

Danser BH. 1933. *Thaumasianthes* eine neue Loranthaceengattung aus den Philippinen. Recueil des Travaux Botaniques Néerlandais 30:464-474.

**THAUMASIANTHES**  
**A NEW LORANTHACEAE FROM THE PHILIPPINES**  
**BY**  
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Upon a closer examination of the inflorescences of the Philippine Loranthaceae, which have hitherto been placed in the genus *Lepeostegeres*, it has been proved that among them there is one which, in regard to the structure of the flower heads, differs so much from all others that it deserves to be accepted as a type of a new genus, and that there is a second species, which must probably be made to the same genus. For this reason, I first let the diagnosis of the new genus and the transplantation of the species belonging to it follow, in order then to dare to attempt to morphologically interpret the inflorescence.

*Thaumasianthes* Dans., nov. gen. – Inflorescentia capitata; receptaculum elongatum; bracteae decussatae confertae, triadem florum vel superiores florem singulum ferentes; flores triadum omnes sessiles bracteis 3 suffulti, flores laterales bractea maiore naviculata bracteolisque 2 planis, flos medius bractea maiore plana et bracteolis 2 planis. Corolla sympetala profunde 6-partita. Antherae basifixae acutae loculis 4 continuis. Ovarium saccis embryonalibus 3, parenchymate separatis, basi amplis, sursum attenuatis, altitudine disci in apicem globosum inflatis. Cfr. fig. 1 et 2d.

*Thaumasianthes* Dans. nov. gen. – Inflorescence capitate; receptacle elongate; bracts closely decussate, bearing flowers in triads or the upper ones singular; all flowers resting sessile on 3 bracts, the major bracts of lateral flowers naviculate and the bracteoles in 2 planes, major bracts of the middle flowers flat and bracteoles in 2 planes. Corolla sympetalous, deeply 6-parted. Anthers basifixed, acute, locules 4 continuous. Ovary with 3 embryo sacs, separated by parenchyma, base wide, attenuate upwards, high above the disc the apex globose inflated.

Type species: *Thaumasianthes amplifolia* (Merr.)

Dans., nov. comb.; *Loranthus amplifolius* Merr., Phil. J. Sc., bot., 13, p. 277 (1918); *Lepeostegeres amplifolius* Merr., Enum. Phil. Fl. Pl., 2, p. 101 (1923); Dans., Bull. Jard. Bot. Buitenz., ser. 3, 10, p. 320 (1929); Verh. Kon. Akad. Wetensch. Amsterd., afd. Natuurk., 2de sectie, 29, 6, p. 62 (1933).

Probably other species: *Thaumasianthes ovatibractea* (Merr.) Dans., nov. comb.; *Loranthus ovatibracteus* Merr., Phil. J. Sc., bot., 13, p. 278 (1918); *Lepeostegeres ovatibracteus* Merr., Enum. Phil. Fl. Pl., 2, p. 101 (1923); Dans., Bull. Jard. Bot. Buitenz., ser. 3, 10, p. 321 (1929); Verh. Kon. Akad. Wetensch. Amsterd., afd. Natuurk., 2de sectie, 29, 6, p. 63 (1933).

