Epiparasitism in Phoradendron durangense and P. falcatum (Viscaceae)

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EPIPARASITISM IN *PHORADENDRON DURANGENSE* AND *P. FALCATUM* (VISCACEAE)

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ABSTRACT

Phoradendron, the largest mistletoe genus in the New World, extends from temperate North America to temperate South America. Most species are parasitic on terrestrial hosts, but a few occur only, or primarily, on other species of *Phoradendron*. We examined relationships among two obligate epiparasites, *P. durangense* and *P. falcatum*, and their parasitic hosts. Fruit and seed of both epiparasites were small compared to those of their parasitic hosts. Seed of epiparasites was established on parasitic-host stems, leaves, and inflorescences. Shoots developed from the plumular region or from buds on the holdfast or subjacent tissue. The developing endophytic system initially consisted of multiple separate strands that widened, merged, and often entirely displaced its parasitic host from the cambial cylinder. During establishment the epiparasite invaded the cortex, vascular cylinder, and pith of its parasitic host and spread aggressively within host tissues, extending between and into individual host parenchyma cells, eventually isolating host cells or cell groups. The parasitic host showed little visual response to the epiparasite. Endophytic system growth of the epiparasite within its parasitic host was compared to that of a parasitic *Phoradendron* within its terrestrial host. The results indicate growth dynamics similar to those of parasitic species on terrestrial hosts. We conclude that the epiparasite/parasitic-host union should not be regarded as a graft union. The harmonious appearance of the union is a result of the growth of the epiparasite replacing entirely tissues of its parasitic host, with little or no hypertrophy of parasitic-host branches.

Key words: graft union, host/parasite tissue relationships, mistletoe, parasite, Santalaceae, seedling development, Viscaceae.

INTRODUCTION

Parasitism by means of haustorial connections to a host is widespread in the angiosperms, having evolved independently ten or more times (Nickrent et al. 1998). Parasitic species occur in approximately 20 plant families and in total they represent more than 1% of all angiosperms (Heide-Jorgensen 2008). Parasites may be terrestrial, root parasites, or aerial, branch parasites. The largest and most diverse group of aerial parasites, the mistletoes, occurs in five families, Eremolepidaceae, Loranthaceae, Misodendraceae, Santalaceae, and Viscaceae, within the order Santalales. Eremolepidaceae and Viscaceae are sometimes placed within Santalaceae (APG 1998). Viscaceae form a strongly supported monophyletic clade within the broader Santalaceae (Nickrent 2000). Because epiparasitism, the subject of this report, is common within Viscaceae, but uncommon within Santalaceae and Eremolepidaceae, we are treating Viscaceae as a distinct group for convenience of discussion.

The family Viscaceae contains seven genera, including *Arceuthobium* M.Bieb., *Korthalsella* Tiegh., *Notothixos* Oliv., *Phoradendron* Nutt., and *Viscum* L. This report focuses on two epiparasitic mistletoes from the genus *Phoradendron*. *Phoradendron*, the largest genus in Viscaceae, is widespread in the New World. It ranges from Oregon on the West Coast of North America to New Jersey on the East Coast and extends southward across the United States, Mexico, Central America and South America, where it occurs in every country except Chile. Over this vast area the genus is represented by more than 230 species (Kuijt 2003).

Epiparasites (also called hyperparasites) are parasitic plants that grow on other parasitic plants of a different species (this definition excludes self-parasitism, commonly termed autoparasitism). Most epiparasites will grow on both terrestrial, non-parasitic hosts and parasitic hosts (facultative epiparasitism), while a few will grow only on parasitic hosts (obligate epiparasitism; Wiens 2002). Relationships among epiparasites, parasitic hosts, and terrestrial hosts can be complex. *Phoradendron bolleanum* (Seemann) Eichler typically grows on terrestrial hosts, but occurs occasionally as a facultative epiparasite on a number of mistletoe species. In contrast, *Viscum capitellatum* Sm. in Sri Lanka is known only as an obligate epiparasite primarily on the widespread mistletoe, *Dendrophthoe falcata* L.f. (Glatzel and Balasubramaniam 1987). Although the epiparasite has a high degree of host specificity its parasitic host, *D. falcata*, grows on the largest number of terrestrial hosts of any mistletoe, parasitizing more than 320 terrestrial species throughout its range (Singh 1962).

In Viscaceae the haustorial system, termed the endophytic system, is embedded within the host branch. In parasitic species of *Phoradendron* the endophytic system comprises a network of discrete bark strands and sinkers. The bark strands are oriented more-or-less parallel to the branch axis. At intervals elongating bark strands come into contact with the host vascular cambium (or form lateral branches that grow to the cambium) and assume a position within the cambial cylinder. Continued activity of the parasite/host cambium results in the formation of sinkers that extend from the bark strands across the phloem and into the xylem tissue of the host. The result is a highly dissected system that thoroughly permeates host phloem and xylem (Calvin 1967; Calvin et al. 1991; Fineran and Calvin 2000). A comparable endophytic system ground plan is found in the New World *Arceuthobium*

(Kuijt 1960; Sadik et al. 1986; Calvin and Wilson 1996), and the European mistletoe, *Viscum* (Salle 1979, 1983; Smith and Gledhill 1983; Hartmann 1994). The xylary portion of sinkers often have direct tracheary element connections between parasite and host (Kuijt 1960; Salle 1979; Smith and Gledhill 1983; Hartmann 1994; Calvin and Wilson 1995), but direct phloem-to-phloem connections by sieve elements have not been reported in any parasitic mistletoe.

There are many references in the literature to mistletoe epiparasitism, but most are anecdotal in nature. The Mistletoe Center literature database (*www.rms.nau.edu/mistletoe*) has more than 150 references for epiparasitism. Wiens and Calvin (1987) provide a general report on the occurrence of epiparasitism in Viscaceae and Loranthaceae. More recently, Wiens (2002) has described additional examples of epiparasitism in Viscaceae, including the widespread occurrence of epiparasitism in *Phoradendron* species from Mexico. Downey (1998) and Moss (1998) provide reports on the extensive occurrence of epiparasitism in the Australian mistletoes. Some reports describe the epiparasite/parasite union as "graft-like" in nature with the epiparasite producing little or no noticeable reaction in its host (Hamilton and Barlow 1963; Kuijt 1969). Epiparasite/parasitic-host tissue relationships have not been investigated previously and are likely to differ from parasite/terrestrial-host tissue relationships where infected-host branches typically develop extensive hyperplasia. We also examine seedling establishment, shoot growth in relationship to rate of haustorial system growth (as measured by spread of the epiparasite within parasitic-host branches), and the morphology of established epiparasites.

MATERIALS AND METHODS

This report focuses on two *Phoradendron* epiparasites, *P. durangense* Wiens, known only from the Mexican states of Sinaloa and Durango (Wiens 2002), and *P. falcatum* Eichler, a widespread species from Mexico and Guatemala. *Phoradendron durangense* has only one known parasitic host, *P. longifolium* Eichler ex Trel., and is considered an obligate epiparasite. In contrast, *P. falcatum* is reported to have a broad host range, including terrestrial hosts. However, Kuijt (2003) suggests that *P. falcatum* may also be an obligate epiparasite because the primary (immediate) host may have been overlooked in the numerous collections in which terrestrial plants are cited as hosts. We have observed *P. falcatum* in the field at more than twenty sites, and in all cases it was growing on other *Phoradendron* species, including *P. longifolium*, *P. bolleanum*, and *P. forestierae* Robinson & Greenman. Thus, the status of *P. falcatum* as facultative or obligate epiparasite is uncertain.

