A STUDY OF HETEROPHYLLY AND INFLORESCENCE STRUCTURE IN DENDROPHTHORA AND PHORADENDRON (LORANTHACEAE)

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INTRODUCTION

It is not surprising that the mistletoes, being parasitic plants, should show a great range of diversity in the structure of their haustorial organs. These organs, after all, are involved in the act of parasitizing; they form the physiological channel for the materials which the parasite draws from its host. It can therefore be appreciated that such vitally important organs should have evolved in many directions, this evolution being influenced by different endophytic environments when new host species were attacked.

Much more puzzling, however, is the fact that many of the most striking morphological peculiarities in the mistletoe family appear not to be directly connected with the parasitic mode of life. The most outstanding of these are related to the flower and fruit, and a few of such features may be briefly referred to here: the absence of true ovules; behavior of the embryo sac (cf. MAHESHWARI, JOHRI and DIXIT, 1957); radical anther modifications in *Arceuthobium, Viscum,* and *Korthalsella;* the highly efficient explosive fruit of *Arceuthobium;* green endosperm, absence of rootcap, and presence of stomata on radicles of some Viscoideae (cf. KUIJT); and the peculiar inflorescence of *Dendrophthora* and *Phoradendron.* Before the full significance of such peculiarities can be appreciated, the structural variability of the organs involved needs to be explored in detail. I herewith present my observations on the morphology of the unusual inflorescences of the American genera *Dendrophthora* and *Phoradendron,* together forming the tribe Phoradendreae of the Viscoideae. I include some notes on the heterophylly so conspicuous and varied in many species of these genera, a phenomenon frequently important but sometimes used incautiously in the taxonomy of the Phoradendreae, and which is still poorly known in detail. It will be seen later that there are more relations between the seemingly separate topics of heterophylly and inflorescence morphology than meet the eye.

A few words must be said about the taxonomy of the two genera. The only distinction between *Dendrophthora* and *Phoradendron* which

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difficulties will be discovered in due time. I am fully aware of the arbitrary character of such definitions and circumscriptions; but their usefulness as points of reference will, I hope, be better appreciated as the discussion proceeds. Finally, I wish to warn against the misuse of the term *internode* by EICHLER (1868) and TRELEASE (1916). Both speak of the insertion of several pairs of cataphylls per *internode* or *foliage internode*. Such an extension of the concept internode is, I think, quite unwarranted and indeed confusing. The places of insertion of cataphylls, prophylls, scale-leaves and foliage leaves alike must be regarded as nodes; the areas between two successive nodes, as internodes, in accordance with ordinary morphological usage.
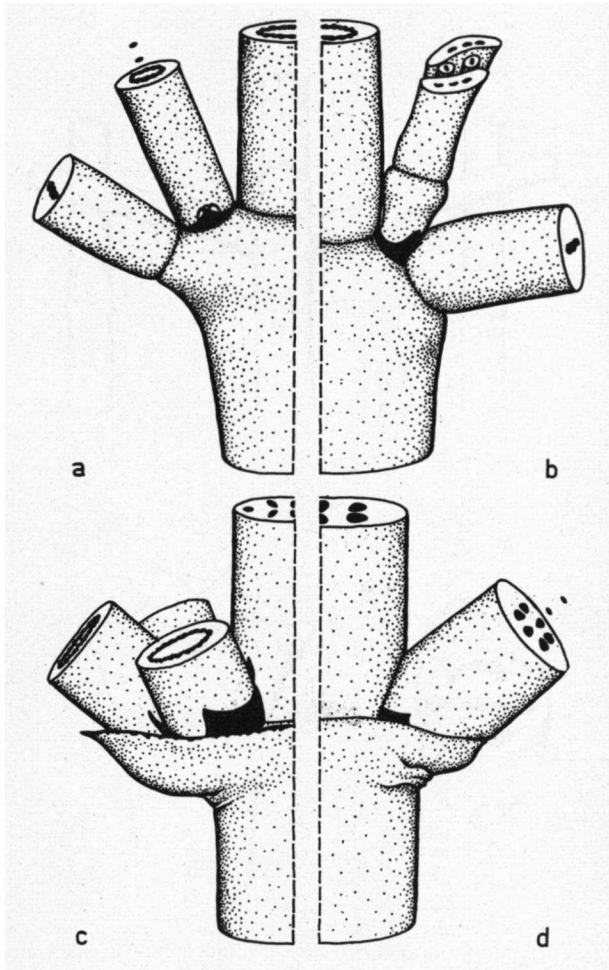

Fig. 1. Prophylls (in black) of a. *P. serotinum*, — b. *P. pauciflorum*, — c. *P. californicum*, — d. *P. juniperinum*. Dots above cut stem surfaces indicate the position of next higher appendages (× 7).

Prophylls   The prophylls of the Phoradendreae are, as in many other Dicotyledons, minute structures. They are usually most clearly visible when young (Fig. 1b). Even then they may not be more than slight protuberances of the same color as, and not visibly delimited from the bulging shape of the node from which they arise. This is true, for example, in the species *P. villosum, P. macrophyllum,* and *P. serotinum* (Fig. 1a). In *P. densum* and *P. pauciflorum* the prophylls are somewhat more conspicuous (Fig. 1b). In the two latter species, which have expanded foliage, it is often easier to scrutinize herbarium material for prophylls because these organs are situated on the shoulder of the node, between the basal constriction of the subtending leaf and the also constricted base of the following internode of the main axis (Figs. 1a, b). In the "leafless" species, however, the pro-
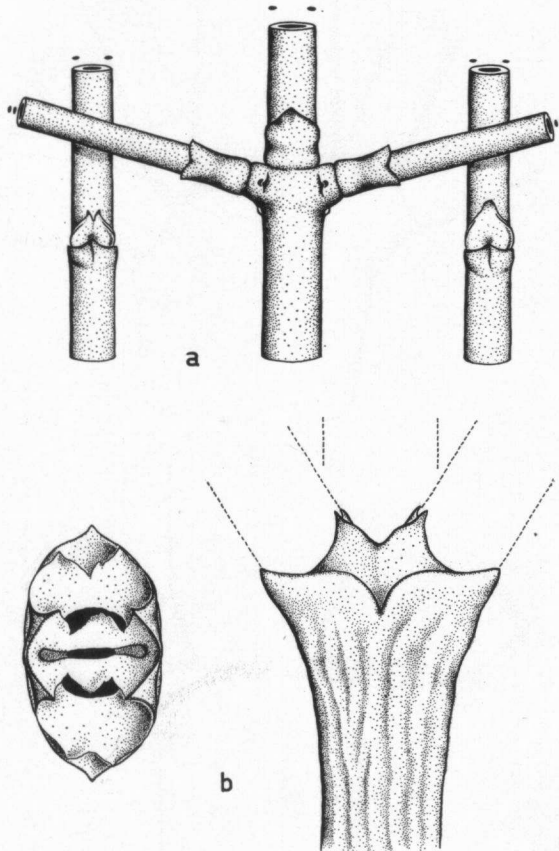

Fig. 2.   a. Fusion of prophylls (left and right) in *D. remotiflora,* von Türckheim 2916, at U (× 3; lateral branches removed). Center: vaginae cataphyllares in *D. poeppigii,* Krukoff 6011, at U (× 3). Black spots indicate the positions of the next higher appendages. — b. Fused prophyll-pairs in *D. nipensis,* Morton & Acuna 3038, at K (× 6). Left, top view; right, lateral view. Main and lateral branches removed (broken lines).
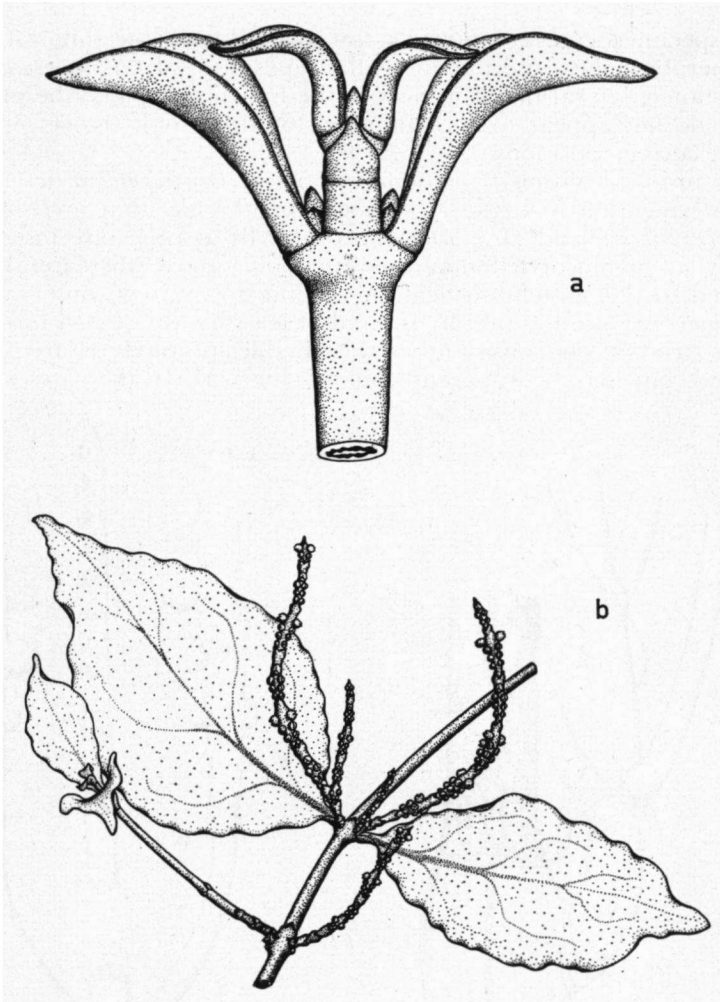
Fig. 3.   a. Young foliage leaves and cataphylls of *P. piperoides* from Puerto Limón, Costa Rica (× 5). Kuijt 1529. — b. Mature branch of same (× ½).

phylls are usually at least partly obscured by the fused margins of the subtending scale-leaves (Figs. 1c and 1d). If branches develop in the axils of the prophylls of a primary lateral, such branches have their own pair of prophylls (Fig. 1c), or these may be wanting (see the secondary inflorescences of *P. pauciflorum*, Fig. 12b). In *D. biserrula* (Fig. 4a) the prophylls of secondary laterals are clearly visible as dark brown little teeth, even when these secondary branches do not themselves develop.

On older nodes it becomes progressively more difficult to discern the prophylls which may be obliterated or pushed aside by the expansion of the node. Indeed the position of prophylls on an herba-

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rium specimen can, at times, be traced only from the inflorescences or other branches inserted in axillary positions. In *P. cheirocarpum*, for instance, lateral inflorescences of the fourth order may be present which do not appear to be subtended by any prophylls, yet emerge in the correct positions.

The fusion of prophylls in some species of *Dendrophthora* deserves a separate mention. URBAN (1896) mentions the fact that in *D. opuntioides*, *D. dahceri*, and *D. gracilis* the prophylls at times are fused and occupy a "monocotyledonous" position, i.e. above the lateral axis, opposed to the subtending leaf. According to my own observations, *D. domingensis* also has prophylls fused at least basally. In *D. remotiflora* this is true more consistently: the double prophyll is frequently notched, but may be apparently single (Fig. 2a). In the cases known
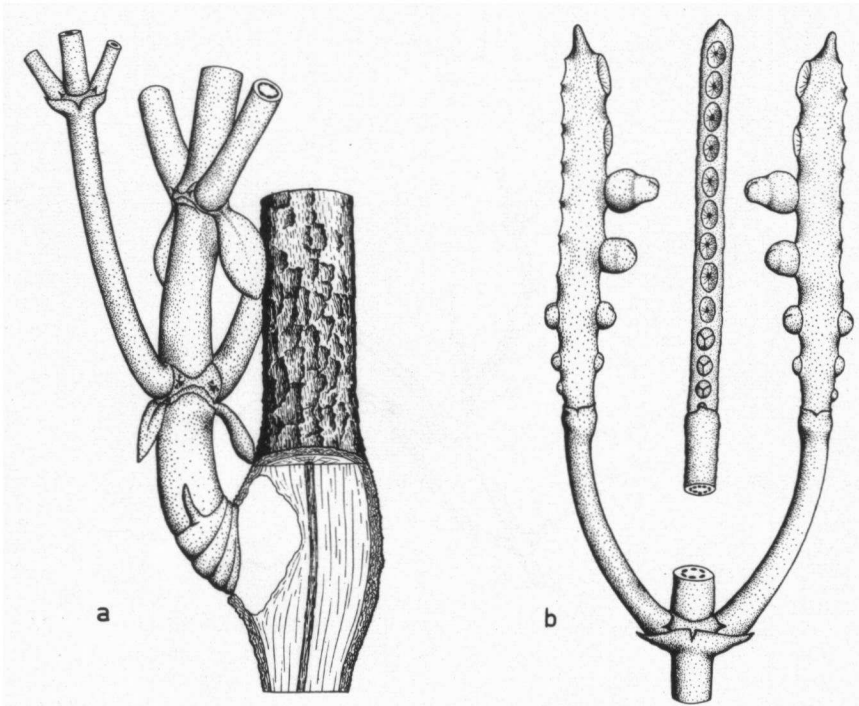

Fig. 4. *D. biserrula* (Kuijt 1532) on *Vaccinium consanguineum*, Volcán Irazú, Costa Rica. — a. Basal portion of young plant; haustorial organ left blank (× 1). — b. Lateral and median views of spikes (× 2).

to me the double organ is paper-thin and almost translucent, with a narrow upturned lateral edge. The process of fusion has gone one step further yet in *D. nipensis* (Fig. 2b) and some specimens of *D. domingensis*, where the four prophylls borne on one node form a single structure of, as it were, three toothed cups, the lateral ones containing the lateral axes, the middle cup the percurrent axis. Such a multiple structure gives the impression of being a very short internode.
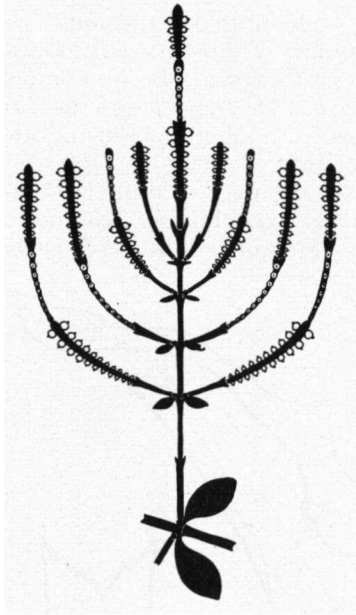
Fig. 5. Reconstruction of part of a plant of *D. paucifolia*, Williams 1530 (isotype, UC). Phyllotaxy must be thought of as decussate throughout ($\times$ ½).

