

Pattern analysis in pseudanthia *

REGINE CLASSEN-BOCKHOFF

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Abstract: Pseudanthia occur in more than 40 angiosperm families. With regard to the underlying inflorescence structure they can be classified into the following groups: (a) floral and (b) hyperfloral pseudanthia, each with (c) or without (d) pseudocorollas. Pseudanthia have developed along independent evolutionary lines and are not bound to a particular inflorescence structure. They are the result of (a) the specific morphological predisposition of the taxon concerned, (b) aggregation and diminution of the flowers, giving rise to the formation of an attraction unit (for animal pollination), (c) variation, and (d) selection. Ontogenetical abbreviation is regarded to play an essential role in the origin and elaboration of pseudanthia.

Floral attraction units (“blossoms”, German: “Blumen”) are usually single flowers (German: “Blüten”). They exhibit an attractive peripheral corolla and a sexual



Fig. 1. Analogous similarity between *A* a flower and *B* an inflorescence. *A* *Anemone hepatica* (*Ranunculaceae*; BG Aachen), *B* *Cosmos bipinnatus* (*Asteraceae*; BG Aachen). c Carpel, lf ligulate flower, p petal, s stamen, tf tubular flower

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Table 1. List of genera with pseudanthia. Bold face: inflorescences with high similarity to individual flowers; ^a VOGEL, pers. comm.; ^b STRUIK (1987: 18); ^c *Spathanthus bicolor* DUCKE (MAGUIRE, WURDACK & BUNTING 37521, B)

Dicotyledons	Euphorbiaceae	Dalechampia	Nyctaginaceae	Bougainvillea	Monocotyledons
Amaranthaceae	<i>Gomphrena</i> <i>Ptilotus</i>	Euphorbia <i>Monadenium</i>	<i>Plantaginaceae</i>	<i>Plantago</i>	<i>Alliaceae</i> <i>Allium</i>
Apiaceae	gen. div., e.g., Actinotus <i>Alepeidea</i> <i>Astrantia</i> <i>Xanthosia</i>	Pedilanthus <i>Synadenium</i> <i>Trifolium</i> <i>Azara</i>	<i>Proteaceae</i>	gen. div., e.g., <i>Mimetes</i> Orothamnus <i>Protea</i> <i>Serruria</i>	<i>Amaryllidaceae</i> Haemanthus Scadoxus gen. div. Acrolepis <i>Ficinia</i>
Asteraceae	<i>Fabaceae</i> <i>Flacourtiaceae</i> <i>Globulariaceae</i>	<i>Globularia</i>	<i>Rhamnaceae</i>	<i>Phyllica</i> Spyridium	<i>Cyperaceae</i> <i>Carludovica</i> <i>Cyclanthus</i> <i>Ludovia</i>
Bruniaceae	<i>Goodeniaceae</i> <i>Hamamelidaceae</i>	<i>Brunonia</i> <i>Loropetalum</i> Parrotiopsis Rhodoleia	<i>Rubiaceae</i>	<i>Cephaelis</i> Cephalanthus <i>Nauclera</i>	<i>Dasyopogonaceae</i> Dasyopogon
Campanulaceae	<i>Loranthaceae</i> <i>Mimosaceae</i>	<i>Amyema</i> Calliandra <i>Dichrostachys</i>	<i>Rutaceae</i>	<i>Chorilaena</i> Diplolaena <i>Euchaetis</i>	<i>Mesanthemum</i> <i>Paepalanthus</i> Syngonanthus
Cornaceae	<i>Cornus</i>	<i>Mimosa</i>	<i>Salicaceae</i>	<i>Salix</i>	<i>Androcymbium</i> ^b <i>Dauberya</i> ^b
Cunoniaceae	Callicoma	Neptunia <i>Parkia</i>	<i>Saururaceae</i>	Anemopsis <i>Houttuynia</i>	Thalia <i>Marantaceae</i>
Davidiaceae	<i>Davidia</i>	<i>Dorstenia</i>	<i>Sterculiaceae</i>	Lasiopetalum	Rhizanthella <i>Orchidaceae</i> Cirrhopetalum
Dipsacaceae	Cephalaria <i>Knaulia</i> <i>Scabiosa</i> <i>Succisa</i>	Actinodium <i>Darwinia</i> <i>Metaleuca</i>	<i>Thymelaeaceae</i> <i>Verbenaceae</i>	Pimelea <i>Congea</i> Sphenodesme Symphorema	<i>Pandanaceae</i> <i>Pontederiaceae</i> <i>Rapateaceae</i>
Ericaceae	<i>Cavendishia</i> ^a				<i>Spathanthus</i> ^c <i>Tacca</i> <i>Zingiberaceae</i> Nicolaia <i>Achrasma</i>

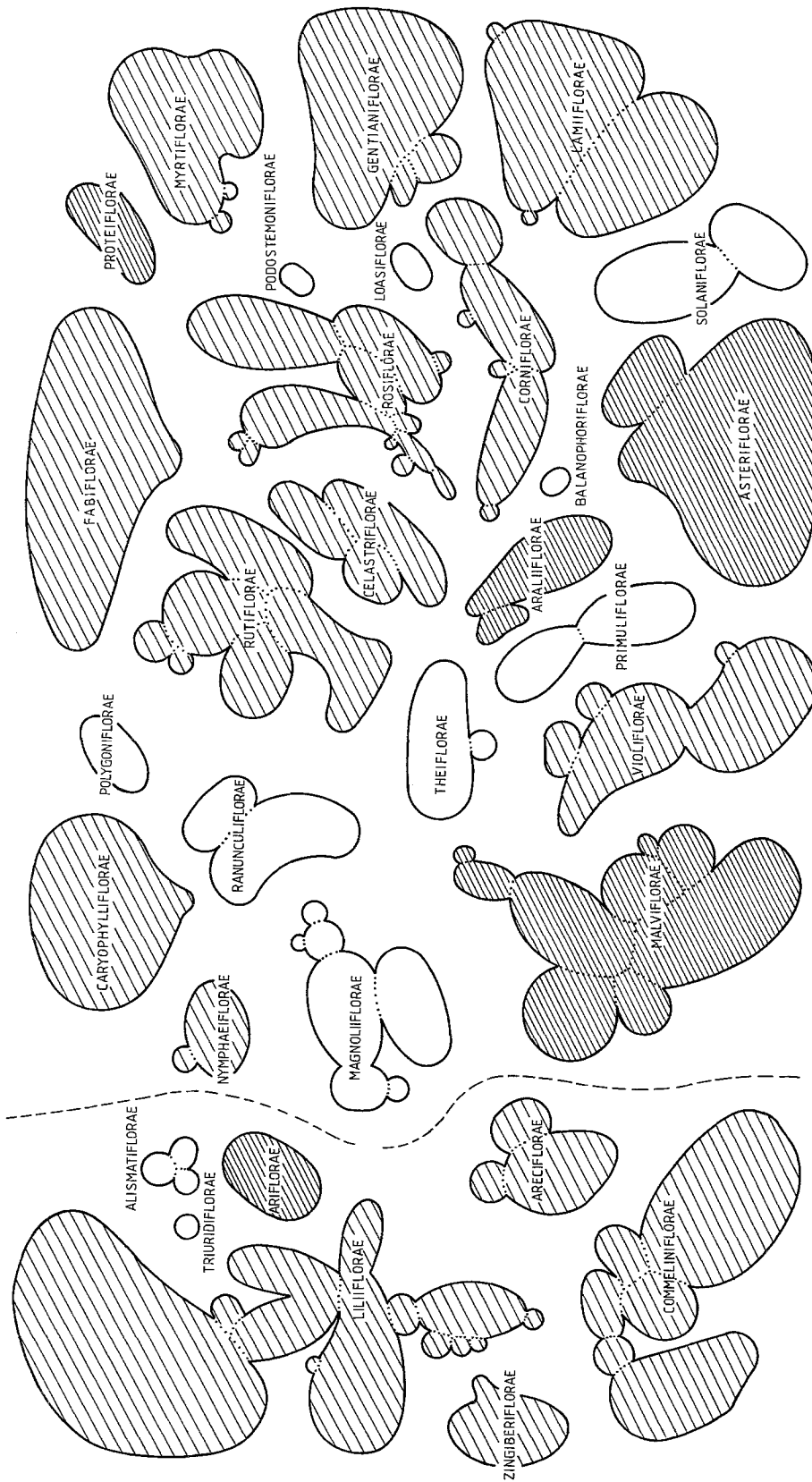


Fig. 2. Distribution of the genera with pseudanthia within the angiosperms (diagram according to DAHLGREN 1980). Tightly hatched: groups with more than 10 genera with pseudanthia

centre of stamens and carpels (Fig. 1 A). Within an inflorescence, the attractivity of the individual flowers gets reduced with the increase of aggregation. Lastly, the aggregated flowers form a new unit which we refer to as inflorescence-blossom or pseudanthium (Fig. 1 B).

It is well known that the formation of pseudanthia has occurred many times in evolution (cf. JOHOW 1884, GOOD 1956), and can be regarded as a general trend in angiosperm evolution (cf. LEPPIK 1969). The best known examples are the flower heads of the *Compositae*. The most important steps of the transformation are: (a) aggregation and inconspicuousness of the individual flowers, (b) floral differentiation and (c) integration of extrafloral bracts (TROLL 1928, GOEBEL 1931, GOOD 1956, FROEBE & ULRICH 1978, CLASSEN 1984).

The interpretation of the phenomenon itself, however, poses manifold problems. According to TROLL (1928), an immanent "Gestalttrieb" causes the formation of similar structures more or less independent of function. GOOD (1956) has noted that similar functions may result in similar forms, but he, too, does not equate analogy with adaptation. He supposes the aggregation to be the most important impulse for forming flowerlike inflorescences which are basically nothing but the passive results of a general aggregation tendency. In our days the interpretation of LEPPIK (1969) favouring the functional aspect, is widely accepted. He postulates that the flowerlike design of inflorescences is the result of a "pseudanthic recapitulation" which means the evolutionary repetition of a well-established pollination pattern.

All interpretations proposed so far are highly generalized. They do not sufficiently take into account that each taxon has its individual constraints and its individual evolutionary history. One has to be aware that different impulses may cause similar transformation within different taxonomic groups. Therefore, before turning to the question: Why have flowerlike inflorescences evolved? We first have to answer the following questions: What is the precise organization and design of the pseudanthia? What are the evolutionary steps within a special group? And: which potentialities and restrictions are inherent to a certain phylogenetic group?

The present paper refers to the first question. The wide morphological diversity of pseudanthia is illustrated by numerous examples. Little known pseudanthia are presented in more detail than well known ones. In view of the synoptical character of the present paper it is not necessary or possible to refer to all the material and literature in full detail. The relevant genera and their distribution within the angiosperms are represented in Table 1 and Fig. 2. The paper continues the work started by FROEBE & ULRICH (1978) and already carried out by the author (CLASSEN 1984–1988). Details of the individual modes of transformation will be the subject of a separate paper.

Material

The investigated plant material originates from the following sources:

Botanical Gardens: Aachen, Amsterdam, Berlin-Dahlem, Bochum Bogor, Bonn, Canberra, Cibodas, Hamburg, Kirstenbosch, Krefeld, Mainz, München, Perth, Pretoria, Singapore.

Herbaria: Berlin-Dahlem (B), Bogor (BO), Bruxelles (BR), Canberra (CANB), Cape Town (BOL, NBG), Leiden (L), München (M), Nairobi (EA), Paris (P), Perth (PERTH), Pretoria (PRE), Singapore (SING), Wien (W, WU).

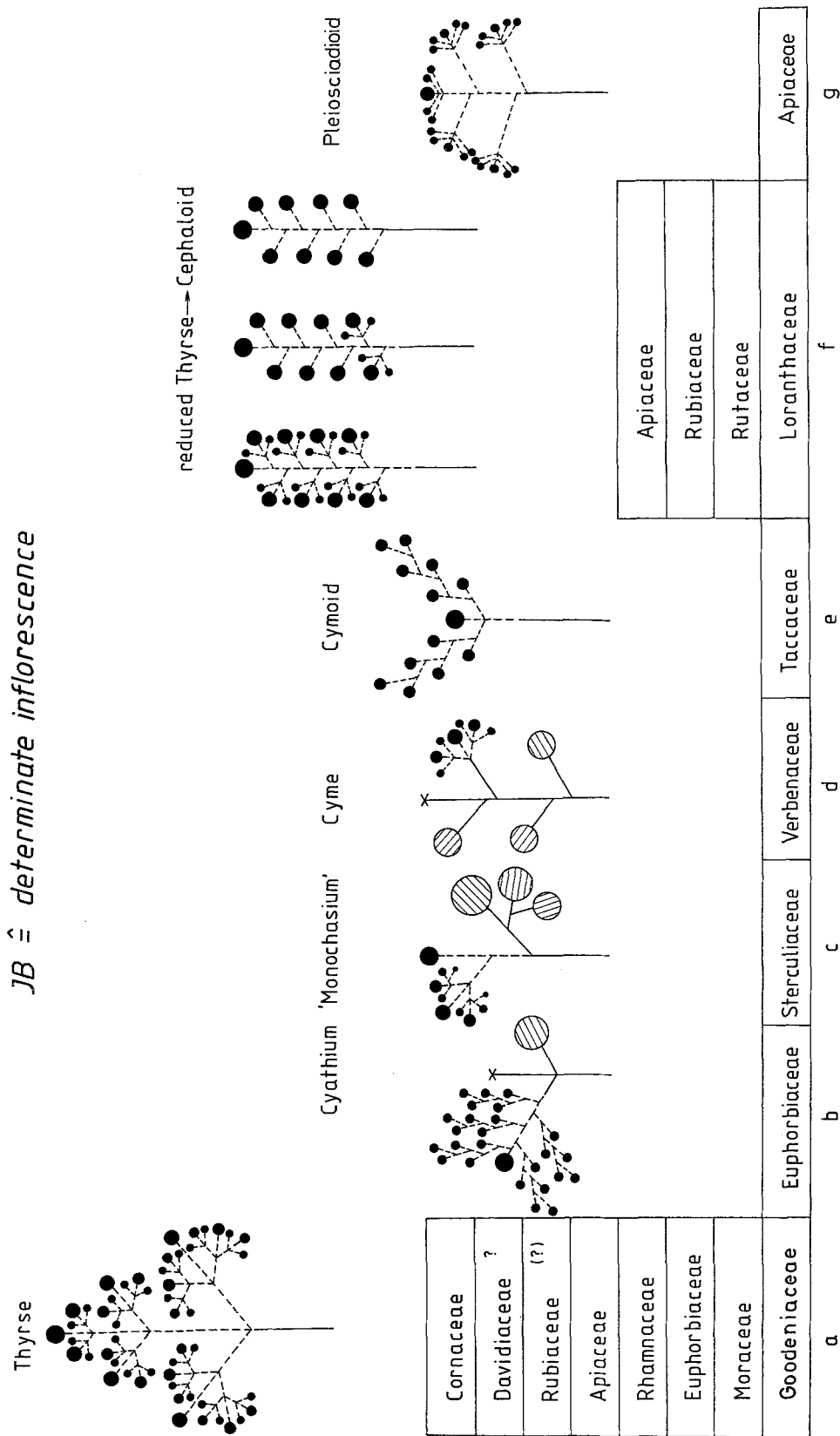


Fig. 3 a-g. Determinate inflorescences as structural basis for pseudanthia. ? Structure of the inflorescence not clear. JB inflorescence

I myself collected many species in SE. Asia, W. Australia, E. and S. Africa in the field. Voucher specimens are deposited in the Herbarium of the Botanical Institute of the Rheinisch-Westfälische Technische Hochschule Aachen (HAQ).

