INFLORESCENCE MORPHOLOGY OF LORANTHACEAE -
AN EVOLUTIONARY SYNTHESIS

'The distinction and arrangement of genera among the Loranthaceae is based for a rather great part upon the structure of the inflorescence.' (Danser, 1931)

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CONTENTS

SUMMARY

A systematized survey of inflorescence structure is presented of *Loranthaceae, s.s.,* on a world-wide basis, starting with New World taxa and continuing with Old World ones. In each case, material is arranged to reflect a presumed evolutionary sequence. This sequence uses as its starting point the solitary sessile flower subtended by a foliage leaf, leading to the evolution of a determinate inflorescence with ebracteolate lateral monads, and eventually to indeterminate inflorescence types successively bearing ebracteolate and bracteolate lateral monads and, in many groups, eventually triads. Various trends in condensation to umbels and capitula have emerged occasionally, as well as other reductional phenomena and other modifications. The unit inflorescence of *Loranthaceae* is thus regarded as a fundamentally axillary structure, and not a modified leafy branch.

1. INTRODUCTION

My current preoccupation with the inflorescences of *Loranthaceae, s.s.*, is a direct outgrowth of the revision of *Cladocolea* a few years ago (Kuijt 1975a). At that time I was surprised to learn that the great majority of species in that genus possess clearly determinate inflorescences. This seemed to represent a considerable departure in the family. In the Flora Brasiliensis, Eichler (1868) had stated explicity: 'Flores nunquam terminales, rarissime genuine axillares sunt ...', a statement repeated ('Die Blüthen sind stets seitlichen Ursprungs') for the family in his classical Blüthendiagramme (Eichler 1875). It is clear that Eichler was unaware of the earlier illustration of *Peraxilla colensoi* (Hooker 1844), in which an unequivocally determinate inflorescence is portrayed. Subsequent workers in *Loranthaceae*, including the eminent B. H. Danser in his extensive paleotropical studies, accepted Eichler's view. If individual workers like Van Tieghem (1895c) and Barlow (1966) referred to terminal flowers on inflorescences, the discrepancy between this and Eichler's writings does not seem to have been noted. Similarly, when I found that the inflorescence of *Struthanthus polystachyus* was determinate (Kuijt, 1964a) I attributed no special significance to it. The treatment of mistletoe inflorescences in my book (Kuijt, 1969), it should be admitted, is a decidely cavalier one, being at least very incomplete.

A taxonomic clarification is immediately necessary here. My present treatment excludes *Viscaceae*, a family still often regarded as no more than a subfamily, *Viscoideae*, of *Loranthaceae, s.l.* In contrast to most plants of the present study, the great majority of Viscacean genera have determinate inflorescences (see, for example, *Arceuthobium*: Kuijt, 1970), the indeterminate spikes of *Phoradendron* and *Dendrophthora* constituting remarkable departures (Kuijt, 1959). A third, purely American family, *Eremolepidaceae*, may well be a very early offshoot of *Loranthaceae*. Especially since recent palynological work (Feuer & Kuijt 1979) implies affinities to the New Zealand *Tupeia* (*Loranthaceae*), brief reference is made to *Eremolepidaceae* in the present article.

There is, unfortunately, no generally accepted subfamilial framework into which we can hang considerations dealing with inflorescence morphology. Ignoring the various chaotic rearrangements in Van Tieghem's work, the major ideas in this area are derived from Engler (1935), Danser (1931, 1933a), Barlow (1964), and Barlow and Wiens (1971). There is no need to go into details here, although it may be said that the position of *Nuytsia* on the one hand and of the endosperm-less *Psittacanthus* group on the other have been notable points of contention. In addition, however, the stated criteria used to separate major clusters of genera have often been extrapolated rather casually to genera not adequately known. We see, for example, characters of the ovary used in Barlow's (1964) key to Tribe *Lorantheae* which have not been tested for a large number of genera included; similarly, we find Danser (1933a) implying that cotyledons remain hidden in the endosperm during germination of a number of genera (especially of the New World) where we now know the situation to be quite different. The absence of a reliable systematic framework places great emphasis on accurate and cautious reporting of morphological information.

When we now search for a sure general, morphological footing upon which to base an analysis of Loranthaceous inflorescences, we also meet with considerable dissapointment. It remains a surprising fact that, while the theoretical literature on

the angiosperm flower is vast, that on the angiosperm inflorescence has not moved beyong an extremely skeletal and fragmentary level. Part of the reason for this lag is undoubtedly the fact that a study of inflorescences must of necessity be a more wholistic effort than a study of the flower; i.e., from a conceptual point of view the flower allows itself to be dissociated from the rest of the plant rather easily, while inflorescence studies must frequently take into account the branching patterns of the vegetative parts of the plant as well. This is indeed difficult to do for the vast number of tropical and other plants which are normally accessible to us only via the herbarium. Furthermore, a good deal of information on inflorescences lies scattered throughout the systematic literature and is not easily retrieved and summarized. All this would not be serious if there had been terminological consistency, which there clearly has not. It is by no means automatic that the terms panicle and cyme, for instance, are directly comparable from author to author. I would refer the reader to Rickett (1944) and Briggs and Johnson (1979) for historical summaries of the major concepts involved.

Grafted onto the developments up to Rickett's time, there appeared in 1964 and 1969 the first (and thus far, the only) two volumes of Wilhelm Troll's 'Die Infloreszenzen'. They initiate an ambitious program, and are richly illustrated with photographs and careful analytical drawings. It is neither possible nor necessary to evaluate Troll's work here. It should be mentioned, however, that a rather difficult terminology is used by Troll and his students, and this has undoubtedly contributed to the relatively low popularity and/or understanding of his work abroad. At a time when interpreters of plant structure continuously search for evolutionary significance – sometimes obsessively so – Troll rather isolated his contributions by maintaining a strictly formalistic perspective. The two published volumes, as far as I can ascertain, possess no reference to *Loranthaceae*. I have found it often difficult, and never illuminating, to find equivalents of Loranthaceous structures in Troll's published work. I therefore prefer to cast my observations into a form largely independent of Troll's terminology. For an elucidation of the latter the reader is referred to Weberling (1965). A thoughtful critique of Troll's earlier work was published by Stauffer (1963), and the recent work of Briggs and Johnson on *Myrtaceae* (1979) provides a very helpful summary and critique of concepts and terms used by Troll and his students, along with a comprehensive glossary.

My focus throughout this study has been rather to bring conceptual unity into this aspect within *Loranthaceae*, not to make comparisons across family boundaries. I have no doubt that the material presented here can provide raw material for such comparisons, but I leave them to others better acquainted with angiosperms generally.

The purpose of the present study may thus be said to be twofold. I hope, first of all, to make an intelligible survey of the remarkable diversity of Loranthaceous inflorescence types. At the same time I hope to discover, where possible, any evolutionary tendencies which might give this diversity meaning and integrity.

The study of inflorescences of *Loranthaceae* may be said to begin with the publication of the Flora Brasiliensis volume on mistletoes (Eichler, 1868). As mentioned above, Eichler begins by stating that terminal flowers do not occur in *Loranthaceae*, which we now know to be incorrect. He distinguishes two categories, a raceme of pedicellate single flowers (monads) and raceme of pedunculate triads. Within the first category he recognizes that the individual flowers may be ebracteolate or bracteolate. Among the ebracteolate ones he further distinguishes a

raceme ('*sensu vulgari...*'), a spike, a capitulum, and an umbel, the latter sometimes 1- or 2-rayed by reduction. Among the inflorescences with bracteolate single flowers no further subtypes are recognized. Among '*racemus pedunculis trifloris*' a similar (but not altogether clear) distinction into ebracteolate vs. bracteolate flowers is made, and the former type is further subdivided as to whether median and/or lateral flowers of a triad are pedicellate or sessile. Eichler also comes forward with an unusual and elaborate interpretation of the inflorescence of *Psittacanthus*, an interpretation which was to be repeated in his 'Blüthendiagramme' (Eichler, 1875) and which would much later influence Danser's (1933b) analysis of *Thaumasianthes*. It is altogether too easy, by way of hindsight, to criticize Eichler's typology, but that serves no purpose. Nevertheless, not in the least through the superb illustrations accompanying the text, Eichler clearly focusses on a number of essential features such as the construction of triads, dyads, and monads as the basic vocabulary of inflorescence structure. It will be seen in the present study that Eichler's vocabulary is as useful today as it was a hundred years ago. The uncritical use of the term 'ombellule' for this triad in Van Tieghem's work in later years shed little light on the subject, and may even have led Danser's (1933b) thinking astray. Danser was cautious enough, however, to reject the more extreme interpretations of Van Tieghem, and pointed to the need for more meticulous inflorescence analysis. Danser himself was thoroughly convinced of the systematic importance of inflorescences especially at the generic level, as can be seen at the head of this article and elsewhere in Danser's work.

The only other source of inflorescence information is to be found in the various systematic monographs and regional treatments in the family. Morphological interpretations in such works must be accepted gingerly, even though they may contain valuable materials. The two major regional studies by Barlow (1966, 1974) fall into this category. They for the first time provide some significant facts about inflorescences of a few of the primitive genera, and the second also contains an elaborate conceptual scheme for the inflorescences of *Amyema* which will concern us elsewhere.

It is, of course, neither possible nor desirable to meet the purposes of this study without using a modicum of established terms. It is essential, however, that I indicate the precise meaning which I assign these terms.

First of all, I follow Troll in including certain determinate systems within the concept raceme; Loranthaceous racemes may or may not be determinate. A practice of contrasting cymoid versus racemose inflorescences is deeply ingrained in many inflorescence discussions, but does not serve us well in our family. A raceme thus is accepted as a simple, elongated axis bearing stalked, single, lateral flowers, whether a terminal flower is present or not. Both types are present in the family, sometimes in very closely related species. I am also taking the liberty, as Danser does, to use the phrase 'raceme of triads' or 'raceme of dyads' for comparable situations where the single lateral flowers are 'replaced' by stalked triads or dyads as repetitive units. A spike is an elongated simple inflorescence with sessile flowers, whatever their arrangement, and whether or not it is provided with a terminal flower. The existence of transitional forms, sometimes within a single individual, makes such flexibility advisable. Similarly, I will speak of umbels of monads, dyads, and triads and even tetrads in some cases.

A determinate inflorescence is one in which the primary axis terminates in a single flower; it would seem to correspond to the monotelic inflorescence as utilized by

Weberling (1965). In contrast, an indeterminate inflorescence is one lacking such a terminal flower, the apex thus aborting; it probably corresponds to Weberling's use of the polytelic inflorescence at least as far as *Loranthaceae* are concerned.

My use of the umbel and the capitulum are not, I believe, different from standard usage. The former refers to a number of morphologically equivalent single flowers (bracteolate or not) or other units attached to a single node at the apex of a peduncle. The capitulum is different from the umbel only in that the flowers or comparable units are sessile rather than stalked. Thus even in a capitulum subunits like triads may be recognizable.

The terms monad, dyad, triad, and tetrad require special attention as they are the building blocks of most *Loranthaceous* inflorescences; furthermore, their interpretation is by no means as simple as might be thought. All we can say about them generally is that they are units bearing one, two, three, or four flowers each, respectively. They may represent a subdivision of a larger inflorescence or they may, in some instances, represent the entire inflorescence. The occurrence of bracts, bracteoles, and articulations plays an important role in recognizing different types of these structures. The terms are morphologically non-committal in the sense that they are purely descriptive and imply nothing beyond such phytographical facts.

The most common type of monad is as a lateral unit to a raceme or spike. In a number of these cases monads are no more than sessile flowers of a spike (for example, in *Trithecanthera*, *Loranthus*, and some *Cladocolea* species). The pedicellate condition of monads is more common; in practically all African and very large numbers of Asiatic and Australian species, as well as a sprinkling of neotropical ones (*Tristerix*, *Dendropemon*, and two or three species of *Cladocolea*) pedicellate flowers may be subtended by a bract, with or without bracteoles (sometimes both within the same genus). It is the rule that the subtending bract is fused with the length of the pedicel, thus apparently subtending the flower directly. Exceptions are seen, for instance, in the three pedicellate *Cladocolea* species, *C. harlingii*, *C. pedicellata*, and *C. diversifolia* as well as in some New Zealand plants. The same 'recaulescence' (Troll, 1964, p. 1:127) is seen in nearly all dyads, triads, and tetrads (see exceptions noted below). In only one case, as far as I know (*Cladocolea pedicellata*, Kuijt 1975a), is there what Troll calls 'concaulescence', i.e., partial fusion of a pedicel or peduncle with the inflorescence axis. Monads are associated in umbels in a number of instances in the Old World; the only occurrence of this in the New World seems to be the remarkable *Psittacanthus palmeri* from northern Mexico, but a different interpretation as presented below qualifies this exception. Where we have solitary, sessile axillary flowers the concept of monad (and indeed of inflorescence) loses its meaning. However, there are a number of cases of stalked monads occupying axillary or comparably 'primary' positions, and these are frequently very difficult to interpret. Especially in *Sogerianthe* and other members of the *Amyema* complex this situation is troublesome, and the non-committal term 'monad' is thus very useful. Strictly speaking we may also use 'monad' for a one flowered portion of any dyad, triad or tetrad, but in most instances this is not especially helpful.

Dyads are easily dealt with as they occur in two types, the first more directly related to monads, the second to triads. In most cases where we find an axillary stalk terminating in a dichotomy each branch of which has a single flower, the entire structure may be called a dyad but is really no more than a pair of monads together forming (with the peduncle) the entire inflorescence (for example, species of *Lysiana*

and *Taxillus*). The affinity is thus with a raceme or umbel. The other type of dyad is a unit which is lateral to an inflorescence axis, and is comparable to a lateral triad except that the median flower has failed to develop; this is common, for example, in *Psittacanthus* and *Aetanthus*, and in the Old World is known from *Tetradyas*. The two types of dyads can normally (but perhaps not always) be distinguished in that the peduncle of the former is ebracteate while that of the latter bears a recaulescent bract.

Triads as defined above exist in several forms which must be carefully distinguished and are best visualized by means of specific examples. The first type is exemplified by the primary inflorescence of *Cladocolea dimorpha*, where we see a peduncle terminated by a median flower flanked by two bracteate lateral flowers (Fig. 2 – 2). It clearly represents an entire, determinate inflorescence: the three flowers lie in one plane, the median flower lacks a separate bract, and the entire triad occupies a primary, axillary position. In a second type of triad, occupying a primary position also, the peduncle is not usually terminated by a recognizable bract although a rim may indicate a much reduced pair of leafy organs; *Amyema sanguinea* and *A. quaternifolia* are examples. The distinguishing feature of this type of triad is the fact that all three flowers are morphologically equivalent; each is borne on a pedicel at the tip of which there is a recaulescent bract. It is clear that this triad must be viewed as a small umbel. A very different variant of this second type is the sort of 3-rayed umbel which has become a subunit of the compound umbel of *Amyema pendula* (Fig. 24 – 1) and *A. miquelii*. Here the three flowers each are borne by a recaulescent bract. The latter is always placed between two rays of the umbel (the additional occurrence, in some plants, of a fourth flower is referred to below).

The third type of triad is a lateral unit subordinate to the (usually simple) inflorescence as a whole. It has one median and two lateral flowers. The bract is recaulescent with the triad peduncle as far as the point of attachment of lateral flowers (except in *Struthanthus interruptus*: Kuijt, 1975b, *Papuanthes*, and possibly *Lampas*: Danser, 1931). The median flower may have a pedicel beyond this point or be sessile. Lateral flowers are commonly pedicellate, but are at any rate subtended by (recaulescent) bracteoles which are in the nature of prophylls to the median flower (many lateral flowers are thus seemingly sessile). Lateral flowers in this triad are usually placed somewhat closer to the main inflorescence axis. Numerous examples are present in *Psittacanthus*, *Struthanthus*, *Phthirusa*, *Nuytsia*, *Amylotheca*, and other genera. It should be emphasized that the lateral flowers of this triad are not morphologically equivalent to the median one but rather are secondary to it; their smaller size and later development often document this fact. These triads may be sessile or virtually so, in extreme cases apparently leaving the three flowers individually sessile on the inflorescence axis (*Struthanthus polystachyus*, Fig. 4 – 4).

Aside from 4-rayed umbels or contracted racemes which, in a casual fashion, might be called tetrads (although this is not at all helpful) the tetrad seems to be restricted to *Amyema*. Even within that genus it is rare as an inflorescence unit (Barlow, 1974), being known only in about half a dozen species. It might be mentioned that *A. fitzgeraldii*, listed as having a capitulum in Barlow's paper, should be added to that author's list of *Amyema* species having tetrads; in fact, its tetrad would seem to be of some special significance.

A dichasium, following Rickett (1944) and other, refers to a flower cluster formed

by an apparent dichotomy beneath a terminal flower. A simple dichasium (frequently also called a cyme) has a single flower on each of its two lateral branches, and thus consists of three flowers in total. It is the only type of dichasium existing in *Loranthaceae*. Both the first and the last types of triads described above might be referred to as cymes, although this is not done in the present paper.

   The reader may already have noticed that in the above general comments I have abstained from referring to one inflorescence or its unit as being derived from others by reduction. It has become an almost mechanical reaction in the minds of many morphologists to regard simpler structures as being reductions from more complex ones; it is apparently an easier mental process to visualize the gradual evolutionary disappearance of organs, than their addition. Within context of problems of floral vascularization, Carlquist (1969) has written: 'The uniformity with which workers always choose to hypothesize a reduction series is little short of hilarious', concluding that 'Increase in vascularization of flowers should be expected as often as reduction'. In the course of this work it has become clear that this preference for reduction is a nearly unquestioned and frequently undetected bias of systematic and morphological thought. It takes little meditation to discover the weakness of such a position: clearly, the complex structure used as a starting point must have had a prior evolutionary history from a simple base in order to reach a level of complexity. There is scarcely a writer in *Loranthaceae* who doesn't fall into this trap. In vain do we look for an example where even the eminent Danser provides an evolutionary connection which leads from simple to complex. Barlow (1966) gives an elaborate evolutionary scheme for the inflorescences of *Amyema* based on the assumption that the compound umbel is the evolutionary starting point[1]. Numerous other examples could be mentioned. It is especially tempting, apparently, to look upon bracteolate monads as being reductions from triads. I know of not a single case in *Loranthaceae* where an author has taken an opposite point of view, one which a priori is surely at least equally logical, namely that evolutionary progress has frequently entailed the addition of bracteoles to a simple monad, and later (or perhaps simultaneously) the two additional flowers in the axils of these prophyllar bracteoles. Yet this is precisely what my studies of neotropical *Loranthaceae* indicate to me, and part of the present study represents an effort to discover whether this evolutionary view contributes to an understanding of Loranthaceous inflorescences in general. In this I do not, however, deny reduction a respectable position in morphological thinking. Reduction is kept in reserve, as it were, as a method of phylogenetic reconstruction, while giving priority to elaborative trends, and it is necessary that the reader is aware of this bias in what follows. It would, of course, be ludicrous to deny the importance of reduction as an 'active evolutionary principle' especially in parasitic plants (cf. Kuijt, 1969).

1.1. THE DELIMITATION OF INFLORESCENCES IN LORANTHACEAE

   The question of homology will emerge repeatedly in the following discussions. We therefore need to say something about the manner in which inflorescences even

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[1] 'The solitary flower is more primitive than the inflorescence, the highest form of the latter being the umbel and the capitulum' (No. 9 of the Bessey-Hutchinson dicta as cited by Davis & Heywood, 1963, p. 36).

in a reduced state may be distinguished from subordinate parts of others. In what way, for example, is the 3-flowered (primary) inflorescence of *Cladocolea dimorpha* different from the standard, lateral triad of *Struthanthus*? A precise definition of the inflorescence of *Loranthaceae*, unfortunately, may well be impossible, as the great number of exceptions and qualifications would make a definition quite top-heavy. I consider it therefore more useful to state the most important criteria separately. It might be said parenthetically that the inflorescence of *Loranthaceae*, fortunately, is almost always clearly set apart from the rest of the plant, and thus we are not faced with the sort of problems present in families such as *Labiatae* and *Scrophulariaceae*.

The first criterion is that an inflorescence must either stand at the end of a leafy branch or be axillary to a foliage leaf (squamate species are very rare, and are here ignored). This would seem to be obvious but will at least avoid confusion between part-inflorescences and entire inflorescences, as in the question concerning the 'terminal triad' of some *Struthanthus species* discussed elsewhere. Included are also the rare instances where a single species may show inflorescences of both positions, as in *Tripodanthus acutifolius*. Not even this criterion can cover all cases, as the inflorescence of some species of *Amyema* and *Sogerianthe* emerge directly from epicortical roots; but in these cases little confusion exists as to the limits of the inflorescence. A somewhat similar situation exists in *Tristerix aphyllus*.

A second criterion of entire inflorescences in *Loranthaceae* is a degree of radial symmetry; i.e., structures lacking such symmetry are only part-inflorescences. The lateral triad of *Struthanthus*, and the bracteolate monad of *Tristerix tetrandrus*, are thus excluded from consideration as they are bilaterally symmetrical only. Some monads (as in *Cladocolea harlingii*) produce difficulties but are already screened out by the application of the first criterion. The unusual basal triad described in *Cladocolea pedicellata* (Kuijt, 1975a) is awkward with regard to both criteria but is recognizably equivalent to a normal monad, and may be accounted for by the next criterion.

A third and perhaps more difficult criterion is that an inflorescence must correspond to a single growth-phase of the plant, or at least fall within it. The curious raceme of *Cladocolea pedicellata* is clearly such a unit. The raceme of *Tristerix aphyllus* produces basal and sometimes terminal branch-inflorescences, but a single growth-phase produces a clearly circumscribed unit comparable to the inflorescences of related forms.

A fourth criterion is of uneven application but occasionally may be of significant assistance in defining the inflorescence as, again, in the otherwise difficult case of *Cladocolea pedicellata*. As first described in my *Cladocolea* revision (Kuijt, 1975a), numerous species of that genus have inflorescences (and vegetative innovations) which appear to originate in an endogenous fashion, as shown by the irregularly torn 'crater' of corky tissues investing the base. Whether or not this represents true endogeny does not concern us here: what is important is that, where flower-bearing branches are concerned, this crater can be used as a diagnostic feature for the inflorescence as a whole. This character is by no means restricted to *Cladocolea* and finds a variable expression in many other genera; it is especially strongly developed in *Amyema* and its nearest relatives, and no less than dramatic in *Cyne*.

The discussion below begins with an analysis of the *Cladocolea-Struthanthus* complex which is pivotal to the present study. The other small-flowered American genera that are undoubtedly related to this complex follow next. The genera *Tripodanthus*, *Gaiadendron*, *Notanthera*, and *Desmaria* are then discussed together,

followed by *Tristerix* and *Ligaria*. The variable *Psittacanthus-Aetanthus* group concludes the treatment of New World *Loranthaceae*. Thus this grouping has some semblance to systematic relationships.

The treatment of Old World taxa is more arbitrary, as the mutual affinities of the larger groups are often not clear to me. The exclusively American *Eremolepidaceae*, as mentioned earlier, are briefly summarized in a separate section.

2. LORANTHACEAE OF THE NEW WORLD

2.1. THE CLADOCOLEA-STRUTHANTHUS COMPLEX

Ignoring the several exceptions mentioned elsewhere these two genera may be distinguished largely on the basis of the inflorescence. *Cladocolea* has a determinate spike or raceme of single flowers which are either sessile (excepting the terminal one) or rarely pedicellate, the flowers being ebracteolate; *Struthanthus* is characterized by an indeterminate raceme (sometimes approaching a spike or umbel) of bracteolate, dichasial triads.

The first key to an understanding of the complex mutual relationships of these two genera lies in the species pair *C. harlingii* − *S. orbicularis*, the former being highly localized in Prov. Loja of Ecuador and (very rarely) adjacent Peru, and the latter species being extremely widespread in nearly all continental, humid tropical areas of the New World, at lower elevations. The overall similarity of the two species is extremely striking: in leaf shape, angularity vs. tereteness of twigs and inflorescences axes, etc., the species are sufficiently similar to be easily confused. The most interesting correspondence, however, lies in the strategy of parasitic attack. Both species have identical long, trailing innovations, with greatly elongated internodes separated from each other by pairs of hook-shaped, rigid young leaves which are bent back somewhat. It is easy to see how such 'grappling hooks' can come to rest upon surrounding vegetation. When this occurs a fairly rapid growth response sets in which twists the swelling petiole completely around the object.[1] In a short time roots appear from near the node which entwine the captured object and, if the latter is a living branch, soon penetrate it by means of secondary haustoria. This method of attack, first fully described for *S. orbicularis* in Costa Rica (Kuijt, 1964b), eventually leads to the formation of a tough, wiry covering which may smother a small tree and reach across to attack others. There are one or two other species of *Struthanthus* which show the same parastici strategy (for example, *S. rotundatus*) but they are closely related to *S. orbicularis*; beyond this, there are no species in the two genera − and indeed in the family − which behave similarly. The similarities between *S. orbicularis* and *C. harlingii* are too comprehensive to be dismissed as convergence; in fact, without knowing more about the two genera, one would certainly be tempted to place the latter in *Struthanthus*, differing from *S. orbicularis* only in inflorescence structure. To the above should be added one more significant fact: *C. harlingii* has bisexual flowers, while *S. orbicularis* is dioecious.

If the relationship between these two species, even though placed in different genera, appears very close, this impression is clinched by the existence of a third

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[1] The prehensile nature of these leaves was already known to Eichler (1868, p. 68).

species in Peru, Bolivia, and Ecuador, *S. flexilis*. To begin with, *S. flexilis* also shows the same parasitic strategy by means of prehensile petioles. Morphologically, it represents a perfect intermediate between *S. orbicularis* and *C. harlingii*. Its inflorescence has 6 — 8 nearly sessile triads decussately arranged on a quadrangular axis, which, however, terminates in a single sessile flower flanked by two ebracteolate single flowers (Fig. 5 — 3). These lateral flowers are also sessile but subtended by caducous scale leaves which are decussate with the nearest pair of triads. It is, indeed, as if the tip of the *C. harlingii* inflorescence has been grafted onto a typical one of *Struthanthus*. The species is dioecious.

Leaving in abeyance for the present the taxonomic urge to place all three species immediately together in *Struthanthus* we can at least agree that an uninterrupted series exists. Can we make a convincing case for reading this series in one or the other direction? I would maintain that we can, and that the direction is clearly indicated by sex distribution. Most botanists would agree that a bisexual flower can evolve into a unisexual one, but not vice versa. As Takhtadzhian (1969), among others, states: '... the basic type of angiosperm flower was bisexual, and ... the unisexual type is derived and secondary'. I feel it is safe to propose that the *Cladocolea* inflorescence type must be more primitive than the typical one of *Struthanthus*.

The admitted weakness of the above argument is that sex distribution, in the evolution of the inflorescence, need not have been coupled with any particular structural configuration. It might be argued that the common ancestor of *C. harlingii*, *S. flexilis*, and *S. orbicularis* was a plant with bisexual flowers and an *S. flexilis*-like inflorescence, which evolved in the *S. orbicularis* direction by developing dioecy and 'dropping' the terminal inflorescence portion, and separately evolved in the *C. harlingii* direction by having all triads reduced to ebracteolate monads. I know of no facts which are dissonant with this interpretation, and can only say that it does not attract me as it seems once again to begin with a complex situation to derive, by reduction, a simpler one. If this were the only connection between the two genera an alternative explanation might be more convincing, but we shall see it is not; and I feel the existence of several parallel 'bridges' between the two genera strengthens an interpretation leading from simpler to more complex.

The relationships between *Struthanthus polystachyus* and *Cladocolea lenticellata* provides a remarkably parallel case to the above, the two cases nevertheless being quite independently convincing. This case, also, is touched upon in my *Cladocolea* monograph (Kuijt, 1975a). *C. lenticellata* (previously called *C. archeri*) is a species of fairly high elevations, and is restricted to Ecuador, Columbia, and Peru; *S. polystachyus* occurs in the same area at much lower elevations but has a far larger geographic extent, finding its northern limit in Costa Rica (Kuijt, 1964a). Once again, the two species have a remarkable similarity, which only reinforces itself upon closer scrutiny, involving various morphological features of stems and leaves, including the occurrence of leaf sclereids otherwise rare or absent in both genera. Most convincing, however, is the persistence of a number of prominent chartaceous bracts at the base of the inflorescence. *C. lenticellata* has bisexual flowers; *S. polystachyus* is dioecious. The situation is so closely comparable to that of *S. orbicularis* — *C. harlingii* that the conclusion again seems reasonable that *S. polystachyus* is derived from a *C. lenticellata*-like ancestor, or from that species directly. *S. polystachyus* itself, in a sense, is an intermediate between the two genera: some years ago (Kuijt, 1964a) I made the isolated observation that its spikes have a

single terminal flower and two single lateral ones, precisely as that described for *S. flexilis* above.