Collections of *P. durangense* were made in 1985, 1988, and 2006 at sites from 18 km E of La Capilla del Taxte, Sinaloa, eastward into Durango, Mexico. In 1988 we collected 39 infections of *P. durangense* at several locations in the vicinity of El Palmito, Sinaloa, Mexico for comparative analyses. We collected infections of different sizes in order to measure endophytic system spread of the epiparasite within its parasitic host, and compared these values to endophytic system growth of *P. juniperinum* Engelm. within its terrestrial host (Calvin et al. 1991). At all of the sites studied the parasitic host was *P. longifolium*.

Specimens of *P. falcatum* were first collected in 1985 at two sites in Oaxaca, Mexico, one NW and one NE of Oaxaca City. In 1988 we made a second trip to collect *P. falcatum*. On this trip more than a dozen infections were collected near Tequila, Jalisco, in proximity to Volcán Tequila. In this region *P. falcatum* occurred on both *P. longifolium* and *P. bolleanum*. Voucher specimens for our 1985, 1988, and 2006 trips are in our collections stored at RSA. Vouchers of the 2006 collections of *P. durangense* and its host *P. longifolium* are also filed at the Herbaria del Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR), Instituto Politécnico Nacional, Unidad Durango in the town of Durango, Mexico.

Collected endophytic system materials were placed in formalin–propionic acid–alcohol (FPA) containing a few drops of DMSO. In the laboratory preserved tissues were dehydrated, embedded in paraffin and mounted on wooden blocks. Mounted specimens were trimmed to expose plant tissue and, if woody, soaked overnight (or longer) in water containing 1–3 drops of detergent prior to sectioning. Sections were cut at 10–12 μm and attached to microscope slides. These slides were stained with either safranin–fast green (Jensen 1962) or with tannic acid–ferric chloride–lacmoid (Cheadle et al. 1953).

Shoots and infected host branches of 39 epiparasites were collected to determine the growth of epiparasitic shoots and endophytic systems. Shoots of *P. durangense* were air dried in the field and on return to the laboratory were oven dried for 72 hr at 60°C. Shoot dry weights were then recorded. Spread of the epiparasite in branches of its parasitic host was analyzed by taking hand sections at 1 mm intervals through entire infections. Free-hand sections at each interval were mounted on slides, stained, and examined for presence of the epiparasite using a light microscope. Microscopy and photography were done using a Zeiss Standard Universal microscope (Oberkochen/Württemberg, Germany). Images were captured using 35 mm film and digitized.

When studying tissue relationships between mistletoes and their hosts it is often difficult to distinguish between cells and tissues of the two plants. This is especially true in epiparasite/parasitic-host combinations where the two species belong to the same genus. We used several criteria to distinguish between epiparasite and parasitic-host tissues. These criteria were (1) cell lineages, (2) cell orientation, (3) cell size, (4) cell wall characteristics, (5) affinity for biological stains, (6) nuclear characteristics, (7) presence and distribution of necrotic tissues, (8) vessel member characteristics, (9) cell types present, (10) intracellular and/or intercellular contents, and (11) patterns of primary and/or secondary fluorescence. Although any one criterion when used alone may not have been adequate to distinguish between species, when used in combination they provided an effective means of differentiating between an epiparasite and its parasitic host.

Phoradendron epiparasites can also be difficult to recognize in the field. Several features were used to identify epiparasites: (1) seedling features such as cotyledons, (2) positional criteria such as growth from internodes, inflorescences or leaves, (3) distinct morphological characters such as epidermal features, and (4) examination of freehand transverse cuts through the parasitic-host stem to reveal epiparasite tissue.

Throughout the text we refer to the epiparasitic mistletoe either as the *epiparasite* or by its species name, and its mistletoe

host either as the *parasitic host*, or by its species name. The host of the parasitic mistletoe is referred to either as the *terrestrial host* or by its generic name. Mistletoes were assumed to be obligate epiparasites if they were observed and have been reported as growing only on parasitic hosts, and regarded as facultative epiparasites if they grew primarily on terrestrial hosts and occasionally on parasitic hosts.

<div style="text-align:center">RESULTS</div>

Comparative Morphology of Epiparasite versus Parasitic-Host Shoots

   Phoradendron longifolium was a common parasite in pine/ oak forests along the western side of the Sierra Madre Occidental in southern Sinaloa, Mexico. Plants of *P. longifolium* were rough textured, had a grayish cast and formed large, pendant masses of shoots that reached 5 m or more in length (Fig. 1). Because of their size, shape, and dull gray-green color older infections were quite visible even at a distance. This growth pattern contrasted with the pattern observed in *P. durangense*, an obligate epiparasite of *P. longifolium*. Shoots of the epiparasite projected outward (Fig. 1) from the pendant masses of *P. longifolium* shoots and curved upward (Fig. 2), ultimately forming broad, somewhat circular masses of green foliage with growing shoots projecting from the mass. The two species could be distinguished based on differences in plant habit such as shape and the clear separation in space of the epiparasite and its parasitic host even though their respective shoots were similar in appearance when examined closely.

   Vegetative shoots and overall habit of *P. falcatum* were easily distinguished from those of their parasitic hosts. Plants of *P. falcatum* formed large pendant yellowish-green masses, and had large, often sickle-shaped leaves and long internodes that were prominently flattened and were up to 2 cm wide just below the node. These characteristics contrasted with the grayish, long and slender shoots of its parasitic host, *P. longifolium*, and the reddish-brown, relatively short, squamate shoots of *P. bolleanum*.

   Epiparasites and their parasitic hosts of both species pairs were easily distinguished based on differences in fruit morphology. Within each epiparasite/parasitic-host pair, fruits ripened concurrently and those of the epiparasite were much smaller. Fruits of *P. falcatum* and some of its parasitic hosts also differed in color (Fig. 3). Birds fed on fruits of both plants as evidenced by the presence of dispersed seed masses containing seed of both the epiparasite and parasitic host. Dispersed seed of the epiparasite and its parasitic host each occurred in masses of 5–15 closely spaced seed (Fig. 4). This pattern of seed distribution is one of the three seed dispersal patterns recognized by Restrepo (1987). Seed of both epiparasites were smaller than those of their parasitic hosts (Fig. 4).

Establishment of Epiparasites on Parasitic-Host Branches

   In older stems of the epiparasite and its parasitic host the epidermis was replaced by the cuticular epithelium, a secondary protective covering characteristic of Viscaceae (Wilson and Calvin 2003). It was often difficult to determine the boundary between the two species after development of a cuticular epithelium (Fig. 5). To further confound interpretations, epiparasites often established near nodes and could be confused with parasitic-host shoots that developed from axillary buds (Fig. 5). In this example, parasitic-host inflorescences developed in axillary positions. Plants that established along internodes could be distinguished more easily from shoots of the host based on their position (Fig. 6). In addition, in this specimen the small, persistent cotyledons of the epiparasite were still clearly visible near the base of the plumular shoot (*c*, Fig. 6), providing unequivocal evidence that the plant developed from seed deposited on its parasitic host.