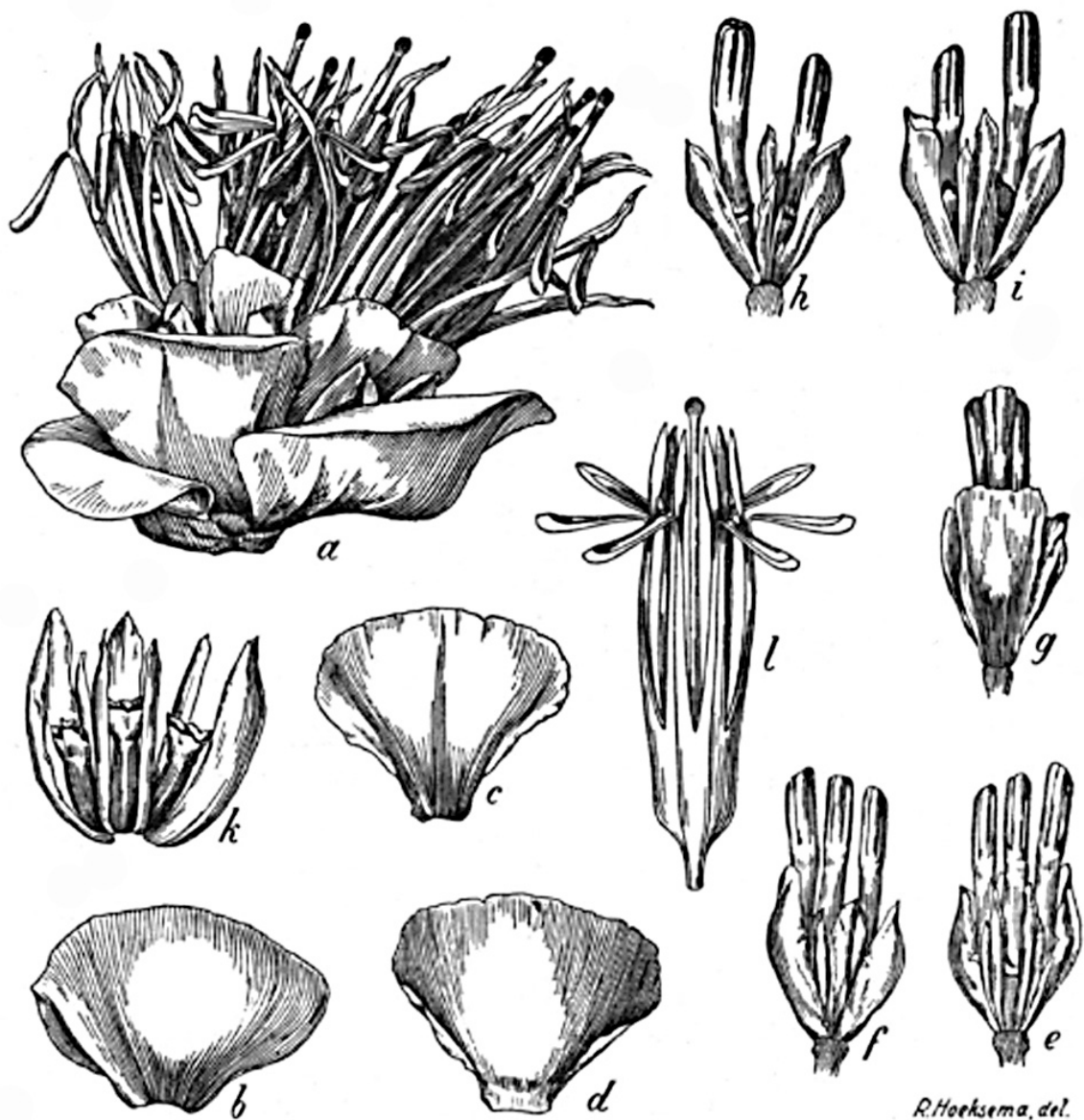


FIG. 1. *Thaumasianthes amplifolia* (Merr.) Dans. ; a. Inflorescence with z.T. flowered, z.T. opened flowers; b. bracts of the outer pair; c. bracts of the second pair seen from the outside; d. the same seen from the inside; e. Flower triad of the outer pair from the outside; f. the same from the inside; G. Flower triad of the third pair with bract, from the outside; h. general receptacle with the upper triads reduced to a flower and associated bracts and bracteoles; i. the same from the other side; k. flowered triad of the second head, which lacks the outer bracteoles of the side flowers. Everything 2x nat. size.

Another species, formerly called *Lepeostegeres*, was found to belong to the genus *Cyne*. It should be called: *Cyne capitulifera* (Merr.) Dans. nov. comb.; *Loranthus capituliferus* Merr., Phil. J. Sc., Bot., 7, p. 264 (1912); *Lepeostegeres capituliferus* Merr., En. Phil. Fl. Pl., 2, p. 101 (1923).

There is thus only one *Lepeostegeres* species, *Lepeostegeres congestiflorus* (Merr.) Merr., remaining for the Philippines.

The inflorescence of *Thaumasianthes* (see Fig. 1) is not a true head; the common receptacle is not flat, but elongated, with flattened internodes on the side of the flowers, and all the bracts bear flowers. The bracts are decussed, as is to be expected with a Loranthacee. In the two inflorescences I studied I found 5 pairs, of which the outer 2 or 3 pairs carried a complete triad of flowers, the rest, as we shall see, a more or less reduced triad.

