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NEW SPECIES OF *PHORADENDRON* (VISCACEAE) FROM MEXICO AND GUATEMALA AND A SYNOPSIS OF SPECIES IN SECTION *PAUCIFLORAE*

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**Abstract**

As presently interpreted *Phoradendron* section *Pauciflorae* consists of 15 species. These mistletoes parasitize primarily conifers. We describe seven new species, make status changes for four species, and provide information on the hosts and distribution of all members of the section. New species described are: *Phoradendron abietinum* Wiens, on *Abies durangensis* in Chihuahua, Durango, and Jalisco, Mexico; *P. acuminatum* Wiens, on *Cupressus lusitanica* in Guatemala; *P. flavomarginatum* Wiens, on *Juniperus flaccida* in Nuevo Leon, Mexico; *P. hawksworthii* Wiens, on *Juniperus* in New Mexico, west Texas, and Coahuila, Mexico; *P. olivae* Wiens, on *Cupressus lusitanica* in Colima and Jalisco, Mexico; *P. rufescens* Wiens, on *Juniperus spp.* in San Luis Potosí, Mexico; and *P. sedifolium* Wiens on *Cupressus lusitanica* in Chiapas, and Hidalgo, Mexico. Three taxa previously recognized as subspecies are raised to specific rank: *P. densum* Torr. ex Trel., *P. pauciflorum* Torr., and *P. libocedri* (Engelm.) Howell. Also *P. saltillense* Trel., which had been placed in synonymy under *P. bolleanum* subsp. *densum*, is accorded species status. In addition, three new epiparasitic species of *Phoradendron* are described. Epiparasitic mistletoes are known to parasitize only other species of mistletoes—in this instance *Phoradendron* or *Cladocolea* (Loranthaceae).

Key words: epiparasitism, new species, parasitic plants, *Phoradendron*, Viscaceae.

**Introduction**

Since the publication of the acataphyllous species of *Phoradendron* (Wiens 1964), considerable additional information has accumulated regarding sect. *Pauciflorae*. This is primarily the result of our extensive field studies in Mexico and Guatemala over the course of approximately 26 years. All the taxa discussed here have been studied in the field and the critical, defining characteristics of the new species were evaluated at the population level. In addition to reporting new species, several taxa previously recognized as subspecies in 1964 are elevated to species status and one species, *Phoradendron saltillense* Trel., previously synonymized under *P. bolleanum* (Wiens 1964), is also accorded species status. There are no subspecies presently recognized among these species. We include a synopsis of the species currently included in section *Pauciflorae* (Table 1), and a key to the species.

The earlier taxonomic conservatism of Wiens (1964), who gave subspecific recognition to a number of taxa now regarded as species, was partially a reaction to the numerous species named by Trelease (1916); however, the classification of taxa as subspecies that are widely distributed over thousands of kilometers seems inappropriate for subspecific recognition. We suspect that additional research will demarcate the existence of geographically definable elements (subspecies) within some of the wide ranging species, e.g., the populations of *P. densum* occurring in central Arizona on *Cupressus*, and perhaps various population systems of the widespread *P. saltillense* in northern Mexico.

**Materials and Methods**

The morphological differences most useful in the construction of keys for separating the species, often leaf size, are notoriously variable characters. Nonetheless, leaf size tends to fall out statistically, as well as internode length, since the latter is generally a correlate of overall plant size. Characters, such as stature and size, are not especially useful for constructing keys, but are still important features in defining the species, along with host differences. The specifics of these quantitative features are described in Wiens (1964), or in the descriptions of the new species presented herein. The problem is well illustrated by the relationship between *P. juniperinum* and *P. libocedri.*
The latter species has internodes that are significantly longer than those of *P. juniperinum*, and long internodes are correlated with the distinctive pendulous habit. Yet neither morphology nor molecular data (Ashworth 2000) identify clear-cut interspecific differences.

In addition to the description of new species in sect. *Pauciflora*, we also include descriptions of three new species of epiparasitic species of *Phoradendron*, *i.e.*, mistletoes that are known to parasitize only other mistletoes. In this instance the host mistletoes are either other species of *Phoradendron* or *Cladocolea* (Loranthaceae). The subject of epiparasitism is a fascinating phenomenon deserving of further study. More detailed information on the subject is available in Wiens (1964).

Unfortunately, Kuijt (pers. comm., 1996) has indicated that there are potential nomenclatural difficulties with the maintenance of the name *Pauciflora* as a section of *Phoradendron* sensu Wiens (1964). This issue will not be addressed here, as there is no question of the species involved or the cohesiveness of the group, regardless of what name is ultimately attached to it.

### RESULTS AND DISCUSSION

The species of section *Pauciflora* (Wiens 1964) parasitize primarily *Juniperus, Cupressus*, and to a lesser extent, *Abies*. Members of the group are typically reduced in terms of their overall size, as well as their floral and vegetative features, when compared to most other members of *Phoradendron*. Overall the species are rarely over 0.5 m high (exceptions are *P. acuminatum* and *P. olivae*, which may be over 1 m). Reduced overall size is typically correlated with shortened internode lengths and widths (mostly < 25 × 4 mm). The leaves are likewise either comparatively small (mostly < 25 × 8 mm) or reduced to scales. The length of the inflorescence, the number of fertile internodes produced, and the number of flowers per fertile internode are also relatively small in comparison with species in other sections. The staminate inflorescences are usually < 10 mm long with mostly 1–2 (3) fertile internodes, with each fertile internode commonly bearing < 20 flowers. The pistillate inflorescences typically have 1 (2) fertile internodes, and consistently produce only two flowers per fertile internode; two pistillate flowers per fertile internode is the best single morphological feature defining sect. *Pauciflora*. In addition to the morphological and host affinities that characterize the group, Ashworth (2000) showed that molecular data also confirm the uniformity of the group, as well as its monophyletic origin.

### CHANGES IN TAXONOMIC STATUS

Specimens are cited only for those species for which we have significant new distributional data. For distributional information of other species, see Wiens (1964).


*Phoradendron densum*, as here defined, occurs on *Juniperus* and *Cupressus* and has a distribution ranging from southern Oregon (Jackson Co.) throughout California to the Sierra San Pedro Martir, Baja California Norte, Mexico. There are interesting outlying populations in central Arizona on *Cupressus* (Coconino, Yavapai, Maricopa, and Gila Counties), that de-
serve further study as possible subspecies. The known elevational range is 200–2300 m.