Pattern analysis

Determinate inflorescences (Fig. 3). According to Fig. 3 a there are several families with pseudanthia based on a more or less complex thyrse. The elements are branches (of different order), flowers and leaves/bracts. The internodes must remain extremely short to guarantee that the richly branched nature of the inflorescence is masked. This high degree of aggregation often causes a reduction of flower size. The individual flower becomes inconspicuous and the whole cluster of flowers then acts as a new individual unit.

In *Cephalanthus* and *Nauclea* (*Rubiaceae*), the globular pincushion-shaped pseudanthia exclusively result from the aggregation of very small, filiform flowers. The original inflorescence structure is completely masked and not recognizable any more.

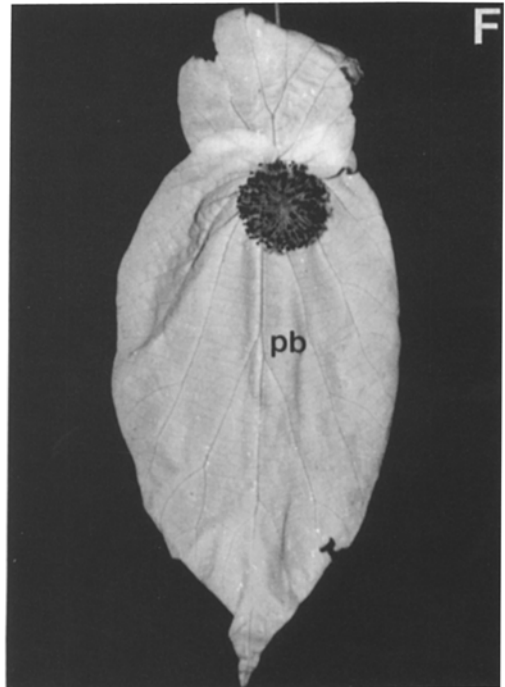
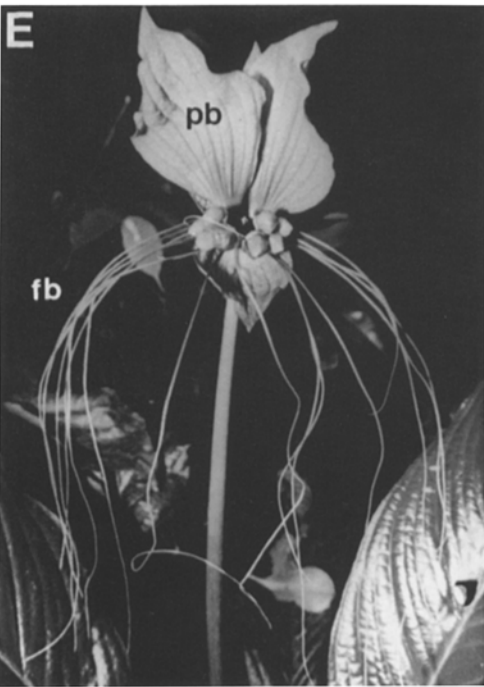
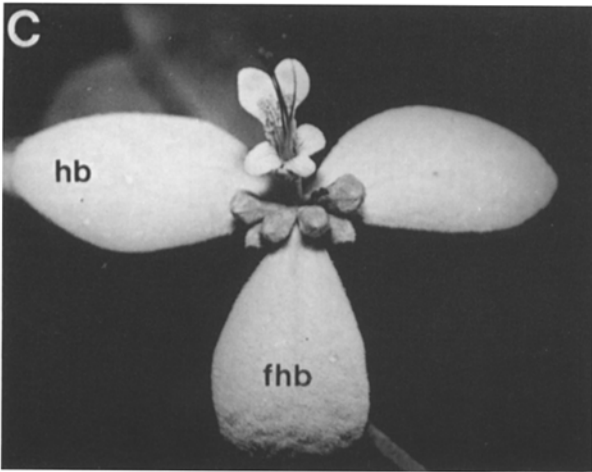
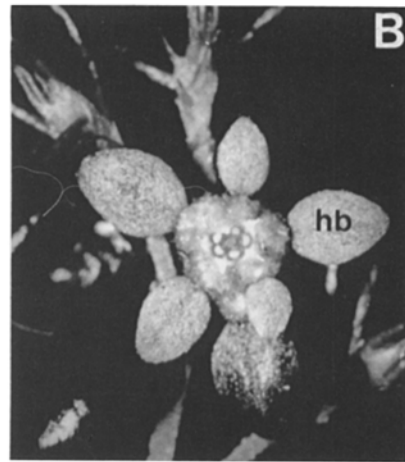
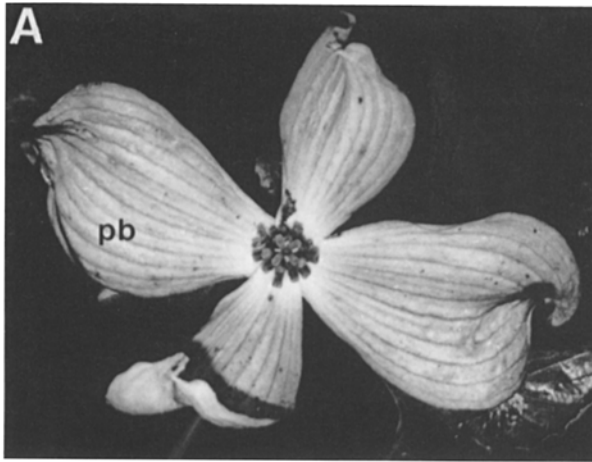
Besides aggregation and inconspicuousness of flowers, bracts within or below the inflorescence often have a great impact on the design of the inflorescence-blossom.

In *Spyridium* (*Rhamnaceae*; Fig. 4 B) – as well as in *Dorstenia* (*Moraceae*) and *Brunonia* (*Goodeniaceae*) – all flower-subtending bracts are arranged peripherally (Fig. 6 A', B', B"). This is a first step to subdivide an inflorescence into a "centre" and a "periphery". In some *Spyridium* spp., additionally, bract dimorphism occur. The proximal bracts subtending the partial-inflorescences are enlarged and covered with white hairs, thus forming a loose, irregular pseudocorolla (Figs. 4 B and 6 A, B).

In *Actinotus leucocephalus* (*Apiaceae*; Fig. 9 A), the Australian "flannel flower", the woolly pseudocorolla is composed of the proximal flower-subtending bracts of the thyrse (FROEBE 1979: 58 f). The white colour results from a dense film of dead hairs covering the adaxial side of the bracts. In comparison to *Spyridium*, a comparable bract dimorphism is lacking since the inner, distal bracts are totally suppressed. Furthermore, the pseudocorolla of *Actinotus* is quite regular because the bracts – though belonging to branches of different order – are integrated in size and shape.

In *Xanthosia* (Fig. 9 B), another Australian member of *Apiaceae*, the radial symmetry of the pseudanthium does not result from an equivalence of bracts, but from their dissimilarity. The pseudocorolla is not composed of the involucre but of 4 involucella. Though the involucellar bracts belong ontogenetically to the subunits of the inflorescence (FROEBE 1980: 225), they form a pseudocorolla at the rim of the whole "umbel" by unilateral development towards the periphery of the whole set. As Fig. 9 B illustrates the blossom of *X. tomentosa* is composed of one central and four axillary partial-inflorescences. Each of the marginal subunits is characterized by a monosymmetric triad of bracts (pmi). Hence, the radial symmetry of the pseudanthium as a whole is the result of the circular arrangement of these four zygomorphic subunits (comp. FROEBE & ULRICH 1978).

Fig. 4. Determinate thyrses as pseudanthia. A *Cornus florida* (*Cornaceae*; BG Aachen); B *Spyridium phyllicoides* (*Rhamnaceae*; FROEBE & CLASSEN 991, HAQ); C *Congea tomentosa* (*Verbenaceae*; CLASSEN 181, HAQ); D *Lasiopetalum discolor* (*Sterculiaceae*; FROEBE & CLASSEN 757, HAQ); E *Tacca integrifolia* (*Taccaceae*; CLASSEN 235, HAQ); F *Davidia involucrata* (*Davidiaceae*, Stadtgarten Krefeld). The showy elements are bracts. Note the bract fusion in C, the bract dimorphism in E and the three-lobed epicalyx elements in D. ee Epicalyx elements, fb filiform bract, fhb fused hairy bracts, hb hairy bract, pb petaloid bract



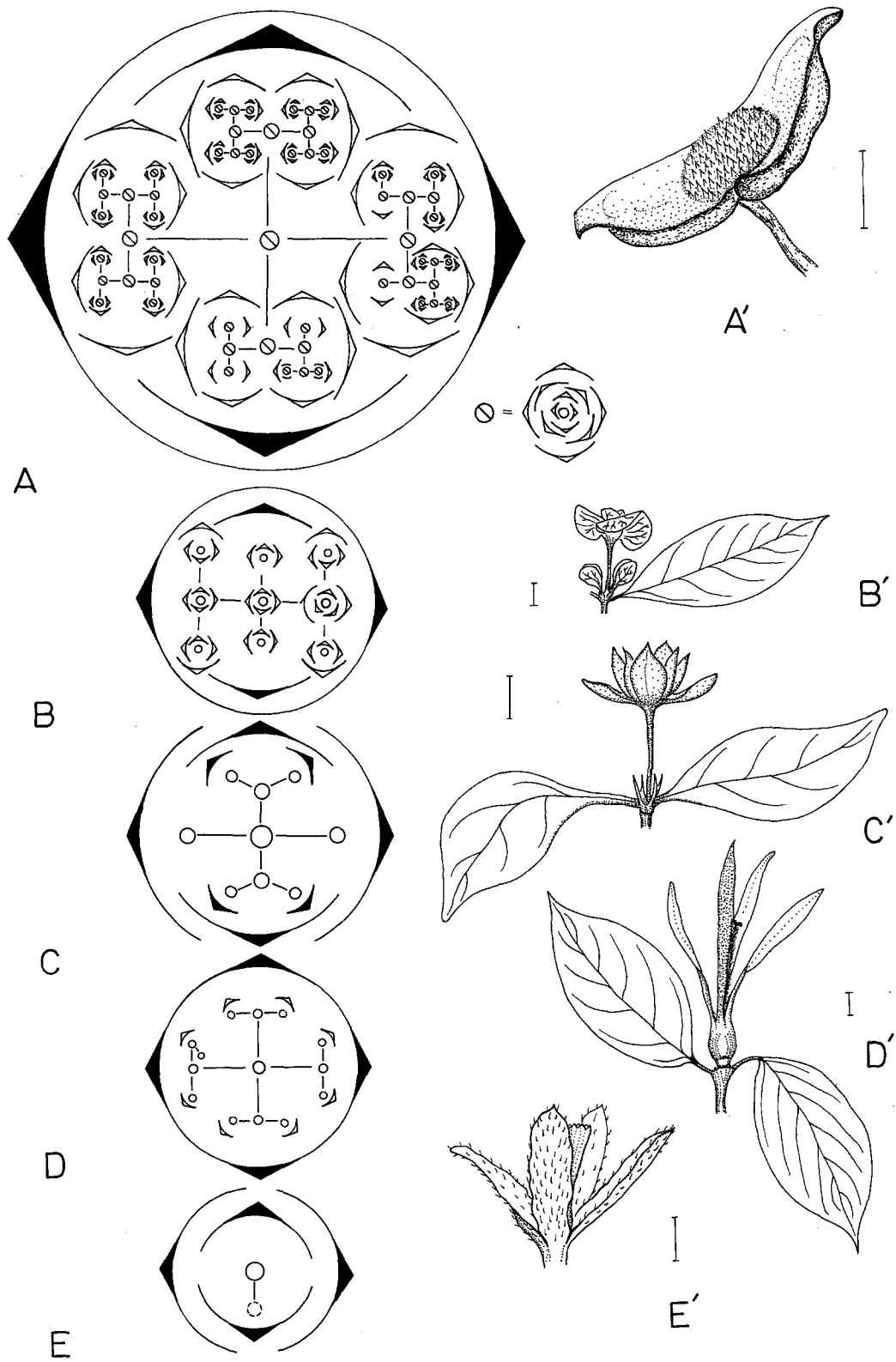


Fig. 5. Thyrses as pseudanthia within the genus *Cephaelis* (Rubiaceae). A, A' *C. tomentosa* (FOSBERG & FASSETT 21782, B); B, B' *C. elata* (ADAMS 5857, Mü); C, C' *C. salicifolia* (VOGL. 860, Mü); D, D' *C. aetantha* (MAGUIRE & FANSHAWE 32091, Mü); E, E' *C. potaroensis* (SANDWITH 1261, B). Bar: 1 cm

