THE CRISTATE INFLORESCENCE OF CHIRITA SECT. MICROCHIRITA (GESNERIACEAE)

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ABSTRACT. A detailed description and an interpretation of the cristate epiphyllous inflorescence of *Chirita elphinstonia* and *C. micromusa* is given. In addition the structure of the whole plant is described in terms of Troll's synflorescence concept. The inflorescence as a whole, which here corresponds to the total plant, is a synflorescence consisting usually of the main florescence and one co-florescence emerging from the axil of the macrocotyledon. The partial florescences are two-flowered and represent cymes of the gesneriaceous type ("double-flowered cymes"), which are reduced to their primary unit consisting of the terminal flower and the front-flower. The development of a number of accessory partial florescences in each leaf axil gives rise to a uniserial, fan-like arrangement (the cristate inflorescence). Evolutionary aspects of this peculiar structure are briefly discussed as well as the possible functional significance.

INTRODUCTION

In his recent revision of *Chirita*, Wood (1974) again draws attention to the peculiar "epiphyllous inflorescence" occurring in certain species of Sect. *Microchirita*. He describes this inflorescence type as follows: "The peduncle of the inflorescence appears fused to the short petiole and the proximal part of the midrib. The pedicels are usually in pairs . . . In appearance the inflorescence is a crest of flowers . . . . An important feature of this type of inflorescence is that the open flowers are always in the same position with respect to the leaf" (p. 125). Since only species with yellow, orange and cream corollas have crested inflorescences, whereas the blue-flowered species (with the exception of *C. barbata*) do not, Wood supposes that there might be an adaptive significance in the relation between flower colour and inflorescence structure.

In the present paper we shall particularly refer to the morphological problems and try to give a valid interpretation of the peculiar epiphyllous inflorescence crest. In addition, we shall cover the inflorescence organization of the whole plant. There we shall concentrate our explanations on *Chirita elphinstonia* Craib and *C. micromusa* B. L. Burtt, which may represent the most impressive examples of crested inflorescences in *Microchirita*. For comparison we shall also touch on *C. hamosa* R. Br., *C. lavandulacea* Stapf and *C. involucrata* Craib. Cultivated material of all the species mentioned here was available for investigation.

Starting from the description cited above we are confronted with the following basic problems. How are we to understand the morphological organization of the cristate inflorescence? How are we to explain morphologically the uniform flower orientation? Why are the pedicels in pairs? For an elucidation of these questions it is necessary to relate the inflorescence structure of *Chirita* to the usual pattern found in Gesneriaceae. Therefore, the general inflorescence structure in the family is described first.

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GENERAL REMARKS ON THE INFLORESCENCE STRUCTURE IN GESNERIACEAE

It is important to point out that the term "inflorescence" is inaccurate for a detailed morphological analysis. Often one reads that certain Gesneriaceae have cymose "inflorescences" (e.g. *Streptocarpus caulescens*), whereas others have racemose ones (e.g. *Smithiantha zebrina*). Morphologically this is not quite correct, because the same term "inflorescence" refers to different morphological structures and levels of homology in these two plants. For a precise morphological statement, therefore, this term must be replaced by a system of exactly defined terms. Troll (1964) has elaborated such a differentiated terminology and taken it as a basis of his "synflorescence" concept. It is not necessary to explain or to discuss this concept here in detail, because Weberling (1965) has given a good abstract of Troll's ideas in English (with illustrations). However, we want to explain briefly the terms adopted in describing Gesneriaceae: "florescence", "partial florescence" and "synflorescence".

First we have to state that the main axis in Gesneriaceae is never terminated by a flower. Therefore, the inflorescence belongs to the "polytelic type" of Troll. (With some essential reservations, which cannot be discussed here, the "polytelic" and the "monotelic" type correspond to the "indefinite" and "definite" inflorescences in the usual sense.) The flower-bearing structures emerging from the axils of the leaves (foliage or bract-like) are characterized by a special cymose structure, to which we will refer later. They are "partial florescences". The whole apical aggregate including the main axis and the partial florescences is the "florescence". In respect to the monopodial structure of the florescence axis, but sympodial structure of the partial florescences, the descriptive term "thyrse" is appropriate for the classification of the florescence. In many cases the inflorescence is of higher complexity representing a system of florescences ("main florescence" + "paracladia" with their "co-florescences"). Such a complex aggregate is termed a "synflorescence" (for an explanatory diagram see Weberling 1965, fig. 2/VI).