   While epiparasites that established on parasitic-host stems were most successful, specimens were also found growing on ephemeral organs such as inflorescences (Fig. 7) and leaves (Fig. 8, 9). Epiparasites that established on leaves occasionally reached sexual maturity, in part because infected leaves generally persisted longer on the parasitic host than did uninfected leaves. In young epiparasitic plants cotyledons were often visible (Fig. 8, 9). In the smaller plant of Fig. 8 one short, pointed cotyledon was visible. Note that the larger, second leaf-pair developed in the opposite plane and directly above the cotyledons. The first internode did not elongate and the first extended internode occurred between leaf pairs two and three (Fig. 8). In the larger plant the cotyledon was oriented directly toward the observer, but can be seen with difficulty (Fig. 9).

   In seedlings and young plants that developed from plumular shoots, cotyledons were persistent and visible for some time following establishment (Fig. 6, 8, 9). A second pattern of seedling establishment is shown in Fig. 10 and 11. In each of these epiparasite seedlings multiple shoots developed at the site of infection. These shoots developed from buds that formed either at the periphery of the holdfast or from newly proliferated endophytic tissue of the epiparasite. The hypocotyl-root axis, with the shoot primordium and cotyledons still enclosed within the necrotic seedling mass (*nsm*, Fig. 10), aborted following invasion into host tissues. The presence of the shrunken seedling mass with enclosed plumular shoot provides proof that the young shoots did not develop from plumular growth. Shoot development from the holdfast or endophytic tissue at the site of the infection was commonly observed in both *P. falcatum* (Fig. 10) and *P. durangense* (Fig. 11). In a given epiparasite population one pattern of seedling establishment was generally predominant.

Morphology of the Epiparasite Endophytic System

   A better understanding of the structural relationships between epiparasites and their parasitic hosts was gained by removing the bark from older infections to expose the wood (Fig. 12, 13). In Fig. 12 an entire infection is visible. The epiparasite had established on a small branch (at arrow) and spread to the main branch where it grew in a primarily basipetal direction. The small branch was necrotic distal to the site of infection and secondary growth of the main branch distal to the infection was minimal (Fig. 12). The endophytic system of the epiparasite was a series of separate strands (Fig. 12) in the portion of the main branch that was most recently infected. Moving in an acropetal direction along the branch, toward the initial infection site, the separate strands
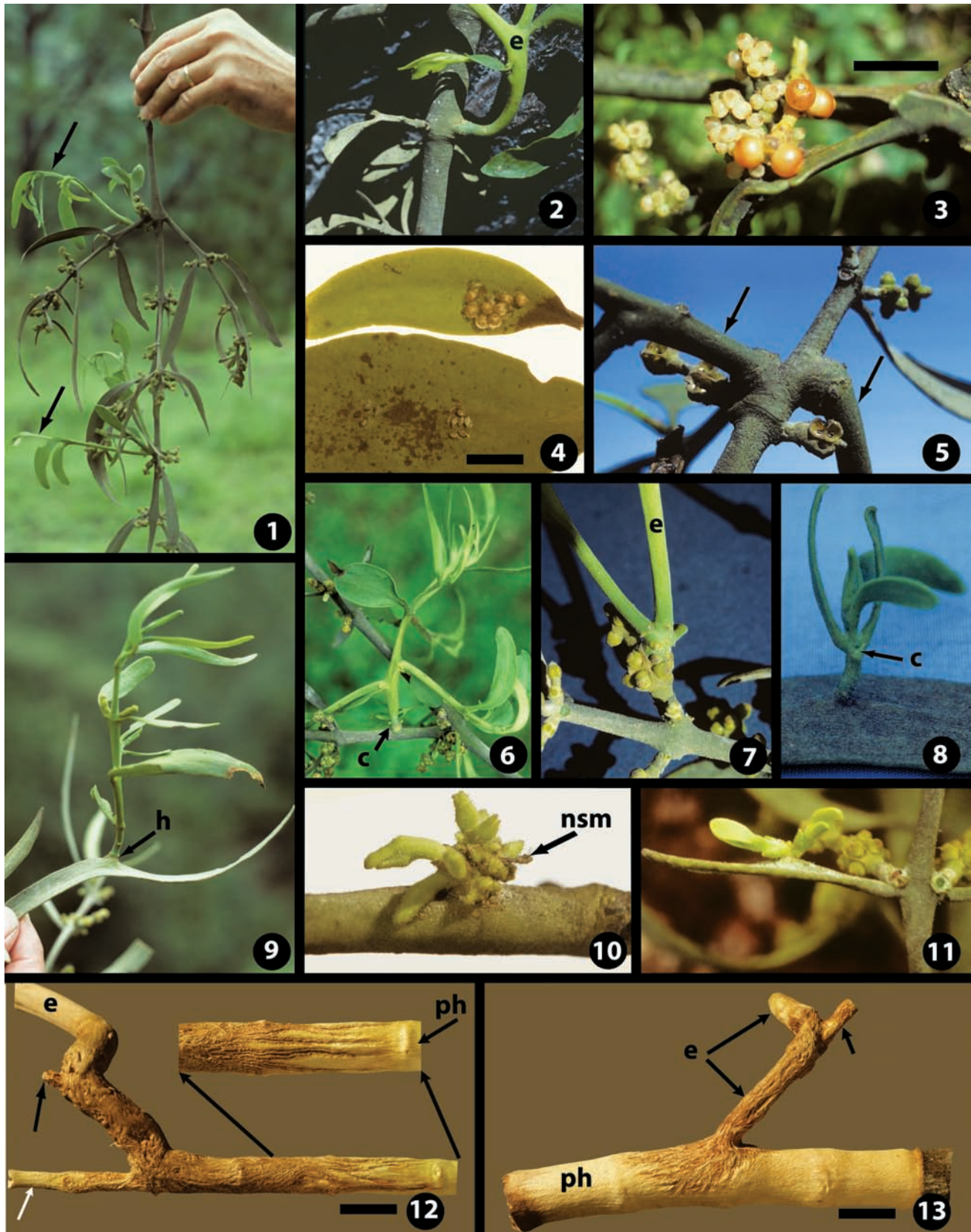
Fig. 1–13. Morphological aspects of epiparasitism in *Phoradendron durangense* and *P. falcatum*.—1–2. *P. durangense*.—1. Pendant *P. longifolium* shoot with epiparasite infections (at arrows).—2. Details of upward curved epiparasite, *e*, shoot.—3–4. *P. falcatum*.—3. White fruit of epiparasite and larger, orange-colored fruit of its parasitic host, *P. reichenbachianum* Oliv.—4. Seed of epiparasite (below) and its parasitic host (above) on mistletoe leaves.—5. Shoot of *P. longifolium* with two *P. durangense* infections (at arrows); note small diameter of parasitic-host

widened and merged, and eventually formed a solid cylinder of epiparasite xylem tissue that completely encircled the parasitic-host wood.

