 25). The outer cortex is a chlorenchyma consisting of two to three layers of radially elongate cells with prominent nuclei and many large chloroplasts (Fig. 24–25). Transverse sections of newly collected stems show a brilliant green chlorenchyma. This region adjoins the inner cortex consisting of large isodiametric parenchyma cells that are highly vacuolate and contain large nuclei but small plastids (Fig. 25). The chlorenchyma of the outer cortex extends the entire length of the internode, and unlike in *Arceuthobium* M.Bieb. (Wilson and Calvin 1996), the upper third of the internode is not significantly wider than the lower third. In older stems of *P. californicum*, druses are abundant in the inner cortex, especially near its boundary with the outer cortex. The cortex also has many astrosclereids and tannin.

Small vascular bundles occur near the boundary between the outer and inner cortex (Fig. 24, unlabeled arrows). These bundles lack the clusters of protophloem and protoxylem fibers characteristic of typical vascular bundles in stems of *P. californicum* (Fig. 24, 26). The differentiated vascular tissue observed in the cortical bundles consists entirely of protoxylem and metaxylem. Tracheary elements of the cortical bundles are often associated with one or a few large, densely staining parenchyma cells (Fig. 26, unlabeled arrow) that typically contain large crystalloid inclusions of various shapes. However, in contrast to druses, the crystalloid inclusions were removed during tissue processing but the remaining organelle retained the crystalloid shape. Also present in these densely stained parenchyma cells are small spherical bodies with perimeters that appear dark blue with lacmoid stain. The cortical vascular bundle seen in Fig. 25 is shown enlarged at a slightly different level in Fig. 27. The bundle has a file of tracheary elements that extend outward to contact the chlorenchyma of the outer cortex. Cortical bundles are abundant in stems but have a rather short functional life because they are more or less obliterated when secondary growth occurs.

DISCUSSION

Seedling Establishment

Our study of seedling establishment in *P. californicum* identified several structural features that occur elsewhere in Santalales, including the holdfast, an adhesive attachment disk with epithelial trichomes, and a collapsed zone (Olson and Kuijt 1986; Heide-Jørgensen 1989, 2008). In *Viscum minimum* Harv., epithelial trichomes often divide perpendicular to their long axis to become bicellular (Heide-Jørgensen 1989), a feature we also observed in *P. californicum* (Fig. 7). In contrast, two loranthaceous species, *Tristerix aphyllus* (DC.) Barlow & Wiens (Mauseth et al. 1985) and *Phthirusa pyrifolia* (HBK) Eichler, have epithelial disks with unicellular trichomes (Dobbins and Kuijt 1974). In *P. californicum*, the division of epithelial trichomes to become bicellular may correlate directly with the extent of trichome elongation because anticlinal divisions occur most frequently in longer trichomes.

←

cavity, *gc*.—7. Higher magnification view of flank of holdfast showing collapsed zone and epithelial trichomes, *et*; the trichome at right has formed a cell plate (unlabeled arrow) and is now bicellular; note also the matrix of amorphous-appearing material at mistletoe-host interface.—8–10. Sections of infected host stem.—8. Section of primary haustorium, *ph*, in host secondary phloem, *hp*, and host secondary xylem, *hx*.—9. Radial section of host stem showing bark strand, *bs*, of mistletoe at juncture with two sinkers, *s*, that contact a host ray, *hr*.—10. Tangential section of host secondary phloem containing mistletoe sinkers; the centrally located sinker and the two sinkers to its right are associated with host rays. Scale bar in 6, 9 = 100 μm; in 7, 10 = 50 μm; in 8 = 200 μm.