Cataphylls Of the cataphylls I shall first deal with those occurring on lateral axes. They are frequently wanting on inflorescences. In all species north of Mexico (e.g. *P. macrophyllum*, Fig. 10a; *P. pauciflorum*, Fig. 12b), in *D. costaricensis* (Fig. 8d), *D. biserrula* (Fig. 4b), *D. ternata* (Fig. 9), and many others, the first pair of appendages above the prophylls is already fertile. In such species as *P. piperoides* (Fig. 6c), *P. crassifolium* (Fig. 14), *D. tetrastachya* (Fig. 7d), two to several pairs of cataphylls may intervene between prophylls and fertile bracts. Fusion of inflorescence cataphylls is the rule.

The cataphylls of vegetative laterals are, of course, more conspicuous because of the contrast with the foliage leaves above them. Those species of *Phoradendron* included by TRELEASE (1916) in his Boreales are without cataphylls. However, I would like to draw attention to the fact that in several species referred by Trelease to the "Brachystachyae" occasionally markedly reduced leaves occur near the base of a lateral branch. This phenomenon can be seen from Trelease's plates 51 (*P. globuliferum*) and 52 (*P. aureum*); I have also observed it in herbarium material of *P. brachystachyum* (Pringle 11160, L) and *P. minutifolium* (K.). We may perhaps regard such leaf reductions as an intermediate situation between presence and complete absence of cataphylls. The plants involved are also geographically intermediate.

In the "Aequatoriales" and in many species of *Dendrophthora* the cataphylls on lateral vegetative axes show a great variety of form, number, and prominence. Especially when only one or two pairs

are found, these are often united into *vaginae cataphyllares* of shallow (*P. piperoides*) to tubular (*D. costaricensis*, *D. poeppigii*) shape. The second or third pairs, if present, become more shallow and more clearly bifid (*P. tonduzii*). In *D. poeppigii* the cataphylls form a conspicuous tube, almost completely obscuring the scar of the small deciduous leaf below (Fig. 2a).

I must now return to the matter of phyllotaxy of the first two pairs of appendages on lateral axes. URBAN (1896) is the only author who speaks of these features. He noticed that in *Dendrophthora* some variation
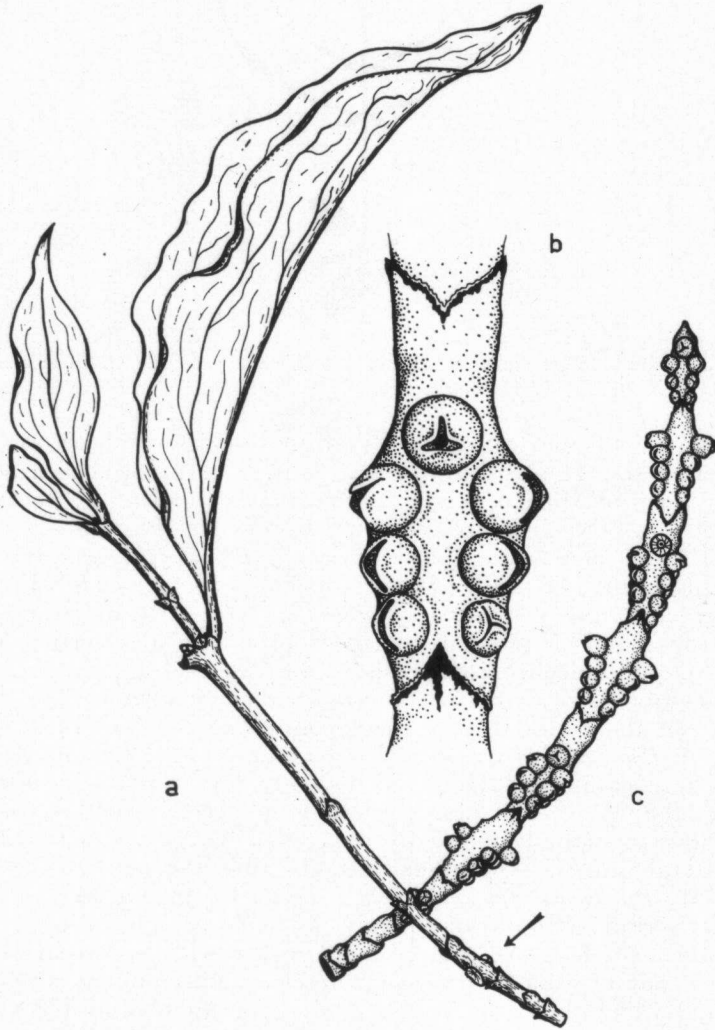

Fig. 6. *P. piperoides.* — a. vegetative lateral branch with pair of aborted flowers (arrow). Baber 2602, UC. — b. and c. Details of spike, Kuijt 1529 (× 1, × 8, and × 2 respectively).
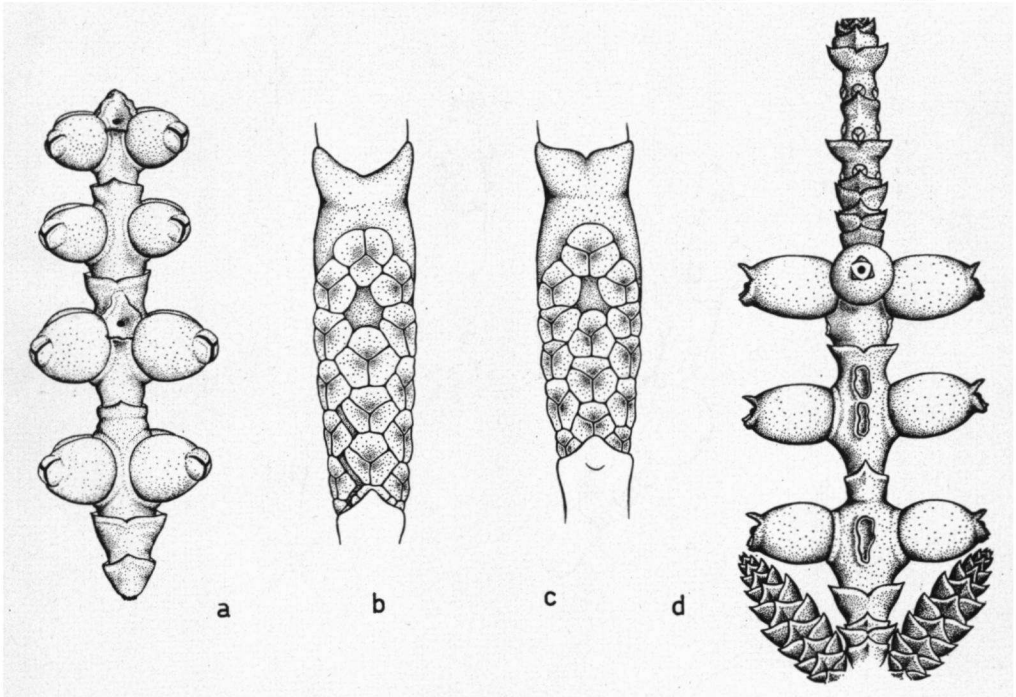
Fig. 7. a. *P. platycaulon* in fruit, the staminate (apical) flowers having fallen away (× 4). Spruce 228, the type, K. — b. & c. *P. tonduzii*, from Tres Rios, Costa Rica (× 6). Demonstrating the orientation of the apical flower b., when the second or more median flowers are absent; c., when the second or no median flower is absent. — d. Primary and young secondary spikes of *D. tetrastachya*, von Türckheim 3108, L (× 2).

exists in the relative positions of the prophylls and the next higher pair of appendages on the lateral axis. In one group of species, a decussate arrangement prevails throughout; i.e. the appendages following the prophylls are in the median plane. In the second group, however, the second pair of appendages stands transversely, in the same plane as the prophylls (distichous therefore), but beyond this second pair again a decussate phyllotaxy follows. Finally, there are those species which have a distichous arrangement throughout, sometimes with the exception of the basal portion of the plant.

Urban then moves on to look at these same features in *Phoradendron*, and concludes that all West Indian and South American species of this genus have one or more pairs of cataphylls or vaginae cataphyllares, the lowest being median in position, decussate thus with the prophylls. A decussate phyllotaxy is here thus the rule throughout the plant. EICHLER (1868), indeed, had regarded this as a generic character. Urban had seen more material from North and Central America, however, and knew this to be incorrect. Again three different arrangements can be recognized, the first two remarkably parallel to the corresponding groups in *Dendrophthora*. Practically all South American
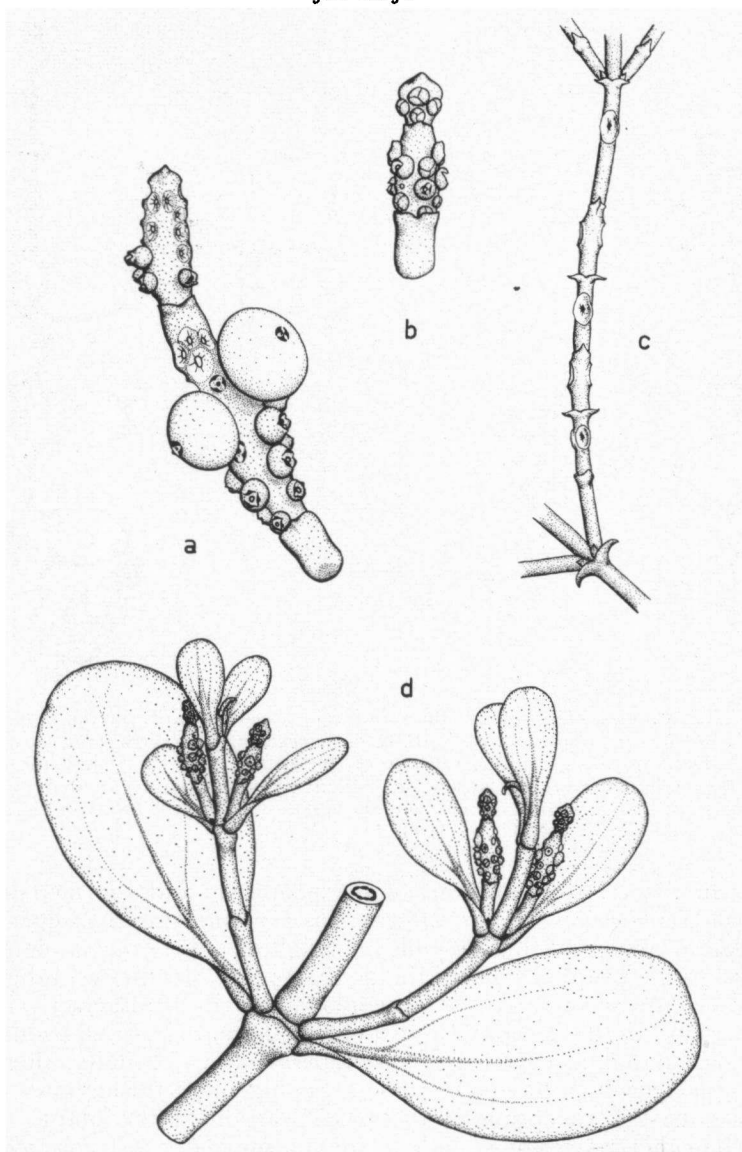
Fig. 8.   a. & b. Inflorescences of *D. costaricensis* (Kuijt 1531) from Volcán Poás,
Costa Rica; a. with mature berries ($\times 2^2/_3$).—c. *D. cupressoides*, branch with floral
cups ($\times 3^1/_3$). Morris s.n., K.—d. Habit of *D. costaricensis* from the same collection
as above. The two large lateral branches are secondary ones to primary inflorescences
which have fallen away ($\times 1^1/_3$).

and West Indian species of *Phoradendron* have, as already stated, a
decussate phyllotaxy throughout. To this group Urban adds *P.
brachystachyum* and *P. tlacolulense* from Mexico. The second group has

prophylls and the following pair of leaves in the same, transverse plane (distichous phyllotaxy), all others decussate. To this group Urban refers *P. serotinum*, *P. bolleanum*, and *P. minutifolium*. Finally, Urban groups together those *Phoradendra* which have scale-like leaves only, such as *P. juniperinum* and *P. californicum*. He also briefly refers to the remarkable fact that the prophylls and the next pair of appendages in *P. californicum* may be either decussate or distichous. I shall later return to this variation in phyllotaxy. I should mention here that Urban did not propose these divisions as natural taxonomic groups, but used them to underline these particular structural details.
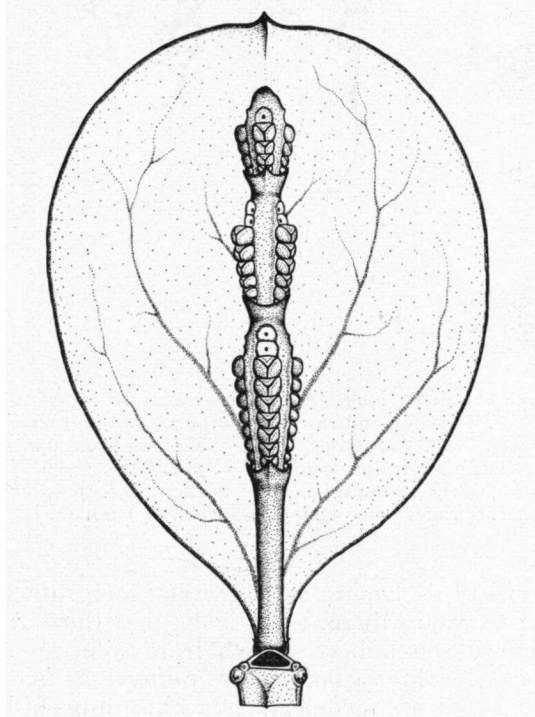

Fig. 9.   Inflorescence (probably staminate) and leaf of *D. ternata*, Fuertes 1523 (the type), U. The two other leaves and two other spikes of the same node have been removed (× 2).