This terminology permits the unequivocal recognition of homologous structures and also the clear description of the more complex inflorescences. In the above mentioned example of *Streptocarpus* and *Smithiantha* the term "inflorescence" refers in the first case to the partial inflorescence, in the second to the florescence! We may regard the florescence as the basic structure, and, in *Streptocarpus* it is a thyrse, in *Smithiantha* a raceme. This implies that at the level of the partial florescence in the one case these structures are really branched (cymes), but in the other reduced to solitary flowers. In this way of description the evolutionary change from the one "type" ("cymose") to the other ("racemose") can easily be made clear. We have to add that both examples represent synflorescences!

Since the study of complex inflorescences makes it essential to include the structure of the whole plant, it also provides a way " to comprehend more exactly something of that complex of characters which is commonly circumscribed by the word 'habit' " (Weberling 1965, p. 220). As we shall show below, the 'habit' of *Chirita elphinstonia* and *C. micromusa* can most easily and exactly be described in terms of the synflorescence concept.

Of special interest in Gesneriaceae is the structure of the partial florescences. In the Old World members as well as in the New World ones (cf. especially

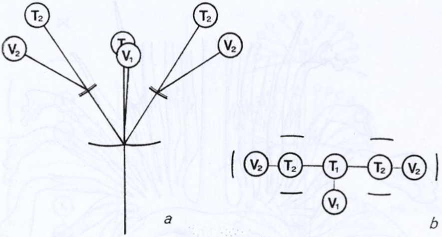

FIG. 1. a, b, diagrams of a dichasium with front-flowers. T, terminal flower of a cyme unit; V, front-flower ("Vorblüte").

Goebel 1931, Troll 1964, Burtt 1970, Hilliard & Burtt 1971, Weber 1973, Wiehler in press)—and even in a few Scrophulariaceae—the cymose partial florescences reveal a unique structure. The units do not seem to end with one flower, but with a flower pair ("pair-", "double-" or "twin-flowered cymes"). Each unit (fig. 1) includes the true terminal flower (T) and the so-called front-flower (V, from the German "Vorblüte"), which arises without a subtending bract in median position at the level of the prophyll branches and is orientated in the same direction as the terminal flower. The diagrams of figure 1 show a dichasium enriched by the front-flowers. With an increase of the unit number there, compound (pair-flowered) dichasia may result and, due to certain symmetry influences, double-cincinni, cincinni etc.

The striking twin-flowered condition in the gesneriaceous cyme, mostly ignored by taxonomists and misinterpreted by morphologists, was clarified in a previous paper (Weber 1973). According to this interpretation the front-flower must be regarded as a true axillary branch of the cyme unit, the bract of which is normally (but just secondarily!) aborted. It is inserted above the prophyll branches (bracts), but by internode contraction it draws toward the latter. The subtending bract of the front-flower, although usually reduced, is apparently the remainder of a dimerous bract whorl with median orientation due to the primarily decussate phyllotaxis in Gesneriaceae and Scrophulariaceae (cf. Haccius 1950, Pennell 1935). For details and a more extensive discussion of the morphological situation see Weber (1973).

THE INFLORESCENCE CREST

A leaf pair of *Chirita elphinstonia* with typical cristate inflorescences is shown in fig. 2. In each crest all flowers are exactly arranged in a row and look in the same direction. This figure also demonstrates clearly the pairing of the flowers.

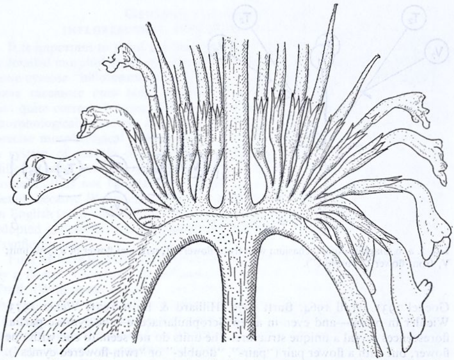

FIG. 2. *Chirita elphinstonia*, leaf pair with the cristate inflorescences. Half of the right leaf is cut off to show the open flower.

Wood (1974) obviously regards such a system as representing an axillary inflorescence (probably partial florescence in our sense), the axis of which ("peduncle") is fused to the petiole. A similar opinion seems to have been held by Boldt (1897). But such an interpretation does not satisfactorily explain the uniserial, fan-like flower arrangement.