The given diagram (Figure 2d) is a combination of the 2 inflorescences examined. The outer 2 pairs of triads are drawn after the first head I analyzed under the binocular microscope. From this little head, the bracts of the inner triads were all too easily detached, so that I could not obtain sufficient security as to their position. The inner 3 pairs of bracts and triads have therefore been drawn from the other head, from the inner parts of which my assistant Mr. J. C. Mekel has delivered a complete series of microtome sections. In this second head there was still a deviation in the extremities of two pairs of triads, which was not included in the figure. Seven out of the eight lateral flowers of these triads lacked the bracts (compare Fig. 1k). However, where in one of the flowers the bracteoles were present and the disappearance of these bracteoles is the first reduction phenomenon of the triads, I hardly attach any morphological value to this finding. Moreover, it might be possible that part of the bracteole had already fallen off with this already spent head.

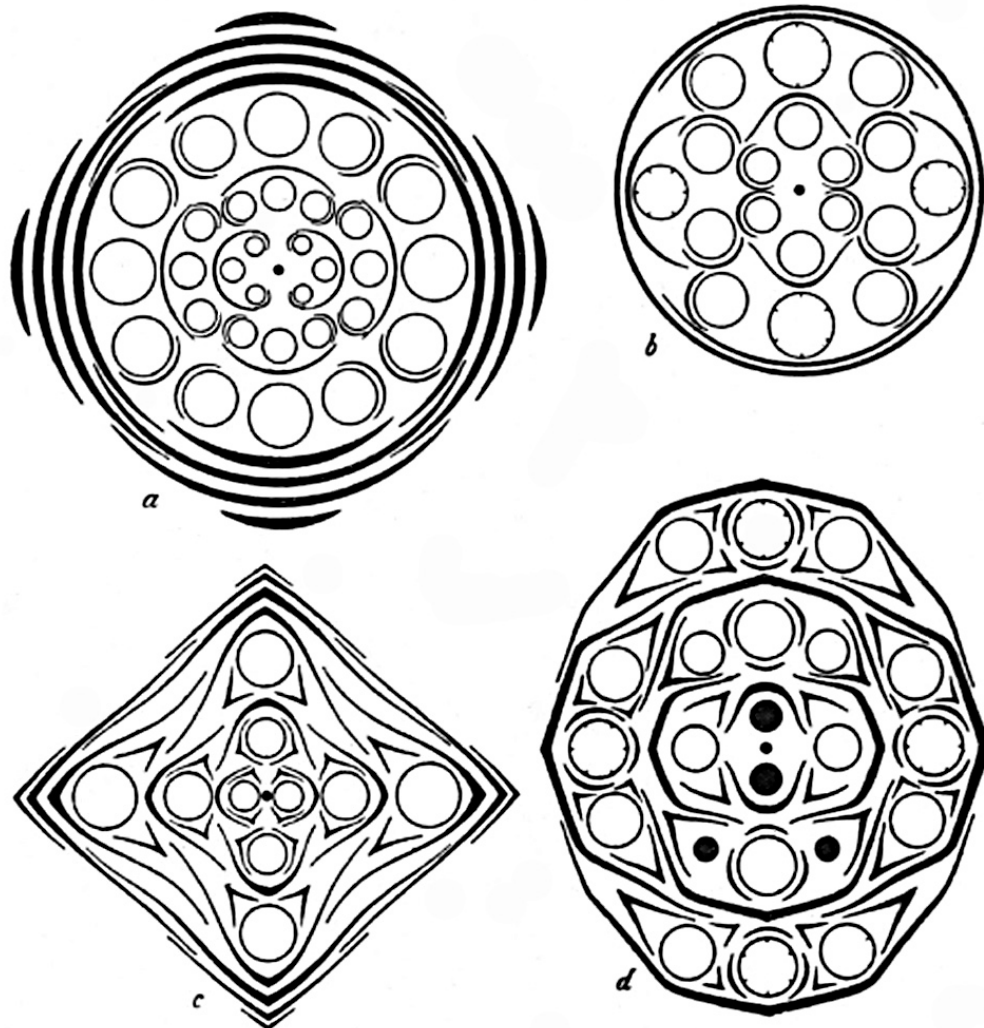


FIG. 2. Diagram of Elytrantheae inflorescences; a. *Lepeostegeres*; b. *Cyne*; c. *Lepidaria*; d. *Thaumasianthes*.

Considering now a complete triad of *Thaumasianthes*, we see that each main bract bears three flowers and that each flower is again surrounded by 3 bracts. If in Loranthaceae with affinity to *Thaumasianthes* a flower is surrounded by 3 bracts, we consider these bracts to be a bract with 2 bracteoles, and I would like to speak here of the bract and the two bracteoles of each flower. Thus, the middle flower then has a flat bract pointing to the rear and 2 obliquely inclined bracteoles, the lateral flowers a laterally directed, strongly keeled bract and one toward the rear and one towards the front, a narrow, flat bracteole.

