

Cataphylls and taxonomy in *Phoradendron* and *Dendrophthora* (Viscaceae)

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SUMMARY

The occurrence of basal cataphylls is surveyed in *Phoradendron* and *Dendrophthora* (Viscaceae). It is shown that, in the former genus, there is a great deal of irregularity in this regard, rendering the maintenance of Trelease's distinction between his Boreales and Aequatoriales extremely difficult, and at times misleading or even impossible. In both Trelease's groups, a number of cataphyll irregularities are detailed. Some of these appear to represent the development of basal cataphylls from acataphyllous stock, but in other cases it seems that acataphyllous species have evolved from ancestors bearing such organs. In each genus, the lowest foliar organs of lateral stems are positioned in one of two phyllotactic patterns, transverse or median. The systematic importance of this difference is almost exclusively at the species level. In both the occurrence of basal cataphylls and in basal phyllotaxy the type species of *Phoradendron*, *P. californicum*, occupies an anomalous position in the genus; nomenclatural consequences are briefly indicated.

Key-words: basal phyllotaxy, cataphylls, *Dendrophthora*, nomenclature, *Phoradendron*.

INTRODUCTION

In many species of the closely related genera *Dendrophthora* and *Phoradendron*, each lateral branch bears at least one pair of scale-like leaves as its first pair of foliar organs. It was Eichler (1868) who first paid serious attention to these structures which he called cataphylls or, when laterally fused, 'vaginae cataphyllares'. Both he and Urban (1896) made extensive use of cataphylls at the specific level, but did not concern themselves with their taxonomic significance elsewhere.

This situation was dramatically altered in *Phoradendron* by Trelease (1916) who based his primary subdivision of the genus into Boreales and Aequatoriales nearly exclusively on the absence vs. presence, respectively, of basal cataphylls. These organs, Trelease wrote, 'afford by their presence or absence what proves to be one of the most important characters for the primary subdivisions of the genus *Phoradendron*'. In fact, none of the other features in Trelease's diagnoses of Boreales and Aequatoriales hold true consistently, thus sharpening the focus on the validity of the cataphyll criterion, nor has the geographic distinction implied in Trelease's names remained inviolate (see below). However, most workers in *Phoradendron* have essentially followed Trelease's system, even though doubts have been expressed (Kuijt 1959) and even though, since Trelease's

monograph, acataphyllous species have been identified in South America. I have found a number of additional irregularities, mostly in Mexican species, which bear on this question and which are reported below. It is the main purpose of the present paper to show the inadequacy of the presence or absence of basal cataphylls as an infrageneric character. I hope to focus attention, furthermore, on the phyllotaxy of the lowest basal cataphylls (or the foliage leaves found in that position) as an important taxonomic character, this being a feature which Urban studied extensively, but which Trelease ignored completely. Briefly, there are two patterns of phyllotaxy: *median basal phyllotaxy*, in which the lowest foliar organs on a lateral branch are in the plane which passes through the main stem and lateral axis; and *transverse basal phyllotaxy*, where these foliar organs are placed perpendicularly to that plane, and thus in the same plane that passes through the prophylls which are invariably present.

It seems certain that Trelease took his cue from Urban with regard to the systematic importance of basal cataphylls, for it was the latter who, nearly 20 years earlier, had pointed out this difference between North American and neotropical species. Trelease formalized in nomenclature what Urban had described morphologically for *Phoradendron*. We find no acknowledgment to Urban's study in Trelease's work, except where it concerns the former's taxonomic analysis of Caribbean forms.

A limited number of species of *Phoradendron* and *Dendrophthora* also have another type of cataphyll called *intercalary cataphylls*, but these structures are always additional to basal cataphylls, and do not affect my argument. Another important taxonomic feature is the number of similar structures (often called sterile bracts) subtending inflorescences, which may vary significantly between species. There seems to be no general correlation between such basal scale leaves on vegetative branches and inflorescences, for there are numerous cataphyllous species of *Phoradendron* which have simple inflorescence peduncles.

Whether or not basal cataphylls are present in any Phoradendreae, there always are two prophylls in each foliar axil (Kuijt 1959). Occasionally these structures are quite prominent, as in *P. argentinum* (including *P. ernstianum*) (Kuijt 1986, Fig. 11b), rivalling the basal cataphylls in size. They may even be laterally fused into a single structure, as in *D. domingensis* (Spreng.) Eichler (Kuijt 1959). Prophylls are invariably transverse in position, and normally cannot be mistaken for cataphylls. Finally, basal cataphylls in some species or specimens may be placed so low in the axil that they may escape detection; see, for example, the basal cataphylls of *Phoradendron* sp. in Fig. 1a, where the only remnant of the pair of cataphylls is a slim, irregularly torn crown of tissue.

A special problem is posed in the definition or recognition of basal cataphylls in species which are entirely squamate to begin with, such as *P. aphyllum*, *P. californicum*, *P. poeppigii*, *P. rusbyi* and others. It might be objected that basal cataphylls cannot truly be designated where expanded foliage is absent. That, however, is not quite true. *P. poeppigii* (Tiegh). Kuijt and the closely related *P. tunaeforme* (DC.) Eichler, for example, are squamate species which have very conspicuous basal cataphylls which are of the fused, tubular type. Similarly, the crowding of the lowest pairs of scale leaves in some plants of *P. californicum* leaves little doubt that we are concerned here with basal cataphylls (Kuijt 1996). In *P. aphyllum*, there is neither such crowding nor a discernible difference in morphology.

