

**A NOTE ON HETEROPHYLLY AND BRANCHING PATTERNS
IN THE AMYEMA COMPLEX (LORANTHACEAE)**

JOB KUIJT

University of Lethbridge, Canada

SUMMARY

Attention is drawn to the unusual distribution of flowers and inflorescences in a number of species, and to certain peculiarities of branching and phyllotaxy. The latter are explained by a heterophylly which so far has escaped notice, involving the formation and early disappearance of a pair of minute intercalary cataphylls. A similar branching pattern and flower distribution is evident in *Helicanthes*.

The genus *Amyema* and its nearest relatives undoubtedly constitute the most difficult complex of *Loranthaceae* in the Old World, especially with regard to generic circumscription. Much difference of opinion has existed in this latter regard. Ignoring the eight or nine additional genera proposed, mostly by the prolific creator of Loranthaceous generic names Van Tieghem, the two most important workers dealing with the complex have been Danser (1931, 1933) and Barlow (1966, 1974). Danser regarded the genera *Dicymanthes*, *Diplatia*, *Distrianthes*, *Tetradyas*, *Papuanthes*, *Rhizomonanthes* and *Sogerianthe* as 'extreme forms of the polymorphous genus *Amyema*'. He stressed the need, however, for more detailed investigations of several of these genera to achieve both more reliable generic limits and a more accurate placement in the system of *Loranthaceae*. Barlow's work has followed Danser in these views generally although *Dicymanthes* and *Rhizomonanthes* are not maintained as separate genera (Barlow 1974; the latter genus was nomenclaturally apparently overlooked by Barlow). An infrageneric organization for *Amyema* has not, to my knowledge, been proposed. *Amyema* even in the narrow sense is an exceedingly diverse genus in its inflorescence structure, showing several types which are unique in *Loranthaceae* as a whole. A discussion of these types will follow at a later date within the context of an inflorescence survey of *Loranthaceae* generally.

One of the striking morphological features of *Amyema* lies in the fact that, in the great majority of species, the inflorescences emerge not merely in the axils of leafy organs but rather in a narrow, transverse floriferous zone often completely encircling the stem and including the axillary region of the foliage leaves. In other words, inflorescences on a stem may be found (often profusely, especially on older wood) between the members of a leaf pair. Little attention has been paid to this peculiar feature, which also constitutes an anatomical curiosity in that the inflorescences appear to develop endogenously. The extreme expressions of such inflorescence proliferation are found in those species (*Dicymanthes suluana* Danser and *D. seriata* (Merr.) Danser) where inflorescences are found irregularly along the internodes themselves, very much like the flowers of *Stichianthus minutiflorus* Valetton (*Rubiaceae*; Winkler 1931).

