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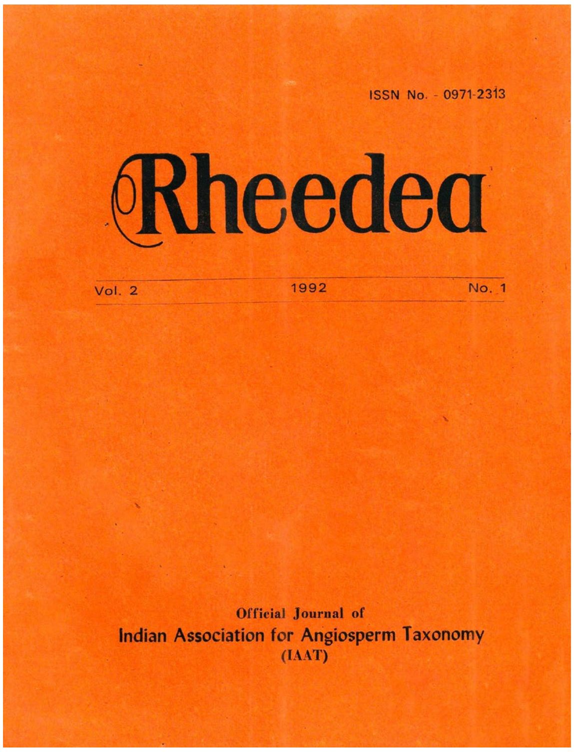
Meeuse A.D.J.



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Anthecology, Chorology, Adaptive features and Taxonomy

A. D. J. Meeuse

(Formerly Hugo de vries laboratorium, University of Amsterdam)
Harrelaers 1, 1852 KT Heiloo, the Netherlands.

Abstract

In the anthecology and chorology certain recurring combinations of features referred to as 'syndromes' are recognised. Most of these are so manifest that they have a predictive value, but one must be aware of the taxonomic aspects principally because so many 'adapted' characteristics form part of these syndromes. Such 'adaptive syndrome elements undoubtedly originated independently, as convergencies in unrelated taxa, but on the other hand, a diversification of syndromes within a certain taxon (at the generic or a higher level) has taken place. The second development has an immediate bearing upon the evaluation of syndrome characteristics in taxonomic studies because the usually correlated syndrome features and their clearly adaptive nature have often misled phanerogamists who over-rated the taxonomic meaning (weight) of such characteristics or character states, which in turn resulted in a higher grading of closely related taxa than they actually deserve. It follows that the not so manifestly 'adaptive' charactes may be better taxonomic pointers. What is perhaps worse is that authors have measured syndrome characteristics by different standards, which has led to inconsistencies. Illustrative examples are given to substantiate this conclusion. Future monographers and compilers of Floras ought to pay heed to the suggestion made in this paper and should not hesitate to disregard the syndrome features in favour of other indications of taxonomic affinities.

INTRODUCTION

Spermatophytes (the Angiosperms in particular) depend on various types of agents, such as wind, water and anthophilous or fungivorous animals for successful pollination and dispersal and, consequently, their survival. The generalities and various aspects of such mutualisms between plants and animals and the adaptive responses of plants to the service of such vectors (and *vice vesa*) are now properly understood (Van der Pijl, Proctor & Yeo, 1973; Faegri & Van der Pijl, 1979; Jones & Little, 1983). Such mutualisms between plants and animals frequently led to specialisations on either side, and even to co-evolution. The anthecological and chorological syndromes provide perhaps the best examples for the adaptation of morphological and anatomical features of the reproductive region, mosty of floral parts, fruits and seeds, pollen grains, and also their more or less distinctive, specialised function in the syndrome. There are also chemical characteristics involved, such as pigmentation of the flowers, ripe fruits or mature seeds, floral scents and physiological ones such as diurnal or crepuscular anthesis, nectar secretion, synchronisation of opening of the anthers and/or receptiveness of the stigma, and the nectar composition. Such anicillary syndrome features will hardly be touched upon here because In practice they are hardly ever adduced in assessing taxonomic affinities.

