Inflorescence morphology and evolution in the genus Picramnia (Simaroubaceae)

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ABSTRACT

PIRANI, J. R. (1993). Inflorescence morphology and evolution in the genus Picramnia (Simaroubaceae). *Candollea* 48: 119-135. In English, English and French abstracts.

The basic aspects of inflorescence morphology in the neotropical genus *Picramnia* (Simaroubaceae) are presented, including characterization of the various inflorescence types (racemes, simple thyrses, diplothyrses and pleiothyrses), their position and mode of growth, as well as some secondary sexual characteristics. The importance of these aspects in infrageneric taxonomy and possible evolutionary trends involved are discussed.

RÉSUMÉ

PIRANI, J. R. (1993). Morphologie de l'inflorescence et évolution du genre Picramnia (Simaroubaceae). *Candollea* 48: 119-135. En anglais, résumés anglais et français.

Les aspects basiques de la morphologie de l'inflorescence chez le genre neotropical *Picramnia* (Simaroubaceae) sont présentés, avec une caractérisation des types (racemes, monothyrses, diplothyrses et pleiothyrses), leur position (latéral ou terminal) et mode de croissance, et quelques caractères sexuels secondaires. L'importance taxonomique de ces aspects ainsi que des éventuelles tendances évolutionnaires sont discutées.

KEY-WORDS: Picramnia — SIMAROUBACEAE — Inflorescence — Angiosperms — Morphology — Taxonomy.

Introduction

The genus *Picramnia* was established by SWARTZ (1788), and is composed of species with a geographical distribution ranging from Mexico and Florida to the tropical and subtropical regions of South America. The woody plants are usually to be found in forest, though a number of species have adapted successfully to open or rocky habitats. *Picramnia* may be distinguished from other genera in the Simaroubaceae by the flowers, which are trimerous to pentamerous (rarely hexamerous), diclinous (in dioecious plants), with stamens opposite the petals and a syncarpous bi- or tricarpellary gynoecium. The fruit is a berry.

The principal works on the morphology and taxonomy of *Picramnia* are: PLANCHON (1846), TULASNE (1847), JADIN (1901) and, above all, ENGLER's monograph (1874) in Martius' "Flora Brasiliensis", and the same author's overall treatment of the Simaroubaceae (ENGLER, 1931). In more recent times our knowledge of the genus has expanded only by way of descriptions of new

taxa and inclusions in local or regional floras (e.g. KILLIP & CUATRECASAS, 1942; MACBRIDE, 1949; PORTER, 1973; PIRANI, 1987a, 1987b, 1988; PIRANI & THOMAS, 1988, and THOMAS, 1988).

The fact remains that various aspects of the flower and inflorescence morphology still demand elucidation. In their work on the morphology of the Simaroubaceae, NAIR & JOSHI (1958) concern themselves exclusively with floral structure in *Ailanthus, Picrasma* and *Brucea;* these three genera belong in subfamily Simarouboideae, and are thus not very closely related to *Picramnia,* the only genus in subfamily Picramnioideae (classification according to ENGLER, 1931 and SCHOLZ, 1964).

This paper forms part of the taxonomic revision of *Picramnia* for Brazil (PIRANI, 1989, 1990); the underlying intention is to cast light on basic aspects of inflorescence morphology in the genus, to characterize the various inflorescence patterns, demonstrating their importance in infrageneric taxonomy, and to discuss possible evolutionary trends involved.

Material and methods

Morphological and taxonomic study was based on the herbarium material listed in PIRANI (1989). There are 19 Brazilian species: *Picramnia andrade-limae* Pirani, *P. bahiensis* Turcz., *P. campestris* Rizz. & Occh., *P. caracasana* Engl., *P. ciliata* Mart., *P. elliptica* Pirani & Thomas, *P. excelsa* Kuhlmann ex Pirani, *P. ferrea* Pirani & Thomas, *P. gardneri* Planch., *P. glazioviana* Engl., *P. grandifolia* Engl., *P. guianensis* (Aubl.) Jansen-Jacobs, *P. juniniana* Macbr., *P. parvifolia* Engl., *P. ramiflora* Planch., and *P. sellowii* Planch. Further to these species, collections of *P. antidesma* Sw., *P. hirsuta* Thomas, *P. monninaefolia* Rusby, *P. nuriensis* Steyerm., *P. pentandra* Sw., *P. polyantha* (Benth.) Planch., and *P. sphaerocarpa* Planch. were also studied.

Flowers and inflorescences fixed in FAA 50% were examined with respect to the following species (voucher material listed): *P. bahiensis (Pirani & Zappi 972* and *976, Pirani & al. 2460* and *2461), P. ciliata (Pirani & al. 2015* and *2493), P. campestris (Giulietti & al. CFCR 6377), P. glazioviana (Pirani & Cordeiro CFSC 7679, Pirani & al. 1406, 2331, 2468), P. oreadica (Pirani, Mello-Silva & Werneck 2016), P. parvifolia (Pirani & al. 408, 1357* and *1358, Robim 379, 380* and *381), and P. sellowii (Pirani & al. 2052).* Also studied were: *P. polyantha (Thomas & Contreras 3785)* and *P. guerrerensis (Thomas 3714),* neither of which is found in Brazil. All the voucher specimens here mentioned are on deposit in the herbarium of the Department of Botany of the University of São Paulo (SPF).

Flowers and inflorescences taken from dry material were rehydrated by boiling; all material was studied with a Wild stereo microscope with camera lucida or photographic apparatus as necessary.

Results and discussion

Inflorescence organization and typology

The inflorescence of *Picramnia* is in essence racemose or indeterminate; in the sense of TROLL (1964) a polytelic inflorescence (blastotelic according to BRIGGS & JOHNSON, 1979). The primary axis, instead of forming a terminal flower (which would be characteristic of a monotelic or anthotelic inflorescence) continues "indefinitely" to form lateral flowers and bracts, and ceases its growth in a rudimentary apex. In those species where the inflorescence is conspicuously branched (Troll's "synflorescence") a "principal florescence" may be made out in the distal zone of the main axis; below this are arranged lateral flowering branches (paraclades) which repeat the morphological organization of the terminal florescence and which are called "coflorescences" by TROLL (op. cit.). In the case of those inflorescences where there are no branches of any importance, only the principal florescence is present.

The levels of inflorescence organization in *Picramnia* at its most complex are as follows (from basic unit to overall structure): flower → cyme (cymule or glomerule) → simple thyrse → diplothyrse → pleiothyrse (Figs. 1a, 2).

The basic units, the flowers, are organized into "partial florescences" (TROLL, 1964; WEBERLING, 1975, 1988); these are very short lateral branches, cymose in growth. This type of growth is defined by WEBERLING (1988) as that in which "branch production is restricted to the axils of prophylls of consecutive orders", and the systems of sympodial ramification which arise from this process constitute cymes (ci in fig. 1a). However, a cyme is a strictly sympodial arrangement in which each lateral flower is preceded by two "bracteoles", these being the prophylls of the axillary ramification. In *Picramnia,* in the axil of one of the prophylls (in a monochasial system) or of both (in a dichasial system) there appear lateral flowers which are also preceeded by two prophylls. If at this stage the system stops in its growth, then the small cyme constitutes a cymule, with two or three flowers; this is the case in many of the species. In most, however, the cymes continue to produce increasing numbers of lateral flowers; the axes of these are always short, thus giving rise to dense glomerules (with from four to about thirty flowers). The basic organizational scheme and the sequence of flower maturation in *Picramnia* is shown in Fig. 1b-d. It should be noted that, as with most dicotyledons (WEBERLING, 1988), there are two prophylls per flower, subopposite and in a position transversal to the axis. Given F_1 as the first terminal flower of the initial branch of the cyme, and F_2 as the flowers produced at the apex of the two lateral branches, and so on, then we shall see that the prophylls of a flower F_{x+} will always be the bracteoles which will subtend the flower F_{x+1} (see Fig. 1b, c).