On the whole I find Urban's morphological categories helpful, but would make some changes. In *Phoradendron*, all of Trelease's Aequatoriales fit in group I (decussate phyllotaxy throughout). In group II, we may place all species occurring in the United States, except *P. californicum*: in *P. serotinum* (Fig. 1a), *P. macrophyllum* (Fig. 10a), *P. villosum*, *P. pauciflorum* (Figs. 12b, and 13a), *P. bolleanum* and *P. juniperinum* (Fig. 1d), the prophylls and the next higher pair of appendages stand in the same, transverse plane. Beyond, the phyllotaxy is uniformly decussate. It is difficult to know what to do with the
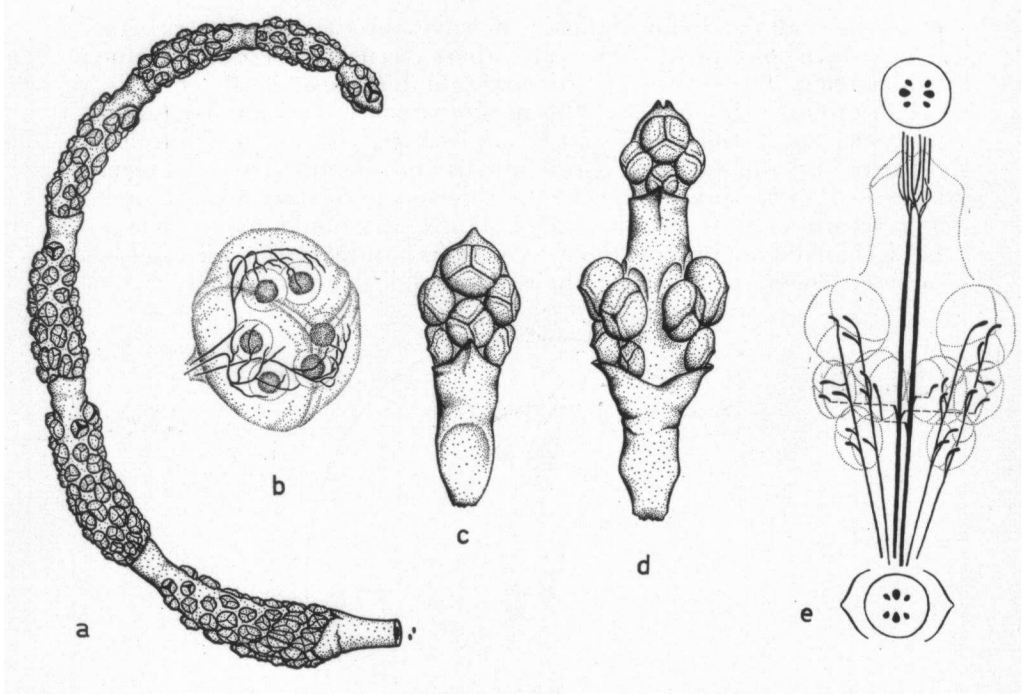
Fig. 10.   a. Large staminate spike of *P. macrophyllum* from Woodlake, California
(× 1¹/₂); Kuijt 1209. Two dots indicate the positions of the subtending prophylls.—
b. Staminate flower of *P. pauciflorum* (× 15), showing vascular structure. Kuijt
1521. — c & d. Staminate inflorescences of *P. pauciflorum* (× 6). — e. Diagram-
matic representation of the vascular structure in the staminate spike of *P. pauciflorum*
(× 10). Lateral traces somewhat pushed away from percurrent ones.

remaining species of the genus, as I have not seen sufficient material.
I should prefer to retain them, tentatively, in a third group, because
of the variation in phyllotaxy known from some of them. Urban
hesitatingly speaks of this variation in *P. californicum* (see above). This
species indeed shows an inconstancy in this respect. For example,
Templeton 1559 (L) shows arrangements typical of group I and II
on the same plant. Rehder 248 (K) from Arizona has decussate
phyllotaxy throughout. Indeed, the decussate arrangement predomi-
nates in the various collections of this species which I have seen. In
P. brachystachyum some plants are predominantly as group I (L 911–
116–133), others as group II (L 911–116–136). In *P. calyculatum, P.
velutinum, P. scaberrimum, P. tlacolulense, P. globuliferum, P. galeottii,
P. diguetii* and *P. uspantanum*, all members of the Boreales, phyllotaxy
again is decussate throughout, as in group I. It is an interesting fact
that these are the most southerly representatives of the Boreales. In the
matter of phyllotaxy therefore we find a continuous cline, from the
Aequatoriales in the south and the adjacent Boreales (group I),
through such species as *P. californicum* and *P. brachystachyum* (variable

phyllotaxy), to the northerly Boreales where phyllotaxy is always as in group II. This morphological cline bridges the gap between the Boreales and Aequatoriales.

In *Dendrophthora* we find a variation in phyllotaxy which parallels that in *Phoradendron*. There are many species (perhaps most) which are decussate throughout, e.g. *D. biserrula* (Fig. 4a), *D. costaricensis* (Fig. 8d), and *D. poeppigii* (Fig. 2a). In *D. grisebachii* (Wright 2652, K), *D. glauca* (Wright 2651, K), and *D. cupressoides* (Morris s.n., K) the phyllotaxy again belongs in group II. In *D. tetrastachya* (Ekman 9540, K) both types of phyllotaxy occur on the same plant! *D. biseriata* (U 031249), though otherwise very close to *D. biserrula*, in contrast to this species belongs in group II. I have the impression, at
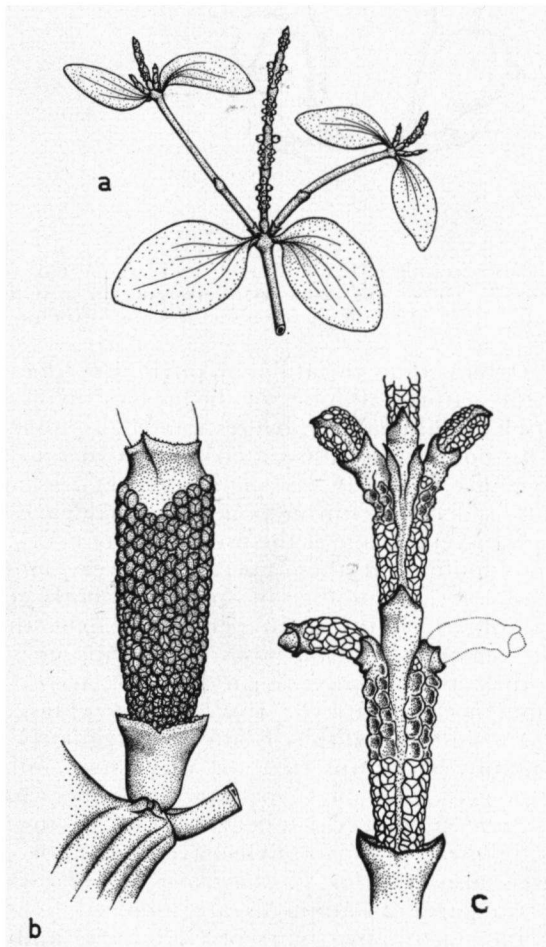

Fig. 11.   a. Dichasial habit in *P. henslovii*, Habel 1868, K (× ¹/₂). — b. Basal internodes of staminate spike of *P. calyculatum*, Pringle 13189, K (× 4). — c. Teratological staminate spike of *P. dimidiatum*, Boschwezen 5308, U (× 4).
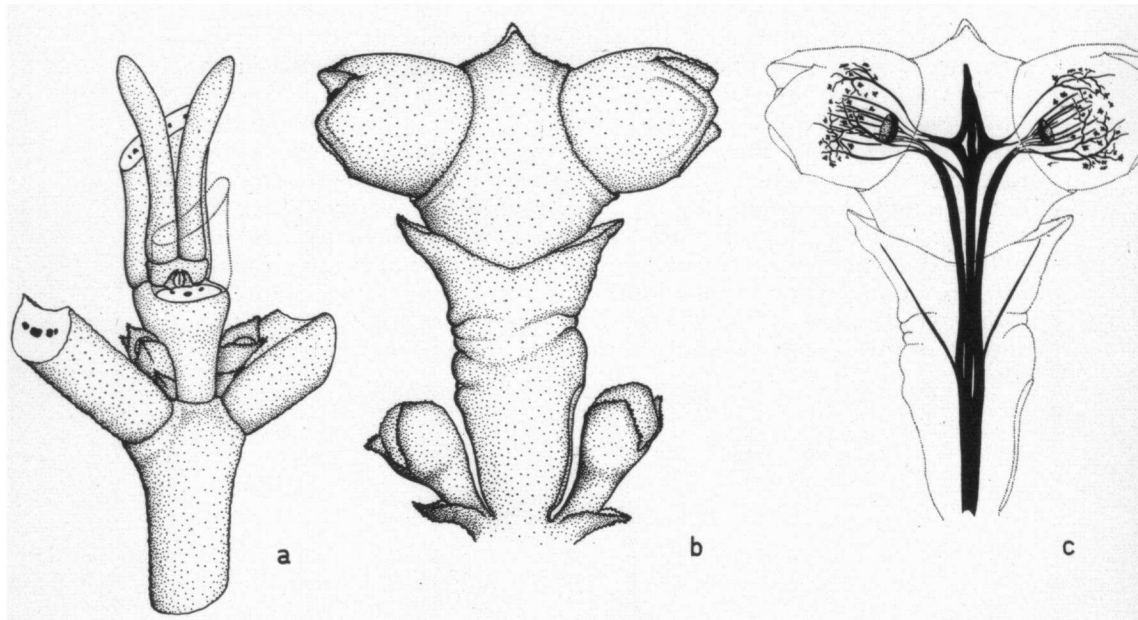
Fig. 12. *P. pauciflorum*, pistillate, Kuijt 1521. — a. Terminal part of branch with young inflorescences (× 5). — b. Primary inflorescence in fruit flanked by two young ones. (× 10). — c. Lateral view of the vascular structure of b (× 10)

least in *Dendrophthora*, that variation in phyllotaxy does not always correspond to the natural affinities of the species involved; that this variation in itself should not be overestimated as to its taxonomic significance. This point is also illustrated in the two European species of the related genus *Viscum*, *V. album* L. and *V. cruciatum* Sieb. ex Boiss. The former is decussate throughout; the basal leaves of the latter are in the same transverse plane as the prophylls (TUBEUF, 1923, p. 94). Yet there is no doubt that these species are very closely related.

There are, however, a number of species in both genera which also possess cataphylls on the main percurrent axis: these may be called *intercalary cataphylls*. For purposes of description it is useful to arrange them diagrammatically, as in Fig. 15, according to their increasing prominence of cataphylls. In *P. piperoides* (Figs. 3b and 15a), *D. poeppigii* (Fig. 2a), etc., cataphylls alternate regularly with foliage leaves. The cataphylls are inserted on very short internodes, the foliage leaves on very long ones, so that the former may easily be overlooked and the phyllotaxy appears distichous in *P. piperoides*. In *D. poeppigii* the intercalary cataphylls have fused to become vaginae (Fig. 2a); this is also true for *P. platycaulon* and *P. surinamense*. In *P. paradoxum*, two pairs of cataphylls are followed by two pairs of foliage leaves; then again two pairs of cataphylls, and so on. The lowest of a pair of these cataphylls is quite basal, the upper pair inserted at approximately equal distances to the foliage leaves above and below.