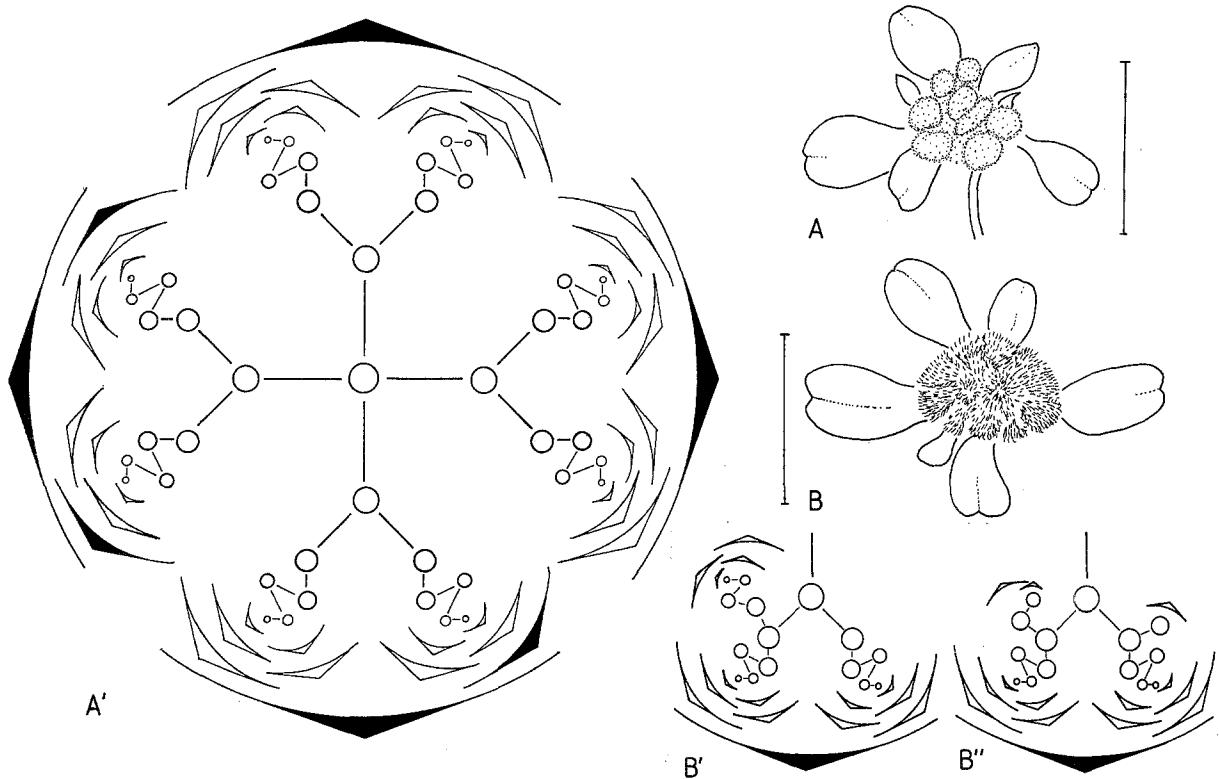


Fig. 6. Pseudanthia within the genus *Spyridium* (*Rhamnaceae*). A, A' *S. coactilifolium* (SCHODDE 327, B); B-B'' *S. halmaturinum* (SCHODDE 521, Mü; KASPIEW 1057, B). Note the peripheral position of the bracts. The black colour indicates the showy bracts. Bar: 0.5 cm

In *Cornus* (*Cornaceae*; Fig. 4 A) and *Davidia* (*Davidiaceae*; Fig. 4 F) the whitish colour of the showy bracts is caused by the total lack of chlorophyll. Most of the flower-like *Cornus* spp. have tetramerous pseudocorollas which directly result from decussation already present in the vegetative region of the plant (cf. JAHNKE 1986: 27–52). The pseudanthium of the “handkerchief-tree” *Davidia involucrata* (Fig. 4 F) is composed of a pincushion-shaped flower cluster and of two large flag-like bracts hanging down on long stalks. Density and reduction of the flowers has proceeded so far that the real nature of the inflorescence has not been identified even by ontogenetic studies (JAHNKE 1986: 103).

Coloured bracts – mainly pink, red and yellow – are present in the inflorescence-blossoms of *Dalechampia* (*Euphorbiaceae*) and *Cephaelis* (*Rubiaceae*).

In *Dalechampia spathulata* (Fig. 7 D) two showy leaves (prophylls α and β) surround a thyrses which is subdivided into a proximal female zone and a zygomorphic centre. Part of the centre (towards α) is male while the other part (towards β) is a bright yellow cushion (c) which allures perfume for euglossine bees (ARMBRUSTER & WEBSTER 1979). As MICHAELIS (1924) and recently FROEBE & al. (1983) have shown, this cushion is homologous to bracts.

In *Cephaelis* the flowers form head-like aggregates and are surrounded by two to eight coloured bracts (Fig. 5). Total flower number varies from one to many (Fig. 5 A–E). Starting from inflorescences with numerous sterile bracts (Fig. 5 A, B) a reduction tendency in flower and bract number is evident in *Cephaelis*. Similar reductions have been described

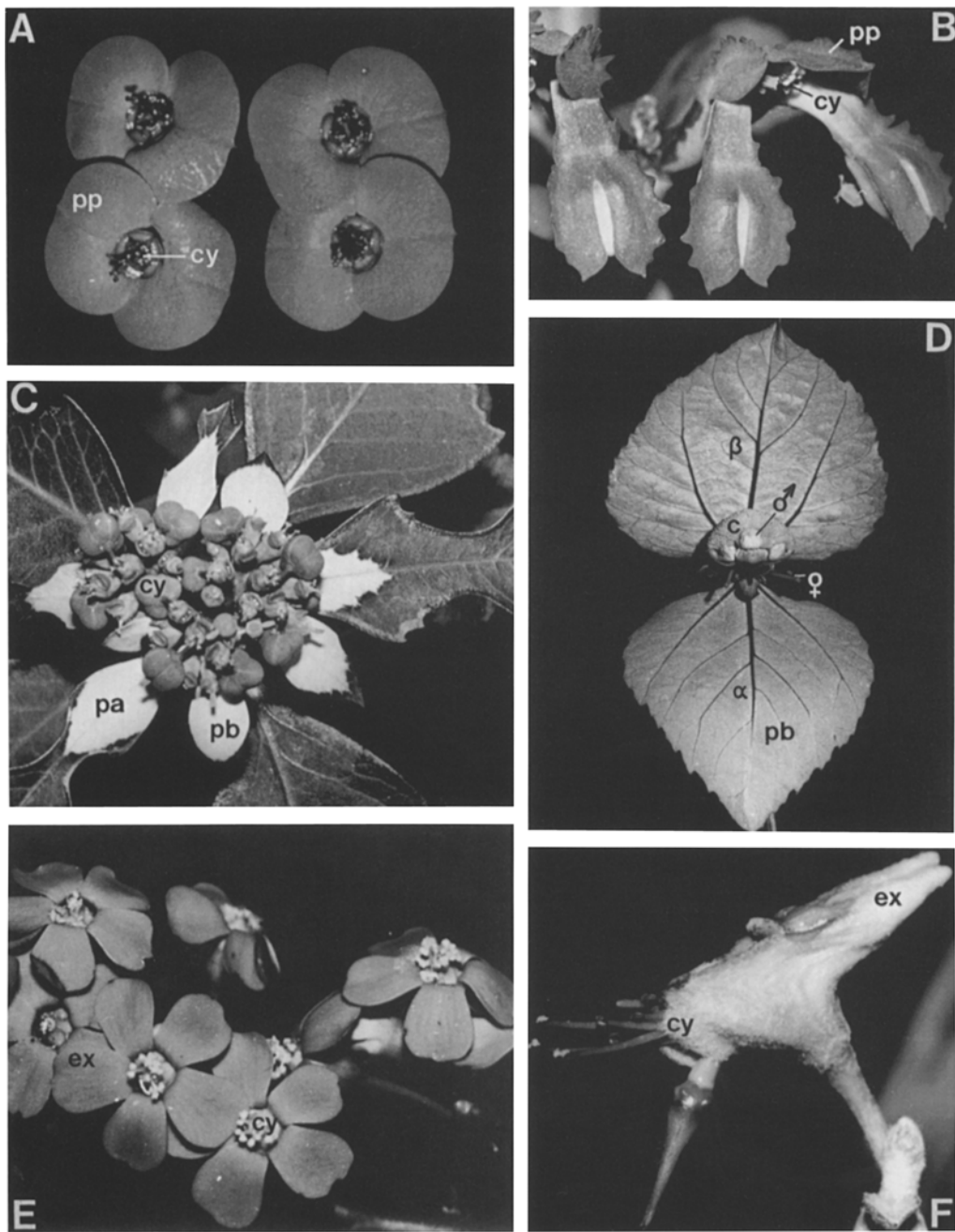


Fig. 7. Pseudanthia within the *Euphorbiaceae*. *A* *Euphorbia milii* (BG Aachen); *B* *Monadenium coccineum* (BG Berlin-Dahlem); *C* *Euphorbia heterophylla* (BG Pretoria; CLASSEN & FROEBE 1494, HAQ); *D* *Dalechampia spathulata* (BG Aachen); *E* *Euphorbia fulgens* (BG Aachen); *F* *Pedilanthus macrocarpus* (BG Aachen). The showy elements are prophylls (*A*, *B*), bracts (*C*, *D*), stipular excrescences (*E*, *F*); the inflorescence is a cyathium (*A*, *B*, *E*, *F*), a cluster of cyathia (*C*), a thyse (*D*). α , β Prophylls, c cushion, cy cyathium, ex excrescence, pa petaloid area on foliage leaf, pb petaloid bract, pp petaloid prophyll

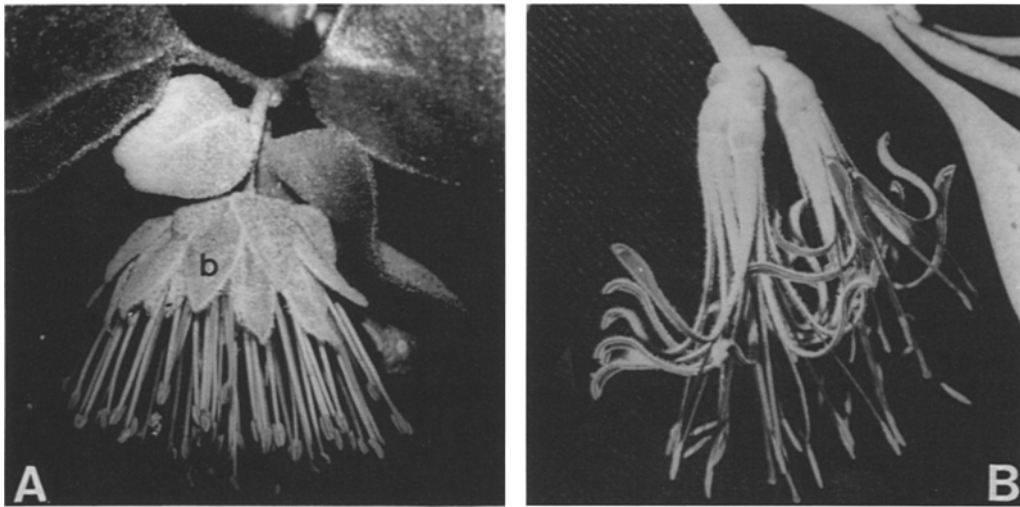


Fig. 8. Pseudanthia of *Diplolaena microcephala* (*Rutaceae*; FROEBE & CLASSEN 646, HAQ) (A) and *Amyema nestor* (*Loranthaceae*; CLASSEN 1054, HAQ) (B). b Coloured bract

for other genera of *Rubiaceae* (WEBERLING 1977). Reduction seems to be a general trend in the family and may be regarded as a suitable predisposition for forming inflorescence-blossoms. In contrast to the pseudanthia described above, in *Cephaelis aetantha* a remarkable improvement takes place: the bracts are fused, looking like petals of a sympetalous corolla (Fig. 5D, D').

As a special type of a thyrses the cyathium (Fig. 3b) occurs exclusively within the *Euphorbiaceae-Euphorbieae*. It is morphologically characterized by the flowerlike arrangement of the unisexual flowers which can be regarded as extreme reductions of pentamerous hermaphroditic flowers (MICHAELIS 1924). The following examples demonstrate that the showy elements of the cyathium are variable:

In *Euphorbia milii* (Fig. 7A) and *Monadenium coccineum* (Fig. 7B) the two prophylls are coloured forming a deep red pseudocorolla.

In *Euphorbia pulcherrima* a cluster of cyathia is surrounded by large red leaves which, in size and shape, are similar to the foliage leaves of the plant.

In *Euphorbia heterophylla* (Fig. 7C), a further step towards symmetry is realized. The pseudocorolla is regular though the distal leaves are of different size. The different size is compensated by a gradation of colour: the smallest bracts are completely red, while the larger leaves are frondose at the top and coloured at the base. The red areas (pa) have the same size as the red bracts (pb), thus imitating them and together with them forming the regular pseudocorolla.

In *Euphorbia fulgens* (Fig. 7E), a completely different mode of forming an attractive pseudocorolla is realized. The red elements are not leaves, but stipular excrescences (HOPPE & UHLARZ 1982).

In *Pedilanthus* (Fig. 7F), the zygomorphic, ornithophilous pseudanthia can be derived from the radial pattern of *E. fulgens* by fusion, monosymmetrical growth and tubular development of the bracts and excrescences (DRESSLER 1957, HOPPE 1985).

Inflorescences formed by the terminal flower and one paracladium (Fig. 3c) are characteristic of the Australian genus *Lasiopetalum* (*Sterculiaceae*).