Having established two bridges between the two genera, it is natural to search for more. Indeed, a third acceptable one seems to exist in Mexico. A number of species of *Cladocolea* in that area are characterized by a curious structural feature apparently not known outside Mexico (except for the unrelated instance of *Ileostylus* in New Zealand). I am referring to the strangely contorted style (cf. Kuijt, 1975a; Fig. 1 – 3 of the present paper), especially in the female flower of many species. Whatever its functional significance may be, it is a very striking feature (the style does not straighten out but remains in the same condition until it falls). This condition in Mexico is not, however, limited to *Cladocolea*; there are several species of *Struthanthus* in the same region which have similarly contorted styles. Indeed the genus *Spirostylis*, now a synonym of *Struthanthus*, was named after one such species (Kuijt, 1975b). In this case the *Cladocolea* species concerned, like *Struthanthus*, are dioecious, and a possible intergeneric bridge might not be postulated if it were not for two facts. The first of these is the fact that one *Cladocolea*, *C. pedicellata*, sometimes produces a dichasial triad in the lower portion of the inflorescence (Fig. 1 – 3); this fact might, of course, be dismissed as a teratological feature. The second fact is not so casually dismissed: once again there exists an intermediate species of *Struthanthus*, *S. deppeanus*, to make the intergeneric bridge more credible (Fig. 4 – 2). The inflorescence is determinate, but instead of the dichasial triads seen below, the top of the raceme features pedicellate, ebracteolate monads in decussating pairs. Curiously, the subtending bracts are concaulous, while the triads below have separate (caducous) bracts, like the triads of *S. interruptus* (Kuijt, 1975b). While this third bridge between *Cladocolea* and *Struthanthus* may not have quite the 'structural strength' of the earlier two, its credibility, I feel, is much enhanced by the latter's existence.

Whether there are still further intergeneric bridges I cannot say. I have earlier alluded to the possibility that *S. palmeri* and *C. pringlei* might be similarly related (Kuijt, 1975a), and the new species *S. condensatus* would seem to lend some support to this idea (Kuijt, 1980a).

My interpretation of the direction of intergeneric bridges between *Cladocolea* and *Struthanthus* derives some additional bracing from a comparison of a few other aspects. Using the 'Bessey-Hutchinson' dicta as formulated by Davis & Heywood (1963) we can see that a number of structural features stamp *Cladocolea* as somewhat more primitive than *Struthanthus*. *Cladocolea* has several species with solitary axillary flowers and several with bisexual flowers, *Struthanthus* none. Several species of *Cladocolea* have monomorphic stamens, but no *Struthanthus* species do. Again, numerous *Cladocolea* species have alternate phyllotaxy, a condition not known for *Struthanthus*. Finally, most species of *Cladocolea* seem to lack roots which develop from the stem, while such (more advanced) roots may well be typical of all *Struthanthus*. This is not to deny the existence, in individual *Cladocolea* species, of advanced traits not present in *Struthanthus*, as the branching pattern of *C. microphylla* and *C. dimorpha*, but the overall picture certainly points to *Struthanthus* as the more derived genus of the two.

If the concept of *Struthanthus* as a polyphyletic entity as outlined above is agreed upon, is there any a prior reason why elements from other genera might not evolve in the same direction? Indeed, the difficult taxonomic relationships existing with *Phthirusa* might well be of this nature. *Phthirusa* generally has bisexual flowers, but

two or more species (e.g., *P. retroflexa*, thus far known as *P. adunca*) have become dioecious and have even evolved the branch-borne epicortical roots otherwise characteristic of *Struthanthus*, and not of *Phthirusa* species with bisexual flowers. We might even speculate that the remarkable *Tripodanthus flagellaris*, while 'still' having bisexual flowers, is only that feature removed from the *Struthanthus* syndrome. Is it conceivable also, that *S. panamensis*, which fits so poorly in 'normal' *Struthanthus* because of bisexual flowers and inflorescence characteristics, represents yet another independent branch leading into the *Struthanthus* 'pool'? The possibility emerges that the *Struthanthus* constellation of characters — an indetermine inflorescence of paired, dichasial triads, stem-roots, dioecy, and mostly low-elevation preference — represents what might be called an evolutionary sink in the neotropical area.

Should the above vision of a polyphyletic *Struthanthus* prove acceptable it would, of course, give little satisfaction to taxonomists: at least, it provides little help in the delimitation of the genera involved. To be more specific, if the relationships between *Cladocolea* and *Struthanthus* are as delimited above, it may well be impossible to draw intergeneric frontiers which are natural. However, at least the taxonomic difficulties involved might be better understood even if they cannot be satisfactorily resolved.

It should be pointed out that in *Cladocolea* there is no necessary connection between the evolution of triads and of the indeterminate inflorescence. In three separate, unrelated species an indeterminate spike with lateral monads may be seen (*C. biflora*; Kuijt, 1980a; *C. cupulata* and *C. mcvaughii*; Kuijt, 1975a) (Fig. 3 – 1). In *C. mcvaughii* and *C. biflora* the flowers are clearly ebracteolate. Inflorescence morphology of *C. cupulata* is more puzzling, however, even though they are consistently indeterminate. It appears that each of the four flowers is held in a cupule which shows faint traces of bracteole-like marginal prominences. Should the latter indeed be bracteoles the inflorescence would be the only bracteolate one in *Cladocolea*. These three species clearly represent derivative situations, a fact especially obvious in *C. biflora*, the only species among all small-flowered neotropical *Loranthaceae* with gamopetalous flowers.

Before leaving the inflorescences of *Cladocolea* and *Struthanthus* there are several other points to be made. First of all, a solitary instance of a compound inflorescence has been observed in *C. loniceroides* in which individual spikes are organized in a larger system (Kuijt, 1975a). *In Struthanthus*, as illustrated by Eichler (1868), there are two or three species with compound inflorescences, and the same is true (but perhaps more regularly so) in some species of *Phthirusa* and one of *Oryctanthus* (see below).

Two curious instances have been found where two morphologically different inflorescences are produced, in regular sequence, on the same plant (Kuijt, 1975a). In *Cladocolea dimorpha* one type of inflorescence, called the primary one, emerges from the axils of foliage leaves, is always 3-flowered, and lacks foliage leaves on its own axis; the other type, the secondary inflorescence, bears 3 – 5 flowers and 2 – 4 foliage leaves, and develops on older, leafless wood. A similar situation prevails in *C. oligantha*. These are the only known cases of true inflorescence dimorphism in *Loranthaceae*, and are not to be confused with the variation which exists in certain Old World taxa (see below); nor is the phenomenon related to sexual differentiation, as both species have bisexual flowers.

The triads of *Struthanthus* vary with regard to the length of both peduncles and

pedicels. The former may be rather long, quite short, or, more rarely, absent. The latter case is illustrated in Fig. 4 – 4, where the three flowers appear to emerge directly from the main inflorescence axis. In the great majority of *Struthanthus* species the lateral flowers are pedicellate and the median one is sessile. In contrast to Barlow & Wiens' (1973) statement, however, there are some *Struthanthus* species with pedicellate median flowers. One of these, *S. vulgaris*, may be seen in Eichler (1868, p. 27), and another is *S. deppeanus* from Mexico (Fig. 4 – 2).

2.1.1. TENTATIVE INFLORESCENCES THESES

The above analysis of the *Cladocolea-Struthanthus* complex allows for two general theses with regard to tendencies in inflorescence evolution which, in the discussions which are to follow, will be used as guide lines. While they may appear to be somewhat premature at this point I should like to put them forward now to be tested by further material in this paper; I shall return to them in the Discussion.
1. The determinate inflorescence of *Loranthaceae* represents an ancestral condition, the indeterminate a more derived one.
2. In *Loranthaceae*, monads as lateral inflorescence units are generally more primitive than triads in that position.

2.2. OTHER SMALL-FLOWERED NEOTROPICAL GENERA[1]

In the remaining neotropical genera with small flowers we should first refer to the curious monotypic genus *Ixocactus* (Kuijt, 1967). Its flowers are single, sessile, and axillary in precisely the same way as, for instance, those of *Cladocolea clandestina*; we can thus not speak of inflorescences. Prophylls associated with the axillary flower usually subtend flowers also.

All other genera involved in this group have indeterminate racemes or spikes. The small (2 species) Brazilian genus *Oryctina* was originally founded upon the belief that the lateral flowers were ebracteolate (Van Tieghem, 1895a), a notion accepted in all but one subsequent reference to the genus. In 1976 I hesitated to accept this notion, but Rizzini (1977) once again confirmed it. Nevertheless, I have recently shown that flowers of both species are unquestionably bracteolate (Kuijt, 1980c) even though the bracteoles of *O. scabrida* are difficult to identify in older material. A very peculiar feature in *O. scabrida* is the occurrence of compound spikes (Eichler, 1868; Kuijt, 1976) in which some of the scale-leaves in the mid-area of the main spike subtend secondary spikes instead. As very little material of the two species is extant we do not know whether these compound spikes represent teratological structures or not.

Racemes or spikes where bracteoles are clearly identifiable on monads occur in several genera. In *Oryctanthus* and *Maracanthus* such monads are simply sessile flowers axillary to the spike's scale-leaves, and flanked by the prophyllar bracteoles which may or may not extend beyond the rim of the subtending leaf (Fig. 4 – 5). In *Dendropemon* (Fig. 6 – 2) and *Struthanthus panamensis* (Fig. 6 – 1) each monad, with its two bracteoles, is elevated on a pedicel. The three leafy organs subtending the flower may be connate to form a compound cupule, but the bracteoles are always recognizable as such by their smaller size and/or their prophyllar position.

In *Phthirusa*, finally, we find precisely the same conditions as in the majority of

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[1] Palynological work in progress (Feuer and Kuijt, in preparation), indicates that these genera are indeed closely related to one another and to Cladocolea and Struthanthus.

Struthanthus species: an indeterminate raceme or spike of bracteolate triads. The number of triads varies very considerably, some being reduced to four or perhaps even two, in which case the flowers may be very crowded in the leaf axil.

The inflorescence of *Phthirusa pyrifolia* has been analyzed rather carefully (Kuijt and Weberling, 1972). The triad has developed beyond the standard Loranthaceous form in that the lateral flowers themselves are also provided with prophyllar bracteoles each (Fig. 6 — 4, 5). Even a normal triad usually shows the 'inner' (near-median) two of these four bracteoles to have one or two extremely minute leafy organs which I suggest are bracteoles of the third order (Fig. 6 — 4). That this is so is indicated by the rare occurrence, at the base of extremely vigorous inflorescences, of 5-flowered 'pentads' which show two further flowers to have differentiated (Fig. 6 — 5), each cradled by these minute prophyllar organs. It is the only known case in *Loranthaceae* of this type of inflorescence unit.

In a number of species the leafy branch terminates in a squamate section occupied by a number of pedunculate racemes, and we can thus speak of compound racemes. The best known example is *O. alveolatus* as illustrated in the Flora Brasiliensis (Eichler, 1868, pl. 29). In *Phthirusa rufa*, as shown in the same work (Pl. 16), a similar arrangement has evolved, and the same is true for what is perhaps another species of *Phthirusa, Furarium disjectifolium* (unpublished information). In all these cases we are concerned with a new arrangement of spikes or racemes which are otherwise not different. In some other species, however, there is a compound inflorescence which involves a structural alteration of constituent portions. In *Phthirusa robusta* (Fig. 6 — 3), the basal two pairs of triads of axillary racemes have been 'replaced' by four racemes. Whether a terminal, compound arrangement also is present I do not know. In one of the most common species of *Phthirusa, P. retroflexa*, such a compounding has occurred and, additionally, some of the lowest axillary racemes may show the same basal branching (Fig. 7 — 3). This is one of the very few instances in which strict delimitation of the floriferous portion in *Loranthaceae* seems impossible (see also note on *Cladocolea loniceroides* on p. 12).

2.3. TRIPODANTHUS, GAIADENDRON, NOTANTHERA, AND DESMARIA

Fully differentiated triads characterize racemes of *Tripodanthus, Gaiadendron, Notanthera*, and *Desmaria*. In the first genus all three flowers are pedicellate, while in the others only the lateral flowers are, and often on very short stalks only. Bracts and bracteoles in *Tripodanthus* are very inconspicuous, in the others, rather prominent. In *Gaiadendron* the bracts and bracteoles are foliaceous and sometimes rather large, lending a very distinctive appearance to the inflorescence even when in fruit, where these organs have somewhat enlarged. In early stages, the bracteoles in this genus appear to protect the young flowers (Fig. 10 — 4).

In both species of *Tripodanthus*, however, the inflorescence seems to be determinate (because of the brittleness and crowded conditions of flowers on herbarium specimens I cannot be absolutely sure that this is always so). It is a notable fact that this is correctly indicated in Eichler's (1868) illustration of *T. acutifolius*, while he denied the existence of determinate inflorescences in the family in the accompanying text (for another such discrepancy, cf. *Amyema*). The stalked terminal flower is followed by either two or four ebracteolate monads, below which only triads are found. Thus the raceme is very much the same as several of the exceptional *Struthanthus* inflorescences discussed above, and like many *Gaiandendron* ones (see below). In *T. acutifolius* such monads are decussate in

arrangement, but in *T. flagellaris* they are always alternate (Fig. 8 – 1). Some racemes in the latter species may, in fact, be indeterminate, the aborted apex being flanked by one or more monads. In this same species, racemes develop individually on short shoots which are leafy below, while in the former one, except for some caducous scale leaves below, the racemes are leafless and found in a small cluster at the end of a leafy shoot, or sometimes singly in many leaf axils along it (the latter is illustrated in Eichler, 1868, Pl. 12). The habit of the two species, also because of the voluble, root-bearing branches of *T. flagellaris*, is thus very different.

In *Gaiadendron* populations in Central America inflorescences are commonly determinate. The apices of such racemes may take a variety of forms. In one situation, the uppermost triads may be followed by a pair of ebracteolate monads, these in turn followed by the terminal flower which may or may not have two small bracts decussating with the monads (Fig. 10 – 2, 3). Other inflorescences terminate in the same way except that monads are minutely bracteolate (Fig. 10 – 1). A combination is possible in racemes where we find above the triads first a pair of bracteolate monads, then a pair of ebracteolate monads, and finally the terminal flower (Fig. 10 – 3). My impression is that in South America only indeterminate racemes of triads occur. I can offer no explanation for this intriguing geographical pattern of variation.

Desmaria plants are characterized by a dimorphism of shoots, viz., long shoots and short shoots. The latter form spurs on older wood which develop for several years and eventually bear a terminal inflorescence each. At that time, two or more pairs of foliage leaves develop first, followed by a series of regular lateral triads which in due course bear fruit. These triads are thus not axillary to the involucral foliage leaves (as Van Tieghem, 1895d, had indicated), as also shown by the concaulescent bract of each triad. The outstanding feature of the inflorescence of *Desmaria* thus is its developmental relationship to a spur-shoot of several years' duration. In this I am assuming that the apex of the raceme aborts: that we cannot take this for granted, however, is shown by *Tristerix aphyllus* (see below).

2.4. TRISTERIX

The inflorescence of *Tristerix* is simply an indeterminate raceme of monads, the recaulescent bracts usually conspicuous, especially in the foliaceous bracts of *T. longebracteatus* (Fig. 8 – 2). In all but two species bracteoles are absent. However, in *T. grandiflorus* I have observed a minute bracteole occasionally subtending a flower (Fig. 8 – 4). In *T. tetrandrus* and *T. aphyllus* the monads are bracteolate (Fig. 8 – 6, 7). The position of the racemes is terminal to shoots in all species, but small, leafy inflorescences often occur in the leaf axils near the tip of the shoot, especially in *T. tetrandrus* and *T. verticellatus*. Long vegetative innovations later develop from below, extending beyond the older ones and again terminating in racemes.

The remarkable *T. aphyllus*, parasitic on large, columnar cacti in northern and central Chile, is almost completely leafless: its leaves are few and reduced to minute scales. Nearly the entire (visible) plant can be called an inflorescence which, as in other *Tristerix species*, is a raceme with rather few flowers. Below the flower-bearing portion of the raceme, one or more axillary buds develop in the second season, growing into additional inflorescences (Fig. 9 – 2). These in turn have a few basal leaves from the axils of which a third crop of flowers may be produced, and so forth for an undetermined number of seasons. While this system is somewhat condensed, it is not in principle different from that of other species of *Tristerix*. What is

different, however, is the fact that the tip of the raceme, instead of aborting, may be no more than temporarily arrested (Fig. 9 − 1), and may grow into a new raceme also. How common this is I do not know, but scrutiny of the plants in the field indicates the phenomenon to be not at all exceptional.

2.5. LIGARIA

The monotypic *Ligaria* has had a rather complex history, and has been much misinterpreted. In addition to its first and final assignments to *Loranthus* and *Ligaria*, respectively, it has also been placed in *Phrygilanthus* and *Psittacanthus*. Placement in *Phrygilanthus* (as done by Eichler, 1868) is not possible for a number of reasons, the most unambiguous one being the fact that this genus was nomenclaturally superfluous when published (Barlow & Wiens, 1973). Bentham & Hooker (1883) were not able to demonstrate the presence of endosperm in the seed of *Ligaria* and thus allied it to *Psittacanthus*. Van Tieghem confirmed this fact, and consequently placed his genus *Ligaria* within tribe *Psittacantheae* (Van Tieghem, 1895b). More recently, however, Bhatnagar and Chandra (1968) have shown convincingly that endosperm is indeed present in the mature seed. Rather than casting doubt on the validity of this character for *Psittacanthus*, as the latter authors do, I concur with Barlow & Wiens that this feature unequivocally removes *Ligaria* from the vicinity of *Psittacanthus*.

Van Tieghem (1895b) produced a very elaborate interpretation of the inflorescence, an interpretation which Eichler apparently shared. Van Tieghem regarded the axillary flower as an indeterminate raceme reduced to its ultimate, lateral flower. Thus the involucral cupule which subtends the flower by implication represents the fusion of one bract and two bracteoles, a situation which Van Tieghem compares to a monad of *Dendropemon*. Where more axillary flowers develop he views them as representing additional lateral flowers of the original raceme.

There are a number of reasons why this is not an acceptable interpretation. Careful scrutiny of the involucre shows that we are not concerned with one bract and two bracteoles. These three organs are, instead, morphologically equivalent: in fact, there are cases where there are four instead of three, as in the terminal flower of Fig. 9 − 4 (the callosed, brown tips of involucral lobes are reliable markers of foliar units, as the foliage leaves themselves also have such tips). The existence of four involucral bracts is quite incompatible with the concept of a bracteolate monad. Another fact which would be difficult to explain is that, where more than one axillary flower is present, there is no sign of a common peduncle which would correspond to a common inflorescence axis. I have not observed more than two additional axillary flowers; and these always occupy a prophyllar position. This is also true where such a pair of flowers flanks a vegetative innovation rather than an axillary flower. In all such cases the additional flowers (often there is only one) emerge directly from the axil of the subtending leaf.

Van Tieghem already observed that a floral penduncle occasionally bears a small leaf near the halfway point (see Fig. 9 − 3). In especially vigorous plants such a leaf may subtend a sessile flower which is flanked by two distinct prophylls but not by an involucre (Fig. 9 − 4). This situation is not comparable to the symmetrical dyad illustrated by Eichler (1868) which, since I have not been able to find anything like it in scrutinizing large numbers of specimens, I hold to be teratological. The 2-flowered inflorescences and those with an additional sterile leaf render Van

Tieghem's interpretation especially difficult, as one of the flowers is clearly terminal. A presumed pedunculate, lateral monad would not have any such additional organs.

My interpretation of *Ligaria* favors the concept of a determinate, (usually) one-flowered inflorescence with an involucre of 3 − 4 bracts. As Barlow & Wiens (1973) already indicated, this involucral cupule is very distinct from the cupule of many *Psittacanthus* species, where it represents an expansion of the terminal portion of a peduncle or pedicel.

The floriferous twigs of *Ligaria* may or may not branch in the first season, but all branch tips eventually seem to abort, producing a sympodial branch system.

2.6. PSITTACANTHUS AND AETANTHUS

The most complex genus in the New World, from the vantage point of inflorescence structure, is *Psittacanthus*. The small, closely related genus *Aetanthus*, as we shall see, poses no particular problems. The basic repeating unit in *Psittacantheae* is a standard, lateral triad, but these triads are arranged in a variety of ways, and may be reduced to dyads. Furthermore, there are several species which require special attention. This applies especially to *P. pusillus* and two peculiar species in northern Mexico, *P. sonorae* and *P. palmeri*, the latter being described as having a simple umbel of monads.

The various *Psittacanthus* inflorescence types are here regarded as derived from a raceme of triads of pedicellate flowers (Fig. 13 − 2). As in *Amyema* below, it appears useful to regard this generalized raceme as being made up of either paired or tripled triads. This latitude is acceptable because of the great variation in vegetative phyllotaxy: while the majority of species is decussate, others have their leaves whorled in threes or fours, and in some species the leaves are irregularly scattered. The basic type of inflorescence, a raceme of triads, is exemplified by such species as *P. cordatus*, *P. peronopetalus*, *P. schiedeanus*, *P. calyculatus*, and numerous others. The flowers in each triad have become sessile or nearly so in *P. cucullaris*, which is further discussed below. In some species, as in *P. cucullaris*, (Eichler, 1868, Pl. 7) the uppermost leaf axils may have small inflorescences which together form an integrated compound inflorescence.

A contraction of the main inflorescence axis, accompanied by a reduction in the number of triad-bearing nodes, has produced an umbel of triads in many species. This umbel may possess two, three, or four triads. Whether the latter type represents a single remaining node of an originally verticellate raceme, or two successive nodes of two triads each is here of no great moment, as both conditions might occur. In species like *P. drepanophyllus* and *P. acinarius* the latter is clearly the case (see illustrations in Eichler, 1868), and possibly also in *P. plagiophyllus*, *P. robustus*, and *P. collum-cygni*. The 2-rayed 'umbel' can also be seen as the basal remnant of the raceme and is found, for example, in *P. pinguis*, *P. biternatus*, *P. glaucocoma*, *P. grandifolius*, and *P. crassifolius*.

In each of these umbels the median flower of the triad has a tendency to disappear resulting, therefore, in umbels of dyads. Thus in *P. warmingii* and *P. ramiflorus* we find a 3-rayed umbel of dyads, and in *P. siphon* at least an approximation of a 4-rayed one. There are also a number of species with 2-rayed umbels of dyads, e.g., *P. dichrous*[1] and *P. lamprophyllus*, and probably all species of *Aetanthus*. In the latter

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[1] In this species, and in *P. claviceps*, dyads and triads may both occur on the same plant (Urban 1898).

two *Psittacanthus* species the peduncle uniting the two dyads is so short that it may easily be overlooked, so that it then seems as if individual dyads are directly attached to the stem.

The recently described *P. pusillus* (Kuijt, 1978) occupies what appears to be a unique position in the genus as far as inflorescences are concerned. Along a leafy innovation which aborts apically, small axillary inflorescences originate which in most cases seem to be nothing but dyads (Fig. 11 – 5). That these dyads are entire, not part-inflorescences is shown by their emergence from an axillary crater, and by the distinctness of their peduncles from the axillant leaves. In other words, the whole innovation cannot possibly be thought of as an inflorescence.

It might, of course, be suggested that such a single, truly axillary dyad in reality represents a simple racemic condition involving two monads, the terminal flower having aborted. Such a situation would be quite unexpected in *Psittacanthus* and, in fact, difficult to accommodate there. The true situation would seem to be indicated by the fact that the peduncle actually has two internodes (Fig. 11 – 5). The simplest explanation would therefore entail two pedunculate dyads on a common peduncle where one pedunculate dyad aborts. That this is the correct interpretation is shown by a rary inflorescence which indeed bears two dyads on a common peduncle (Fig. 11 – 5). I know of no other instance in the New World where such an asymmetrical reduction has taken place. It does occur in several instances in the paleotropics, however, as discussed elsewhere.

Psittacanthus sonorae of northern Mexico has an inflorescence composed of dyads of another sort. The dyad peduncle is long and at first sight seems to terminate in a terete, fleshy leaf. The latter is no other than the bract which has become foliar (normal foliage leaves are also terete). The two pedicellate flowers spring from that point where the peduncle-bract combination continues as a mere bract, each flower being subtended by a small but recognizable bracteole. In other words, *P. sonorae* simply has a raceme of dyads.

The other species from northern Mexico, *P. palmeri*, appears at first impossible to accommodate within the general *Psittacanthus* inflorescence scheme. Its inflorescence is described as an umbel of pedicellate monads subtended by an involucre of foliage leaves (Van Tieghem, 1895a). It is not altogether surprising that Van Tieghem erected a new, monotypic genus for such an extraordinary plant.

It turns out, however, that the inflorescence of *P. palmeri* has been misinterpreted, and that it constitutes no great deviation from *Psittacanthus* especially when placed alongside *P. sonorae*, a close relative. One of the problems is that the fleshy nature of *P. palmeri* renders it exceptionally brittle when dry, even in a family which is notorious for this feature. I have yet to see a complete *P. palmeri* inflorescence in any herbarium. The most complete one I have found is illustrated in Fig. 12 – 1 and demonstrates a number of interesting points. It may first be observed that, of the four 'involucral' leaves, one pair is inserted higher on the axis than the other pair. Since both pairs have axillary flowers, the inflorescence is not so much an umbel as an abbreviated raceme. The second important feature is the fact that the flowers are not single but paired in the axils of leaves. Finally, below each ovary we find not just a pedicel, but also an asymmetrical bracteole. My choice of the latter term already points the way to the solution of the riddle: the two axillary flowers of each leaf represent the two lateral flowers of a dyad the peduncle of which has disappeared. Since we must assume that the primary bract, as in all other species of *Psittacanthus*, must originally have been fused with that peduncle, we have here an

unusual case of a secondarily distinct bract. At any rate, the inflorescence of *P. palmeri* is an (abbreviated) raceme of dyads, not a simple umbel.

It is interesting to see how closely a teratological specimen of *P. schiedeanus* may approach the *P. palmeri* situation (Fig. 11 – 3). Here three distinct pedicellate flowers, together clearly representing a sessile triad without peduncle, emerge directly from the axil of a foliage leaf. While teratological specimens are always to be interpreted cautiously, this one demonstrates that no great genetic change has been involved to reach the *P. palmeri* situation. Disappearance of the median flower of the triad, a common phenomenon in the genus, is the remaining distinguishing feature.

The uncertain situation involving the Honduran '*Phrygilanthus nudus*' should be mentioned at this point. The species was described as such; however, *Phrygilanthus* as a generic name cannot be maintained (Barlow and Wiens, 1973), leaving the species in limbo except for the fact that Barlow and Wiens suggest that it may be a *Psittacanthus*. This would indeed seem to be the most likely possibility; unfortunately, the description of the only known specimen makes this transfer difficult, as the flowers are said to be arranged in umbels of 5 – 6 pedicellate flowers each subtended by an obliquely dilated cupule (Molina, 1952). The flowers are also said to be 5-merous, a condition not otherwise known in *Psittacanthus*. This description is reminiscent of the South American genus *Tristerix*. Instead, I suspect that there are some serious flaws in Molina's diagnosis. Except for the 5-merous condition of the flower, all of Molina's statements are compatible with my re-interpretation of the inflorescence of *P. palmeri*, and I would suggest that *P. nudus* be seen in the same light until more adequate material becomes available.