The next structural level of the complex synflorescence of *Picramnia,* above the cyme, is the thyrse: a raceme in which the axillary flowers have been substituted by cymes in the form of cymules or glomerules. The term "thyrse" was coined by Linnaeus (TROLL, 1964; WEBERLING, 1988), but was first given its definition in todays's sense by DE CANDOLLE (1827), who described it as "composed of small cymes along an axis of indefinite growth". In a work specifically about this type of inflorescence, LEE (1967) characterized it as a "panicle of cymes" or, rather more exactly, as an inflorescence of "determinate cymules with the branches alternating along the axis". However, TROLL (1964) and WEBERLING (1988) define the thyrse exclusively as a "complex (or compound) inflorescence with cymose partial inflorescences", and restrict the term panicle to inflorescences having "racemose partial inflorescences". BRIGGS & JOHNSON (1979) rather similarly define the thyrse as a "blastotelic (that is, polytelic) inflorescence with a multinodal principal axis bearing lateral cymes (commonly lateral dichasia)". It should be noted that TROLL (1969), parallel to his definition of the thyrse as a polytelic inflorescence, analyzes a series of "monotelic thyrses", to which he gives the name of "thyrsoids", generally adopted by his followers, including BRIGGS & JOHNSON (1979). Thyrses and thrysoids are common in numerous dicot families and display a large variety of subtypes, particularly in the Anacardiaceae, Sapindaceae and Meliaceae, families related to the Simaroubaceae.

In the schematic synflorescence of *Picramnia* shown in Fig. 1, the distal sector is a thyrse (by Troll's definition), and forms the principal florescence (FP); below the zone marked H_1, which is a hiatus in the organization, the various lateral cymes are substituted by coflorescences (CF) in the form of thyrses which repeat the pattern of the principal florescence alternately along the axis. The number of nodes is variable, in such a way that the terminal unit (FP) normally has more cymes than the more distal lateral units (CF); the length of the latter and the number of their cymes gradually increase towards the base of the principal axis (Fig. 1a). The internodes of the more distal lateral thyrses are much smaller, and it may be difficult to establish the exact limits of the region of hiatus H_1.

There is on the axis of this same synflorescence a further structural hiatus (H_2, Fig. 1a), separating the two regions A and B, which display the same pattern and degree of ramification (though B is less well developed than A). In the proximal region of the axis lateral axes, C, D etc., are often formed; these are structurally analogous to A and B. Occasionally, only region A is present.

Given this, we may define and characterize all the inflorescence types found in *Picramnia;* these are shown in Fig. 2.
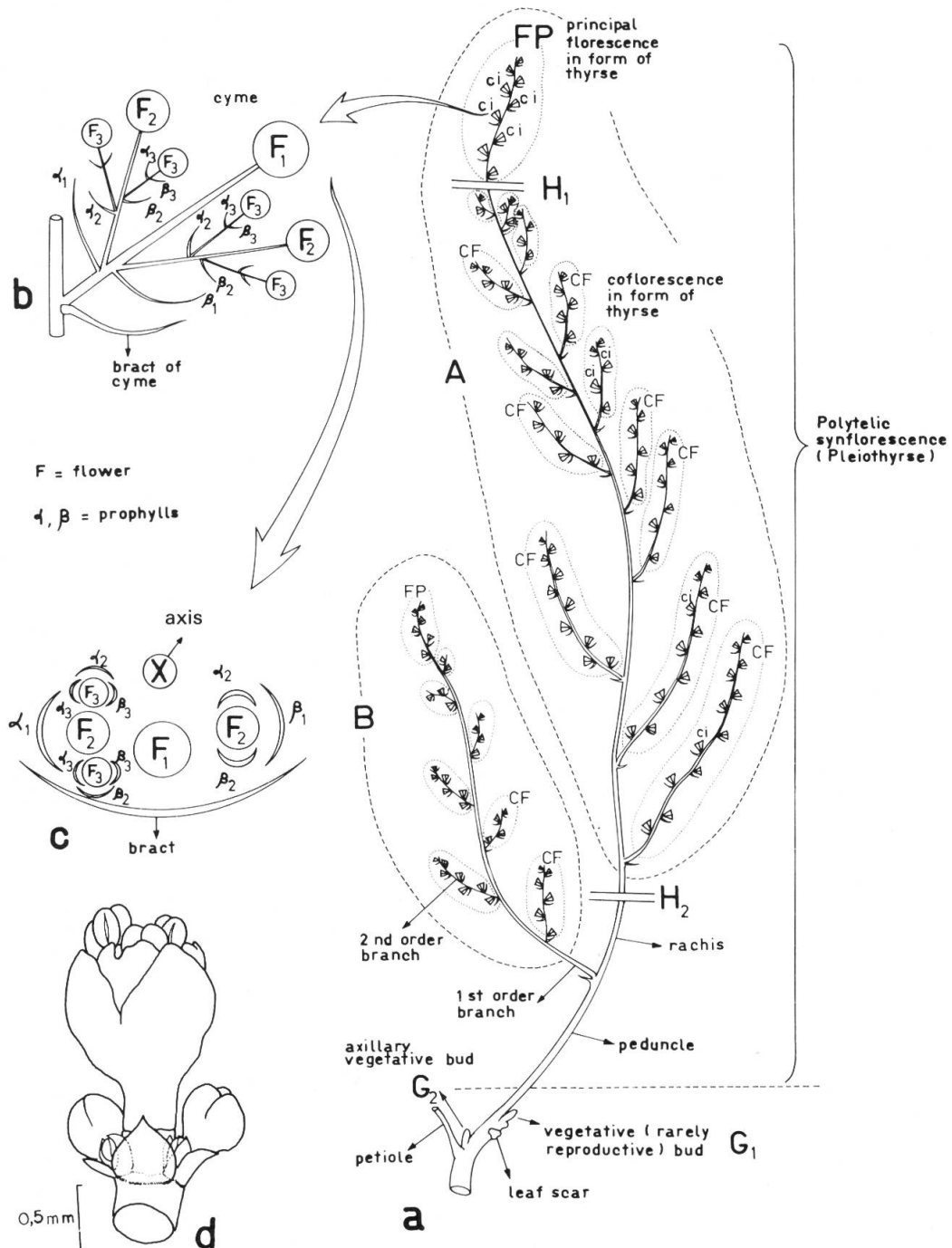
Fig. 1. — Inflorescence structure in *Picramnia*.