In *Lasiopetalum discolor* (Fig. 4D), the inflorescence is transformed into a composite-like blossom (CLASSEN 1988). The white pseudocorolla is composed of epicalyces consisting

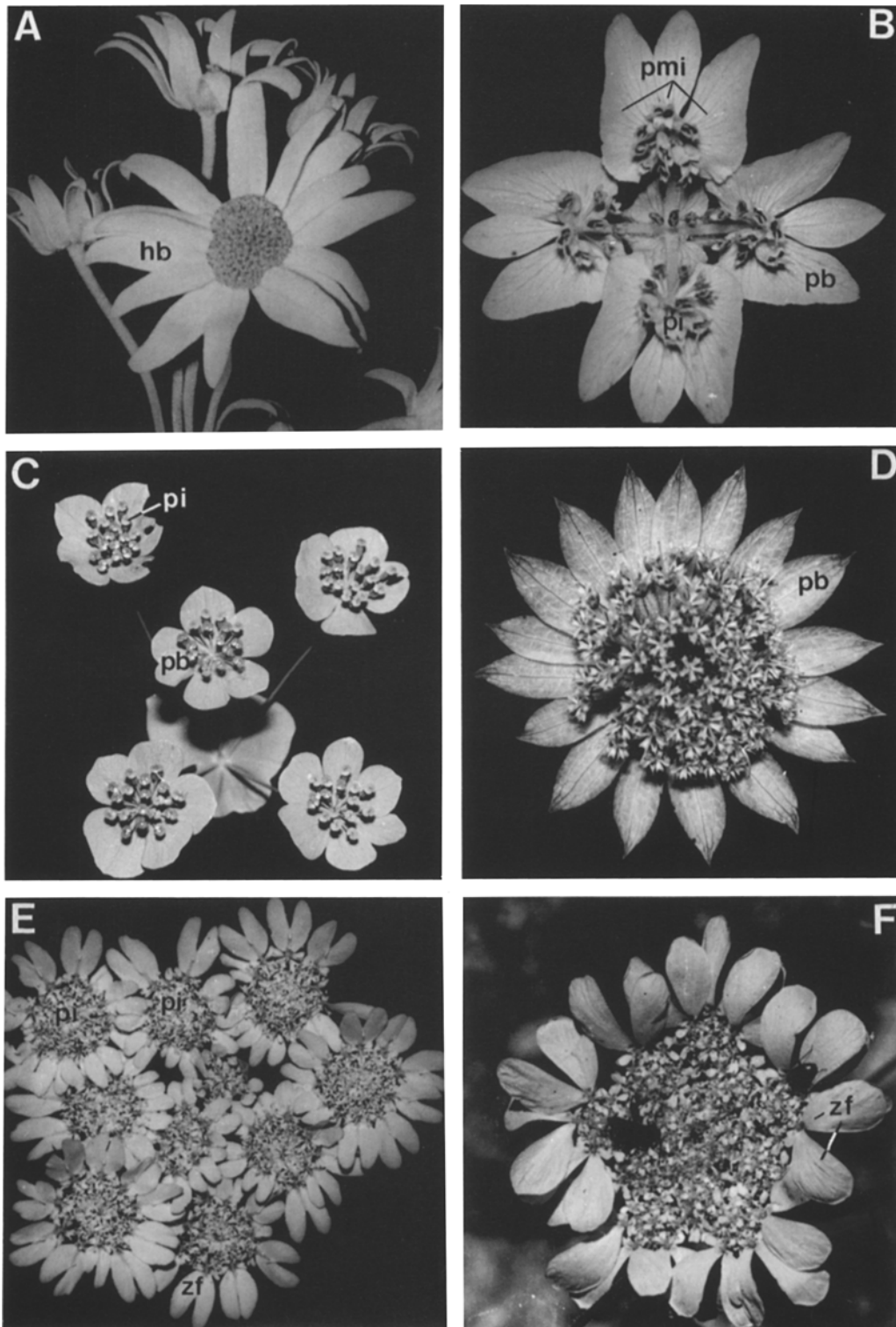


Fig. 9. Pseudanthia within the *Apiaceae*. *A* *Actinotus leucocephalus* (CLASSEN 1062, HAQ); *B* *Xanthosia tomentosa* (FROEBE & CLASSEN 405, HAQ); *C* *Bupleurum aureum* (BG Mainz); *D* *Astrantia minor* (BG Aachen); *E* *Lisaea strigosa* (CLASSEN 1730, HAQ); *F* *Tordylium officinale* (CLASSEN 1702, HAQ). The showy elements are involucral bracts (*A*, *D*), involucellar bracts (*B*, *C*), zygomorphic flowers (*E*, *F*); the inflorescence is a thyrse (*A*, *B*), a sciadioid (*C*, *E*), a pleiosciadioid (*D*, *F*). hb Hairy bract, pb petaloid bract, pi partial inflorescence, pmi petaloid monosymmetric involucrellum, zf zygomorphic flower

of three elements (ee). The segments are densely covered with hairs. The radial arrangement and the trimerous structure indicate that the epicalyces are homologous to bistipulate bracts.

Determinate partial-inflorescences (cymes) of an indeterminate thyrse form pseudanthia within the *Symphoremoideae* (*Verbenaceae*) (Fig. 3 d).

In *Sphenodesme* and *Symphorema* the inflorescence-blossoms are hexamerous, in *Congea*, they are tetra- and trimerous. The showy elements are white or pink, hairy during anthesis and papery when dispersing the diaspores. They correspond to the flower subtending bracts. The hexamerous and tetramerous pseudocorollas result directly from the branching pattern of the cymes which is dichasial in *Sphenodesme* and *Symphorema* (2 bracts of 1st order, 4 bracts of 2nd order) and partly dichasial in *Congea* (2 bracts of 1st order, 2 bracts of 2nd order). Some *Congea* spp. are characterized by trimerous pseudocorollas which are, however, of different origin: in *C. connata* one of the bracts of 2nd order is inhibited and only three bracts are well-developed. In *C. tomentosa* both bracts of 2nd order develop, but they are congenitally fused and thus imitate a single bract in the adult state (Fig. 4 C, fhs; CLASSEN 1986).

A cymoid (Fig. 3 e) is the structural basis for the pseudanthia of the *Taccaceae*.

In *Tacca integrifolia* (Fig. 4 E) the peculiar form is caused by a bract dimorphism: the first prophylls are large, white and erect (pb) while all the consecutive bracts are filiform, brownish and pendulous (fb; cf. KAUSMANN 1951, DRENTH 1972).

As Fig. 3 f illustrates pseudanthia may be also based on highly reduced inflorescences or even sciadioids or cephaloids (*Cephaelis*, *Rubiaceae*: Fig. 5; *Amyema*, *Loranthaceae*: Fig. 8 B).

In *Diplolaena* (*Rutaceae*, Fig. 8 A) ontogenetic studies have revealed that the dense head-like flower aggregate is a reduced panicle/thyrse (CLASSEN-BOCKHOFF & al. 1990).

In the *Apiaceae*, the pleiosciadioid (Fig. 3 g) is the characteristic inflorescence. Within the family, however, there is an enormous variability in both the organization of the inflorescence and the elements of the pseudocorolla (cf. FROEBE & ULRICH 1978).

In *Alepidea*, *Hacquetia*, *Astrantia*, and other *Apiaceae-Saniculoideae*, the pseudanthia are formed by highly condensed and reduced pleiosciadioids (Fig. 9 D; FROEBE 1964). The petaloid elements are involucre bracts.

In *Bupleurum*, a member of the *Apiaceae-Apioideae*, the sciadioids of the pleiosciadioid form separate pseudanthia (Fig. 9 C). The showy elements are involucellar bracts.

In *Lisaea strigosa* (Fig. 9 E) and *Tordylium officinale* (Fig. 9 F), the pseudocorollas consist of floral elements (petals). Floral dimorphism often occurs in *Apiaceae-Apioideae* (cf., FROEBE 1980), but only a few species have inflorescences with floral dimorphism and with dense flower aggregation. Such pseudanthia occur both on the level of a sciadioid (*Lisaea*) and of a pleiosciadioid (*Tordylium*).

Indeterminate inflorescences (Fig. 10). According to the morphological concepts of TROLL (1964), WEBERLING (1981), MARESQUELLE (1970), and SELL (1976), indeterminate inflorescences originate from determinate inflorescences by truncation. This process is often combined with disjunction and homogenization. An inflorescence of originally conjunct construction thus develops as a disjunct system of homogeneous partial-inflorescences. The subunits become more or less separated from each other and appear as individual units. Thus, on a high level of generalization, indeterminate inflorescence tend to form pseudanthia on the base of their partial-inflorescences.

Figure 10 demonstrates this tendency: there are only few taxa which form inflorescence-blossoms on the base of an indeterminate thyrse (Fig. 10 a, b). Examples occur within the *Liliales*, *Apiaceae-Hydrocotyloideae* (FROEBE 1979), and

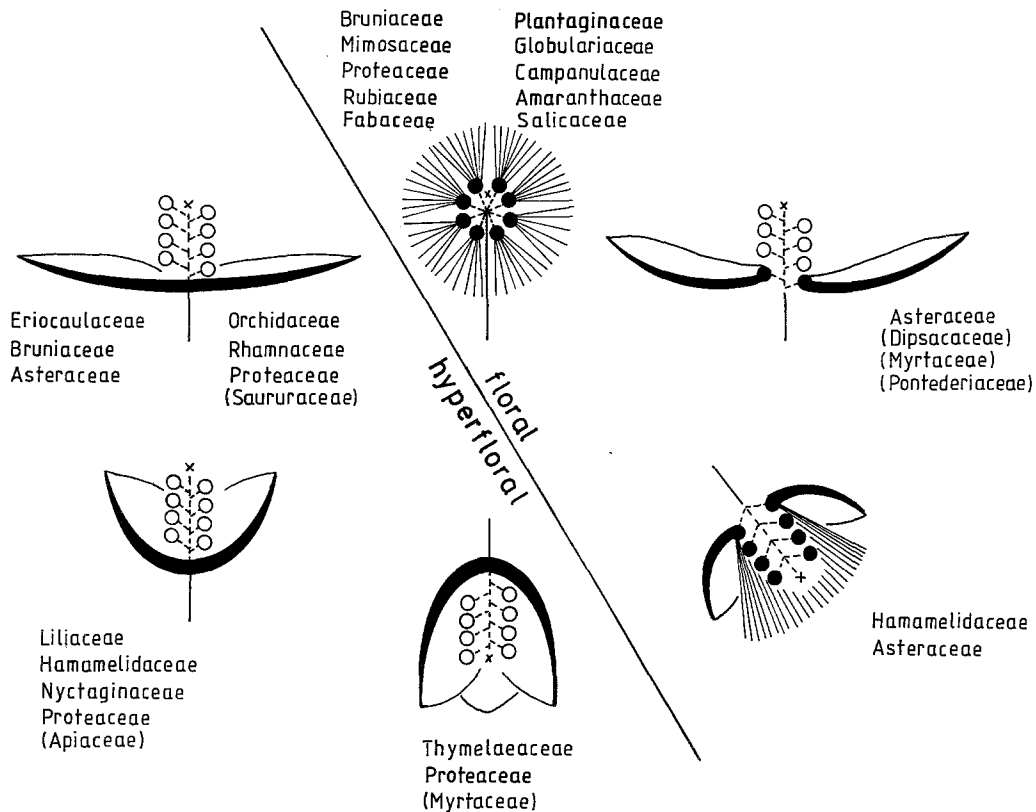


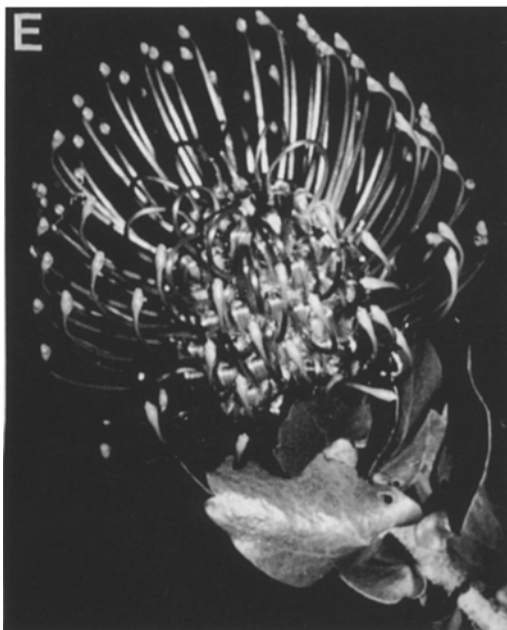
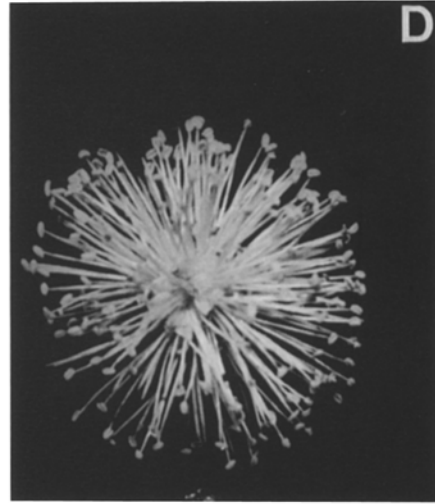
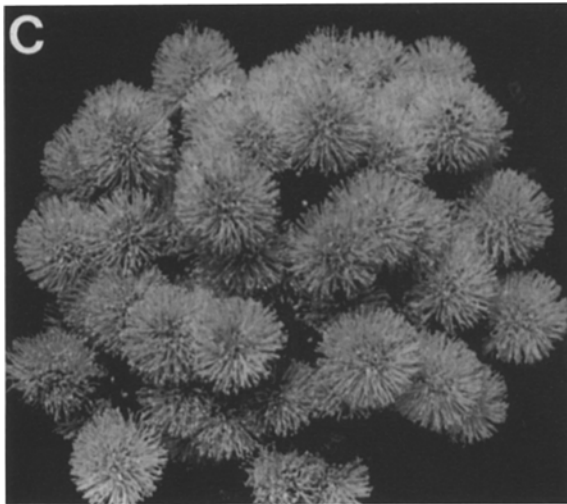
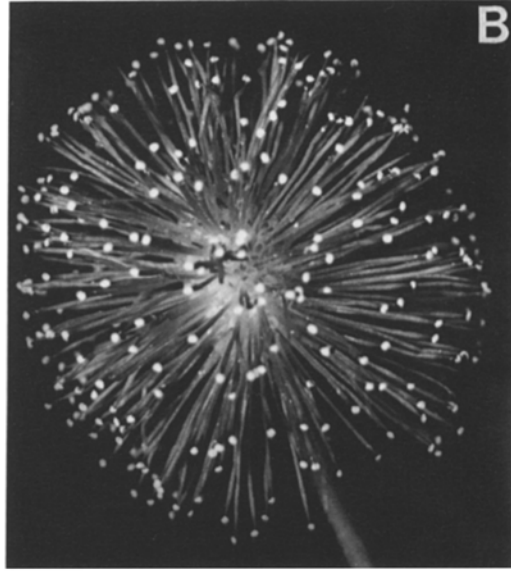
Fig. 11. Cephalia as blossoms. Schematic summary of the different forms realized within this group. The pseudanthia are composed exclusively of flowers (“floral”) or of flowers and extrafloral bracts (“hyperfloral”); the parenthesis indicates that the underlying inflorescence is not a cephalium s.str., but another simple inflorescence (Fig. 10 b β – d); solid black: showy elements

probably within the *Cunoniaceae* (unpubl.) (Fig. 12 D), *Dasypogonaceae*, and *Cyclanthaceae* (HARLING 1946).