Known hosts are Juniperus californica, J. occidentalis, J. osteosperma, Cupressus arizonica, C. bakeri, C. forbesii, C. goveniana, C. macnabiana, C. macrocarpa, C. montana, and C. sargenti. Phoradendron densum was reported on Pinus monophylla in the Mt. Pinos area of Ventura County, California (McMinn 1939), but this host has not been confirmed. The reports of P. densum in New Mexico and west Texas (Wiens 1964) are based on populations now transferred to P. hawsworthii.


We now consider P. libocedri a distinct species. It is an obligate parasite of Calocedrus (Libocedrus) decurrens, and it co-occurs in the Lake Tahoe region of California with P. juniperinum, which infects Juniperus occidentalis; each mistletoe is restricted to its particular host in this area. Also, P. libocedri becomes pendulous with age, and is a larger plant than P. juniperinum. This size difference is reflected in the longer internodes of P. libocedri (> 10 mm) (Wiens 1964). The distribution of P. libocedri ranges from southern Oregon (Jackson County), southward in both the Cascade and Sierra Nevada cordillera to southern California and Baja California Norte to the Sierra Juarez and Sierra San Pedro Martir (Wiggins 1980). An outlier population occurs on San Benito Peak in the south Coast Range in Monterey County (Raven 1957). The known elevational range is 400–1900 m.


We give species status to this taxon because it differs from P. densum in a number of features: leaf size, color, hosts, and distribution (Wiens 1964). The distributional range of P. pauciflorum extends from the central Sierra Nevada of California (Calaveras County) southward to the Transverse Ranges of southern California and to the Sierra San Pedro Martir in Baja California. Throughout its distribution it is a consistent parasite of Abies, especially A. concolor. An extreme outlying population occurs in southern Arizona in the Santa Catalina Mountains (Pima County) and it has also been recorded in the nearby Rincon Mountains (Bowers and McLaughlin 1987). Abies concolor is the typical host of P. pauciflorum throughout its range, but in the Sierra San Pedro Martir in Baja California it rarely parasitizes Cupressus montana, where this tree is associated with infected Abies concolor (Hawsworth and Wiens 1966). There is also a report of autotoparasitism in this species (Felix 1970), which is an uncommon phenomenon among mistletoes in general. The known elevational range is 1400–2600 m.


We recognize P. saltillense as a distinct species since it differs from typical P. bolleanum in leaf shape, color, hosts, and distribution, and from P. densum in leaf size, hosts, and distribution. Its relationship to P. hawsworthii is discussed under that species. The distribution of P. saltillense ranges from eastern and east central Mexico in Coahuila, Nuevo Leon, San Luis Potosi, and Puebla, on both Juniperus and Cupressus hosts. This species is separated from the closest known P. densum populations in central Arizona by more than 1000 km. The known hosts of P. saltillense are Cupressus arizonica, C. benthamii, C. flaccida, Juniperus deppeana, and J. saltillense. The species is common in the Sierra del Carmen in northern Coahuila, just east of the Chisos Mountains in Big Bend National Park, Texas, and might be expected in Texas. The known elevational range is 1850–2850 m.

Noteworthy collections examined.—MEXICO: COAHUILA: Mpio. Arteaga, 5 km E of Las Vegas, on C. arizonica. Bailey in 1982 (FPF); Sierra de la Marta, on Cupressus sp., Robert & Passini 43-4288 in 1975 (IBUG); Sierra de la Madera, Desiderio Cyn, on C. arizonica, Hawksworth et al. 1512 in 1975 (FPF) and on J. flaccida, Hawksworth et al. 1515 in 1975 (FPF); Sierra del Carmen: 1 mi W of Asseradero Maderas del Carmen (Ocampo) on J. deppeana, Hawksworth et al. 1035 in 1967 (FPF); 0.5 mi W of Asseradero Maderas del Carmen (Ocampo) on J. flaccida, Hawksworth et al. 1036 in 1967 (FPF); 2 mi W of Asseradero Maderas del Carmen (Ocampo) on J. deppeana, Hawksworth et al. 1040 in 1967 (FPF); 5 mi W of Asseradero Maderas del Carmen (Ocampo), on C. arizonica, Hawksworth et al. 1028 in 1967 (FPF); 15.9 mi S of Saltillo on Juniperus, Clark et al. 672, in 1967 (FPF); 40 mi S of Saltillo, on Hwy 57, on Juniperus, Wiens & Cameron 2607 in 1959 (RSA); Hwy 57 near San Roberto, on J. monosperma, Villareal 560 in 1987 (IBUG); 12 mi S of General Cepeda, on J. flaccida, Hawksworth & Wiens 399 in 1963 (FPF); Sierra de Parras en El Capulin, on J. saltillense, Rodriguez & Carranza 214 in 1981 (IBUG).—NUEO LEON: 6 mi S of Hwy 58 on Hwy 69, on Juniperus, Hawksworth & Wiens 1832 in 1978 (FPF).—SAN LUIS POTOSI: 8 km ENE of San Bartolo, on Juniperus, Hawksworth et al. in 1979 (FPF).—PUEBLA: Cerro de los Humeros, on C. benthamii, Chazaro & Charazo 4318 in 1986 (IBUG); 2 km NE of Guadalupe Sarabia, on C. benthamii, Oliva et al. Hor-36 in 1981 (IBUG).

NOTES ON HOSTS AND DISTRIBUTION

Phoradendron bolleanum (Seem.) Eichler

This species has the widest geographical distribution of any species in sect. Pauciflorae in Mexico. It occurs throughout the Sierra Madre Occidental from Chihuahua.
hual to Jalisco, including the states of Sonora, Durango, Sinaloa, Nayarit, and in central Mexico in Hidalgo and Querétaro. The report of it in Texas (Wiens 1964) was based on collections now transferred to *P. hawksworthii*. The known elevational range is 1900–2500 m.