This paper represents a summary and synthesis of individual observations made over many years, partly in the field, but mostly in herbaria while carrying out taxonomic work. I have arranged my observations roughly in a sequence leading from constancy

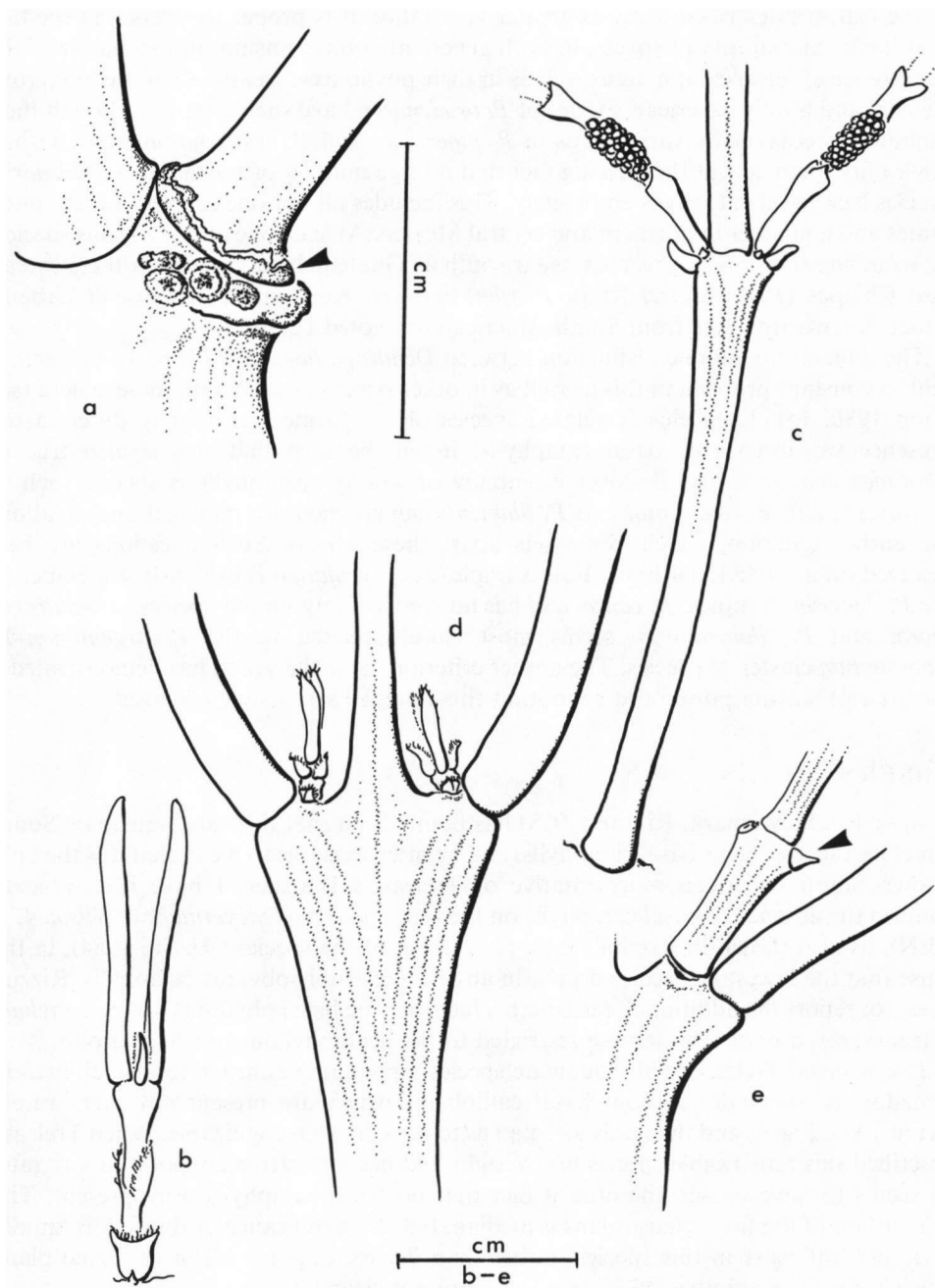


Fig. 1. (a) *Phoradendron* sp., Laughlin 202 (DS). Lateral branch with very low remnant of basal cataphylls (arrow). (b–e) *Phoradendron calyculatum*; Cházaro & Hernandez 4140, LEA (b–d), Cházaro 3321, LEA (e). (b) Young branch with two pairs of basal cataphylls. (c) Lateral branch with high, fertile basal cataphylls. (d) A pair of young axillary branches, each with one pair of basal cataphylls. (e) Lateral branch with one pair of caducous basal cataphylls (arrow).

in the features described towards greater variability. It is proper to stress first the fact that the great majority of species in both genera are quite constant in the matter of the occurrence of basal cataphylls as well as in their phyllotaxy. Nearly all of the numerous Central and South American species of *Phoradendron* have such organs, although their number is occasionally variable, as in *P. piperoides* and *P. semivenosum* Rizz. Urban (1896) first pointed out the striking fact that a large number of northern *Phoradendron* species lack basal cataphylls completely. This includes all but one species in the United States and a number in northern and central Mexico. At least one acataphyllous species, *P. velutinum* (DC.) Nutt., reaches as far south as Guatemala, and several others extend into Chiapas (*P. breedlovei* Kuijt, *P. ramosissimum* Kuijt and *P. robinsonii* Urban). Other noteworthy facts from South American are noted below.

The difficult taxonomic distinction between *Dendrophthora* and *Phoradendron* represents a constant problem in this as well as in other papers dealing with these genera (see Kuijt 1986: 15). Even closely related species of the former genus may differ in the presence vs. absence of basal cataphylls; it will be seen that this is also true in *Phoradendron*. When we discover essentially or wholly acataphyllous species such as *P. calyculatum*, *P. canzacotoi* and *P. filamentosum* sp. ined. we may feel uneasy about the anther criterion, which alone sets apart these genera. Such questions are best resolved on an individual basis. For example, *P. calyculatum* is evidently a member of the *P. dipterum* complex; *P. canzacotoi* has no convincingly similar species in *Dendrophthora*; and *P. filamentosum* seems most closely related to the *P. argentinum*-*P. mucronatum* cluster of species. The anther criterion, over the years, has demonstrated a remarkable staying power and cannot, at this time, be seriously challenged.

OBSERVATIONS

P. aphyllum Steyermark. Rizzini (1978) has pointed out that this rare, squamate South American species lacks basal cataphylls, and he interprets this to mean that it is the only known South American representative of Trelease's Boreales. I have been able to confirm the absence of basal cataphylls on the type specimen (*Steyermark & Nilson 473*, VEN), as also shown in Rizzini's later illustration of the species (Rizzini 1984), in the sense that the lowest leaf scales do not in any way resemble obvious cataphylls. Rizzini does not report the additional, remarkable fact that the basal phyllotaxy of *P. aphyllum* is transverse, a pattern otherwise restricted to the acataphyllous northern group.