In the more inward triads, the bracteoles of the lateral flowers disappear first, then the side flowers themselves, then the remaining parts, until at last in the inner triads there is only a rudimentary flower left in the axil of the main bract.

The individual flowers are essentially identical to those of the genus *Lepeostegeres* (see Bull Jard Bot. Buitenz, ser. 3, 11, p. 458-459, and Fig. 3 on p. 261). The calyx tube (the portion of the calyx, which has fused with the ovary) is somewhat funnel-shaped and edged by the lateral pressure of the flowers standing around. The calyculus (the free part) is quite long, and like *Lepeostegeres* fringed and irregularly serrated. The corolla is 6-parted, sympetalous, with a short tube and above the exit point of the sharply bent corners. I have not been able to find in *Thaumasianthes* an S-shaped curvature of the corolla lobes before the crown opens, as occurs in *Lepeostegeres*. The anthers are long and pointed and show 4 unchambered loculi. The style breaks off above the disc; I did not find a beak-like style rudiment on the ovary of past-flowering [ausgeblüten] flowers, which is so characteristic of most Elytranthinae. The microtome preparations produced by Mr. Mekel of herbarium material soaked in ammonia solution still show the internal structure of the ovary in sufficient quantities to be able to determine that *Thaumasianthes* agrees with *Lepeostegeres* in the construction of the ovary. At the base of the ovary, 3 embryo sacs are separated by parenchyma; they narrow up and thicken at the top (at the height of the disc and below the point where the style breaks off) again club-shaped. *Thaumasianthes* belongs to the Elytranthinae.

Only the structure of the inflorescence of *Thaumasianthes* is yet to be explained. For this purpose we want to compare this inflorescence with those of the nearest related Elytranthinae.

*Lepeostegeres* (Figure 2a) has a real capitulum. The flowers are all sessile or very short-stalked on a flat common receptacle and are surrounded by a sheath of decussate sterile bracts. The flowers have very rudimentary or no bracts, with the exception of the external triads, which are apparently placed in the axils of the inner involucre bracts. The position of the flowers on the receptacle is in principle very simple; they are in decussate triads.

This is most evident in the fruit formation of certain species. In some species, the flowers are completely sessile and the fruits remain sessile on the receptacle. In most species, however, the flowers are very short-stalked and elongate the small pedicels upon fruiting, in such a way that the lateral fruits of the triads get longer pedicels than the middle. In the only Philippine species, the common receptacle now elongates, the involucre falls off early, and there are also rudimentary bracts and bracteoles here and there, so that there is nothing left of the capitulum-shaped inflorescence, and the capitulum has returned its basic form as a raceme or spike from decussate triads. This inflorescence, as occurs in *Amylotheca* (Fig. 3a), shows as the only peculiarity that with it, as with all Loranthoideae, the bracts and bracteoles are postponed to the apex of the internodes, at whose base we expect them. Hereby is completely explained the stretched inflorescence of *Amylotheca* and thus also the same construction, but merged into a capitulum of *Lepeostegeres*.

The inflorescence of *Cyne* (Figure 2b) is another variation of the same scheme. Here, too, we find a receptacle with some decussate pairs of flower triads. The difference with *Lepeostegeres* is

that the bracts and bracteoles are developed on all flowers and that an involucre of decussate bracts is absent and replaced by an undivided calyptra, which is in no way composed of bracts.

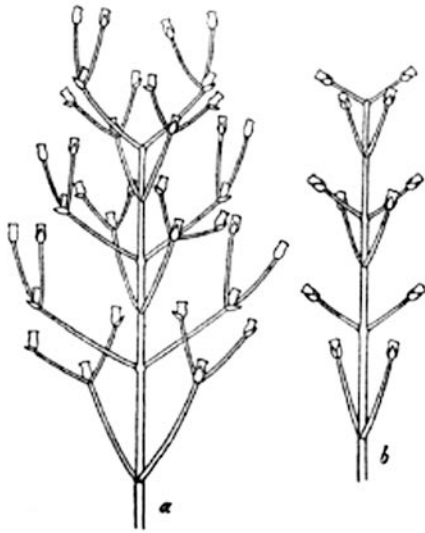


Fig. 3. Schematic representation of some Elytranthinae inflorescences; a. *Amylotheca*; b. *Macrosolen*.