a, schematic representation of a branch apex with a polytelic terminal synflorescence (pleiothyrse): **ci,** partial florescence (cyme) $\bigtriangledown$; **FP,** principal florescence (thyrse); **CF,** coflorescences (thyrses); **A,** sector between H_1 and H_2 with coflorescences in simple thyrses (haplothyrses); **B,** proximal sector, below H_2, where the ramification(s) repeat(s) the form of the distal sector; H_1, hiatus in synflorescence architecture, separating the apical simple thyrse **(FP)** from zone **A**; H_2, hiatus in architecture separating zones **A** and **B**.

b, c, schematic representation of a cyme: **b,** vertical projection; **c,** horizontal projection; F_1, first flower; F_2, second flower; α_1, first of the two prophylls of F_1 (subtending bract of F_2); β_1, second of the two prophylls of F_1 (subtending bract of F_2); α_2, β_2, prophylls of F_2 (prophylls of F_x are always subtending bracts of F_{x+1}).

d, cyme of *P. glazioviana (Pirani & al. 1406),* showing bract, prophylls, and the much-contracted axes which give the glomeruli-form appearance.
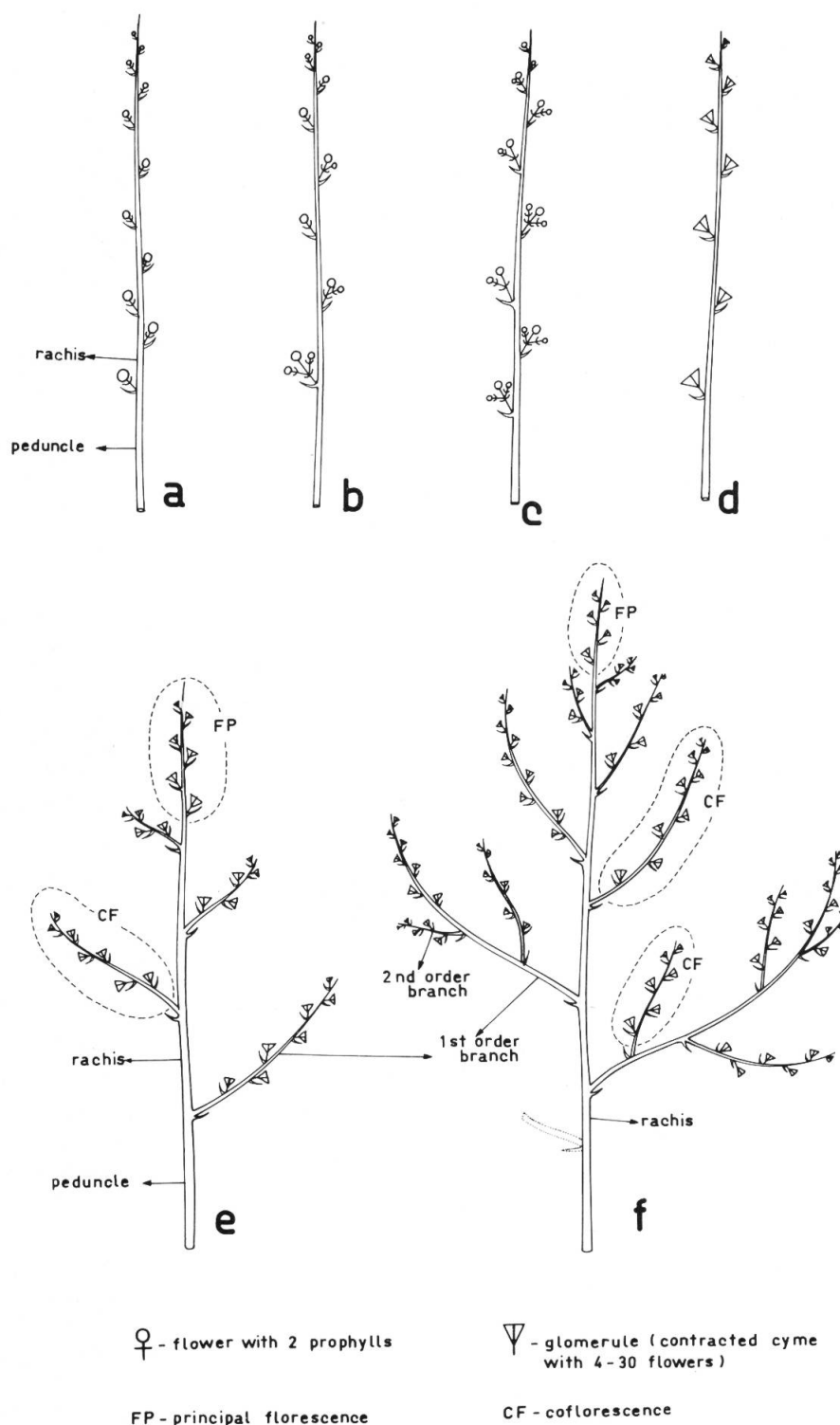
Fig. 2. — Inflorescence typology in *Picramnia*.
a, raceme; **b-d,** simple thyrses (monothyrses or haplothyrses): **c,** the lateral units are cymules with 2 or 3 flowers; **d,** the lateral units are contracted cymes with from 4 to 30 flowers (glomerules); **b,** intermediate form between type **c** and a raceme **a; e,** diplothyrse, in which the coflorescences (**CF**) repeat the pattern of the principal florescence (**FP**). In this case, the lateral units are always cymes or cymules; **f,** pleiothyrse, in which the proximal first order branches follow the ramification pattern of the distal zone.

1. Synflorescences of the type described above; to these we shall give the general name of compound or branching thyrses. TROLL (1964) and WEBERLING (1988) distinguish two varieties:

a)   the diplothyrse (Fig. 2e), in which the distal portion, with a certain number of cymes, forms a simple thyrse (monothyrse or haplothyrse according to the classification of the authors mentioned above), while one or several branches originating at the nodes beneath are also coflorescences in the form of simple thyrses (in Troll's classification these are called special thyrses or infrathyrses);

b)   the pleiothyrse (Figs. 1a, 2f), in which one or more proximal branches of the rhachis represent a repetition of the distal zone above them, as they possess a terminal florescence and one or several thyrsic coflorescences.

These two variations of the "compound thyrse" may occur in one and the same species, and are often related with sexual dimorphism. Diplothyrses and pleiothyrses are typical of the species with trimerous flowers, in which they may display very profuse branching; diplothyrses also occur in numerous tetramerous and pentamerous species — *P. sellowii, P. caracasana* and *P. gardneri,* for example.

2. Inflorescences of the simple thyrse type (monothyrses or haplothyrses, according to the classification of WEBERLING, 1988). Here, only the region corresponding to the principal florescence (FP) of the preceding type is present. Thus the simple thyrse is formed of an indeterminate axis (at times very long in certain species), the lateral branches of which are highly contracted cymes (Figs. 2c, d). The degree of development achieved by the cymes is very variable, and frequently characterizes the species. So in many species the lateral cymes are many-flowered, but as the internodes are much contracted, they appear as dense glomerules, forming the simple thyrse with glomerules (Fig. 2d). In other cases, each lateral branch forms only one terminal flower (F_1) and two lateral flowers (F_2), of which one may be suppressed. In this case we have a simple thyrse with cymules (Fig. 2c — the cymule, diminutive of cyme, is the simplest cyme, with 3 flowers in a dichasial structure and 2 flowers in a monochasial structure).