P. canzacoto Trelease. This squamate species, apparently endemic to a small area in Ecuador, is essentially without basal cataphylls, which are present only very rarely (Kuijt 1986, Fig. 1) and then only so small as to be scarcely recognizable. When Trelease described this remarkable species his eyesight had become extremely poor; at any rate, he seems to have missed the crucial fact that no basal cataphylls were present. The orientation of the first foliar organs is median, but the significance of this fact is limited since the leaf pairs in this species, rather than decussating, are all in the same plane (distichous). The affinities of *P. canzacotoi* are not clear.

P. filamentosum, sp. ined. This as yet underscribed Bolivian plant species (*Acevedo-R. 6572*, LEA, US) is variable with regard to basal cataphylls, even on the same individual. Most branches lack these structures completely, but some have one pair. Intermediate situation also exist where the first pair of foliar organs is very short and needle-like. The position of any of these basal organs is median. While at first the plant is reminiscent of *Dendrophthora*, the anthers are clearly bilocular, placing it in *Phoradendron*.

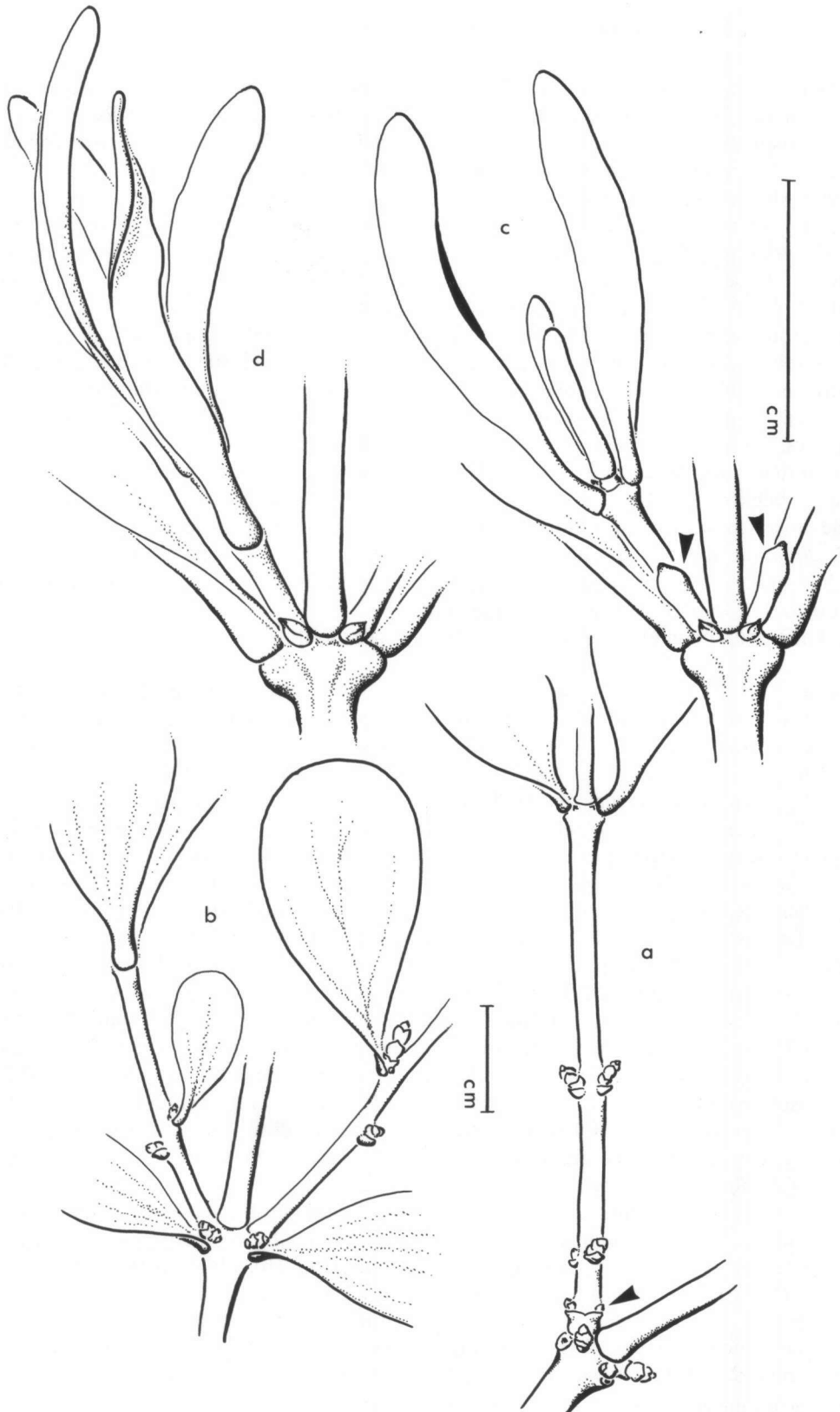
The *P. dipterum* Eichler assemblage. The majority of this group of species have regular, more or less tubular, rather conspicuous basal cataphylls (usually only one pair), as in *P. dipterum* Eichler and *P. fasciculatum* Kuijt, clearly set apart from foliage leaves. There are three extremely rare species apparently belonging to this group of hyperparasitic species which appear to be squamate (additionally, *P. fasciculatum* is nearly so), and which are very fragile. In fact, the only extant specimens of all three are badly fragmented, making statements about basal cataphylls somewhat speculative in two of these three species. I hope that additional future collections can clarify the situation. A fourth, leafy species of the group, *P. calyculatum* Trel., has been traditionally misplaced in *Boreales* for reasons that are relevant here (see below).

A related, unusual morphological feature of this species cluster must be mentioned here to avoid confusion. Elsewhere in the genus, the germinating seedling develops a normal, single stem from which all further branching takes place (except in those species, such as *P. aphyllum*, *P. juniperinum* and others, where additional shoots are generated from the endophyte). We do not know how the seedling of the *P. dipterum* group behaves; what we do know is that a curious basal cushion is formed external to the host from which additional shoots are formed (see *P. aequatoris*, Kuijt 1986; *P. dipterum* and *P. fasciculatum*, Kuijt 1987; *P. iltisorum* Kuijt, Kuijt 1990). Such additional, secondary shoots are not subtended by basal cataphylls even though upper branches have them, as in *P. fasciculatum*.