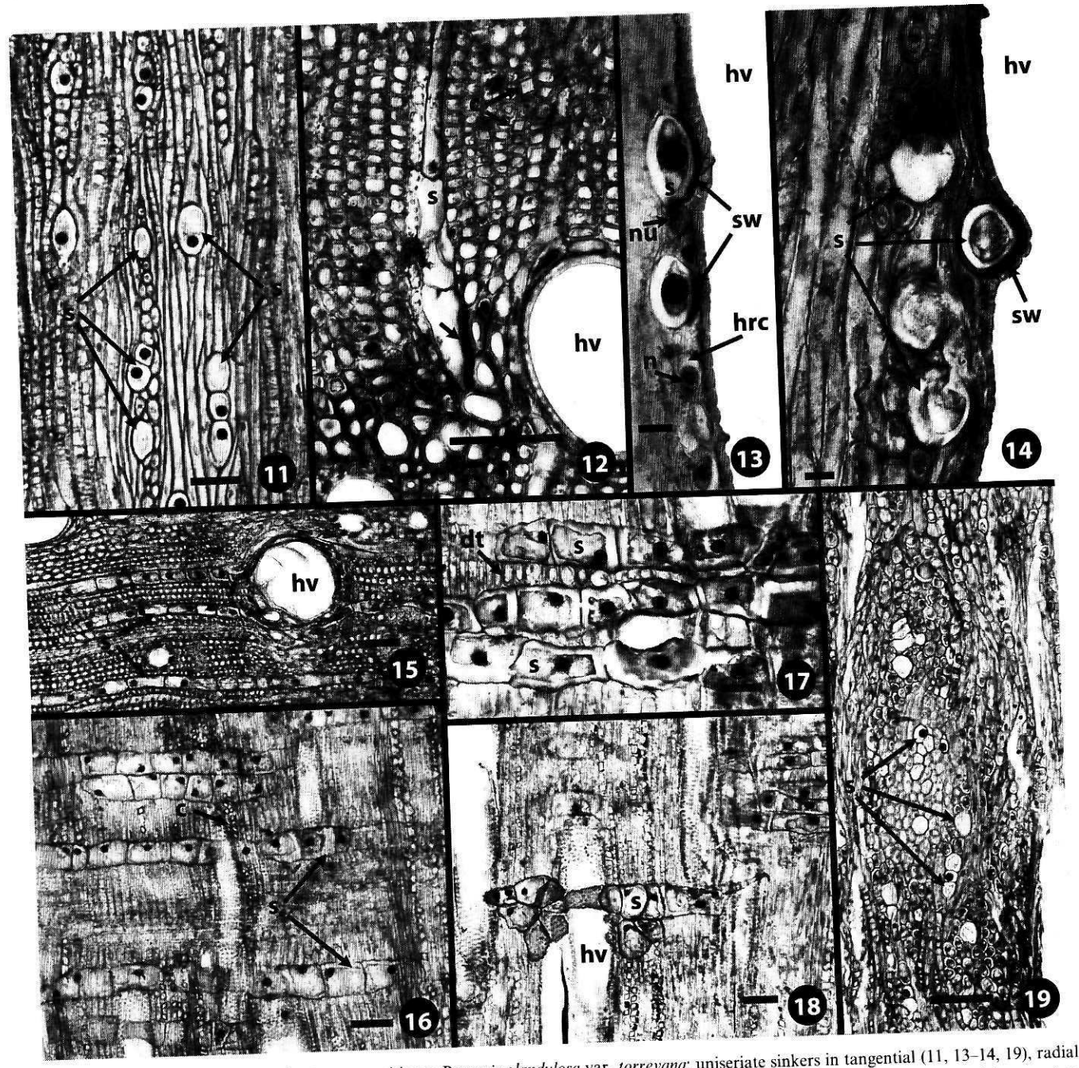

Fig. 11–19. *Phoradendron californicum* parasitic on *Prosopis glandulosa* var. *torreyana*: uniseriate sinkers in tangential (11, 13–14, 19), radial (16–18), and transverse sections (12, 15) of host wood.—11. At left three sinkers, *s*, associated with host ray, versus at right two sinkers, not so associated.—12. Sinker with necrotic cells at end; note shape and prominent differential wall thickening (unlabeled arrow) in terminal cell on side by large host vessel, *hv*; note also crystals, *c*, in host wood and dense staining of host cells near end of sinker.—13–14. Transfer cells.—13. Cells with thick secondary cell walls, *sw*, in part contiguous with host vessel; note that protoplasts of sinker cells have drawn away from cell walls only on side opposite thick-walled labyrinth and that sinker cells are associated with host ray cells, *hrc*; note also that host ray cells have prominent nuclei, *n*, and nucleoli, *nu*.—14. Sinker with prominent secondary cell wall near bulge into host vessel.—15. Radially elongate sinkers with cells having prominent nuclei; note that large host vessel has altered somewhat the radial course of sinkers.—16. Sinkers, one or two cells high; note abundant prismatic crystals in host.—17. Middle row of sinker cells contacting lowermost row of cells at left and uppermost row at right; declining tier, *dt*, of cambial derivatives at upper left.—18. Sinker locally proliferated near host vessel; at different tangential sections this sinker would appear as one, two, or three cells high.—19. Large aggregate parenchyma of host with several separate mistletoe sinkers. Scale bar in 11, 12, 15, 16, 18 = 50 μm; in 13, 14 = 10 μm; in 17 = 25 μm; in 19 = 100 μm.

A prominent broad zone of collapsed cells occurs in the attached holdfast of *P. californicum* (Fig. 6–7). In *Viscum minimum*, a zone of collapsed cells forms in the mature holdfast prior to penetration of the host and then, as the intrusive structure contacts the host, more layers of compressed cells accumulate in this zone (Heide-Jørgensen 1989). We studied only a small number of seedlings of *P. californicum* and were able to determine the presence and position but not the timing of collapsed zone formation.