In *Nicolaia elatior* (*Zingiberaceae*) only some axillary buds show that the “simple” head is not as simple as it looks like (KUNZE 1985). The special construction of the pseudanthium enables bird pollination: the sterile top of the massive “head” offers a place for landing and perching, while the main axis of the inflorescence elongates to the same extent as the flowers start to open. Thus, the distance between the bill of the bird and the nectar in the flower remains constant (cf. CLASSEN 1987).

The cephalium is the type of the indeterminate inflorescences from which pseudanthia have most frequently developed (Fig. 10). If we put together all comparable systems (spadix, spica etc.; Fig. 10 b – e) it is evident that about 50% of all families with pseudanthia form pseudanthia on the base of simple indeterminate inflorescences (cf. Fig. 21).

An overview of the huge variety of forms realized within this group is given in Fig. 11: pincushions (Fig. 12 B, C, E, F), discs (Figs. 13 A, D, and 16 A – C), bowls (Fig. 16 D), bells (Fig. 16 F), monosymmetric (Figs. 13 B and 16 E) and individual forms (Figs. 13 C, E, and 15 A – C). The main elements are flowers and parts of flowers (Fig. 11, floral) or showy bracts (Fig. 11, hyperfloral). Within the pincush-



ions, which are not differentiated into a centre and a pseudocorolla, floral structures predominate: mainly long stamina (Fig. 12 A – D), but also styles (Fig. 12 E), needle-like petals or thin petals with long hairs (Fig. 12 F).

The habit of the differentiated pseudanthia depends on the form of the pseudocorolla which is composed of (a) flowers (“floral”) or (b) extrafloral bracts (“hyperfloral”).

a) Floral pseudocorollas. Differentiated pseudanthia not always result from flower dimorphism, but also from a special arrangement and flowering sequence of exclusively zygomorphic flowers.

In the *Proteaceae*, buds and open flowers look so different that the pseudanthium appears differentiated into a centre and a pseudocorolla (cf. *Leucadendron reflexum*, Fig. 13 E).

In the *Asteraceae-Cichorioideae*, the circular arrangement of exclusively ligulate flowers results in the well known dandelion pattern. The more the total amount of flowers is reduced – esp. if there is only one circle of ligulate flowers (*Mycelis muralis*, *Prenanthes purpurea*, etc.) – the more the pseudanthium resembles a single flower.

In *Rhodoleia championi*, which constitutes a monotypic subfamily within the *Hamelidaceae* (cf. PORSCH 1923, DOCTERS VAN LEEUWEN 1927, ENDRESS 1977), numerous cephalia are arranged in a globular cluster (Fig. 13 C). Each cephalium is composed of 5 – 10 zygomorphic flowers arranged in a circle. Each flower contains 2 – 3 well-developed petals which are oriented towards the periphery of the whole inflorescence. They form altogether a floral pseudocorolla (Fig. 14 A). The stamens of all flowers together form a “polyandric” centre which masks totally the real number of flowers.

Structural flower dimorphism is always combined with functional differentiation: some flowers operate as sexual elements, the others as attraction structures.

In some *Dipsacaceae* (Fig. 13 D) and in many *Asteraceae-Asteroideae* (Fig. 1 B), the pseudocorolla is composed of zygomorphic flowers the ensemble of which surround a dense field of small tubular flowers. TROLL (1928) has shown in detail how far the synorganization of the participating flowers may go and which steps of modification cause the surprising similarity between the pseudanthia of the *Compositae* and flowers of certain *Ranunculaceae* or *Mesembryanthemaceae*.

In *Actinodium cunninghamii* (Fig. 13 A), the inflorescence looks like a daisy. However, this Australian plant belongs to the *Myrtaceae*. It is formed by a sciadium (Fig. 10b β) (BRIGGS & JOHNSON 1979: 201). All flowers are stalked, tubular and have two prophylls. The marginal flowers are sterile and characterized by enlarged and purely white sepals and petals. The showiness of the marginal flowers, is additionally increased by the two prophylls which are also white and enlarged.

The sterile flowers of a florally differentiated pseudanthium most often act as showy elements. However, as the *Mimosaceae* show, they can also function as nectar cups or odorous flowers.

In *Calliandra surinamensis* (Fig. 15 B) the central flowers are sterile. Their filament tubes are much larger than in the marginal flowers and are capable of storing nectar.

Fig. 12. Pincushion-shaped blossoms of different morphological nature. *A* *Neviusia alabamensis* (*Rosaceae*, BG Amsterdam); *B* *Mimosa pudica* (*Mimosaceae*, BG Aachen); *C* *Berzelia intermedia* (*Bruniaceae*; CLASSEN & FROEBE 1381, HAQ); *D* *Callicoma serratifolia* (*Cunoniaceae*; CLASSEN 129, HAQ), *E* *Leucospermum cordifolium* (*Proteaceae*, BG Kirstenbosch); *F* *Ptilotus* spec. (*Amaranthaceae*; FROEBE & CLASSEN 723, HAQ). The organization is a flower (*A*), a cephalium (*B*, *C*, *E*, *F*), a reduced thyrse (*D*); the showy elements are stamina (*A* – *D*), styles (*E*), hairy petals (*F*)

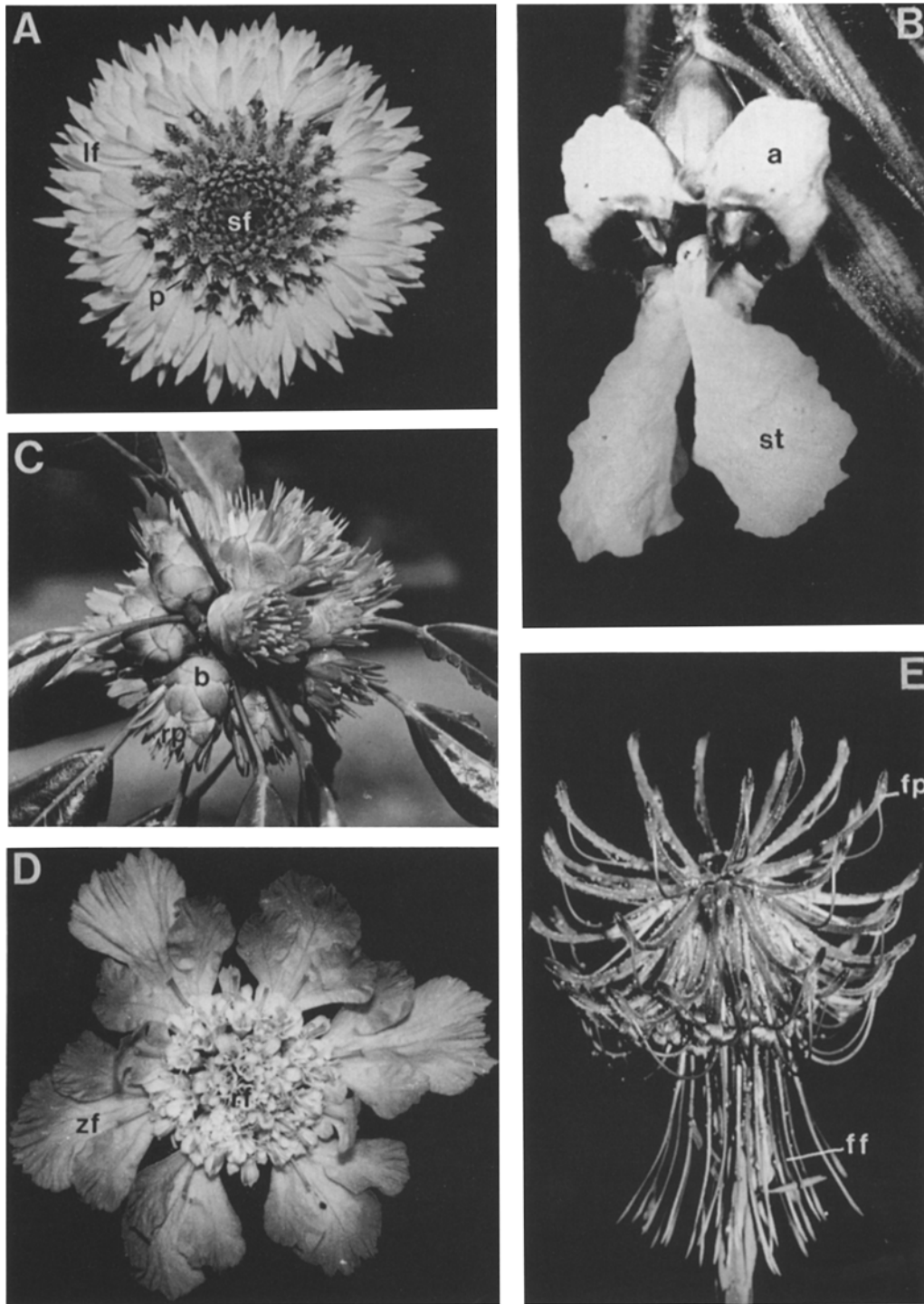


Fig. 13. Simple indeterminate inflorescences as floral differentiated pseudanthia. *A* *Actinodium cunninghamii* (Myrtaceae; FROEBE & CLASSEN 810, HAQ); *B* *Thalia geniculata* (Marantaceae; CLASSEN 146, HAQ); *C* *Rhodoleia championi* (Hamamelidaceae; CLASSEN 128, HAQ); *D* *Scabiosa caucasica* (Dipsacaceae, BG Mainz); *E* *Leucospermum reflexum* (Proteaceae, BG Kirstenbosch). In *A* and *D* the floral pseudocorolla is formed by a true flower dimorphism, in *B*, *C*, and *E* it is the special arrangement of zygomorphic resp. asymmetric flowers causing floral subdivision. Note that the showy elements in *B* are exclusively staminodes. a Appendage of the callose staminode, b bract, ff flower (floral stage), fp flower (prefloral stage), lf large marginal flowers, p prophyll, rf radial flowers, rp red petals, sf small central flowers, st outer staminode, zf zygomorphic flower

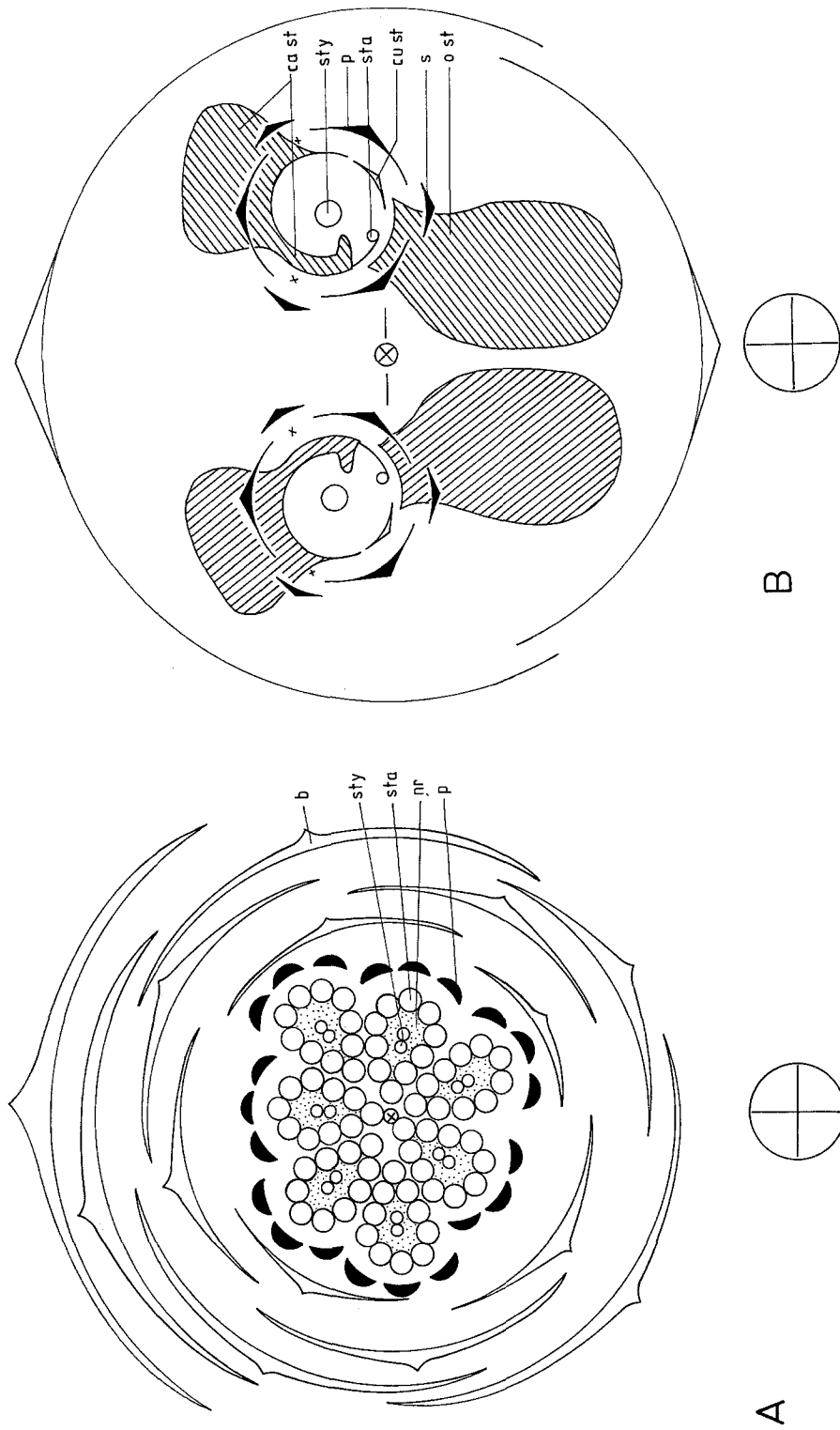


Fig. 14. Diagrams of the pseudanthia of *Rhodoleia championi* (*Hamamelidaceae*; CLASSEN 128, HAQ) (A) and *Thalia geniculata* (*Marantaceae*; CLASSEN 146, HAQ) (B). b Bract, ca st callose staminode, cu st cucullate staminode, nr nectar reservoir, o st outer staminode, p petal, s sepal, sta stamen, sty style. Solid black (A)/hatching (B): showy elements