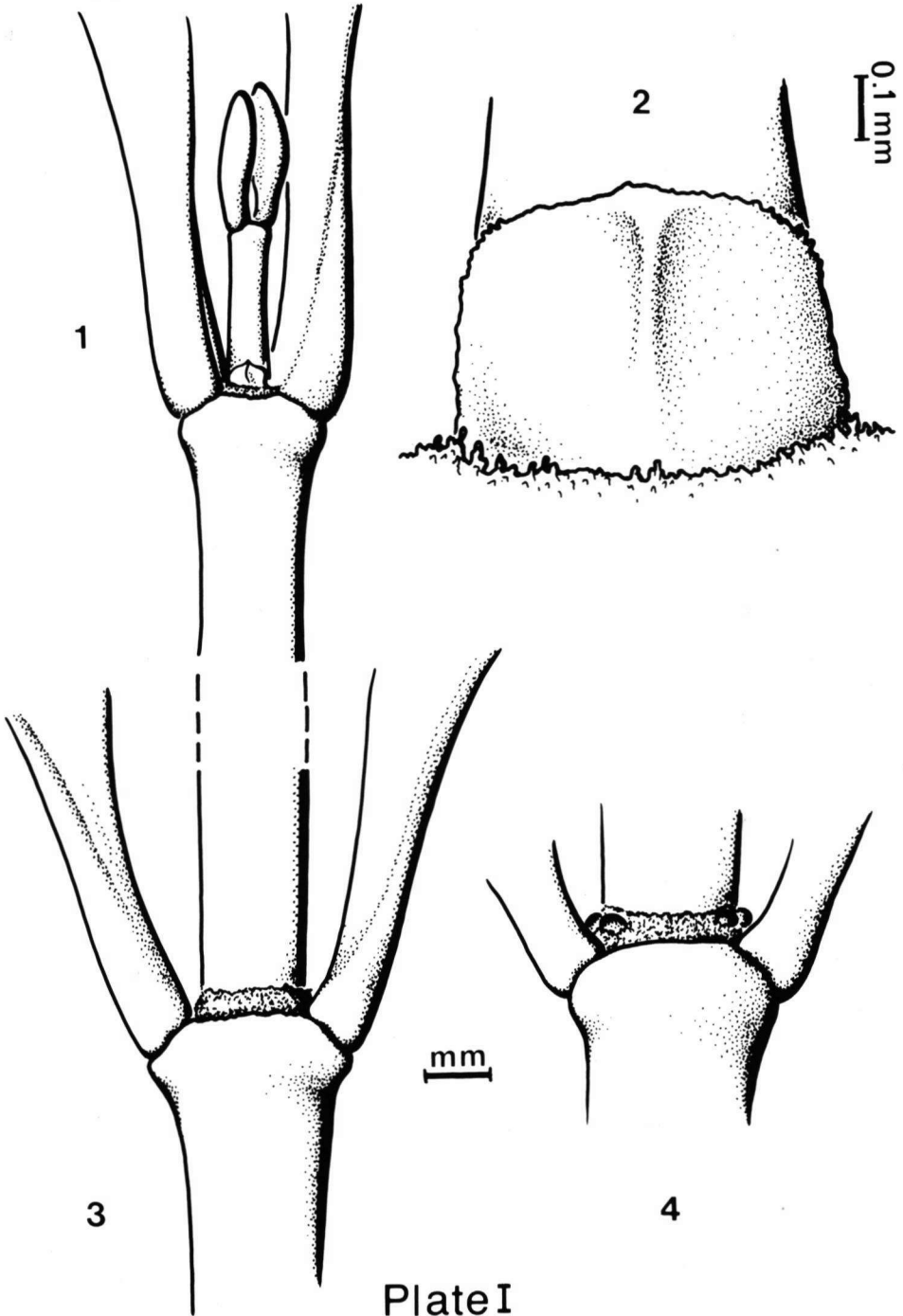
Plate I. *Sogerianthe versicolor*, Brass 3227, L. — Fig. 1. Young branch tip showing position of intercalary cataphylls between two successive pairs of foliage leaves. — Fig. 2. Cataphyll from Fig. 1, enlarged. — Fig. 3. The next lower node from Fig. 1, showing disappearance of cataphylls and prominence of young flower zone. — Fig. 4. Emergence of four flowers from the flower zone, all in approximately prophyllar positions.

In a number of *Amyema* species inflorescences or flowers may emerge directly from epicortical roots¹). In these latter instances there can be no doubt of the endogenous origin of flowers or inflorescences, a phenomenon known from a number of quite unrelated angiospermic parasites (Kuijt 1969). Even in those species showing strictly nodal flowering there is some evidence of such an endogenous origin, as the structures involved may be invested by irregular flaps of corky tissue, which have apparently been ruptured during emergence. Such flaps in *Sogerianthe* are referred to as 'chaffy scales' by Barlow (1974), but the implied leafy nature is not appropriate. This apparent endogeny as a phenomenon cannot be taken at face value, nor is it rare in *Loranthaceae* in general, as we find traces of it in numerous genera both in the New and Old Worlds. In some species of the neotropical *Cladocolea*, for example, it is very pronounced for inflorescences as well as vegetative innovations (Kuijt 1975). In *Misodendrum* (*Misodendraceae*), several species show the same phenomenon, but Hooker (1846) was able to show that axillary buds were covered over secondarily by a caplike tissue through which the bud eventually emerges. In *Cladocolea* there is evidence of a matting together of perhaps glandular hairs in the axillary region, drying to a hard, protective cushion covering the axillary area. The implication of all this is, therefore, that in *Amyema*, also, what appears to be endogeny at the flowering nodes may in fact not be this at all. (As mentioned above, however, it is difficult to understand how the flowering from internodes and roots can be anything but true endogeny). Interestingly enough, there is usually a conspicuous hairy covering in the young flowering zones of these plants. It needs no emphasis that a proper anatomical study is needed to elucidate these features.