In *P. fendlerianum* two or three pairs of intercalary cataphylls follow upon each other, after which a pair of foliage leaves; then again a sequence of cataphylls, and so on. Approximately every third pair consists of foliage leaves, we might say, the others being cataphylls. Again the first pair of such a cataphyll series is basal, the others more evenly spaced between successive pairs of foliage leaves. The situation here differs from that in *P. paradoxum* only in that in the former one pair, in the latter two pairs of foliage leaves are inserted between two successive series of cataphylls. If it is true, as Trelease suggests, that that these names belong to different sexes of the same species, this would be an interesting case of sexual dimorphism. It is unfortunate that the two species have not been collected very often, so that the question cannot at present be clarified.
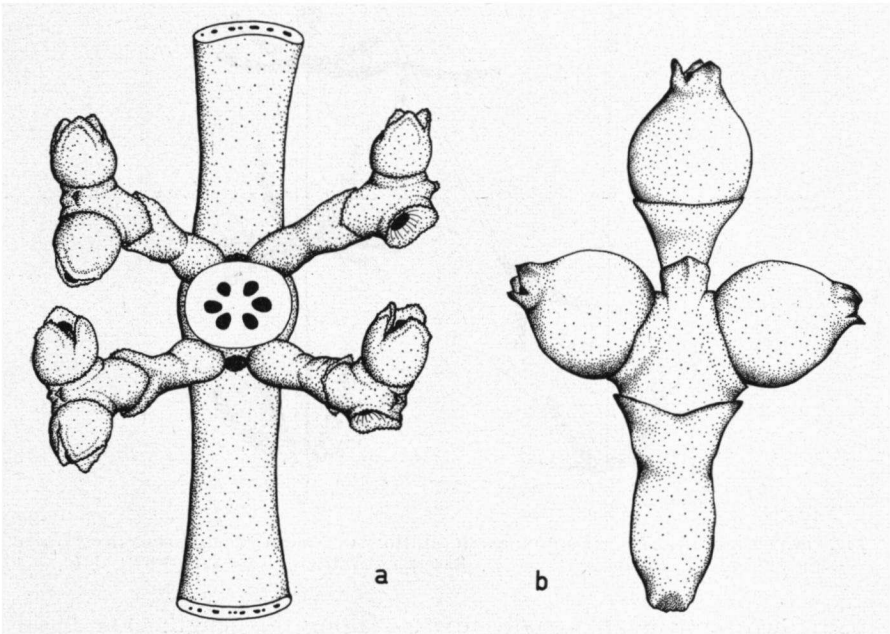
Fig. 13. *P. pauciflorum*, pistillate, Kuijt 1521. — a. Four secondary spikes in fruit the primary ones having fallen away (× 4). — b. Teratological spike with single terminal, pedicellate flower (× 7).

In the types of intercalary cataphylls mentioned so far, only the foliage leaves subtend inflorescences. Cataphylls are not always sterile in other species, however. In *P. craspedophyllum* (Fig. 15d), for example, we find two pairs of cataphylls between every two successive pairs of foliage leaves, as in *P. fendlerianum*. The first pair of cataphylls is basal and sterile; the second, about midway between the foliage leaves, subtends inflorescences. The latter occur also in the axils of foliage leaves. The most advanced condition is seen in *P. crassifolium* (Fig. 14). Here the distance between two successive pairs of expanded leaves corresponds to one season's growth. Three or four

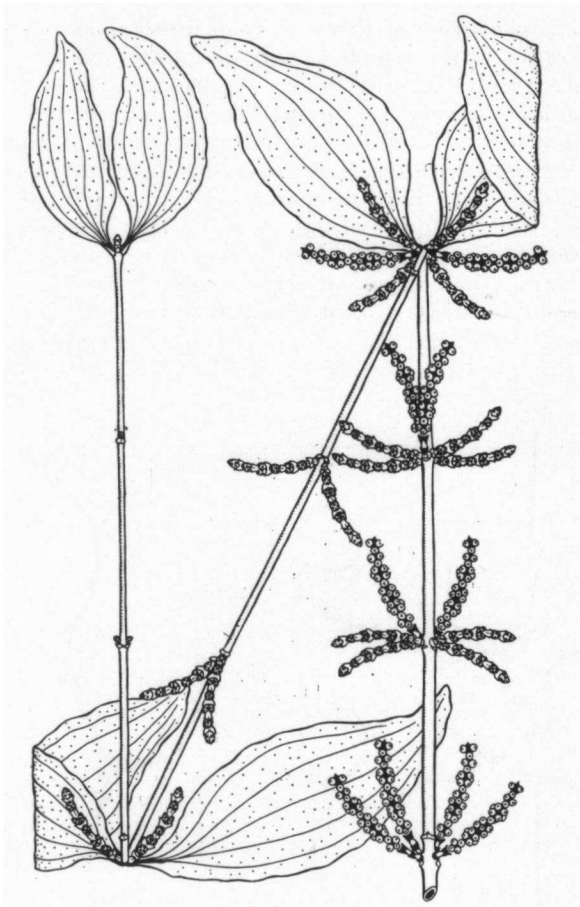Fig. 14. Diagrammatic representation of the succession of inflorescences on a branch of *P. crassifolium* (× ¹/₂). Based on Williams & Assis 6879, UC.

pairs of cataphylls are usually inserted along this length. The basal pair again crowns a very short internode, and is invariably sterile. The remaining cataphylls, as well as the foliage leaves, subtend inflorescences. In basipetal direction we therefore find portions of the main axis with successively more advanced inflorescences: first, a section with only inflorescence buds in the axils; then, fully developed inflorescences; finally, inflorescences in fruit and, in the axils of their prophylls, new inflorescences. The inflorescences axillary to foliage leaves always correspond in age to the inflorescences directly below. I shall later have occasion to return briefly to *P. crassifolium*, as it offers other points of interest.

From my own observations it seems that in those species of *Phoradendron* which possess intercalary cataphylls, the vegetative laterals bear at least as many as the sterile ones found in sequence on the main

axis. In *P. piperoides* there are usually 1–5 pairs on lateral branches (Figs. 3b and 6a) occasionally up to 8 or 9 pairs (UC 142083). I have not as yet seen critical specimens of other types except *P. crassifolium* which has as few as one sterile pair of cataphylls on some vegetative laterals, as many as 4 or 5 on others. There are many species, of course, which have one (e.g. *P. liga, P. herbert-smithii, P. martianum*) or two (e.g. *P. quadrangulare*) pairs of cataphylls on lateral shoots, and none on the main axis.

It would indeed be very interesting to know at what age these types of heterophylly first appear. I suspect intercalary cataphylls to be absent from the juvenile aspect of plants which at maturity have them. This is only a suggestion, however, and only those botanists acquainted with the species in the field are in a position to supply such data. This also applies to that group of *Phoradendra* with a dichasial ("dichotomous") habit: from mature branches it is impossible to say whether such plants can develop intercalary cataphylls, because the axis terminates in an inflorescence. Only in young plants can be seen whether or not these cataphylls are a feature of the species.

Scale-leaves Reduction of leaf size is a very common feature in parasitic flowering plants. We see it conspicuously in *Cuscuta*, in *Cassytha*, in Balanophoraceae, Orobanchaceae, Lennoaceae, Rafflesi-aceae. It is rather rare in Santalaceae (*Chorethrum, Daenikera, Phacellaris*) and among the parasitic members of Scrophulariaceae (*Lathraea*), and
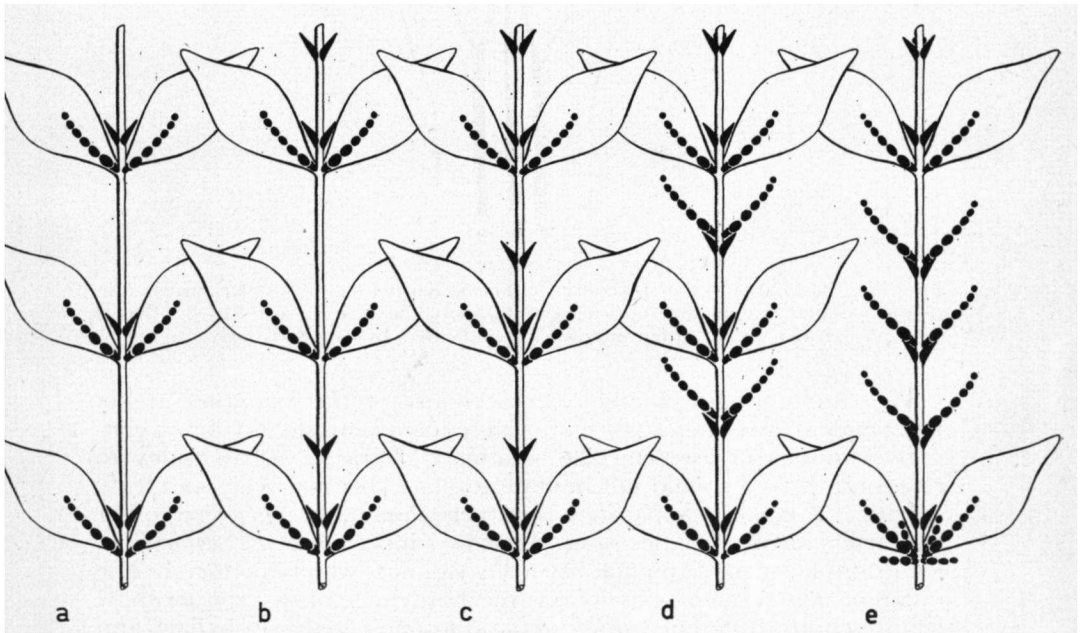

Fig. 15. Heterophylly and inflorescence position. Cataphylls and inflorescences are drawn in black. — a. Trelease's "Percurrentes" (cf. *P. piperoides*, Fig. 3b). b. *P. paradoxum.* — c. *P. fendlerianum, P. fanshawei,* and possibly *P. jenmanii.* — d. *P. craspedophyllum.* — e. *P. crassifolium* (cf. Fig. 14).

is known from Myzodendraceae in *Myzodendron* subgenus *Gymnophyton*. In Loranthaceae some genera are completely squamate (*Arceuthobium*, *Eubrachion*, and *Korthalsella*). Others have one or very few scale-leaved species (*Phrygilanthus aphyllus; Viscum minimum, V. articulatum, V. capense*). *Phoradendron* also has several squamate species, and *Dendrophthora* seems predominantly scale-leaved.
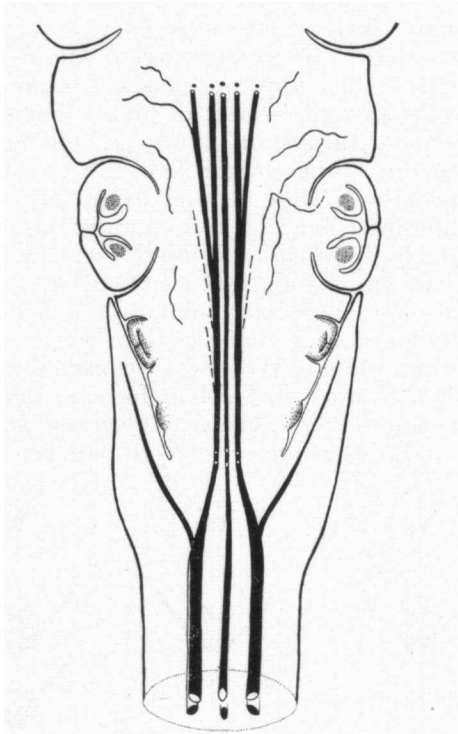
Fig. 16. Basal area of the spike of *D. biserrula*, Kuijt 1532 (× 8). Reconstruction of the vascular system and optical section. Only the nearest series of bundles is drawn fully; other bundles are indicated by cut ends only.

We cannot doubt, therefore, that many of the examples are of independent evolutionary origin. Consequently we should be exceedingly cautious in assessing the squamate character as an index to relationship, and should not hesitate to place together scaly and leafy species, or make a separation between squamate species, if other characters justify such decisions. Trelease's inclusion of *P. californicum*, for example, in his Aphyllae is in my opinion wholly artificial. The inflorescence, stamens, phyllotaxy and host range of this species show features quite different from comparable ones in the Aphyllae, and indeed in the Pauciflorae. Whatever the true position of *P. californicum* be, it can scarcely be where Trelease places it on the basis of its squamate habit.

There are, as far as I know, four species of *Phoradendron* with scale leaves: *P. californicum*, *P. juniperinum* (incl. *P. ligatum* and *P. libocedri*) *P. fragile*, and *P. tunaeforme*. Trelease places the first two in the Boreales; the last two in the Aequatoriales as they possess cataphylls on both lateral and percurrent axes. The fact that the cataphylls in these two species are fused and tubular like those of many leafy species seems to imply that the development of cataphylls and that of scale leaves are separate phenomena.

In the genus *Dendrophthora* there are a large number of squamate species. Of these may be mentioned *D. biserrula*, *D. domingensis*, *D. opuntioides*, *D. gracilis*, *D. cupressoides*, *D. squamigera*.