3. Inflorescences in the form of a raceme or bothrium. In some species there arises an inflorescence of the sort which has been described in he literature on the genus as a raceme (Fig. 2a, 3a); this comes about through the simplification of a thyrse with cymules and formation of the terminal flower only of each lateral branch. In an inflorescence of this type, in the axils of each of the various bracts of the main axis there is a single flower, at the base of which 1 or 2 prophylls may be made out. These may be easily deciduous or at times apparently absent. The absence of one or both prophylls is a matter in need of illumination by further and more detailed study. Evidence that these racemes probably originate from thyrses with cymules comes from the presence of the prophylls, and above all from the occurrence, regular in certain species, of a number of two-flowered — rarely three-flowered — cymules along the main racemose axis (Fig. 2b). This inflorescence type, the most simplified of those found in *Picramnia,* is the pattern basic to some species: *P. ramiflora, P. guianensis, P. oreadica* subsp. *penduliflora.* However, it is very common for 1, 2 or 3 flowers in addition to the original one (giving rise to a cymule) to develop at some at least of the nodes of the axis. Thus there is a final predominance over racemes proper of a transitional type. This is a simple thyrse which bears along its main axis cymules, principally at the median and proximal nodes, and monads (Fig. 2b). In *P. latifolia,* the racemes and thyrses are basically of this type, but there also appear forms with almost sessile flowers which give rise to spicate racemes.

When we compare these facts with the relevant morphological and taxonomic literature, we note that the inflorescence of *Picramnia* has been inaccurately described. PLANCHON (1846) described it as having "glomerate or fasciculate flowers gathered in spikes" which were "not infrequently geminate and ramose"; ENGLER (1874, 1931) showed it as having "fascicules or glomerules which form pseudo-spikes or pseudo-racemes", or "racemes gathered in panicles". For SMALL (1911) and BRIZICKY (1962), the flowers are arranged in "spike-like or raceme-like panicles". KILLIP & CUATRECASAS IN CUATRECASAS (1942), in their description of *P. platystachya,* refer to "simple pseudo-racemose or slightly racemose panicles". Thus the interpretation of the inflorescence of *Picramnia* as being racemes or panicles; it is the same in all works previous or subsequent

to those mentioned, including PORTER (1973), PIRANI (1985, 1987a, 1987b, 1988), and THOMAS (1988). In fact, as we have seen, there are species with true racemes; in the remaining cases the inflorescence is always racemose (in the sense of being polytelic). Even the thyrses have been considered by a number of authors as special types (mixed, according to LEE, 1967) of panicle; this, however, was refuted by the school of Troll. What was obscure or imperfectly understood in this literature was the cymose character of the basic inflorescence units in most of the species of *Picramnia*. This was only suggested "en passant" by TULASNE (1847, p. 263) and is enlarged upon here. The interpretation of the glomerules of *Picramnia,* so characteristic of the genus, as being contracted cymes which are sub-sessile and at times reduced to few-flowered cymules, previously known as "fascicles", was not arrived at, probably due to the much-reduced dimensions of the internodes, prophylls, and of the flowers themselves (see Figs. 3e and 4c, d).

The typological classification here adopted for the inflorescences of *Picramnia* follows in general terms the terminology proposed by TROLL (1964) and WEBERLING (1965, 1988); this rests upon solid empirical foundations and is fully accepted by Stützel (pers. comm.). The distinction used here for certain subtypes is to some extent arbitrary, and aims simply at a degree of simplification for better systematization and more succinct morphological description. So the distinction between racemes and simple thyrses with few-flowered cymules is not strict, as all these forms may appear in the same species or even in the same inflorescence. The name "simple thyrse" (that is, haplothyrse or monothyrse), referring to the characteristic type of most species in the genus, is used here in preference to the terms "pseudo-raceme" and "pseudo-spike", formerly used by a number of authors (e.g. ENGLER, 1874; CUATRECASAS, 1942). The reasons for this are as follows:

a)   the principle authorities on the subject of inflorescence morphology have not investigated this type (this includes TROLL, 1964, 1969; WEBERLING, 1965, 1988; FOSTER & GIFFORD, 1974; BRIGGS & JOHNSON, 1979).

b)   In a recent work on the floral ontogeny of the Leguminosae, TUCKER (1987) affirms that the term "pseudo-raceme" has been used indiscriminately: it sould be restricted to indeterminate inflorescences where each first order bract on the primary axis subtends basically 3 (in fact from 2 to 12) flowers, thus being "technically a panicle". In the view of the same author each group of flowers (basically a triad) of the pseudo-raceme forms a "short shoot", or "partial florescence", in which each flower is subtended abaxially by one second order bract. Each partial florescence is racemose, not cymose, in its development; in this lies the main divergence with the scheme of the thyrsic inflorescences of *Picramnia.*

c)   In a recent morphological study of the inflorescence of *Rinorea* (Violaceae) HEKKING (1988) recognized as a "pseudo-raceme" an inflorescence with a terminal flower, isolated lateral flowers in the distal portion, and 1-3 flowered cymules in the proximal portion.

d)   Even so, there is no precise and uniform definition of "pseudoraceme"; furthermore, as we have shown, true racemes (bothria) also occur in some species of *Picramnia.*

It is also important to point out that there is no fully stable separation between simple thyrses and branching thyrses (be they diplothyrses or pleiothyrses). In many species formation or not of one or more coflorescences (lateral thyrses) is not a fully established character (as in many other cases), and varies in accordance with factors which have yet to be studied. In other words, and following the system of TROLL (1964), the inflorescences in certain species may in some cases form an "enrichment zone" or "parachadial zone". In species like *P. latifolia, P. juniniana,* and *P. oreadica,* the formation of compound thyrses (in this case diplothyrses) is an occasional occurrence, while the contrary is true of *P. sellowii.* In *P. gardneri* simple and compound thyrses occur with more or less the same frequency, although there is an evident correlation between the types and a degree of sexual dimorphism (in this species the staminate inflorescences are larger and more branched than the pistillate).

Fig. 3. — Inflorescences of *Picramnia*.