The inflorescence of *Lepidaria* (Fig. 2c, see also Bull Jard Bot. Buitenz, ser., 3, 11, p 261, Fig. 3) is at first sight similar to that of *Lepeostegeres*, but shows on closer inspection some more important differences. In the species with many-flowered heads (subg. *Strobilaria* Dans., Verh. Kon. Akad. Wetensch. Amsterd., afd. Natuurk., 2de sectie 29, 4, p. 16, 1933), the inflorescences are still not real capitula, because the common receptacle is still elongated; however, a real involucre of sterile bracts is present. The inner bracts each carry only one flower, which is placed between two bracteoles. In the species of the subgenus *Lepidella* (tc.) The number of flowers is only 4 or sometimes even only 2, and we also find a flat common receptacle, so we have here a real capitulum. In the Philippine species of this subgenus flowers are missing the bracteoles, flowers

are missing the bracteoles, in the species from the western part of the Malay Archipelago, however, they are present, as in the subgenus *Strobilaria*. This inflorescence is now to be regarded as the compacted state of the raceme or spike of triads of which the middle flower is reduced, as occurs in the genera *Elytranthe* and *Macrosolen* (Fig. 3b), and where these again are derived without difficulty from the inflorescence of *Amylotheca* (Fig. 3a), the inflorescence of *Lepidaria* is morphologically completely interpreted.

We can see from the primitive inflorescence of the genus *Amylotheca* on the one hand directly the inflorescences of *Lepeostegeres* and *Cyne* are derived, on the other hand on the inflorescences of *Macrosolen* and *Elytranthe* also the capitulum of *Lepidaria*.

However, it is not possible to trace the capitulum of *Thaumasianthes* back to the same basic groundplan. Consider again Fig. 2d. The position of the bracts on the main spindle is quite normal. In the axil of each bract, we now find a triad, and each flower of these triads is, as we have already noted, surrounded by one bract and two bracteoles. The question now is whether it is possible to regard the triads of *Thaumasianthes* as dichasia. This is unlikely for two reasons. First, second-order bracteoles on the lateral flowers of the dichasia are completely unknown in the Elytranthinae. Secondly, the bracteoles of the middle flower would remain completely unexplained.

I believe we do not need to see any dichasia in the triads of *Thaumasianthes*, but we must consider them a reduced inflorescence of higher order. This assumption is generally not daring. It occurs in many other plant families that initially strongly composite inflorescences are also weaker and are merged into always entangled total inflorescences. Thus we see that the capitula of the composites, though a many-flowered system, have become weaker in many genera, and are united to greater total inflorescences. An extreme case is the jug-shaped inflorescences of *Echinops*, which are composed of a greater number of capitula reduced to a small size. An even more beautiful case is found in the Australian composite *Angianthus myosuroides*, which we find shown and described in Velenovsky (Vergl. Morphologie der Pflanzen, 3, p. 814, Fig. 501). Here

the heads are 2- or even only 1-flowered and put together in an spike, so that this composite carries its flowers almost in spikes rather than in capitula. Also in the Lorantheae similar examples are known, albeit less apt ones. Thus, in the genus *Taxillus* the flowers are made in simple umbels. In some species, e.g. *Taxillus glaucus* (Thunb.) Dans., these umbels are only few-flowered, after the ends of the branches mostly single-flowered, and then rather dense, so that the flowers stand in this way in simple, leafy terminal spikes.

A complaint against this derivation is the fact that the flower of *Thaumasianthes* is not similar to that of *Macrosolen*, *Elytranthe* or *Lepidaria*, but rather that of *Lepeostegeres* or *Cyne*. Moreover, if the head of *Cyne* does not have an envelope of sterile bracts, I prefer to think of the triads of *Thaumasianthes* as derived from the capitula of *Cyne*. At the same time, the triads of this genus would be reduced to one flower, as triads easily do in weaker development.

If, according to the above, we want to give the genera *Thaumasianthes* and *Cyne* their proper place in my system of Elytranthinae (Verh. Kon. Akad. Wetensch., Amsterd., afd. Natuurk., sectie 2, 29, 6, p. 4) this system thus suffers the following change.

3a Flowers in triads, which are united into larger inflorescences.

4a inflorescence a raceme, spike or umbel of triads.

5a Anthers basifixed ..... *Amylotheca*

5b Anthers dorsifixed (but immobile)..... *Loxanthera*

4b Inflorescence a head-shaped umbel of triads surrounded by a common cup ..... *Lampas*

4c Inflorescence a simple head.