We identified in *P. californicum* one holdfast structure, the gland (Fig. 6), considered absent in the Viscaceae clade (Olson and Kuijt 1986), although present in other parasitic Santalales (Fineran 1963; Kuijt 1977). In *Phthirusa pyrifolia*, the gland first appears as a glandular mass of tissue (Dobbins and Kuijt 1974: Fig. 1) and later as a cavity (Kuijt and Toth 1976). The intrusive organ of the parasite develops proximal to (above) the gland and grows through it on its way to the host (Dobbins and Kuijt 1974: Fig. 4–5). Thus, the gland is ephemeral in nature and its presence could be easily missed. Neither Heide-Jørgensen (1989) for *Viscum minimum* nor Ramm et al. (2000) and Sallé (1975, 1983) for *V. album* reported a gland at any stage of seedling establishment. If our interpretation is correct, namely, that the lens-shaped cavity seen in *P. californicum* is a haustorial gland cavity, then the Viscaceae clade is not unique among Santalales in lacking haustorial glands, as suggested by Olson and Kuijt (1986).

Malécot et al. (2004) proposed that parasitism via haustoria has arisen only once in Santalales, a mostly parasitic order, and that reversals from parasitism to the non-parasitic condition are unlikely. Thus, parasitism in Santalales, an order with over 2200 species (Heide-Jørgensen 1989; Nickrent et al. 2010) may be viewed as a single derived character. Morphological and anatomical studies throughout Santalales have shown a remarkable similarity in haustorial structure, regardless of family (Kuijt and Toth 1976; Kuijt 1977; Fineran 1991; Heide-Jørgensen 2008). For example, the collapsed zone of cells and, with our findings, haustorial glands occur commonly throughout the parasitic members of the order. A broad survey employing electron microscopy has shown that a unique type of tracheary elements, graniferous tracheary elements, is universally present in Santalales (Fineran 1985). That such common haustorial structural characters persist throughout the order indicates that the haustorium, once established, was conservative in its evolution. This suggests that the gland is likely to be present in haustoria of other taxa in the Viscaceae clade. The reported absence of a gland in *Viscum minimum* (Olson and Kuijt 1986; Heide-Jørgensen 1989) may be related to the diminutive size of the plant, the ephemeral nature of the gland, or even evolutionary loss.