In the course of general studies of the inflorescence of *Loranthaceae* it has become evident that the overall structure of the members of the *Amyema* complex has been inadequately explored; I am referring especially to branching patterns and their relationships to the position of inflorescences. While I cannot pretend that an understanding of this morphological aspect is the key to systematic analysis of the complex, there is no doubt that it will be an essential tool for this purpose. My present contribution is based on herbarium material only which, when we are concerned with the position of branches particularly, can be rather misleading.

My original attention was focussed on *Sogerianthe*, where two puzzling features are present neither of which seem to have been recorded in the literature. The branches of these plants frequently bifurcate. On a percurrent stem, however, each two successive pairs of foliage leaves are always aligned in the same plane rather than at perpendicular planes as would be expected from plants with decussate

¹) See, for example, *A. curvifolium* (Krause) Danser and *A. hastifolium* (Ridl.) Danser (together constituting Danser's *Rhizomonanthes*) and *A. dilatipes* Barlow. Flowers in *Distrianthes* (and perhaps also the inflorescences of the above three species) are seen both on the epicortical roots and in the axils of leaves.



phyllotaxy (Plate I). Secondly, more often than not the innovations arising at a node (often apparently from the flowering zone) are placed *p e r p e n d i c u l a r l y* to the nearest foliage leaves, not in their axils (Plate II). In other words, such branches *a l t e r n a t e* with the nearest foliage leaves, arising *b e t w e e n* the members of a pair. As mentioned earlier, this feature is not always obvious in pressed material; especially if only one of the two innovations develops, its orientation is often altered somewhat to be aligned with the internode below, and it may appear to be percurrent.

A solution accounting for both of these aberrant features presented itself with a particularly good specimen of *Sogerianthe versicolor* Danser (*Brass* 3227, Solomon Islands, L) which has young twigs in the process of elongating (Plate I). The fact is that, on a percurrent branch, two successive pairs of foliage leaves are separated by an extremely inconspicuous, caducous pair of intercalary cataphylls which can be seen only for a very brief period. Each cataphyll is a minute, brownish scale, keeled dorsally, and about 0.5 mm long (fig. 2). Even before the foliage leaves are fully expanded the cataphylls have fallen, possibly through the production of the corky material in the flowering zone between it and the node of the foliage leaves below (fig. 3). Both because of the cork and because of the considerable swelling of the node before flowering, the cataphylls leave no discernible scars. In the collection cited above there are at least ten successive pairs of foliage leaves along a single shoot, all in the same plane.

It can be seen, therefore, that these intercalary cataphylls provide a common explanation for both of the above mentioned features. Regular decussate phyllotaxy does, in fact, exist but successive pairs of foliage leaves find themselves in the same plane (on percurrent branches) through the intercalation of a pair of caducous cataphylls. Innovations seem to originate most frequently in axillary positions to these cataphylls, and thus alternate in position with the nearest foliage leaves.

The observed phenomenon immediately calls to mind the parallel one which exists in several species of the neotropical genus *Phoradendron* of *Viscaceae* (Kuijt 1959), especially the common *P. piperoides* (H.B.K.) Trel. In *Phoradendron*, however, intercalary cataphylls are persistent, and never seem to subtend innovations, although in a few more elaborate species such as *P. crassifolium* (DC.) Eichl. inflorescences regularly stand in the axils of some intercalary cataphylls. No flowers have been seen in cataphyll axils of *Sogerianthe*.

The sequence of flowering in a single flowering zone is difficult to observe in pressed material. I am assuming that the flowers in the axils of foliage leaves are the first or at least among the first to mature. The next flowers to appear are certainly those found immediately flanking the petiole (fig. 4). It is tempting to designate these positions as prophyllar, but in some they seem to be too far to the side for this and not at all above the petiolar base, and such a designation may therefore not be correct. I have not observed any regular pattern in the further development of the flowering zone.