a, b, staminate raceme of *P. ramiflora* Planch. (**a,** detail; **b,** lateral position on shoot); **c,** terminal staminate pleiothyrse of *P. sellowii* Planch. subsp. *sellowii;* **d,** terminal and lateral simple thyrses on a shoot of *P. juniniana* Macbr.; **e,** part of a thyrse of *P. gardneri* Planch. showing three dense, multiflowered cymes; **f,** terminal staminate pleiothyrses of *P. parvifolia* Engl. (**a, b,** from *Martins 10054;* **c,** from *Hassler 6622;* **d,** from *Williams 13918;* **e,** from *Ule s.n.* (R 71006); **f,** from *Hoehne 6161*).
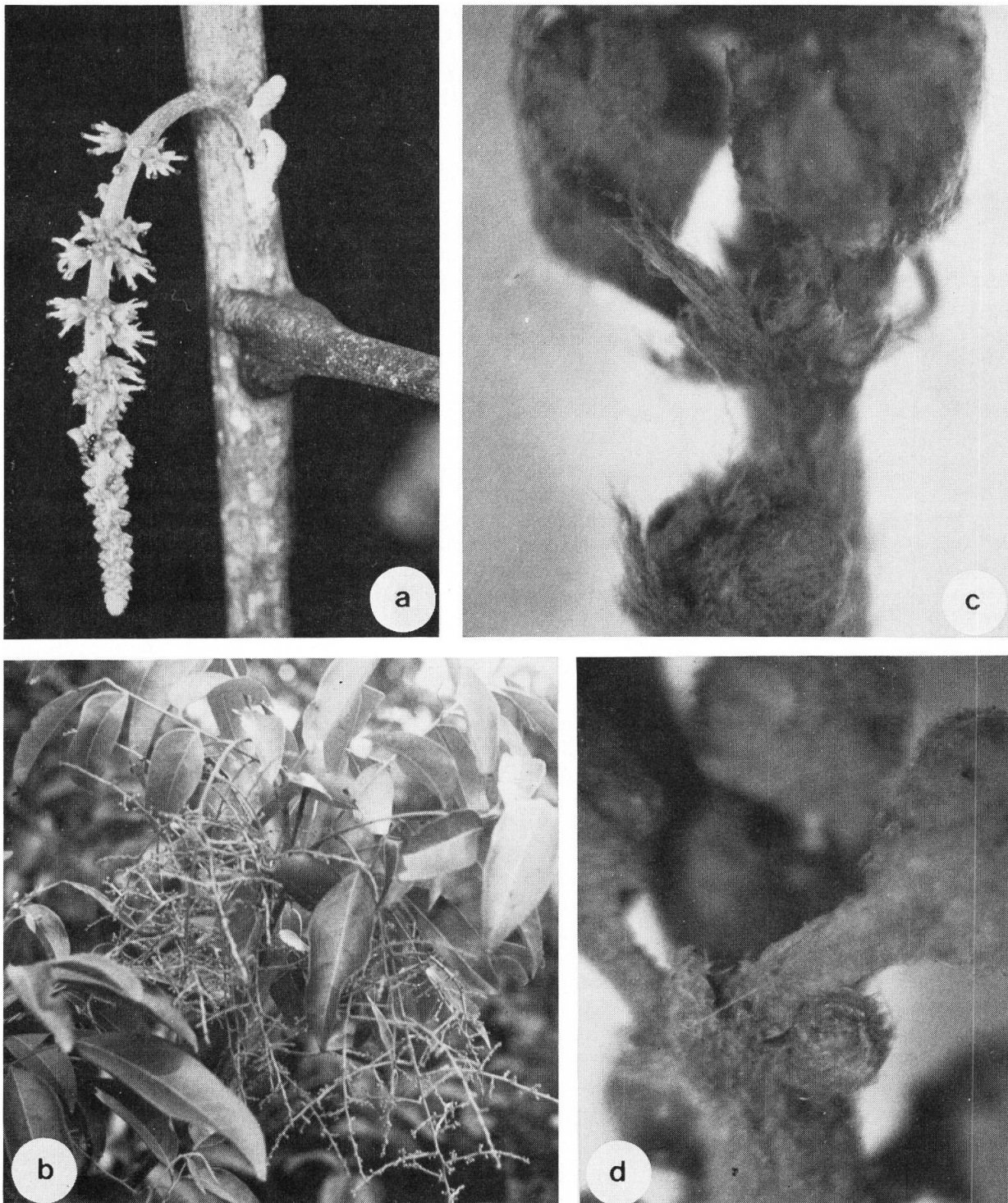
Fig. 4. — Inflorescences of *Picramnia*.
a, lateral staminate racemes of *P. latifolia* Tul.; **b**, terminal pleiothyrses of *P. bahiensis* Turcz.; **c, d**, details of lateral cymes, with bract and prophylls, from a thyrse of *P. glazioviana* Engl. (**a**, from *Thomas & al. 4727;* **b**, from *Pirani & Zappi 976;* **c, d**, *Pirani & al. 1406* (**c**, 22.5 ×, **d**, 30 ×).

Bracts and prophylls

Bracts (hypsophylls) are present at all the nodes of the axis in a simple inflorescence (bothrium and thyrse); they subtend isolated flowers (in a bothrium) and cymes (in a thyrse). In complex inflorescences (diplothyrses and pleiothyrses) it is obvious that bracts also form at the nodes of the axis of each coflorescence, as also at the base.

The bracts are always much reduced, linear-lanceolate, pilose on the outer surface, and generally persistent. Thus the inflorescence in *Picramnia* is never frondose (sensu TROLL, 1964), that is, it never has expanded foliar organs with the appearance of leaves. In a Mexican species (*P. polyantha* (Benth.) Planchon), some of the bracts are expanded into a narrow oblanceolate photosynthesizing blade; even so, they are short (up to 1.5 cm) and never differentiated into a pinnate structure; the synflorescence thus remains bracteose and not frondose in aspect.

Sporadically, one or more leaves may form in the so-called "inhibition zone" (TROLL, 1964, WEBERLING, 1965, 1988), situated at the base of the terminal synflorescence; in size and number of leaflets these are conspicuously smaller than the leaves produced before the onset of flowering. Even so, the inhibition zone is always very abrupt, and the inflorescence axis is quite distinct from the vegetative portion of the stem.

Occasionally there may appear a number of sterile bracts on the peduncle; these are here referred to as "peduncular bracts", and have been observed in *P. ferrea* and *P. oreadica*.

In the inflorescence of *Picramnia,* each axis which will form a terminal flower produces two reduced leaves, the prophylls, which are transversal-opposite in position, and are identical to the prophylls (the two first leaves) of other branches. According to TROLL (1964), BRIGGS & JOHNSON (1979) and WEBERLING (1988), the internode which precedes the prophyllary node is the hypopode, while the internode above the node is the epipode. These internodes are evident in the flower pedicel of *Picramnia,* since the node is well articulated, although the articulation of the pedicel at times falls to correspond exactly to the point from which the prophylls emerge. In addition, the epipode is usually veryx short, so that the prophylls are very proximal in their position. At times the epipode itself is hardly elongated, and gives rise to subsessile flowers (particularly in *P. latifolia*). The flowers which arise from the axils of the two prophylls of the primary flower also bear second order prophylls, thus continuing the sympodium.

BRIGGS & JOHNSON (1979) comment that the term "bracteole" has been applied to a variety of bract-like structures which are not in fact always homologous, and is thus "insufficiently precise". In the view of these authors, "bracteole" should designate only "empty" foliar structures (that is, those without axillary buds, or where the buds are finally undeveloped) on an axis which terminates in a flower. They also state that in the case of these buds giving rise to flowers, the bracteoles will constitute prophylls. In *Picramnia,* since the development of the axillary buds of the first prophylls may be limited or not in one and the same species (as we have seen), and since the term bracteole has no place in the school of thought begun by TROLL (1964, 1969), we shall always call the foliar structures which precede each flower by the name of prophylls.

By contrast with the bracts, which are normally persistent on the infrutescence, prophylls are frequently deciduous.

Inflorescence position and mode of growth

The production of flower-bearing axes in *Picramnia* may come from the apex of the stem branch (terminal inflorescence) or from lateral buds (ramiflorous and cauliflorous inflorescences).