5a Capitulum with a involucre of decussate bracts. .... *Lepeostegeres*

5b Capitulum with hood-shaped involucre in one piec ..... *Cyne*

4d Inflorescence a clustered capitulum, all bracts with 3 flowers or the interior with fewer flowers, all flowers with 1 bract and 2 bracteoles. .... *Thaumasianthes*

3b Unchanged.

3c Falls away.

Probably the case of *Thaumasianthes* has an analogue in the South American genus *Loranthus*, which is usually named after Martius *Psittacanthus*. It does not concern a capitulum-shaped inflorescence, but a stretched raceme of triads. Nevertheless, Eichler comes to a completely similar diagram of the triads (compare Fig. 4F, drawn after Eichler in Mart., Fl. bras., 5, 2, plate I, 51, with the inscribed letters from Eichler, Blütendiagr., 2, p. 550, in order to keep the association with the quotation taken from this work.) We then read in Eichler (Blütendiagr., 2, pp. 550-551):

“B. Secondary flowers with prophylls. This case is characteristic of the South American group *Psittacanthus*, which is characterized by the fact that the primordial flower is also provided with a special covering (Fig. 235 D and F at i). "... Thus we see in Fig. 235 D. in the bract of the primary flower I, which grew up to the departure of the secondary flowers, and in the secondary flowers II, which were pushed a little farther back, a 3-toothed or 3-sided shell, consisting of their likewise grown a special covering bract a and b and their sterile prophylls  $\alpha'$   $\beta'$  resp.  $\alpha_1$   $\beta_1$  (cf. Fig. 235F) and thus represents the same structure as we find in Fig. 235B in primordial blooming. But what is the meaning of the sheath i at the primary flower? It can not be formed from the covering bract and bracteoles because the covering bract b stands at the bottom of the branching point of the triad (cf. Fig. 235D), but the bracteoles have grown up as cover bracts of the secondary flowers and are stuck in the 3-toothed cup, which enclose the ovary; thus, in the primordial flower, the sheath i must be of a morphological character other than that of the secondary. It now usually shows 3 teeth, which are oriented towards the covering bract b as  $\frac{1}{2}$ ; These may, however, have been produced by the pressure exerted on each other by the flowers of the triad, which are densely packed

together when young, but they may indicate a composition of 3 straight leaf organs. I can not decide the question; but in any case I would like to assume that the sheath as a whole is of a phyllomatic (not just a discoid or the like) character!"