The more conspicuous syndrome features, such as the floral morphology and certain fruit and seed characteristics, have drawn the attention of taxonomists so much that they used them in their diagnoses wtthout sufficiently taking the strongly 'adaptive' nature and reciprocal correlation of syndrome elements into account.

Since syndrome elements appear to be often correlated (*e. g.*, a long and narrow corolla tube with a red pigmentation, a relatively less viscous nectar, and absence of scent in ornithophily) the diagnostic meaning of each separate element is not much greater than that of the aggregate because this is inherited as a complex, for instance through linkages in the genome, or as a 'super-gene'. A better understanding of the principal syndrome types and a recognition of the taxonomic consequences will certainly help systematists when it comes to evaluating relationships and delimiting higher taxa.

Adaptive morphological features

It is generally accepted that organisms exhibit features so clearly suited to a specific function, called 'adaptation'. The ultimate, specialised ('advanced') phenetic features often become so much different from their respective, plausible ecological and morphological prototypes, that the taxa involved seem to be rather far apart also in a taxonomical sense. This is not unexpected, because the adaptive features in question are so diverse and often so conspicuous that they were deemed to be more significant than they actually are. As already mentioned above, the incidence of the same syndromes in unrelated groups (*e. g.*, in Monocots and Dicots), clearly based on convergent evolution, is another warning against a taxonomic over-rating of syndrome features.

The morphological elements in the anthecological and chrological syndromes involve principally inflorescence, floral parts, the fruit wall, the seed coat and seed appendages. The morphological features are to be understood in a somewhat wider sense including not only shape, symmetry, etc. but also size, specific weight, consistency, surface patterns (sculpturing etc.), and reactions upon desiccaton or moistening. In this paper I prefer to use the term 'blossom' rather than 'flower,' also for aggregates of conventional 'flowers' such as the heads of Compositae and cyathia of Euphorbiaceae to avoid unnecessary connotations. In cases where biotic agents are concerned, the syndromes (which, as mentioned before, include morphological, phytochemical and physiological features) are no doubt the products of co-evolution often leading to a strong mutualistic relation. The greater the specialisation, the stronger the mutual adaptation and the more evident the syndrome. However, not all syndromes are mutualistic, especially when abiotic vectors are involved. Autogamy and autochory have no element of mutuality. Even in cases where biotic agents are involved the relation need not always be mutualistic in the sense that the animal vector does not benefit from the relationship—it may even be a nuisance in case of epizoochory when a fruit or seed bears hooks or spines. For the purpose of the present paper a more general classification of the syndrome will suffice, for the pollination and dispersal syndromes involving the abiotio factors, wind and water, and syndromes in which animals are vectors. Roughly speaking the major groups of animals comprise: Hymenoptera (mainly the apioids or 'bees' in the widest sense), various orders of Coleoptera, butterflies, moths (the hawk-moths or Sphingidae forming a special group), birds and mammals. Self-pollinating and autochorous plants are left out of consideration here. The syndromes usually reflect the senses of the animal vectors (sight. smell, tactile perception). A plant taxonomist must remember that there are, in a broad sense, three principal types of zoophilous blossoms (see Fig. 1, a-f):

(a) 'open blossoms', which are bowl-, cup- to saucer-shaped, or nearly flat on top with exposed genitalia, such as those of *Ranunculus* and related genera, many members of the Compositae, Umbelliferae, Saxifragales, Rosales and Liliales such as Alliaceae, where blossoms are unspecialised as regards the pollinators; when compound, they often form 'pincushion blossoms';

(b) 'gullet blossoms', with a rather short to moderately long and more or less tubular part and a zygomorphic corolla that is more or less clearly bilabiate. They are usually melittophilous or visited by flies with a long enough proboscis, for whom the lower lip provides a landing platform. Sometimes they are ornithophilous and/or sphingophilous in which case the lower or seemingly lower lip is reflexed as in several tubiflorous Sympetalae: Bignoniaceae, Labiatae, Scrophulariaceae etc.; representatives of the melittophilous and of the other subtypes are also found in *e. g.*, papilionid, Leguminosae, Polygalaceae, and several monocotyledonous taxa (especially in Orchidaceae);

(c) 'tube blossoms' with a more or less elongate and narrow tube and a spreading, usually more or less actinomorphic limb (typical of Rubiaceae but also found in some members of the Scrophulariales, Solanales and Liliales, see Fig. 2, a, f). Blossoms with spurs are functionally of the same type.