A similar phenomenon is shown in Fig. 13 where an epiparasite infected a small parasitic-host branch that developed laterally from a larger branch. The epiparasite had spread from the small branch toward and into the larger branch. In the small branch the epiparasite had overgrown the wood of its host as it displaced the host from the vascular cambium. In the larger, more recently infected branch the epiparasite extended both basipetally and circumferentially. At the margins of the infection several narrow strands were present, similar to those shown in Fig. 12. The elongation of these narrow strands was responsible for the continued spread of the epiparasite within the parasitic-host branch. Over time this infection is expected to completely encircle the larger host branch and take over the production of vascular tissues in this host branch region. The small branch was necrotic distal to the site of infection and the epiparasite appeared to occupy a terminal position on the parasitic-host branch. Each of the eleven mature infections of *P. falcatum* analyzed occupied a pseudoterminal position on branches of their *P. bolleanum* host. Pseudoterminal infections were observed infrequently in *P. durangense*.

Macroanatomy of the Epiparasitic Endophytic System and Spread within the Parasitic Host

The morphological features of the epiparasite endophytic system described above were illustrated anatomically (Fig. 14, 15) in a transverse section through an infected parasitic-host stem. In the outer region of the stem the cuticular epithelium, cortex, and primary and secondary phloem of the parasitic host were visible (Fig. 14). A bundle of primary phloem fibers was present and to its left a cluster of thick-walled sclereids. The same sclereid cluster was visible in Fig. 15. Below the sclereid cluster the secondary phloem of the parasitic host was contiguous tangentially with the more densely stained outermost layer of epiparasite meristematic cells (Fig. 15). Internal to the meristematic layer, radial files of epiparasite vessels were embedded within a densely stained parenchyma. At the outer limit of matured vessels a few partially differentiated vessel members were present, illustrating the centrifugal differentiation of epiparasite xylem within the parasitic-host stem. Below the region of differentiated epiparasite xylem was a large strand of epiparasite parenchyma tissue (*ftp*, Fig. 15) bounded on three flanks by parasitic-host wood. At the level of stem shown in Fig. 15, several similarly positioned parenchyma strands were present at the innermost boundary of the epiparasite. These strands of parenchyma are the differentiated product of the individual elongating strands shown in Fig. 12.

Details of the epiparasite parenchyma strand (*ftp*, Fig. 15) are shown in Fig. 16. The individual parenchyma cells had bands of lignified secondary wall material adjacent to their lumina and were interpreted to be flange-type parenchyma cells (Fineran 1996). Prominent cell features included a dense cytoplasm, large nuclei, and (particularly in cells at the parasitic-host interface) abundant starch. The tissue had small intercellular spaces, and necrotic tissue (*nt*, Fig. 16) was often present at the parasitic-host interface. Epiparasite parenchyma was visible in radial sections through infected stems (Fig. 17) where the parenchyma was contiguous with sclerenchyma fibers, vessel members and parenchyma of its parasitic host. Both tracheary elements and sclerenchyma fibers were absent in the first-formed tissue of epiparasite strands; instead all cells differentiated into parenchyma (Fig. 15–17).

During growth of the epiparasite's endophytic system new cells that were formed above the parenchyma strand matured as vessel members as well as parenchyma (Fig. 15, 17). The enlarging strands also added tissues tangentially and subsequently merged with adjacent strands. Tissue differentiation was more diverse in the variable width regions where strands enlarged tangentially and merged (Fig. 18). Here epiparasite tracheary elements as well as parenchyma were present at the interface with parasitic-host wood. Note that the wood of the parasitic host had an abundance of living, thick-walled sclerenchyma fibers (Fig. 16, 18). Sclerenchyma fibers were also present in epiparasite wood but generally formed some distance from the interface (later in development). Elongate epiparasite fibers (upper right, Fig. 17) appeared to be structurally distinct from those of the parasitic host because they were of the gelatinous type (Esau 1965).

The epiparasite spread aggressively in the primary tissues of the host, particularly in leaves and inflorescences, both of which had limited secondary growth. The extent of spread was illustrated dramatically in transverse sections through a petiole of an infected parasitic host leaf (Fig. 19). The epiparasite was present on both the dorsal and ventral side of the infected bundle as well as in the meristematic region between differentiated xylem and phloem (Fig. 19). The epiparasite had also spread intrusively into host ground parenchyma adjacent to the bundle (Fig. 19, 20). Frequently, parasitic-host parenchyma cells became isolated within proliferated masses of epiparasite tissue (Fig. 21), essentially becoming idioblasts within their own plant body. The isolated parasitic-host cells often were enlarged, contained atypical contents, deposited unusual secondary walls, were necrotic, and/or lacked visible living contents. In an adjacent vascular bundle the epiparasite