Anatomy of the Endophytic System

Table 1 compares the sinker systems of the acataphyllous, squamate *P. californicum*, the acataphyllous, squamate *P. juniperinum*, the acataphyllous, leafy *P. serotinum*, and the cataphyllous, squamate *P. fragile*.

The similarities and differences between *P. californicum* and the other three species raise two questions. (1) Because both *P. californicum* and *P. fragile* have a dimorphic sinker system and are squamate, could a dimorphic sinker system be shared among all squamate species? The answer is no! Although also squamate, *P. juniperinum* has only multiseriate sinkers. Ashworth (2000*b*) showed that the squamate condition in *Phoradendron* has arisen independently at least twice. The occurrence of squamate species of *Phoradendron* in several of the proposed natural alliances recognized by Kuijt (2003) suggests that the squamate condition has arisen repeatedly in the genus. (2) Because both *P. californicum* and *P. fragile* have a dimorphic sinker system, whereas *P. serotinum* and *P. juniperinum* have only a unimorphic multiseriate sinker system, does this suggest that *P. californicum* may be more closely aligned with the cataphyllous group of species? Several lines of evidence indicate this. Ashworth's (2000*a*,*b*) molecular work places *P. californicum* in the cataphyllous alliance. Furthermore, this species, though generally regarded as acataphyllous, is often cataphyllous (Kuijt 2003: p. 4, Fig. 66). Finally, the biseriate inflorescence (Ashworth 2000*b*: Fig. 3) found in *P. californicum* is shared with cataphyllous species. Unfortunately, little is known about the structure of the endophytic system in the mainly tropical cataphyllous species of *Phoradendron*. Thus, the systematic importance of the dimorphic sinker system shared by *P. californicum* and *P. fragile* awaits a comparative survey of the structure of the endophytic system across a broad range of species in the genus.

Differences in cellular organization between uniseriate and multiseriate sinkers present in *P. californicum* may allow for functional specialization. Uniseriate sinkers are commonly associated with host rays and contain only parenchyma cells, some of which are transfer cells, whereas multiseriate sinkers lack thick-walled transfer cells, are much less abundant, and contain both tracheary elements and parenchyma. The prevalence of uniseriate sinkers in *P. californicum* was quantified by Schmid and Lindemann (1979) who found a ratio of uniseriate-to-multiseriate sinkers approaching 40 : 1. In contrast, *P. serotinum* has only multiseriate sinkers that also contain both tracheary elements and parenchyma cells, but the latter are specialized in the form of flange cells and flange-type transfer cells (Fineran and Calvin 2000). These structural differences in the sinker system suggest that: (1) In *P. californicum* each sinker type has discrete functions. (2) The discrete functions of the dimorphic sinker system of *P. californicum* are combined in the unimorphic, multiseriate sinkers of *P. serotinum*.

Studies have provided information for *P. serotinum* on movement of materials between sinkers and host tissue. In its multiseriate sinkers, (1) parenchyma predominates at the mistletoe-host wood interface for both mistletoe (95%) and host, *Juglans* L. (71%), (2) direct tracheary-element connections are present, and (3) interface contact with host rays is minimal, occupying less than 2% of the sinker perimeter (Calvin and Wilson 1995). Cut host stems immersed in water containing lanthanum ions, an apoplastic marker, confirmed the transfer of tracer across the apoplastic continuum and into the walls of parenchyma cells of the parasite (Fineran and Calvin, unpubl. data). Vessel-to-vessel connections in *P. serotinum* should provide for bulk flow between mistletoe and host, whereas the abundance of flange-type transfer cells likely reflects sites where solutes are loaded into the mistletoe. We hypothesize that in *P. californicum* the transfer cells of uniseriate sinkers and the direct vessel-to-vessel, parasite-host connections in multiseriate sinkers function much like those in the multiseriate sinkers of *P. serotinum*, the significant difference being that in the transition to a unimorphic sinker system there has been a dramatic shift away from association with the ray system of the host.