In the section, *P. bolleeanum* is unique because it commonly parasiizes two diverse hosts, a conifer (*Juniperus* spp.) and an angiosperm (*Arbutus*) (Wiens 1964; Hawksworth and Wiens 1966). We know of no other instance where a mistletoe is restricted to two such diverse hosts. Trelease (1916) questioned whether the same mistletoe actually occurred on two such distantly related species. Without experimental evidence the question remains moot. We find, however, no morphological basis for a separation of the two populations on the two hosts. Although infection of *Juniperus* and *Arbutus* frequently occurs together, we have also observed a number of instances from Chihuahua to Jalisco, where only one of the two hosts is parasitized, even though the other host is present. For example, in Jalisco we have found *P. bolleaanum* only on *Arbutus* (also occasionally on associated *Arctostaphylos*), but *Juniperus* also occurs in the same area (Cházaro pers. comm., 1989). This suggests the possibility of two host races, and areas where both hosts are infected may simply represent instances of the co-occurrence of the two host races. Such morphologically indistinguishable host races are known in the related dwarf mistletoes (*Arceuthobium*) (Hawksworth and Wiens 1996). Controlled cross-inoculation experiments are necessary to resolve the problem.

Although this mistletoe is typically bright brownish, some greenish populations were observed in central Chihuahua (Hawksworth and Cibrian 1985).

*Phoradendron capitellatum* (Torr.) ex Trelease

This highly distinctive parasite of junipers is characterized by its small, densely stellate-pubescent leaves. The distribution of *P. capitellatum* is restricted to central and southeastern Arizona, southwestern New Mexico, northeastern Sonora, and northwestern Chihuahua. The known elevational range is 800–1700 m.

The hosts of *P. capitellatum* include *Juniperus deppeana*, *J. erythrocarpa*, *J. monosperma*, and *J. osteosperma*. Typically, *P. capitellatum* occurs at elevations below *P. juniperinum*, but the two species sometimes co-occur, and rarely parasitize the same host tree, e.g., on the south side of the Santa Catalina Mountains, Pima County, Arizona (Gilbertson pers. comm., 1978). For whatever reason, *P. capitellatum* tends to be under-collected, so we cite a number of collections to give a better understanding of its distribution.

**Noteworthy collections examined.—**U.S.A. ARIZONA, Cochise Co.: Guadalupe Mts, Guadalupe Cyn, on *J. erythrocarpa*, Gilbertson 7756 in 1967 (FPF); Chiricahua Mts, Paradise, Blumer 1524 in 1906 (MO); Gila Co.: 5 mi S of Payson, Wiens 2707 in 1960 (RSA); Tonto National Monument, Strong 118 in 1961 (ASU); Pinal Co.: 5 mi E of Superior on Hwy 60, on *J. erythrocarpa*, Hawksworth 2149 in 1986 (FPF); Graham Co.: Graham Mts, Tripp Cyn, on *J. deppeana*, Hawksworth & Lightle 145 in 1962 (FPF); Galiuro Mts, 1 mi N of Deer Cr Cabin, on *J. deppeana*, Mathiasen 7702 in 1977 (FPF); Peloncillo Mts, Microwave Tower, 11.5 air miles NW of Duncan, Holmgren & Holmgren 7073 in 1973 (WU); Greenlee Co.: 8 mi NE of Guthrie on Rte 78, on *J. erythrocarpa*, Hawksworth & Bailey 1771 in 1977 (FPF); near Clifton, Greene in 1880 (MO); Pima Co.: Santa Catalina Mts, Molina Basin, on *J. erythrocarpa*, Hawksworth & Gilbertson 1808 in 1977 (FPF); Santa Cruz Co.: Pajarito Mts., 1.7 mi S of Pajarito Peak, on *J. deppeana*, Van De Vender & Toolin s.n. in 1981 (ARIZ, FPF); Yavapai Co.: 8 mi W of Sedona, on Hwy 89, Wiens 2692 in 1960 (RSA); 10 mi E of Camp Verde on Pine Rd, Wiens 2699 in 1960 (RSA). NEW MEXICO. Grant Co.: Summit Mts, 10 mi E of Duncan on East Mine Camp Rd, on *J. erythrocarpa*, Hawksworth & Bailey 1772 in 1977 (FPF); Hidalgo Co.: Steins Pass, Tumney in 1895 (UC); Guadalupe Cyn, on *J. erythrocarpa*, Hawksworth 1624 in 1975 (FPF); Lightning Dock Mtn, 18 mi S of Lordsburg, on *J. erythrocarpa*, Hawksworth s.n. in 1985 (FPF); Luna Co.: Florida Mts, N slope, on *J. erythrocarpa*, Mathiasen 75-53 in 1975 (FPF); Crook Mts, near Crook Peak, on *J. erythrocarpa*, Hawksworth & Bailey 1762 in 1977 (FPF).—MEXICO. CHIHUAHUA: Sierra de Moscos, Chaising et al. 3851 in 1979 (FPF, TEX). SONORA: Palm Cyn, 13 mi SE of Magdalena, on *J. deppeana*, Mathiasen 7604 in 1976 (FPF).

*Phoradendron juniperinum* Engelm.

This distinctive scale-leaved species has the broadest distribution of any member of section *Pauciflorae*, and ranges from Oregon southward and eastward to California, Nevada, Utah, western Colorado, Arizona, New Mexico, and western Texas into Chihuahua and Durango in northwestern Mexico. It occurs in the Chisos Mts, but has not been reported from adjacent Coahuila. The known elevational range is 1000–1600 m.

Common hosts of *P. juniperinum* include *Juniperus californica*, *J. deppeana*, *J. erythrocarpa*, *J. flaccida*, *J. monosperma*, *J. occidentalis*, *J. osteosperma*, and *J. scopulorum*. *Cupressus arizonica* is commonly parasitized in central Chihuahua, but this host is only rarely infected in Arizona (Hawksworth and Wiens 1966). Other rare hosts are *Cupressus bakeri* in California (Hawksworth and Wiens 1966) and *Chamaebatia millefolium* (Rosaceae) in Arizona (Hawksworth 1952; Hawksworth and Mathiasen 1978).

Geographically, *P. juniperinum* co-occurs with *P. capitellatum* in Arizona, with *P. hawksworthii* in New Mexico, and with *P. densum* in California. Natural hybrids between *P. densum* × *P. juniperinum* that are apparently sterile F1 plants are known in the Inyo Mts. of California (Wiens and DeDecker 1972) and San Bernardino Mts. (Vasek pers. comm., 1973). These are among the few reports of natural hybridization for mistletoes.