The three squamate species and one leafy species meriting attention are the following:

- (a) *P. rusbyi*: this species was first described as a *Phoradendron*, but Trelease (1916) transferred it, without comment, to *Dendrophthora*. I have recently (Kuijt 1994) been able to clarify the situation; the relevant fact here is that this squamate hyperparasite, which almost certainly is a *Phoradendron* of the *P. dipterum* alliance, lacks basal cataphylls completely, as illustrated in the above note.
- (b) *P. aequatoris* and *P. iltisorum*: each of these two species is a squamate hyperparasite of other mistletoe species, as are the other members of the complex. The former is known from two Ecuadorian specimens, the latter based on a single collection from Oaxaca. These fragmentary specimens give no certainty, but it is highly probable that, as in *P. calyculatum* and *P. rusbyi*, they lack cataphylls.
- (c) *P. calyculatum*: the pitfalls of a strict adherence to the cataphyll criterion as an infrageneric feature are shown by the case of *P. calyculatum*, a large, flat-stemmed mistletoe from Central Mexico. Trelease (1916) and Wiens (1964)—although the latter with some trepidation—included the species in *Boreales*, as it lacks basal cataphylls. It has been known for a long time that the species is (perhaps exclusively) hyperparasitic on other mistletoes. It clearly represents a member of the *P. dipterum* group of hyperparasites of southern affinity in which flattening of the stem has become greatly exaggerated. Its inflorescences are exactly like those of *P. dipterum*, except that they are longer.

It is therefore significant that, while basal cataphylls are generally absent in this species, there are rare instances where they are retained. One small lateral branch of *Cházaro 4140* (LEA) has two pairs of cataphylls (Fig. 1b), while a mature one above it (Fig. 1c) has a pair of striking cataphylls at 3.5 cm which subtend inflorescences. On the second sheet of the same collection at LEA, two axillary branches clearly have one pair of cataphylls each (Fig. 1d). In several instances in this specimen and *Camp 225* (LEA) from Oaxaca, a lateral branch starts with an unusually short



internode which seems to have had caducous cataphylls (Fig. 1e) as in *P. dolichocarpum* Kuijt (see below). The great majority of basal internodes in this species, however, bear ordinary foliage leaves. The specimen *Steyermark 747432* (NY) is similarly variable, having some lateral branches with, and others without basal cataphylls; a single branch bears two pairs of basal cataphylls.

- (d) *P. dipterum*: one of the three isotypes of *P. glaziovii* Urb. (= *P. dipterum* Eichler) at P also has two vigorous, low lateral branches that are totally acataphyllous. The disappearance of basal cataphylls thus seems to be a general trend of the *P. dipterum* alliance.

P. parietarioides Trel. In this plant from the northern Andes we see another unrecognized case of a taxonomically isolated species which is essentially acataphyllous (Kuijt 1986), even though Trelease's (1916) protologue speaks of such structures. The great majority of lateral stems lacks cataphylls altogether. Rarely, a single pair is present in a very low position; in the even more infrequent cases in which they are placed 6–8 mm above the axil, these cataphylls subtend one inflorescence each. Thus, we glimpse the same relationship between position and the occurrence of subtended inflorescences that we will see in *P. forestierae*, below.

P. argentinum Urb. The main geographic range of *P. argentinum* is east of the Andes, and plants there are consistently cataphyllous. In Peru and Ecuador, however, the species appears to be rare and has, in the past, been referred to as *P. ernstianum* Patsch. (Kuijt 1986). It is here that much variation exists. A Peruvian collection, *Edwin & Schunke V. 3732* (BM, F), is completely without basal cataphylls. Yet, two further Peruvian specimens (*Diaz S. 2063* LEA) and *Gentry et al. 22777*, (MO) have more lateral branches with than without these organs. In Ecuador, the great majority of lateral branches also lack them, but basal cataphylls are present very occasionally (Kuijt 1986). The first foliar organs, in all cases, are in a median position. The closest relative of *P. argentinum* is undoubtedly *P. mucronatum* (DC.) Krug & Urban, which always has regular basal cataphylls, also of a median orientation.

P. vernicosum Greenm. A species of southern affinities, *P. vernicosum* nearly always has one pair of extremely low and inconspicuous basal cataphylls. Occasionally, it has branches without such organs, as in the Costa Rican collection *Haber 9973* (MO). It is also fairly common for this species to produce inflorescences in the axils of basal cataphylls. The Nicaraguan collections, *Moreno 766 & 2003* (LEA), for example, have numerous lateral branches with up to 3 pairs of fertile basal cataphylls each, sometimes including a very low pair (Fig. 2a). It appears that those basal cataphylls which are much higher (to 1.5 cm) than normal ones are invariably fertile. Curiously, in *Moreno 9862* (LEA), also from Nicaragua, two lateral branches at one node show no normal basal cataphylls but, at about 1 and 2 cm, they each subtend one fertile cataphyll and, somewhat displaced upwardly, a small, fertile, expanded leaf (Fig. 2b; see also the similar situation illustrated for *P. breedlovei* Kuijt, Kuijt 1990, Fig. 13). Even where this species has only one, low pair of basal cataphylls we often find a small bud in their

Fig. 2. (a, b) *Phoradendron vernicosum*, *Moreno 20003* and *9862*, respectively (both LEA). (a) Lateral branch with three pairs of basal cataphylls, all fertile but the lowest ones (arrow) possibly dormant. (b) Lateral branches, in each case of lowest pair of foliar organs made up of one fertile cataphyll and one expanded leaf. (c, d) *Phoradendron* aff. *galeottii*, *Tenorio 983* (LEA). (c) Lateral branches each with one pair of transverse basal cataphylls (arrows). (d) Lateral branch lacking basal cataphylls.

axils which apparently remains dormant. In other words, *P. vernicosum* is extremely variable in its basal cataphylls. The position of the lowest foliar organs is always median.