There are many intermediates and border-line cases. A special form is the 'batflower' type which combines a broad, more or less actinomorphic to gullet-type corolla which accommodates the head of the visitor and a rather wide and often curved tube, which stores the usually appreciable amount of nectar and accomodates the snout and tongue of the vector (see Dobat & Peikert - Holle 1985).

'Open blossoms' can accomodate not only visitors of some or all anthopilous groups of insects with a short proboscis, but also those with longer sucking mouth parts, whereas, 'gullet flowers' are more specialised and accomodate visitors with mouth parts of an adequate length: certain kinds of flies, anthopilous birds and butterflies (when diurnal) or hawk-moths (usually crepuscular, less often diurnal). However, the latter groups of visitors, especially the long-tongued ones, usually prefer tube flowers.

Additional syndrome characters, such as the presence of a pleasant or evil odour (or absence of a scent in ornithophilous blossoms), pigmentation of the corolla, absence or presence of nectar guides,

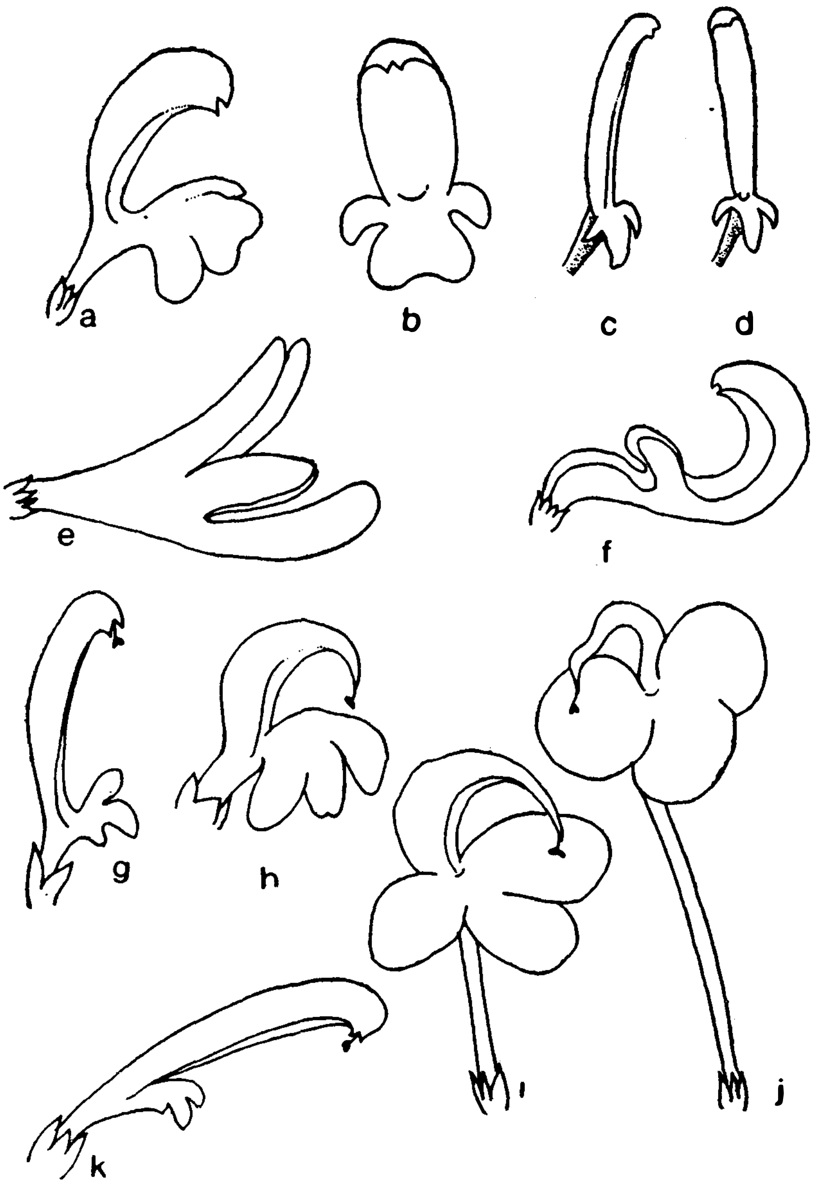

Fig. 1. Various adaptions of corolla types; a, b: gullet flower, side and frontal view; c, d: transition to ornithophily/sphingophily; e: more 'open' type, g: 'upside down' gullent type; g-k: corolla types in *Pedicularis*, g: basic gullet type, changing into ornithophilous/psychophilous type (h-j) and transition towards ornithophily/sphingophily (k). Explanation in text.

quantity and quality of the nectar, time and duration of the anthesis and special morphological adaptations such as cauliflory, special position or arrangement of the blossom, (*e. g.*, flagelliflory in chiropterophilous taxa, presence of a 'perch' in Old-World ornithophiles), are usually not considered to be of taxonomic significance, as stated before. Indeed they are mostly representative examples of convergent evolution, but possibly may indicate a relationship in special cases.

Anthecological syndromes

The best possible approach to understand anthecological syndromes is to search for examples of a divergent anthecological evolution within a single taxon. The most illustrative example, that can also serve as a yardstick for similar cases, is the genus *Pedicularis* (Scrophulariaceae). The overall floral morphology was surveyed by Sprague (1962), who rightly assumed that its original, anthecological