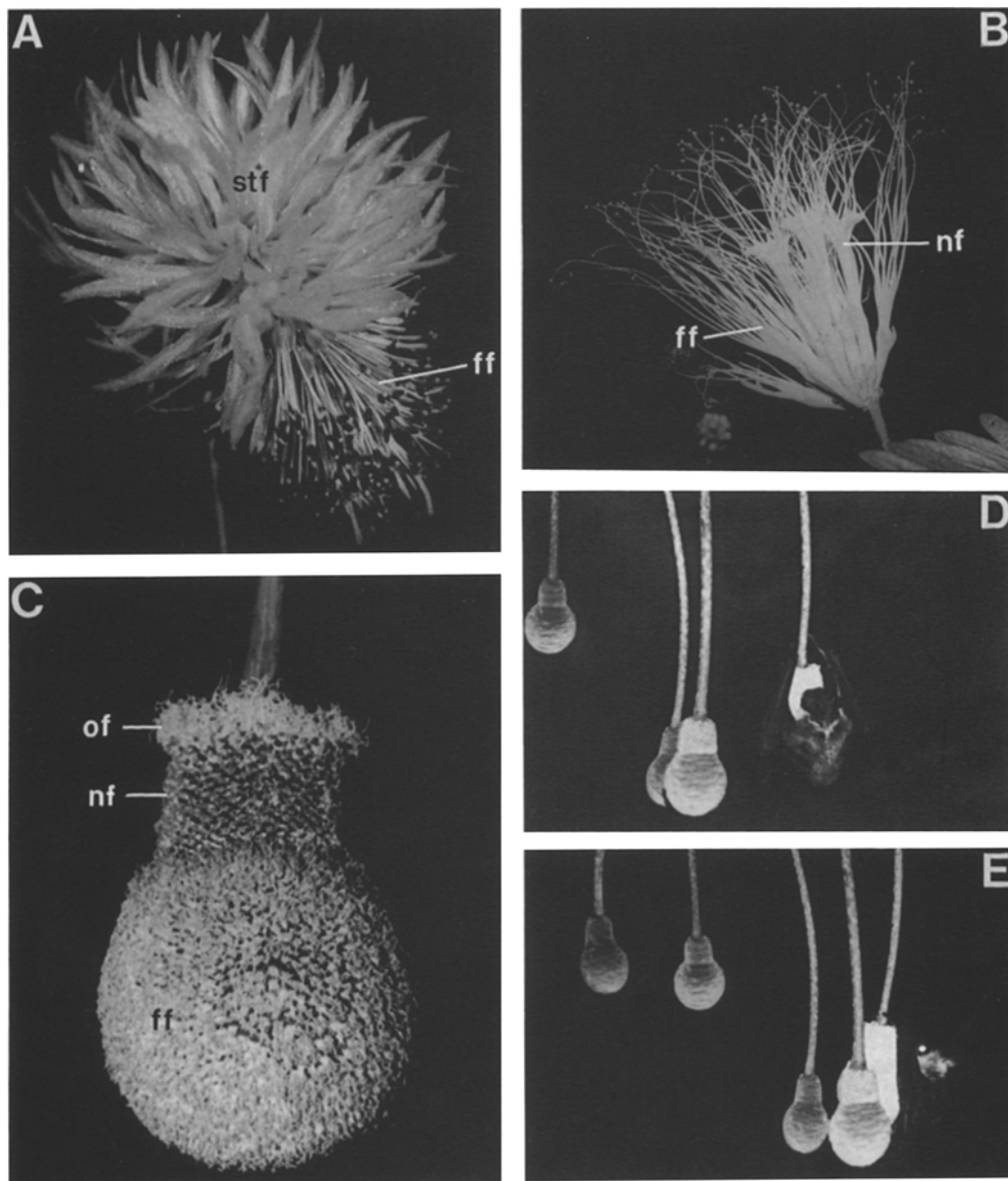
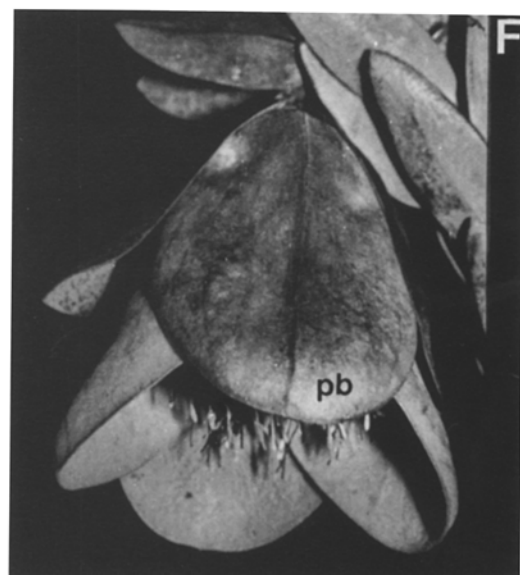
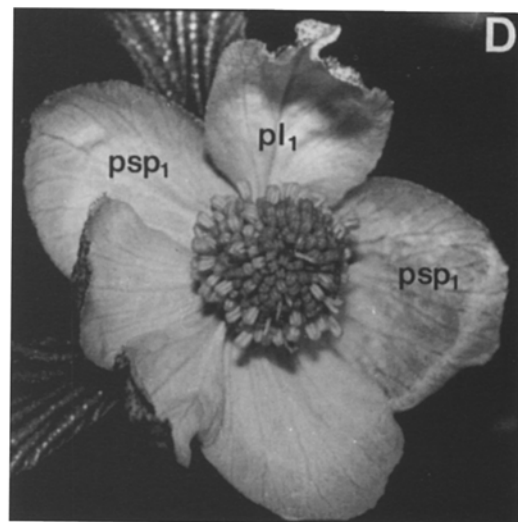
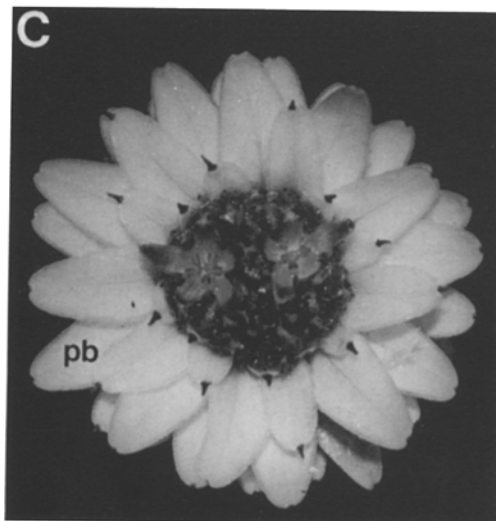
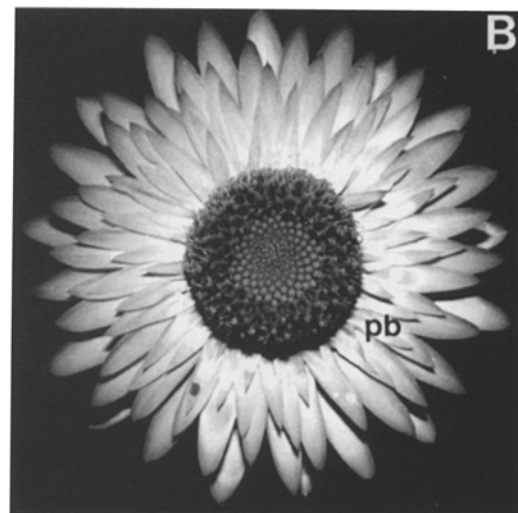
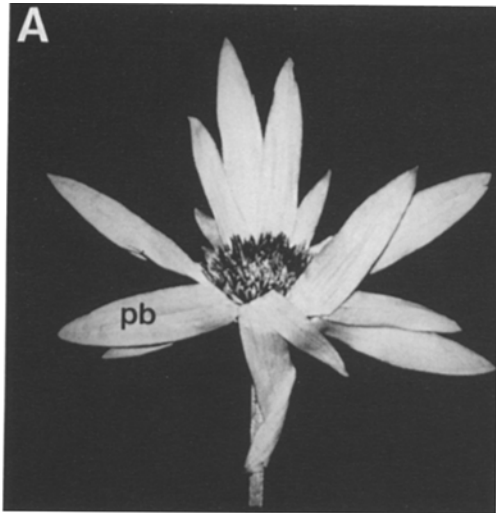


Fig. 15. The different types of flower dimorphism within the pseudanthia of the *Mimosaceae*. *A* *Neptunia plena* (CLASSEN 113, HAQ); *B* *Calliandra surinamensis* (CLASSEN 63, HAQ); *C–E* *Parkia* cf. *javanica* (CLASSEN 193, HAQ) – in *D* and *E* visited by *Eonycteris spelaea*. ff fertile flower, nf nectariferous flower, of odourous flower, stf staminodial flower

Fig. 16. Cephalia as pseudanthia with extrafloral pseudocorollas. *A* *Mesanthemum prescottianum* (*Eriocaulaceae*; SCHNELL 1828, W); *B* *Helichrysum bracteatum* (*Asteraceae*, BG Aachen); *C* *Staavia dodii* (*Bruniaceae*; CLASSEN & FROEBE 1321, HAQ); *D* *Parrotiopsis jacquemontiana* (*Hamamelidaceae*, BG Mainz); *E* *Mimetes hirta* (*Proteaceae*, BG Kirstenbosch); *F* *Pimelea physodes* (*Thymelaeaceae*; FROEBE & CLASSEN 808, HAQ). Note the two bistipulate bracts in *D*. pb Petaloid bract, pl petaloid lamina, psp petaloid stipule



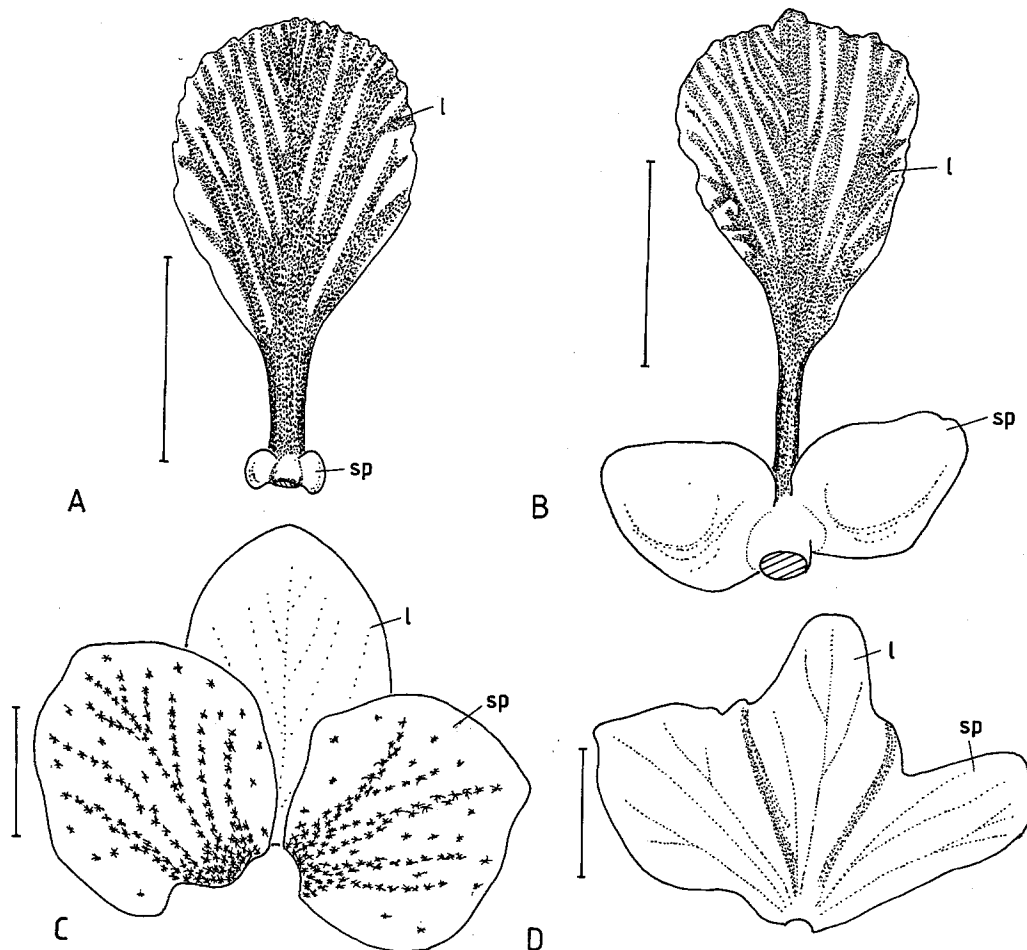


Fig. 17. Leaf-metamorphosis of *Parrotiopsis jacquemontiana* (Hamamelidaceae, BG Mainz). A frondose leaf, B single transitional leaf of foliage character, C, D showy three-lobed bracts. l Lamina, sp stipule. Bar: 1 cm

In *Neptunia plena* (Fig. 15 A) the proximal flowers are sterile. They have flat staminodes instead of fertile stamens. Besides their bright yellow colour the staminodes are attractive for insects because of their intensive, sweet odour.

In *Parkia*, there are three kinds of flowers (Fig. 15 C) odorous (of), nectar-producing (nf), and fertile flowers (ff). As VOGEL (1968) has pointed out, the sequential arrangement of the three flower types is directly connected with the process of pollination: the scent allures bats which cling to the pincushion-like heads and are powdered with pollen while lapping up the nectar from the top (Fig. 15 C–E).

b) Extrafloral pseudocorollas. Extrafloral pseudocorollas are composed of bracts. Quite often phyllotaxis remains unchanged and then transitional organs may be present. However, if leaf metamorphosis changes abruptly and if the showy bracts differ distinctly from the frondose leaves, both the inflorescence and the bracts form a functional unit separate from the vegetative part of the plant.