P. aff. galeottii Trel. The specimen under scrutiny is *Tenorio* L. 983 (LEA) from Durango. It is perhaps related to *P. galeottii* but differs significantly in several respects which do not concern us here. It is dioecious, triseriate where there are enough flowers to show this feature, and somewhat hairy. These features, in addition to its overall similarity to *P. lanatum* Trel. and *P. galeottii*, leave little doubt as to its affinity with the northern group.

It is therefore surprising to find that many, but not all, lateral branches bear conspicuous and well-formed basal cataphylls (Fig. 2c). Other branches on the same plant lack these structures completely (Fig. 2d). Another fact of considerable interest is that this collection, unlike the other two species mentioned above, has its lowest foliar organs (whatever their form) of lateral shoots in a consistently *transverse* position, as in the great majority of northern species. We thus have two morphological features one of which (the occurrence of cataphylls) argues for an affinity with species south of Chiapas, the other (basal phyllotaxy) indicating northern affinities.

P. rhipsalinum Rzed. This rare and highly unusual species has extremely long and slender internodes, making observations on basal phyllotaxy a little difficult. It appears, however, that both patterns coexist. The lowest foliar organs of lateral shoots may be either transverse or median; in contrast, inflorescences always seem to show a median pattern.

The plant is said to lack cataphylls (Calderón de R. & Rzedowski 1972) but, in reality, some basal cataphylls are present on the US isotype (*Rzedowski* 28087; Fig. 3a) as well as on the P paratype (*Rzedowski* 31510) and other known specimens (*Rzedowski* 33410, 34405, *Englemann s.n.8.*, all MEXU). These cataphylls are placed far above the leaf axil (1–7 cm), the highest ones seen (Fig. 3a) subtending buds. This species may be a distant relative of *P. bolleanum* (both species occur on conifers).

P. brachystachyum (DC.) Nutt. (incl. *P. riberense* Wiggins), *P. bolleanum* (Seem.) Eichler, *P. robinsonii* Urban and *P. velutinum* (DC.) Nutt. The US isotype of *P. riberense* (*Wiggins* 5654), while mostly acataphyllous, bears some branches with one or two pairs of basal cataphylls, each subtending an axillary bud (Fig. 3b). In *P. bolleanum*, a single specimen has been seen in which the lowest leaves on lateral branches are greatly reduced, in some cases to scale leaves (*Baker & Steinmann* 10427, from Sonora, LEA). For *P. robinsonii* a cataphyllous branch is illustrated, all cataphylls being fertile (*Pringle* 9467, K; Fig. 4b). In *P. velutinum* (DC.) Nutt. also normal basal cataphylls may exceptionally be formed (Fig. 3c). The illustration shows a secondary lateral branch bearing one pair of cataphylls adjacent to two primary laterals which, as usual, lack such organs. There is no doubt that all four of these species are of northern affinity.

P. dolichocarpum Kuijt. This recently described species from Michoacan has several unusual cataphyll features. Most lateral branches have one pair of conspicuous basal cataphylls, but on other branches these are replaced by small, expanded leaves. Where cataphylls are developed they are eventually deciduous, a feature not known elsewhere in the genus (Kuijt 1990). Since this species, in contrast to others in the northern group, has biseriate flowers and is also unusual in having median basal phyllotaxy, it truly seems to form an intermediate between Trelease's two alliances.

P. californicum Nutt. *P. californicum* has traditionally been placed in Trelease's *Boreales*, for it was considered to be acataphyllous. We find it placed next to another