*Phoradendron minutifolium* Urban

In 1959 this mistletoe was known only from the
type locality near Perote, Sierra Madre Oriental, Veracruz, Mexico. Phoradendron minutifolium, however, is now known to have a wide, but apparently localized, distribution in Mexico. It is most common in central Mexico (Tlaxcala and Veracruz) and in the Sierra Madre Occidental in southern Chihuahua and Durango. A widely disjunct population occurs in the Sierra del Carmen of northern Coahuila, where it co-occurs with P. saltillense on junipers and the two mistletoes have been found parasitizing the same tree. The Sierra del Carmen is just across the border from Big Bend National Park, Texas, and P. minutifolium might be expected to occur there. The known elevational range is 2000–2750 m.

The closest relative of P. minutifolium appears to be P. olivae. Phoradendron olivae has even smaller leaves (ca. 2 mm)—but these are still expanded (as opposed to scales)—whereas P. minutifolium typically has leaves ca. 2–4 mm long. P. olivae is known only from one locality in Jalisco, near the Colima border, where it parasitizes Cupressus lusitanica.


NEW SPECIES IN SECTION PAUCIFLORAE

Phoradendron abietinum Wiens, sp. nov.


Plantae maturae frutices globosos 3–4 dm altos efformantes, furcatae dioeciae, acataphyllae; internodia 12–18 mm longa, 2–3 mm lata; folia sublinearia, adaxialiter applanata, abaxialiter rotundata, praeipue in juventute minute puberula, ca. 12–19 mm longi, 2–3 mm lati, ad apicem saepe attenuate, ad apicem acuminate, ad basim sessilia; inflorescentia staminate et florae ignotae; inflorescentia pis-tillata plerunque 4–6 in nodo quoque, segmentis 1–2 per inflorescentiam quamque, segmentis singulis flores 2, interdum 3 ferentibus; anthesis et fructus ignota.

Host: Abies durangensis

Distribution: Coniferous forests of the Sierra Madre Occidental from southern Chihuahua, through Durango to northern Jalisco. The known elevational range is 2600–2850 m.

Discussion: Phoradendron abietinum is distinguish-able from P. bolleanum, with which it sometimes co-occurs, by a number of features: host, shoot color, and leaf and floral morphology. In fact, P. abietinum perhaps resembles most closely the Guatemalan species, P. acuminatum, especially the leaves (see discussion under the latter species). Phoradendron abietinum is yellow-green, a color common to most species of the section, whereas P. bolleanum is typically rusty brownish, especially the leaves, a feature that makes P. bolleanum easily detectable on the host plant from a considerable distance. The leaves of P. bolleanum tend to be oblong to occasionally sub-oblanceolate, with a rounded to obtuse apex, whereas the leaves of P. abietinum are generally linear with an attenuated, acuminate apex, abaxially rounded, but flattened adaxially; in P. bolleanum the leaves are dorsiventrally flattened. The perianth lobes of P. abietinum (which remain adnate to the fruit during development) have a minute basal tube 0.2–0.3 mm long and the lobes remain erect or sometimes reflex at the midpoint. The style is mostly cylindrical, but some lateral compression may occur. By contrast, the perianth lobes on the fruit of P. bolleanum are free and strongly inflexed distally and the style is only slightly elongated. These are minute structures, usually < 0.1 mm long, but the relative differences are nonetheless considerable.

The occurrence of a mistletoe specific to such a rare tree as Abies durangensis presents an interesting evolutionary situation. Although the host tree is known from only a few widely scattered localities in the Sierra Madre Occidental (Martinez 1963), all the populations of A. durangensis we have surveyed are parasitized by P. abietinum. The dispersal of host specific mistletoes between small, highly disjunct populations would appear to be difficult. Thus, the occurrence of this mistletoe on A. durangensis is perhaps best explained in terms of the parasite becoming evolutionarily "stranded" along with its host. In fact, the presence of a host specific mistletoe on such a rare species supports the proposition that the host at one time had a larger, more continuous distribution.

Specimens examined: CHIHUAHUA: Cerro Mohinora, Conkle a.s.n. in 1985 (FPF); near Guadalupe y Calvo, Oliva s.n. in 1987 (FPF). DURANGO: Puerto Buenos Aires, near km 54 W of El Salto, Hwy 40, Wiens & Hawksworth 4422 in 1969 (FPF), and Hawksworth et al. 1420 in 1972 (FPF); Mpio Otaez, 16 km SW of Altares on Banome Rd, Hawksworth & Reid 2247 in 1987 (FPF). JALISCO: Mpio Mexquitic, 40 km NW of Bolanos, Flores et al. 1609 in 1989 (FPF, IBUG).

Phoradendron acuminatum Wiens, sp. nov.

Holotype (US): GUATEMALA: SOLOLA: 12 km E of Nahualan, Pan American Hwy near km 146; mixed broadleaf-conifer forest, elevation 2500 m; parasite on Cupressus lusitanica, Wiens & Hawksworth 4396 in 1969. Isotypes: EAP, ENCB, MEXU, MO, RSA.

Plantae maturae massas pendulas usque ad 2 m longas efforman-
tes, furcatae, dioeciae, acataphyllae; internodia 15-25 mm longa; folia linearia, 15-20 mm longa, ca. 2 mm lata, abaxialiter appianata, adaxialiter rotundata, ad basim sessilia, ad apicem acuminata; inflorescentia staminata ignota; inflorescentia pistillata ca. 5 mm longa, pendunculo ca. 1 mm longo praedita, in segmenta fertilia 1-2 de­
cussatim dispositis divisa: segmento quoque Flores 2 ferente se­
mentis et bractis minute ciliatis navicularibus flores parce superan­tibus subentis; anthesis probabiliter Juli–Septembro; fructus rosae­
albidus, orbicularis, 4–5 mm diam; in Cupresso et Junipero parasiti­
ticum.

**Hosts:** Cupressus lusitanica, rarely Juniperus spp.

**Distribution:** Broadleaf-coniferous woodlands of north­ern Guatemala; possibly also in southern Mexico. The known elevational range is 2500–3150 m.