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branch distal to infections.—6–9. Sites of *P. durangense* establishment.—6. On stem internode; note cotyledon, *c*.—7. On inflorescence.—8–9. On leaves.—8. Persistent cotyledon is visible.—9. The holdfast, *h*, is prominent.—10–11. Epiparasite seedling shoots developed from buds at holdfast region.—10. *P. falcatum* on stem, necrotic seedling mass, *nsm*, is visible.—11. *P. durangense* on leaf.—12–13. *P. falcatum* infections on branches of its parasitic host, *P. bolleanum*, from which bark had been removed.—12. Epiparasite established on small lateral branch (at arrow) and spread basipetally into larger branch where most growth was also basipetal; note diminished growth of larger parasitic-host, *ph*, branch (white arrow) distal to infection. The enlarged reverse side of parasitic-host branch (above) shows details of most recent portion of infection; note that the epiparasite appears as several discrete strands that later widen and merge.—13. Epiparasite established on smaller diameter lateral branch (at unlabelled arrow) and spread to larger diameter branch. The small branch was necrotic distal to the site of infection. Bars in Fig. 3, 4, 12, 13 = 1 cm.
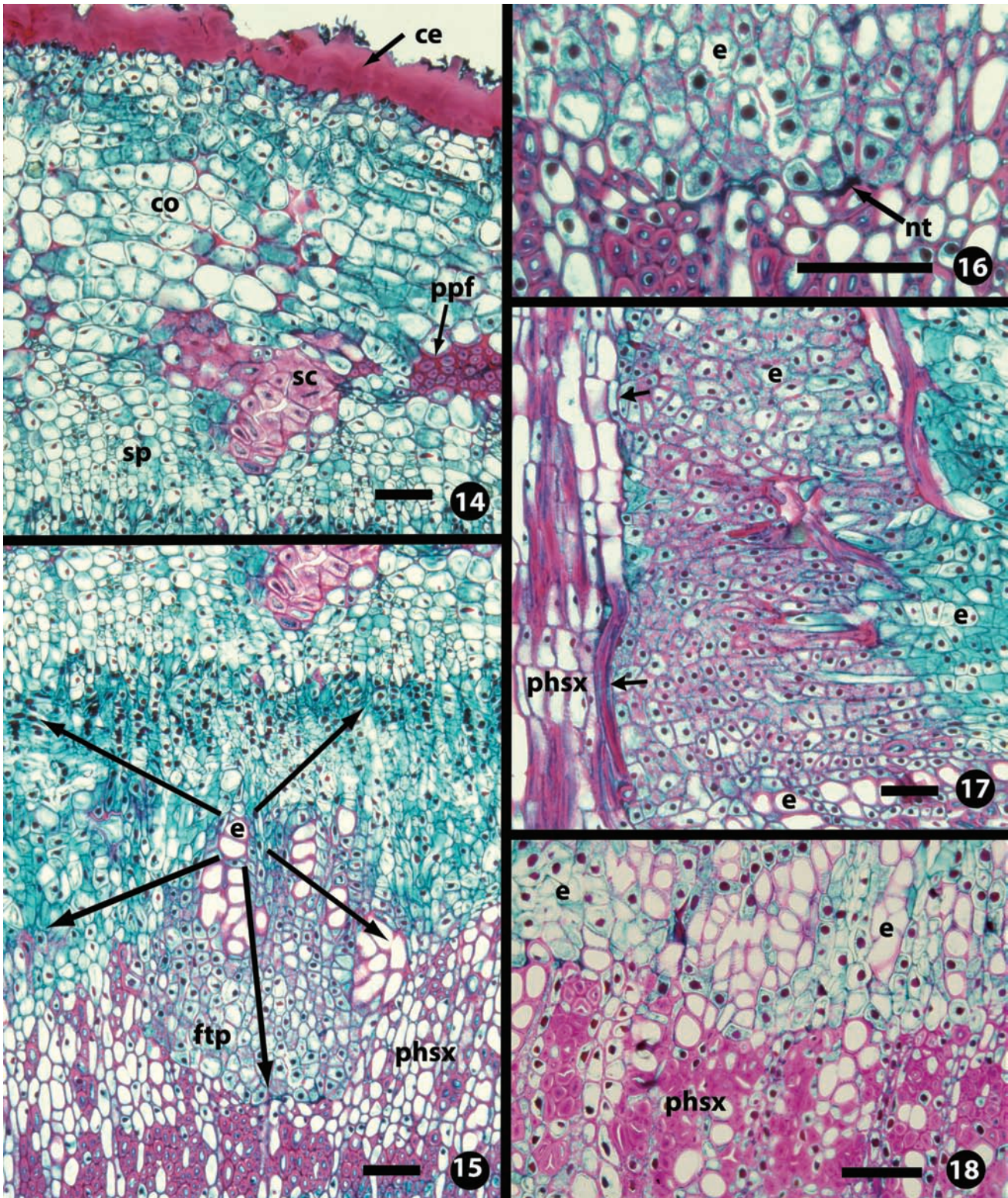
Fig. 14–18.   *Phoradendron durangense* as seen in transverse (14–16, 18) and radial longitudinal (17) sections of a *P. longifolium* stem.—14. Near periphery of stem showing cuticular epithelium, *ce*, cortex, *co*, primary phloem fibers, *ppf*, sclereid cluster, *sc*, and secondary phloem, *sp*, of parasitic host.—15. A view taken closer to the center of the parasitic-host stem; the sclereid cluster at top of figure is the same cell cluster as seen in Fig. 14. Interior to the host secondary phloem is the epiparasite, *e*, with an outer region of densely stained meristematic cells. The epiparasite xylem contains radial files of vessel members (near center of figure) and beneath these a large mass of flange-type parenchyma, *ftp*, devoid of tracheary elements and fibers. Parasitic-host secondary xylem, *phsx*, is visible near bottom of figure; note abundance of sclerenchyma fibers in parasitic-host wood.—16. Enlarged view of the flange-type parenchyma seen in Fig. 15; note presence of dense cytoplasm with large nuclei, secondary cell walls, and necrotic tissue, *nt*, at tangential boundary with parasitic-host wood.—17. Epiparasite parenchyma tissue contiguous

had grown intrusively into a cluster of primary phloem fibers, and subsequent meristematic activity had separated the fibers into two groups (Fig. 22).

A salient feature of the epiparasite was its ability to invade living cells of its parasitic host. In the example shown, the epiparasite had penetrated the thick primary cell wall of a parasitic-host parenchyma cell (Fig. 23). Several epiparasite cells occupied a major portion of the parasitic-host cell lumen and the resulting lens-shaped, parasitic-host cell protoplast occupied a small volume opposite the site of epiparasite penetration (Fig. 23). The protoplast of the host cell contained abundant small starch grains on the side adjacent to the epiparasite (Fig. 23) and its dense cytoplasm contained a prominent nucleus that was not clearly visible at this focal level. The birefringent starch grains were of a distinctly different shape than grains present elsewhere in host tissue. The complex relationships of the epiparasite to host vasculature will be reported separately.

Is the Epiparasite/Parasitic-host Union Graft-like in Nature?

The absence of significant swelling of infected parasitic-host branches has been considered characteristic of the epiparasite/parasitic-host union. In most cases, however, at least minimal swelling was evident in the epiparasitic infections studied. Swelling was localized (Fig. 5), occurring primarily in close proximity to the union, or diffuse extending a significant distance acropetally and/or basipetally along the parasitic-host branch. We determined the spread of the epiparasite within its parasitic host and compared this spread to that of a parasite on its terrestrial host, where considerable host branch swelling typically occurs. Baseline endophytic-system spread/shoot dry weight ratios were established previously for *Phoradendron juniperinum* Engelm. ex A.Gray growing on a terrestrial host, *Juniperus* L. (Calvin et al. 1991).

The 39 *P. durangense* infections collected to examine growth of epiparasite shoots and endophytic systems were separated into five shoot dry-weight classes (Table 1). In both unstained and stained sections uninfected stem segments (Fig. 24) could be readily distinguished from infected stem segments (Fig. 25). In infected branch portions the epiparasite was often present in the parasitic-host cortex, vasculature and pith, including pith rays (Fig. 25). The epiparasite also was visible to the unaided eye in freehand transverse sections through infected branches (Fig. 26), a technique that proved useful on occasion for distinguishing between epiparasite and parasitic-host branches in the field, especially in *P. durangense*.

Our analyses of endophytic system spread and shoot growth in *P. durangense* illustrated that the overall pattern of longitudinal spread of the epiparasite within branches of its parasitic host mirrored that of parasitic infections of *P. juniperinum* growing on a terrestrial host, *Juniperus* (Fig. 27). Note that the spread of the epiparasite, while less than that of lateral parasitic infections, was initially greater than that of parasitic infections that had become pseudoterminal on branches of their terrestrial host. Note also that the rate of spread of the epiparasite diminished more rapidly than in either pseudoterminal or lateral infections of the parasitic mistletoe, and subsequently mirrored more closely that of pseudoterminal infections.

DISCUSSION

Phoradendron, with 234 species (Kuijt 2003), is the largest mistletoe genus in the New World, and arguably in the World. If the closely related, sympatric *Dendrophthora* Eichler with approximately 120 species (Kuijt 2000, pers. comm.) were merged into *Phoradendron*, a change supported by the molecular work of Ashworth (2000), the total number of species would exceed 350. The genus ranges from temperate North America to temperate South America, with the greatest species diversity found in the tropics. Over this vast range the genus parasitizes not only hardwoods but also several conifers (Geils et al. 2002). The fruit of *Phoradendron*, a pseudoberry, is bird dispersed. It is likely that facultative epiparasitism is common because parasitic species are abundant and many have overlapping fruiting seasons. Much less common, but widespread in the Neotropics, is obligate epiparasitism. A striking feature of obligate epiparasitism in *Phoradendron* is that most species grow on other species of the same genus (Wiens 2002; Kuijt 2003).