Ashworth's (2000*b*) molecular work indicates that the northern, acataphyllous alliance, which includes *P. serotinum*, is a derived group with respect to the cataphyllous clade where *P. californicum* was resolved. Weber (1980), in his studies of the gross morphology of haustorial systems of Australian and New Zealand Loranthaceae, concluded that the diverse haustorial systems observed represented functionally equiva-

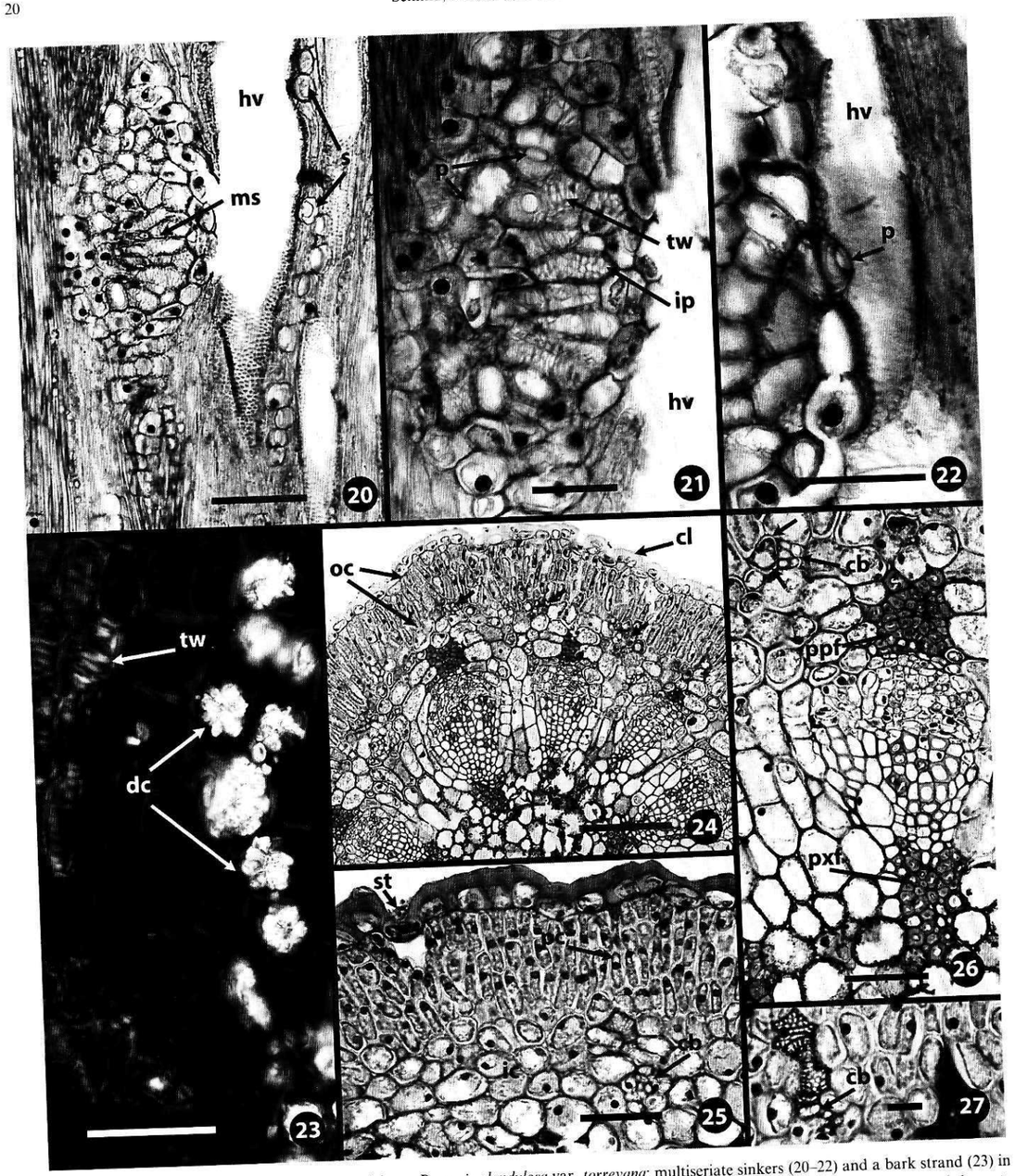

Fig. 20–27. *Phoradendron californicum* parasitic on *Prosopis glandulosa* var. *torreyana*: multiseriate sinkers (20–22) and a bark strand (23) in radial sections of host wood; transections of aerial stems of mistletoe (24–27).—20. Large multiseriate sinker, *ms*, contacting host vessel, *hv*; note how sinker narrows at its margins; note also abundant uniseriate sinkers, *s*, contacting other side of host vessel.—21. Higher magnification view of sinker showing vessel elements with simple perforation plates, *p*, alternate intervascular pitting, *ip*, and spiral thickenings of tertiary wall, *tw*.—22. Simple perforation plate connecting vessel elements of mistletoe and host.—23. Older bark strand with druse crystals, *dc*, in parenchyma cells, and tertiary-wall spiral thickenings in vessel elements.—24. Older stem with thick cuticular layer, *cl*, palisade chlorenchyma in outer cortex, *oc*, and cortical vascular bundles (unlabeled arrows).—25. Higher magnification view of stem showing sunken stoma, *st*, palisade chlorenchyma of outer cortex with large nuclei and prominent chloroplasts, inner cortex, *ic*, with isodiametric parenchyma cells, and a cortical bundle, *cb*.—26. Regular vascular bundle with secondary growth and fibers of primary phloem, *ppf*, and primary xylem, *pxf*; at upper left is a cortical bundle with its conducting elements next to a large, densely-stained parenchyma cell (unlabeled arrows) that had contained a large crystalloid inclusion.—27. ←