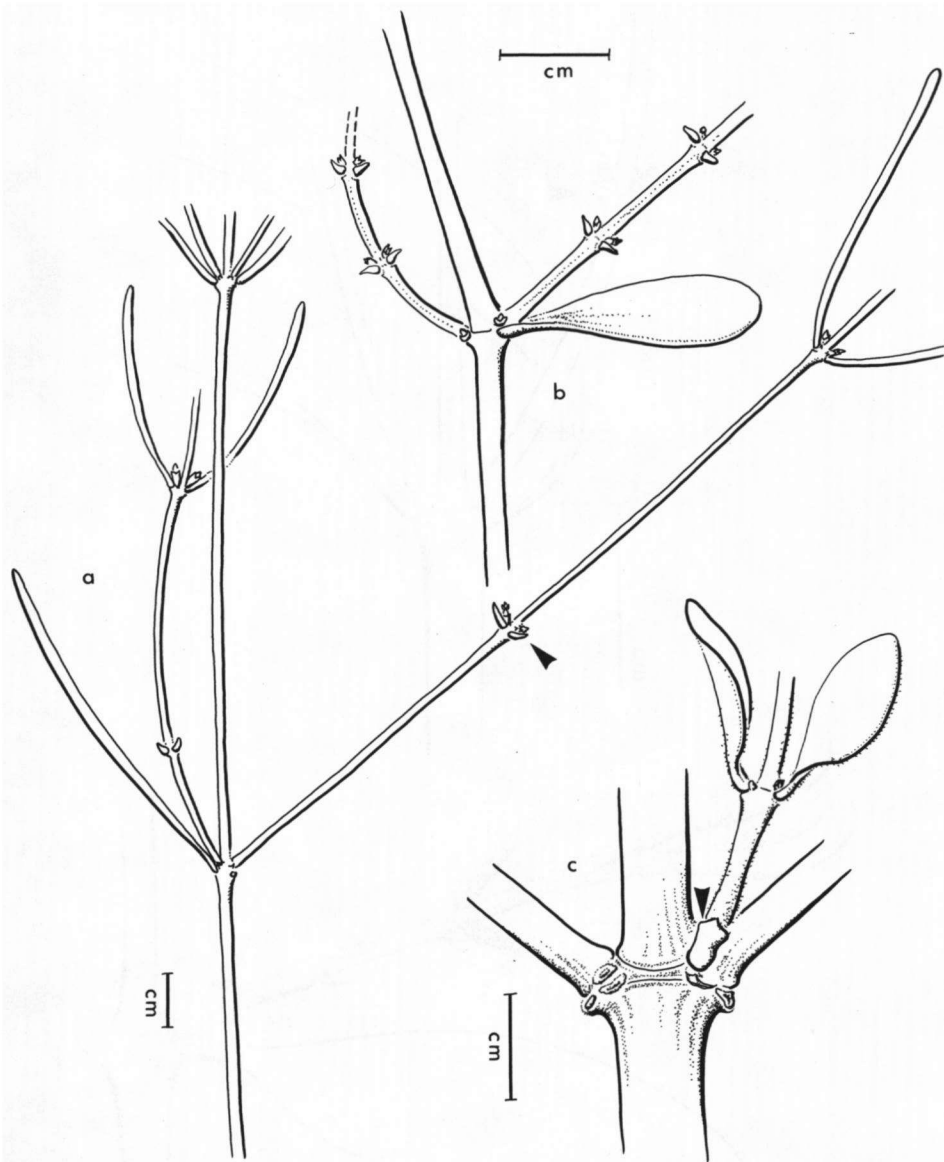


Fig. 3. (a) *Phoradendron rhipsalinum*, Rzedowski 28087 (US). Two lateral branches with one pair each of basal cataphylls, one pair of which is fertile (arrow). (b) *Phoradendron brachystachyum*, Wiggins 5654 (US). Lateral branches with two pairs of fertile cataphylls each. (c) *P. velutinum*, House 1144 (LEA). Secondary lateral branch with one pair of basal cataphylls (arrow), the primary lateral branches being without.

squamate species, *P. juniperinum* Engelm., in Trelease's treatment. I expressed doubts about such an affinity more than 35 years ago, partly because flower seriation is very different in *P. californicum*. It now appears that such doubts were fully justified (Kuijt 1996). Many specimens of this mistletoe do indeed have basal cataphylls, and both phyllotactic patterns occur, sometimes even on the same plant. Even inflorescences occasionally have basal cataphylls. The most telling point is the discovery of a new

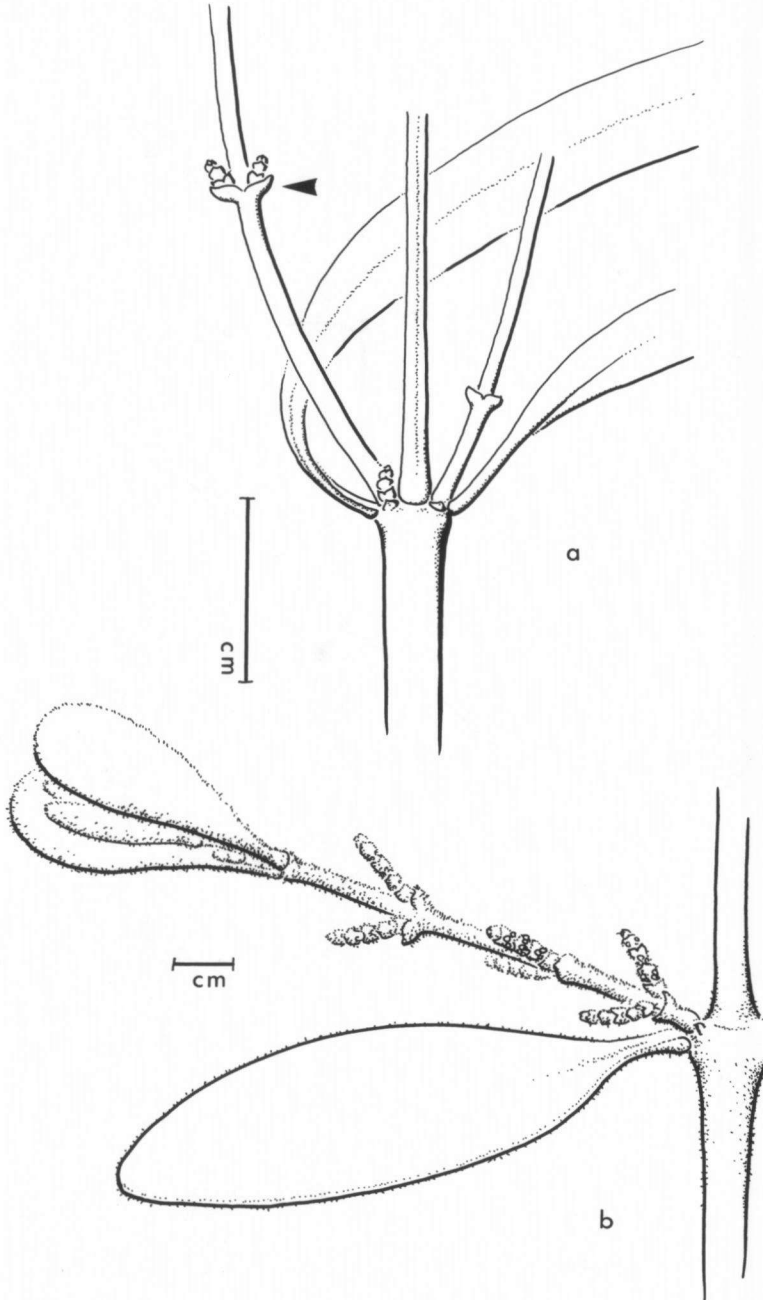


Fig. 4. (a) *Phoradendron forestierae* Robins. & Greenm., *Camp 2334* (LEA). Unusually high basal cataphylls, only the highest ones (arrow) fertile. (b) *Phoradendron robinsonii* Urban, *Pringle 9467* (K). Lateral branch with three pairs of basal cataphylls, all fertile.

Mexican species, *P. olae* Kuijt, which is undoubtedly closely related to *P. californicum*, but which has well differentiated basal cataphylls of a median phyllotaxy. This new species thus unequivocally shows the southern, cataphyllous affinities of *P. californicum*.

The fact that the affinities of the type species of the genus have been seriously misunderstood has significant nomenclatural consequences.

