

## The Reiteration of the Miniaturised Model in some Complex Inflorescences

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### Abstract

The complex inflorescence of *Calathea lutea* (AUBL.) SPRENG. (*Marantaceae*) consists of 2 or 3 bundles of spike-like partial inflorescences. In this complex inflorescence, the branching pattern of the drepanium occurs of two different levels: in each bundle the spike-like inflorescences are arranged in a drepanium and in the lower part of each spike-like partial inflorescence dyads are arranged in drepania. Inflorescences of comparable complexity are observed among the *Euphorbiaceae*, *Poaceae* and *Asteraceae*. It turns out that in these reputedly highly specialized families, the basic flowering unit, once it has undergone evolutionary processes of simplification, reduction and contraction, appears in the form of a miniaturised model, the architectural structure of which is then reiterated throughout the flower bearing ramification system of the plant.

Key-words: inflorescences, miniaturised model, reiteration, *Marantaceae*

### *La réitération du modèle miniaturisé dans quelques inflorescences complexes*

Résumé: L'inflorescence complexe de *Calathea lutea* (AUBL.) SPRENG. (*Marantaceae*) est constituée de 2 à 3 faisceaux d'inflorescences partielles spiciformes. Dans cette inflorescence complexe, la structure du drepanium se manifeste à deux niveaux: dans chaque faisceau, les inflorescences spiciformes sont disposées selon un drepanium et dans la région inférieure de chaque inflorescence spiciforme, les diades sont agencées selon des drepaniums. Des inflorescences d'une complexité comparable sont observées parmi les *Euphorbiaceae*, les *Poaceae* et les *Asteraceae*. Il s'avère que dans ces familles réputées comme très spécialisées, l'unité de floraison fondamentale, après avoir subi des processus phylogénétiques de simplification, de réduction et de contraction, se présente sous la forme d'un "modèle miniaturisé"; dont le programme architectural est alors réitéré au niveau de l'ensemble du système reproducteur de la plante.

Mots-clés: inflorescences, modèle miniaturisé, réitération, *Marantaceae*

The analysis of highly complex inflorescences, and, in particular, of those of the *Marantaceae* shows how difficult it often is to interpret the various components of such inflorescences. Thus, the authors who followed the ideas of TROLL (1964, 1969) and of WEBERLING (1965, 1981) sometimes have been led to conclusions, and above all, to a typology, of a controversial nature. The recent works of ANDERSSON (1976), KUNZE (1985) and KIRCHOFF (1986) on the *Marantaceae* led us to observe in this reputedly highly evolved

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ORSTOM Fonds Documentaire

N° 38.311 ex 1

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family, that the morphology of the flowering unit and consequently, of the main inflorescence, could be interpreted differently according to whether one adopted a purely typological standpoint or a biological and phylogenetic one. More generally speaking, it is the case for taxa which have reached a high level of evolution in Angiosperms.

This point will not be discussed in this paper; it will be developed in a forthcoming study. Our aim is primarily to show how the architecture of a very reduced flowering unit can repeat itself throughout the whole inflorescence of a species. This reduction results from evolutionary processes of simplification and of contraction known among the flowering plants. We have already investigated these processes several times (e.g. SELL 1976, 1980; SELL & CREMERS 1987). Indeed, in numerous families, one observes for example, that the ramifications of a panicle get more and more simple and that this "homogenization" (SELL 1976) leads to the raceme. Often such a raceme is reduced to a pauciflorous inflorescence (see the example of *Berberidaceae* in TROLL 1969, p. 496–508), the ultimate step being the single-flowered raceme (see the example of *Costoneaster* in SELL 1976, p. 252–253). This is paralleled, in some case, by non-elongation of the different axes of such a reduced inflorescence and leads to a condensed inflorescence. Thus the basic inflorescence, that we call "flowering unit", is encountered as a "miniaturised model". The processes of simplification (or homogenization), reduction and contraction are various kinds of evolutionary alterations in developmental events that result in modified mature structures. The cyathium of *Euphorbiaceae*, the spikelet of *Poaceae*, some heads of *Asteraceae* are some well-known examples of such miniaturised models. The analysis of the very complex inflorescences of *Marantaceae* shows a less classical example. It essentially helps us to discover the reiteration of this model at various levels in the inflorescence. This will be demonstrated with the example of *Calathea lutea* (AUBL.) SPRENG., and then with a few other taxa from the *Euphorbiaceae*, *Poaceae* and *Asteraceae*.