Most common in the genus is the terminal position, which is also the only position in most of those species where it occurs. Figure 1a shows us a branch, the apex of which forms a pleiothyrse, and at the base of which we may make out a petiole scar with a bud in its axil. This is clear evidence that the entire distal system from that point on forms in effect the complete synflorescence and not just part of it. The axillary bud G_1 (Fig. 1a) may occasionally form a further synflorescence, adjacent to and concomitant with the first. Generally, however, this bud (or the bud of the node below, G2) brings about the renewal of vegetative growth, and forms a branch with leaves. As this often happens when the plant is in full flower, the inflorescence thus takes up a sub-terminal or

lateral position, but analysis of the branching pattern shows it to be distally formed. This mode of growth, called "overtopping" by some authors (WEBERLING, 1988, Stutzel pers. comm.), and "lateral growth" by others (KORIBA, 1958) is the rule for most species, and was first described clearly in *Picramnia* by URBAN (1926): "Inflorescentiae initio terminales sed ramulo proximo axillari saepius mox evoluto et elongato laterales" (for *P. macrocarpa* Urban).

Branch flowering or ramiflory, in which non-frondose inflorescences (that is, those without expanded foliar organs and which bear only reduced bracts) arise from dormant lateral buds on the woody part of branches formed previously but recently (according to the definition of BRIGGS & JOHNSON, 1979) occurs in *P. latifolia, P. ramiflora, P. juniniana* and *P. magnifolia.* In the last of these species, and sporadically in the other three, the condition known as stem flowering or cauliflory (sensu BRIGGS & JOHNSON, 1979) is also found. Here, non-frondose inflorescences are formed from lateral buds situated on the trunk, which is well-developed through growth over a long period. According to collectors' references, *P. magnifolia* may produce thyrses even on the base of the stem. In branch flowering species, it is easy to observe the supra-axillary position of the lateral inflorescence, above the petiole or the scar traces left by leaves which have fallen earlier (figs. 3b, 4a). In the case of stem flowering in *P. magnifolia,* this state is hidden by the greater development of the bark and the consequent "disappearance" of the petiole scars.

Branch flowering inflorescences may be single or fasciculate, not just in the same species but in the same individual.

Although it is an important character for taxonomy, the branch flowering condition in *P. latifolia* and *P. juniniana* is not fully established, and these species frequently display terminal and truly lateral inflorescences, even on the same branch (see Fig. 3d).

The attitude of the flowers is affected not only by the position of the inflorescence, but also by its orientation and the relative elongation of its axis. In *Picramnia* the inflorescences are at their emergence first ascending, whether they be racemes or complex thyrses; in most species they soon become pendant due to elongation. In *P. campestris* and *P. campestris* and *P. oreadica* subsp. *oreadica,* the inflorescence remains erect, even when fruiting sets in. The length of the primary axis varies from species to species and is of taxonomic significance, but it may vary greatly within a species. Among the species with (essentially) simple thyrses, some display limited axis elongation (36 cm at the most in *P. juniniana, P. elliptica, P. ramiflora, P. oreadica* and *P. ferrea,* to mention just some), while the thyrses of *P. gardneri* subsp. *septentrionalis* and the non-Brazilian species *P. connaroides* Tul. may reach from 50 to as much as 100 cm! In those species with diplothyrses and pleiothyrses maximum elongation always occurs in the primary axis, though some of the lateral thyrses may also grow a lot; in these cases short and medium-sized inflorescences are predominant, reaching 40 cm in *P. excelsa.* With relation to the differential development of the coflorescences and infrathyrses, ramification follows a basitonic pattern (by the definition of WEBERLING, 1988); branches are more developed closer to the base (Fig. 1a).

With regard to mode of flowering, the inflorescences of *Picramnia* are polytelic, thus general maturation of the flowers is acropetal — from base to apex. It should be remembered, however, that as we are almost always dealing with thyrses, an acropetal sequence of primary flowers which reach anthesis first is then followed by a secondary sequence of maturation of the secondary flowers of the cymose partial florescences, the glomerules. In these, the terminal flower opens before the lateral ones, a consequence of the organs of this terminal flower having arisen directly from the apical meristem of the inflorescence, while the lateral flowers of the cyme are formed from the apices of lateral axes. It is not uncommon for the flowers in the axils of the last prophylls differentiated in the glomerule to be greatly retarded in their maturation or even aborted. In species with very dense glomerules such as *P. gardneri, P. elliptica* and *P. juniniana,* a large number of flowers appear never to complete their development. On the other hand, even in species with racemes or simple thyrses such as *P. latifolia* and *P. ramiflora,* it may occasionally happen that an entire distal portion with bracts and well-formed buds does not mature, and thus remains on the apex of the infrutescence.

Authors such as STEPHENSON (1981), WYATT (1982) and BAWA & WEBB (1984) have discussed a number of aspects of the adaptive significance of various inflorescence types and modes of flowering. It is suggested that the number of flowers and their spatial and temporal arrangement

determine pollination and fruiting levels in natural populations. With regard to inflorescence architecture and mode of flowering, WYATT (1982) notes that these factors have a direct effect on the quality of subsequent generations: indeterminate inflorescences, for example, such as those of *Picramnia,* have few flowers maturing on any one day, thus extending the flowering period and the greater possibility of crossing with different individuals (thus implying the formation of embryos with different genomes on just one plant!).

Secondary sexual characteristics

Dioecism is a fully established condition in almost all species of *Picramnia;* the exceptions are a few cases of subdioecism through the occasional formation of perfect (monoclinous) flowers on plants which are otherwise pistillate or staminate. Reference to polygamy in *Picramnia* was first made by FAWCETT & RENDLE (1920), later by LEMÉ (1952); after this the matter has received no further attention. We would draw attention in the present work to a potential capacity for pollen production in pistillate inflorescences in *P. oreadica, P. latifolia* and *P. parvifolia.* In one specimen of *P. oreadica* (*Glaziou 20870,* at C, K and P), almost all the flowers are monoclinous.

A number of secondary sexual characteristics may be seen in *Picramnia,* in association with the condition of dioecism. Of note is dimorphism in the inflorescence: in all species with trimerous flowers so far studied, and in most with pentamerous flowers, the staminate inflorescences are larger and/or more branched than the pistillate, and are composed of far more flowers (Fig. 3c, f). In those species where the pleiothyrse appears, the rule is the pleiothyrse in the staminate and the diplothyrse in the pistillate individual. In general terms this has been reported as being he commonest case in tropical dioecious plants, by LLOYD & WEBB (1977), BAWA & OPLER (1975), BAWA (1977, 1980) and OPLER & BAWA (1978).

There are notable exceptions to the dimorphic model displayed in the inflorescences of *Picramnia;* these are the ramiflorous species, *P. latifolia, P. ramiflora, P. magnifolia* and *P. juniniana.* Here there is no observable dimorphism or, in the first two of these species, the pistillate inflorescences are larger.