blossom was of the 'gullet' type for the simple reason that this type prevails in many groups of the Scrophulariales. The corolla pigmentation and many case histories indicate that the most primitive species of *Pedicularis* were melittophilous and, at least nowadays, nearly always associated with bumble bees (*Bombus*). The genitalia are nearly or completely hidden in the roof of the upper corolla lip. In some species the upper lip becomes much flattened or almost sausage-shaped; the latter shape may, I think, at least in some cases reflect pollination by 'buzzing' or bumble bees, (see Buchmann, 1983), but the 'gullet' type persists. Two lines of advancement can be discerned, one in which the upper lip becomes relatively longer (thus protruding beyond the lower lip) and straighter; the lateral lobes of the corolla having been reduced to small appendages and the central part of the lower lip becoming more or less reflexed. With a concomitant change of the corolla pigmentation (which must orginally have been white to pink, mauve or purple, less often yellow) to orange or red, and with the loss of a nectar guide in the throat, the syndrome became ornithophilous (associated with humming birds in this case). The other trend was towards a broadening and lateral spreading of the lobes of the lower lip with a gradual lengthening of the corolla tube, the tip of the upper lip bending towards the throat, and a change in corolla pigmentation to red. The nactar guide disappeared and presumably the blossoms which were originally axillary became aggregated towards the tips of the stems and fully exposed. The syndromes thus ultimately become psychophilous when the corolla tube became too narrow for anthopilous birds or, alternatively, sphingopilous (in this case visited by diurnal, hawk-moth species). Fig. 1, g-f illustrates the plausible evolutionary trends. As far as I could ascertain, the genus *Pedicularis* has not been dismembered, most probably because there are intermediates linking the various corolla types.

Examples

As an example of a convergence of syndrome features the case ot *Deplanchea* (Bignoniaceae) and *Faradaya* (Verbenaceae) may be mentioned. At least one species of *Deplanchea* was described as a *Faradaya* because the blossoms are so strinkingly similar (Van Steenis, 1977). The ovarial structure and the fruit morphology are, of course, decisive. There must be several similar cases.