### Materials and Methods

The plants of *Calathea lutea* (AUBL.) SPRENG. were collected in the north-east French Guyana, in the region of St. George of Oyapoc (Herb. De Granville 4504). They were growing in secondary vegetation along the edges of swampy forests. They were introduced into the botanical garden of the Centre ORSTOM of Cayenne. Thus, the observations were made on several living plants. The detailed observations were effected using a binocular.

### *Calathea lutea* (AUBL.) SPRENG

The flowering system is constituted of 2 or 3 bundles of compact spike-like inflorescences (Fig. 1) which, at first sight, evoke the picture of axes emerging from accessory buds. The morphologic analysis in figure 1A, however, displays the normal axillary branching of a drepanium (Fig. 2B & C).

In text books the term "drepanium" is generally so closely associated with the three other types of monochasial branching i.e. helicoid and scorpioïd cymes and rhipidium (see in particular MÜLLER-DOBLIES 1977), that the drepanium is often also considered a cymose branching pattern. On this base, we firstly thought to call this structure a thyrses. But after discussion with WEBERLING and MÜLLER-DOBLIES, we are led to the conclusion that a thyrses cannot be involved since the drepanium does not fulfill the definition of cymose branching. In fact, the ramification of the drepanium does not take place from the axil of a prophyll, but from the axil of the second leaf, the interphyll, in our figure 2. Thus, such a drepanium constitutes a racemose inflorescence. The proximal internode (internode delimited by a bract or an interphyll and the next interphyll) of the various scapes is