Fritsch (1904), Velenovsky (1907) and Goebel (1931) have elaborated a better conception than the interpretation just mentioned. They regard the inflorescence crest as a system of individual and morphologically independent elements and, therefore, do not consider the flowers are borne on a common axis. They start from the well-known phenomenon that in many plants (also in many Gesneriaceae) the leaf axils do not bear only one shoot (branch, flower) but two or more. The arrangement of such "accessory shoots" (a term coined by Roeper 1826, in contrast to "adventitious"!) is most characteristic: in the Dicotyledons it is serial (uniserial or more rarely biserial) and in the Monocotyledons (with a few exceptions) it is collateral. The development and arrangement of the accessory buds is achieved by a certain, genetically fixed, mode of "fractionation" of the axillary meristem (cf. Hagemann 1970). Since the whole axillary meristem is not used up by the "legitimate" first bud, the remaining meristem portion regenerates and develops another bud. There again may remain some meristem tissue etc. In this way a considerable number of axillary shoots may be developed (for details see Sandt 1925, Troll 1937).

It is obvious that there is no space for a great number of shoots in the strict leaf axil and so, as in *Chirita*, the enlarging meristem may be displaced to

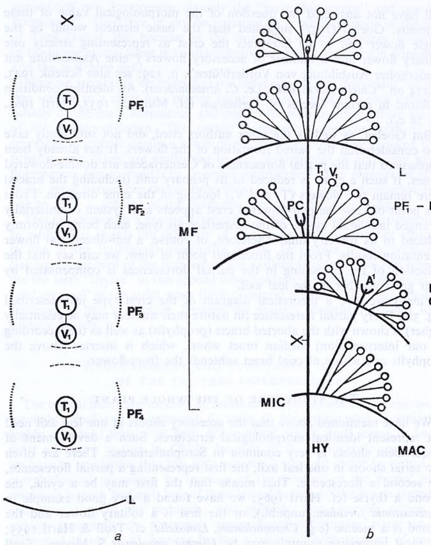

FIG. 3. *Chirita elphinstonia* and *C. micromusa*. a, interpretive diagram of an axillary inflorescence aggregate ("inflorescence crest"). Dotted lines: the aborted transverse and the theoretical median bract whorl, the abaxial bract of the latter bearing the front-flower; b, diagram of the synflorescence, which corresponds to the whole plant. PF, partial florescence; L, subtending leaf; X, axis of the florescence; MF, main florescence; PC, paracladium (because of the lack of vegetative region it is identical with the CoF—co-florescence); A, A′, open apex of the main florescence and the co-florescence respectively; HY, hypocotyl; MAC, macrocotyledon; MIC, microcotyledon. Other symbols as in fig. 1.

the petiole*. From that a somewhat "epiphyllous" position of the shoots results. Usually all structures borne in a leaf axil are morphologically equivalent, but "heteromorphy" is not rare (see p. 226).

Now we are able to understand the cristate inflorescence as an aggregate of individual elements in contrast to a continuous branching system, but we

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* In this case the oldest buds are nearest the axil. In contrast, the serial buds of *Robinia*, *Gymnocladus*, *Juglans* etc. shift up the shoot axis with the oldest buds furthest from the axil.

still have not answered the question of the morphological value of these elements. Goebel (1931) suggested that the basic element would be the single flower and so he interprets the crest as representing strictly one axillary flower and a number of accessory flowers ("eine Axillarblüte mit wiederholter Ausbildung von Vorderblüten", p. 129; see also Schenk 1943, p. 274 on "*Chirita horsfieldii*", i.e. *C. lavandulacea*). An identical condition is found in certain species of *Verbascum* (cf. Murbeck 1933, Hartl 1965, fig. 28 c_1).

But Goebel, as well as the other authors cited, did not sufficiently take into consideration the paired formation of the flowers. It has already been emphasised that the partial florescences of Gesneriaceae are double-flowered cymes. If such a cyme is reduced to its primary unit (including the bracts) there remain two flowers (T_1 and V_1) looking in the same direction. From this point of view the pair-flowered crest appears as a system of uniserially arranged individual cymes of the gesneriaceous type, each being uniformly reduced to its primary unit. Therefore, of course, a uni-directional flower orientation results. From the functional point of view, we can say that the reduction of the branching in the partial florescences is compensated by their great number in the leaf axil.