In contrast with epiparasitism by Viscaceae worldwide, neotropical *Phoradendron* species occur primarily as epiparasites of other *Phoradendron*. Based on the herbarium survey of Downey (1998), Australian species of Viscaceae rarely parasitize other Viscaceae, preferring instead members of the mistletoe family Loranthaceae, as do epiparasitic members of Loranthaceae. Less than ten percent of epiparasitism events in two of the Australian Viscaceae, *Viscum* and *Notothixos* (epiparasitism is rare in *Korthalsella*), involve other Viscaceae. In contrast, Loranthaceae serve as hosts to 88% of Viscaceae epiparasites and 61% of Loranthaceae epiparasites. If the related Santalaceae sensu stricto are excluded as hosts, nearly 92 percent of Viscaceae and 98 percent of Loranthaceae epiparasites in Australia occur on other Loranthaceae. A similar preference of Viscaceae for Loranthaceae hosts is reported for Africa (Visser 1982; Polhill and Wiens 1998), Malesia (Barlow 1997), Sri Lanka (Glatzel and Balasubramaniam 1987; Wiens 1987) and Taiwan (Chiu and Chen 1995, pers. comm.). Thus, the extensive intra-genus epiparasitism of *Phoradendron* in the Neotropics represents a unique phenomenon in mistletoe epiparasitism worldwide.

We illustrate that fruits (Fig. 3) and seed (Fig. 4) of the two *Phoradendron* epiparasites are small in comparison to those of their *Phoradendron* parasitic hosts. Similar size differences occur also in Loranthaceae where the obligately epiparasitic South African mistletoe, *Agelanthus pungu* (De Wild.) Polhill & Wiens, grows on the parasitic host, *Plicosepalus kalachariensis* (Schinz) Danser. The mean dry weight of oven dried fruits of the epiparasite was 0.03 g while that of its parasitic

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with fibers (lower arrow), vessel members (above lower arrow), and parenchyma (upper arrow) of parasitic-host secondary xylem.—18. Vessel members and parenchyma differentiate at the interface with parasitic host secondary xylem in regions between the initial parenchymatous strands. Bars in Fig. 14–18 = 130 μm.
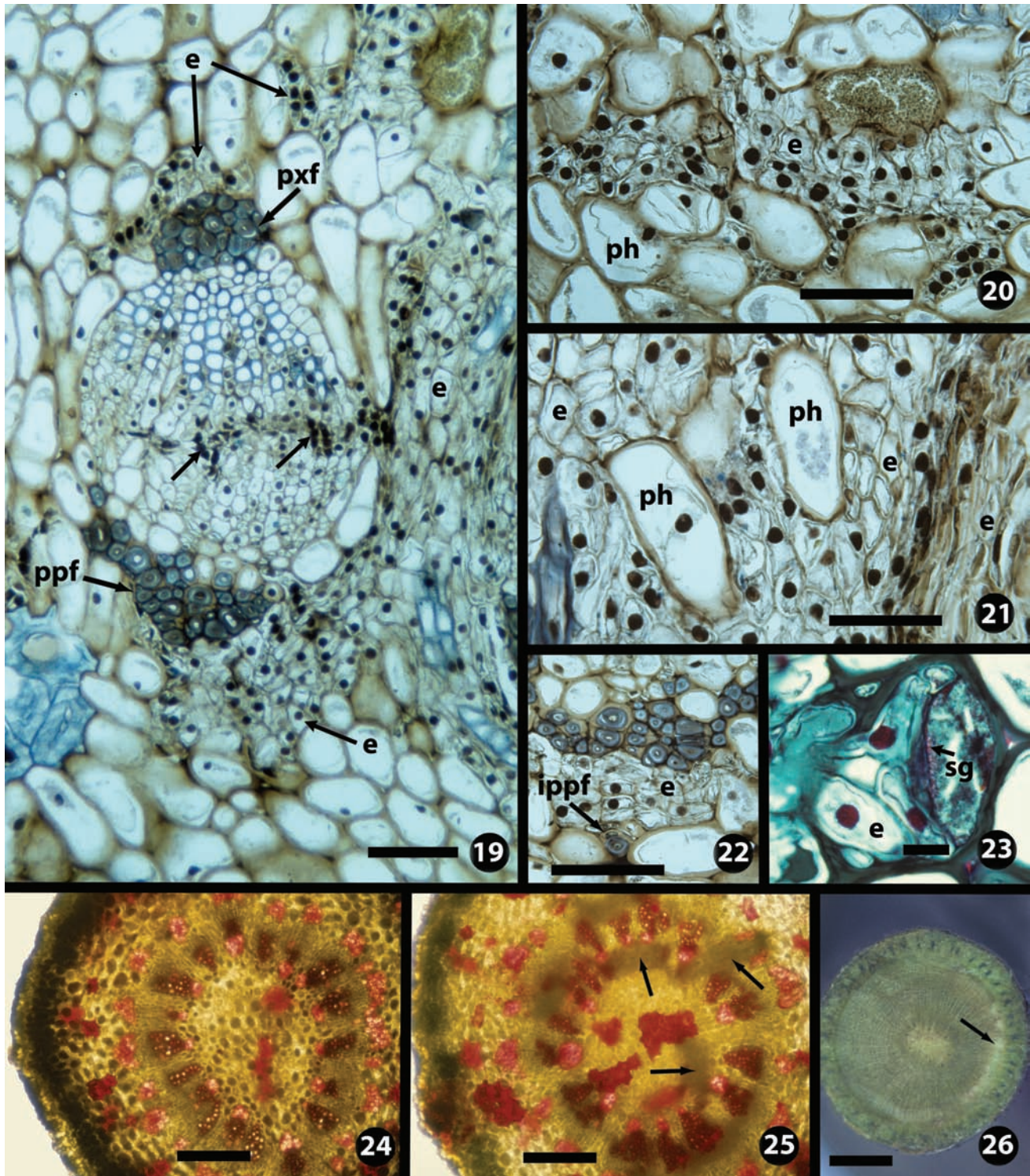
Fig. 19–26.   *Phoradendron durangense* as seen in transverse sections through *P. longifolium* petioles (19–22) and stems (23–26).—19. Infected vascular bundle of parasitic host; the epiparasite, *e*, is contiguous with the primary xylem fibers, *pxf*, and primary phloem fibers, *ppf*, and is present in the meristematic region between matured vascular tissues (at unlabelled arrows).—20. Epiparasite in the ground tissue of its parasitic host, *ph*; note the extent of intrusive cell growth.—21. Enlarged parasitic-host cells partially or completely isolated within a mass of epiparasite tissue.—22. Epiparasite has grown intrusively into a bundle of primary phloem fibers; subsequent meristematic activity has isolated a few fibers, *ippf*, external to the main bundle. —23. Parasitic host cortical parenchyma cell invaded by epiparasite; note that the epiparasite has proliferated within the lumen of the parasitic-host cell such that the now lens-shaped parasitic-host cell contains an abundance of small starch grains, *sg*, at its interface with the epiparasite.—24, 25. Freehand section through uninfected, 24, and infected, 25, regions of parasitic-host stem; note that the epiparasite (at arrows) is present in cortex, vascular tissue, pith rays and pith of its infected parasitic host.—26. Freehand cut through parasitic-host stem with secondary growth; the epiparasite is visible (at arrow), in proximity to the shared cambial zone. Bars in Fig. 19–22 = 143 μm, in Fig. 23 = 28 μm, in Fig. 24, 25 = 1 mm, in Fig. 26 = 3.5 mm.