**Discussion:** Morphologically this species is most closely related to *P. sedifolium*, a parasite on Cupressus in the Chiapas and Hidalgo highlands, Mexico. The two species are readily distinguished, however, by the short (mean = 9.3 mm long) , markedly succulent, glaucous leaves of *P. sedifolium*. In *P. acuminatum* the leaves are longer (mean = 16.0 mm long) and lack significant succulence or glaucousness. Also, *P. acu­minatum* is a much larger plant often a meter or more high, whereas *P. sedifolium* is a smaller plant rarely larger than 5 dm high. The berries of *P. acuminatum* are pink, and larger (ca. 4 mm) than those of *P. sedi­folium* which are white and smaller (ca. 3 mm).

*Phoradendron acuminatum* also shows some mor­phological resemblance to *P. abietinum*, but differs from that species by its occurrence primarily on Cupressus (secondarily on Juniperus), whereas *P. abie­
tinum* is known only from Abies; *P. acuminatum* is also a larger plant than *P. abietinum*, sometimes forming masses a meter or more in length and character­istically producing severe infestations in Cupressus, where it may occupy a large proportion of the crown in host trees. *Phoradendron abietinum* is a relatively small plant producing globose bushes 2–5 dm in di­ameter. In *P. acuminatum*, the leaves are mostly a dull, brownish green, generally less than 3 mm wide and the internodes fuscous, whereas in *P. abietinum*, the leaves are usually more than 3 mm wide and both the blades and internodes are yellowish green.

An interesting characteristic of *P. acuminatum* is its role as a host for two epiparasitic species of *Phora­
dendron*, i.e., species that parasite only other species of mistletoes: cf. *P. auriculatum* Trel. and *P. calycu­
latum* Trel. Infrogeneric epiparasitism in *Phoraden­
dron* is a fascinating phenomenon; for further details see the discussion under new epiparasitic species of *Phoradendron*.

E. Clark (pers. comm., 1973) found that this mistle­
toe causes frequent mortality in cypress in Guatemala, particularly in the Department of San Marcos.

**Specimens examined:** GUATEMALA: HUEHUETENANGO: 25 km N of Huehuetenango, on Rd to Chimal, on C. standleyi, Wiens & Hawksworth 4408 in 1969 (FPF); Paquix, on J. standleyi, Clark & Ramirez s.n. in 1972 (FPF). SAN MARCOS: Mpio Bosque del Astillero, El Cascajo, on C. lusitanica, Clark s.n. in 1972 (FPF); between Cumbre Cotzic and Serchil, on C. lusitanica, Clark & Ra­
mirez s.n. in 1972. SOLOLA: 10 km W of Nahuala, on C. lusitanica, Clark & Ramirez s.n. in 1972 (FPF).

*Phoradendron flavomarginatum* Wiens, sp. nov.

**Holotype (US):** MEXICO: NUEVO LEON: Rd to San Francisco, 10.8 mi E of Hwy 61 turnoff at km 80, N of the town of Doctor Arroyo, elevation 2400 m, parasite on Juniperus flaccida, Wiens 7779 in 1995.

**Isotypes:** MEXU, UC, MO.

Plantae usque 1 m alta, brevem pubescentes; dioeciae, acataphyllae; caules in maturitate lignescentes, et teretes; internodia ca. 18 mm longa; folia linearia-oblonga, sessilia ca. 25 (35) mm longa, 3 mm lata; inflorescentia staminata ca. 6–8 mm longa, segmentis 1–2, cum 8–15 floribus; inflorescentia pistillata ca. 2 mm longa, segmentis 1, cum 2 flores; anthesis July (?)-September; fructus ovatus, albus, 4–5 mm in; in Juniperus flaccida parasiticum.

**Hosts:** known only on Juniperus flaccida.

**Distribution:** known only from several populations near the type locality, where it is locally abundant.

**Discussion:** *Phoradendron flavomarginatum* is se­parated elevationally and by host from *P. saltillense*, which is the common *Phoradendron* at lower elevations in this region. There is considerable variation in *P. saltillense* throughout its extensive distribution. These two species appear separable on the basis of morphology as well as host and elevation. *Phoraden­
dron flavomarginatum* can become a large, brownish plant and becomes pendulous with age (1 m long), whereas *P. saltillense* is typically ca. 3–4 dm high, more or less globose, as well as yellow-green, the common color of most species of sect. *Pauciflorae*. The leaves of *P. flavomarginatum* are generally longer (ca. 25 mm) than those of *P. saltillense* (ca. 15 mm) and have a pale yellow margin (hand lens needed). The leaves of *P. flavomarginatum* tend to become oblan­ceolate, while those of *P. saltillense* are generally linear-oblong. When living, the leaves of *P. flavomargin­atum* are also thinner by about ½ than those of *P. saltillense*, whose leaves are also slightly succulent. Preliminary observations in September suggest that *P. saltillense* produces continuous, successional crops of flowers, a feature not presently known among species of sect. *Pauciflorae*. This possibility requires further study.

*Phoradendron hawkworthii* Wiens, sp. nov.


**Holotype (US):** TEXAS: BREWSTER CO: Big Bend National Park, Chisos Mts, The Basin (near campground), oak-juniper woodland, elevation 1650 m. Parasite on Juniperus flaccida, but also on *J. dep-
range does not appear to overlap with that of *P. hawksworthii*. **Phoradendron capitellatum** occurs from the Cook and Florida Mountains westward to central Arizona, whereas *P. hawksworthii* is found in New Mexico only east of the Rio Grande Valley in the San Andreas, Cornudas, and Sacramento Mountains.

**Phoradendron juniperinum** usually occurs at elevations above that of *P. hawksworthii*, but these two mistletoes sometimes co-occur, and rarely infect the same host tree, which was observed in La Luz Canyon, Otero County, New Mexico.


**Phoradendron olivae** Wiens, sp. nov.

**Holotype (IBUG):** MEXICO: JALISCO: Mpio Minatitlán, Sierra de Mimatitlán, Cerro Grande, 14 km N of Colima-Minatitlán Hwy, on Rd to Terrero, elevation 2000 m, on *Cupressus lusitanica*, Wiens, Hawksworth, Chazaro, Oliva 7051 in 1989. Isotypes: FPF.