Cortical bundle as seen in Fig. 25 but enlarged here, and at a slightly different level; note pitted tracheary elements extending into outer cortical parenchyma. Scale bar in 20, 25, 26 = 100 μm; in 21–23 = 50 μm; in 24 = 200 μm; in 27 = 30 μm.

lent systems, but with strikingly different morphologies. Our anatomical studies revealed a similar pattern where the haustorial systems of *P. californicum* and *P. serotinum* are functionally equivalent but morphologically divergent. We suggest that these salient structural differences may reflect evolutionary trends in sinker morphology in *Phoradendron.*

The more abundant sinker type in *P. californicum* is the uniseriate, with most sinkers occurring in association with host rays. When infected host rays are examined in tangential sections through host wood, more than one sinker may be present in a single ray. However, when examined in radial sections of infected wood it is clear that in many cases what appear as separate sinkers at one tangential level are parts of a single sinker at another level. One option would be to consider all parasitic cells in a single host ray to comprise a single sinker, but there is evidence that some host rays do contain two or more independent sinkers. A second option is to adopt the terminology of Srivastava and Esau (1961*a*,*b*) to describe sinkers of *Arceuthobium* present in rays of its host, *Pinus* L. Focus was on rays of the host rather than on sinkers of the parasite; that is, any host ray that contained parasitic tissue was an "infected ray." In at least some species of *Phoradendron*, as *P. californicum*, where sinker autonomy is uncertain, use of infected ray would be descriptively more accurate.