It is of considerable interest that another (monotypic) genus, *Helicanthes*, which Danser did not consider closely related to *Sogerianthe* or *Amyema*, shows precisely the same branching pattern as described above. Since material of *Helicanthes* is scarce I cannot be certain that all branching is as described for *Sogerianthe* above, but, certainly most of it is (Plate III). Young innovations arise in positions between the members of a leaf-pair. The first flower (only a scar in fig 10, directly above the crescent-shaped leaf scar) is in a primary axillary position, but subsequent ones

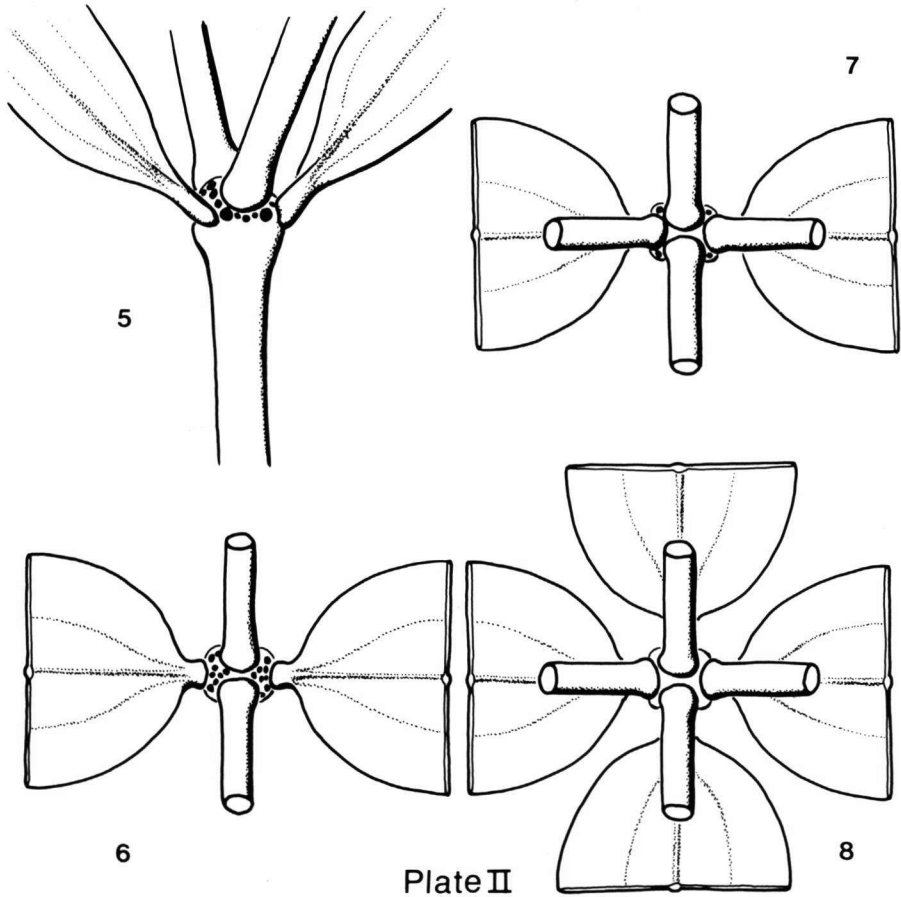
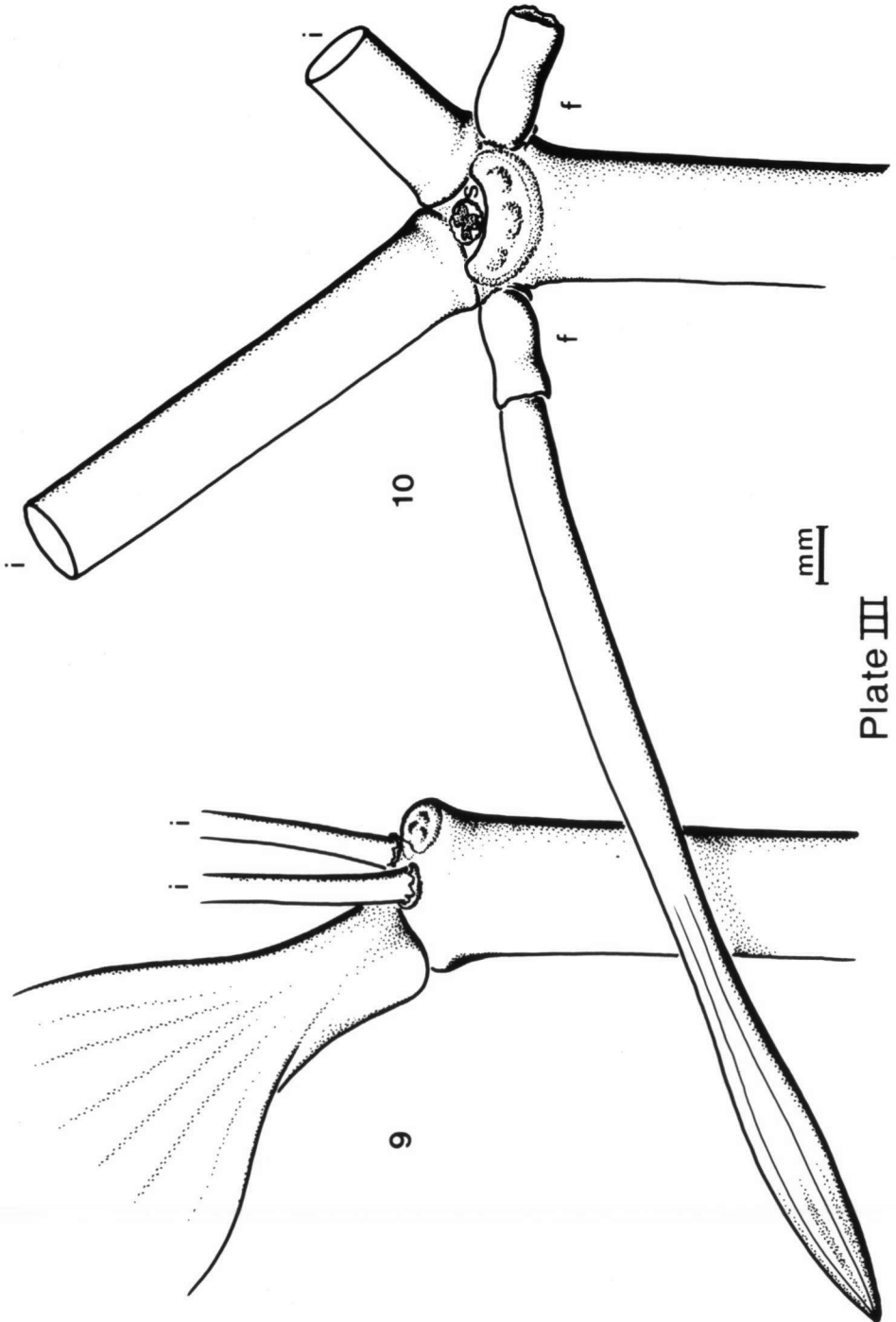