**Phoradendron capitellatum** is also a parasite of junipers in southern New Mexico, but its distribution

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**peana** and *J. pinchotii*. Hawksworth, Lightle, & Lampei 1044 in 1967. Isotypes: ARIZ, CAS, COLO, ENCB, FPF, GH, RSA, UC, UTC.

Plants 1-2.5 dm altae, dioeciae, acataphyllae; bases ramorum in maturitate lignose. glabrea vel in partibus junioribus puberulentae; internodia 6-12 mm longa, folia ob lanceolate-linearia, subsessilia vel sessilia, 6-25 mm longa, 1.5-3 mm lata, ad apicem obtusa vel rotundata; inflorescentia staminate et segmento uno floribus 3-6 prae ditio constituta; inflorescentia staminate et segmento uno floribus 3-6 prae ditio constituta; inflorescentia pistillata et segmento uno cum floribus 3 constituta; anthesis paene Julio–Septembro; fructus albus vel roseolus, orbicularis, 4 mm lata; in *Juniperus* parasiticum.

The species is named for Frank G. Hawksworth, life-long student of mistletoes, particularly the genus *Arceuthobium*.

**Hosts:** *Juniperus ashei*, *J. deppeana*, *J. erythrocarpa*, *J. flaccida*, *J. monosperma*, and *J. pinchotii*.

**Distribution:** Juniper-pinyon woodlands; common in west Texas, but localized in southern New Mexico, and known from only one locality in Coahuila. *Phoradendron hawksworthii* was reported from NW of Carizzo, Lincoln Co., New Mexico, but attempts to locate this population were unsuccessful, and no extant populations are presently known in Lincoln County. The known elevational range is 1550-2000 m.

**Discussion:** *Phoradendron hawksworthii* shows affinities to *P. bolleanum*, *P. densum*, and *P. saltillense*. It differs from *P. densum*, with which it has been confused in the past, by its shorter internodes (mean 9.0 mm, range 6-12 mm, versus a mean of 11 mm and a range of 6-17 mm in *P. densum*). Such differences in internode length are generally positively correlated with total plant size. Finally, the number of fertile internodes per staminate inflorescence is apparently only one in *P. hawksworthii*, an uncommon characteristic in the section. *Phoradendron* typically has two fertile internodes on the staminate inflorescences.

**Phoradendron hawksworthii** is distinguishable from *P. saltillense* primarily by its narrower leaves (ca. 2 mm wide). Occasionally the young leaves of *P. hawksworthii* also show a tendency toward tereteness, with older leaves becoming flattened adaxially, but rounded abaxially. In *P. saltillense* the leaves are typically flattened dorsiventrally and usually exceed 3 mm in width. In *P. hawksworthii* young leaves are often mucronulate in the extreme, the micro itself being only 0.2-0.3 mm long. Newly emerging leaves generally do not exhibit this feature, which apparently originates during mid-ontogeny. The micro is also fugacious, and is largely absent on mature leaves; however, the apex of old leaves often exhibits a minute scar at the tip, presumably resulting from the loss of the micro. Geographically, *P. hawksworthii* and *P. saltillense* approach each other in the Sierra del Carmen, but do not appear to co-occur there.

**Phoradendron capitellatum** is also a parasite of junipers in southern New Mexico, but its distributional
The species is named for Hector Oliva Rivera of the University of Veracruz, Cordoba, and student of Mexican mistletoes.

Host: Cupressus lusitanica.

Distribution: Known only from the vicinity of El Sauz and Terrero, Sierra de Mamitlán, Jalisco, and in adjacent Colima. The known elevational range is 2000–2300 m.

Discussion: The species most closely resembles Phoradendron minutifolium, but is distinguishable from that species by (1) its smaller, almost scale-like leaves ca. 2 mm long, whereas the leaves of Phoradendron minutifolium are 3–5 mm long; (2) its much larger size, and open habit, forming pendulous masses over 1 m long, as compared to Phoradendron minutifolium which is rarely larger than 0.5 m high. This size difference is again reflected by the internode lengths, averaging 18 mm in P. olivae, but only 8 mm in Phoradendron minutifolium; (3) the host difference—P. olivae is known only on Cupressus and Phoradendron, and known to parasitize only Juniperus; and (4) the known distribution of P. olivae is far to the west and south of Phoradendron minutifolium and occurs at higher elevations.


Phoradendron rufescens Wiens, sp. nov.

Holotype (US): MEXICO: SAN LUIS POTOSI: 22 km E of Zaragoza on Rd to La Cuevas mine, elevation 2150 m, on Juniperus flacceda. Wiens, Hawksworth, Bailey, and Mathiasen 5244, in 1975. Isotypes: ENCB, FPF, MO, RSA, UT.

Plantaes usque ad 6–7 dm altae, dioeciae, acathaphyllae; bases caulorum solium in maturitate ligneoscentes, teretes usque parum applanatae, glabrae; internodia 15–25 mm longa; folia linearia usque sublanceolata, 7–15 mm longa, 1,5–2,5 mm lata, minuta et breviter pubescentia, in maturitate applanata, sed in juventute adaxialiter subrotundata, ad basim sessilia, ad apicem acutum usque rotundata, interdum mucronulata; inflorescentia staminata ca. 10 mm longa, segmentis duobis 6–17 flores ferentes, pedunculo 3–4 mm longo; inflorescentia pistillata ca. 10 mm longa, segmentis fertilibus flores duas ferentes, pedunculo ca. 3 mm longo, segmentis perianthii in sexibus ambis conspice rufis, anthesia in mensibus Januario–Februaria (?); fructus orbicularis, 4–5 mm diam., rufo-roseus; in Juniper parasiticum.

Hosts: Juniperus flacceda and J. deppeana.

Distribution: Juniper-pinyon woodlands of San Luis Potosi, Querétaro, and Hidalgo. The known elevational range is 2100–2200 m.

Discussion: This is one of the most distinctive species in section Pauciflora. It is perhaps most closely related to P. bolleanum, from which it is easily distinguished by the rusty-brown color of the perianth segments, and the dense short pubescence, which give the plants a somewhat scabrous character. The berries are bright, reddish-pink.


Phoradendron sedifolium Wiens, sp. nov.

Holotype (US): MEXICO: CHIAPAS: 24 km south-east of San Cristobal de Las Casas on Hwy 190; elevation 2100 m, parasite on Cupressus lusitanica. Wiens, Hawksworth, Player & Hermann 5012 in 1975. Isotypes: ENCB, FPF, MO, RSA, UT.