DISCUSSION AND CONCLUSION

Basal phyllotaxy

As stated above, Urban (1896) was the first to make observations in this regard. It was mostly within context of *Dendrophthora* that he studied his material, but he also looked at some species of *Phoradendron*. He found that all South American species of the latter genus (all with basal cataphylls) are invariably median; that what we now call *Boreales* (lacking basal cataphylls) are all transverse, with at least one exception, *P. brachystachyum*, which is median (the other species he mentions, *P. tlacolulense*, is conspecific with *P. brachystachyum*). I have confirmed the situation for that species: all specimens at LEA are median. Urban also recognized the variable situation in *P. californicum*. Here he feels that his material is inadequate, to be sure, but he points out that, if *P. californicum* is variable in this regard, it is the only such species in both *Dendrophthora* and *Phoradendron*. To Urban's one consistently median exception (*P. brachystachyum*), I can now add five others: *P. lanatum*, *P. ramosissimum* Kuijt (as drawn in Kuijt 1990, Fig. 21), *P. robinsonii*, *P. teretifolium* Kuijt (as drawn in Kuijt 1990, Fig. 23), and *P. velutinum*, all species from Central and Southern Mexico. Two further species that may well have northern affinities also have median basal phyllotaxy, *P. dolichocarpum* and *P. forestierae* (see the protologue of the former for peculiarities; the latter has variable basal cataphylls as illustrated in this paper). As mentioned before, *P. rhipsalinum*, also of northern affinities, may have mixed transverse and median basal phyllotaxy. Interestingly, *P. calyculatum* also has strictly median basal leafy organs, like *P. dipterum* and probably all species south of Guatemala (exception: *P. aphyllum*), and in contrast to typical *Boreales*. The systematic meaning of this difference is uncertain, but the above Mesoamerican species in this respect seem to represent transitions between northern and southern groups. However, the above cluster of median or variable species in no way corresponds to a systematic one; especially *P. californicum*, *P. rhipsalinum*, and *P. teretifolium* seem to be quite isolated in the genus.

Cataphyll characters in *Dendrophthora* are perhaps of even less utility above the species level than in *Phoradendron*, even though they are extremely important in defining species there. Again, I refer the reader to Urban's observations of a century ago (Urban 1896). In my *Dendrophthora* monograph (Kuijt 1961) I confirmed and somewhat extended his observations. At that time I pointed out a curious geographic coincidence: among those species with uniseriate flowers, insular (Caribbean) species showed transverse basal phyllotaxy, while continental ones had a median pattern. Not all species fitted that coincidence, but the known exceptions at the time had complicating morphological features, or were placed only doubtfully in the uniseriate group to begin with, such as *D. tetrastachya* and *D. ternata*. (*D. constricta*, listed as an exception, in fact is not so, as it has transverse phyllotaxy; but *D. cubensis*, similarly listed, has clear median phyllotaxy and is certainly an exception). In subsequent years, however, the clarity of this geographic contrast had faded. While some continental uniseriate species described since 1961 have been of the median type (see *D. fastigiata* Kuijt, Kuijt 1986; *D. davidsei* Kuijt and *D. talamancana* Kuijt, Kuijt 1987), others are characterized by transverse phyllotaxy (see *D. luerii* Kuijt and *D. polyantha* Kuijt, Kuijt 1986). In other

words, the geographic pattern involved is no more than a trend, and seems devoid of supraspecific use. Among the bi- and triseriate species of *Dendrophthora*, the majority of continental ones have median phyllotaxy (e.g. *D. dimorpha* Kuijt, *D. dalstroemii* Kuijt, *D. obliqua* (Presl) Wiens, *D. chrysostachya* (Presl) Urban, and many others), but a number of transverse species are known such as *D. cuneifolia* Kuijt, *D. densifolia* Kuijt, *D. clavata* (Benth.) Urban, *D. bulbifera* Kuijt, and *D. pearcei* (Rusby) Kuijt. In summary, it is only at the species level that basal phyllotaxy is useful. Even here, at least one species, *D. tetrastachya*, may show either pattern (two Cuban specimens, *Ekman 19132* and *2517* (LEA), are median and transverse, respectively).

The fact that the *position* of appendages is not related to their *form* is shown by *Phoradendron* sp. (Fig. 2c, d). In this species also, a single individual may bear lateral branches with or without basal cataphylls; the position of the lowest appendages, whether foliage leaves or leaf scales (including those on inflorescence pedicels), is always transverse.

Fertile cataphylls

A few species of *Phoradendron* have intercalary cataphylls which are fertile, i.e. subtend inflorescences. The best known example is *P. crassifolium* (DC.) Eichler. However, basal cataphylls have been regarded as uniformly sterile since Eichler (1868). While this seems to be generally true, exceptions to this rule are occasionally found. The most striking species in this regard is perhaps the recently described *P. lentii* Kuijt (Kuijt 1990), in which this feature is combined with a dichotomous habit. In the present paper other, more occasional examples are seen in *P. calyculatum* (Fig. 1c), *Phoradendron* sp. (Fig. 4a), *P. rhipsalinus* (Fig. 3a), *P. brachystachyum* (Fig. 3b), and *P. robinsonii* (Fig. 4b). The phenomenon also rarely occurs in *P. parietarioides*. Finally, I have also observed it in *P. mucronatum* (DC.) Krug & Urban (*Krapovickas & Cristóbal 12999*, P) and, more frequently, in *D. karuaiana* (Steyerm.) Kuijt (Kuijt 1990). In the acataphyllous northern group, the basal leaves of a lateral branch routinely subtend inflorescences or shoots.

Other genera of Viscaceae

The morphological aspects which are the subject of my present contribution are of no comparable importance in other genera of Viscaceae. In fact, nothing like basal cataphylls is present in those genera save *Ginalloa* and *Notothixos*, where plants consistently develop one pair of basal cataphylls on lateral branches (for *Notothixos*, see p. 6 and Fig. 3 in Barlow 1983). As also visible from that Figure, basal cataphylls in *Notothixos* are always of a median position. The orientation of the lowest foliar organs on laterals of *Viscum* also seems to be uniformly median in the several species I have been able to inspect. In *Arceuthobium*, curiously, all species seem to be of the transverse type, instead (see the illustrations in Kuijt 1970). In neither *Arceuthobium* nor *Korthalsella* are prophylls present, but some species of the former genus (e.g. *A. americanum*) have collateral branches in those positions. For *Korthalsella*, I have no information available on basal phyllotaxy, and Danser's (1937) revision neither refers to, nor illustrates, these aspects; however, my impression from inspecting very few specimens is that phyllotaxy corresponds to that in *Arceuthobium*. In summary, both the occurrence of basal cataphylls and basal phyllotaxy varies between these genera, but each genus appears to be consistent within itself.