There remains, finally, the question of the cupule in *Psittacanthus*. This structure, of variable prominence in different species, especially in South America, has led some of the best students of *Loranthaceae* astray (see, for example, Eichler, 1868, 1875, and Danser 1933b). The pedicels of many species even in more northerly areas have a distinct tendency to expand at the apex, just below the ovary. This is what earned one species the rather misleading name *P. calyculatus* — misleading in that the proper calyculus is a structure surmounting the ovary rather than subtending it. In several South American species the cupule has completely or partly enveloped the ovary (especially in *P. cordatus* and *P. cucullaris*), in one case even hiding the mature fruit. It is possible that the cupules, at least the larger ones, have their own vascular supply. Had only the two lateral flowers had such a cupule, or had the cupule of the median one been fused with its primary bract, all might have been well; however, the large median bract subtends all three flowers (which are more or less sessile) but is quite distinct from their cupules. One feature which is particularly deceptive is the fact that the margin of the median cupule is usually somewhat irregularly toothed, thus suggesting the fusion of three foliar organs. This conformation produces serious problems in interpretation when compared to other *Loranthaceae*, especially to other species of *Psittacanthus*.

Eichler supplied a solution to the dilemma which at that time was unique in *Loranthaceae*. He interpolated a trio of bracts which, upon fusion, would result in the median cupule, the lateral cupules each being the result of fusion of three bracts as well, of which the outermost one in each case corresponded to a prophyllar bracteole. This conception radically changes the nature of the triad, as it implies a morphological equivalence among the three flowers of a triad. The logical conclusion of this concept was not, however, drawn by Eichler but by Van Tieghem

(1895b & c): the triad in these and some other *Loranthaceae* now came to represent an 'ombellule' of equivalent members: a terminal (fourth) flower has aborted. Van Tieghem may well have derived this idea from one of the details of Eichler's authoritative illustrations (1868, Plate 1, Fig. 41), showing precisely such a 4-flowered determinate inflorescence in *Amyema pendula*. While Danser (1933b), unfortunately, followed Eichler too closely in this elaborate explanation, he nevertheless rejected as very improbable Van Tieghem's view of the triad as the remnant of an umbel with aborted terminal flower, and urged postponement of extreme interpretations until a better foundation of fact exists.

There is a much simpler and much more satisfactory explanation of the *Psittacanthus* cupule, one which is more closely in harmony with the morphology of other *Loranthaceae*. It is a view already implicit in the above description of the expansion of the top of the pedicel. If the cupule of the median flower shows marginal teeth, this may be a simple 'pressure effect' engendered during its early ontogeny; the ridges correspond to space available in otherwise crowded surroundings. In his earliest writings on the subject Eichler (1868) himself, in fact, mentions this idea, and cannot quite decide between it and the 'foliar bracts hypothesis', even though his sympathies lie in the latter direction. In his 'Blüthendiagramme' Eichler (1875) is much less cautious and simply states that the cupules represent three fused bracts each.

In the case of the cupules of lateral flowers the true state of affairs can be seen in very young triads (Fig. 12 — 2), where the bracteoles are relatively very prominent. As time proceeds, the lateral cupules seem to catch up with the bracteoles (Fig. 12 — 3). In some cases they develop marginal teeth (Fig. 12 — 4) but in others they are quite smooth-margined. Even in old cupules with mature flowers or fruits the bracteoles retain their identity although fused with the cupules (Fig. 12 — 5, 6). In contrast to Eichler's contentions, no convincing case for a further set of bracteoles (of the second order) can be made. In other words, the triad of *P. cucullaris* and *P. cordatus* is in no significant way different from the standard Loranthaceous triad as depicted, for example, in many of Eichler's own illustrations, except for the evolutionary addition of a cupule to each of the three flowers, this cupule being an outgrowth of the tip of the pedicel.

3. LORANTHACEAE OF THE OLD WORLD

The inflorescences of the *Loranthaceae* of the Old World are generally more diverse than those of the New, and are consequently difficult to present in a clearly organized scheme. One of the problems here is that there are several species within which much variation exists, as in *Tupeia*; in others, morphological interpretation is very difficult. There are also far more genera of *Loranthaceae* in the Old World than in the New. In an effort to follow the treatment of the taxa of the New World, I will follow as much as possible the same sequence from presumed primitive conditions to more advanced ones.

3.1 NEW ZEALAND TAXA AND MUELLERINA[1].

One inflorescence type which seems generally absent from the Old World (at least

[1] The occurrence of *Muellerina* in New Zealand is questionable (Barlow 1966).

as a consistent feature) is the determinate one with lateral monads. The solitary exception to this rule is *Alepis flavida*.

Alepis flavida is described as having a single axillary inflorescence subtended by a few decussate pairs of deciduous scale leaves (Barlow, 1966). The single, terminal flower is followed by several decussate pairs of lateral flowers. Each flower is pedicellate and subtended by a bract and a pair of bracteoles all of which are deciduous, the bracteoles being placed directly below the ovary. In other words, this would make the inflorescence a determinate raceme with bracteolate monads.

Scrutiny of herbarium material has added some important details. First of all, the racemes are subtended not only by several pairs of scale leaves but also by a clearly marked pair of brown prophyllar scales. The lower flowers are indeed bracteolate, these organs and the bract itself leaving brown and somewhat callused scars when falling (Fig. 14–2, 3). The uppermost monads, however, do not have bracteoles (Fig. 14–1); in fact, even a bract or its scar is difficult to locate, although a slight swelling occurs at those nodes. There is thus some variation within each inflorescence, the presumedly more advanced condition characterizing the lower portion.

From the situation in *Alepis* it is only a small step to that of *Peraxilla*, the two genera apparently being closely related (Barlow, 1966). Barlow indicates that the inflorescence of *Peraxilla* is a spike of 1 to 5 flowers – in other words, a terminal flower which is either solitary or accompanied by 1 or 2 pairs of lateral, sessile flowers in the axils of deciduous bracts. This description again requires some amplification (see also Hooker, 1844).

My impression is that flower number to a large extent is an individual feature. The possibility that nutrient status or host species influences the number of flowers cannot, however, be excluded. At any rate, in some collections (e.g., *Elphick s.n.*, Herb. Univ. Canterbury), 5-flowered spikes are normal; in some (e.g., *Petrie s.n.* and *Hamilton s.n.*, *WELTU 3582* and *3580*, respectively), 3-flowered ones predominate; while in at least some others (*Holloway s.n.*, *OTAGO U 002074*), mostly 1-flowered inflorescences occur. In the latter specimen we sometimes find the solitary flowers on a pedicl of a single internode, at other times the pedicel is articulate in the middle, showing it to consist of two internodes. The pedicel terminates in two conspicuous lobes which are prophyllar in orientation (Fig. 14–6). All the above are *P. colensoi*. The two specimens of *P. tetrapetala* which I have seen (*Franklin s.n.*, and *Kirk s.n.*, *WELTU 3583* and *3589*, respectively) have all or nearly all 1-flowered inflorescences; again there are two scar-like areas in prophyllar positions at the top of the pedicel. In both *Alepis* and *Peraxilla* the tips of branches frequently (always ?) abort (see Fig. 14–5, 5, and Hooker, 1844, for *Peraxilla*), the branching pattern thus becoming bifurcate or at least sympodial.

One consistent difference between the two genera lies in the origin of inflorescences. In *Alepis*, as stated, there are two distinct prophylls; no further modification is visible in the axillary region. In *Peraxilla* an axillary bulge is formed bearing short, superficial hairs but no evident prophylls (Fig. 14–5). This axillary cushion is of exactly the same nature as comparable ones in *Cladocolea* (Kuijt, 1975a) and others in that it harbors the primordial flower or inflorescence which later breaks through this covering, leaving an irregular, two lobed rim of sclerotic or corky tissue (Fig. 14–6). Nothing of the sort is visible in *Alepis*.

In *Tupeia* the same bifurcate habit is seen, but here the direct cause is different: the inflorescence is terminal, the 2 or 4 (rarely 6) axillary innovations from the foliage

leaves below eventually overtopping it and each again terminating in one or two pairs of leaves plus terminal inflorescence (separately, there also are vigorous leafy, strictly vegetative long shoots which abort at the tips). The inflorescence is always determinate (Fig. 14 − 9). In some plants (e.g., *Knox s.n., WELTU 11223*) all lateral units are 1-flowered. In the majority of plants, however, the lowest lateral units are triads instead. These triads are the standard ones which we have encountered in the New World in that they combine a median (in this case pedicellate) flower with two lateral, also pedicellate ones. A curious feature in *Tupeia* is the fact that the flowers often lack subtending bracts completely. In some cases, however, flat, linear flower bracts are present; in others a minute, articulate scale-leaf may be seen below the flower. The flower-bearing nodes of the inflorescence are strongly articulate, and the 'absence' of flower bracts, as in *Alepis*, seems to be a reductional phenomenon.

The most variable genus in New Zealand with respect to inflorescence morphology is *Ileostylus*. Since it has always been tempting to compare the genus with *Tupeia* it might be appropriate to say first that the two differ strikingly in the way inflorescences originate. That of *Tupeia* has a regular origin as a lateral branch, where it is basally flanked by two prophylls. The inflorescence of *Ileostylus*, in contrast, has a similar pseudo-endogenous development as that of *Peraxilla*. A capsule-like, light brown cover forms over the bud which splits off as the latter expands. The process appears irregular in some (*Curran s.n., WELTU 3603*), but in others the capsule is somewhat pointed and splits in a median fashion (*Knox s.n., WELTU 11225*). The capsule may also be rounded (*McKann s.n., WELTU 9095*).

The indeterminate raceme of triads is always the most common one. Sometimes, however, such an inflorescence is topped by a pair of pedicellate monads, or even a single, pedicellate terminal flower. I have no doubt that the two lateral monads and the terminal flower are sometimes combined in the same inflorescence. Always at least the lower part of the raceme is triadic in organization. The triads are each supplied with a normal recaulescent bract and two recaulescent bracteoles (lateral flowers), the median flower being pedicellate.

Quite different from the other New Zealand taxa is *Trilepidea*, a monotypic genus now probably extinct. Since I have not seen adequate material of it, I have redrawn Barlow's (1966) illustration of the inflorescence (Fig. 14 − 8), and also base my remarks on his description. The inflorescence is a short, indeterminate raceme with 2 − 4 decussate flowers, and is subtended by a series of basal scale-leaves, terminating in a sterile tip with recognizable, aborted leafy organs. Each flower is borne by one recaulescent bract and two bracteoles. *Trilepidea* is thus unique in New Zealand *Loranthaceae* in being consistently indeterminate and in having bracteolate monads.

The Australian genus *Muellerina* is here included not because of any presumed affinity with New Zealand taxa (this is not precluded; see the cytotaxonomic evidence in Barlow and Wiens, 1971) but because of its similarity in inflorescence variability. The inflorescence is an indeterminate raceme (not determinate, as Barlow and Wiens, 1973, write) which occupies a terminal position. From the two leaf axils below, new lateral shoots are produced which, after producing a pair of leaves, again terminate in an inflorescence. Thus a strictly bifurcate habit characterizes *Muellerina* as it does, for example, *Tupeia*. In *M. bidwillii* the raceme bears only two (rarely four) flowers, namely two (4) pedicellate, ebracteolate monads. In *M. celastroides* and frequently in *M. eucalyptoides* the raceme instead bears 4 triads which have a sessile median and pedicellate lateral flowers. In some

areas (especially in Queensland: Barlow, 1966) the raceme bears 4 pedicellate, ebracteolate monads only. Mixed racemes also occur with 4 triads below and two monads above.

3.2. INDETERMINATE INFLORESCENCES WITH EBRACTEOLATE MONADS

There are rather a large number of Old World taxa which are characterized by indeterminate inflorescences with ebracteolate monads and, frequently, recaulescent bracts. This includes all African taxa which, partly because of taxonomic complexities, are not listed separately here (see Wiens, 1979, for Southern Africa). From elsewhere we include the genera *Barathranthus*, *Cecarria*, *Dendrophthoe*, *Helixanthera*, *Kingella*, *Loranthus*, *Lysiana*, *Scurrula*, *Taxillus*, *Tolypanthus*, *Trithecanthera*, and probably *Papuanthes*.

It is necessary here to interpolate a brief note with regard to *Loranthus europaeus*. This, the only European member of the family, and the type species of the type genus, is still inadequately known from our perspective. It has always been considered to possess an indeterminate inflorescence, and this is undoubtedly correct in many cases. However, I was surprised to discover that inflorescences may, upon occasion, be truly determinate. An unequivocal, female example is illustrated in Fig. 15 − 4. At least one male collection has been seen where determinate inflorescences are also common (*Baenitz s.n.*, CAS). Taking into account the sessile nature of the flowers, the terminal inflorescence and the consequent bifurcate branching pattern, as well as the dioecious condition, we can suddenly see that *Loranthus europaeus* and *Tupeia antarctica* may be very closely related, indeed. While such a close affinity at first sight seems to be denied by geographic distance it must be remembered that *Loranthus* also occurs in parts of South-East Asia.

The great majority of species in the larger genera of this catagory (*Helixanthera*, *Dendrophthoe*, and *Scurrula*), have elongated racemes with numerous flowers. Representative illustrations of these may be found in Danser (1931); a few-flowered species of *Helixanthera*, *H. ligustrina*, is shown in Fig. 15 − 2. Fig. 15 − 3 shows a different collection of the same species where the primary axillary inflorescence is 2-flowered only. Below it, in prophyllar positions, are two structures which I would interpret as secondary racemes each reduced to the inflorescence axis and a single, pedicellate flower. The fact that each is articulate (made up of two internodes) makes it impossible to regard them as simply the lowest two monads of the main inflorescence (for other examples of asymmetrical reduction, see under *Amyema*, *Lysiana*, and *Psittacanthus*).

In some species of *Helixanthera* and *Dendrophthoe* the pedicels are little or not at all developed, and we can speak of spikes. This we also find in *Kingella* and *Loranthus* (Danser, 1933a). Probably the largest spike in Loranthaceae occurs in *Trithecanthera* from Borneo. The floriferous portion of it may be up to 12 cm long, and is followed by a curious sterile portion about twice as long (Danser, 1931). A prominent bract clasps the base of each flower. Danser does not state this fact, but the inflorescence seems to hang down and the flowers, which may be up to 15 cm long, stand erect above the long, sterile tail. It would be interesting to know if the sterile tail serves as a perch for nectar-collecting birds.

Contraction to an umbel has occurred in a number of unrelated groups, for example in *Taxillus*. Small umbels are known also in African taxa, as in the one here illustrated, *Globimetula* (Fig. 15 − 1). In *Cecarria* the inflorescence is also described as a 2-flowered umbel which rarely is a 4-flowered raceme or spike (Barlow &

Wiens, 1973). It would seem more likely that the 2-flowered condition is derived from a raceme, also. The variability of this inflorescence invites a more careful analysis when materials become available.

The Australian genus *Lysiana* warrants a few separate comments. There is little doubt that its inflorescence is basically a few-rayed umbel, as seen especially in the occasionally 3-rayed ones of *L. subfalcata* (Fig. 16 – 1), although Barlow (1963) speaks of occasional 3- or 4-flowered racemes. The concaulescent bracts of many *Lysiana* species are especially clear, the decurrent base running down all the way to the inflorescence axis. In most cases the umbel has only two rays (Figs. 16 – 2, 3). In *L. exocarpi* the pedicel is extremely short, and one-rayed 'umbels' are quite common (Fig. 16 – 4). It seems clear that this represents an asymmetrical type of reduction. The resultant reduced inflorescence is identical to those in some species of *Amyema* and *Sogerianthe*. In *L. murrayi* (Fig. 16 – 5) the flowers are long-pedicellate and, at first sight, appear to emerge directly from the axil, usually in pairs. When these pedicels are removed, however, we see an extremely short, cushion-like peduncle to which the pedicels are attached. In other words, the flowers (which, when paired, have a prophyllar position as shown by the concaulescent bracts) are not morphologically axillary even though they seem to be. This is true also where a single 'axillary' flower develops. In this species the ovary is clasped not only by the free part of the bract but also by an irregularly toothed extension of the pedicel, which is very reminiscent of the *Sogerianthe* situation to be discussed later.

In *Barathranthus* the inflorescence is called a *capitulum* by Danser (1931) but the material I have seen does not allow for confirmation, partly because of the small size of the inflorescence. There seems to be no reason to doubt Danser's description of *Barathranthus*, which is thus one of the very few paleotropical genera characterized by capitula of ebracteolate monads.

A final, small genus also characterized by a type of capitulum is *Tolypanthus*. Its inflorescences are borne on short peduncles below which a corky crater-rim is discernible. They appear to develop in a transverse zone as in many *Amyema* species, eventually nearly engirdling the node. The number of involucral bracts is 3 or 4; these bracts are nearly free in species such as *T. involucratus* (Fig. 17 – 1) and *T. gardneri*, but concrescent in *T. lageniferus*. It does not seem to have been noted by earlier authors that the involucral bracts in reality are greatly expanded floral bracts, one flower being sessile on the base of each bract (Fig. 17 – 1, below); the flowers are anything but ebracteate (cf. Wiens, 1973).

3.3. INDETERMINATE INFLORESCENCES WITH BRACTEOLATE MONADS

As a further step in development there are a number of taxa which have indeterminate inflorescences of monads, these latter being provided with bracteoles. Of these, *Trilepidea* has already been referred to under 3.1. In the same section *Alepis* is mentioned, at least the lower monads of which are bracteolate. *Amylotheca* *s.s.* sometimes has bracteolate monads (Barlow, 1966, 1974) but, since triads predominate, more correctly belongs in the following section.

The simplest condition is met in the rare, monotypic Australian genus *Atkinsonia* which possesses an indeterminate raceme with short-stalked, bracteolate monads. This inflorescence is comparable to that of *Elytranthe* and *Lepidaria* except that there the monads are sessile, and that the inflorescence in the latter is capitulate. In *Macrosolen* both these conditions occur; in fact, its inflorescence varies from a raceme to a spike, to an umbel and nearly to a capitulum (Danser, 1931). A true

capitulum is seen in *Lepidaria* (Danser, 1931, Fig. 8), even though the basal portion of all flowers is hidden by a set of large, imbricate involucral bracts.

The genus *Papuanthes* from New Guinea is characterized by a short-rayed umbel (Danser, 1931) in which the flowers are protected by bracts. In this case there are only two, very broad bracts, which are fused nearly to the halfway point. Each flower is said to be bracteolate. Unfortunately, material of this curious genus is extremely scarce, and puzzling facts such as the articulation on each pedicel cannot be further studied at this moment.

3.4. INDETERMINATE INFLORESCENCES WITH BRACTEOLATE TRIADS OR DYADS, INCLUDING THAUMASIANTHES

There are at least a dozen Old World genera in which we find indeterminate inflorescences with fully differentiated lateral triads of the dichasial type. Since none of these (except *Nuytsia*) show recognizable affinities with New World taxa, the evolution of triads must thus have proceeded independently in the two hemispheres.

First, a correction: Danser (1933a, p. 18) indicated that the African *Amyema subalata* has an inflorescence made up of triads. In the herbarium at Copenhagen there are three specimens from Zaire (*Lebrun 2010, 4019*, and *Louis 10078*, all originating from the Brussel Herbarium (BR) where De Wildeman, the author of the species, worked). The plants show an indeterminate, small raceme which sometimes has three flowers, each flower bracteate. No lateral triad of any sort is visible, and I conclude De Wildeman's analysis was in error. This would leave all African *Loranthaceae* monadic and ebracteolate.

Secondly, an omission: or, rather, a postponement. Many species of *Amyema* fall into the present category. The problems in that genus are so complex, however, that a separate section is devoted to it (3.5).

Thirdly, an irregularity: the rare genus *Thaumasianthes* has problems of interpretation specifically its own. The inflorescence is triadic but not uniformly so. A discussion of this curious inflorescence is placed at the end of the present section.

Proceeding now to the details of inflorescences in this category, we can first state that triads are decussate in arrangement in *Nuytsia, Decaisnina, Amylotheca*, and *Loxanthera*. In *Amylotheca* the flowers tend to be erect on more or less spreading inflorescence axes (see illustrations in Danser, 1931). All three flowers may be sessile in some *Decaisnina*, but more commonly in this genus as well as in *Nuytsia* and *Amylotheca* only the lateral ones are pedicellate. All three flowers of the triad are pedicellate in *Loxanthera* (Danser, 1931).

I have not encountered examples where triads are grouped on spikes, as in some neotropical species. In *Lampas* they form a short-rayed umbel remarkable in that the bracts are not recaulescent with the pedicels (Danser, 1931). The situation clearly approaches a capitulum.

In a number of genera triads are arranged in capitula. In *Dicymanthes* (if the genus is recognized as separate from *Amyema*) these capitula, as the name suggests, are composed of a pair of triads on a short common peduncle (Fig. 17 – 3). In two species there is a further remarkable development: most inflorescences emerge directly from the internodes without any reference to leaves, very much like *Stichianthus minutiflorus* Valeton (*Rubiaceae*: Winkler, 1931).

Three of the four genera with triadic capitula (*Diplatia* Fig. 17 – 2; *Distrianthes*, Fig. 18 – 1; and *Lepeostegeres*, Fig. 18 – 3) have evolved a system of prominent bracts which ensheath the flowers. In the latter genus the young inflorescences are

placed in a very prominent crater-like rim (Fig. 18 – 2). At that stage only two bracts are visible. At or near anthesis the 16 – 50 flowers have emerged and the other two pairs of bracts are also visible. The flowers are arranged in triads; in some plants the bracteoles are recognizable as very slender organs about 2 mm long, but in others they seem to be totally absent (Fig. 18 – 4). The outermost four triads are placed in the axils of the innermost four bracts, and the remaining triads are in more or less regular decussate positions in the more central area (Danser, 1931; Schaeppi, 1945). In the remaining two genera there are only two large bracts, broad, flat and free in *Diplatia* (Fig. 17 – 2), but pointed, navicular and basally concrescent in *Distrianthes* (Fig. 18 – 1). In the former, the inflorescences are always axillary in position; in the latter, they may be found in flower zones at the nodes or directly on the epicortical roots. In each case six flowers are arranged in two axillary triads.

This leaves us with the remarkable genus *Cyne*, the flower arrangement of which until now has not been known. The inflorescence is a sessile capitulum which in its earlier stages is completely encased by a leathery capsule (Fig. 19 – 1). This capsule is composed of corky tissue apparently lacking any vascular tissue, and thus is comparable to (but much larger than) the various other corky coverings which occur on flowers and inflorescences of many other *Loranthaceae*, both in the Old World and the New. The capsule eventually splits and falls off through the expansion of the flowers, leaving a circular scar below the inflorescence. The capsule is thus not, as Danser (1929) implied, of a foliar nature.

The capitulum of *C. banahaensis* bears twelve flowers, consisting of a central cluster of four surrounded by a whorl of eight (Figs. 19 – 2, 3, 4). What thus appears to be a very unusual arrangement upon closer scrutiny resolves itself into four regular, sessile triads. In the outer whorl are placed the outer two triads, each with a large bract and two smaller bracteoles; additionally, the two median flowers of the inner triads are placed in the same whorl. Thus the inner cluster of four flowers consists of the four lateral flowers of the inner two triads. The placement of bracts and bracteoles on the capitulum leaves no room for other interpretations. In *C. alternifolia* the capitulum appears to bear six flowers, which we may assume to be two triads.

One further modification has evolved in *Tetradyas*, a monotypic genus endemic to the Sogeri region of eastern New Guinea. I am not sure that any collection beyond the type collection has been made in the intervening years, and I am thus dependent upon Danser's data. The inflorescence is a capitulum with 8 flowers arranged in 4 dyads. Each dyad is partly enveloped by a broad bract on the outside and two smaller bracteoles on the inside, the bracteoles each accompanying a lateral flower. Danser noted a group of 8 very young flower buds in the axil of one of the involucral bracts and concluded that the inflorescence can therefore proliferate. It is to be hoped that new and more extensive collections will shed more light on this unique genus.

There finally remains yet another rare, monotypic genus, *Thaumasianthes*, which is known from the Philippines only. It was described by Danser (1933b) on the basis of very scant materials, and no further collections seem to have been made since that time. This is very unfortunate: the facts which Danser reports are most unusual but, as he was aware, need confirmation on a more extensive scale than can be provided. I shall start with a resumé of Danser's comments, and try to place it in the general context of the ideas which I have developed. This is best done with reference to the inflorescence diagram in Danser (1933b).

The inflorescence of *Thaumasianthes*, like those of several other paleotropical genera, is characterized by a number of large, broad, decussate bracts which obscure the basal portions of the flowers. All bracts are floriferous. The lowest four bracts each subtend an axillary triad. The median flower of each triad is surrounded by three distinct bracteoles which are narrow and elongate, extending far beyond the ovary. Lateral flowers are situated in the axil of a keeled, prophyllar bracteole on each side of the median flower, but also themselves possess a pair of small, slightly keeled bracteoles of the second order; these are displaced somewhat in the direction of the median flower. There is nothing particularly unusual about such a triad except for the three bracteoles flanking the median flower, which in position are somewhat reminiscent of the three elongated, bract-like structures encircling the terminal flower of the tetrad in *Amyema dilatipes* (Fig. 20 – 1, 2, 6). The bracteoles of the second order flanking the lateral flowers may not be found elsewhere in paleotropical *Loranthaceae*, but identical ones are reported from *Phthirusa pyrifolia* (Kuijt and Weberling 1972). Danser places what we may call the median bracteoles in such a way that one is directly adaxial to the median flower. The fifth and sixth bracts also subtend one triad each, these being different from the lower ones only in lacking bracteoles of the second order. The seventh and eighth bracts possess one flower each, provided only with a pair of bracteoles. The single flowers belonging to the ninth and tenth bracts seem to be ebracteolate, but since they are immature this cannot be taken for granted. The inflorescence as a whole is indeterminate. Thus far the data provided by Danser.

The main features to be noted, in summary, are (1) the second-order bracteoles; (2) the curious median bracteoles; and (3) the remarkable transition within a single inflorescence from complex triads below to monads above.

It is my good fortune to have discovered a new specimen of *Thaumasianthes amplifolius*, enabling me to report on the structure of a single, mature inflorescence (Fig. 20). The inflorescence was not complete, and the profusion of bract-like organs leaves a few uncertainties. I might add that my dissection of this inflorescence confirms my great admiration for the work of Danser whose observations here, as in most other places, are substantially correct.

The bracts are very fleshy and decrease rapidly in size, especially in width, beyond the first four. They are decussately arranged. The lowest four bracts are essentially as Danser describes them. Each bears a triad of sessile flowers with nine associated bracteoles. The outermost two are different in size and shape from the other seven: they are very strongly keeled, rather thick, and much broader. More importantly, their insertion encloses, in each case, two of the remaining bracteoles.

Thus there are seven bracteoles of more or less the same shape and size. They are somewhat keeled, and approximately 1 cm long. Beyond the four which, as said above, are associated with the two largest ones, there are three which are placed as Danser indicated: one on the adaxial, and two on the abaxial side of the median flower. Danser was thus correct in stating that each flower of the triad was accompanied by three bracteoles.

At a somewhat higher level Danser refers to triads which are like the lower ones except that the lateral flowers possess no bracteoles of the second order. In my specimen this was also true but the median flower now seems to have only its two abaxial bracteoles. On the other side of the inflorescence the companion bract subtended only one flower: bracteoles of the first order were present and, in addition, one bracteole in a position abaxial to the single flower. In the next higher

pair of bracts, one subtended an axillary complex exactly like the last-mentioned one except that the single bracteole now occupied an adaxial position instead (Fig. 20 – 6).

At the apex of the inflorescence stood a solitary flower (Fig. 20 – 5). It was accompanied, first of all, by a rather stout bract. Opposing the latter were two bracteoles, and one very small bracteole stood to the side.

It can thus be seen that the main outlines of Danser's analysis are confirmed. Differences lie in the bracteoles, the number and position of which appear to be somewhat more variable than Danser thought; and in the single, apparently terminal flower.

It is quite clear that Danser's view of this curious inflorescence is strongly influenced by Eichler's interpretion (1868, 1875) of the inflorescence of the neotropical *Psittacanthus*, which has been discussed in section 2.6. The inflorescence of *Thaumasianthes*, Danser writes, represents a reduction from a more compound one. The upper, single axillary flowers are reduced triads; the disappearance of the median bracteoles is the first event in the reduction of triads. The original inflorescence had triads in which every flower was flanked by three bracteoles. Danser then refers to Eichler's similar interpretation of *Psittacanthus*.