Perhaps the more interesting species, however, are those which have greatly reduced foliage leaves still larger than scale leaves. It is possible that in such species the same evolutionary processes are still at work which in others have already achieved the squamate habit. In some of these "intermediate" species we may discover a gradient
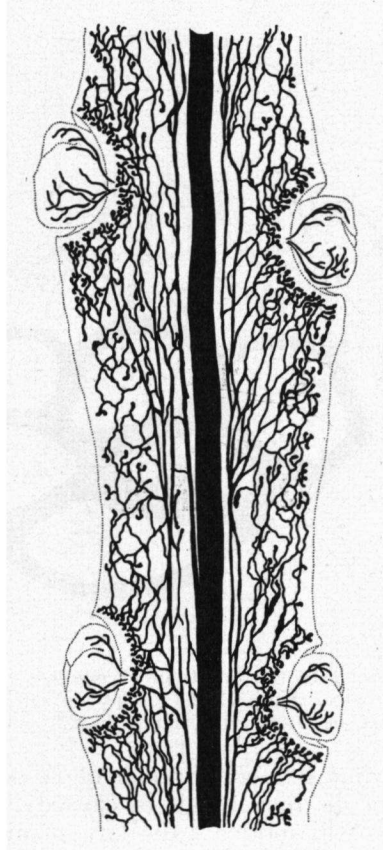
Fig. 17.   Lateral view of cleared section of fertile internode of *D. flagelliformis*, Fuertes 374, U (× 8).
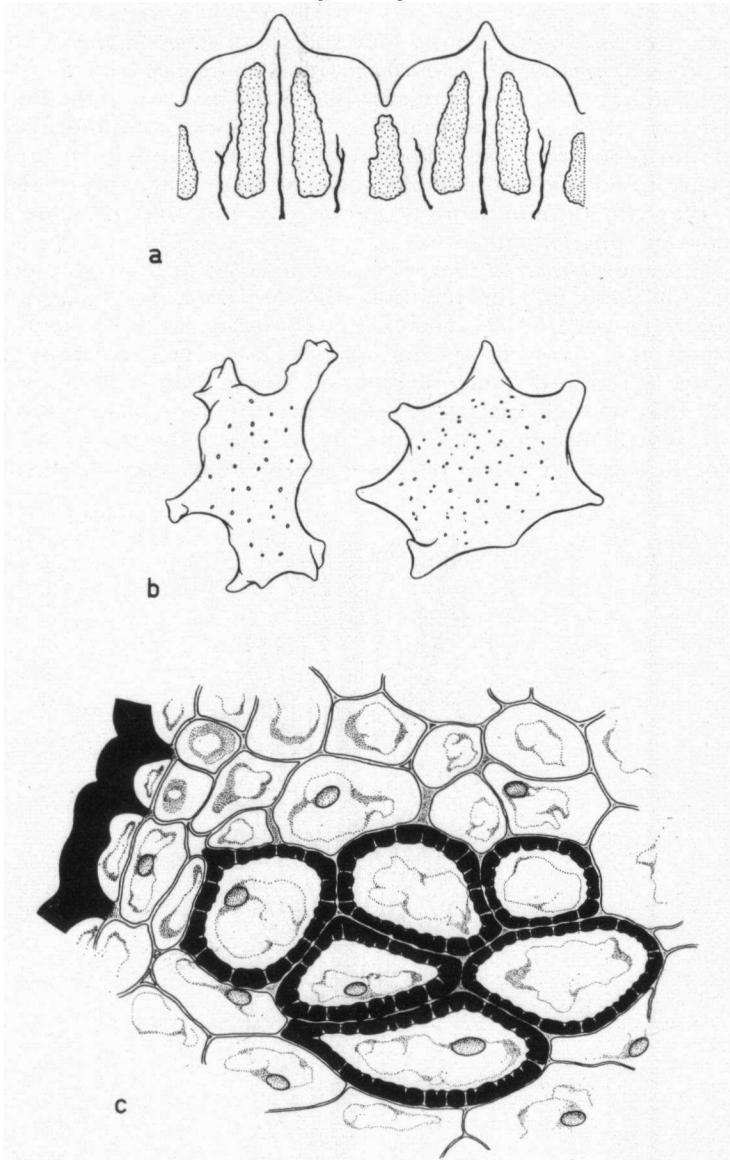
Fig. 18.   a. Sclereid fields in the bracts of *P. piperoides* (× 15). — b. Sclereids from the spike of *D. biserrula*, Kuijt 1532 (× 150). — c. Cluster of sclereids in the spike of *D. biserrula*, Kuijt 1532 (× 150).

in leaf size. Following a lateral branch of *D. paucifolia* (Fig. 5) we find after the prophylls first a pair of cataphylls. The next pair of appendages, however, is suddenly the largest on that branch. From there on to the terminal inflorescence there is a steady decline in the size of leaves until the last ones are quite scale-like. The same pattern

holds true for *D. biseriata*. Now it is interesting that a very closely related species, *D. biserrula*, seems to be in an even later stage of leaf reduction. It is commonly known as a completely squamate species. When one has the opportunity to inspect a young plant (Fig. 4a), however, the same gradient of leaf size is found for the base of a plant of this species, as that outlined for a branch of *D. paucifolia*. The lowest leaves are very small (cotyledons do not persist). Above these small scales, expanded though small foliage leaves suddenly appear, becoming smaller at the higher nodes until only scale leaves remain.

It again appears, therefore, that the development of cataphylls and reduction of foliage leaves to scale-leaves are two distinct evolutionary processes. The former seems to progress in an acropetal, the latter in a basipetal direction in the plants just mentioned. Indeed, the fact that many species have both cataphylls and foliage leaves shows the independence of the two processes. The circumscription of the concepts cataphyll and scale leaf on pp. 508–509 will now perhaps be better appreciated.

Entirely different patterns of heterophylly are, however, possible. In *D. grisebachii* we find series of 1–4 pairs of fully expanded foliage leaves near the base of the plant, and sometimes also higher up, immediately below the terminal inflorescence. These upper foliage leaves are separated by scale leaves from the foliage leaves at the base of the plant. No gradient occurs here. This is also true for *D. flagelliformis* where the base of the plant has large leaves which are suddenly, without transitional forms, replaced by scale leaves when we approach the inflorescences.

Any attempt to ascribe function to the cataphylls of the Phoradendreae appears doomed to failure by the very multiplicity these organs demonstrate in prominence, position, and frequency. It is easy to say that in *P. crassifolium* each series of cataphylls and that in *D. costaricensis* the basal cataphylls of lateral branches create a certain amount of space in which the inflorescences can better fulfill their function. At least some species of *Phoradendron* are entomophilous and a more prominent position of the spikes could amount to a real advantage. But what possible function could the majority of cataphylls have, supported as they are by internodes so short as to not provide any extra space whatsoever? Especially in such a case as *D. poeppigii*, a leafless species, the basal cataphylls could not be of any significance in this regard. The same seemingly inconsequential consistency and variation are to be seen in the petal positions of the flowers of these genera, a topic to be discussed in the next section.

II. ORGANOGRAPHY OF THE INFLORESCENCE

The inflorescence of the Phoradendreae is basically a succession of internodes with scale-like leaves arranged decussately. One or more terminal internodes are fertile; at least one, frequently several internodes above the prophylls are sterile. Flowers are arranged in "flower areas" each topped by a single apical flower above each scale-leaf of

the fertile internodes, not truly axillary thus but rather distributed along the internode. The flowers are completely sessile in cup- or collar-like outgrowths on the axis of the inflorescence.

EICHLER (1868) recognized three general types of inflorescences in *Phoradendron* which were delimited on the basis of the seriation of flowers. The first, the "2 × 2 type", had on one side of each fertile internode two series of flowers topped by a single, apical flower which stood exactly above the subtending bract. In the second, the "2 × 3 type", the apical flower was followed by a median, longitudinal series of flowers occupying the space between the two lateral series. In Eichler's third category we find elaborations of the second type into the "2 × 5, 2 × 7, and 2 × 9 types", which can be visualized by adding two, four and six additional lateral series to the three series of the previous ("2 × 3") type. These three categories are used by Eichler as aids to description, not as natural taxonomic groups. His remarks on the inflorescence of *Dendrophthora* are very incomplete.

VAN TIEGHEM (1896b), on the contrary, made a taxonomic sub-division of each of the two genera on the basis of inflorescence morphology alone. In *Phoradendron* he recognized four sections. Section *Hexanthum* consists of species having only six flowers per fertile internode, one pistillate for each of the four lateral series, and one apical, median, staminate flower above each of the two bracts. Section *Tetrastichum* conforms to the remainder of the "2 × 2 type" of Eichler (to whom van Tieghem does not refer), with lateral series having more than one flower, except that the apical flowers are said to be staminate, the lateral ones pistillate. In section *Hexastichum* we find those species having three series of flowers above each bract, staminate and pistillate flowers being present in each series. Finally, section *Polystichum* contains those species having more than three series above each bract; this section can thus be equated to Eichler's third type.

A similar subdivision was proposed for *Dendrophthora*. Section *Diantha* unites all species having not more than two flowers, one above each bract, per internode. In section *Disira* this one flower per bract is followed by a single series of varying extent, each series containing staminate and pistillate flowers. The plants of section *Hexasira* develop three series of flowers per bract, each series having several flowers. In those cases where sexual dimorphism of inflorescences occurs, the staminate inflorescence, having the greater number of flowers, determines taxonomic position. In addition the new genus *Distichella* was segregated, differing from *Dendrophthora* in being distichous, and containing the species *D. opuntioides* and *D. gracilis*.

I shall not waste many words on Van Tieghem's taxonomic contentions; indeed URBAN (1896) has already pointed out the unnaturalness of such groups. When so much morphological variation is subordinated to so few characters the resulting taxonomic system can only be artificial and unworkable.

Morphologically, Eichler's three categories are fairly useful. Eichler was, however, poorly acquainted with North American species;

furthermore, the inflorescences of *Dendrophthora* are not incorporated, or at most fit very awkwardly into his scheme. Van Tieghem's sections are, in my opinion, as bad morphologically as taxonomically. Furthermore, they are based on inaccurate observations and/or incomplete material. For example, the facts of sex distribution along a fertile internode which are implied for *P. latifolium* (= *P. piperoides*) in the section *Tetrastichum* are demonstrably incomplete or wrong; although they may possibly hold for other species. I have little choice, therefore, but group the inflorescences of *Dendrophthora* and *Phoradendron* in a manner which I consider more logical. Like Eichler, I do not wish such a scheme to be primarily a taxonomic one.

I wish to point out first a few features which are *not* taken into account in the classification below. The first of these are the number of fertile internodes per spike, and the number of flowers per series. These two features I know to vary greatly within some species, or differ between some closely related species and should, on the whole, perhaps not be taken too seriously. The distribution of staminate and pistillate flowers along an internode may be a constant character at the species level; but it would be difficult to incorporate such data in a general typology, not in the least because they are difficult to ascertain from herbarium material. In fact, the inflorescence types outlined below should not be adhered to rigidly, as different types are sometimes present on one inflorescence.

Type 1a. Apical flower followed by 2 lateral series; median series absent. By far the most common type in *Phoradendron* especially in the Aequatoriales; in the Boreales known only from *P. californicum*. In *Dendrophthora* it is found regularly only in *D. aequatoris* [1]. Sometimes found together with the next type, even on the same inflorescence (e.g. *P. tonduzii*). Where flower position is consistent, the apical flower is $^2/_1$, all flowers of the lateral series $^1/_2$ [2]). This is true for *P. demerarae* (Jenman 2546); uniformly in *P. racemosum*; in *P. anceps* (U 031029); in *P. tonduzii* when the median series is wanting; and in *D. aequatoris* (K). In others, however, though the apical flower always seems to be $^2/_1$, the lateral flowers may be quite irregular in position. This applies especially to the plants of *P. piperoides* which I have seen at Puerto Limón, Costa Rica. Here lateral flowers, though often $^1/_2$, are also frequently bipartite, and then usually $^1/_1$ (Figs. 6b and c). The regularity which EICHLER (1868, see Tab. 31, ser. I, Fig. 1) implies for *P. piperoides* (*P. latifolium*) in any case is not evident in all plants of this species.

[1]   I seriously doubt the appropriateness of Trelease's assignment (without any discussion) of this species to *Dendrophthora*. Indeed, URBAN (1897) described it as *Phoradendron aequatoris*, and clearly spoke of a bilocular anther dehiscent by two pores.

[2]   I am following EICHLER (1868) in the denotation of flower position. As a rule flowers are tripartite. When one perianth member of a flower is distal on the internode and the two others are inserted below, the flower position is said to be $^1/_2$ (e.g. the apical flower of Fig. 7c). When the opposite occurs we speak of a ⚏ position (e.g. the apical flower of Fig. 7b).

It needs to be pointed out here that an inflorescence showing only three flowers (one median and two lateral) per bract cannot automatically be placed in this category. It is the position of the fourth and following flowers which is significant here. Where, as in the staminate spike of *P. juniperinum,* the fourth flower has a median position the inflorescence clearly belongs to the next, the 1b type. In *P. californicum* fertile internodes having four or more flowers per bract are exceedingly rare; and for this reason a rather outstanding feature of this species has remained undescribed. Where we do find a luxuriantly developed plant (e.g., Monnet 1128, Remy s.n., staminate, P; and Alexander, Kellogg and Carter 2002, pistillate, K), the fourth and later flowers of each bract are located in the *lateral* series. *P. californicum,* therefore, apparently alone in the Boreales, has a 1a inflorescence.