The present studies (Fig. 10 b β –d) show that extrafloral pseudocorollas are common (cf. Fig. 11) exhibiting surprising similarities among pseudanthia of dif-

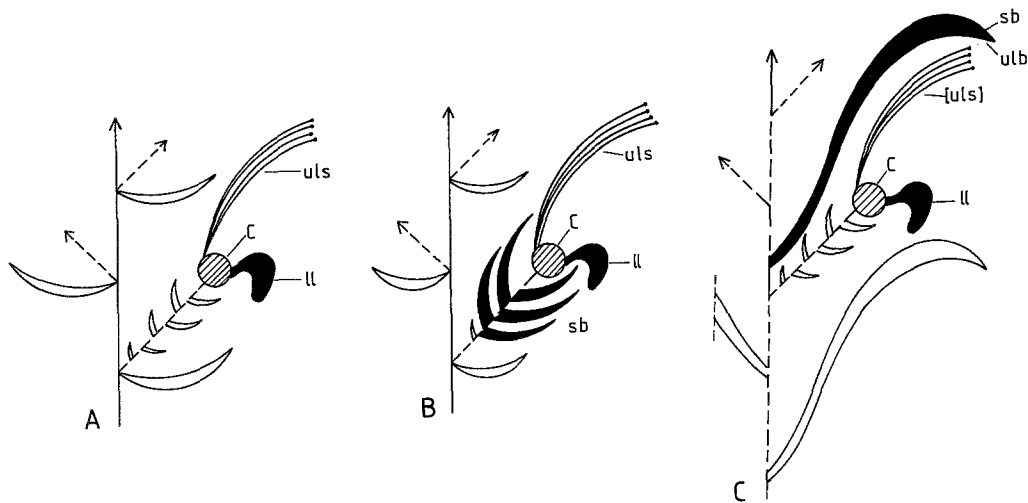


Fig. 18. The different forms of pseudanthia within the genus *Mimetes* (*Proteaceae*), schematically. A *M. hottentottica* (ROUSSEAU 1976); B *M. hirta* (BG Kirstenbosch); C *M. cucullata* (BG Kirstenbosch). c Cephalium, ll lower lip composed of the petals of all flowers, sb showy bract, ulb upper lip formed by a showy bract, uls upper lip composed of the styles of all flowers

ferent families: *Helichrysum*-like pseudanthia occur within the *Asteraceae*, *Bruniaceae* and *Eriocaulaceae* (Fig. 16 A–C). Bell-shaped pseudanthia, even of same size and reddish colour occur within the *Proteaceae* (*Orothamnus zeyheri*), *Myrtaceae* (*Darwinia spec. div.*), and *Thymelaeaceae* (*Pimelea physodes*, Fig. 16 F).

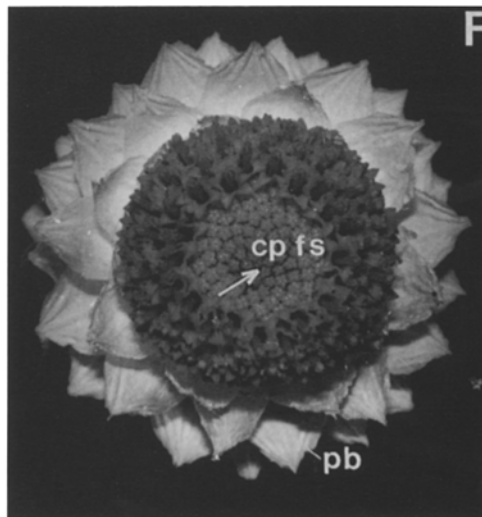
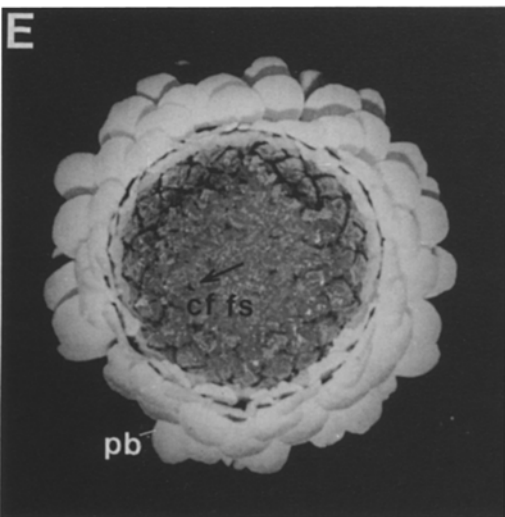
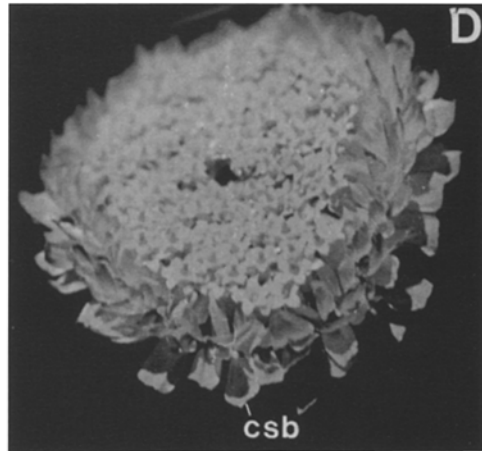
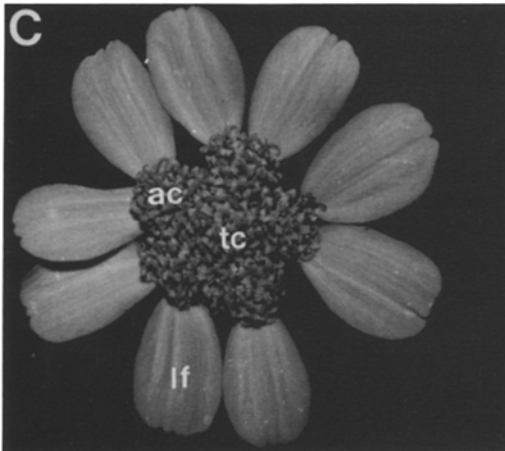
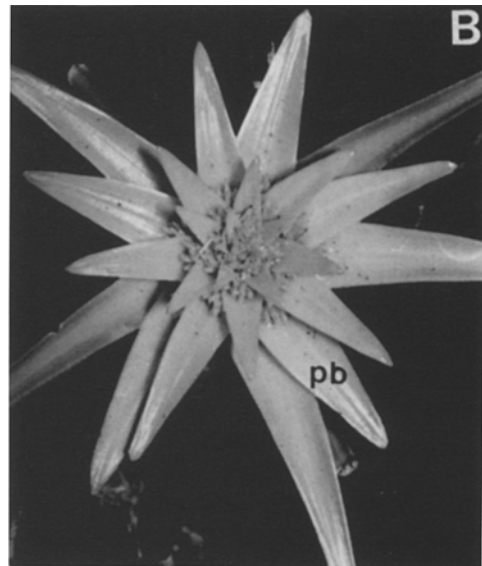
The morphology of the extrafloral pseudocorolla is rarely spectacular. However, there are two exceptions:

In *Parrotiopsis jacquemontiana* (Fig. 16 D), which belongs to the apetalous group of the *Hamamelidaceae* (cf. ENDRESS 1970), the pseudocorolla is hexamerous. However, it is not composed of six individual bracts but of two leaves only. As the leaf metamorphosis illustrates (Fig. 17) the foliage leaves have small and inconspicuous stipules. These enlarge in the transitional zone and, finally, loose their chlorophyll (Fig. 16 D, pl, psp). The two “trimerous” distal leaves are close to each other and thus form the seemingly “hexamerous” pseudocorolla.

In *Mimetes* (*Proteaceae*), the cephalium is composed of about 10 zygomorphic flowers, which altogether form a bilabiate pseudanthium (Figs. 16 E and 18) (VOGEL 1954, ROURKE 1984). The erect styles function as upper lip (Fig. 18 A, uls) while the woolly petals of all flowers together form the lower lip (Fig. 18 A, ll). In *M. hirta*, red and yellow bracts intensify the showiness of the inflorescence (Figs. 16 E and 18 B). In *M. cucullata*, the same or even a better effect is achieved: the subtending bract of the next (upper) cephalium (Fig. 18 C, sb) is red and turned down. It covers the head and functions as a showy upper lip (ulb). Thus elements of different origin (cephalium + subtending bract of another cephalium) form a functional unit, pointing to a high degree of synorganization.

According to Fig. 10 e, even much reduced, viz. two-flowered inflorescences are able to form pseudanthia. They are excellent examples for studies on symmetry because the two flowers are symmetrically arranged to each other.

In *Hydrothrix gardneri* (*Pontederiaceae*; RUTISHAUSER 1983), the individual flowers are monosymmetric and form, just as in *Rhodoleia* and the *Cichorioideae*, a new polysymmetric unit.



In *Thalia geniculata* (*Marantaceae*; Fig. 13 B) the two flowers are asymmetric forming together a new zygomorphic unit (Fig. 14 B). In both taxa, *Hydrothrix* and *Thalia*, the pseudanthium has a higher level of symmetry than the individual flowers. Within the monocotyledons *Thalia* has an exceptional position because it is the only genus that forms zygomorphic pseudanthia with exclusively floral elements. The elements are also of considerable interest: as it is well known from the zingiberaceous relationship, staminodes substitute functionally petals. In *Thalia* the outer staminodes (o st) form the white flag. Additionally, the callose inner staminodes (ca st) have appendages which are enlarged and of violet colour (cf. ANDERSSON 1981).

Just as flowers may aggregate to form head-like inflorescences, the inflorescences themselves may aggregate to head-like inflorescence-clusters (cf. Fig. 10 f). And, just as inflorescences proceed to pseudanthia, the clusters may do so as well. Apart from the *Umbelliferae* (cf. Fig. 3 g) such inflorescences are composed of modified racemes: spadices (*Pandanaceae*, Fig. 19 A), sciadia (*Apiaceae*), spicae (*Cyperaceae*, Fig. 19 B), and cephalia (*Asteraceae*, *Amaranthaceae*, *Bruniaceae*). Most often the pseudocorolla is extrafloral and composed of the sterile distal bracts being aggregated and being white or coloured. However, some *Asteraceae* show more complicated pseudocorollas:

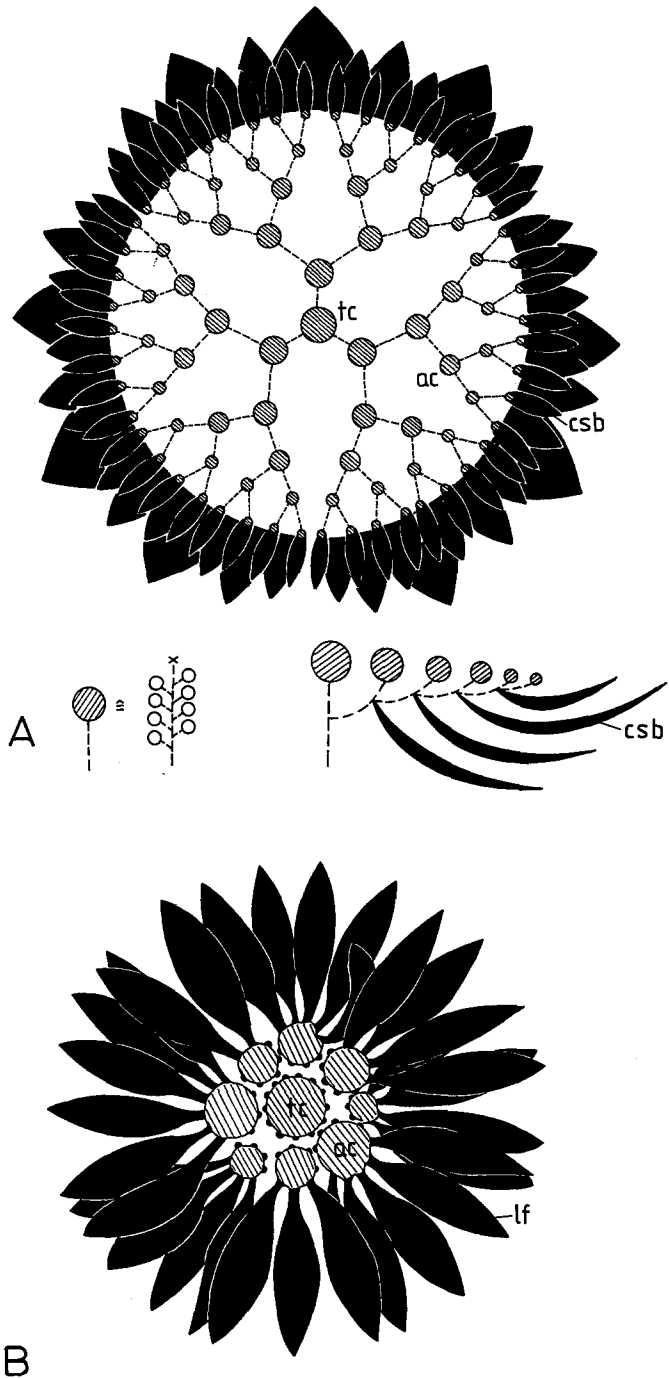
In *Myriocephalus stuartii* and *M. guerinae* (Fig. 19 D), two Australian everlastings, the pseudanthia are composed of about 100 cephalia which are arranged in a flat pleiocymoid (Fig. 20 A). The extrafloral pseudocorolla is formed by the subtending bracts of all cephalia, that means by bracts of different order (Fig. 20 A: csb). The bracts are rather small and yellow in *M. guerinae*, but large and white in *M. stuartii*. The pseudanthium of the related *M. helichrysoides* (Fig. 19 E), has basically the same complex inflorescence structure. However, the cephalia are reduced (2–5 flowers), sessile and arranged on a “super-receptaculum”. The resemblance to a simple cephalium is very great (cf. Fig. 19 F). Only the centrifugal flowering sequence indicates the complex structure.

In *Syncephalanthia decipiens* and *Eroeda* (= *Oedera*) *capensis* the compound heads are surrounded by floral pseudocorollas. As in the *Asteraceae* both floral dimorphism and aggregated inflorescences occur frequently, it is unexpected that pleiocephalia with floral pseudocorollas are so rare. In fact, *Syncephalanthia* and *Eroeda* are the only known examples.

The pseudanthium of *Syncephalanthia decipiens* (Fig. 19 C) is composed of 6 disc-like aggregated cephalia (cf. TROLL 1928: 143 f). The central head has exclusively tubular flowers while each of the axillary cephalia has additionally two ligulate flowers. As all the ligules are oriented towards the periphery, the result is a radial pseudanthium with ten rays.