Plantaes 3–4 cm altae, dioeciae, acathaphyllae; bases caulorum solium in maturitate ligneoscentes, teretes usque parum applanatae, glabrae; intermediina 6–15 mm longa; folia linearia usque sublanceolata, 6–12 mm longa, 2–3 mm lata, in vivo valde succosa; incrementum novum conspicue griseo-glaucum, abaxialiter applanata sed parum proximam versus leniter elevatum, adaxialiter rotundatum, ad basim sessile, ad apicem acutum usque rotundatum, interdum mucronulatum, margine in juventute interdum minute ciliato; inflorescentia staminata ca. 4 mm longa, segmento uno (rado 2) 6–7 flores ferentes, pendunculo 1–1.5 mm longo; inflorescentia pistillata ca. 3 mm longo, segmento uno flores duas ferentes, pendunculo 1–1.5 mm longo; anthesia in mensibus Januario–Februaria; fructus ovatus albus, 3 mm diam.; in Cupresso parasiticum.

Hosts: Known only on Cupressus lusitanica.

Distribution: Broad-leaf coniferous forests of the Chiapan and Hidalgan highlands. The known elevational range is 1850–2200 m.

Discussion: This species most closely resembles P. acuminatum from Guatemala, but is readily separated from that species (even though they occur on the same host) by the characteristics mentioned in the discussion under P. acuminatum. Phoradendron sedifolium is also a host for one of the epiparasitic species of Phoradendron (P. calyculatum) which also regularly parasitizes P. acuminatum.

Specimens examined: MEXICO: HIDALGO: 18 km N of Metepec on Rd to Tenango de Doria, on Cupressus lusitana; Wiens & Hawksworth 5524 in 1979 (FPF; UT); Rio Moctezuma, Magana 571 (ENCB).

ARTIFICIAL KEY TO THE SPECIES OF PHORADENDRON SECTION PAUCIFLORA

a. Leaves < 5 mm long or leafless
b. Leaves reduced to scales
c. Parasic mostly on Juniperus (occasionally on Cupressus); internodes usually less than 1 cm long; older plants mostly globose

P. juniperinum
NEW EPILACHNARIS SPECIES OF PHORADENDRON IN MEXICO

**Phoradendron calvinii** Wiens, sp. nov.

*Holotype (US): MEXICO: JALISCO: Mpio Minatitlán, Cerro Grande, 18 km N of Colima Hwy, on Rd to Terrero, elevation 2060 m, Wiens 7774 in 1995. Isotypes: IBUG, MEXU, FPF, MO, RSA.

Plantae maturitae pendulas usque ad 2 m longa efformiantes, dioeciae, acathyllae; internodia 80–120 mm longa, 3–4 mm lata, folia lanceolata, falcate, 120–130 (165) mm longa, 15–45 mm lata; inflorescentia staminea 90–110 mm longa, 2 mm lata, segmentis 3–5; inflorescentia pistillata ca. 35 mm longa, 3–4 mm lata, segmentis 3–5; fructus albus, 3 mm alta. In *Phoradendron longifolium* parasiticum.

The species is named for Prof. Clyde L. Calvin, lifelong student of mistletoe anatomy, particularly the haustorial systems.

*Host:* *P. longifolium*, but also occasionally on *P. cf. reichenbachianum.*

*Distribution:* Known only from the type locality.

*Discussion:* This amazing species parallels the size of the large epiparasite, *P. calyculatum*, forming huge, pendulous masses exceeding 2 m in length and parasitizing primarily *P. longifolium*, and to a lesser extent another species with which it co-occurs. *Phoradendron calvinii* is readily distinguished from *P. calyculatum*, with which it also co-occurs, by its long, thin stamine inflorescences that reach lengths up to 110 mm, but are only 2 mm wide. These inflorescences are borne on peduncles ca. 15 mm long and comprise 3–5 fertile segments, each bearing hundreds of flowers. The fruits are small (ca. 2 mm) as are the seeds, which is typical of all epiparasitic Viscaceae so far known. The fruits of *P. calvinii* are also distinguished by the persistent sepals that form a short collar (1 mm) around the minute (< 0.5 mm) style.

**Phoradendron chazaroi** Wiens, sp. nov.

*Holotype (US): MEXICO: JALISCO: 5 km S of Quila on Rd to Tecolotlán, elevation 1960 m, epipar- asite on Cladocolea grahamii (Loranthaceae) on Quercus obtusata. Wiens, Chazaro, Hawksworth, Oliva 7047 in 1989. Isotypes: IBUG, MEXU, MO, UC, RSA.

Plantae ca. 1.5 (2) dm altae, monoeccia, cataphyllis, glabrae, internodia 35–40 mm longa, 2–3 mm lata; folia 50–55 mm longa, 6–8 mm lata, lanceolate-elliptica; inflorescentia 20–25 mm longa, in segmento fertilia 2–3, segmento cum flores 12–16; fructus ignota; in *Cladocolea grahamii* parasiticum.

The species is named for Miguel Chazaro Basañez, student of Mexican mistletoes.

*Host:* Known only from *Cladocolea grahamii* (Loranthaceae)

*Distribution:* Western Jalisco

*Discussion:* The plants branch profusely from a “basal cushion” when young, but the “cushion” becomes obscure in older plants. The young shoots are quadrangular, and often occur in whorls of 3–6, with the basal internode of each shoot bearing a sheathing cataphyll ca. 3 mm high. The inflorescences are often whorled with 3–8 inflorescences per node, with 2–3