Phylogenetic aspects

On the basis of data collected for this paper and facts from PIRANI (1989), we may propose some comparative conjectures as regards what are presumed to be specialized and primitive conditions in *Picramnia.*

Pentamerous flowers (5 sepals + 5 petals + 5 stamens) are the basic pattern for the genus, as for the rest of the Simaroubaceae. Pentamerism is also established in the genus *Alvaradoa* (subfamily Alvaradoideae), the flowers of which are extremely like those of *Picramnia* (CRONQUIST, 1944). However, there still exists in *Picramnia* a certain flexibility in this respect, and tetramerous or even rare hexamerous flowers may on occasion appear. This potential in the ancestral stock was probably the starting point from which the consistently tetramerous or trimerous lines were derived; many of these species still maintain a capacity for flexibility.

Similarly, we may postulate flexibility as a primitive condition for the inflorescence structure of *Picramnia,* and in a number of existing taxa this — the terminal diplothyrse — is still preserved. Although the closest genus, *Alvaradoa,* has racemes, those species of *Picramnia* with the broadest range of distribution have branching terminal thyrses, while in the family as a whole there is a predominance of branching terminal to subterminal inflorescences. These are often put down as being "paniculate", but are in effect thyrsic, at least in genera such as *Simarouba, Simaba, Picrolemma* and *Ailanthus* (personal observations) and, according to the illustrations in ENGLER (1931), in *Odyenda, Hannoa, Harrisonia* and *Desbordesia.* Even in the genera with racemes, these racemes are usually gathered into panicles (e.g. *Mannia, Soulamea, Klainedoxa* fide ENGLER, 1931).

Starting with the basic terminal diplothyrse (Fig. 5a) we may detect the principal tendencies:

1a.   towards reduction of the branching of the thyrse, resulting in a monothyrse (or simple thyrse, Fig. 5c);

1b.   towards a continuation of the previous tendency, reduction of the lateral cymes of the monothyrse to 2-3-flowered cymules or to monads, thus giving rise to even more simplified monothyrses (Fig. 5d, e) or to racemes (Fig. 5f);

2.   towards an increase in the degree of branching, giving rise to the pleiothyrse (Fig. 5b). In most of the species which have followed this direction — most notably all the Brazilian and some Central American trimerous species — this tendency has become established in the staminate inflorescences, while the pistillate inflorescences generally preserve the primitive diplothyrse, a good example of secondary sexual differentiation. The pleiothyrse is here interpreted as a derivative structure on the principle of correlation: it is found in those taxa which unite a series of other derivative characters such as trimerism, obcordate petals, enclosed stamens and a 3(-4) carpelled gynoecium. On the other hand the pleiothyrse is absent in pentamerous species with diplothyrses, which are considered to be closer to the ancestral pattern;

3.   parallel to the evolution of the simple thyrse, we have starting from the terminal position (Fig. 6a), the initial stage of a transitory movement towards simultaneous production of terminal, subterminal and lateral inflorescences (Fig. 6b), and at a stage of greater specialization, stabilization of an effectively and exclusively lateral position (branch flowering and stem flowering, Figs. 6c, d).

Apparently divergent tendencies in inflorescence evolution within the same taxon (genus or family) such as those discussed here (reduced and increased complexity) have been noted elsewhere by other authorities (e.g. BRIGGS & JOHNSON, 1979 for the Myrtaceae, WEBERLING, 1988 for various families of Myrtales, and HEKKING, 1988 for *Rinorea* in the Violaceae).

The tendency observed in most species of *Picramnia* is towards reduction; this may occur as reduction of:

a) nodes of first and second order axes
b) degree of internode elongation
c) degree of branching and/or
d) number of flowers (by abortion).

Emphasis must be placed on the flexibility of the basic pattern as well as on the four modes of simplification given above; this has made possible the establishment of a variety of derived patterns such as diplothyrses with few branches and having cymules (Fig. 5a), or haplothyrses which have kept their dense glomerules (Fig. 5c), or racemes, representing the extreme of reduction in the genus (Fig. 5f).

The strongest corroboration of this proposal regarding inflorescence evolution in *Picramnia* lies exactly in this flexibility or instability: even species with typical simple thyrses retain their genetic potential for the production of lateral thyrsic coflorescences. This potential is expressed, regularly or occasionally, and in varying degree in *P. latifolia, P. oreadica, P. juniniana* and *P. gardneri* among others. The interpretation of the "monads" of racemes and ramemiform thyrses as being the final stage of reduction from glomuleriform cymes is borne out by the frequent presence of flower buds in the prophyllary axils of the lateral flowers; these buds may or not complete their development into functional flowers. This occurs regularly in *P. latifolia, P. oreadica* subsp. *penduliflora,* and sporadically in *P. ramiflora* and *P. ferrea.*