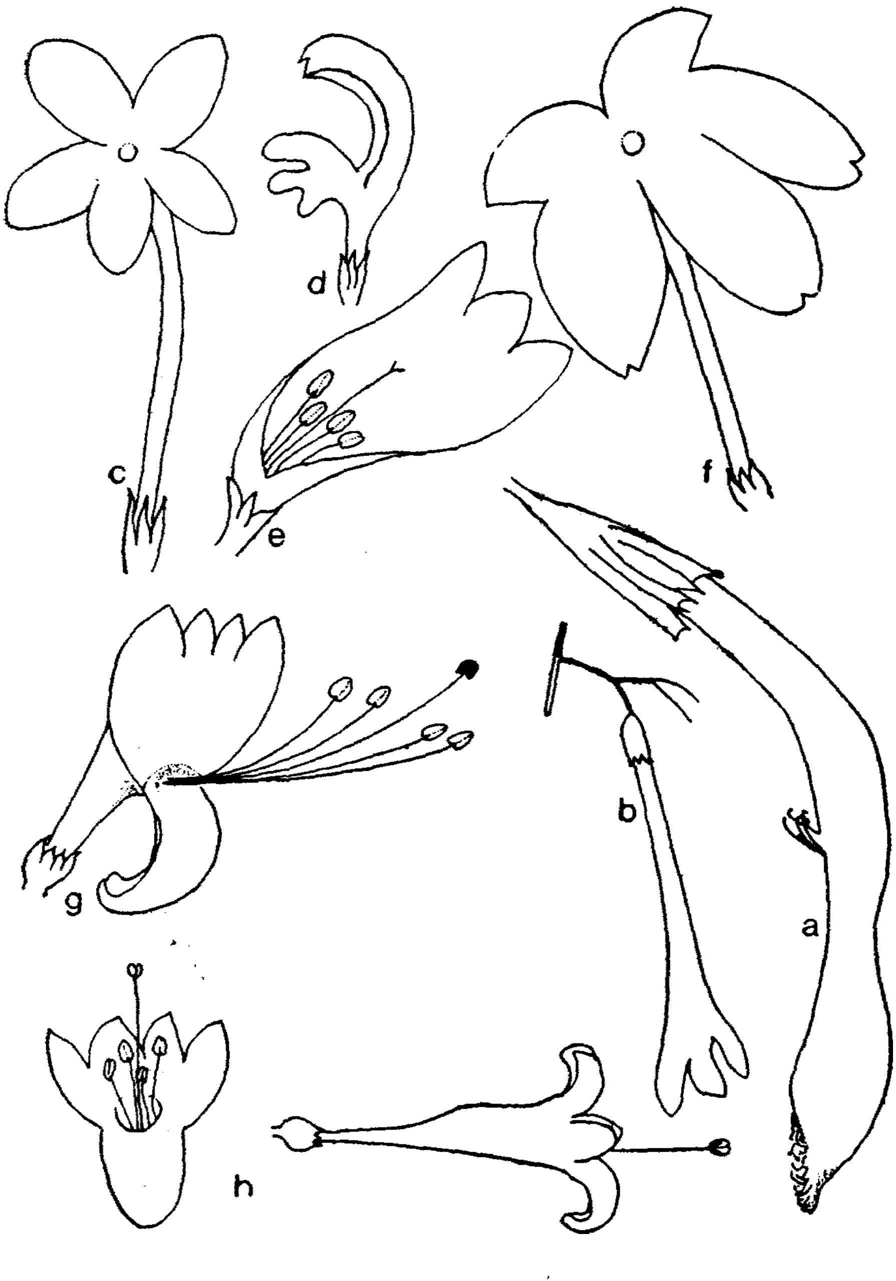

Fig. 2. a. b: Tube flowers of (a) *Leonotis* and (b) *Gardoquia*; c-h divergent evolution of syndrome types: c. *Ruspolia* and d. *Ruttya*; e. *Blepharis* and f. *Crossandra*, g. *Lonicera*, *L. periclymenum* type (gullet type) and h. *L. sempervirens* (tube flower, ornithopilous).