It should be noted that the original triads as viewed by Danser (and, in addition to Eichler, also by Van Tieghem, 1895b) is something quite different from the lateral triads which we know from such genera as *Struthanthus*, *Amylotheca*, *Nuytsia*, and many others. In those groups there is a primary flower and two lateral, secondary flowers. The above views of *Thaumasianthes* and *Psittacanthus*, on the contrary, are based on the existence of an umbel of three morphologically equivalent flowers, each with three bracteoles of an involucral nature. Van Tieghem actually takes one further step to postulate the earlier disappearance of a fourth, terminal flower from this 'ombellule', a step which Danser cautiously refrains from taking.

Danser's interpretation (and Eichler's of *Psittacanthus*) is awkward, as he himself obviously sensed. For one thing it takes no account of the striking dimorphism within the nine bracteoles, and of the constant position of the largest two. It also fails to cope with the fact that the position of the three bracteoles of each flower differs between median and lateral flowers. The bracteoles are evenly spaced for the former but not so for the latter. Each lateral flower has one large, keeled bracteole which partly encloses two smaller ones toward the median flower.

The correct interpretation, it seems to me, equates the triads of *Thaumasianthes* with those occurring commonly in many other *Loranthaceae*. I reject the concept of a more compound inflorescence from which that of *Thaumasianthes* (or *Psittacanthus*) is derived by means of reduction. Without the median flower, I am convinced that Danser and Eichler would have seen that each lateral flower is subtended by one prophyllar bracteole, and has two such bracteoles of its own on the other side (i.e., a pair of prophyllar bracteoles of the second order). This is identical to some situations in the triads of *Phthirusa* where the latter bracteoles may (rarely) even subtend flowers of the third order (Kuijt and Weberling, 1972). This interpretation also accounts for the fact that the second-order bracteoles nestle within the larger bracteole rather than meeting marginally. There seems to be no real alternative to this interpretation: the two large bracteoles are undeniably bracteoles to the median flower; the two lateral flowers are situated normally, and are thus not equivalent to the primary one; and the four bracteoles belonging to the lateral flowers are also normal in position.

This simpler interpretation, of course, fails to account for the curious median bracteoles, which in number vary from one to three, in the same way that my interpretation of *Psittacanthus* fails to provide an organ-derived explanation of the median cupule. The variability in number and (to some extent) in position of median bracteoles, however, warrants some caution in their interpretation. In the last analysis there may be no alternative to regard them as a 'de novo' development, as the *Psittacanthus* cupule clearly is.

There remains the question of the 'terminal' flower illustrated in Fig. 20–5. Danser believed the inflorescence to be indeterminate, and it may be that he is correct in that, also. The fact that the flower in question is subtended by a bract is not conclusive either way: on the one hand, the uppermost lateral flower may, in species such as *Cladocolea mcvaughii*, occupy a pseudoterminal position; on the other hand, truly terminal flowers in a number of cases in *Cladocolea* are subtended by a separate internode (Kuijt, 1975a). One reason to consider, in this case, the possibility of a terminal flower is the fact that it is significantly larger than any of the adjacent ones; however, unlike the triadic flowers below, these upper ones had not yet opened. This question is only one of several which require better material before *Thaumasianthes* can be adequately understood.

3.5. THE AMYEMA COMPLEX

The genus *Amyema* consists of some 90 species distributed throughout the Malay Archipelago, the Philippines, Australia, possibly with one or two species in Africa (Danser, 1933a). The greatest concentration of species is in New Guinea and adjacent areas. Major regional treatments may be found in Danser (1931, 1933a) and Barlow (1966, 1974).

The genus is exceptionally complex; generic concepts have not been stable, and significant changes may still be necessary in the future. My present focus, of course, is not on such changes but rather on the diversity and relationships of inflorescences. For such a task we need to consider also the other genera of what might be referred to as the *Amyema* complex. This consists of at least the following taxa: *Amyema*, *Dactyliophora*, *Dicymanthes*, *Diplatia*, *Distrianthes*, *Papuanthes*, *Rhizomonanthes*, *Sogerianthe*, and *Tetradyas*. Several of these have already been detailed in the previous section. It should be said that even Danser regarded this as a tentative assemblage; he was not certain, for example, that *Tetradyas* and *Papuanthes* were truly related to *Amyema* (Danser, 1933a). The paucity of subsequent collections in several of these genera does not allow us to move beyond Danser's uncertainty. It is conceivable that *Cyne*, already discussed above, also belongs in this assemblage.

Although Danser relied heavily on the inflorescence for taxonomic characters especially at the generic level, it remained to Barlow (1966) to provide a synthesis of various *Amyema* inflorescence types. Barlow's basic assumption, as evident in his Fig. 5 and also stated elsewhere, is that the inflorescence of *Amyema* is primarily a pedunculate, many-rayed compound umbel of triads which by a process of reduction has resulted in the numerous simpler types. This reduction refers to a decrease in the number of flowers per constituent unit, the median flower of triads having a tendency to disappear first; to reduction in the number of rays of simple and compound umbels; and to contraction of various peduncles and pedicels. I have mentioned earlier my trepidation in accepting reduction as the sole or major evolutionary trend, and thus find it difficult to accept Barlow's version in its

entirety. I will therefore attempt to replace it with one which to me seems closer to evolutionary reality; however, it will be seen that I do not reject all features of Barlow's construction.

The starting point of my argument lies in the observation that phyllotaxy in the *Amyema* complex is diverse; beyond some instances of scattered leaves (Barlow, 1974), leaves are paired or in whorls. In a previous paper I have already shown how deceptive phyllotaxy can be in the complex (Kuijt, 1980b), but the truly whorled as well as the paired conditions are each clearly established. For example, whorled phyllotaxy is found in *A. dilatipes* and *A. scandens*. My point here is that this phyllotactic variability has a bearing on the branching patterns of inflorescences.

I would propose as the fundamental inflorescence type a simple umbel of 2 or 3 ebracteolate monads; for reasons stated above there seems no need to choose between the two forms. In all probability this inflorescence represents a somewhat derived condition from an earlier racemic one involving successive single, whorled or paired monads, an inflorescence type common in other *Loranthaceae*, but this need not concern us within the *Amyema* complex.

Perhaps the major trend has been one which is also seen in numerous other genera throughout *Loranthaceae*: the evolutionary change from monads to dichasial triads, which amounts to the development of two lateral flowers in the axils of the bracteoles of such a monad. Thus the plant is provided with a pair or a whorl of such triads, a condition known in numerous species.

Two major, further changes have affected these structures. A rather simple change is the contraction of pedicels of lateral flowers, resulting in a trio of sessile flowers, the median and its bract being recognizable as primary over the lateral ones and their bracteoles (there is no a priori reason why this sessile condition might not instead have led to the pedicellate one, but the question is not significant in the overall scheme). In some instances in *Amyema* even the triadic peduncles have disappeared, giving us a small, pedunculate capitulum made up of two completely sessile triads, as in *A. maidenii* (Fig. 22 – 1) and *A. tetrapetala* (Fig. 22 – 2), and also in *Dicymanthes* (Fig. 17 – 3). It is easy to see how the genera *Diplatia* and *Distrianthes* are modifications of this type, differing only in the development of the two primary bracts into a pair of large, protective organs ensheathing the basal portion of the six flowers. The other kind of evolutionary change which has taken place is again one which is seen in triads elsewhere in *Loranthaceae* (see especially *Psittacanthus* and *Aetanthus*): it is the disappearance of the median flower of the triad, reducing it to a dichasial dyad. Many species of *Amyema* show this change.

A special problem is here poised by *A. gibberula* in which the entire inflorescence consists of such a dichasial dyad — supported, however, by a clearly articulate peduncle (Fig. 22 – 4)[1]. It is probable that this inflorescence represents one further step in reduction, namely the disappearance of all but one of the dichasia. Such an asymmetrical reduction seems unusual, and I would hesitate to support the idea if other explanations had not been lacking. A further difficulty lies in *A. seemeniana*, where we find the entire inflorescence consisting of an ebracteate dichasium. In *A. gibberula* the dichasium is clearly a lateral unit, but this cannot be assumed in *A. seemeniana*.

The unifloral condition occurs in both *Amyema* and *Sogerianthe*. In the former genus it is known from at least *A. finisterrae* (Fig. 23 – 1) and *A. hastifolia* (Figs.

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[1] Barlow (1966, Fig. 5) erroneously illustrates this dyad as being ebracteate.

23 — 2, 3), introducing a serious difficulty (see the key to genera in Barlow, 1974) in distinguishing such species from *Sogerianthe* where all species are unifloral. The peduncle is articulate in all but one of the unifloral species. In the *Sogerianthe* species to which this applies, the pedicel above the articulation terminates in what Danser (1933) and Barlow (1974) have regarded as 2 or 3 bracts, the upper 2 sometimes being concrescent. Danser also suggested the possibility that these three structures may represent one bract and two bracteoles. The lower internode (peduncle) is bractless; in *S. versicolor* (Fig. 23 — 9) it is the only internode, the bracteate pedicel apparently having disappeared.

There is much variation in the upper bract(s) in *Sogerianthe*. In the majority of cases it seems indeed as if two basally concrescent bracteoles are present (Figs. 23 — 6, 7). In others, however, the bilobed condition is clearly brought about by a split in what during the early stages of floral development was a single organ (Figs. 23 — 5 and 23 — 8, below), and others yet show a single 'upper bract' in the mature condition (Figs. 23 — 4 and 23 — 8, above). In *Amyema finisterrae* (Fig. 23 — 1) the 'upper bract' seems to be no more than a fringed rim of the pedicel.

Returning now to the common 2-flowered condition of *A. gibberula* (Fig. 22 — 4, right) we could theoretically derive the *A. seemeniana* inflorescence (Fig. 22 — 5) from it if the dyad peduncle were to disappear. Further deletions of one monad and the second one's pedicel would give us the condition of *S. versicolor* (Fig. 23 — 9). Conversely, a deletion of only one of the monads would result in a situation essentially like the other unifloral species mentioned. This (admittedly very elaborate) explanation still leaves unexplained the 'upper bract(s)' of *Sogerianthe*.

There is an alternative interpretation of the unifloral condition in the *Amyema* complex which starts with the assumption that these inflorescences are derived directly from a simple umbellate or racemic condition as represented at the very base of Fig. 26. This would mean that the inflorescences of the *A. seemeniana* — *A. squarrosa* group (Fig. 22 — 5) are the most primitive in the entire *Amyema* complex. The same derivation of the articulate and inarticulate unifloral types might apply as described above, but the preceding evolutionary history would have been very different, indeed. I have included both alternative possibilities in Fig. 26.

But what of the 'upper bract' of *Sogerianthe*? As we have seen elsewhere (especially in *Psittacanthus*), the pedicel of *Loranthaceae* may expand considerably at its distal end; in some species of *Psittacanthus* the entire ovary is hidden by this cupule. In *Cladocolea cupulata* a similar cupule has developed asymmetrically (Kuijt, 1975a), and this is even more clearly the case in the newly described *C. biflora* (Kuijt, 1980a). In *Barathranthus*, also, a similar cupule has evolved (Johri, Agrawal & Garg, 1957). Even more relevant would seem to be *Lysiana murrayi* (Fig. 16 — 5), where the top of the pedicel forms irregularly dentate projections around the 'open' side of the ovary. Surely the step from this type of investment to the admittedly quite variable 'upper bract' of *Sogerianthe* is not a great one. In other words, I am suggesting that we are concerned with various evolutionary steps leading to the *de novo* addition of a bract-like structure above the primary bract. The apparently intermediate situation in *Amyema finisterrae* (Fig. 23 — 1) is particularly suggestive of this notion. It would be interesting to know whether this 'upper bract' is vasculated, even though this need not sway or judgement as to its morphological nature.

There exists an apparently unrelated genus in India, *Helicanthes*, in which inflorescence reduction seems to have gone one last step further[1]. Here the pedical has disappeared completely, although the flower is still subtended by an exceedingly inconspicuous bract. This bract lacks vascular strands (Johri, Agrawal and Garg, 1957). Actually, there is some reason to believe that *Helicanthes* may be related to *Sogerianthe* or at least *Amyema* (Kuijt, 1980b). In any event, it seems safe to view *Helicanthes* as representing the ultimate reduction of an inflorescence to a single, sessile flower. If this is correct, *Heliçanthes* (which is undoubtedly highly specialized) represents a secondary return to that condition.

In speaking of the triadic subunits of the compound inflorescence in *Amyema* we need to recognize first of all that there are two quite different morphological types. The first one is exemplified by *A. clavipes* and *A. lucasii* as illustrated in Fig. 21. This triad is in no way different from the standard lateral triad which we have met in *Psittacanthus*, *Gaiadendron*, and numerous other genera, and requires no further description. Not surprisingly, in some species (especially in *A. gibberula*, Fig. 22 – 4), these triads have been reduced to dyads, the median flowers having disappeared.

The second type of triad is unique in *Loranthaceae*, and can perhaps be best understood by first considering the equally unique tetrad which is related to it (Fig. 24 – 2). The entire tetrad of *A. pendula*, for instance, is subtended by a primary bract fused with the length of the tetrad peduncle. At the end of the latter we find a 3-rayed umbel, each flower on a bracteate pedicel. The orientation of these rays is such that one points directly to the inflorescence peduncle, the other two pointing obliquely outwards. Where the three pedicels join is the fourth flower, which is sessile. Interestingly, some plants of *A. pendula* lack the central flower but are otherwise similar (Fig. 24 – 1); *A. miquelii* shows the same variation. The resultant triad thus is quite different from the first, dichasial type. It is a true umbel with three morphologically equivalent pedicellate flowers. It is possible to suggest that the flower nearest the main peduncle represents an evolutionary addition to a standard triad. Against this there are at least two arguments: first of all, the position of the other two rays is very unusual; and secondly, in rare instances, there may be a fourth ray (Barlow, 1966). There is therefore no clear equivalence between the two types of triads; they represent quite separate developments.

The explanation of the second type may well lie in the inflorescence of an ususual Australian species, *A. fitzgeraldii* (Fig. 24 – 3). It has simple, axillary umbels which, except for the absence of a recaulescent bract, are comparable to the tetrads of *A. pendula*, *A. miquelii*, *A. dilatipes* (Fig. 25), and others: in other words, a 3-rayed umbel plus a terminal or central, sessile flower. Without wishing to designate *A. fitzgeraldii* as the ancestor of these other species it seems clear that a derivation via such a type of simple, axillary umbel is the most acceptable explanation of that compound umbel.

In a sense this explanation only begs the question: what is a determinate, umbel-like inflorescence doing in the *Amyema* complex? That the inflorescence is determinate cannot be doubted. To relate this tetrad back to the determinate inflorescence or to the single axillary flowers which I assume to be ultimately

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[1] The reference to a raceme with whorled flowers in Johri, Agawal and Garg (1957) rests on a misinterpretation.

ancestral to all *Loranthaceae*, would seem to be altogehter unreasonable. The question cannot here be resolved, but I would rather assume that the central, sessile flower represents a transformation of the apex of the umbel. This would mean that this umbel is an inflorescence which has become determinate secondarily. We have already seen that, along a different line of development, this is probably also true for those species of the *Amyema* complex which have solitary flowers.

In *Dactyliophora*, finally, the major difference from some of the more complex *Amyema* species lies in the fact that the inflorescence consists not of one, but of a series of whorls of triads. The structure of the triad corresponds to the dichasial type, i.e., the triads are not umbellate units as in *A. miquelii*. Another indication of close affinity is the fact that in *Dactyliophora*, also, inflorescences may be borne in the axils of foliage leaves as well as directly on the epicortical roots (Danser, 1931).

4. EREMOLEPIDACEAE

A brief summary of the inflorescences of *Eremolepidaceae* is here included in view of recent palynological data which suggest (Feuer and Kuijt, 1979) an ancient connection, via *Tupeia*, to *Loranthaceae*. Karyological data also support this *Tupeia-Lepidoceras* connection (Barlow and Wiens, 1971). The possibility has therefore emerged that *Eremolepidaceae* represent a very early offshoot of pre-*Loranthaceae*. Again largely on the basis of palynological data, *Lepidoceras* is here included in this small, exclusively American family.

Thus the family consists of *Eubrachion*, *Antidaphne*, *Eremolepis*, and *Lepidoceras*. In *Eubrachion* and *Eremolepis* the inflorescence is simply a short spike, with persistent or largely deciduous basal scale leaves, respectively; however, *Eremolepsis wrightii* has its spikes assembled in a compound, terminal inflorescence. In both genera spikes seem to be indeterminate, but Engler (1935) illustrates what appear to be terminal flowers. I have not been able to ascertain the fact, as good materials are very scarce; my impression is that individual spikes are indeterminate.

In *Lepidoceras kingii* we encounter significant differences between male and female plants. The former possess indeterminate racemes which, as they expand, lose their large, papery bracts each of which subtends a single pedicellate flower. These racemes are placed singly in the axils of foliage leaves but also in secondary positions on leafless portions further down. The axillary (and terminal) buds at the tips of the vigorous branches instead become leafy innovations the leaves of which will subtend a further crop of racemes in the following season. At least in *L. squamifer* many racemes also develop from terminal buds of smaller leafy shoots, but leaves and flowers belong to different seasons. In female plants at least the floriferous bracts persist and expand into leafy organs, and instead of speaking of an inflorescence we can alternatively regard the flowers as solitary in the axils of expanding bracts. Whether the tip of the 'inflorescence' may continue vegetative or reproductive growth I do not know. The male plant has thus evolved a more clearly defined inflorescence than the female, which is also the case in the following genus.

The male flowers of *Antidaphne* ar arranged in small, indeterminate racemes from which the scale leaves fall away during expansion (Fig. 27 – 2). The racemes, like those of *Lepidoceras*, are thus very much like catkins. Female flowers occur in a spike in which the fertile scale leaves subtend one or more sessile flowers (Fig. 27 – 1). The tip of this spike, however, bears several small foliage leaves also

subtending axillary flowers. The apex of this spike may, following anthesis, continue growth into a normal, leafy shoot, a phenomenon recently called *auxotely* by Briggs and Johnson (1979). This is by no means invariable, many spikes apparently falling away after fruit maturation. The flower-bearing part of the spike also elongates considerably in those which proliferate terminally. In the female *Antidaphne*, therefore, as in *Lepidoceras*, the definition of the inflorescence remains equivocal. When supernumerary inflorescences are present in *Antidaphne* (Fig. 27 – 3), they appear to be placed irregularly in the leaf axil. I have observed the same auxotely in one Ecuadorian specimen of *Eremolepis*, which is monoecious instead.

When we now look at *Eremolepidaceae* as a whole we can thus say that in taxa where we can speak of inflorescences the latter are simple, at least mostly indeterminate and characterized by single, axillary flowers. The information suggests an ancestral solitary, axillary flower in both families, in *Eremolepidaceae* many of these together resulting in an inflorescence, but in *Loranthaceae* each individually evolving into an axillary inflorescence. This difference in no way detracts from the evolutionary connection suggested in the first paragraph of this section.

5. DISCUSSION

The profusion of inflorescence types in *Loranthaceae* as detailed above is perhaps one of the most striking features of the family. It is no exaggeration to say that few clearly natural families have evolved this degree of structural diversity in the inflorescence.

There are at least two essential functions which involve the inflorescence, pollination and seed dispersal. Both of these functions in *Loranthaceae* are filled in a highly specialized fashion, involving the presentation of flowers to (in the great majority of cases) birds for pollination, and of fruits also to birds (but not usually the same ones) for seed dispersal. The relationship of frugivorous birds to mistletoe, as is well known, has especially interesting features (cf. Kuijt, 1969) and in fact amounts to an obligate dependence of mistletoes on birds in all *Loranthaceous* genera except *Nuytsia*. Considering the vital, dual importance of the inflorescence it is not altogether surprising that so much evolutionary experimentation has taken place.

The question might be raised whether the evolution of an indeterminate inflorescence of triads from a determinate one of monads has anything to do with changing pollination systems. Even though very few careful observations have been made especially in the New World, it is common knowledge that large-flowered mistletoe species are predominantly ornithophilous and small-flowered species entomophilous, while plants with intermediate flower sizes have both types of visitors. *Gaiadendron*, for example, has frequent bird visitors (Kuijt, 1963) but insects are also common, and the flowers have a strong, sweet fragrance. Confounding this question, however, is the fact that all *Loranthaceae* (except *Nuytsia floribunda*) have fruits that are dispersed primarily by birds of many sizes, no matter what type of inflorescence bears the fruits.

In the New World, entomophilous *Loranthaceae* are indifferently distributed over those with determinate vs. indeterminate types and those with monads vs. triads. The large-flowered ones all have indeterminate inflorescences with monads,

dyads, or triads. The solitary exception here is *Ligaria* which I have interpreted as having a one-flowered, determinate inflorescence. In Africa all species are characterized by monads, and all inflorescences are indeterminate; all may well be ornithophilous. In other parts of the world the situation is too complex or poorly known to allow for analysis. The meager result of this line of thought thus allows us to say no more than that ornithophilous inflorescences tend to be indeterminate. An 'adaptive' explanation of the postulated inflorescence evolution in terms of changing systems of presentation of pollen, nectar and fruits seems thus not possible with our present information.

This is not to deny that in some *Loranthaceae* post-floral developments take place which are clearly adaptive. In *Struthanthus orbicularis*, *S. costaricensis* (Fig. 5 – 5), and *S. crassipes* the lateral floral pedicels enlarge and elongate strikingly, thus making the ripened fruits more visible to visiting birds. Individual fruits of *Lepeostegeres* are said to be elevated from the capitulum in a similar fashion (Danser, 1933c). The inflorescence axis itself in *Cladocolea mcvaughii* elongates considerably during fruit maturation (Kuijt, 1975a). In *C. microphylla* (Kuijt, op. cit.) the foliar bracts fall before the fruits mature, undoubtedly making the latter more visible. Such developments are not always amenable to obvious explanations, however, as is shown by the enlargement of foliaceous bracts and bracteoles of *Gaiadendron* while the fruit matures, which has the opposite effect. Even more puzzling is the fact that in the related *Nuytsia* the triad peduncles enlarge considerably after fertilization (Barlow, 1966), as the winged fruits of this genus do not seem to be dispersed by animals who would thus find them easier to locate.

We can thus see that post-floral developments increasing the visibility of ripe fruits are relatively rare in *Loranthaceae*. Considering the absolute dependence of all but one species on avian disseminators, this is surprising. It probably means that the plants rely largely on the extremely variable and often bright colors of the ripe fruit to attract birds.

With regard to flowers it is much more obvious that many bird-pollinated mistletoes have evolved a flower-presentation which facilitates bird visits; this is especially so in neotropical taxa which are visited by hummingbirds. Flower clusters are at the tips of branches, or hang down well below them, beyond the leaves, in nearly all species of *Tristerix*, *Aetanthus*, and *Psittacanthus*, and this is true even for *Gaiadendron* and *Tripodanthus* which are only partly ornithophilous. In contrast, the purely entomophilous groups such as *Phthirusa*, *Struthanthus*, *Ileostylus*, and *Cladocolea* have inflorescences (or individual flowers) which are often surrounded by foliage.

In numerous *Loranthaceae* an organization has evolved where the flowers, instead of projecting beyond the leaves, are placed well below them. In other words, here flowers develop only (or mostly) on older wood from which the leaves have already fallen, a type of cauliflory therefore. The effect, of course, is similar in that leaves no longer impede the movement of birds, and flowers are more clearly visible. Good examples are seen in *Psittacanthus ramiflorus* (Kuijt, 1980a) and several *Dendrophthoe* species (Danser, 1931), and in the morphologically extraordinary production of flowers or inflorescences from epicortical roots in a number of taxa in the *Amyema* complex, including *Distrianthes* (Fig. 18 – 1; Danser, 1931) and the species which Danser (1933a) placed in *Rhizomonanthes*; in *Dactyliophora*; and in several *Amyema* species (e.g., *A. hastifolia*, Fig. 23 – 2; *A. dilatipes*, Fig. 25 – 1). An equally extraordinary but different solution to the same problem has evolved in

Dicymanthes where most inflorescences sprout directly from the elongated internodes without reference to the leaves (Fig. 17 – 3).

Once again, however, I suspect that the actual placement of flowers and inflorescences, while frequently important for the attraction of birds, is less so than the frequently very striking color schemes of the flowers themsleves. There exists no survey of color patterns in the flowers of tropical *Loranthaceae*, but their brilliance is well known to most botanical visitors and has been much commented on.

A phenomenon of frequent occurrence in *Loranthaceae*, both in the Old and New Worlds, is the sympodial branching habit, in which growth is resumed from lower, axillary buds rather than from an apical bud. Where the phyllotaxy is decussate the resulting branching pattern is bifurcate. This is, in different taxa, achieved in two very different ways. In the first case the shoot apex simply aborts; examples exist in *Cladocolea dimorpha, C. hintonii, C. microphylla* and others of that genus; in *Tapinanthus natalitius* from South Africa; in numerous species of the *Amyema* complex (Kuijt, 1980b); in *Peraxilla tetrapetala* (Fig. 14 – 5, 6), and *P. colensoi* (Hooker, 1844), in *Cyne* (Fig. 19 – 1); in *Lepeostegeres* (Fig. 18 – 2); probably in *Oryctanthus grandis* (Kuijt, 1976) and many others. An alternative method achieving the same branching pattern is followed by *Loranthus europaeus, Tupeia antarctica, Muellerina,* and nearly all species of *Psittacanthus* (Fig. 11 – 2) and *Tristerix* of the New World. The inflorescence is here placed at the tip of the branch, allowing lower lateral buds to develop into leafy shoots which themselves again terminate in an inflorescence. It is interesting, by the way, that in mistletoe taxa outside *Loranthaceae* similar developments have taken place independently, as in species of *Arceuthobium* (Kuijt, 1970), *Dendrophthora* (Kuijt, 1961), *Viscum, Phoradendron,* and even *Misodendrum* (Kuijt, 1969).

When more than one inflorescence develops in the axil of a foliage leaf the secondary inflorescences may occupy either a prophyllar or a superimposed position. In some species, as in *Phthirusa pyrifolia,* both may occasionally be seen even in the same leaf axil. The superimposed position is the more unusual; I have noted it in species of *Phthirusa* (Kuijt & Weberling, 1972), *Cladocolea* (Kuijt, 1975a, fig. 21a), *Struthanthus* (Kuijt, 1964a, fig. 37), *Oryctanthus* (Kuijt, 1964a, fig. 11), *Oryctina* (Rizzini, 1977, fig. 1), and for individual flowers, in *Ixocactus* (Kuijt, 1967). It is of some interest to note that all the examples cited are small-flowered neotropical *Loranthaceae.* In *Eremolepidaceae* neither pattern seems to exist, additional inflorescences in *Antidaphne* being placed in an apparently random fashion (Fig. 27 – 3).

In a number of places in *Loranthaceae* inflorescences have begun to be grouped in higher units of organization, and we may speak of compound inflorescences. Some rather exceptional instances of this have been pointed out in *Phthirusa, Cladocolea, Struthanthus, Oryctina,* and *Oryctanthus.* Vigorous flowering shoots of *Tripodanthus acutifolius* may also show such a tendency. Perhaps the most obvious examples of compound inflorescences are seen in *Psittacanthus* where the great majority of species show a clustering and integration of individual inflorescences at the tip of a shoot which becomes a unified, larger arrangement. Illustrations of all examples mentioned (except *Cladocolea*) may be seen in Eichler's Flora Brasiliensis. A different feature is the terminal proliferation or auxotely which seems to occur occasionally in *Tristerix aphyllus.*

It is clear from the detailed coverage of inflorescences presented above that the inflorescence of *Loranthaceae* is fundamentally an axillary structure, and not a

modification of a leafy, flower-bearing branch. Where more complex arrangements exist these are derivative. In other words, it appears again that generally reduction has played no more than a subordinate role, and that the inflorescence has developed as a result of elaboration from a more simple, axillary complex. It is no doubt thanks to this fact that it is easy, in the majority of cases, to circumscribe the inflorescence in the family: boundaries between the inflorescence and the surrounding leafy portions of the plant tend to be very sharp. The curious pseudo-endogenous origin of inflorescences in many taxa, both in the New and Old Worlds, contributes much to this separateness, as it frequently leaves a distinctly corky crater around the base of the stalk. The extreme of this development is visible in *Cyne* (Fig. 19 – 1). No systematic meaning seems to attach to this feature, as even within a genus (*Psittacanthus, Cladocolea*) much variation may occur. The phenomenon seems not or scarcely to exist where basal scale leaves ensheath the base of the inflorescence (exception: *Struthanthus panamensis*). Among such species are *Alepis flavida, Atkinsonia ligustrina*, and *Trilepidea* (Barlow, 1966), *Cladocolea lenticellata* (*C. archeri*) and *C. roraimensis* (Kuijt, 1975a), *Struthanthus polystachyus* (Kuijt, 1964a) and *S. lojae* (Kuijt, 1980a), and species of *Macrosolen* (Barlow, 1974) and *Helixanthera* (Danser, 1931). The caducous nature of these bracts, for example in *Gaiadendron*, frequently makes it difficult to recognize this feature.