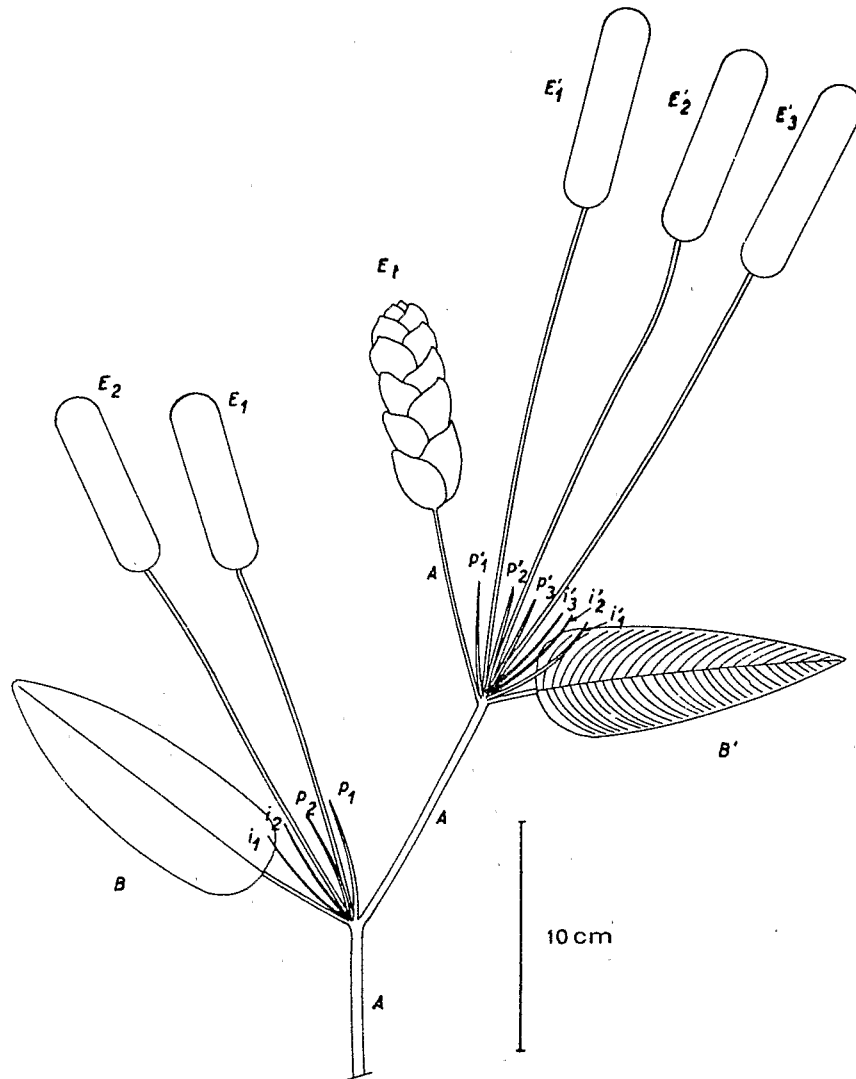


Fig. 1. Half-schematic representation of the inflorescences of *Calathea lutea* (AUBL.) SPRENG. Et = terminal spike-like inflorescence; E1, E2, E1', E2', E3' = spike-like inflorescences; p1, p2, p1', p2', p3' = prophylls; i1, i2, i1', i2', i3' = interphylls; B, B' = bracts; A = main axis.

extremely short, virtually non existing. The inflorescence axis itself is crowned by a terminal spike-like inflorescence (Et in Fig. 1 and Fig. 2) which emerges from the final bundle and which is recognizable by its position opposite to the last bract.

The inflorescence complex thus forms a raceme of drepania, i.e. a compound raceme of spike-like inflorescences which displays a paniculate structure.

As regards now the spike-like inflorescence (Fig. 3A), the schemes proposed by the various authors quoted previously agree in the essential features. SCHUMANN (1902) described such an inflorescence as a serial set of drepanium-like structure (Seite 8: "seriale Schar von sichelartigem Bau"); in a similar way, KUNZE (1985) calls it drepanium-like sequences ("sichelige Verbände"). Each bract bears one or more pairs of flowers or dyads (Fig. 3B).

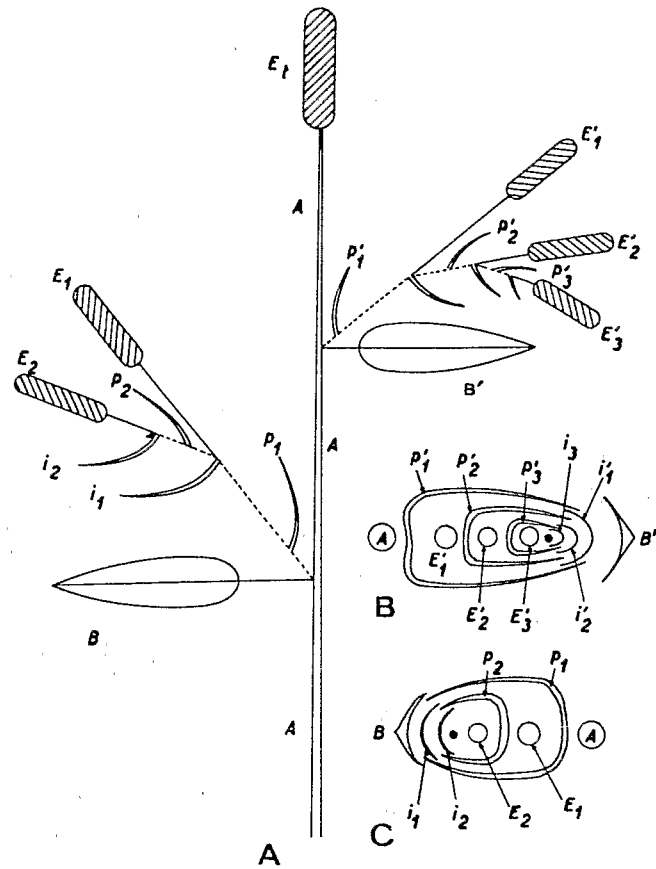


Fig. 2. Schematic representation of the inflorescence complex and diagrams of the 2 bundles of spike-like inflorescences of *Calathea lutea* (AUBL.) SPRENG. Dotted lines show the non-elongated parts of the axes; same symbols as for Fig. 1.