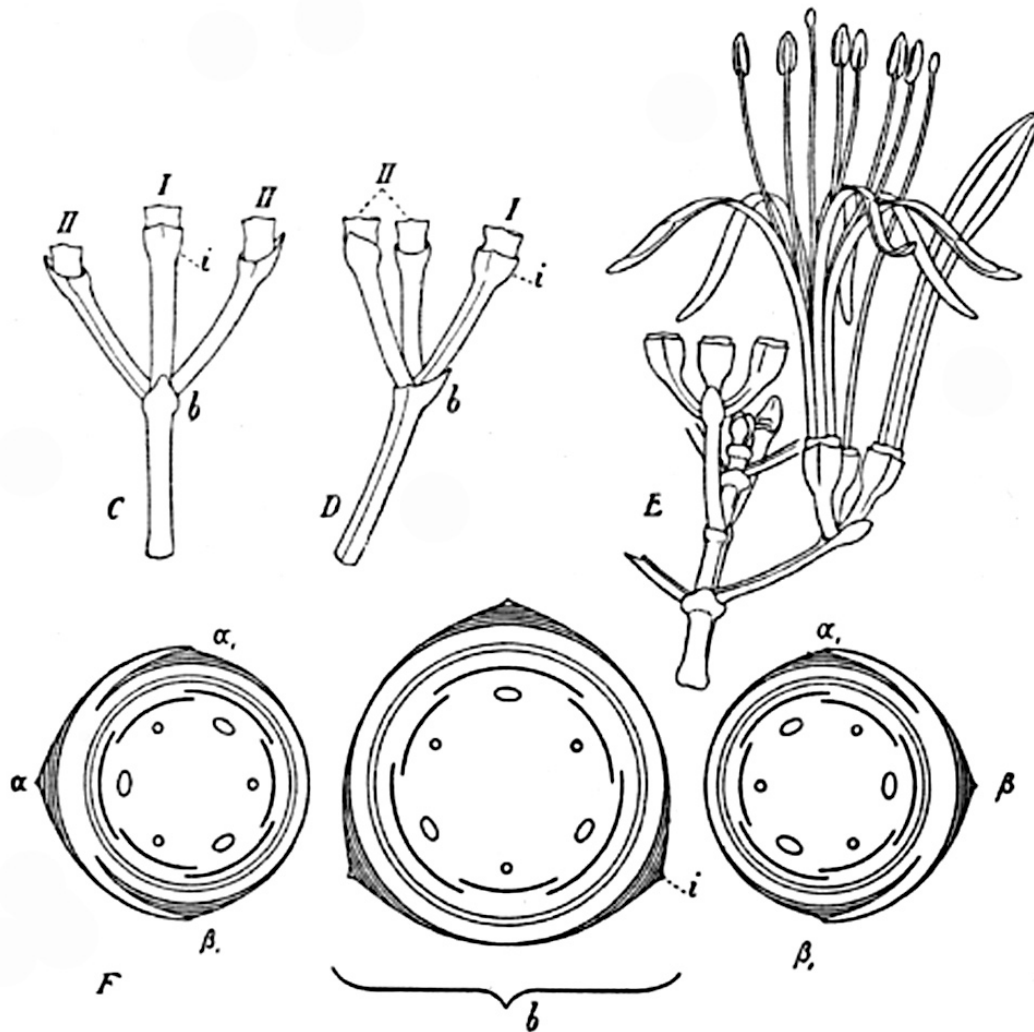


Fig. 4. *Loranthus* s.s. (= *Psittacanthus* Mart.) C. Flower triad from the outside; the same from the left side; E. complete inflorescence; F. Diagram of a flower triad. Further explanation in the text. C, D, E after Eichler, in Martius' *Flora Brasiliensis*, plates I, 44 and plates VIII, 26.

It can be seen that all this could also apply to the case of *Thaumasianthes*, with the exception of the remark that the sheath of the middle flower of the triads is possibly an axial formation, for in *Thaumasianthes* this covering, like that of the lateral flowers, consists of completely separate leaf-like organs.

Before I venture to make an analogous explanation for the *Thaumasianthes* for this inflorescence, I would first like to mention what Van Tieghem notes about the inflorescence of *Loranthus* (sensu *Psittacanthus* Mart.) (Bull. Soc. Bot. Fr., 42, p 349-350). He says in the discussion of his split genus *Glossidea*:

“First, what is the true nature of these triads? The three flowers being alike, pedicelled all three, and wrapped in a cupule more or less deep, we see that they are tripartite cymules with an aborted central flower. The primary pedicel, conerescent with the mother's bract in all its length, produces above it a pair of lateral bracts, then a posterior bract, in opposition to the mother's bract, after which it aborts without forming the terminal flower. In the axil of each of the three secondary bracts thus formed, a secondary pedicel is formed, conerescent with it in all its length, and terminating in a flower. The three flowers of the umbel are therefore lateral to the same head, the terminal having aborted. Considering the umbels as consisting of two lateral flowers and a terminal flower, Eichler has made the presence of a cupule at the base of this terminal flower inexplicable.

Second, what is the cupule that surrounds the base of each flower? Eichler admits that the secondary pedicel, before ending with the flower, produces two lateral bracts of third order, conerescent between them and with the secondary bract, and that the cupule is, consequently, formed of three bracts, as it takes place for example, for the flowers that terminate the primary pedicels of *Dendropemon* and *Ligaria*. If so, the existence of these two third-order bracts would be unique in the Loranthaceae. In fact, the cupule is formed of only one bract, which is the mother's bract of the flower, bracting and cupuliform bract here, as it is often elsewhere, especially in the Dendrophthoeae.”

Van Tieghem rightly prefers to consider the three flowers of the triads as equivalent. But then he assumes that the triads are trichasia with aborted middle flowers. However, it seems to me that this is very unlikely, because trichasia are very rare in the Loranthaceae, and quite unknown among the relatives of the genus in question. Van Tieghem's assumption is also very bold that the sheaths of all flowers were formed from a single bract, and that each bract was more or less three-pointed, and thus only apparently formed by the union of three leaf-like structures. I must confess that I can not prove the inaccuracy of Van Tieghem's assumptions, but that they are in conflict with everything we are used to seeing in the Loranthaceae.

I would like to give a similar explanation for the inflorescence of *Loranthus* (sensu *Psittacanthus* Mart.) as that of *Thaumasianthes*. We must then accept the following.