Finally we give a theoretical diagram of the crest type just described (fig. 3a). Every partial florescence (in nature their number may be essentially higher) is shown with the aborted bracts (prophylls) as well as the (according to our interpretation) median bract whorl, which is inserted above the prophylls and whose abaxial bract subtends the front-flower.

THE STRUCTURE OF THE WHOLE PLANT

We have mentioned above that the accessory shoots of one leaf axil need not represent identical morphological structures. Such a development of inequivalent shoots is very common in Scrophulariaceae. There are often two serial shoots in one leaf axil, the first representing a partial florescence, the second a florescence. That means that the first may be a cyme, the second a thyrse (cf. Hartl 1965; we have found a very good example in *Chaenostoma foetidum*, unpubl.), or the first is a solitary flower and the second is a raceme (e.g. *Chaenorhinum*, *Limosella*, cf. Troll & Hartl 1955; the most impressive example may be *Hiernia angolensis* S. Moore). Troll (1969) has recently observed the reverse condition in *Verbascum thapsus*: in the region of paracladia ("enriching field", cf. Weberling 1965) after the axillary thyrse there occur accessory inflorescences of cymose character—that is, partial florescences.

We are concerned with the same phenomenon in these *Chirita* species. In the axil of the macrocotyledon, and often of the next leaf pair (primary leaves), the first axillary shoot is a florescence representing in repetition of the main florescence an open thyrse, whereas all following shoots are two-flowered partial florescences. Usually only the florescence of the macrocotyledon develops, but its number of nodes is reduced to one or two. The florescences of the primary leaves regularly remain in the stage of buds.

So in *Chirita elphinstonia* and *C. micromusa* the total inflorescence, which is identical with the whole plant because from all leaves (with exception of the tiny microcotyledon) there emerge flower-bearing structures, usually consists of two florescences, namely the "main florescence" and one "co-florescence". Therefore, it can be regarded as a synflorescence in the sense of Troll (1964). But because of the two types of inflorescence structures in the lower leaves, there is no sharp boundary between the main florescence and the enriching field.

Now we are able to describe the total inflorescence and the "habit" of these two species in a short and precise manner: it is a synflorescence consisting usually of the main florescence and one co-florescence arising from the axil of the macrocotyledon. The partial florescences are two-flowered and represent morphologically a cyme of the gesneriaceous type reduced to its primary unit. They are multiplied by the development of accessory partial florescences (up to eight!) in uniserial arrangement. The number of nodes in the main florescence ranges from three to five, in the co-florescence from one to two. A scheme of the synflorescence is reproduced in fig 3b.

This restatement is a precise description and a simple basis for comparison. In addition it avoids the difficulty of classifying the inflorescence structure in one of the traditional descriptive terms. In respect to the florescence (taking no account of the increase of the axillary structures) we can scarcely use the term "thyrse" in this special case, because the partial florescences are not "cymose" in the strict sense (lack of lateral branches), but also the term "raceme" is not applicable, because the axillary structures are not really solitary flowers.

EVOLUTIONARY AND FUNCTIONAL ASPECTS OF THE CRISTATE INFLORESCENCE

The typical inflorescence crest as found in *C. elphinstonia* and *C. micromusa* (probably similar in *C. marcanii*, *C. viola*, *C. bimaculata* etc.) is certainly a highly advanced feature in Sect. *Microchirita*, which itself seems to be the most advanced section in *Chirita* because of its monocarpic species. But we have to emphasise that this inflorescence is brought about by only a few morphological processes: by increase of the number of the partial inflorescences in each leaf axil, loss of their lateral branches (the bracts included) and shortening of the peduncles and pedicels. Some species within the section apparently do represent intermediate evolutionary steps: in the cultivated plants of *C. hamosa* R. Br. a relatively high number of partial florescences is present on one leaf but these for the most part were found to have bracts and lateral branches. (A diagram of an "epiphyllous" aggregate is given in fig. 4c; in this species the front-flower V_1 is often subtended by a bract, see PF_3 in our diagram. For detailed information see Weber 1973 under "*Chirita* aff. *hamosa*".)*

In *C. lavandulacea* Stapf usually only two partial florescences are developed in a leaf axil: the adaxial mostly contains three to four flowers (T_1, V_1, T_2) with relatively long pedicels (on the other hand the peduncle is extremely short). The bracts are very small or even lacking. In the additional

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* According to the diagnoses, the "inflorescence" of *C. hamosa* R. Br. should not have bracts and lateral branches. Therefore, the plant was named in Weber 1973 "*Chirita* aff. *hamosa*". But using Wood's key, there is no doubt that the name of *C. hamosa* is correct. Moreover, we evidently had at hand the same seed material (Utrecht) as Wood, who also mentions that this species is "confusingly variable" (p. 193).