These basal, chartaceous bracts are very different from the foliaceous, involucral bracts which have evolved in a variety of other *Loranthaceae*. In the New World there are only a couple of species of *Cladocolea* (Kuijt, 1975a) which fall in this category. In the Old World there are some genera with several pairs of imbricate bracts (*Lepidaria, Lepeostegeres*, and *Thaumasianthes*). In others the bracts are fewer, valvate, and often basally connate (*Diplatia, Distrianthes*, and *Tolypanthus*).

The apparent absence of bracteal organs subtending lateral inflorescence units in various taxa is somewhat puzzling. In the stalked monads and triads of numerous groups this impression is misleading because of the recaulescence of bracts; it simply means that an articulation develops at the base of the peduncle/pedicel which includes the fused bract. In three New Zealand groups, however, we are concerned with a true absence of bracts: *Ileostylus, Tupeia* (Fig. 14 – 9), and the upper inflorescence portions of *Alepis* (Fig. 14 – 1). In *Tupeia*, all different stages of bracteal reduction can be seen even on the same inflorescence, especially in some male specimens: some lateral units are subtended by long, flat, narrow bracts, others by minute, nail-like ones, and others yet are quite ebracteate.

The cupule of certain species of *Psittacanthus* has already been discussed under that genus. Quite aside from the problematic situation in *Thaumasianthes*, the evolution of similar cupules is evident in a few other *Loranthaceae* as well. In some species of *Dendropemon* and to some extent in the curious *Struthanthus panamensis* the bract and bracteoles are basally concrescent and clasp the flower or fruit (Fig. 6 – 1). In *Cladocolea biflora* (Kuijt, 1980a) and, to a lesser extent, *C. cupulata* (Kuijt, 1975a) the fruit is placed in a comparable cup (Fig. 2 – 1, 3 – 1). Similarities are found in several species of *Phthirusa*. The extreme in this genus is seen in what might well be an undescribed species (Fig. 7 – 1, 2) in which the entire triad is transformed into a pedunculate, triple, compound cupule.

I have said little about the direction of anthesis in the inflorescence of *Loranthaceae*, partly because the herbarium material to which, for many species, I have been limited is unsatisfactory for this purpose. A basipetal sequence of flowering is commonly considered to be characteristic of determinate inflorescences

and, conversely, an acropetal sequence of indeterminate ones. My observations show that this is generally true also for *Loranthaceae*. The terminal flower normally opens first in *Cladocolea*, as can be seen in numerous illustrations of my monograph (Kuijt, 1975a). It is just as true that the pattern is acropetal in the indeterminate racemes of *Struthanthus*, *Phthirusa*, *Gaiadendron*, and many others. However, in Costa Rican populations of *Gaiadendron* determinate inflorescences are common, and these are also acropetal in anthesis. In this connection the species with 'intermediate' inflorescences, i.e., those which have only partly achieved the transformation from a determinate to an indeterminate inflorescence, would be of much interest if adequate material could be studied. Aside from *Gaiadendron*, the only one of these species where I have seen something relevant is *S. flexilis* (Fig. 5 – 3) where in several inflorescences the petals still adhered only in the mid-region. In other words, anthesis in at least that species starts more or less simultaneously at both ends; it is both basipetal and acropetal, its intermediacy having carried through to its flowering sequence.

In all this it is clear that the original Eichlerian vocabulary of monads, dyads, and triads, if careful morphological analyses are adhered to, has withstood the test of time. Even though not all interpretations by Eichler can be followed at present, inflorescence interpretations in *Loranthaceae* must always rest on the foundations laid by Eichler. There would seem to be only two instances where this basic vocabulary falls short. The first is in the median bracteoles of *Thaumasianthes*; the second, in the tetradic and certain related triadic species of *Amyema*.

I should like to return now to the two theses which I put forward in a tentative fashion early in this study (p. 13) when discussing the variation in inflorescence structure in the *Cladocolea-Struthanthus* complex. At that time I reached the conclusion that indeterminate inflorescences and triads were derived, respectively, from determinate inflorescences and monads. These theses have been used as general guides in my survey. They cannot be evaluated in the proper sense, as there is no unanimity in most cases as to what genera are primitive, and what advanced. Even if this had been so it is clear that mosaic evolution as defined by Takhtadzhian (1969) has taken place in many taxa. There is little question, for example, that in the genera *Gaiadendron* and *Nuytsia*, which are generally regarded as primitive, advanced features (triadic, indeterminate inflorescences and, in *Nuytsia*, the dry, winged fruit) are associated with primitive ones (those associated with germination; cf. Kuijt, 1963). Conversely, it might be suggested that *Cladocolea harlingii* seems to combine a remarkably primitive inflorescence with a very highly advanced type of parasitic strategy. However, the theses may be validated to some extent (quite aside from the external support available for No. 1; see, for example, Stebbins, 1974, pp. 261 – 282; Rickett, 1944) by the degree to which they facilitate a comprehensive picture of inflorescence evolution in the family. In order to accomplish this we need to retrieve some facts from the above survey of taxa.

There is, first of all, the relationship within the *Cladocolea-Struthanthus* complex as outlined previously. Even though no proof is possible, I would nevertheless suggest that the 'bridges' between these two genera do not allow for a convincing alternative explanation to the one proposed.

Secondly, of special interest are those species which, within one and the same inflorescence, show variability in basic structure, and those species where significant variations are encountered between different inflorescences, whether on the same plant or different plants. Such facts have been pointed out in the survey but may be

gathered together here. There are, first of all, a number of cases noted which seem to be of an exceptional nature in the species involved, even though it would not be proper to call them teratological. In such cases either the apex or the base of the inflorescence shows the unusual feature. The inflorescence variation in *Gaiadendron* also appears to be a geographic feature (see under 2.3). In *Cladocolea pedicellata* I have pointed out the rare triad at the base of the raceme (Fig. 1 – 3), and in *Phthirusa pyrifolia* exceptionally vigorous plants may produce a pentad instead of a triad, in the same position (Fig. 6 – 5).

More importantly, there are a number of instances where such variation is a normal characteristic of the entire species. In *Struthanthus flexilis*, *S. polystachyus*, and *S. lojae* we find a strictly determinate spike, with one or two pairs of monads directly below the terminal flower but only triads further down. In *S. deppeanus* we may find the same, but the terminal flower does not always develop. Similar conditions obtain in *Ileostylus*. In both species of *Tripodanthus*, even though all flowers are pedicellate and triads pedunculate, precisely the same distribution of terminal flowers, monads, and triads occurs, although I am not certain of its constancy. In *Thaumasianthes*, while some uncertainties persist, it cannot be doubted that the triads occupy the basal positions and monads the upper positions within the inflorescence. In *Tupeia* and *Muellerina* a similar pattern of variation exists, always the triads, where present, occupying a basal position and the monads near the apex. In *Alepis* all lateral units are monads, but only the lower ones are bracteolate. The situation in *Lampas* (Danser 1931), *Lepeostegeres*, and *Taxillus* (Danser 1933b) is uncertain but may, upon closer scrutiny, yield further examples of variation within inflorescences. An instance which I have not been able to follow up myself is the occurrence of both dyads and triads in the inflorescences of two species of *Psittacanthus* as claimed by Urban (1898), and the situation in *Loranthus europaeus* is inadequately known.

Among all these examples [1] there exists one important common denominator: those conditions which, following my thesis No. 2, are regarded as more advanced are always nearest the base of the inflorescence; and, conversely, primitive conditions, where present, are found nearest the apex. The *Phthirusa* pentad is undoubtedly an advanced condition, and is near the base. Triads in mixed inflorescences are invariably at the base, and monads near the tip. If some monads are bracteolate and others on the same inflorescence are not, the former are nearest the base and the latter near the apex. This constancy thus provides us with an extension of the second thesis. The situation in *Alepis* and *Gaiadendron*, furthermore, would suggest that bracteoles are an evolutionary addition to originally ebracteolate monads. If this principle were extended to the numerous *Loranthaceae* with bracteolate monads (see Appendix II) we would oppose the generally accepted notion in the family to the effect that such monads are reduced triads.

A few words need to be said here about the idea of the 'terminal triad' as mentioned in, e.g., Barlow (1966) for *Ileostylus*. The idea has also been suggested to me in personal discussions that we need not, in inflorescences such as those of *Struthanthus polystachyus* and *S. flexilis*, speak of a determinate inflorescence at all

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[1] The instances where a spike of monads may or may not bear a terminal flower, as in *Loranthus europaeus* and *Cladocolea mcvaughii*, stand outside this consideration.

if we regard the terminal flower and its two accompanying monads together as yet another triad. There are several reasons why such an equation is not appropriate. First of all, the dichasial lateral triad which we have followed through the family is always associated with a recaulescent, subtending bract. Secondly, the notion would not make any sense in any of the species (especially in *Cladocolea*) where the terminal flower is followed by one, two, or more pairs of lateral monads; yet, morphologically, this 'terminal triad' is identical to that of those *Struthanthus* species where it is followed by lateral triads. And what about inflorescences where, as in *S. deppeanus* (Fig. 4 – 2) and *Ileostylus*, the terminal flower of this 'triad' may or may not be present? The concept has even less weight in those species of *Cladocolea* where phyllotaxy is alternate and a 'terminal triad' cannot be delineated at all. It seems far more meaningful to accept the evolutionary relationship between monads and triads defined in my second thesis.

Another topic which requires some consolidation here is the status of the solitary flower in *Loranthaceae*. It is my contention that in the dozen or more species of *Loranthaceae* where flowers are solitary some represent the primitive condition, but others may be reversals and thus correspond to an advanced condition. All species in this category in the New World, I would suggest, belong to the former group (*Cladocolea clandestina*, *C. inconspicua*, *C. inorna*, *Ixocactus hutchisonii*, and *Ligaria cuneifolia*). This view is difficult to defend for *Ligaria* — a taxonomically isolated and probably relictual genus (Barlow and Wiens, 1973) — except that there is no associated evidence of reduction as there is in some of the paleotropical forms mentioned below. *Ixocactus* is nearly identical in this regard to the *Cladocolea* species mentioned (cf. Kuijt, 1967, Fig. 9, with Kuijt, 1975a, Figs. 18c, 19a). In the case of the latter there are cogent reasons for placing them within the primitive group of the genus (Kuijt, 1975a, p. 269); this rationale utilizes four separate morphological criteria which are independent of inflorescence features. It thus seems more logical to accept this solitary, axillary condition of the flower as a primitive condition rather than a highly advanced one.

In the Old World we need to consider *Sogerianthe*, *Helicanthes*, and some instances of *Amyema*, *Lysiana*, *Muellerina*, and *Peraxilla*. In the latter genus, spikes more commonly have 2 or 4 lateral flowers in addition to the terminal one. The inflorescence, except for the occurrence of bracteoles, is thus generally comparable to that of *Cladocolea*. I suggest therefore that in *Peraxilla*, also, we are concerned with primitive conditions, i.o.w., with a primitively solitary flower which is in various stages of evolving into a determinate spike. In the remaining taxa, the situation is quite different. The peculiar branching patterns and flower emergence in *Sogerianthe*, *Helicanthes*, and those *Amyema* species that concern us here (Kuijt, 1980b) leave little doubt that we are concerned with a highly advanced group. What is more important is the fact that a complete morphocline exists from simple umbels bearing numerous monads with concaulescent bracts to similar umbels with 3, 2, and eventually one ray (see Fig. 26). Since both the latter form and that with an inarticulate stalk coexist in *Sogerianthe* (compare Fig. 23 – 4 and 23 – 9) it would again seem logical to accept this as the ultimate state of reduction in this series, even though this idea contradicts or modifies the Bessey-Hutchinson dictum quoted on p. 7. In *Lysiana* we undoubtedly have a derived situation also, as shown by the common occurrence of 2-rayed umbels and by the fact that the genus 'is one of the most advanced and reduced genera of *Elytrantheae*' (Barlow, 1966).

We have thus reached a point where it becomes possible to expand somewhat on the two original theses, which are here restated for *Loranthaceae* as a whole.

1. The determinate inflorescence represents an ancestral condition, the indeterminate a more derived one.
2. Monads as lateral inflorescence units are generally more primitive than triads in that position.

To these we may add, as based on the above discussion:

3. Dyads as lateral units are derived from triads in that position (cf. *Aetanthus, Psittacanthus* spp., *Tetradyas, Amyema* spp.).
4. Where internal variation exists along an individual inflorescence axis, the latter's base tends to show more advanced features than the apex.
5. Lateral monads with bracteoles are more advanced than those without.
6. Recaulescent bracts are usually more advanced than free ones.
7. In all probability the solitary, axillary, sessile flower represents a more primitive condition than the various inflorescence types.

It is an unfortunate fact that there is no fossil evidence, as far as I know, to aid us in our search for the primitive loranthaceous inflorescence. Indeed, inflorescences are probably among the most unlikely plant structures to be preserved in this way. Among *Olacaceae*, from which family *Loranthaceae* is almost certainly derived (Kuijt, 1968), inflorescences are very simple but have not been studied in much detail (Sleumer, 1935). It is interesting to find, however, that the inflorescence of at least tribe *Couleae* is a determinate raceme even though secondary branches add complexity in the lower regions (Stauffer, 1961). In *Eremolepidaceae*, which may constitue a very early offshoot of *Loranthaceae*, we find sessile axillary flowers and simple spikes and racemes. The only thing that can be deduced from these facts is that they provide no evidence which clashes with our emerging conception of the primitive inflorescence of *Loranthaceae*.

In summary, a comprehensive view of inflorescence evolution in *Loranthaceae* would thus entail the following steps:

1. The ancestral condition is represented by a solitary sessile flower in the axil of a foliage leaf. It is likely that this flower was small and insect-pollinated.
2. A pedicel evolves, elevating the flower.
3. The pedicel/peduncle becomes articulate, the one or two bracts terminating the first internode eventually subtending as many lateral flowers. The latter in some cases evolve pedicels also.
4. Additional internodes and lateral flowers are added to form a more elongated spike or raceme.
5. Recaulescence of bracts.
6. In some, formation of bracteoles to lateral flowers, in prophyllar positions; and, either simultaneously or subsequently, the formation of lateral flowers in their axils, thus completing the triads.
7. In some instances, lateral flowers evolve bracteoles of a second order; those of the first order may become recaulescent; in others, the median flower aborts, resulting in a dyad.
8. Loss of the terminal flower, i.e., transformation of the determinate inflorescence into an indeterminate one.

The above sequence, however, must not be seen as rigid and invariable, as exemplified by the numerous groups in which the change to indeterminacy has taken place on inflorescences bearing monads. It is clear also that various

modifications have occurred here and there which cannot be placed in a general outline such as the above, these modifications including cases of apparent reversion. The above elements and approximate sequence of evolutionary events thus would seem to constitute a conception with which the preceeding account of factual details is in substantial accordance; a conception which, in turn, may aid those who attempt the challenging task of establishing affinities between the genera of *Loranthaceae*.

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INDEX

SPECIES AND GENERA OF LORANTHACEAE AND EREMOLEPIDACEAE REFERRED TO IN TEXT AND/OR ILLUSTRATIONS

ACKNOWLEDGEMENTS

APPENDIX I

Summary of inflorescence structure of Loranthaceae.

Taxa of the New World are underlined; the question of determinate vs. indeterminate inflorescences is ignored. Brackets indicate the fact that a particular inflorescence type occurs only rarely, or not in all members; however, not all deviations or exceptions are included. In the left column, M = ebracteolate monad; ⟨M⟩ = bracteolate monad; ⟨T⟩ = bracteolate, dichasial triad; and ⟨D⟩ = bracteolate, dichasial dyad.

	RACEME	SPIKE	UMBEL	CAPITULUM
M	Tristerix spp. Cladocolea spp. (Alepis) Kingella Scurrula Helixanthera spp. Dendrophthoe spp. (Cecarria) (Muellerina) Tupeia All Africa spp.	Cladocolea spp. Trithecanthera Dendrophthoe spp. Helixanthera spp. Loranthus	Cecarria Dendrophthoe spp. Taxillus (Amyema) Lysiana	Barathranthus Tolypanthus
⟨M⟩	Tristerix spp. Dendropemon Struthanthus panamensis Macrosolen Amylotheca spp. Atkinsonia (Alepis) (Ileostylus)	Oryctanthus Oryctina Maracanthus Elytranthe Trilepidea (Peraxilla)	(Macrosolen) Papuanthes Sogerianthe?	(Macrosolen) Lepidaria
⟨T⟩	(Tripodanthus) Gaiadendron Notanthera Psittacanthus spp. (Struthanthus spp.) Phthirusa spp. Amylotheca Decaisnina Loxanthera Nuytsia (Muellerina) (Ileostylus) (Tupeia)	Struthanthus spp. Phthirusa spp.	Struthanthus spp. Psittacanthus spp. Desmaria Lampas Amyema spp.	Lepeostegeres Distrianthes Dicymanthes Diplatia (Amyema) Thaumasianthes Cyne?
⟨D⟩	Psittacanthus spp.		"Phrygilanthus" nudus? Psittacanthus palmeri Aetanthus Amyema spp.	Tetradyas

Other, or inadequately known	NEW WORLD: Ligaria
	            Cladocolea spp.
	            Ixocactus
			OLD WORLD: Amyema spp.
			            Sogerianthe?
			            Helicanthes
				Dactylophora
				Cyne?

APPENDIX II

Inflorescences interpreted as determinate (Loranthaceae) (including solitary axillary flowers).

The text should be consulted for full details. Taxa followed by asterisks have determinate inflorescences occasionally or in only some species (*).

Alepis
Amyema fitzgeraldii
Cladocolea spp.
Gaiadendron (Central America)
Ileostylus (*)
Ixocactus
Ligaria
Loranthus europaeus (*)

Peraxilla
Struthanthus deppeanus (*?)
S. flexilis
S. liebmanni (*?)
S. lojae
S. polystachyus
Tripodanthus
Tupeia
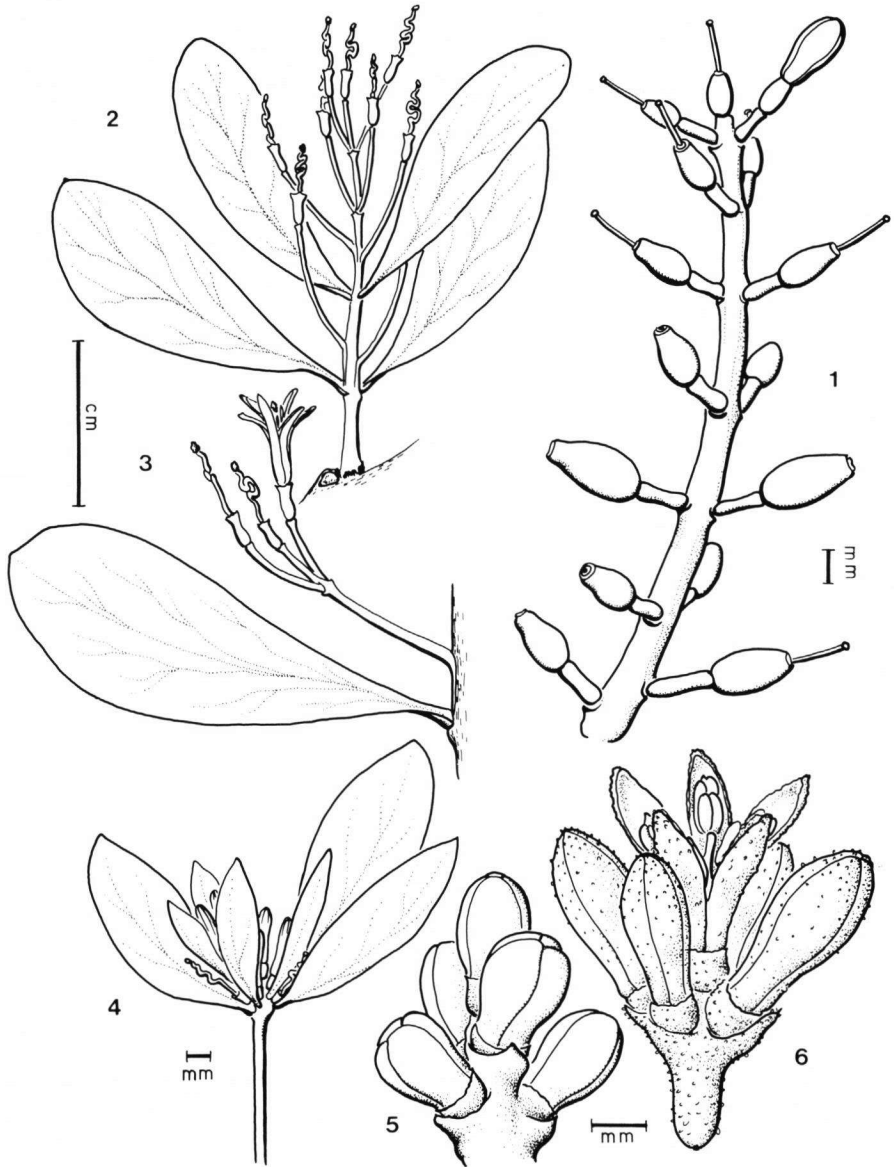
Fig. 1 — *Cladocolea*, after Kuijt 1975a. — 1. *C. harlingii.* — 2. *C. pedicellata*, entire infloresence. — 3. Same, triad at base of infloresence. — 4. *C. loniceroides.* — 5. *C. coyucae.* — 6. *C. stricta.*