Type 1b. Above each bract flowers are inserted in three series, one median and two lateral. This type is found predominantly in the Boreales, e.g. in all species north of the Mexican border with the exception of *P. californicum.* It is also very common in the Aequatoriales. In addition, I have seen it in the following species of *Dendrophthora: D. costaricensis* (Figs. 8b and d), *D. buxifolia* (staminate), *D. chryso-stachya, D. clavata, D. elliptica, D. epiviscum,* and *D. subtrinervis.*

Flower position in this type shows some interesting features some of which may here be recorded. In the staminate inflorescence of *P. pauciflorum* the apical flower is $^2/_1$, all others rather uniformly $^1/_2$ (Figs. 10c and d). The pistillate inflorescence of the same species bears only one flower per bract, and this flower strangely enough usually has the $^1/_2$ position (Fig. 2b). The (bisexual) spike of *D. costaricensis* (Fig. 8b) behaves like the staminate one of *P. pauciflorum,* though with occasional irregularities. In *P. tonduzii* (staminate), where usually three series are found per bract, all flowers are $^1/_2$ where the median series reaches up to the apical flower. It frequently happens, however, that the first one or more median flowers following the apical flower are absent, the median series being resumed below. In such cases the terminal flower commonly is $^2/_1$, all others $^1/_2$; in other identical situations all flowers are $^1/_2$ (Figs. 7b and 7c). The inversion of the apical flower is reasonably consistent, however, and was already noted by EICHLER (1868).

In some species, especially in the larger Boreales (e.g. *P. macro-phyllum,* Fig. 10a), the three series of each bract quickly loose their identity: the basic triplet pattern is not repeated regularly, flowers occur at irregular positions until no series can be recognized at all. The two flower areas of an internode may even coalesce below, flowers evidently being produced by a continuous intercalary meristematic ring at the base of the internode. The position of even the apical flowers of such spikes seems to be quite irregular.

Type 1c. This is really a modification of the previous type, 2, 4, or 6 additional lateral series per bract being added. I have seen

very few of such inflorescences and Eichler mentions only *P. tomentosum* and *D. clavata* as having 5 series per bract.

In the *D. clavata* specimens at Kew (Hartweg 1044, Triana 2780, 4584, Holton 658, Tracey 119, 470, Balls 5730, Fendler 1114) I have seen only the 1b type, though with occasional irregularities. The type is not otherwise known from *Dendrophthora*. In *P. calyculatum* (staminate), 9 series are originally present above each bract (Fig. 11b). From the beginning both flower areas are coalesced and not separable. The series retain their identity for some distance downwards, but eventually become confused. Other species included in this type are *P. falcatum* and *P. robinsonii*. In the latter species (Pringle 9467, K) the lower flowers of an internode seem to be arranged in helices, a phenomenon also faintly discernable in *P. calyculatum* (Fig. 7b) and *P. macrophyllum* (Fig. 10a). Again, in these species there seems to be a continuous ring of florigenic meristem at the base of such internodes. Flower position in *P. calyculatum* is at first regularly $^1/_2$ but becomes irregular when seriation does. *P. tomentosum* and *D. clavata* (both 5 series per bract) are shown as being $^1/_2$ throughout in the Flora Brasiliensis, but I have not seen any material of *P. tomentosum*. In the *D. clavata* specimens cited above flower position was frequently irregular but otherwise $^1/_2$.

Type 2a. Flowers in a single median series only; therefore two series per internode. This is perhaps the most common type in *Dendrophthora* (e.g. Fig. 4b). It is not known from *Phoradendron*. Only in *P. jenmanii* (Ayliffe 14320, K) the inflorescence sometimes approaches this type. Often there are only 2 flowers of the basic triplet pattern in this species, the second flower apparently "taking advantage" of the absence of the third, and being developed towards a more median position, and sometimes directly below the apical flower. There is, however, so much variation in these features in *P. jenmanii* that the species cannot truly be accepted in this category.

Flower position in this type shows a remarkable consistency: only the $^1/_2$ position is found. I have seen no exceptions to this rule.

In very large staminate inflorescences of *D. domingensis* (Fuertes 1857, U) and *D. remotiflora* (v. Türckheim 2916, U) this median series sometimes proliferates laterally somewhat at the very base of the internode, so that a third or even a fourth series develops. Occasionally these additional series are in an intermedian position as in type 2c (see also below).

Type 2b. This type is really a unique modification of 2a, to my knowledge found only in *D. ternata*. Again, a single median series is present; but instead of being decussate the bracts (as well as the foliage leaves) occur in alternating whorls of three. There are therefore three series of flowers per internode. All flowers are $^1/_2$ (Fig. 9).

Type 2c. Flowers in four series per internode. One median series is found above each bract; in addition, there is one series above each sinus, or line of fusion, of the bracts. The latter series we may refer

to as *intermedian series* (Fig. 7d). Strangely enough these intermedian series sometimes begin at a higher point on the internode than the median one, and also stop earlier. Flower position is $^1/_2$ throughout (Fig. 7d). I know this unusual type regularly only from two closely allied species of *Dendrophthora*, *D. sessilifolia* and *D. tetrastachya*.

There are species of *Phoradendron* which at first glance seem to belong in this category. In *P. platycaulon*, for instance, only three flowers develop per bract, one flower in each of three series. The apical flower is staminate and falls away very early. When the two other flowers (or four per internode) mature into berries, the scar and shallow cup of the apical flower is almost completely obliterated (Fig. 7a) and the inflorescence appears truly tetrastichous. On closer examination it can be seen, however, that these berries are in a lateral and not in a median or intermedian position.

It must be admitted that some of URBAN's (1896, pp. 284–285) remarks are disagreeable to the above typology. For a number of species Urban here describes irregularities which I have not seen, or at least not to the same degree. I have spoken of lateral proliferation in *D. domingensis* and *D. remotiflora* under type 2a. Urban reports the same for *D. biserrula* and *D. squamigera*, and even more conspicuously for *D. lindeniana*, *D. gracilis*, and *D. opuntioides*. Similar irregularities are cited for *D. buxifolia*, *D. chrysostachya*, *D. elliptica*, and others. I have seen lateral proliferations of this sort in *D. gracilis* (collector illegible, K) in *D. opuntioides* (Nicholl 55, K); but I have not seen the aberrant situations in *D. lindeniana* (Fendler 1113, K), or in any species with a 1b inflorescence. I wish to put on record a few collections of the latter type where, in contrast to Urban's observations, I have seen no irregularities: *D. buxifolia* (Wright 220, 221, p.p., K), *D. epiviscum* (Wright 221 p.p., K), *D. chrysostachya* (Lechler 1927, Balls 7265, K), *D. elliptica* (Gardner 437, 5727, Glaziou 3642, 6894, 8726, 17023, K). Among these aberrant forms Urban also lists *D. sessilifolia*, which I have placed under type 2b because of the regular intermedian series (Wright s.n., 1301, K). To what extent teratology here plays a role cannot as yet be decided. I suspect, however, that most of these irregularities are comparable to the ones discussed under type 1b.

Sex distribution on inflorescences

The identification of staminate or pistillate flowers from herbarium material is usually very difficult, if not impossible. Not only the small size of both flowers and anthers, but also the occurrence of prominent vestigial gynoecia make sex determination difficult unless fresh or preserved inflorescences are at hand. My statements on this topic are therefore partly based on indications in the literature which may not always prove entirely reliable; or the original author may have underestimated variability in this respect. Field observations can add much important information here.

There are many species, first of all, which exhibit a strictly dioecious distribution. This dioeciousness does not correspond with any known

taxonomic boundaries. It is true that all of Trelease's Boreales are dioecious; but such species are also known from more southerly areas, in the Aequatoriales (according to Trelease, *P. wattii* is dioecious), and also in some species of *Dendrophthora* (e.g. *D. domingensis, D. opuntioides*).

Both staminate and pistillate spikes sometimes grow on the same plant. An example of this is *D. clavata*.

Bisexual spikes are present in both the Aequatoriales and in *Dendrophthora*. Within a single spike there may be a great constancy in the positions of staminate and pistillate flowers. In the *Phoradendron* cited by Trelease under *P. polygynum* (Fendler 1104) the lowest fertile internode bears staminate flowers only, all others pistillate ones. A similarity is seen in those inflorescences of *D. clavata*, which have one staminate and one pistillate internode, the latter being terminal. *D. clavata* appears to be unique in having such bisexual as well as completely unisexual spikes of each sex, even on the same plant (Hartweg 1044, K). KARSTEN (1859) claims that the apical flower above each bract of his *P. polygynum* is staminate, all others pistillate. In *P. platycaulon* (Fig. 7a) and others a similar pattern is present (see under inflorescence Type 2c.). *D. costaricensis* has not one, but three staminate flowers at the apex; strangely enough the oldest pistillate flower just below opens before the apical staminate flower on the same internode. In other species yet, such as *D. biserrula*, the lowest flowers are staminate, the upper ones pistillate.

Unisexual spikes can usually be easily distinguished from those of the opposite sex. The staminate spike always bears more flowers per internode, and sometimes more internodes per spike. These features can be seen in almost any of the North American species (*P. pauciflorum*, Figs. 10c and 10d; *P. macrophyllum*, Fig. 10a), but often also in *Dendrophthora*, for example *D. buxifolia, D. opuntioides, D. domingensis*, and *D. constricta*. As far as I am aware the staminate and pistillate spikes always are of the same type, though in the case of pistillate spikes with one flower per bract this can only be inferred.

Inflorescence and flower position

A few words may be said on the position of inflorescences on the plant. The most common situation is that which can be followed in Figs. 12a, 12b, and 13a for *P. pauciflorum*. Here inflorescences replace primary lateral branches, secondary spikes develop in the prophylls of primary ones, etc., in regular succession. Inflorescences of higher than the fourth order (*P. cheirocarpum*) are not known to me. Where intercalary cataphylls are present this regular sequence is interrupted, the lowest of the intercalary cataphylls being sterile in all cases. In a rather large number of species of *Phoradendron* (*P. henslovii*, for example) and in *D. poeppigii* shoots terminate in inflorescences, two lateral branches grow out at the base of such a spike, and a dichasial "compound inflorescence" is obtained (Fig. 11a). Thus a habit results differing from that of *Viscum album* only in the presence of two pairs of cataphylls on each lateral branch.

Indeed, there are many other instances where we may speak of compound inflorescences, where spikes are arranged in a constant pattern and together form a unit. *P. crassifolium* (Fig. 14) certainly is a case in point: the space between two successive pairs of foliage leaves forms a reproductive unit which is recreated annually. It is interesting to see that the spikes of this species are inserted somewhat above the cataphylls, and not truly axillary; perhaps this displacement is comparable to that of flowers by an intercalary meristem to the strange position they occupy in the spikes? Another type of compound inflorescence is very common in *Dendrophthora:* a shoot apex is replaced by a spike, and all laterals, instead of continuing vegetative growth as in the dichasial types mentioned above, also become spikes which arrange themselves symmetrically around the main axis (Fig. 5 for *D. paucifolia;* otherwise found in *D. cupulata, D. epiviscum, D. biserrula, D. flagelliformis,* and many others). In *D. biserrula* this symmetry is carried to such an extent that the two spikes developing from one node frequently are exact mirror-images (Fig. 4b), berries and flowers being present in precisely corresponding positions. Perhaps we can also think of *D. cupressoides* as having compound inflorescences: in this species the apical meristem of the spike simply retains its activity, and soon branches into ordinary vegetative growth (Fig. 8c). In the specimen of *D. tetrastachya* at Leiden (v. Türckheim 3108) several inflorescences have continued into a second inflorescence, built on top of the old one (Fig. 7d). In the Kew specimen of the same collection, however, nothing of the sort is in evidence, so that I do not know whether the Leiden specimen is teratological. To teratology must perhaps also be relegated what TRELEASE (1916) calls *P. piperoides* f. *composita,* with "a somewhat branched spike in some cases". I have not seen the specimen in question (Ule 4800) but I assume it to be of the same type as that of *P. dimidiatum* as illustrated in Fig. 11c. Here a small lateral spike occupies the place of each apical flower (even prophyll-like structures may be seen) of the main inflorescence. Interesting is also the inflorescence of *P. pauciflorum* drawn in Fig. 13b where the apical meristem of the spike has formed a pedicellate flower; and the *D. constricta* spike (Wright 220b, K) which, like the spikes of *D. cupressoides,* continues into a normal vegetative branch.

We may finally return briefly to the question of flower orientation, surely one of the most puzzling features of the Phoradendreae. Eichler, however hesitatingly, has speculated on the underlying causes of the consistencies and differences in the positions of floral segments. The ideas about torsion of flowers prevalent in those days are now, however, known to be without adequate factual basis or at least greatly over-simplified. The causal mechanism of phyllotaxy is nevertheless a matter of continuing controversy (WARDLAW, 1952), though experimental work is unearthing interesting new facts.