The triad of *Loranthus* is neither a dichasium nor a trichasium, but a 3-rayed umbel reduced to the middle flower dichasium, in which the bracts of the lateral flowers have remained. This is not a bold assumption. In *Macrosolen*, for example, the whole inflorescence, which is originally a cluster of triads diminished to the middle flower, may be reduced in the same way to a 4 to 2-rayed umbel of flowers with a bract and 2 bracteoles, e.g. in *Macrosolen avenis* (Bl.) Dan. The umbels of *Loranthus* have now rejoined together to form one cluster, and the inflorescence formed in this way has either remained so, or reduced again in various ways. Eichler's plates in Martius' Flora Brasiliensis V, 2, show the following series of cases.

1. Plate 7, *Loranthus cucullaris* Lam. The clusters of 3-rayed umbels diminished to the middle flower dichasia are terminal and axillary and are not further reduced. Also, the leaf-like development of the bracts of the triads is primitive.
2. Plate 8, *Loranthus cordatus* Schultes. The same raceme has become axillary.
3. Plates 2 and 6, *Loranthus clusifolius* (Eichl.)<sup>1</sup>) and *L. cinctus* Schult. As before, but the umbels have become 2-rays.
4. Plate 3, *Loranthus robustus* Schult. The cluster of 3-pronged umbels is contracted into a 4-pronged umbel of 3-pronged umbels.
5. Plate 4, *Loranthus Warmingii* (Eichl.)<sup>2</sup>) The main inflorescence is further reduced to a 3-rayed umbel of 3-rayed umbels.
6. Plate 5, *Loranthus dichrous* Schult. The whole inflorescence is further reduced to a 2-rayed umbel of 2-pointed umbels.



The fifth case also has special interest in that through it the somewhat peculiar assumption (at the first sight) that partial inflorescences are obliquely developed 3-rayed umbels loses its peculiarity, because the main inflorescence during the reduction can also go through the stage of a 3-rayed, crooked umbel.

However, I want to immediately draw attention to some complaints against my statement, which I can not quite eliminate as desired.

First, I assumed that the triads of *Loranthus* (sensu *Psittacanthus* Mart.) are 3-rayed umbels. If this is true, then the rays are equal in relation to the axis of the umbel, and the three flowers must therefore have the same position with respect to this axis. This is not the case in the diagram Eichler gives of the triad. The middle flower is turned towards a smaller petal of the outer circle of the bract, while the lateral flowers are turned towards a larger one of the inner circle.

Second, the bracts of the central flower, as Eichler draws them in the diagram and describes them emphatically in the accompanying text, are oriented as  $\frac{1}{2}$  in relation to the main axis of the inflorescence, and not, as my assumption suggests, as  $\frac{2}{1}$ .

I would like to note the following.

Both complaints are eliminated if we only assume that the outward-directed ray of the triad is originally the ray of the umbel that faces the main axis of the inflorescence. However, I recognize that this is a somewhat peculiar assumption.

Further, we must be careful that in the pictures of Eichler, of which the lower part drawings have been made by himself (see p.134, c & d at the bottom), the orientation of the bracts in certain cases seems to be  $\frac{2}{1}$  as in Plate I, Fig. 44a, C at I (our Fig. 4C, at i) and Plate 4, Fig. (26), while in other pictures the orientation is clearly visible as  $\frac{1}{2}$ , in others again not clearly.

Also, Eichler (see our Fig. 4F) draws and describes the petals of *Loranthus* as placed in 2 circles of 3, and the petals of the outer circle slightly larger than those of the inner circle. I have never observed such a difference between outer and inner smaller petals in the Loranthaceae of the Malay archipelago.

In any case, it can be seen that different genera of Loranthaceae can behave differently in significant ways and that much of the Loranthaceae morphology has not been sufficiently studied. It is therefore better for me to postpone too far-reaching consideration of the construction of the Loranthacean inflorescences until further investigations have reached our relevant knowledge.

Finally, I would like to thank my highly esteemed colleague Professor Dr. J. C. Schoute for some valuable information concerning the morphology of the inflorescences in general, to my assistant, Mr. J. C. Mekel, for the disinterested manner in which he put his great skill at the service of my investigation, Mr. R. Hoeksema, the draftsman of our laboratory for the careful execution of the pictures.

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<sup>1</sup>) *Loranthus clusiifolius* (Eichl.) Dans., nov. comb.; Willd., ex Eichl., in Mart., Fl. bras., V, 2, p. 30 (1868) in synonymis; *Psittacanthus clusiaefolius* Eichl., in Mart., Fl. bras., V, 2, p. 30, t. 5 (1868).

<sup>2</sup>) *Loranthus Warmingii* (Eichl.) Dans., nov. comb.; *Psittacanthus Warmingii* Eichl., in Mart., Fl. bras., V, 2, p. 36, t. 4 (1868).