Fig. 2 — *Cladocolea*, after Kuijt 1980a (2–1) and Kuijt 1975a (others). — 1. *C. biflora*. — 2, 3. *C. dimorpha*, primary and secondary inflorescences, respectively. — 4. *C. clandestina*. — 5. *C. grahamii*. — 6. *C. inconspicua*.
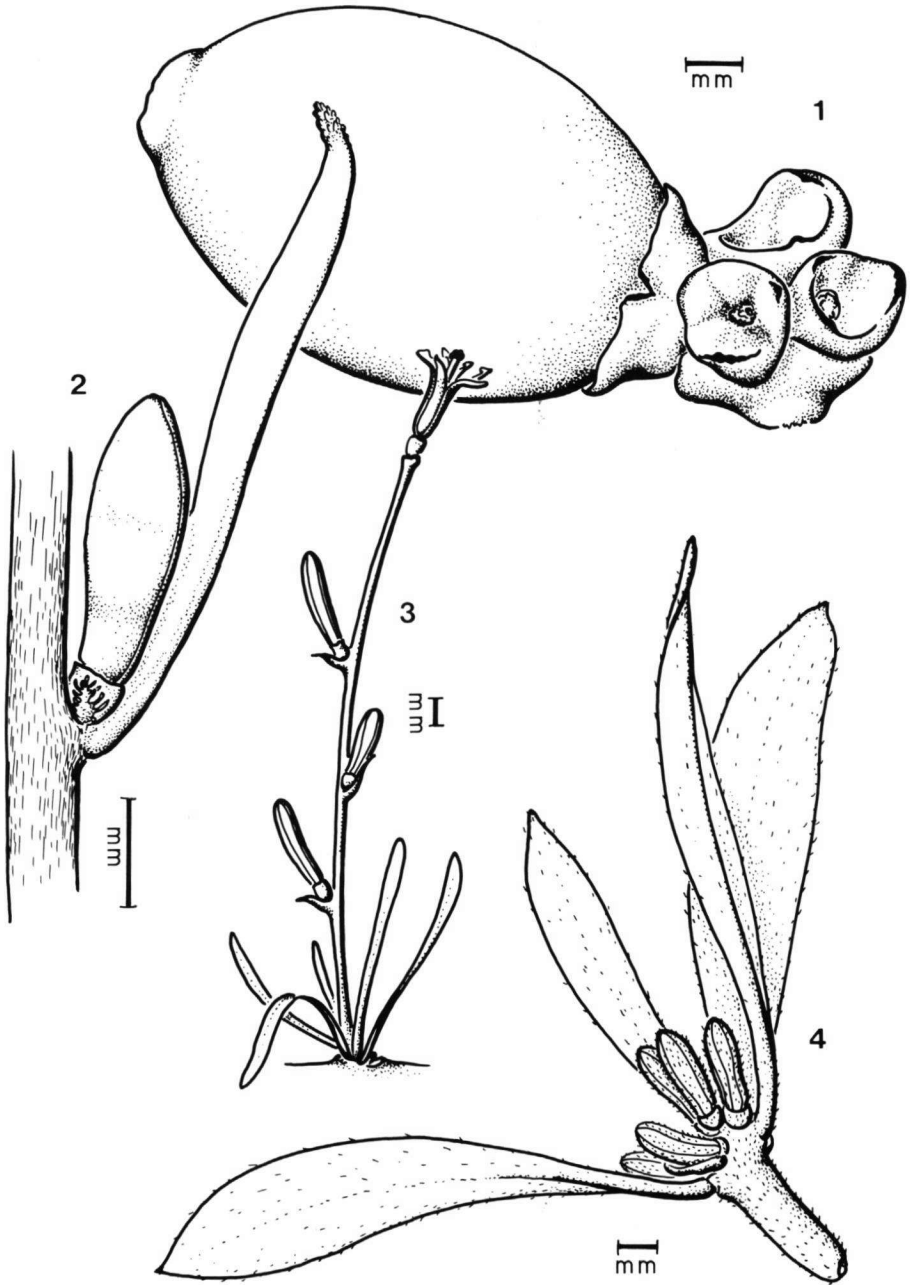
Fig. 3 — *Cladocolea*, after Kuijt 1975a. — 1. *C. cupulata.* — 2. *C. inorna.* — 3. *C. gracilis.* — 4. *C. microphylla.*
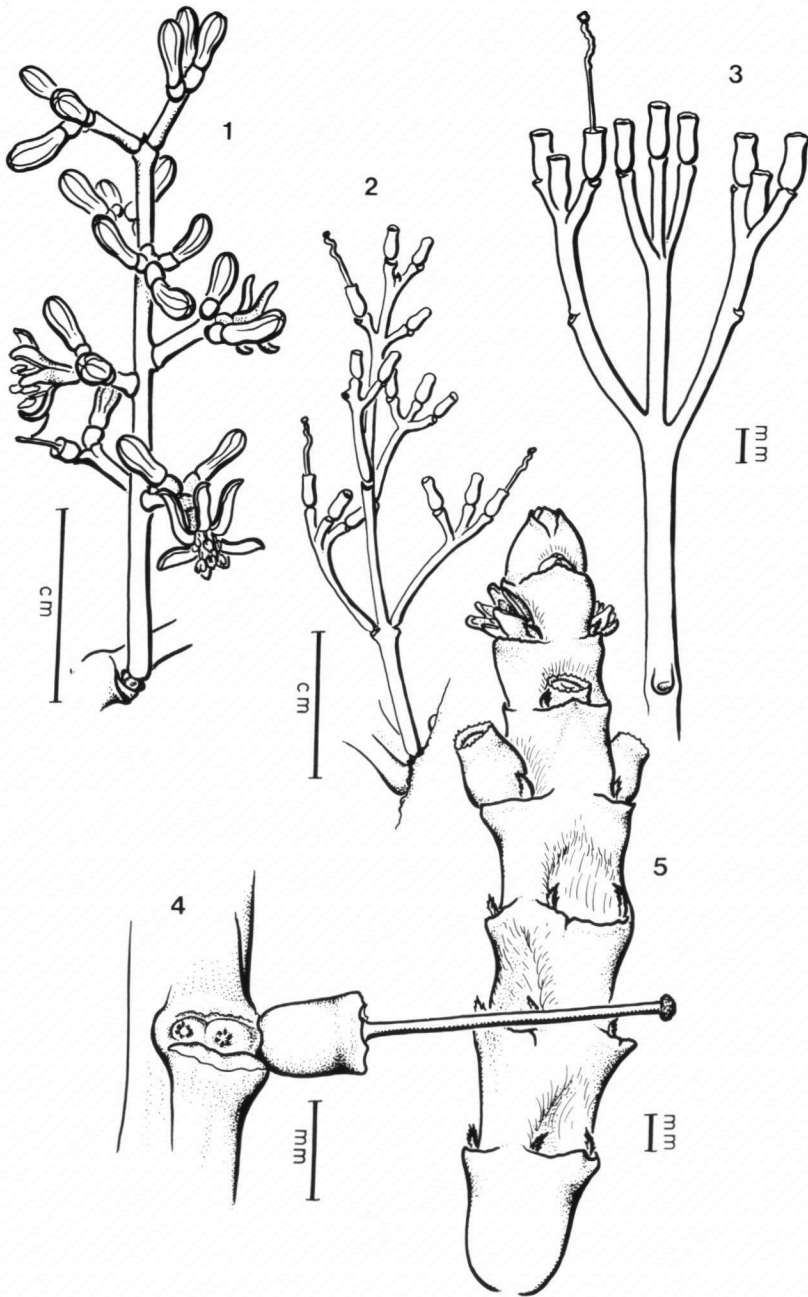
Fig. 4   *Struthanthus* and *Oryctanthus*. — 1. *S. marginatus*, after Kuijt 1964a. — 2. *S. deppeanus*. *Stanford et al. 2106*, WTU. — 3. *S. liebmanni*, tip of raceme. *Liebmann s.n.*, P. — 4. *S. polystachyus*, sessile triad. *Kuijt 2558*, UBC. — 5. *O. asplundii*, after Kuijt 1976.
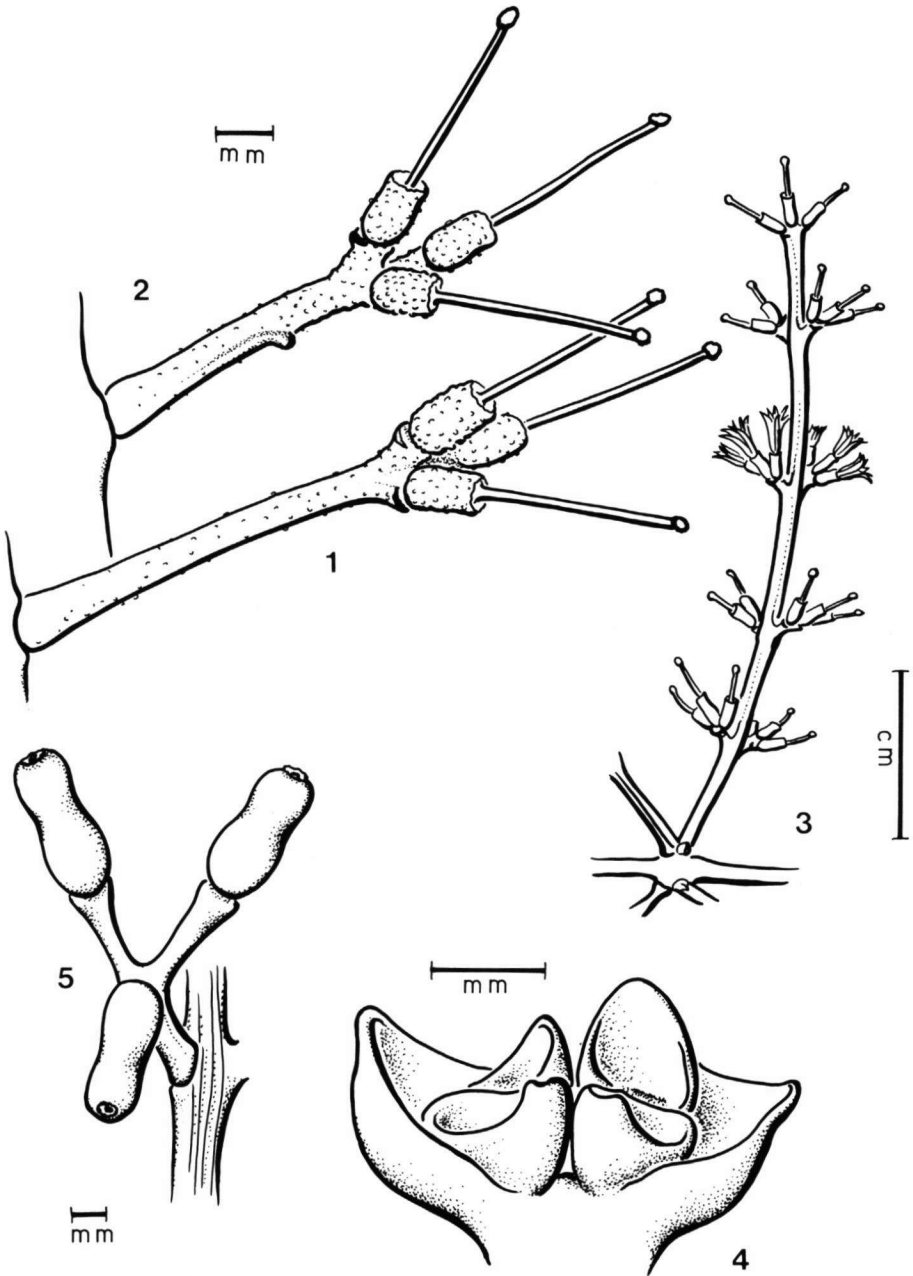
Fig. 5 — *Struthanthus.* — 1, 2. *S. papillosus,* two triads from upper and lower portion of raceme, respectively, showing different positions of bract. *v. Tuerckheim II.1240,* L. — 3. *S. flexilis,* after Kuijt 1980a. — 4. *S. condensatus,* entire inflorescence, after Kuijt 1980a. — 5. *S. costaricensis,* showing postflorally expanded pedicels and peduncle of triad, after Kuijt 1964a.
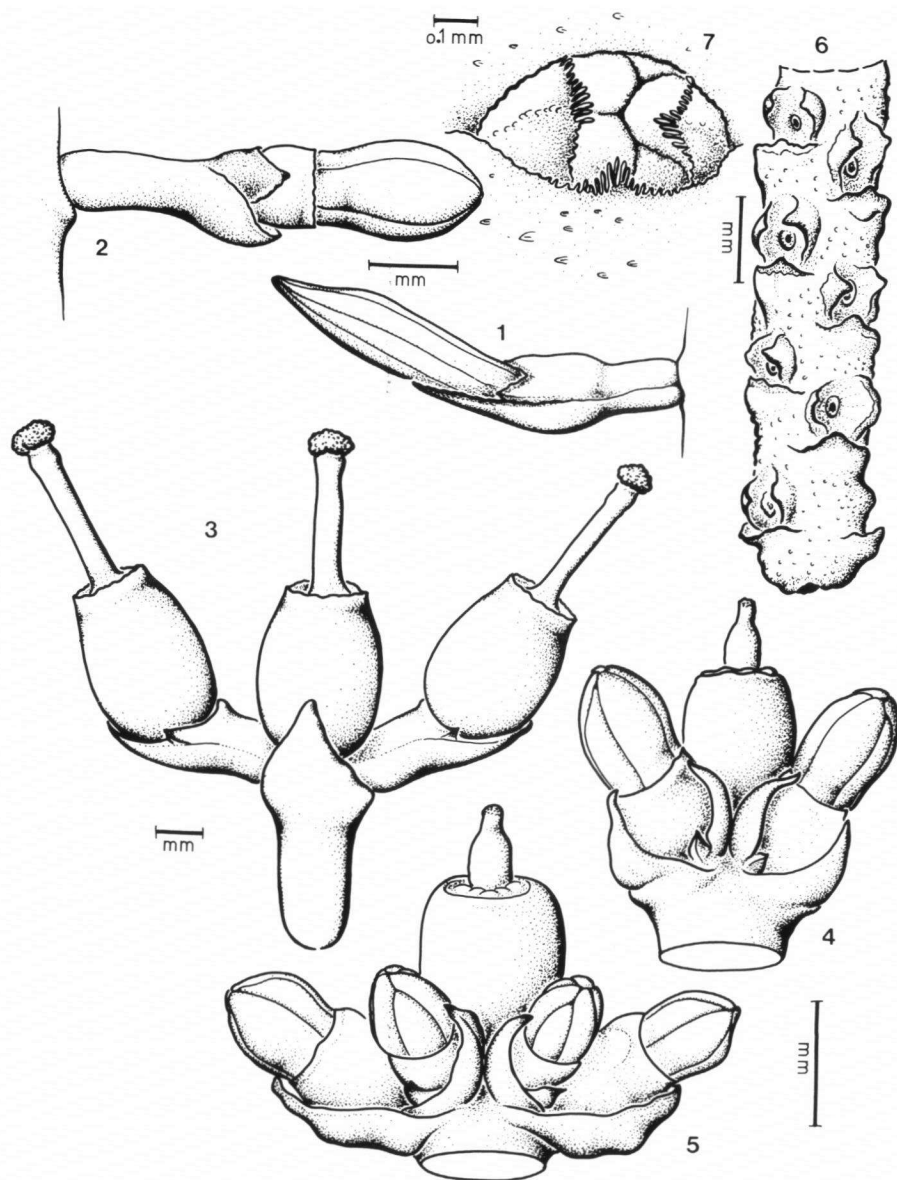
Fig. 6 — *Struthanthus, Dendropemon, Phthirusa,* and *Oryctina.* — 1. *Struthanthus panamensis,* monad. *Almeda 3536,* MO. — 2. *Dendropemon constantiae,* monad. *Cicuro et al. 6040,* MO. — 3. *Phthirusa robusta. Lugo 91,* S. — 4, 5. *Phthirusa pyrifolia,* triad and pentad, adaxial views, after Kuijt and Weberling 1972. — 6, 7. *Oryctina subaphylla,* portion of old spike and flower bud. *Anderson et al. 36949,* LEA.
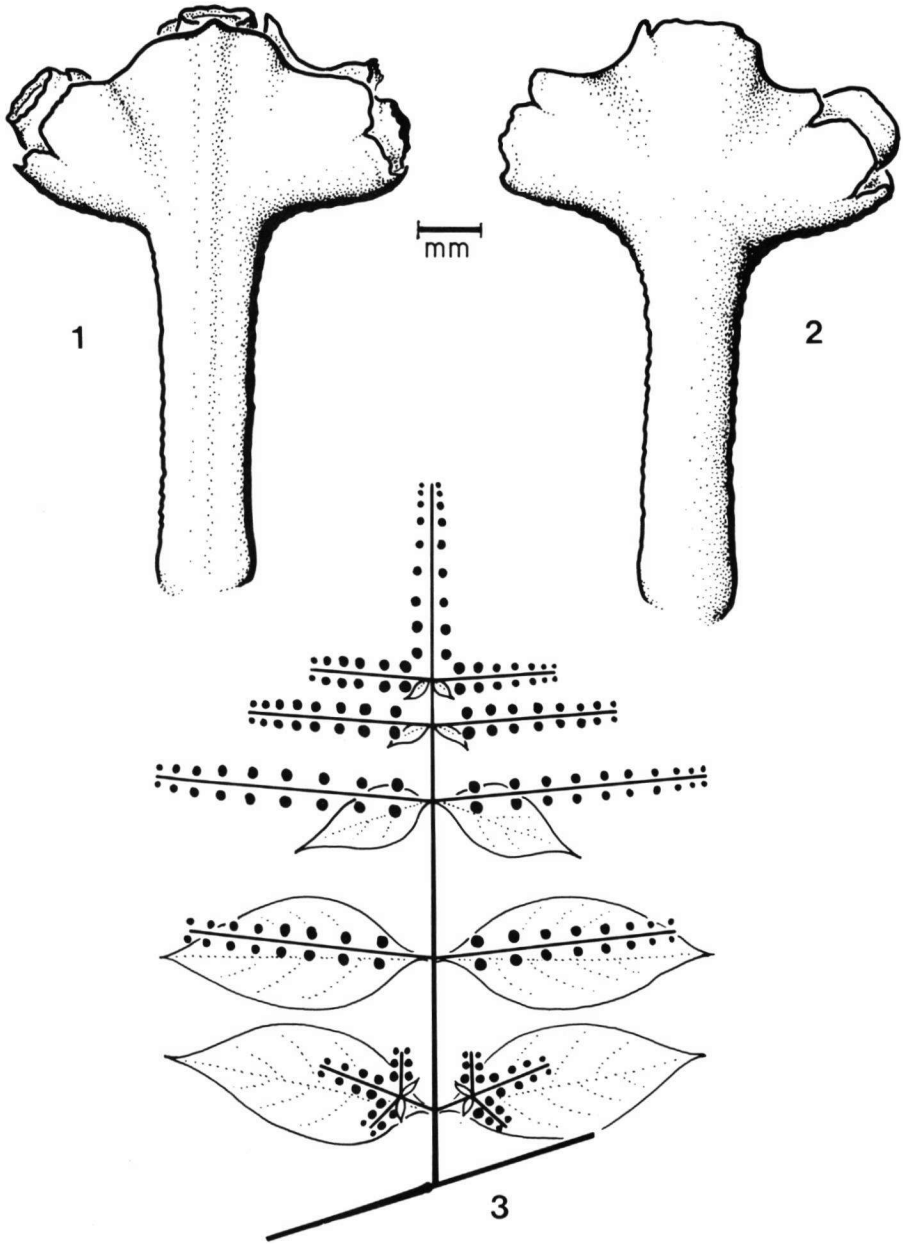
Fig. 7 — *Phthirusa.* — 1, 2. *Phthirusa sp.*, triad seen from below and above, respectively, to show fusion of bracts and bracteoles. *Sastre 6407*, P. — 3. *P. retroflexa*, diagrammatic representation of compound inflorescence, based on *Broadway 4689*, U. Each solid circle represents a triad.

Fig. 8 — *Tripodanthus* and *Tristerix*. — 1. *Tripodanthus flagellaris. Delvitto-Belgeno 27.663*, Herb. Ruiz Leal, Mendoza, Argentina. — 2, 3. *Tristerix longebracteatus*, monads. Ecuador, *Cuenca*; and *Cleef and 't Hart 250*, U, respectively. — 4. *Tristerix grandiflorus*, monad showing rare bracteole. *Holm-Nielsen*, Ecuador. — 5. *Tristerix tetrandrus*, inflorescence with all monads partly cut away, showing aborted apex. Chile, Prov. Concepción, 8 km W of Florida. — 6, 7. *Tristerix aphyllus*, inflorescence and monad, the latter showing persistent apical bud (arrow), the former showing position of lateral inflorescence bud (arrow). Chile, Fallerones.