It must be remembered, however, that the flowers of the Phoradendreae originate under conditions quite different from those of subapically formed organs. Most importantly, these flowers are traceable, not to an *apical* meristem, but to an *intercalary* one. All

except perhaps the apical flowers are formed just above the *mature scale leaf*. Which of the surrounding organs, whether bracts or older flowers, determines flower orientation remains a matter of conjecture. Even more puzzling is the variable position of the apical flower of *P. tonduzii;* for here it often appears as if the apical flower by its position ($^1/_2$ or $^2/_1$) determines the presence or absence, respectively, of the next few flowers of the median series. The apical flower in *P. juniperinum* and *P. pauciflorum* (which also have 1b inflorescences) is, on the contrary, of a $^2/_1$ position. When such discrepancy is found between two species having the same type of inflorescence we can scarcely make any generalizations as to the dynamics of flower position. Indeed, a more detailed study of the origin of flowers is needed before any hypothesis can be constructed. We shall have to know, for example, whether in a $^1/_2$ flower the apical perianth member is initiated before the others, or all three simultaneously. Until then we can do no more than draw a few general conclusions, though admitting the existence of exceptions:

1. a single median or intermedian series has flowers of a $^1/_2$ position.
2. in type 1a, the apical flower is most commonly $^2/_1$, those of the lateral series $^1/_2$.
3. if seriation is complete in 1b, all flowers are of the $^1/_2$ position.

These three points may be combined by saying that flower position in general is $^1/_2$, with the exception of the apical flowers of 1a inflorescences which are $^2/_1$.

4. there seems to be a necessary relation between regularity of seriation and regularity of flower position: if seriation deteriorates, the position of floral segments also becomes irregular.
5. the dominant positional effect perhaps emanates from the flower immediately above the one under consideration. This is indicated by the constancy of flower position in lateral series whether a median series is present or not; and by the apparent relation discussed under 4.

In the following part of this paper the vascular structure of the inflorescences of Phoradendreae will be discussed, and its evidence brought to bear upon the question of flower position.

III. ANATOMY

The only previous anatomical work relevant to this study is contained in YORK (1913), who described the vascular structure of the inflorescences of *D. gracilis* and *D. opuntioides*. His observations will be introduced below; be it pointed out here, however, that the species studied by him have inflorescences with only a single median floral series (Type 2a). It cannot be surprising, therefore, that those inflorescences which differ greatly from York's species in external morphology are also different anatomically. Indeed, when considering the facts presented in previous pages it will at once be apparent that the remarks of the present section can be little more than exploratory.

I have attempted to study the vascular structure of several types of spikes, and with varying degrees of thoroughness. None of the descriptions below can claim finality or completeness; each represents a reconstruction or interpretation based on sectioned material, or cleared spikes, or both.

The vascular structure of the flowers appears to be rather uniform. The staminate flowers receive from the axial stele a single trace for each perianth segment. This vascular strand branches several times, the ramifications stopping well within the limits of the perianth segment (Fig. 10b). The sessile anther has no visible vascular supply whatsoever, a feature also found in other Viscoideae: *Arceuthobium* (JOHNSON, 1888), *Viscum album* (TUBEUF, 1923), and *Korthalsella* (MEKEL, 1935). The central cushion is also without vasculation.

The pistillate flower, in addition to such a vascular structure has a number of slender strands emerging from the very base of the flower and together forming a sort of spindle which is open towards the floral apex (Fig. 12c). SMITH and SMITH (1943) state that from ten to twelve traces are present in the pedicel of *P. villosum*, but I have not seen any material of this species. In *P. pauciflorum* the inner strands, which probably are of a carpellary origin, are held apart by a collenchymatous cup situated immediately below the ovarian papilla or mamelon. I have not been able to determine the exact origin of the "carpellary" traces, as they become exceedingly slender where the flower connects with the stem. The spindle formed by them delimits the space later occupied by the endosperm and embryo; indeed, these bundles form a conspicuous and beautiful silvery pattern against the dark green background of the endosperm when the seed is mature (this is also true in *Viscum album*: see TUBEUF, 1923, Fig. 64). Irregularly branched sclereids are present in a halo-like zone in the perianth of the pistillate flower only, but are absent from the remainder of the spikes of *P. pauciflorum*.

In other species of the Phoradendreae, however, sclereids are very abundant, and indeed can render observation of the vascular structure impossible in some cleared material, as in *D. biserrula*. In this species, as well as in *D. costaricensis*, a cortical zone about midway between the heavily cutinized epidermis and the stele contains a very great number of sclereids. They are somewhat branched and lobed, show an abundance of pits, and usually occur in small groups (Fig. 18b and c). They appear to retain a living cytoplasm and normal nucleus long after their secondary walls are heavily lignified in *D. biserrula*. In *P. piperoides* the clusters of sclereids are very large in the flower-bearing parts of the inflorescence. In the bracts of the same species sclereids occur in actual *solid fields* between the vascular traces of the bracts (Fig. 18a), each field uniting many scores of sclereids. Sclereids may also develop in the pith, as in *D. biserrula* and *D. costaricensis*.

The stomata, as typical in Loranthaceae, are transversely oriented on the stem. All superficial cells are covered with a thick cuticle. I can add no more details of the non-lignified tissues except that druses are frequent, especially in the outer cortical region of many species. I

have seen fiber-caps on vascular bundles only in the peduncle of *D. biserrula*. The xylem elements vary greatly in length, and have secondary helical thickenings which tend to coalesce in the shorter elements. Evidence of stretched and obliterated elements is to be found especially in the oldest xylem of the base of a fertile internode. Most xylem elements appear to be vessel members with single terminal perforations. In the xylem of *P. californicum* there are short bulging vessel members each of which contains a large druse, a cell-type which is not known to me from any other plant. The vascular bundles are of the collateral type, but sometimes a group of small cells in the position of internal phloem reminds one of the bicollateral bundles known from *Viscum album* (TUBEUF, 1923).

It is now necessary to recapitulate YORK's (1913) work on the vascular anatomy and floral ontogeny in the spikes of *D. opuntioides* and *D. gracilis*. According to him, 6–14 bundles enter the spike from the main axis, these bundles being arranged in a dictyostelic way. There is no interfascicular cambium. The first fertile bracts receive one trace each, leaving the majority of the bundles to enter the lowest fertile internode. Here, as two parallel rows, they run essentially unchanged into the second fertile internode. In the meantime, however, several branches have been given off. From near the base of the internode, the two bundles closest to each bract (thus together four bundles) give rise to traces which ramify somewhat and are said to terminate in the swollen collar which surrounds the flower. These same four bundles supply three traces for each of the two flowers (YORK's Figs. 7 and 8). I have not myself been able to use material of York's species. Nevertheless, I cannot accept his description without question; it makes an altogether too simple impression. Be that as it may, York's description corresponds only partly with my own observations on other species.

The earliest sign of flower development, according to York, is a bulging out of the periblem of the axis some distance above the axil of the fertile bract. The collar now expands rapidly, almost burying the young flower in the axis. "Two cycles of floral segments develop acropetally on the young axis of the flower. The outer consists of three parts, which are the segments of the perianth; while the inner is composed of two segments, the carpels. The perianth completely covers the apex of the floral axis before the carpels have begun to develop. The two carpels arise as distinct primordia, and upon elongating inclose the moundlike apex of the floral axis between them. At this period of development the flower is still sunken in the axis of the spike, and its various parts are clearly distinct from one another. The apical growth of the floral axis is never active, and the outer region, composed of torus and the basal portion of the carpels, now grows rapidly, and thus the axis with the narrow ovarian cavity about it becomes deeply sunken within the torus." (YORK, 1913, p. 97).

Again, I cannot add to or criticize this description. In my own work I have seen young flowers of several stages, but none of these show the acropetal development, or the longitudinal extension of

floral elements while covering the floral apex. Nor have I seen the near-burial of young flowers. Instead, in *D. biserrula*, the embryonic flowers appear more active than the collar. In even the youngest flower with distinct floral elements, the latter were closely appressed and in fact scarcely separable. Is it possible that we are here faced with a unique floral ontogeny through schizogeny (cleavage)? This seems a fantastic suggestion, but we must keep in mind that Loranthaceae are structurally aberrant in many ways. My own work does not allow critical observations, but the question is obviously one of great interest.

It is in any case true that the vascular bundles of the young flower have to be fitted onto a stelar organization which already exists. Even by the time the archesporium becomes recognizable in the staminate flowers of *D. biserrula* (when the flower begins to emerge above the bract) the flower is still without mature xylem elements.

It is perhaps most logical to consider first two species which have the same (2a) inflorescence which York's species had. Both of these species have a fairly large number of flowers per bract. The first, *D. biserrula*, has only a single fertile internode; the second, *D. flagelliformis*, up to a dozen fertile internodes per inflorescence.

The peduncle, or sterile internode, of the spike of *D. biserrula* contains six, but sometimes five or seven vascular strands arranged in a cylinder (Fig. 16). A single trace leads into each bract. Partly because of the varying number of bundles in the peduncle, and partly because of the density of sclereids there, I have not been able to ascertain the exact origin of the bracteal strands. It is certain, however, that they do connect with the stele at that point, and do not run down alongside it independently as York stated for *D. opuntioides* and *D. gracilis*. The percurrent bundles become extremely slender when entering the fertile internode. By this time they have aligned themselves into two series which are approximately parallel, an arrangement which persists and becomes more obvious in older parts. The traces leading into the flowers spring from the outermost bundles of each series. In addition a few small strands radiate out into the areas between the flowers. They do not branch and are difficult to follow because of their irregular course and slenderness. It is possible that these strands correspond to York's "collar traces". Since they are not, in *D. biserrula*, specifically directed towards the collars, this terminology is here inappropriate. Except for the percurrent bundles, no vasculation occurs below the rim of the bracts. Procambial strands diverging from the stele and extending towards the flowers can, however, be distinguished in this region (broken lines).

In the spike of *D. flagelliformis* a rather startlingly different organization prevails. The fertile internodes of this species are frequently flattened in the median plane of the subtending bracts. A portion of a cleared fertile internode is illustrated in Fig. 17. The skeletal system must be thought of as a double series of vascular bundles, one series partly obscured by the nearest. In the central part of the stem two strong percurrent bundles are present. These have only occasional

and irregular connections with the remaining vascular system, and run into the next higher internode. On either side of this central pair of bundles there is a complex and highly irregular reticulum of slender bundles which ramify and anastomose. Some terminate within the spaces of the reticulum, others near the margins of the flattened stem, but always such vein endings are slightly thickened. A conspicuous aggregation of these vein endings may be seen in the floral cup, not only at the floral pedicel, but also in all other areas of the cup, even in its very margin. Because of the extreme slenderness of floral traces I have been unable to establish their precise origin, but I assume the connections are with some of the aggregating bundles of the reticulum. Although the majority of the veinlets below the flower point in its general direction we can obviously not speak of a vascular supply exclusively associated with the flower. The most central part of the reticulum shows a more consistently longitudinal direction. The reticulum is continued well into the following bracts. This, in turn, makes it difficult to discern the course of the bundles in the transition zone of the next internode. Each of the percurrent bundles forks while giving rise to a single median tract for the bract above it. In addition to the resulting four percurrent bundles a few very slender ones of the reticulum pass into the next internode. A fusion of some of the lateral bundles must somehow take place in the transition zone, as a pair of central percurrent bundles again is present in the next internode, and this pair is arranged in a plane at right angles to the corresponding plane of the previous internode.

We find in this species, therefore, a remarkably deviating axial structure which seems to be an elaboration of the more simple situation as seen in *D. biserrula*. It might be mentioned in passing that the stelar concept has little significance in such structures (cf. also *P. californicum*), as a stele can scarcely be delimited. We can only conjecture as to the functional meaning of the reticular aggregation of bundles near the flower. Could the floral cup here in its early stages somehow function as a placenta for the flower?

The fact that these two species are congeneric with *D. costaricensis* would lead one to suppose that this species, although instead of a 2a inflorescence it has a 1b type, might also show a reticular skeleton of some sort. This supposition turns out to be quite incorrect. The vascular structure of the spike of *D. costaricensis* does not appear to be appreciably different from that of the staminate spike of *P. pauciflorum*, which is to be discussed below. A feature which is more fully developed in the former species, however, is the vasculation of the first bracts. Three traces, often branching, supply these organs in *D. costaricensis;* in *P. pauciflorum* this number is usually, but not always, reduced to one median trace only.

Six bundles enter the first fertile internode of the staminate spike in *P. pauciflorum* (Fig. 10e), these being arranged in two parallel series of three each. The central percurrent bundle of each series is the largest. The large median gaps above the axils of the bracts are formed by the departing median bracteal traces below. If any lateral

traces are present in the bracts they emerge from the other four gaps.

In a general way the origin of the vascular supply of the flowers corresponds to the origin of the bracteal bundles. The bundles leading from the median flowers connect to the two bundles delimiting each median gap. The traces leading from lateral flowers combine with these same bundles or with the percurrent bundles, according to the position of the floral segment involved.

The representation in Fig. 10e is, of course, highly diagrammatic, and is in reality rarely materialized. It is fairly common that, instead of six, five or seven bundles enter the fertile internode. The two bundles above each bract frequently fuse at points between two successive median flowers. In such areas a transection of the spike reveals four main bundles, each of the four gaps issuing traces to the lateral flowers in a cruciform overall pattern. Finally, the four terminating bundles occasionally show a very slight, upturned connection with the percurrent ones. It is of some interest that not all traces depart from longitudinal bundles in the usual upward direction: some turn downward slightly, and appear as if welded onto the larger bundles.

In any case, only two large, percurrent bundles are in evidence just below the next bracts. The departing median trace of each bract there divides each percurrent bundle into two, making four in all. However, in the next internode we find six bundles again arranged in two series, but these series at right angles to the corresponding configuration of the internode below. In the nodal area, therefore, a fusion must have taken place reconstituting a pair of percurrent bundles.