Table 1. Weight class, acropetal and basipetal spread, total spread, and ratio of spread to weight for the endophytic systems of 39 epiparasitic infections of *Phoradendron durangense*. All infections were lateral on parasitic-host branches. $N \geq 6$ for each weight class.

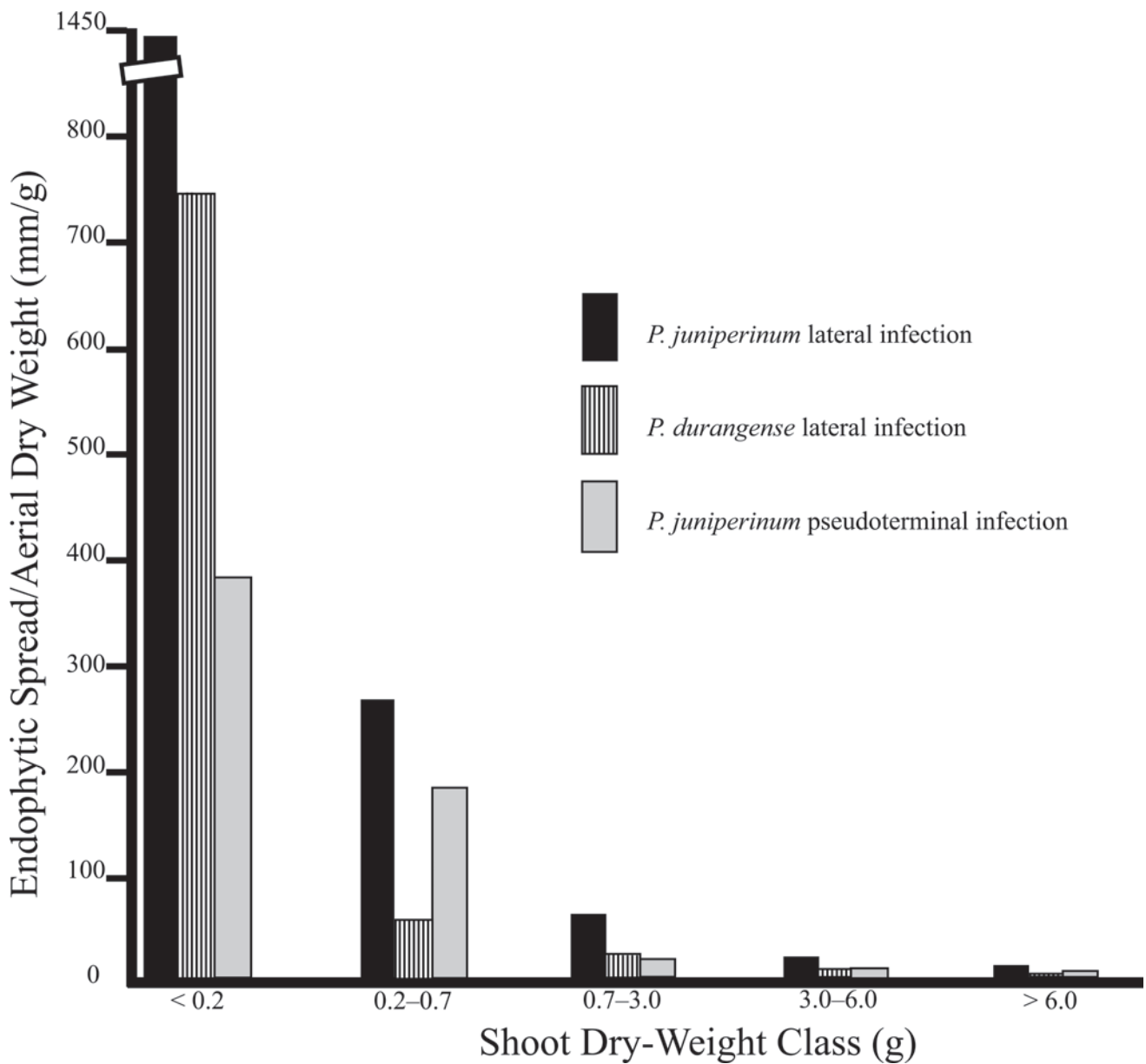| Dry weight class in g	Mean spread in mm			Mean ratio of spread/weight
	Acropetal	Basipetal	Total	
<0.2	6	8	14	746
0.2–0.7	10	13	23	60
0.7–3.0	12	18	30	27
3.0–6.0	19	25	44	10
>6.0	26	31	57	4

Fig. 27. Endophytic system spread/shoot dry-weight ratios for 39 lateral infections of *Phoradendron durangense* on its parasitic host, *P. longifolium*. Infections were assigned to one of five weight classes and extent of endophytic system spread was determined using freehand sections at 1 mm intervals. For comparison purposes spread/shoot dry-weight ratios are also presented for lateral and pseudoterminal infections of *P. juniperinum* on its terrestrial host, *Juniperus*; the five weight classes are identical for epiparasite and parasite infections.

host was 0.24 g ($N = 38$; unpubl.). A marked reduction in fruit size was noted in African obligately epiparasitic *Viscum* species (as compared to parasitic *Viscum* species) when the former were growing on Loranthaceae hosts (D. Wiens, pers. comm.). Thus, the epiparasite fruit/seed size-reduction phenomenon is widespread, occurs in both mistletoe families, and is independent of the plant family of the epiparasite or its parasitic host.

Botanists have long been interested in the significance of seed size in plants. Seed production is viewed as an evolutionary compromise between the size of seed and their number (Lloyd 1987). A large number of small seed improves species dispersal at the expense of successful seedling establishment (Šerá and Šerý 2004). The two *Phoradendron* epiparasites studied, similar to other epiparasites, rely on the production of a large number of small seed. The prodigious production of small fruit with small seed is likely a reflection of the stringent requirements for seedling establishment in the two epiparasites. Because several *Phoradendron* species are typically in fruit simultaneously a higher rate of unsuccessful dispersal would be expected because of seed transfer to a non-compatible parasitic host, particularly in the host-specific *P. durangense*.