Plate II. *Sogerianthe sogerensis*. — Fig. 5. Cruceate branching pattern. — Fig. 6 as seen from above. Flower positions indicated by black dots. *Amyema luzonensis*. — Figs. 7, 8. Variations in cruceate branching pattern, as seen from above.

flank the petiole, and older nodes show a series of flowers or scars very much like those of *Sogerianthe*. Since flowers in *Helicanthes*, again as in *Sogerianthe*, are solitary²⁾, one wonders if the affinity between the two genera might not be much closer than Danser supposed, even if the geographical distribution of the two genera (India, and Eastern New Guinea and island groups to the east, respectively) is quite distinct. I have not been able to ascertain the occurrence of intercalary cataphylls in *Helicanthes*.

²⁾ The statement 'The inflorescence is a raceme with about fifteen sessile flowers arranged in a whorl' (Johri, Agrawal, and Garg 1957, p. 352) is not only self-contradictory but also in error; the authors probably referred to a leafy branch with a nodal whorl of flowers.



While all species of *Sogerianthe* seen appear to have this type of 'cruciate' branching pattern, this is not true for all *Amyema* species. Similarly, there are numerous species of *Amyema* which clearly lack cataphylls. My impression is, however, that cruciate branching and cataphylls always occur together. In those species not showing either we would thus expect a normal, percurrent system, with lateral branches in the axils of decussating foliage leaves. This is seen in several Australian representatives, for example *A. maidenii*. As would be predicted in such species also, the two axillary cushions from which inflorescences emerge at a node are not confluent but quite separate. There are thus two very distinct patterns of ramification in the *Amyema* complex, the systematic significance of which needs to be explored.

The forking habit of many species is based on an early abortion of the shoot apex. In the majority of cases this means that two lateral innovations develop, each of which forms only one pair of foliage leaves, before abortion of its own apex takes place. The entire innovation, in effect, is only a single internode long. Where an apex aborts we see a very blunt area on which sometimes two minute scales can be seen, which are decussate with the foliage leaves, and are placed in a field of short, brownish hairs. It is from this hairy cushion that future flowers or inflorescences originate.

In at least one species of *Amyema*, *A. luzonensis*, two normal innovations in the axils of the foliage leaves may join the two cruciate ones. Thus an apparent whorl of four innovations is present above the two foliage leaves (fig. 7). Also common in this species, even on the same individual, is the occurrence of four foliage leaves under such a quartet of branches (fig. 8).

Strictly speaking, these lateral innovations may already be considered leafy inflorescences; at any rate, the transition to one is not great. In several members of the *Amyema* complex, indeed, specialized inflorescences of this type have evolved, as in *Distrianthes*, *Diplatia*, and *Papuanthes*. In turn, it is possible that the numerous *Amyema* species with compound umbels may have inflorescences of a comparable derivation, involving the reduction of all leafy organs on such branches.

ACKNOWLEDGEMENTS

I should like to acknowledge working facilities at the Rijksherbarium, Leiden, and financial support from the National Science and Engineering Research Council, Canada.

REFERENCES

- BARLOW, B. A. 1966. A revision of the Loranthaceae of Australia and New Zealand. *Austral. J. Bot.* 14: 421–499.
 ——— 1974. A revision of the Loranthaceae of New Guinea and the South-western Pacific. *Austral. J. Bot.* 22: 531–621.
 DANSER, B. H. 1931. The Loranthaceae of the Netherlands Indies. *Bull. Jard. Bot. Buitenzorg, Sér.* 3, 11: 233–519.

Plate III. *Helicanthes elastica*, Wight 35, L. — Fig. 9. Cruciate branching, showing two young innovations (i); one leaf removed. — Fig. 10. Flowering node showing two older innovations (i), an axillary flower scar (s) above a leaf scar, and two flowers (f).

- . 1933. A new system for the genera of Loranthaceae Loranchoideae, with a nomenclator for the Old World species of this subfamily. Verh. Kon. Akad. Wetens. Amsterdam, Afd. Natuurk., 2d Sect., 29: 1–128.
- HOOKE, J. D. 1946. Flora Antarctica. Part II. Loranthaceae, pp. 289–302.
- JOHRI, B. M., J. S. AGRAWAL, and S. GARG. 1957. Morphological and embryological studies in the family Loranthaceae.-I. *Helicanthes elastica* (Desr.) Danser. Phytomorphology 7: 336–354.
- KUJIT, JOB. 1959. A study of heterophylly and inflorescence structure in *Dendrophthora* and *Phoradendron* (Loranthaceae). Acta Bot. Neerl. 8: 506–546.
- . 1969. The biology of parasitic flowering plants. University of California Press, Berkeley and Los Angeles.
- . 1975. The genus *Cladocolea* (Loranthaceae). J. Arn. Arb. 56: 265–335.
- WINKLER, H. 1931. Ueber die eigenartige Stellung der Blüten bei der Rubiacee *Stichianthus minutiflorus* Valet. Planta 13: 85–101.