In *Eroeda capensis* (Fig. 20 B) the number of rays is not strictly fixed. Each of the up to 8 axillary heads form 2–6 large, ligulate flowers. The pseudanthium looks even more like a simple cephalium than in *Syncephalanthia*: the aggregation is denser and the whole inflorescence is surrounded by green bracts imitating a simple involucre (CLASSEN-BOCKHOFF 1991).

Fig. 19. Compound inflorescences as pseudanthia. A *Freycinetia pycnophylla* (*Pandanaceae*, s.n. Mü); B *Ficinia radiata* (*Cyperaceae*; CLASSEN & FROEBE 1299, 1529, HAQ); C *Syncephalanthia decipiens* (*Asteraceae*, BG Aachen); D *Myriocephalus guerinae* (*Asteraceae*; FROEBE & CLASSEN 545, HAQ); E *Myriocephalus helichrysoides* (*Asteraceae*; FROEBE & CLASSEN 1055, HAQ); F for comparison: *Ammobium alatum* (*Asteraceae*, BG Aachen; simple cephalium). ac Axillary cephalium, cf fs centrifugal flowering sequence, cp fs centripetal flowering sequence, csb cephalium-subtending bract, fpb fleshy petaloid bract, lf ligulate flower, pb petaloid bract, tc terminal cephalium



B

Fig. 20. Diagrams of *Asteraceae* with complex organization. *A Myriocephalus stuartii* (LOTHIAN 761, Mü); *B Eroeda capensis* (CLASSEN & FROEBE 1123, 1322, HAQ). Abbreviations see Fig. 19

Conclusions

Pseudanthium types. Though the phenomenon of flower-like inflorescences is known for a long time, it never has been treated in a detailed comparative study. As shown in Fig. 21 pseudanthia can be classified into four types depending on the differentiation level and the construction elements: (a) floral, (b) hyperfloral, each with (c), or without (d) pseudocorollas.

Compared on the family level, within the “pincushions” the floral type predominates over the hyperfloral type; within the pseudanthia differentiated into a “centre” and a “periphery”, extrafloral pseudocorollas are much more frequent than floral ones. Pseudanthia are formed just as frequent by complex inflorescences as by simple ones. According to Figs. 3 and 10 all kinds of inflorescences are able to form “blossoms”. Hence, the phylogenetic steps of transformation are independent of the underlying organization.

Inflorescences. According to the mode of aggregation the pseudanthium is homologous either to the whole synflorescence (sensu TROLL, e.g., *Cornus*, *Tacca*, *Diplolaena*, *Parrotiopsis*) or – more often – to some part of it (e.g., *Congea*, *Bupleurum*, many *Asteraceae*). In the latter case several pseudanthia are produced by one synflorescence. Polytelic synflorescences, which are subdivided a priori into separate units (“florescences”), tend to form pseudanthia on the base of their subunits (cf. Figs. 3 d and 10), while monotelic synflorescences tend to concentrate all flowers in one terminal pool [Fig. 3; exclusively b (?), d].

Showy elements. Figure 22 illustrates which parts of flowers and inflorescences can become petaloid: styles (*Protea*), stamina (*Mimosa*), staminodes (*Thalia*), petals (*Rhodoleia*), sepals (*Actinodium*), epicalyx elements (*Lasiopetalum*), prophylls (*Dalechampia*), simple bracts (*Pimelea*), bistipulate bracts (*Parrotiopsis*), hairs (*Ptilotus*), coloured areas on frondose bracts (*Euphorbia*) and petaloid effigurations (*Euphorbia*).

Extrafloral pseudocorolla. Extrafloral bracts may differ from foliage leaves by the following characters: white colour due to lack of chlorophyll (*Cornus*) or dense cover of dead hairs (*Actinotus*); red or yellow colour (*Darwinia*); strawy nature (*Helichrysum*); smaller (*Ficinia*) or larger (*Staavia*) size than the foliage leaves; different form (*Astrantia*), symmetry (*Xanthosia*) or proportion (*Parrotiopsis*). The extrafloral elements quite often continue the mode of leaf arrangement (phyllotaxis) of the vegetative region. Sometimes it is modified by slight rotation (spirostichy; *Freycinetia*) or seems to be modified by peripheral orientation (*Spyridium*). The extrafloral pseudocorolla is mostly composed of free elements of the same size, form and symmetry. However, bract dimorphism regarding form (*Tacca*) and symmetry (*Xanthosia*) occurs as well as gamophylly (*Cephaelis*), (congenital) fusion of several bracts (*Congea*), and fusion of bracts and effigurations (*Pedilanthus*).

Floral pseudocorolla. Within the pseudanthia with floral pseudocorollas, the marginal flowers are radial (*Actinodium*) or zygomorphic (*Scabiosa*). This is the most common way of effecting floral differentiation. The dominant elements are the petals of the marginal flowers, while staminodes (*Thalia*), styles (*Leucospermum*), or sepals and/or prophylls rarely form a floral pseudocorolla (*Actinodium*). Thus, convergence of flowers and inflorescences is not only based on forming similar blossom-patterns, but also in using comparable elements for attraction.

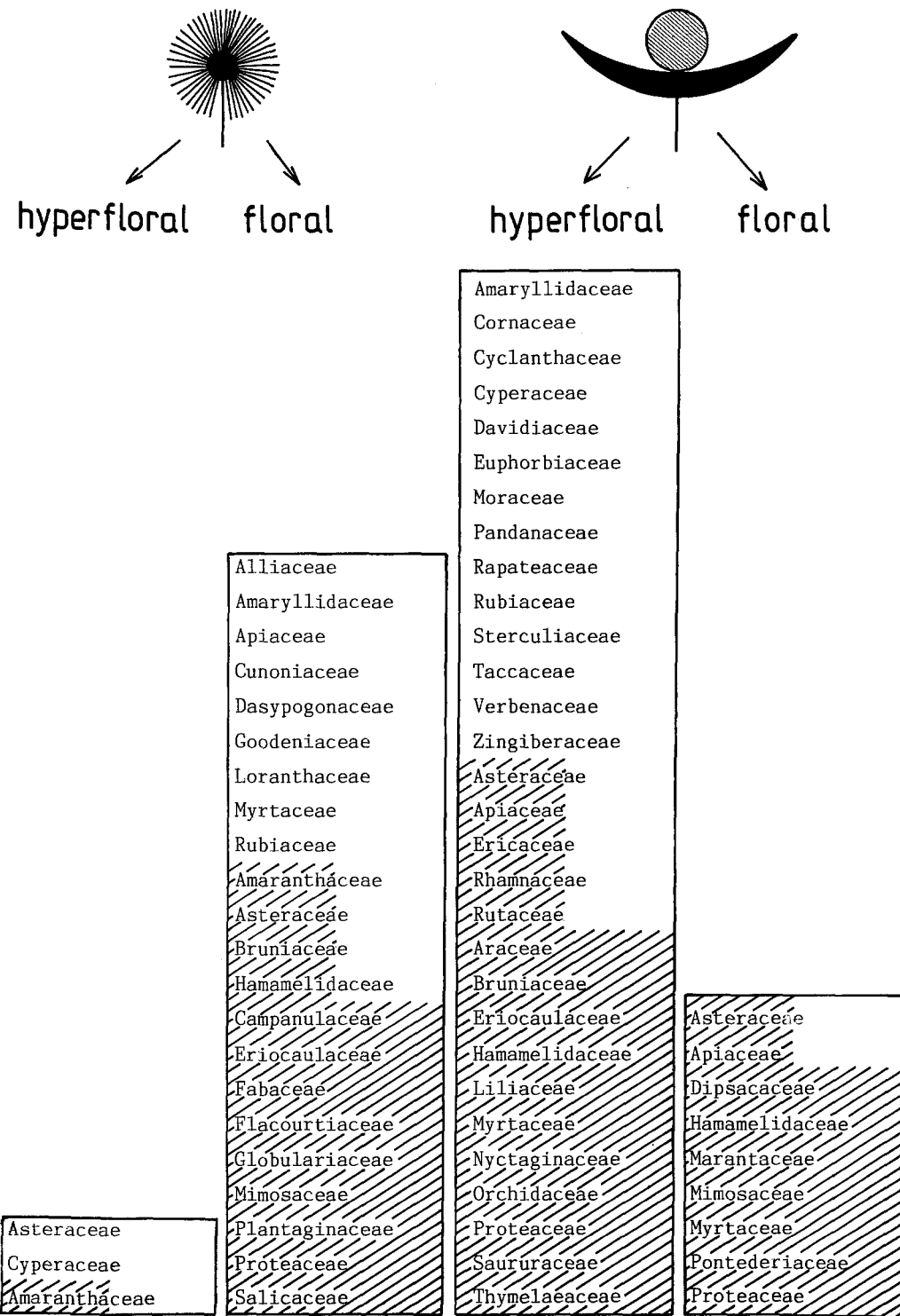


Fig. 21. Distribution of the families with pseudanthia in relation to the four types of pseudanthia. Hatched area: simple inflorescences; clear area: complex inflorescences

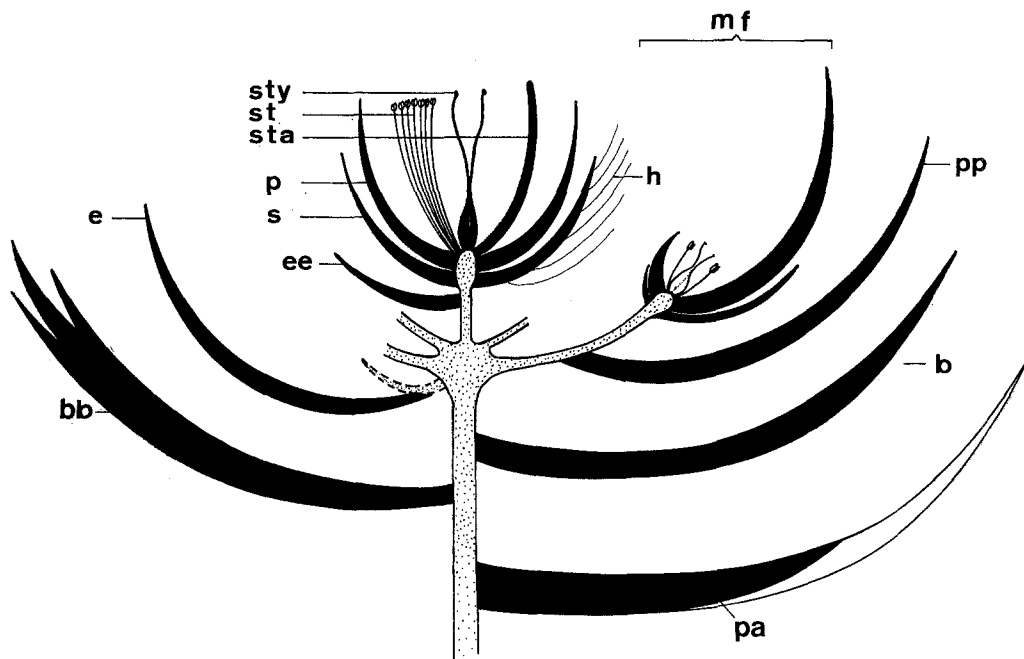


Fig. 22. Idealized combination of construction elements (petaloid structures) forming pseudanthia. b Bract, bb bistipulate bract, e excrescence, ee epicalyx elements, h hairs, mf marginal flower, p petal, pa petaloid area on a foliage leaf, pp prophyll, s sepal, st stamen, sta staminode, sty style

Symmetry. Most of the pseudanthia are radial as a direct consequence of aggregation around a central axis. Radial symmetry in differentiated pseudanthia results from enlarged marginal flowers (*Actinodium/Rhodoleia*) or of the circular arrangement of petaloid bracts (*Staavia*). In complex inflorescences, the bracts may belong to branches of different order, may be of different size and may not be oriented towards the periphery of the inflorescences. The formation of asymmetrical elements (*Xanthosia*), equalization in size (*Symphorema*) and fusion of two elements (*Congea*) enhance radial symmetry.

Zygomorphic patterns result easily from integration of two prophylls (*Dalechampia*) or of a spathe (*Arum*) as showy elements. In addition, unilateral arrangements of zygomorphic flowers (*Mimetes*) and opposite arrangements of asymmetric flowers (*Thalia*) occur as well as secondary shifts towards zygomorphy by ontogenetic modifications (*Pedilanthus*).

Pollination. The similarity of inflorescences and flowers is certainly to some degree the result of comparable adaptations to similar pollinators (cf. LEPPIK 1969). Hence, all types of pollination occur in the pseudanthia. Apart from many unspecialized taxa we find: cantharophily (*Cyclanthaceae*), myophily (*Araceae*), melitophily (nectar: *Thalia*; perfume, resin: *Dalechampia*), psychophily (*Bougainvillea*), sphingophily (*Calliandra*), ornithophily (Old World: *Darwinia*; New World: *Pedilanthus*), and chiropterophily (Old World: *Freycinetia*; New/Old World: *Parkia*). These examples demonstrate the well known fact that a certain pollination type and the responding flower-type does not depend on structural organization.

Aggregation. Selection may influence the form of a structure but finally it is aggregation which actually forms the requisite for repetition. Aggregation can be regarded as a general tendency in nature, that means an expression of neoteny. As flowers are interpreted as "neotenic strobili" (cf. TAKHTAJAN 1959: 26, IHLENFELDT 1971: 96), pseudanthia may represent "neotenic inflorescences". Both systems are characterized by a developmental inhibition of the apex and the internodes. Both systems coincide in site and determination, however, the process of differentiation is distinct, thus resulting in analogous forms.

The present summary shows that the diversity of pseudanthia is enormous. The same blossom-pattern results from different modes of transformation, demonstrating a wide field of analogies. The fact that even within the same genus (*Euphorbia*) different elements are selected for the same function (attraction) indicates a relative unspecific selection of the construction elements. Altogether, pseudanthia are the result of several independent factors: (1) aggregation, which can be regarded as a paedomorphic trend, (2) predisposition to form a "blossom" based on an inflorescence, which depends on the constraints of the taxon involved, (3) variation in the selection of construction elements, and (4) selection by the pollinators.

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Address of the author: Dr REGINE CLASSEN-BOCKHOFF, Botanisches Institut, Rheinisch-Westfälische Technische Hochschule, Aachen, Worringer Weg 1, D-5100 Aachen, Federal Republic of Germany.