The interpretation of such a dyad (Fig. 3D), which is still subject to controversy will not be dealt with here. We shall nevertheless adopt the interpretation of KUNZE (1985) who confers on the dyad the value of an indeterminate biflorous spike which we shall call a spikelet (Fig. 3E and 3F). Triflorous spikelets were observed in *Calathea lutea* (Fig. 3B). Towards the tip of the spike-like inflorescence, the dyads are single in the axil of each bract on the main axis, whereas proximally they occur in twos or fours, arranged in a drepanium, with an extremely short axis (Fig. 3C). As previously, each ramification emerges from an interphyll; thus such a drepanium again constitutes a racemose inflorescence. The spike-like inflorescence of *Calathea lutea* has no terminal dyad, whereas one is present in other species of *Marantaceae* (e.g. *Maranta leuconeura* E. MORR.). Thus, in *Calathea lutea*, a spike-like inflorescence as drawn in figure 3A corresponds to an indeterminate (or polytelic) compound raceme of drepania composed of dyads, which displays a paniculate structure. Thus within each of these compound racemes, we again encounter the structural scheme of each bundle of spike-like inflorescences of the inflorescence complex. The diagrams in figures 2 (B and C) and 3C are indeed quite comparable: one has merely to replace the biflorous spikelets of figure 3C by spike-like inflorescences to obtain the pictures shown in figures 2B or 2C.

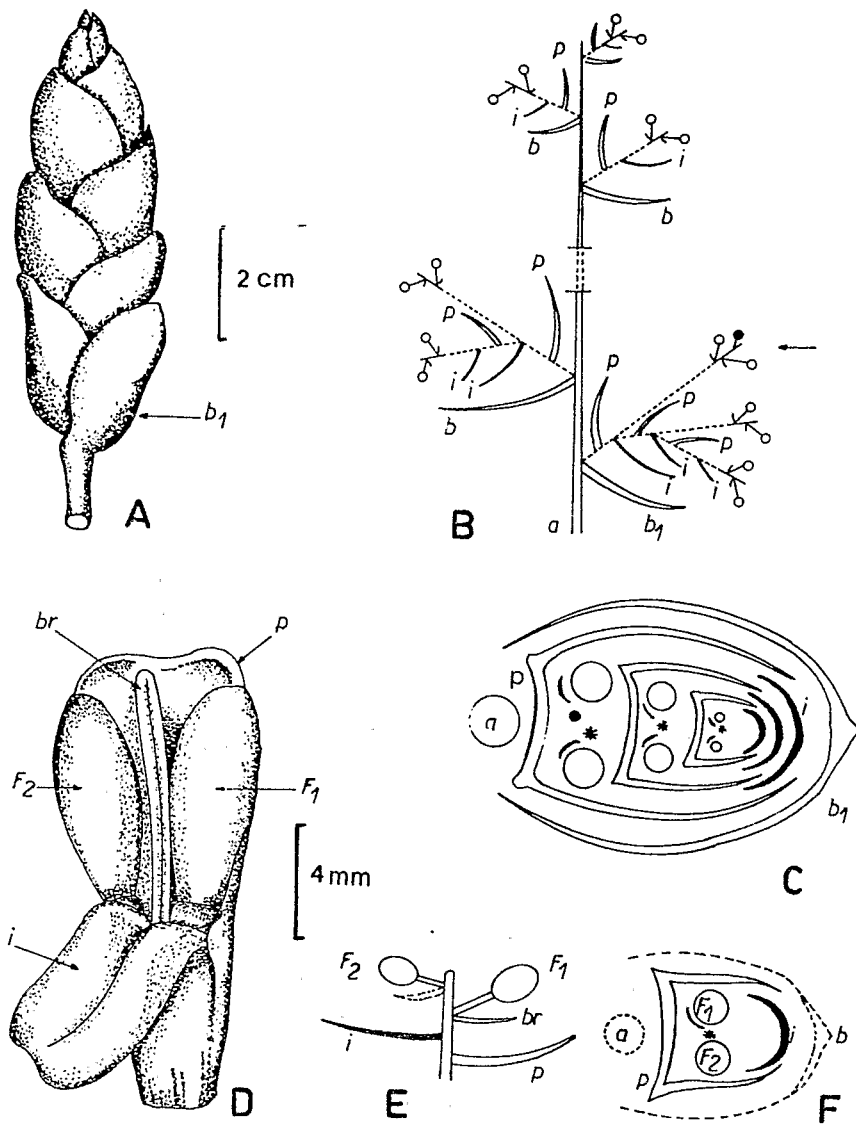


Fig. 3. *Calathea lutea* (AUBL.) SPRENG.