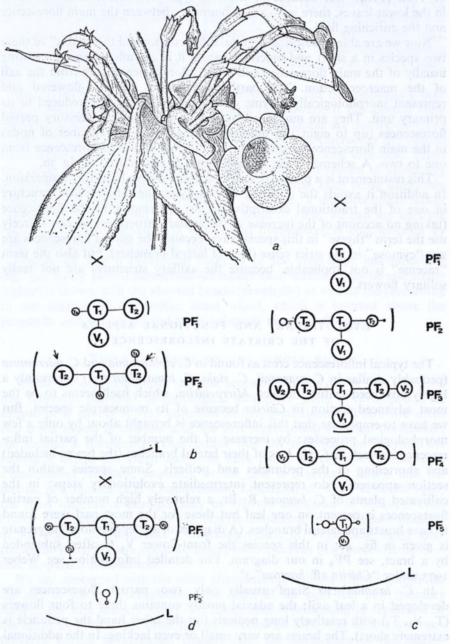

FIG. 4. a, *Chirita lavandulacea*, leaf pair with the inflorescence aggregates; b, diagram of the right inflorescence aggregate in 'a'—arrows: open flowers; c, *Chirita hamosa*, diagram of the axillary inflorescence aggregate; d, *Chirita involucrata*, diagram of an axillary inflorescence aggregate. Symbols see fig. 3.

partial florescences the bracts are of considerable size (fig. 4a, b). (There the number of flowers is often higher than in the first partial florescence and there also can be observed a remarkable amount of variation in branching, but this of less interest in the present connection.)

The most primitive condition within the species dealt with in the present paper is found in *C. involucrata* Craib. There only the "legitimate" primary partial florescence develops (an additional one remains as a bud), in which four flowers open (diagram fig. 4d). The peduncle and the pedicels are relatively long (up to 4 cm and 3 cm, respectively).

The few examples reported here give evidence that it may be possible to draw taxonomic and evolutionary conclusions from exact analysis of the inflorescence structure. For this to be done, of course, more material must be examined and evidence from inflorescence structure has to be paralleled with that from other characters.*

We have already mentioned that the increase of the partial florescence number may parallel and compensate the decrease of the unit number. Furthermore, there seems little doubt that the striking arrangement and uniform orientation of the flowers is also related to pollination ecology. At first it might be expected that the flower fan would always contain a relatively large number of open flowers, which as a whole would form an attraction unit. Cultivated material of *C. elphinstonia* and *C. micromusa* shows this is not the case. There always is only one (or two) flowers per leaf open, which by its short and down-curved stalk sits relatively close to the leaf (fig. 2). However, by the characteristic mode of development, which is reflected by the sequence of flower opening (T_1—V_1—T_1'—V_1'—T_1''—etc.), it is assured that during the whole flowering time of the plant there is always present at least one open flower per leaf.

In respect to the "epiphyllous" position of the open flower we may point out the similar (but not homologous!) situation in certain orchids (particularly in a great number of *Pleurothallis* species). It appears not unlikely that a contrast effect results from the position of the flower ± "on" the leaf lamina—especially in the small-flowered species. Wood's statement, that only flowers with yellow, orange and cream, therefore light-coloured corollas, have the typical crested inflorescences is relevant here. The colour of the blue-flowered exception *Chirita barbata* (see Curtis's Bot. Mag. t. 8200) is very light and pale and the effect may be similar. It must be mentioned that the species investigated are self-pollinating, but this does not necessarily mean that no attractant effect is operative. Self-pollination in *Chirita* is certainly an advanced, and perhaps only accessory, mechanism.

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* There is probably a relation between inflorescence structure and chromosome number! The counts now available for sect. *Microchirita* (see Ratter 1975) indicate that the non-cristate taxa (*C. involucrata*, *C. caliginosa*, *C. sericea* . . .) are diploid ($2n = 18$) while the taxa with cristate inflorescences (*C. micromusa*, *C. hamosa*, *C. bimaculata*, also *C. lavandulacea*) are (aneu–) tetraploid ($2n = 34$).

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