Individual infected rays of *Arceuthobium* often merge, forming large, aggregate units composed of two or more individual infected rays (Srivastava and Esau 1961*a*). This merger results from the lateral or vertical fusion of individual infected rays as they displace fusiform initials from the vascular cambium (Wilson and Calvin 1996). The occurrence of aggregate structures in *P. californicum* that contain sinkers and host cells (Fig. 19) indicates that rays may also merge in infections of the host by *Phoradendron.* However, detailed study of serial sections through several years of growth of infected host wood, as Srivastava and Esau (1961*a*,*b*) did for *Arceuthobium*, would be required to determine whether the aggregate structures observed in *P. californicum* are comparable to the aggregate rays present in *Arceuthobium.*

Anatomy of the Aerial Stem

The stem of *P. californicum* has two features characteristic of the Viscaceae clade of Santalales (Wilson and Calvin 2003): a cuticular epithelium and transverse stomatal orientation. Transverse orientation is uncommon in angiosperms as a whole, but is more common in groups with succulent taxa (Butterfass 1987).

Stem structure in *P. californicum* and *P. serotinum* is strikingly different: most prominently, the outer cortex of *P. californicum* has a two- or three-layered chlorenchyma completely encircling the stem and that small-diameter vascular bundles are present in the cortical parenchyma. The palisade chlorenchyma appears more highly differentiated than the photosynthetic parenchyma present in stems (or leaves) of *P. serotinum.* The cortical bundles of *P. californicum* are also unusual, differing from the large inner vascular bundles of both species in containing only xylem and in lacking fibers. Kuijt (2003) does not mention either the prominent chlorenchyma or the small cortical bundles in his discussion of stem anatomy of *Phoradendron.*

Phoradendron californicum is a desert or arid species. The thick cuticle on the holdfast and aerial shoot, and the trichomes (Kuijt 2003: p. 138) and sunken stomata of the latter, are structures classically presumed to be adaptive to xericity (Evert 2006). Cannon (1904), in fact, surmised that the thick cuticle of the haustorial disk pre-insures against desiccation.

Several structural questions regarding the stem of *P. californicum* need clarification. (1) Is the presence of a chlorenchyma related to the squamate condition in the species? In the squamate dwarf-mistletoe *Arceuthobium*, the leaf base is merged with the stem for about one third of the internode and has a high stomatal density (Wilson and Calvin 1996). Similar to changes in stomatal density of *Arceuthobium* stems, the chlorenchyma in *P. californicum* may reflect a shift in function from the leaf to the stem and/or a merger of the stem and leaf base. (2) What is the significance of the ring of small cortical bundles in the stem of *P. californicum*? Their structure and the nature of their vascular supply need clarification. Cortical bundles also occur in another squamate species, *P. juniperinum* (C. Calvin and C. Wilson, unpubl.), but not in the large-leaved *P. serotinum* (C. Calvin and C. Wilson, unpubl.). (3) What are the structural-functional relationships in *P. californicum*, especially stem anatomy versus transpiration? In particular, how do the squamate shoots, prominently sunken stomata, and cuticular epithelium affect transpiration? Active transpiration is essential in mistletoes to maintain more negative water potentials than in their hosts and thereby assure the flow of water and solutes from host to mistletoe (Ehleringer and Marshall 1995). Perhaps significantly, *P. serotinum* has large foliage leaves with abundant stomata, and species of *Arceuthobium* have squamate shoots with many stomata where the leaf bases merge with the upper portions of the stem internode (Wilson and Calvin 1996). Although *P. californicum* is squamate, the degree of merger of stem and leaf base is unknown. Does the essential function of transpiration in *P. californicum* reside primarily in the reduced leaves? The cuticular epithelium developing on older stems of species of *Phoradendron* and *Arceuthobium* has been shown to severely restrict transpiration from the plant (Wilson and Calvin 2003), unlike the usual periderm with lenticels allowing for gas exchange. We suggest that in *P. californicum* the reduced leaves and young stems have a prominent role in transpiration. By the seventh extended internode of healthy appearing vegetative shoots, stomata were occluded and the system of small cortical bundles was disrupted due to secondary growth.

In summary, our study provides basic structural data on seedling establishment and the anatomy of the aerial stem and the endophytic system of *P. californicum*. Comparisons with the anatomy of three other species of *Phoradendron* (Table 1) allow some tentative evolutionary and functional speculations and present many interesting questions that await further investigation.

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