- A. A spike-like inflorescence.
  - B. Scheme of this inflorescence which is in fact a compound raceme of biflorous spikelets. Unshown part of the axis is dotted; arrow shows a spikelet with 3 flowers.
  - C. Diagram of the whole borne by  $b_1$ .
  - D. A dyad.
  - E. Scheme of dyad shown in  $3D$ .
  - F. Diagram of dyad: dotted, the main axis of the spike-like inflorescence (a) and the bract (b) not shown in E.
- b,  $b_1$  = bracts; p = prophylls; i = interphylls; F1, F2 = flowers; br = bracteoles.

The whole inflorescence of *Calathea lutea* thus displays a highly complex structure since it corresponds to a compound raceme (Fig. 2A) of compound racemes (Fig. 3B) of biflorous spikelets (Fig. 3E). In terms of TROLL's inflorescence morphology, the whole system is a truncate (because a terminal dyad is missing) polytelic synflorescence. But, beyond this successive repetition of racemose structures, the most striking point is the existence of drepanium structures at two different levels of ramification. The drepanium of biflorous spikelets (Fig. 3C) emerges as being characteristic of the *Marantaceae*, since it is observed in all the species studied, both by other authors and by us. This peculiar inflorescence which develops in the axil of the bracts of the spike-like inflorescence (at least of the lower bracts) is very small. It represents, so to speak, the miniaturised model of the inflorescence unit of this family. It can reiterate on a larger scale, as in *Calathea lutea*, where a certain number of these spike-like inflorescences are arranged in a drepanium.

#### Other examples of reiterated models

The main axis of numerous herbaceous species of *Euphorbia*, such as *E. peplus* L. (Fig. 4A), *E. lathyris* L., *E. dulcis* L., *E. amygdaloides* L. is crowned by what is usually called a pleiochasium (see for instance EICHLER 1875/1878, p. 36 and TROLL 1964, p. 113 and p. 221–223), and which in fact is an umbel (Figs. 4A and 4B). This is determinate (or monotelic) since a more or less sessile cyathium is generally observed in its centre. This can abort (e.g. *E. characias* L.) or even not develop (*E. paralias* L., *E. serrata* L., *E. segetalis* L. ...). Each ray of the umbel bears cyathia disposed in a dichasial cyme, in such a way that the whole inflorescence corresponds to a determinate umbel of dichasial cymes of cyathia, in other words, to an umbel-like thyrses of cyathia.

Now, according to the generally accepted interpretation since BROWN (1814, and in NEES VON ESENBECK 1825, p. 55) and WYDLER (1845; see also in particular NOZERAN 1955 p. 82–120 and HOPPE & UHLARZ 1981), the cyathium is itself a determinate umbel (terminal female flower) of 5 scorpioid cymes constituted by perianth-free single-stamen male flowers, i.e. monandrous flowers (Figs. 4C, 4D and 4E), which is equivalent to an umbel-like thyrses of flowers.

Thus, this cyathium represents a miniaturised model whose structure is encountered on the scale of the whole inflorescence: the horizontal section diagrammes 4B and 4E are perfectly comparable, save that the cymes are dichasial at the level of the umbel crowning the main axis, whereas they are scorpioid within the cyathium. In certain species (e.g. *E. segetalis* L.) scorpioid endings are, however, observed on the dichasial cymes of cyathia.

The miniaturised model which the cyathium constitutes results from a series of simplifications, reductions and contractions which have affected the *Euphorbiaceae*, whose original structure corresponded to ramified systems with relatively complete flowers, such as observed in the genera *Hevea*, *Manihot* or *Mercurialis*. Originally, the flowering unit of the *Euphorbiaceae* was the flower; after long intrafamilial evolution, this unit became, beyond any doubt, the cyathium, which represents a characteristic pseudanthium, particularly visible in *E. fulgens* KARW. (Figs. 4F, 4G).