Changes of position of the inflorescence (terminal to lateral), shown in Fig. 6, and of orientation (pendant or erect) represent tendencies which have clearly had a profound effect on the display of flowers and fruits, as also on the basic structure of the inflorescence and the relative elongation of the axis or axes. The evolution of branch flowering and stem flowering may have been partly associated with the need for adequate structures for the support of a lot of heavy fruits, in accordance with the general interpretation of stem flowering in tropical trees proposed by STEBBINS
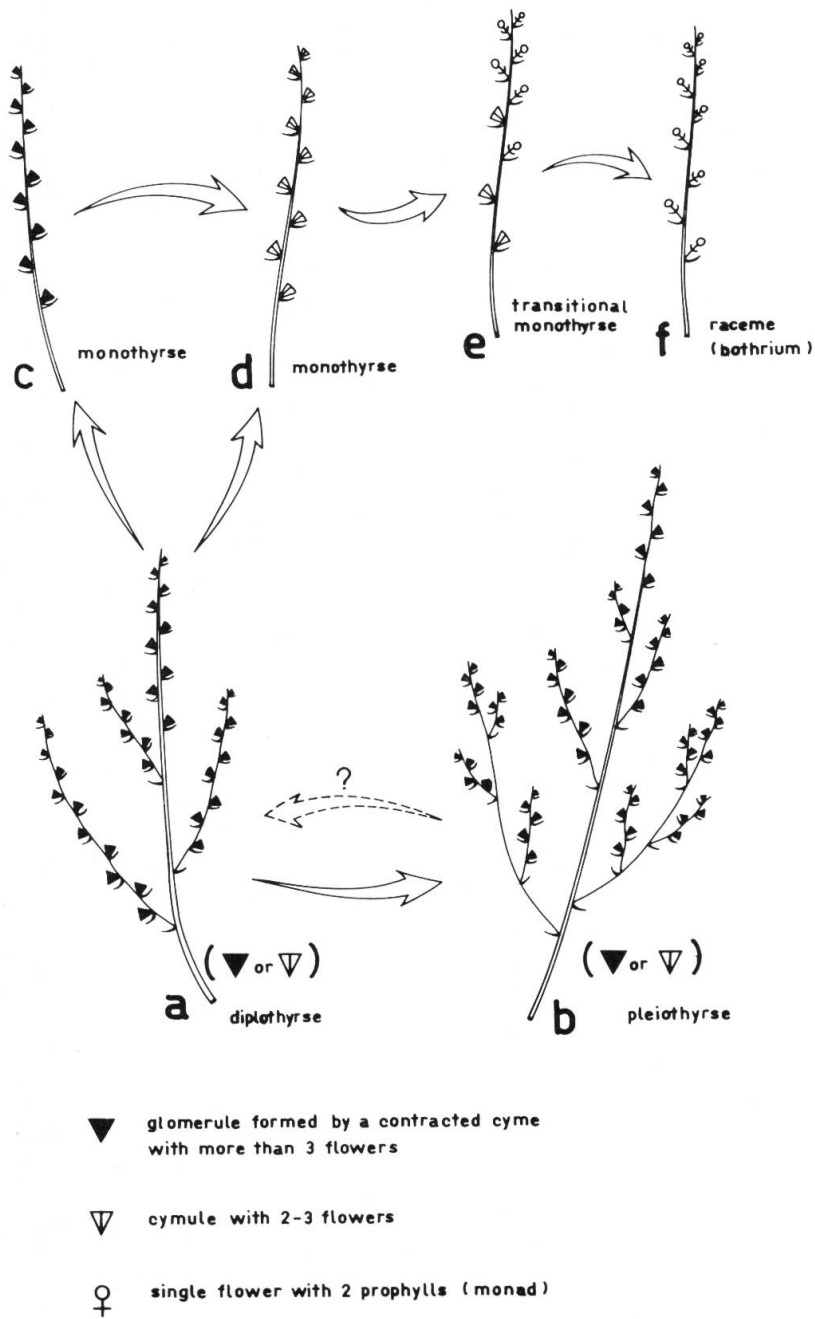
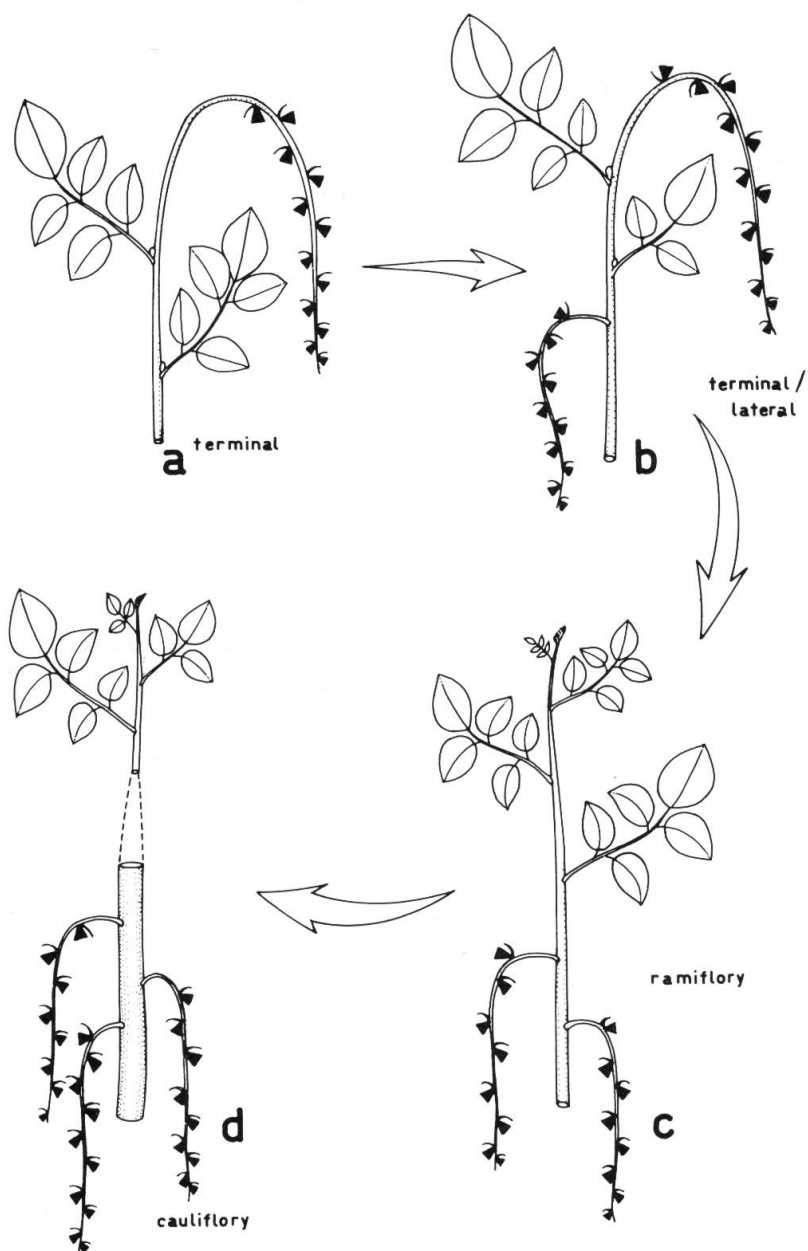Fig. 5. — Evolution of structural patterns in the inflorescence of *Picramnia*.

Fig. 6. — Evolution of inflorescence position in *Picramnia,* from terminal **(a)**, to terminal and lateral **(b)**, to lateral with branch flowering (ramiflory, **c**) or stem flowering (cauliflory, **d**).

(1974) and WYATT (1982). But probably the most important selective pressure concerns the transference of flowers and fruits from a position peripheral to the foliage, to a position within the canopy (in the case of branch flowering); this would no doubt have involved the activities of pollinating and dispersing agents. In the case of stem flowering, the flowers would have moved to the bare parts of the trunk, thus making use of agents from the lower layers of the forest. This explanation is put forward by BRIGGS & JOHNSON (1979) for the Myrtaceae. The erect position of the inflorescence, which is maintained by the infrutescence, is typical of the non-forest species *P. oreadica* subsp. *oreadica* and *P. campestris,* and is certainly the result of pressures of pollination and dispersion in an open habitat. However, as was noted by WYATT (1982) in an overall analysis of the adaptive significance of the various parameters of inflorescence morphology and position, phenological patterns, pollination, and dispersion, many basic questions still await empirical solutions before we can understand the general principles underlying the evolution of reproductive characters in plants.

When one takes into account the general tendencies here commented on, and relates them to biogeographical and taxonomic data, it may be seen that a number of the modifications must have been repeatedly evolved, and in taxa not necessarily closely related. Thus a powerful tendency towards the stabilization of the simple thyrse occurred, for exemple, among the trimerous species of *Picramnia* from Central America, while in the Brazilian species trimerism is consistently associated with the development of at times much branched diplothyrses and pleiothyrses. Up to what point there occured reversals in the direction of appearance of diplothyrses from ancestral forms with pleiothyrses or monothyrses (Fig. 5b→a, c→a) remains doubtful and speculative. The evolution of branch flowering likewise occurred in species with glomerules *(P. juniniana, P. magnifolia)* and in species with cymules or monads *(P. latifolia, P. ramiflora).* The potential (tendency in some cases?) for production of fasciculate inflorescences may be observed in a variety of species, some of them at a considerable taxonomic distance from one another. Thus it is that species with diplothyrses or pleiothyrses and trimerous flowers may on occasion produce a second diplothyrse from a bud located at the base of the first (e.g. in *P. parvifolia* and *P. excelsa*). These "accessory" inflorescences may also form in pentamerous species with branching or simple inflorescences; this is very common in *P. latifolia, P. juniniana* and *P. oreadica.*

In consequence of these extensive parallelisms, various of the well-marked characteristics of inflorescences and flowers should not be used in isolation from one another, or as predominant characters, in the determination of affinities or the delimitation of supra-specific but infra-generic groups. In association with other characters, they are useful for determination at species level, and help in the evaluation of probable relationships between species.

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