Fig. 9 — *Tristerix* and *Ligaria*. — 1. *T. aphyllus*, tip of old inflorescence (upper monad peduncle extending to the right), the apex beginning to proliferate. *Skottsberg and Skottsberg 1463*, GB. — 2. Same, basal portion of old inflorescence (lowest monad scar at arrow), showing proliferation at two lateral buds. — 3. *Ligaria*, flowering branch; Argentina, Prov. Mendoza, San Luis. The arrow indicates a small leaf on the floral pedicel. — 4. Same, 2-flowered inflorescence, the flower on the right being the terminal one, the other lateral and in the axil of a bract. The terminal flower is supported by 4 fused bracts, three of which are here visible.
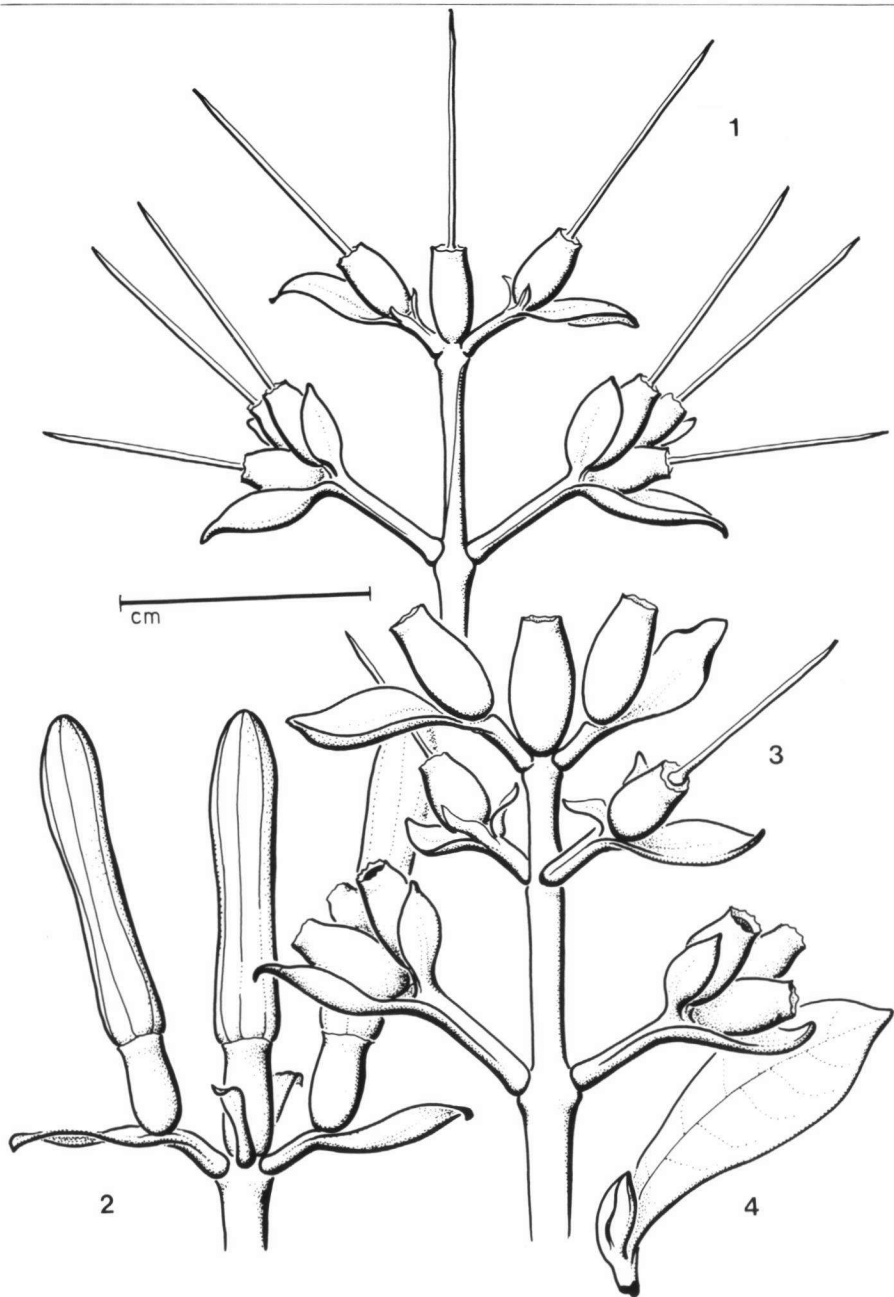
Fig. 10 — *Gaiadendron*: variation of the inflorescence tips in Costa Rica. — 1. Sequence: triad-bracteolate monad-apical flower. *Burger and Liesner 6431*, F. — 2. Sequence: triad (out of view)-ebracteolate monad-apical flower, the latter with two additional bracts. *Kuijt 1534*, UBC. — 3. Sequence: triad-bracteate monad-ebracteolate monad-apical flower. *Raven et al. 20968*, F. — 4. Young triad, showing bracteoles covering the flowers. *Kuijt 2396*, UBC.
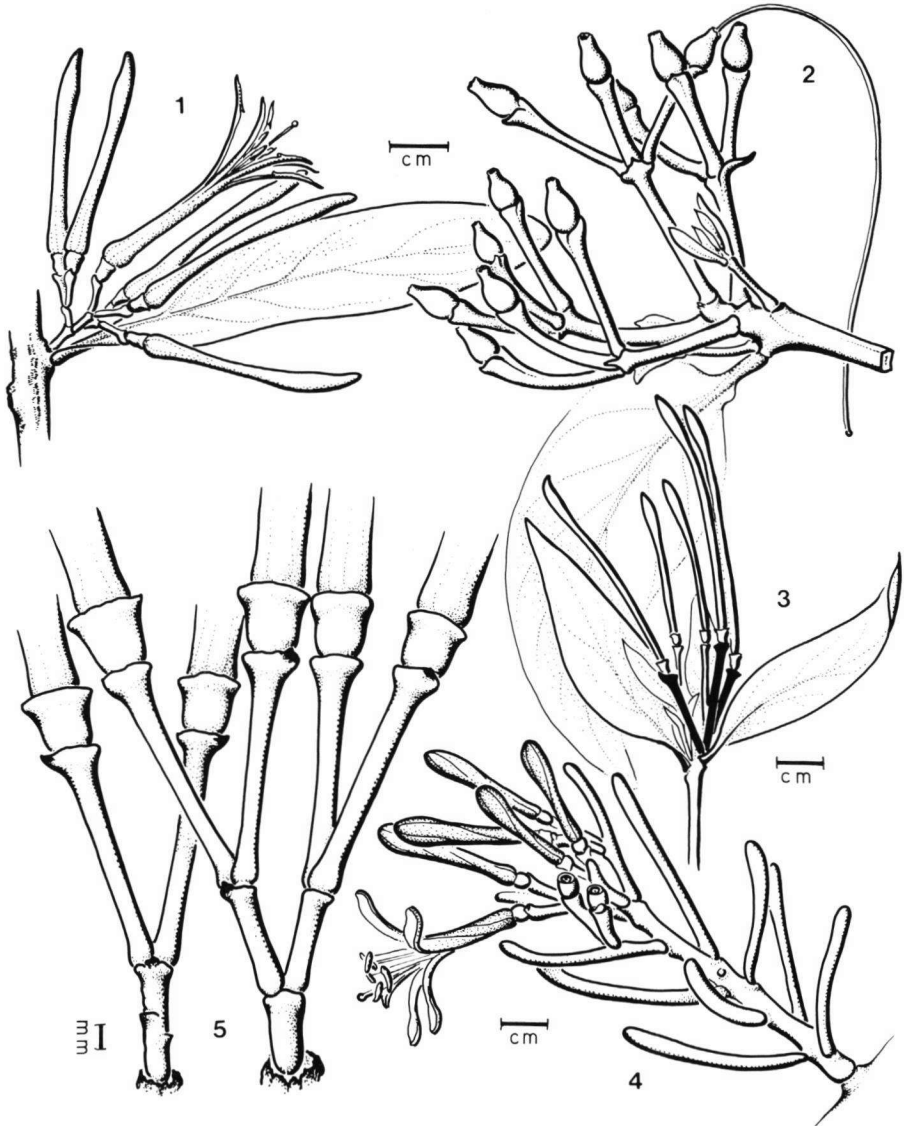
Fig. 11 — *Psittacanthus.* — 1. *P. ramiflorus*, after Kuijt 1964a. — 2. *P. schiedeanus*, after Kuijt 1964a. — 3. *P. schiedeanus*, teratological inflorescence, the leaf on the right subtending three pedicellate flowers (pedicels in black). *Monroy et al. 48*, K. — 4. *P. sonorae*. Mexico, Baja California, Bahia de los Angeles. — 5. *P. pusillus*, two inflorescence forms. *Mori and Kallunki 2192*, MO.
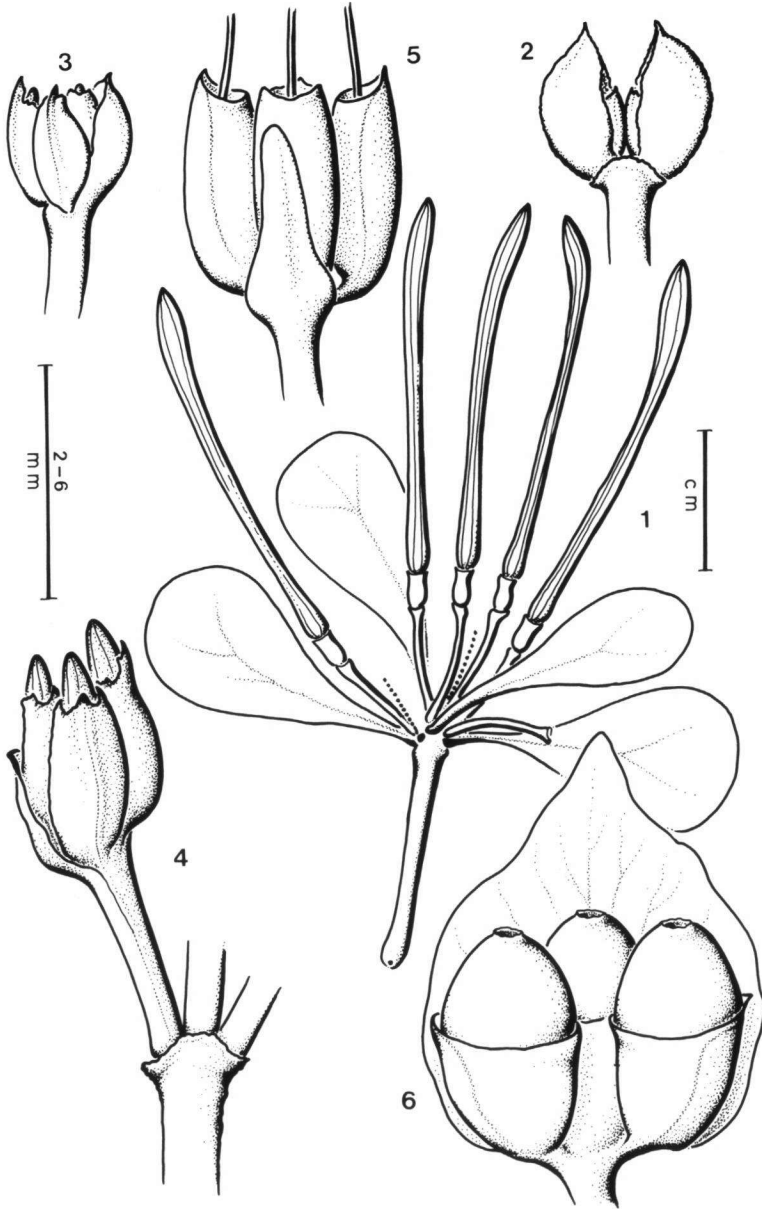
Fig. 12 — *Psittacanthus.* — 1. *P. palmeri*; one missing flower for each of the two leaves on the left is indicated by a dotted line. *Pringle 11701*, K. — 2 through 6. *P. cucullaris. Eggers 14057* (2–4); *Eggers 15295* (5); and *Stahel and Gonggrijp 5617* (6), all L. — 2. Two very young triads at the tip of the inflorescence, the bracteoles still being no more than half as large as the bracts. — 3. A somewhat later stage, from lower on the same inflorescence, the two bracteoles approaching the bract in size. — 4. A still later stage, the cupular form of the bracteoles and the cupule of the median flower (left) being recognizable, and the tips of the three buds emerging. — 5. Mature triad of form with small bract. — 6. Large-bracted triad in fruit.
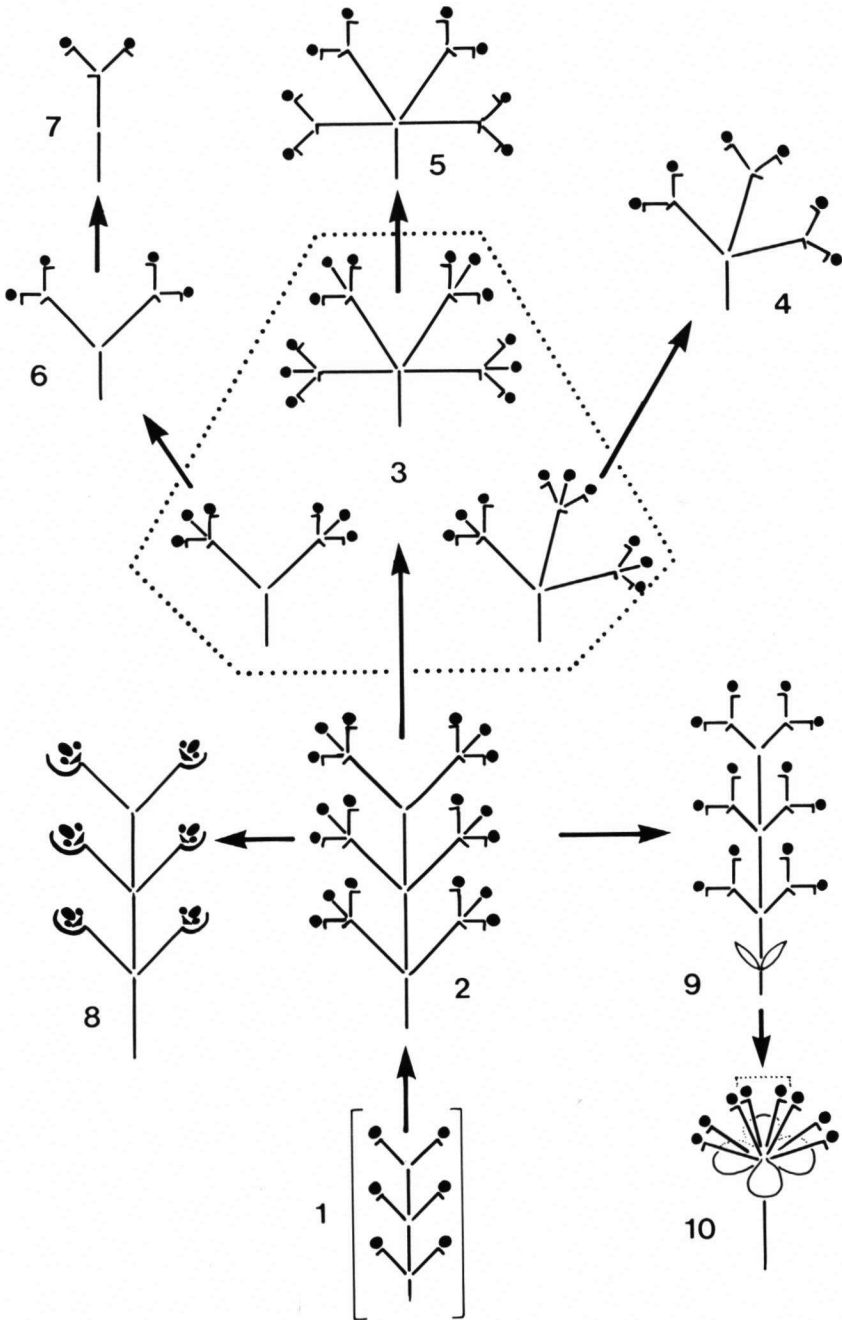
Fig. 13 — Schematic representation of the presumed evolution of the inflorescences of *Psittacanthus* and *Aetanthus*; see text for details. The simple raceme in brackets (1) represents the presumptive ancestral condition.
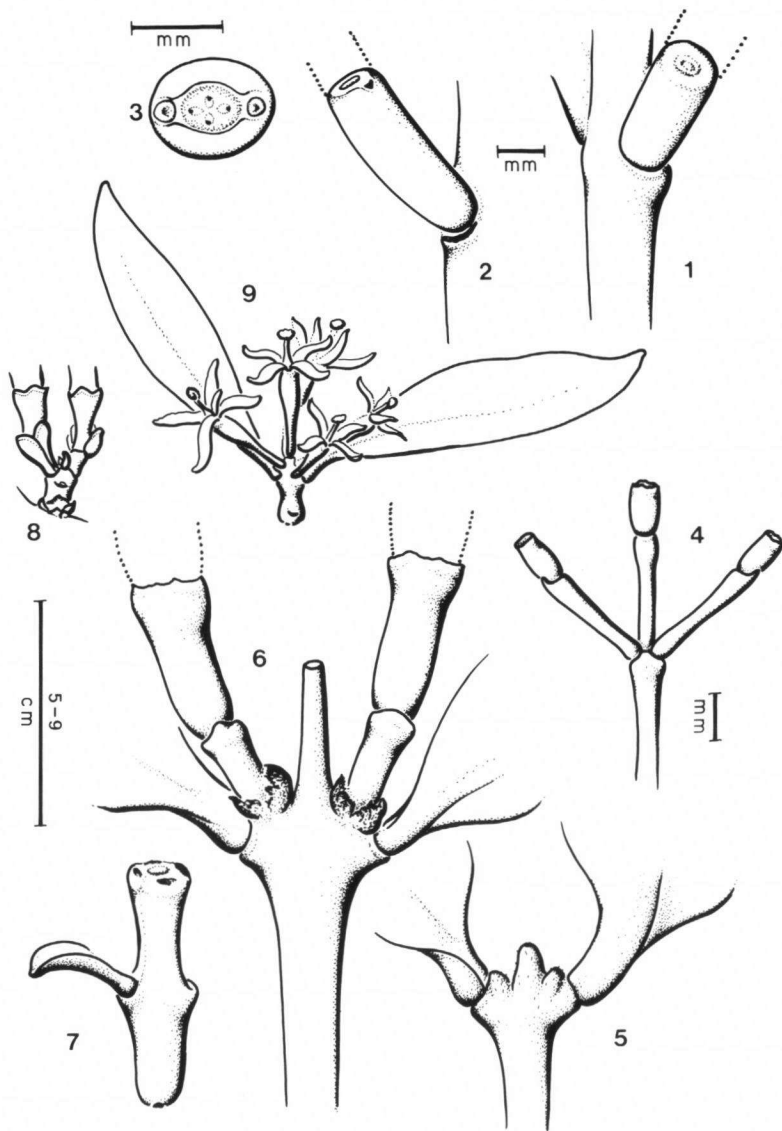
Fig. 14 — *Alepis, Ileostylus, Peraxilla, Trilepidea*, and *Tupeia*. — 1. *Alepis*, pedicel of monad near tip of raceme, showing apparent lack of bracts and bracteoles. *Holloway s.n.*, Herb. Otago University. — 2. Same, lowest part of raceme, showing both bract scar (black) below pedicel and minute bracteole scars, in prophyllar positions, on top of pedicel. — 3. Same as 2; view of pedicel from above, showing flower scar flanked by both bracteole scars. — 4. *Ileostylus*, male, lower triad. *Barker 6745*, Herb. University of Canterbury. — 5. *Peraxilla tatrapetala*, aborted branch tip flanked by two leaves which subtend swollen axillary cushions. *Holloway s.n.*, Herb. Otago University. — 6. Same, with one pedicellate flower in each leaf axil ensheathed by the fissured crater. Note bracteole-like lobes at tip of pedicels. — 7. Same, large peduncle of inflorescence which has borne several flowers. — 8. *Trilepidea*, after Barlow (1966). — 9. *Tupeia*, female. A rather condensed, purely monadic inflorescence; flowers are not subtended by foliage leaves, as the latter have separate axillary buds (not visible in figure). Collection without data.
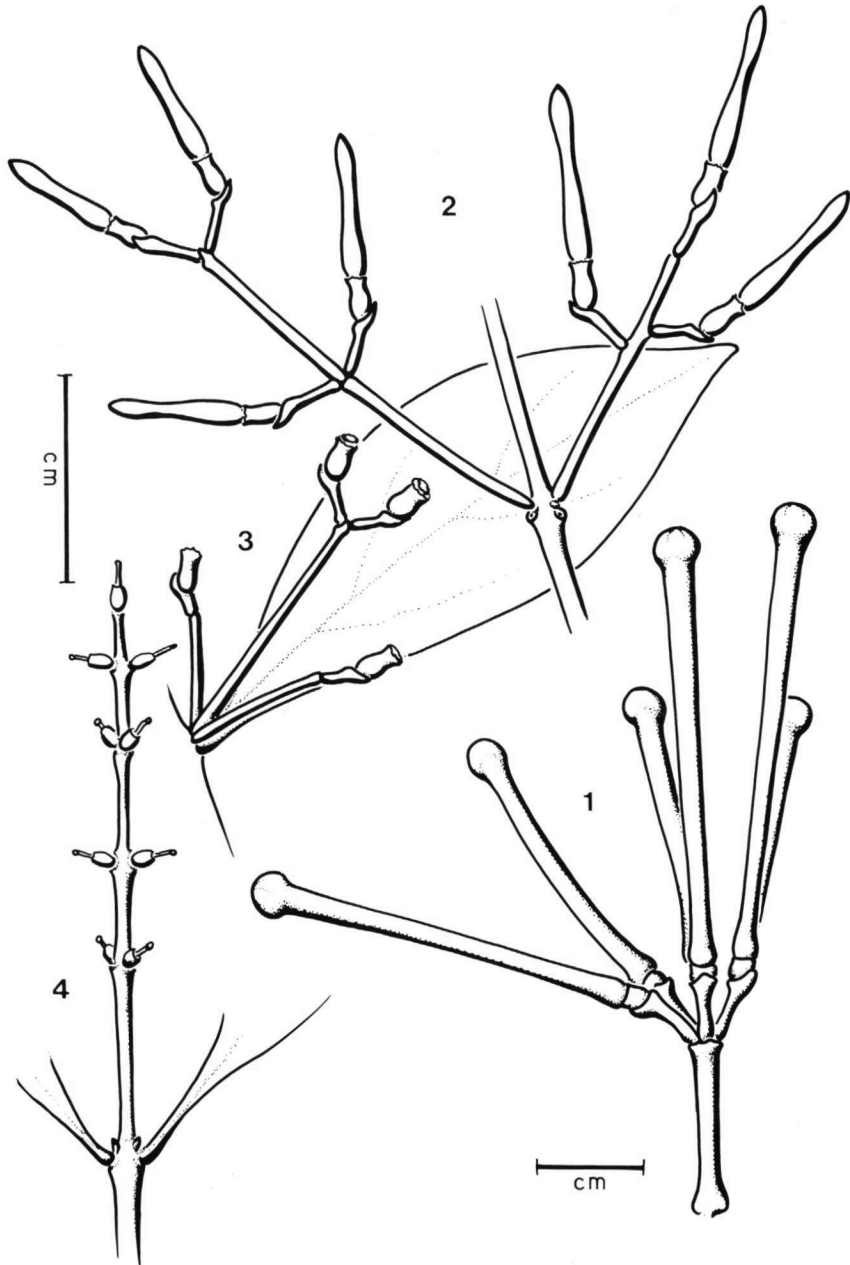
Fig. 15 — *Globimetula, Helixanthera,* and *Loranthus.* — 1. *Globimetula braunii.* Kenya, Broderick Falls, from a photograph courtesy D. Wiens. — 2. *Helixanthera ligustrina. Balansa 2331,* L. — 3. Same. *Tsang 29977,* L. Primary raceme 2-flowered, with two secondary racemes each reduced to a 1-flowered condition (see text). — 4. *Loranthus europaeus,* female, with terminal flower. *Berger s.n.,* CAS.
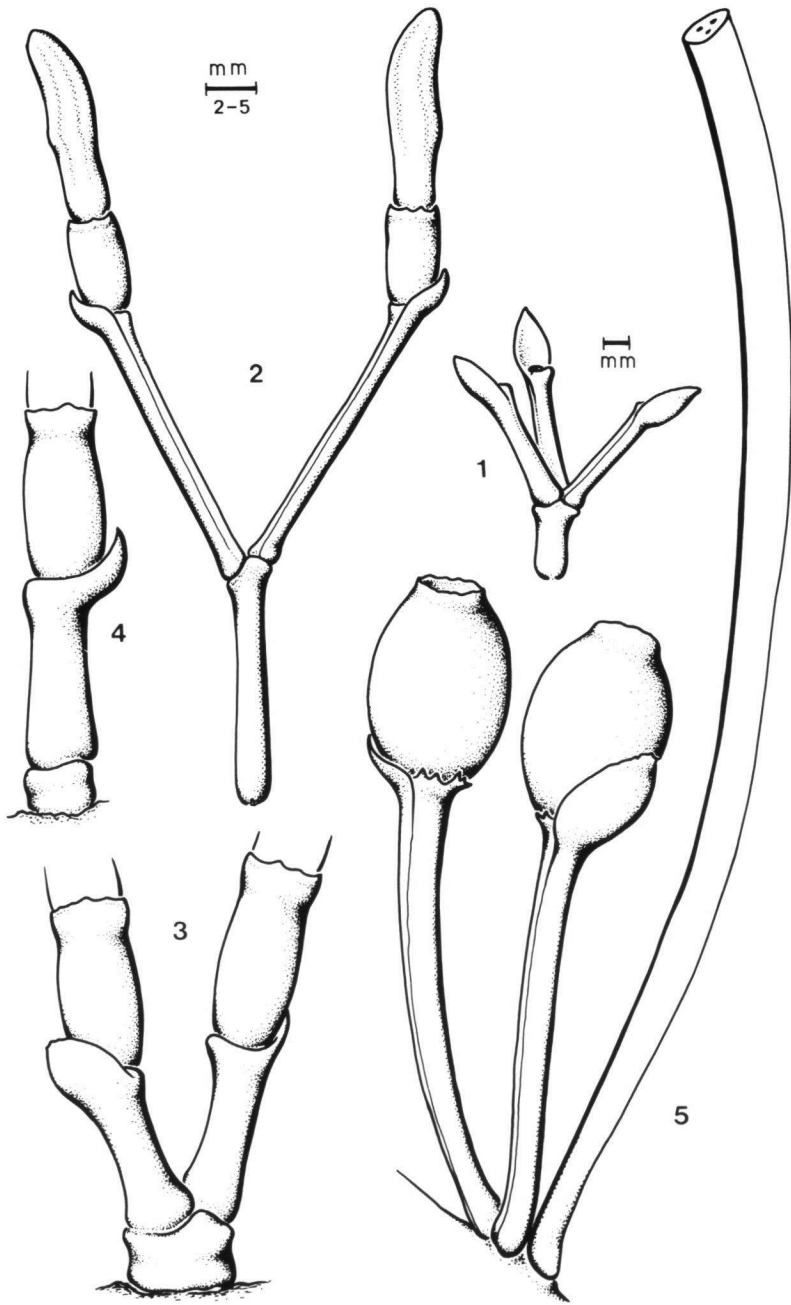
Fig. 16 — *Lysiana.* — 1. *L. subfalcata*, 3-rayed umbel. *Pedley 1181*, L. — 2. *L. linearifolia*, 2-rayed umbel. *Baker Q 828*, L. — 3, 4. *L. exocarpi*, 2- and 1-rayed 'umbels', respectively, with very short peduncles. *Eichler 13682*, L. — 5. *L. murrayi*, 2-rayed 'umbel', the peduncle invisible in the figure. Note also the fringed top of the pedicel. *Lothian 3990*, L.
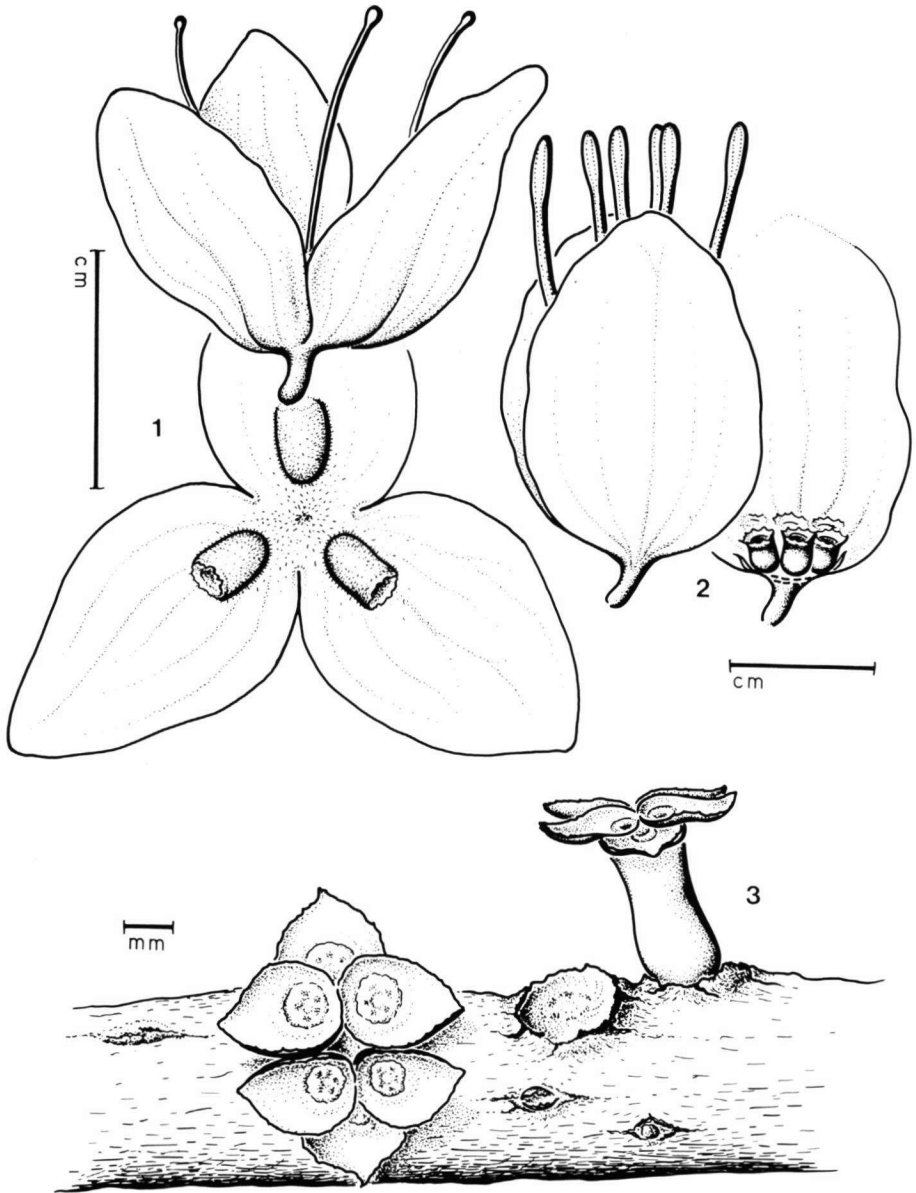
Fig. 17 — *Tolypanthus, Diplatia,* and *Dicymanthes.* — 1. *Tolypanthus involucratus,* seen from aside and from above. *Chand 8323,* L. — 2. *Diplatia furcata,* entire inflorescence and one with the nearest bract removed (broken line) to show triad with bracteoles. *Smith 11625,* L. — 3. *Dicymanthes seriata,* old inflorescences and one inflorescence scar on internode of stem. *Escritor 21380,* L.
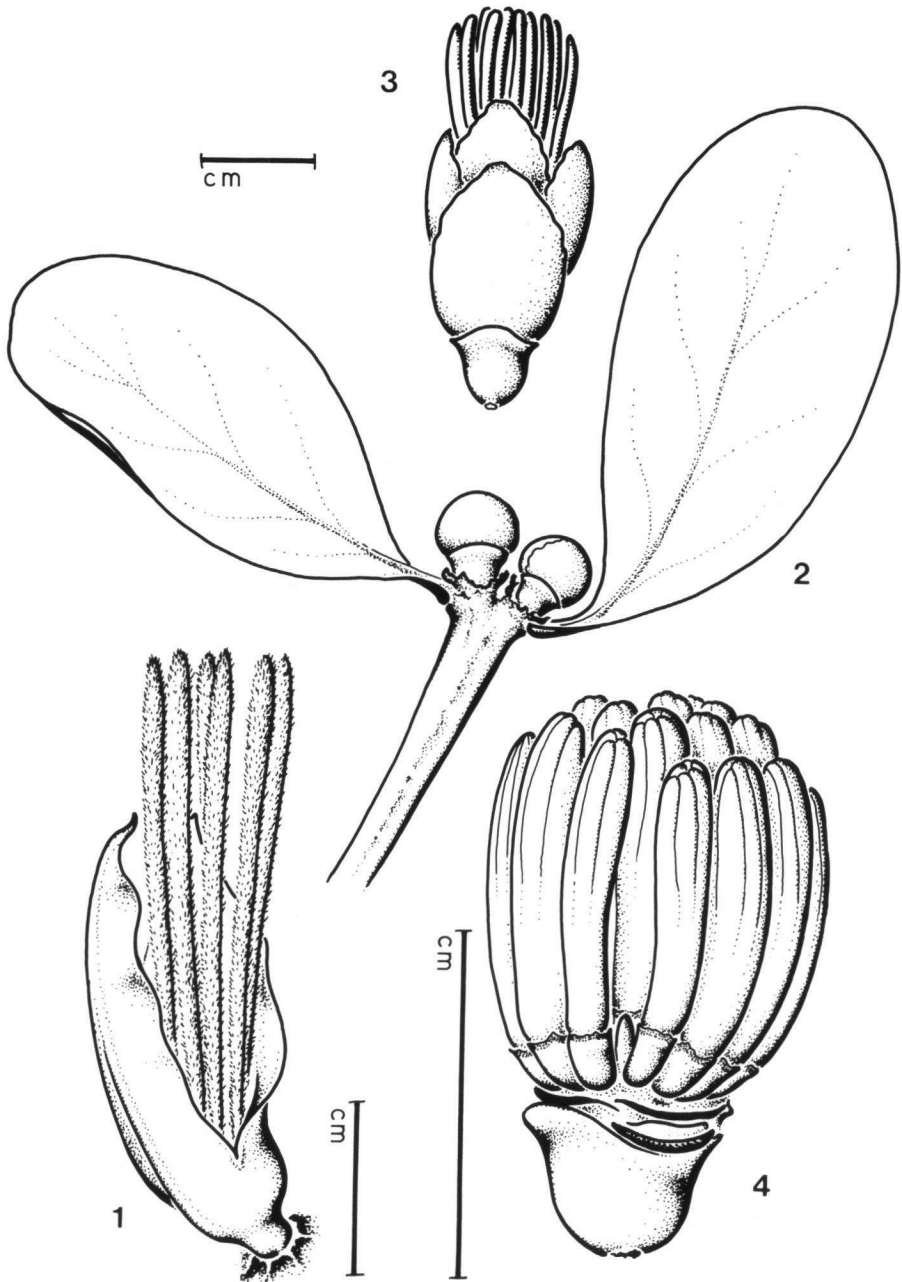
Fig. 18 — *Distrianthes* and *Lepeostegeres*. — 1. *Distrianthes molliflora*, inflorescence on epicortical root. *Clemens 819a*, L. — 2. *Lepeostegeres sp.*, showing two recently emerged young capitula flanking the aborted shoot apex. *Womersley 11718*, K. — 3. Same, inflorescence almost expanded. — 4. *Lepeostegeres sp.*, mature inflorescence with all bracts removed. *Womersley 11426*, K.
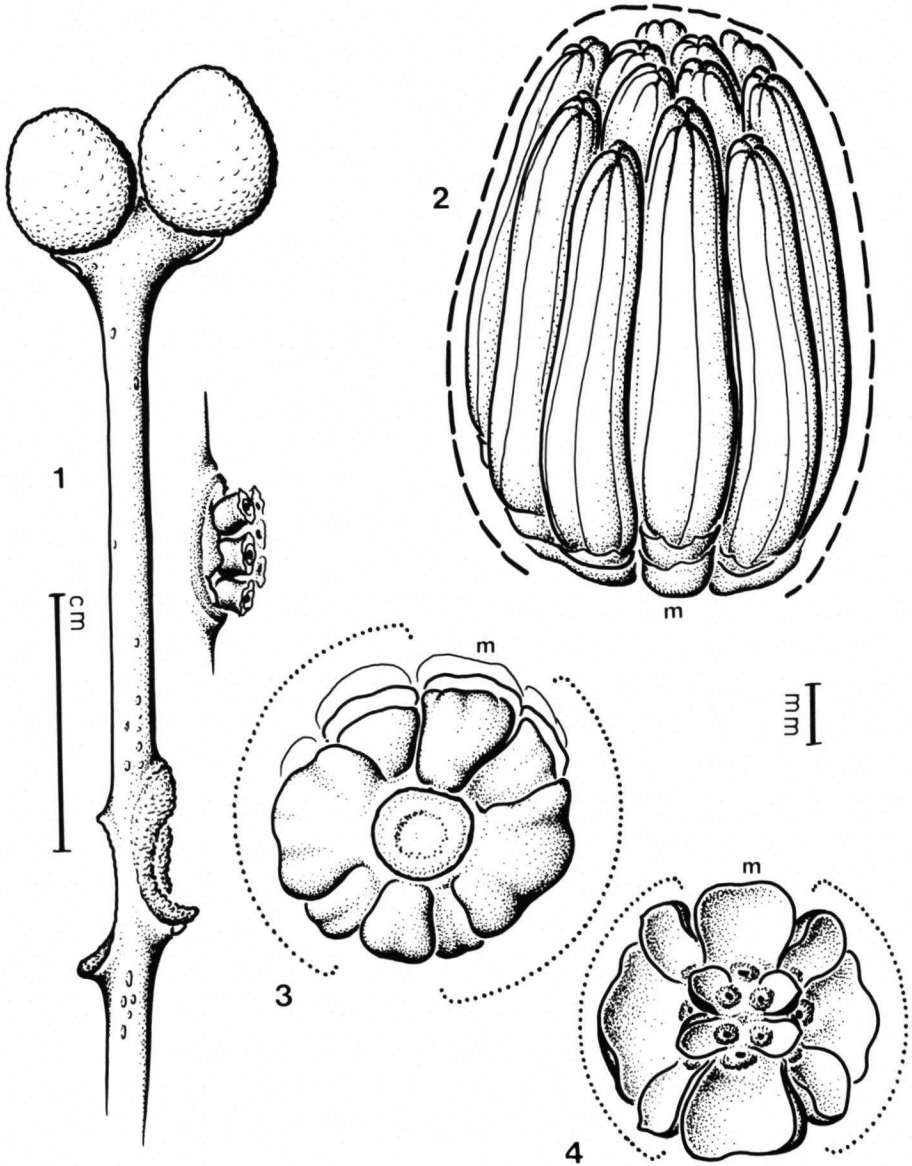