The flowering unit of the *Poaceae* obviously seems to be the spikelet. This spikelet, bereft of any terminal flower, and therefore indeterminate, is more or less floriferous, ranging from the relatively frequent single flower (*Arrhenatherum*, *Agrostis*, *Cynodon*, *Phleum* ...) to the extensive multiple flower (up to 25 flowers in *Lolium multiflorum* LAM.). In this family, the racemose miniaturised model reiterates either in the form of a panicle or that of a spike with all the transitional forms existing between them. The panicle is indeed the structure, itself racemose since it is monopodial, which by simplification and homogenization gives the simple inflorescence with all its diverse aspects (SELL 1981). Thus, in *Lolium perenne* L., the spikelet is reiterated in the form of a spike with a terminal spikelet.

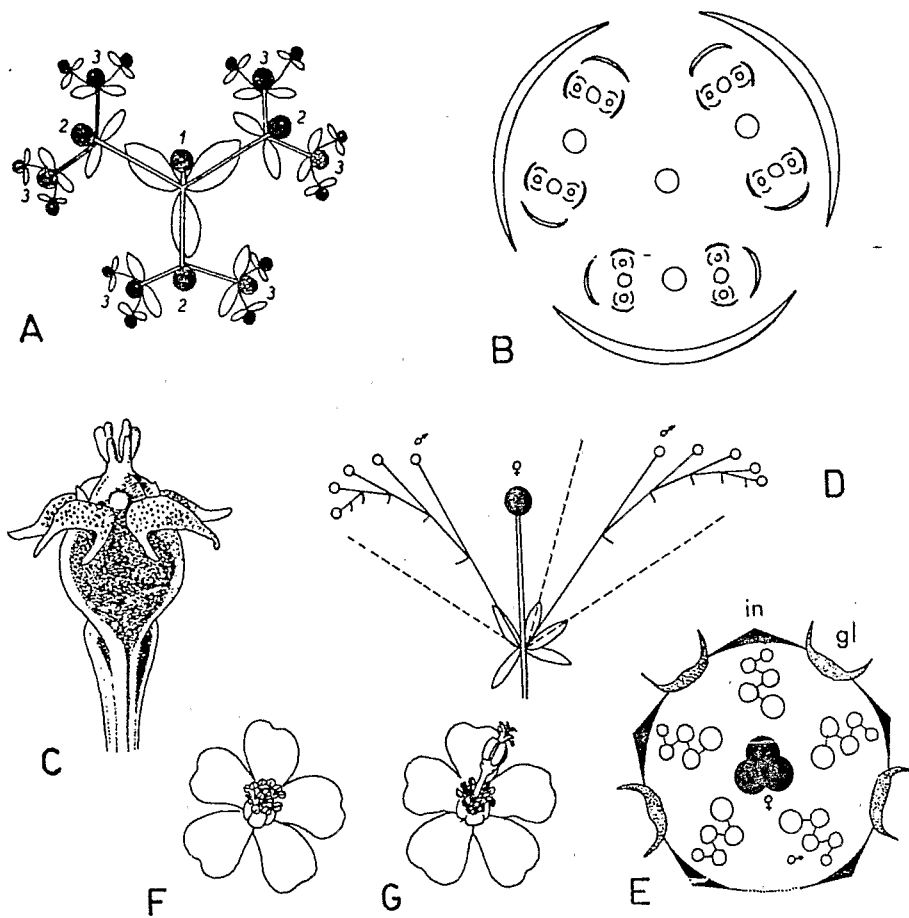


Fig. 4. *Euphorbia*

A to E: *E. peplus* L.

A. Scheme of an inflorescence seen from above: umbel of dichasial cymes of cyathia; the shaded circles represent cyathia.

B. Diagram of inflorescence shown in 4A.

C. Cyathium of female stage (according to TROLL).

D. Scheme of a cyathium (dotted lines represent cymes not shown); ○ = female flower, ● = male flower.

E. Diagram of a cyathium; gl = glande; in = involucre; ○ = female flower, ● = scorpioid cyme of male flowers.

F-G: *E. fulgens* KARW. (according to MANGENOT).