The pistillate spike of *P. pauciflorum* bears only one flower per bract. The four non-percurrent traces may fuse into two bundles soon after giving rise to the single bracteal trace, judging from a lateral view (Fig. 12c). There are four bundles discernible in a transection just below the flowers. The floral traces issue from both the median and the percurrent bundles. The latter run to well above the floral pedicles and terminate abruptly just below the aborted apical meristem. The pistillate spike can thus easily be visualized as a simplified version of the staminate one, both externally (reduction in number of flowers) and internally.

In *P. juniperinum* the staminate fertile internode is extremely short, and the floral traces radiate out from just above its base. The skeletal structure is essentially the same as that in *P. pauciflorum*, however, differing only in being greatly condensed. Except for the floral traces and the percurrent bundles which terminate in a rather broad vascular fan below the inflorescence apex, no vascular bundles are visible in the fertile internode.

Although we have already seen that *P. californicum* differs in many details of external morphology from other northern species of *Phoradendron*, it is nevertheless surprising to find its internal structure to be of such a greatly different organization. A central stele of percurrent bundles is again present in the pistillate spike. It is partly obscured,

however, by a rather dense thicket of ramifying slender bundles which appears to extend throughout the cortex, forming a reticular cylinder around the central stele. This reticular cylinder is present also in the basal sterile internode of the spike (perhaps even in normal vegetative internodes?) and reaches from above the subtending bracts into the next bracts. It is visible even in the most distal portion of the spike just below the aborted apex. It ramifies also into the floral cups, but does not there from the aggregates known from *D. legelliformis*. The vein endings are slightly swollen. The entire reticular cylinder can be visualized as a three-dimensional version of the reticulum of *D. flagelliformis*. In cleared spikes one can also detect the more consistently longitudinal direction of the slender interior veins of the reticulum. Floral vasculation appears little different from that seen in other Phoradendreae.

We find thus in the few species here discussed an entirely unsuspected variation in the anatomical composition of the inflorescence. Species which usually have been regarded as closely related (*P. juniperinum*, *P. californicum*) may show great internal differences. On the other hand, a species of one genus may not differ appreciably in this regard from one of the other genus (*P. pauciflorum*, *D. costaricensis*).

We are also disappointed in our hopes to find in the anatomical construction of spikes clues to the dynamics involved in flower orientation. In *P. pauciflorum*, for example, it would be quite simple to make a "workable" model of the vascular structure if all flowers were differently oriented. In short, there appears to be no necessary relation between stelar structure and flower orientation. Here, as in the organographic aspects of this study, the very diversity of structure prohibits general morphogenetic explanations.

IV. CONCLUDING REMARKS

I have frequently referred to the inflorescences of Phoradendreae as *spikes*. This is in accordance with EICHLER's (1868) discussion as well as RICKETT's (1955) recent definition. Eichler regarded the apical flower of a flower area as comparable to a primary lateral axis, the lateral series of the 1a and 1b types to accessory (secondary) laterals. Type 1c can easily be derived from 1b. Both types 2a and 2b fit into Eichler's hypothesis. It must be admitted, however, that inflorescence 2c provides difficulties in this regard, as the intermedian series is neither median nor lateral; it appears to represent an entirely new development.

The only doubt which, in my opinion, can be thrown upon Eichler's thesis is provided by the vascular reticulum seen in different forms in *D. biserrula*, *D. flagelliformis*, and *P. californicum*, to which can be added York's "collar traces" in *D. opuntioides* and *D. gracilis*. Could it be that in reality we are faced with a more complex inflorescence of which these reticular bundles are vestiges? Are the fertile internodes really internodes, or does each flower in reality represent a node? It seems to me that such an hypothesis has little support. Although

the "collar traces" of York are said to supply the collar, there is no such exclusive relation between reticular bundles and floral cups in the species at my disposal. The facts of floral ontogeny (as far as known) and the consistently decussate phyllotaxy within spikes appear to be quite sufficient to discount any such hypothesis. I believe we have before us, in these reticular stelar proliferations, a most convincing example of a case where the vascular structure is anything but conservative. The teratological specimen of *P. dimidiatum* in Fig. 11c also lends support to Eichler's interpretation, as here a lateral axis takes the place of the apical flower, and *is supplied with prophylls*.

The inflorescence of the Phoradendreae is perhaps not as unique as it seems. Eichler already drew attention to the staminate inflorescence of *Gnetum* where the flowers also appear to arise from a ring-like intercalary meristem. VAN TIEGHEM (1896*a*) also refers to the longitudinal seriation of flowers in *Korthalsella* (Viscoideae), where we may think of one median and two lateral series of one flower each per bract. In *Notothixos* (Viscoideae), an inflorescence unit terminates in a fertile internode which has about five flowers per bract, arranged in a typical 2a fashion. To conclude on the basis of such a similarity that *Notothixos* is closely related to Phoradendreae would indeed be incautious, as evolutionary convergencies abound in the Viscoideae (see below).

We can discern in the evolution of these inflorescences, as inferred from structural details, the evolutionary processes of reduction and elaboration in action simultaneously. Surely we must regard the serial flower production and the vascular reticulum as an elaboration upon simpler situations; and just as certainly does heterophylly, and the reduction of the anther to an evascular sessile pollen sac or pair of pollen sacs indicate reduction. To single out reduction phenomena as the main evolutionary processes surely does not apply in the Phoradendreae, as the main tribal characteristic is one of elaboration (i.e. seriation of flowers).

The present work is not intended as a taxonomic study. Nevertheless, it has certain taxonomic implications. The fragmentary nature of my observations, however, precludes even a partial revision of the two genera involved.

Yet it will be advisable, in my opinion, to look at the subgeneric organization of *Phoradendron* in a manner influenced as little as possible by Trelease's treatment. I am convinced that the primary division of the genus into Boreales and Aequatoriales, even if it will turn out to be a natural one, is at least incorrectly or incompletely defined. The northerly squamate species cannot logically be placed in either subdivision, as all their scale leaves could be regarded as cataphylls. Such species as *P. calyculatum* and *P. falcatum* are nearly indistinguishable morphologically except for one pair of basal cataphylls in the latter. If *D. aequatoris* turns out to belong in *Phoradendron* (cf. footnote, p. 545) it will further embarrass the system, as the species is without cataphylls, yet can scarcely be represented as an Ecuadorian member of the Boreales! In *Dendrophthora* there is at least one species (*D. buxifolia*) which may or may not have basal cataphylls, differing in

this regard even within one plant. In *Dendrophthora*, therefore, the occurrence of cataphylls does not appear to follow lines of affinity.

In his lower infrageneric organization Trelease has made a chaotic confusion between artificial keys and natural groups. He obviously regards these lower divisions as taxa, since he provides each with a formal latin name as well as with a diagnosis, and even with geographical data. Yet I think except for later nomenclatural problems these subdivisions should be regarded as nothing but portions of an artificial key. An example will support my argument. *P. jenmanii* is described (p. 85) as a member of "20.Rigidae". Yet we find it again in the key to "F. Continuae, III. Percurrentes" (p. 143) and even for a third time in the key to "IV. Dichotomae" (p. 156). In a similar way *P. obliquum* and *P. laxiflorum* can be discovered in the keys of three different subdivisions. Surely such groups cannot be held to be natural units! It is unfortunate that, because of the formal diagnosis, future nomenclature is chained to Trelease's names of these subdivisions; but taxonomic concepts should not be led astray by them.

In particular, this study has pointed out the necessity of removing *P. californicum* from the position given to it by Trelease. It differs from its sympatric species in details of phyllotaxy, inflorescence type, inflorescence anatomy, and ecological and host preferences which, taken together, make a reconsideration of its taxonomic position inevitable. Such a reconsideration is futile, however, until the entire genus can be critically revised. The position of *P. californicum* has important nomenclatural implications as it is the type species of *Phoradendron*.

If any feature is conspicuous in the previous pages it surely is the occurrence of evolutionary parallellisms, or convergent evolution, in the structure of Phoradendreae. It is one of the major aspects of orthodox taxonomy to weigh such apparently parallel developments, and to decide which coincides with natural taxonomic boundaries. It is perhaps useful, therefore, to list the most conspicuous convergences in the Phoradendreae:

1. the occurrence of basal cataphylls
2. the 1b type of inflorescence
3. dioecious and monoecious species are present in both genera
4. the position of the first pair of appendages following, and in relation to the position of the prophylls of lateral axes
5. the squamate habit
6. dichasial branching
7. reticular stelar elaborations in the spike.

In the face of these convergences which appear not to be related to taxonomic lines of affinity one naturally is reminded of the slightness of the character which distinguishes *Phoradendron* from *Dendrophthora*, namely the bilocular as contrasted to the unilocular anther. It could

well be that this distinction will one day have to be abandoned; that entirely new boundaries will have to be established in accordance with several of the points listed above and that, in turn, the staminal features will come to be regarded as a convergent evolutionary character which has arisen independently in more than one group.

SUMMARY

Heterophylly is frequent in *Dendrophthora* and *Phoradendron*, and may take many forms. The concepts prophyll, cataphyll, and scale-leaf are briefly discussed and defined as to usage in the Phoradendreae. Various morphological details of patterns of heterophylly, flower orientation and seriation, fusion of prophylls, phyllotaxy, sex distribution and inflorescence position are traced as far as the available material permits. A typology of inflorescences in these two genera is proposed, based on flower seriation.

Anatomical observations on a few species of both genera have revealed striking and unsuspected structural differences between the inflorescences of some seemingly related species, but also similarities which cross the intergeneric boundary. The discovery of "extra-stelar" vascular proliferations in some species of both genera is of particular interest.

ACKNOWLEDGEMENTS

LIST OF PHORADENDREAE REFERRED TO IN THE TEXT
(those illustrated provided with *)

DENDROPHTHORA

D. aequatoris (Urb.) Trel.
D. biseriata Urb.
D. biserrula Eichl.*
D. buxifolia (Lam.) Eichl.
D. chrysostachya (Presl) Urb.
D. clavata (Benth.) Urb.
D. constricta (Griseb.) Eichl.
D. costaricensis Urb.*
D. cupressoides (Macf.) Eichl.*
D. cupulata (DC) Eichl.
D. danceri (v. Tiegh.) Krug Urb.
D. domingensis (Spreng.) Eichl.
D. elliptica (Gardn.) Krug Urb.
D. epiviscum (Griseb.) Eichl.
D. flagelliformis (Lam.) Krug Urb.*

D. glauca (Griseb.) Eichl.
D. gracilis (DC) Eichl.
D. grisebachii Eichl.
D. lindeniana v. Tiegh.
D. nipensis Urb.*
D. opuntioides (L.) Eichl.
D. paucifolia (Rusby) Kuijt,
                    comb. nov.[1])*
D. poeppigii v. Tiegh.*
D. remotiflora Urb.*
D. sessilifolia (Griseb.) Krug Urb.
D. squamigera (Benth.) Kuntze
D. subtrinervis Urb.
D. ternata Urb.*
D. tetrastachya (Griseb.) Urb.*

PHORADENDRON

P. aequatoris Urb.
P. anceps (Spreng.) Gomez de la Maza
P. aureum Trel.
P. bolleanum (Seem.) Eichl.
P. brachystachyum (DC) Trel.
P. californicum Nutt.
P. calyculatum Trel.*
P. cheirocarpum Trel.
P. craspedophyllum Eichl.*
P. crassifolium (Pohl ex DC) Eichl.*
P. demerarae Trel.
P. densum Torr. ex Trel.
P. diguetii v. Tiegh.
P. dimidiatum (Miq.) Eichl.*
P. falcatum Eichl.
P. fanshawei Maguire
P. fendlerianum Eichl.*
P. flavescens = *serotinum**
P. fragile Urb.
P. galeottii Trel.
P. globuliferum Trel.
P. henslovii (Hook. f.) Robinson*
P. herbert-smithii Trel.
P. jenmanii Trel.*
P. juniperinum Engelm.*
P. laxiflorum Ule
P. libocedri cf. *juniperinum*

P. liga (Gillies) Eichl.
P. ligatum cf. *juniperinum*
P. macrophyllum (Engelm.) Cocker.*
P. martianum Trel.
P. minutifol'ium Urb.
P. obliquum (Presl.) Eichl.
P. paradoxum Urb.*
P. pauciflorum Torr.*
P. paucifolium = *Dendrophthora*
P. piperoides (HBK) Trel.*
P. platycaulon Eichl.*
P. polygynum (Karst.) Eichl.
P. quadrangulare (HBK) Krug Urb.
P. racemosum (Aubl.) Northrop
P. robinsonii Urb.
P. scaberrimum Trel.
P. serotinum (Raf.) M. C. Johnston*
P. surinamense Pulle
P. tlacolulense Loes.
P. tomentosum (DC) Gray
P. tonduzii Trel.*
P. tunaeforme (DC) Eichl.
P. uspantanum Trel.
P. velutinum (DC) Trel.
P. villosum (Nutt.) Engelm.
P. wattii Krug Urb.

[1]) *Phoradendron paucifolium* Rusby, Bull. N.Y. Bot. Club **6**: 510. 1910. This recombination has apparently never been made. The isotype at UC (WILLIAMS, 1530) shows it to be closely related to *D. squamigera*, and I therefore do not hesitate to make the transfer although I have not seen the anthers (cf. Fig. 5).

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