Fig. 19 — *Cyne.* — 1. *C. alternifolia*, leafless branch with two large axillary cushions flanking aborted apex, and with two inflorescence scars below; a sessile capitulum drawn to the right. *Elmer 10479*, L. — 2. *C. banahaensis*, nearly mature capitulum removed from its corky capsule (broken line). — 3. The same capitulum as seen from below. — 4. The same capitulum as seen from above, with all flowers removed to show bracts and bracteoles of all four triads. (N.B. The same median flower of one inner triad is labelled with m in each of Figs. 2, 3, and 4. In the latter two figures, the extent of the two outer triads is indicated by means of a dotted line).
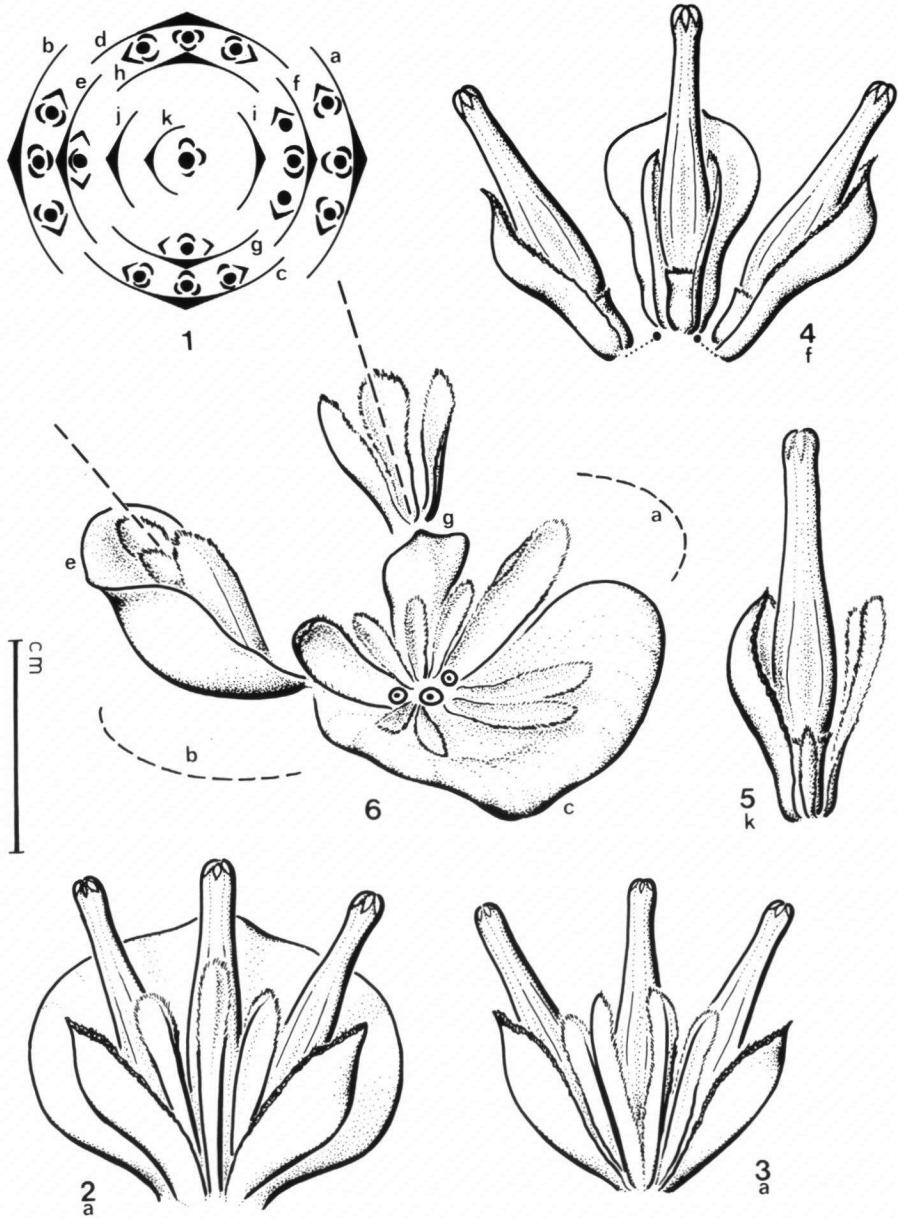
Fig. 20 — *Thaumasianthes amplexifolius. Edaño, B.S. 41765,* K. — 1. Diagram of the inflorescence, the lettering of parts corresponding to that in other figures. Structures subtended by bracts i and j were absent. — 2. Triad a, seen from adaxial side. For the sake of clarity, flowers are indicated in bud; in reality, they were in anthesis. — 3. Same, abaxial side. — 4. Triad f, seen from adaxial side, the two lateral flowers moved aside as shown by dotted line. — 5. 'Terminal' flower (see text). — 6. Some of the major, lower organs of the inflorescence, the lettering corresponding to that in Fig. 20 – 1. The monad complex subtended by bract g displaced upward slightly for clarity of representation. The two broken, straight lines indicate a single flower each, the curved ones bracts.
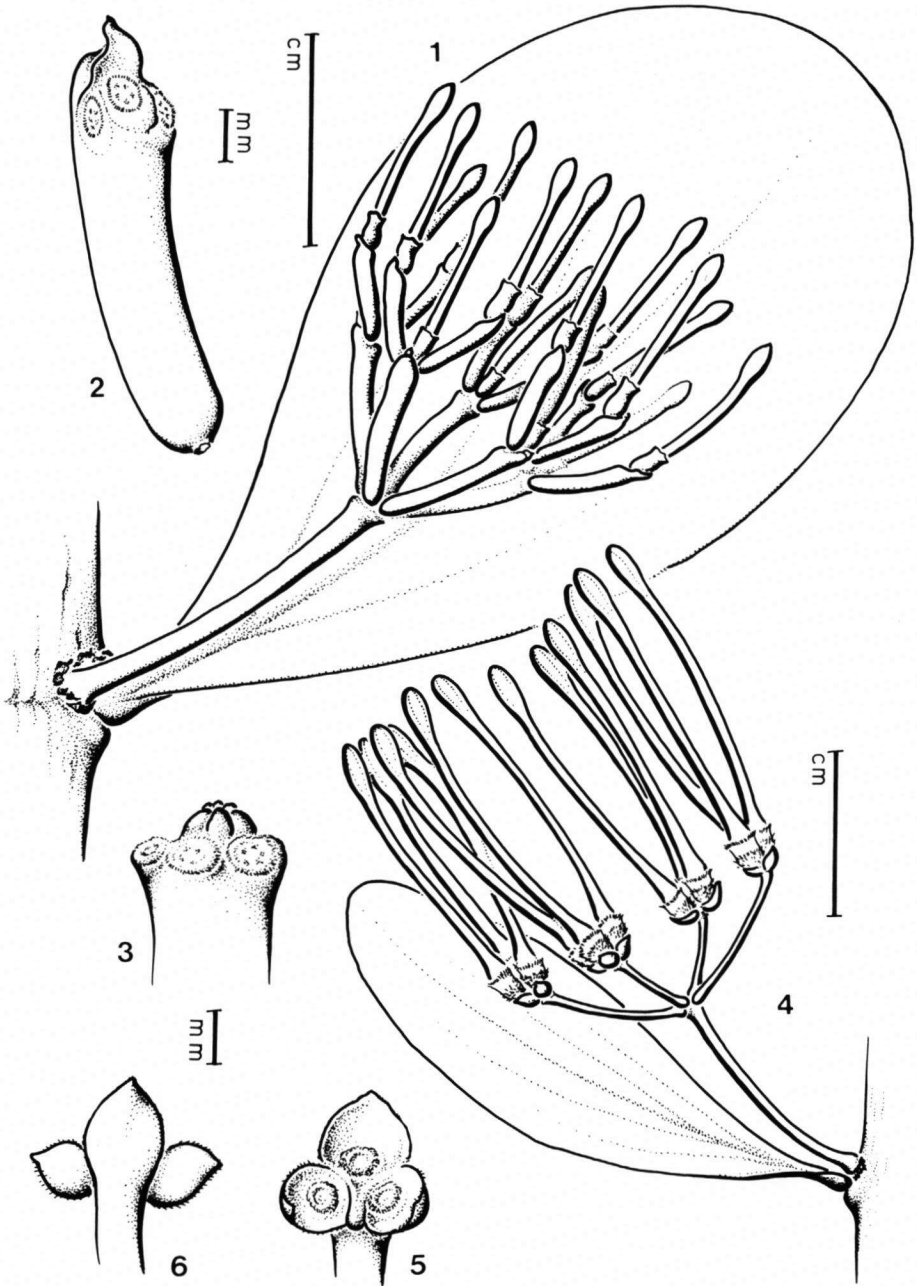
Fig. 21 — *Amyema.* — 1. *A. clavipes*, triads with only lateral flowers pedicellate. *v. Royen NGF 20453*, L. — 2. Same, triad peduncle, showing position of the three flower/pedicel scars. — 3. Same, aborted apex of umbel surrounded by triad scars. — 4. *A. lucasii*, triads with all three flowers sessile. *Constable 4967*, L. — 5, 6. Same, triad seen from above and below, respectively, the flowers removed.
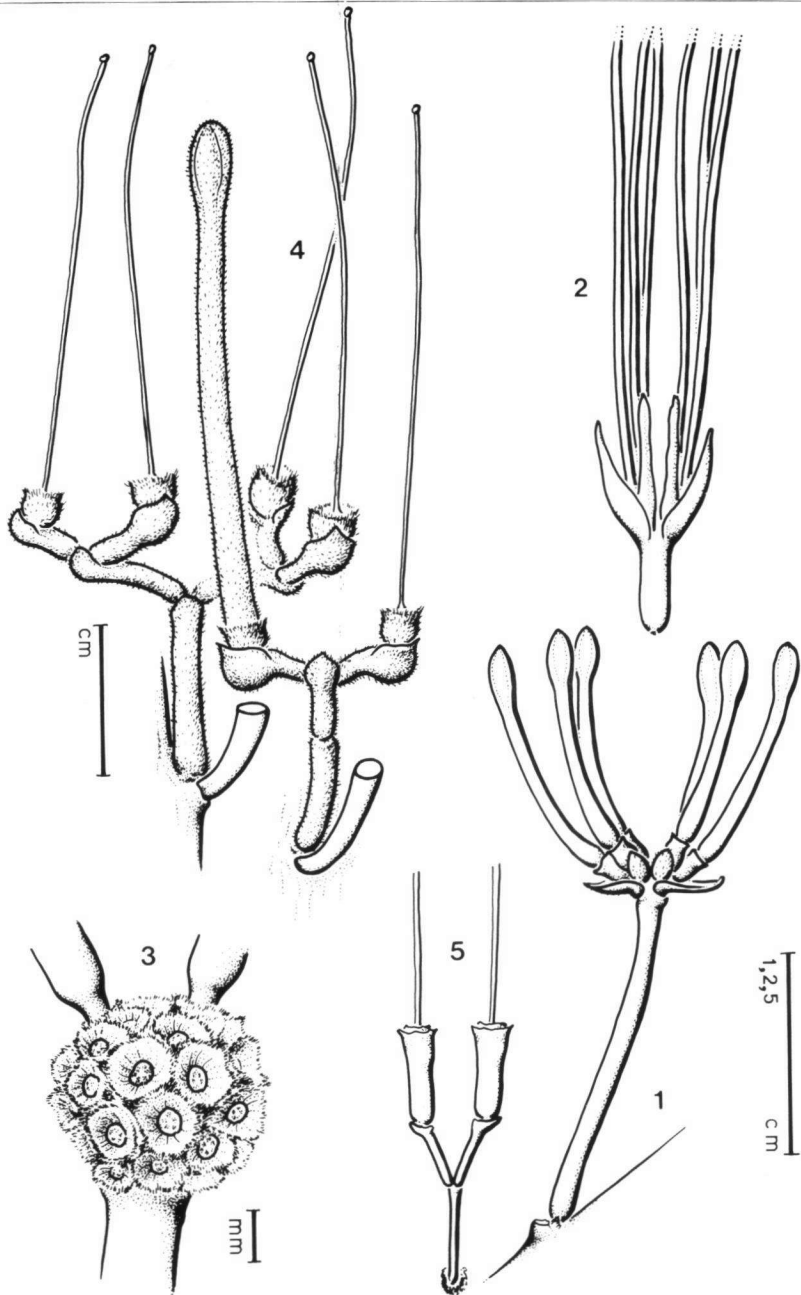
Fig. 22 — *Amyema.* — 1. *A. maidenii*, inflorescence of two sessile triads. *Blake 21294*, L. — 2. *A. tetrapetala*, as in *A. maidenii*. *Womersley 19321*, L. — 3. *A. strongylophylla*, many-rayed umbel of triads, the basal portions of two shown. *Kalkman BW 3426*, L. — 4. *A. gibberula*, inflorescences with two dyads and one dyad. *Lothian 3786*, L. — 5. *A. seemeniana*, inflorescence a 2-rayed simple umbel. *Schodde 3117*, L.
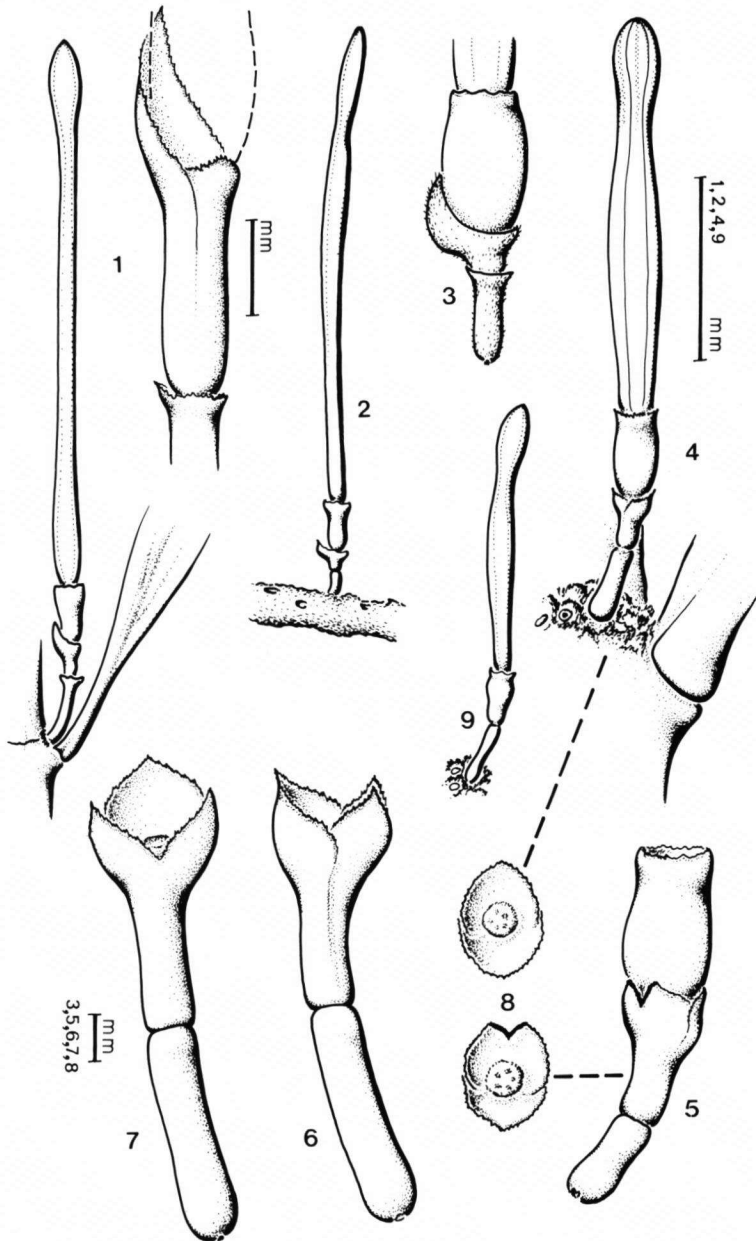
Fig. 23 — *Amyema* and *Sogerianthe*: unifloral types. — 1. *A. finisterrae. Hoogland and Schodde 6732*, L. — 2. *A. hastifolia*, root-borne flower. *Brass 10752*, L. — 3. *A. hastifolia*, enlarged. *Brass 10802*, L. — 4. *S. sogerensis* (note flower zone). Kanis 1093, L. — 5. Same, showing split second bract. *Forbes 715*, L. — 6, 7. Same, showing two views of the common 2-lobed condition of the second bract. *Barlow 974*, L. — 8. Same, views from above of bracts of Fig. 23 – 4 (above) and 23 – 5 (below). — 9. *S. versicolor. Waterhouse 29*, L.
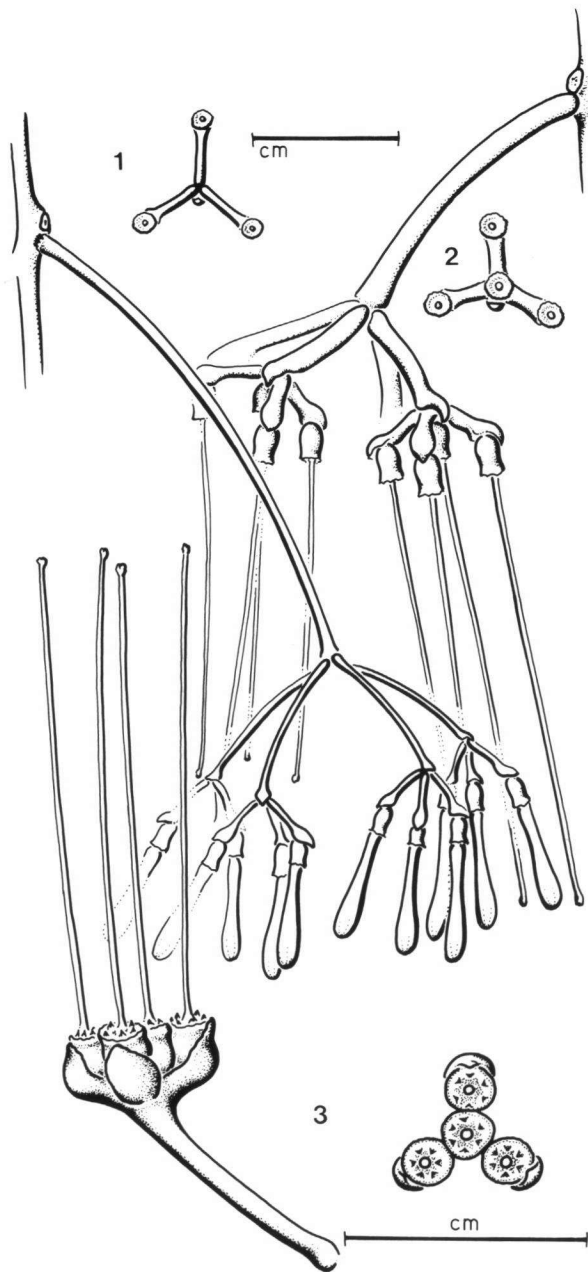
Fig. 24 — *Amyema*. — 1. *A. pendula*, triadic type, with single triad seen from below. *Pedley 1220*, L. — 2. Same, tetradic type, with single tetrad seen from below. *Wilson 781*, L. — 3. *A. fitzgeraldii*, with view from above on the right. *Stauffer and Royce 5339*, L.
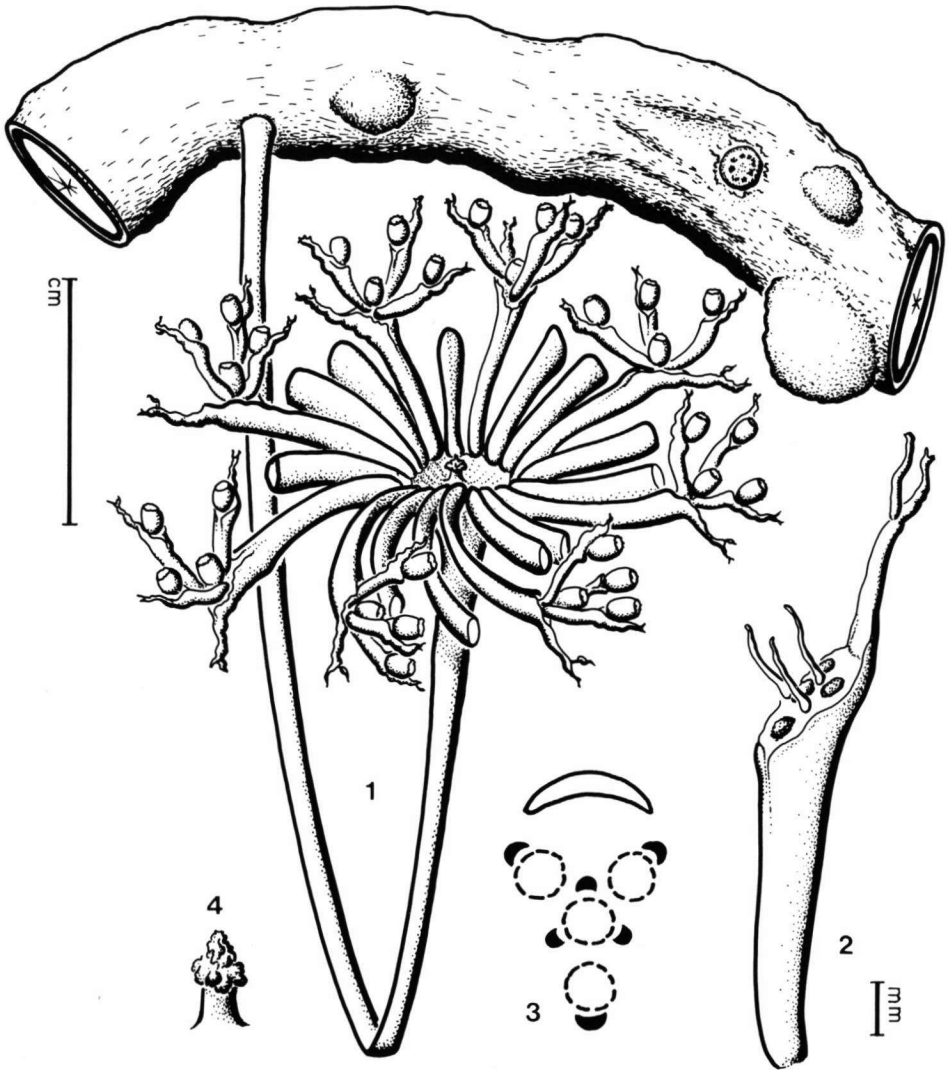
Fig. 25 — *A. dilatipes. v. Balgooy 547*, L. — 1. Inflorescence attached to epicortical root; one scar, and three young inflorescences still within capsules are also visible. For the sake of clarity, a number of tetrads have been cut away, leaving only the base of peduncles. — 2. Tetrad enlarged, with flowers removed. The forked organ on the right is the primary bract. — 3. Diagrammatic representation of Fig. 25 – 2. The primary bract indicated by a white crescent, other bracts in black. — 4. Aborted apex of compound umbel.
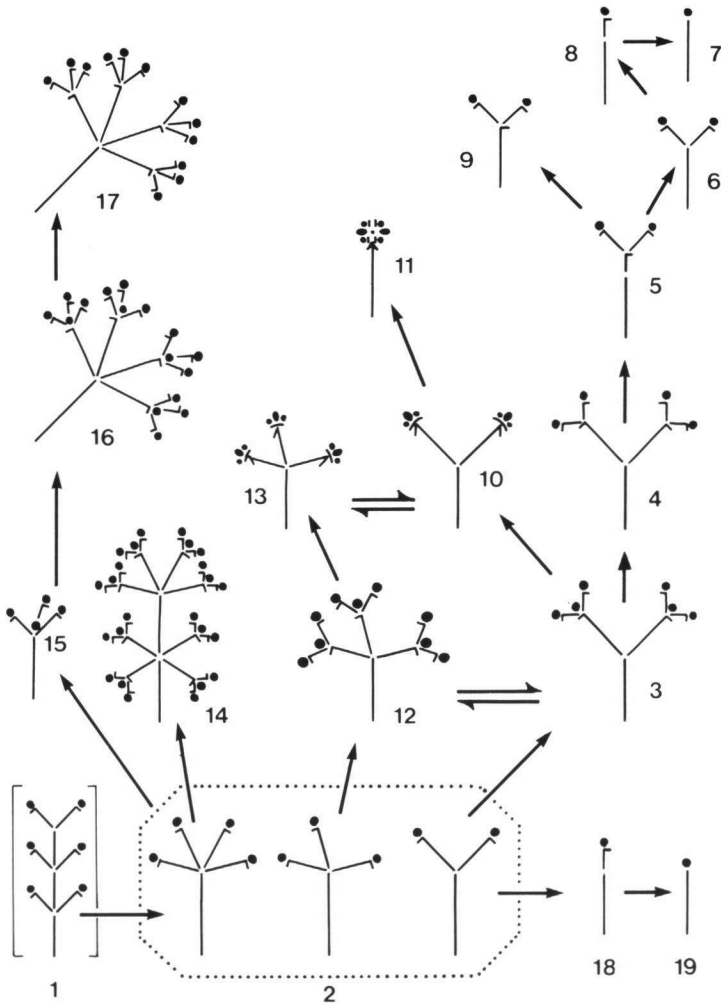
Fig. 26 — *Amyema* and related genera: schematic representation of the presumed evolution of inflorescences. See text for details. — 1. Presumed ancestral raceme of monads with recaulescent bracts. — 2. Simple umbels with two or more rays. — 3. Two-rayed umbel of triads with sessile median flower and pedicellate lateral ones, e.g., *A. quandang*. — 4. Two-rayed umbel of dyads, as in some *A. gibberula*. — 5. One-rayed umbel with dyad, as in most *A. gibberula*. — 6. Simple, two-rayed umbel, as in *A. seemeniana* (but cf. 26 – 2). — 7. One-flowered inflorescence with bracteate, flower and inarticulate pedicel, e.g., *Sogerianthe versicolor* (cf. 26 – 19). — 8. Same, but the pedicel articulate, e.g., *Sogerianthe spp.* and *Amyema spp.* (cf. 26 – 18). — 9. Same as 26 – 6, but one bract subtending both monads. — 10. Two-rayed umbel of triads, all flowers sessile, e.g., *A. hilliana*? — 11. Capitulum made up of two sessile triads of sessile flowers, e.g., *A. maidenii, A. tetrapetala, Dicymanthes*. — 12. As 26 – 3, but with more than two rays, e.g., *A. linophylla* and *A. clavipes*. — 13. As 26 – 12, but all flowers sessile, e.g., *A. lucasii*. — 14. Two or more whorls of several to many triads, of which only the median flowers sessile; *Dactyliophora*. — 15. Simple tetrad, with three peripheral flowers borne on bracteate pedicels, plus central, sessile flower; *A. fitzgeraldii*. — 16. Compound umbel made up of units as in 26 – 15, e.g., *A. dilatipes, A. miquellii*, and some *A. pendula*. — 17. Same as 26 – 16, but without central flowers; some *A. pendula*. — 18. As 26 – 8. — 19. As 26 – 7.
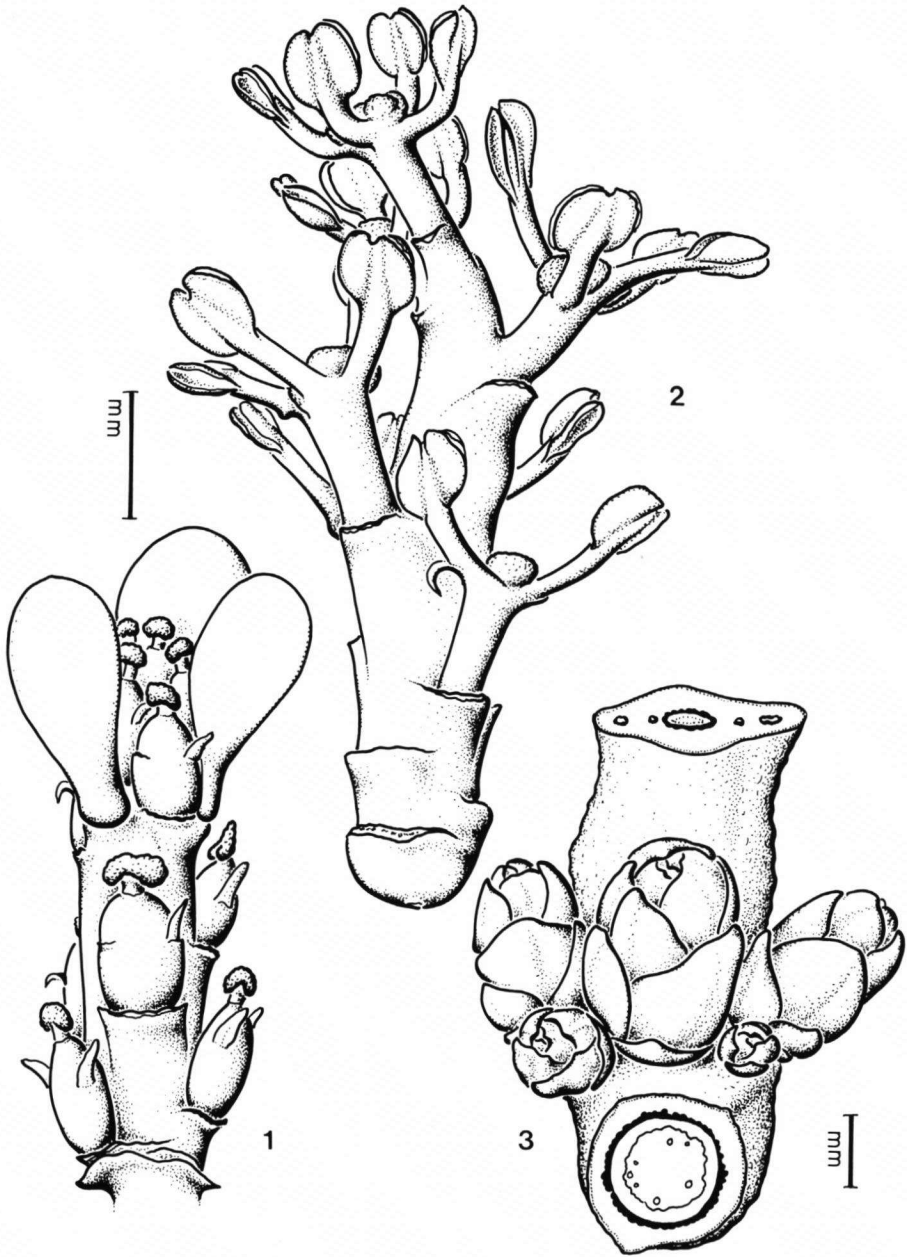
Fig. 27 — *Eremolepidaceae: Antidaphne, Kuijt 2433* as cited in Kuijt 1964a. — 1. Female spike with three embryonic foliage leaves. — 2. Male raceme, the caducous bracts having fallen away. — 3. Young male inflorescences clustered in the axil of a foliage leaf (above); stem in sectional view seen below.