F. Young stage of a cyathium.

G. Adult stage of a cyathium.

Truncation renders such a spike indeterminate in *Secalē cereale* L. In *Paspalum maritimum* TRIN., and in the inflorescence of male flowers of *Zea mays* L., the complexity attains an even higher degree, since indeterminate spikes of spikelets cluster in a terminal raceme crowned with a spike. This terminal spike disappears in *Cynodon dactylon* (L.) PERS. and *Chloris inflata* LINK. The compound racemose inflorescence (triplobotryum) becomes umbel-like in these latter species.

No one would question that the head constitutes the flowering unit of the *Asteraceae*. In certain species, this simple inflorescence, which constitutes the miniaturised model, is reiterated in the form of a raceme or of a spike of heads, with a terminal head, and therefore determinate (*Liatris spicata* (L.) WILLD.) or without one, therefore indeterminate (*Ligularia wilsoniana* (HEMSL.) GREENM.). A further process of contraction then leads to a head of heads (syncephalium) of *Myriocephalus gracilis* BENTH. and of *Syncephalanthia decipiens* BARTL. (see WEBERLING 1981, pp. 318 and 321).

### Conclusions

These few examples of species belonging to families reputed to be highly specialised, testify that an inflorescence structure which has, so to speak, reached an advanced state in its evolution in the form of a miniaturised model (drepanium of *Calathea*, cyathium of *Euphorbia*, spikelet of *Poaceae*, head of *Asteraceae*) and which represents the basic reproductive unit, can reiterate on the scale of the whole plant. There is thus in the genetic heritage of these species an architectural programme which can be reintroduced at one moment or another in the elaboration of the reproductive system. Indeed, such a "miniaturised model" can present for the species a risk of losing its sexuality, as the drepanium of *Marantaceae*, whose flower has only one stamen left, the uniflorous spikelet of some *Poaceae*, the single-flowered head of *Myriocephalus gracilis* BENTH. The reiteration of drepania, cyathia, spikelets and heads is certainly one of the manifestations of the modular growth of the angiosperm body, but could nevertheless represent one of the several reproductive strategies that could come into play to reduce the hypothetical risk of having specialized inflorescences. Thus the reactivations of the architectural programme could constitute one of the measures of safeguard for the species.

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Received June 25, 1991

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Flora (1992) 187: 59–60  
Gustav Fischer Verlag Jena

### Buchbesprechung

NATHO, G., MUELLER, CH., SCHMIDT, H. (Hrsg.): Morphologie und Systematik der Pflanzen. In zwei Teilen (A–K und L–Z). Bearbeitet von R. GROLLE, P. HANELT, H. HÜBEL, B. KAUSSMANN, H. KREISEL, G. NATHO, CH. MUELLER, H. SCHMIDT. Wörterbücher der Biologie, UTB 1522. Gustav Fischer Verlag Stuttgart 1990. – 852 S., 560 Abb., broschiert, DM 44.80.

In den beiden Bänden des vorliegenden Wörterbuchs der Morphologie und Systematik der Pflanzen wurde versucht, eine breite Auswahl relevanter Begriffe aufzunehmen. Wie bei allen vergleichbaren Werken war auch hier durch den möglichen Umfang eine klare Beschränkung notwendig, die eine subjektive Auswahl der etwa 4000 enthaltenen Stichworte erforderte. Erfasst sind einschlägige Termini der Algen, Moose, Farn- und Samenpflanzen. Auch die nicht zu den Pflanzen gehörenden Blaualgen (Cyanobacteria) und Pilze (einschließlich Flechten) werden einbezogen. Bakterien und Begriffe der Cytologie sind hingegen ausgeklammert. Die große Breite der aufgenommenen Organismengruppen erschwert natürlich zusätzlich die Stichwortauswahl. So stellt sich die Frage, ob es nicht günstiger gewesen wäre, Spezialgebiete, für die es schon umfangreiche Wörterbücher gibt, auszuklammern. Das betrifft besonders die Pilze und Flechten.