<table>
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<th>Feature</th>
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<td>c. Parasitic on Calocedrus; internodes usually over 1 cm long; older plants pendulous</td>
<td>..............................................</td>
<td><em>P. libocedri</em></td>
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<tr>
<td>b. Leaves 2–5 mm long, generally expanded</td>
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<td><em>P. minitifolium</em></td>
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<td>d. Parasitic on Juniperus; leaves 3–5 mm long; plants 50–70 cm tall; Coahuila and Chihuahua to Veracruz</td>
<td>..............................................</td>
<td><em>P. minitifolium</em></td>
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<tr>
<td>a. Leaves &gt; 5 mm</td>
<td>..............................................</td>
<td><em>P. olivae</em></td>
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<td>e. Parasitic on Abies</td>
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<td><em>P. pauciflorum</em></td>
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<tr>
<td>f. Parasitic on Abies concolor; leaves 5–8 mm wide; California, Arizona, Baja California</td>
<td>..............................................</td>
<td><em>P. abietinum</em></td>
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<td>g. Parasitic on Abies durangensis; leaves 2–3 mm wide; Durango, Chihuahua</td>
<td>..............................................</td>
<td><em>P. denson</em></td>
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<tr>
<td>h. Leaves usually &lt; 20 mm long; Oregon, California, Baja California</td>
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<td><em>P. multisetosum</em></td>
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<tr>
<td>i. Plants brownish or reddish brown</td>
<td>..............................................</td>
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<td>j. Plants greenish</td>
<td>..............................................</td>
<td><em>P. cupreus</em></td>
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<tr>
<td>k. Leaves ca. 15 mm long, lacking a pale yellow margin; parasitic on various species of Juniperus or Arbutus;</td>
<td>..............................................</td>
<td><em>P. bolleanum</em></td>
</tr>
<tr>
<td>m. Leaves ca. 20–25 mm long, with a pale yellow margin (hand lens needed); parasitic only on <em>J. flaccida</em>; local</td>
<td>..............................................</td>
<td><em>P. flavomarginatum</em></td>
</tr>
<tr>
<td>n. Leaves usually &gt; 10 mm long, ca. 2 mm wide; berries 4 mm in diameter, pinkish; Guatemala</td>
<td>..............................................</td>
<td><em>P. acuminatum</em></td>
</tr>
<tr>
<td>o. Leaves usually &lt; 10 mm long, 2–3 mm wide; berries 3 mm in diameter; Mexico (Hidalgo and Chiapas)</td>
<td>..............................................</td>
<td><em>P. sedifolium</em></td>
</tr>
<tr>
<td>p. Leaves and stems strongly stellate-pubescent; Arizona, New Mexico, NE Sonora, NW Chihuahua</td>
<td>..............................................</td>
<td><em>P. capitellatum</em></td>
</tr>
<tr>
<td>q. Leaves linear, usually &gt; 6 times as long as wide</td>
<td>..............................................</td>
<td><em>P. hawksworthii</em></td>
</tr>
</tbody>
</table>
fertile segments bearing 12–16 flowers. The type collection made on 30 July had berries that were just beginning development, but were probably destined to turn reddish at maturity. Some old seeds at the type collection site were seen on other plants and they appeared to be small (< 2 mm), as is typical of all epiparasites of Viscum and Phoradendron seen by us in Africa, Asia, Australia and Latin America.

At the time of collection no staminate flowers could be found in approximately 35 plants examined. The species is no doubt monoecious and the staminate flowers had likely dehisced at this time. If this is the case, the inflorescences likely bear relatively few staminate flowers, since most of the flowers on the spikes appeared to be developing fruits. In monoecious species of African Viscum, the ratio of pistillate to staminate flowers is often highly skewed (at least 4:1) in favor of pistillate flowers (Polhill and Wiens 1998), often to the point that it is difficult to find staminate flowers. Because the early collectors had only a few pressed samples available for study, at least one such species was originally described as being dioecious. Apparently P. chazaroii also has highly skewed flower ratios in favor of pistillate flowers. The evolutionary implications of such skewed flower ratios should be studied further. The reproductive advantages of high seed production for pioneering species, such as these parasites, would seem obvious. Among dioecious species of various mistletoes, there are a number of examples of species in which the sex ratio is also highly skewed toward pistillate plants (Wiens et al. 1996).

Specimens examined: MEXICO: JALISCO: 14 km S of Tequila on Rd to Volcó n de Tequila, on Cladocolea grahamii, which in turn was parasitizing Quercus castanea, elevation 1860 m, Wiens et al. 7078 in 1989 (IBUG). Chazaro (pers. comm., 1989) indicates that this species also occurs on Nevado de Colima and Volcán de Tequila (Jalisco).

Phoradendron durangense Wiens, sp. nov.

Holotype (US): MEXICO: DURANGO: Mazatlán-Durango Hwy, 1.8 km E of El Palmito, elevation 2200 m, Wiens & Calvin 5993 in 1985. Isotypes: IBUG, MEXU, MO, UC, RSA.

Planta usque ad 0.5 m alta, breve pubescentes, dioeciae, acata phyllaeae; internodia 35–45 (65) mm longa, ca. 10 mm lata; folia linearia-lanceolata, falcate, 70–200 mm longa, 12–25 mm lata; inflorescentia staminata 35–45 mm longa, 2 mm lata; inflorescentia pistillata 25–35 longa, 4–5 mm lata; fructus ignota; in Phoradendron longifolium parasiticum.

Host: P. longifolium; P. durangense was not observed on associated P. schumannii.

Distribution: Collected only from the type locality, but numerous young plants observed near a microwave station on the ridge top ca. 10 km W of El Palmito.

Discussion: Morphologically, P. durangense superficially resembles P. calyculatum, a widespread and common epiparasitic species with a distribution from the Volcá n de Tequila, northern Jalisco, to northern Guatemala. Herbarium specimens of P. durangense could be confused with P. calyculatum, but a number of characteristics separate the two species: P. calyculatum is a much larger plant, often forming pendulous masses over 2 m long, whereas P. durangense is commonly an erect plant, ca. 0.5 m high. Phoradendron calyculatum is grayish-green, due perhaps to the dense, short pubescence typical of the species, whereas P. durangense is brownish-green. The nodes of both species are dilated, but those of P. calyculatum are about twice the width of those of P. durangense (ca. 20 mm vs. 10 mm). The inflorescences of both sexes of P. calyculatum are approximately twice the length of those of P. durangense: staminate ca. 80 mm vs. 40 mm; pistillate ca. 60 vs. 30 mm. Each fertile segment of the inflorescences of P. calyculatum probably bear twice the number of flowers as those of P. durangense, e.g., the fertile pistillate segments of P. calyculatum are ca. 12 mm long, versus ca. 6 mm in P. durangense.

There is also a significant distributional difference between the species, but further collections might alter this situation. Presently P. durangense is the most northward ranging of any of the epiparasitic species of Phoradendron.

Acknowledgments

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