Function of basal cataphylls

No one, as far as I am aware, has commented on the possible adaptive significance of basal cataphylls and, indeed, the question remains quite unresolved. They clearly do not function as bud scales. The only suggestion I can make is that they bear some relationship to the visits of pollinating insects, either at present or in the evolutionary past. The position of occasional, fertile basal cataphylls (i.e. high on later axes) of *P. vernicosum* and a few others is consistent with the idea that these organs function to displace inflorescences on lateral branches away from the main node, which is frequently congested with inflorescences. Nothing, unfortunately, is known about the pollination biology of either *Dendrophthora* or *Phoradendron*; presumably, insect pollination is the rule.

Conclusions

1. Neither the presence nor the absence of basal cataphylls, nor their phyllotaxy, can supply a reliable basis for the delineation of infrageneric taxa in either *Phoradendron* or *Dendrophthora*.

2. The presence or absence of basal cataphylls does not seem to span a very large genetic gulf. There are several instances where, apparently from cataphyllous ancestry, individual, more or less acataphyllous species have arisen:

- (a) *P. canzacotoi*;
- (b) *P. calyculatum*, and perhaps its relatives *P. aequatoris* and *P. iltisiorum*; closely related to *P. dipterum*;
- (c) *P. rusbyi*;
- (d) *P. aphyllum*;
- (e) *P. parietarioides*; and
- (f) *P. filamentosum*, sp. ined.

In some essentially cataphyllous species, such as *P. dipterum* and *P. vernicosum*, acataphyllous branches are occasionally developed; in *P. argentinum*, this seems to be common in its western range. However, there seems to be no way at present to tell whether the acataphyllous condition of northern species is an original or a derived condition. In *Dendrophthora* there are numerous cases where in a closely related species pair, one is cataphyllous and the other is not. Examples of this are seen in *D. ambigua* Kuijt vs. *D. dimorpha* Kuijt; *D. chrysostachya* (Presl) Urban vs. *D. clavata* (Benth.) Urban; and *D. eichleriana* Urban vs. *D. peruviana* Kuijt (see Kuijt 1961, 1990).

In *Phoradendron*, on the other hand, there are instances of cataphylls being formed, however infrequently, in species which are otherwise acataphyllous:

- (a) *P. diguetianum* (*P. riberense*);
- (b) *P. rhipsalinus*;
- (c) *P. bolleanum* (Seem.) Eichler; and
- (d) *P. robertsonii* Urban.

3. Basal phyllotaxy is of limited (*Dendrophthora*) or no (*Phoradendron*) taxonomic significance above the specific level.

4. Contrary to statements in Trelease (1916) the type species of *Phoradendron*, *P. californicum*, frequently has basal cataphylls. It is unique in the genus in its great

variability in both the number and the position of these organs. A newly described Mexican species, *P. olae*, proves that the affinities of this species are with southern cataphyllous species.

5. Some of the observations here reported strongly imply that the absence of basal cataphylls, at least often in South America, is an apomorphic character. This is suggested by the fact that this feature appears in a number of unrelated species, such as *P. canzacotoi*, *P. parietarioides*, *P. rusbyi*, *P. aphyllum*, *P. argentinum*, and *P. calyculatum*, as well as by the fact that these species tend to be systematically isolated in the genus (the first three species) or have close relatives which are clearly cataphyllous (the last two species). It does not necessarily follow that this feature is always apomorphic; in the northern group, it may well have a different significance.

6. The two types of basal phyllotaxy, like the presence/absence of basal cataphylls, do not appear to represent genetic features that are widely separated. This seems to be indicated by several observations: (a) The apparently independent evolution of a transverse pattern in a single, highly advanced, South American species, *P. aphyllum*. It is highly doubtful that this species is related to the northern group in which this pattern is also present; instead, it must represent an evolutionary change from a median ancestry. (b) Variability in *P. californicum*, both in its vegetative and inflorescence structure. (c) Similar variability in *P. rhipsalinum* and the unidentified species illustrated in Fig. 2c and d. (d) The occurrence of both patterns among northern, acataphyllous species.

7. Most of the species in Trelease's *Boreales* appear to form a natural group except for *P. californicum* and *P. calyculatum*, which are to be excluded. The latter species is a member of a cluster of mostly or exclusively hyperparasitic species including *P. dipterum*. Since Trelease's time, some new species have been added to this group, but other new ones are of uncertain position. If *Boreales* is indeed a natural group, it needs to be both redefined and renamed. The systematic organization of the larger, remaining part of the genus is unresolved but cannot be based on cataphyll features only.

8. Nomenclatural consequences—the nomenclatural status of the infrageneric names *Boreales* and *Aequatoriales* depends upon the resolution of two distinct problems, namely the intended meaning of the word 'Division' in Trelease's monograph (p. 19), and the question of ranklessness. If the word 'Division' is held to denote a hierarchical unit, neither *Boreales* Trel. nor *Aequatoriales* Trel. are validity published (International Code of Botanical Nomenclature, Art. 33.5), for a genus cannot be subdivided into Divisions. In that case, the authorities in both cases would become '(Trel.) Engler & Krause' (1935), where they were introduced as subgenera. If, on the contrary, Trelease used 'Division' in the non-hierarchical, more general sense, both Trelease names are rankless; they are validly published in view of Art. 35.2, but they may have no effect on priority except for possible questions of homonymy.

However, in view of Art. 22, neither *Boreales* Trel. (1916) nor *Boreales* (Trel.) Engler & Krause are validly published, as the autonym should have been used. Since, beyond all these considerations and contrary to Trelease's opinion, it is now clear that the affinity of the type of the genus, *P. californicum*, to other northern species is anything but a foregone conclusion, *Boreales* would not necessarily receive this species. Of lesser importance is the fact that all of Trelease's terminations would also seem to be in error, this being correctable.

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