Seedling germination and establishment in *P. durangense* and *P. falcatum* share features with temperate region, parasitic *Phoradendron* species. Study of the leafy *P. villosum* Nutt. and *P. densum* Torr. ex Trel. and the squamate *P. juniperinum* and *P. californicum* Nutt. illustrated a trend of reduced plumular shoot development and concomitant production of multiple shoots from the holdfast region during seedling establishment (Ruhland and Calvin 2001). In *P. villosum* and *P. densum* the plumular shoot developed into the main axis of the plant. In *P. juniperinum* and *P. californicum*, in contrast, growth of the plumular shoot was either reduced or suppressed. In *P. juniperinum* the plumular shoot failed to develop in about 10% of seedlings, whereas in *P. californicum* plumular shoots did not develop in plants from two of the three populations studied but did develop in a small percentage of individuals in the third. Reduction or suppression of plumular shoot growth has also been reported for *Viscum minimum* (Kuijt 1986) and for two Loranthaceae, *Tristerix aphyllus* G.Don (Mauseth et al. 1984) and *Tupeia antarctica* Cham. & Schltdl. (Ruhland and Calvin 2001). This study of seedling development in epiparasites supports that suppression of the plumular shoot and initiation of multiple basal shoots from the holdfast region is derived in Viscaceae (Ashworth 2000; Ruhland and Calvin 2001).

The endophytic system of parasitic *Phoradendron* species consists of more-or-less longitudinally oriented bark strands that form radially oriented sinkers. At intervals newly initiated sinkers come into contact with the host vascular cambium, assume a position within the cambial cylinder, and over time become incorporated into host wood and secondary phloem. Evidence suggests that there is intense competition between parasite and terrestrial host for space within the cambial cylinder because some sinkers widen, others maintain a nearly constant width, and others narrow and may eventually be excluded from the shared cambial cylinder (Calvin 1967). Endophytic system growth is markedly different in *P. durangense* and *P. falcatum*. In these species the elongating bark strands do not grow in the secondary phloem but rather

in undifferentiated cells of the cambial zone. Behind their narrow tips the strands widen rapidly and on branches of small diameter the widening strands merge to form a continuous cylinder, excluding entirely the host from the vascular cambium (Fig. 13). Thereafter xylem and phloem production at that level is solely by the epiparasite.

This change has profound implications for the parasitic-host branch distal to the epiparasite infection. Either the previously formed parasitic-host sieve elements must continue to function for an extended period of time or host photosynthates must move in the infected branch portion through sieve elements of the epiparasite. In *P. falcatum* populations most epiparasite infections had assumed a pseudoterminal position on the host branch due to death of the branch distal to the site of infection. The shift from a lateral to a pseudoterminal position on the host branch occurred but was not as common in *P. durangense*. Death of the host branch end eliminates the need for transport of photosynthates through the infected branch portion. Indeed, diminished photosynthate availability distal to the infection is the most likely cause of distal branch death. The terminalization of infections also occurs regularly in parasitic *Phoradendron* species where it appears that the phenomenon may be inversely correlated with terrestrial-host branch size at the time of infection (Calvin et al. 1991).

In both *P. durangense* and *P. falcatum* the parasitic host shows remarkably few visible tissue incompatibility responses to the presence of the epiparasite. Hypertrophy occurs when epiparasites invade leaves but is due mostly or entirely to proliferation of epiparasite tissues. A major cause of hypertrophy in parasitic mistletoe infections is the stimulation of terrestrial host cambial activity with subsequent xylem production (Calvin et al. 1991; Hartmann 1994). Stimulation of host cambial activity was not a major factor in epiparasitic relationships, in part because the vascular cambium of the epiparasite often replaced entirely that of its parasitic host. The extensive growth of the epiparasite in the cortex and pith of the parasitic host and the invasion and growth of the epiparasite within parasitic-host cells are unusual but have been reported in the parasitic species *Tristerix aphyllus* on its terrestrial Cactaceae host (Mauseth 1984). In this study the host appeared acquiescent, even as its cells and tissues became isolated within epiparasite tissue. Some isolated host cortical cells were unusually large but few host cells showed signs of recent meristematic activity. In both species pairs each species belongs to the same genus, *Phoradendron*. It would be of interest to analyze tissue relationships between a Viscaceae obligate epiparasite growing on a parasitic host in Loranthaceae. Based on the heterografts (*Cucumis* L. on *Cucurbita* L.) analyzed by Tiedemann (1989) one would expect evidence of tissue incompatibility between the epiparasite and its more distantly related parasitic host (Nickrent 2000).

The epiparasite/parasitic-host union has been described as appearing graft-like in nature (Kuijt 1969). To test this hypothesis we compared the endophytic system spread of *P. durangense* infections on its parasitic host, *P. longifolium*, to that of *P. juniperinum* infections on its terrestrial host, *Juniperus*. This comparison illustrates that the epiparasite has a pattern of endophytic system spread similar to that of parasitic species and that the epiparasite spreads aggressively within host tissues. In this comparison the epiparasite spread/shoot dry-weight ratio exceeded that of pseudoterminal

infections of *P. juniperinum* in early stages of establishment but was less than that of lateral parasitic infections (Fig. 27). The results indicate that although the epiparasite/parasitic-host union appears graft-like, the appearance is due to the passivity of the parasitic host to epiparasite invasion instead of failure of the epiparasite to aggressively invade parasitic-host tissues. Although epiparasite/parasitic-host unions may have features present in successful homograft and heterograft unions, such as symplastic continuity between the graft partners (Tiedemann 1989), the unions demonstrate a more aggressive, parasitic nature. Indeed, Pundir (1981) reported that in northern India the presumed obligate epiparasite, *Viscum loranthi* Elmer, is so aggressive and detrimental to its Loranthaceae parasitic hosts (*Dendrophthoe* Mart. and *Scurrula* L.) that the epiparasite has potential for biological control of its parasitic hosts on commercial timber crops.

Two categories of epiparasitism, facultative and obligate, are recognized. We assume that any mistletoe that grows only on other mistletoes (at least in some discrete portion of its range) is an obligate epiparasite. We predict that obligate epiparasites have established symplastic continuity with sieve elements of their parasitic hosts, a feature also shared between successful homo- and heterograft partners (Tiedemann 1989). Based on comparisons of mineral nutrition among epiparasites and their parasitic hosts, Glatzel and Balasubramaniam (1987) predicted symplastic continuity between phloem of the epiparasitic *Viscum capitellatum* and its parasitic host, *Dendrophthoe falcata*. They considered *V. capitellatum* an obligate epiparasite and a phloem feeder. If the preliminary report of symplastic continuity between sieve elements in *P. durangense* and *P. falcatum* and their parasitic hosts (Calvin and Wiens 1987) are documented by rigorous structural studies these Viscaceae species will join the list, albeit short, of obligate epiparasites in which phloem connections to their hosts are likely.

There is indirect evidence from the literature that epiparasitic mistletoes may have obligate status over only a portion of their range. Consider *Notothixos subaureus* Oliv. of eastern Australia (Barlow 1983). In the northern part of its range (21°S and northward) the species occurs mainly on rainforest trees. Further south the species is typically found in open forests, epiparasitic on *Amyema* Tiegh., *Dendrophthoe*, and *Muellerina* Tiegh. (Loranthaceae). Plants from the two regions were each assigned varietal status (Barlow 1983) based on morphological differences, but currently the morphological variation present within the species is not considered consistent with geography. Studies of plants from the two *N. subaureus* regions may provide answers to basic questions about physiological and structural modifications associated with obligate epiparasitism in the mistletoes.

ACKNOWLEDGMENTS

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