Diversification, as in the example of *Pedicularis*, probably occurred also in *Clerodendrum* (Verbenaceae). Although some species were at some time referred to other genera, the present trend is to recognise it as a single Old-World genus. Certain African species of *Clerodendrum* have gullet blossoms with a white to pink or mauve to blue corolla and clearly adapted to melittophily. Other species have usually orange to red blossoms, a long and narrow corolla tube and a subequally 5-lobed, spreading limb and they are almost certainly psychophilous (I have observed specimens of *Papilio* s. l., that perceive red as a separate colour, feeding on such a species). The disposition of the blossoms also differs dipending on the incidence or prevalence of melittophily, psychophily and/or ornithophily. Contemporary taxonomists have maintained *Clerodendrum* as a broad genus in spite of the diversity of anthecological syndromes as we have seen, but in other cases they have separated closely related taxa mainly on account of their different floral morphology.

The acanthaceous *Ruspolia* and *Ruttya* were considered to be different genera although they are closely related as is, for instance, evident from the pollen morphology (a cogent taxonomic pointer in the eurypalynous Acanthaceael). The discovery of a natural hybrid, followed by an artificially produced crossbetween *Ruspolia hypocrateriformis* and *Ruttya ovata* substantiated a close relationship; the sterile hybrid even produced some bivalents in the metaphase in pollen mother cells (Meeuse & De Wet, 1961). Later I obtained a sterile hybrid between *Ruspolia seticalyx* and *Ruttya fruticosa*. The disposition and floral architecture of the two taxa are very different. *Ruttya* has a gullet blossom syndrome, with and either white to pink or yellow to red corolla; in the first case there is a nectar guide and the syndrome is melittophilous and in the other there is no nectar guide and the syndrome is ornithophilous; *Ruspolia* has a red corolla with a long and narrow tube and subequally 5-lobed spreading limb (see Fig. 2, c, d), the blossoms, without nectar guide, being arranged in dense terminal, broadly racemose to subumbellate 'pin cushion' inflorescences, and the genus is clearly psychophilous. Since there are no intermediates, taxonomists will tend to keep the two taxa apart mainly for pragmatic reasons. In other acanthaceous tribes the same contrasting blossom types occur, for instance in the *Blepharis-Crossanda* duo. *Blepharis* has a one-lipped gullet blossom, a blue or more rarely mauvish to white, and rarely yellow corolla with nectar guide; the blossoms are arranged in short-stalked, dense, subspicate inflorescence and the genus is clearly melittophilous (and presumably also pollinated by beeflies or Bombylidae) to sphingophilous. *Crossandra* has yellow-orange to red blossoms without nectar guide, a long and narrow corolla-tube and a limb with three broad-spreading lobes; the flowers are arranged in long-stalked, dense and broadly racemose to subumbellate inflorescences. This genus is clearly psychophilous and presumably sometimes (also?) ornithophilous (see Fig. 2, e-f).

The bignoniaceous genera *Dolichandrone* and *Markhamia* have been distinguished as separate entities (see *e. g.*, Van Steenis, 1977). The former has large, (greenish) white to drab, wide tube-blossoms or rather typical bat blossoms and is completely or mostly chiropterophilous (Dobat & Peikert-Holle, 1985).

According to Van Steenis, *D. spathacea* is night - flowering and has fragrant blossoms. He suggested sphingophily in this species, which needs confirmation. The inflorescence of the African *D. alba* is a perfect example of flagelliflory, characteristic of several bat-pollinated blossoms. *Markhamia* has bilabiate, diurnal, orange to red blossoms in erect and dense inflorescences raised from the canopy, and is manifestly ornithopilous. All or most of the essential features of these two taxa are presumably identical and their separation is more academic than real. Monographers of the Convolvulaceae have consistenly recognised a monotypic genus *Mina.* Its blossoms are borne in almost spike-like, terminal inflorescences and its reddish corolla has a peculiar shape: it is zygomorphic and its tube is dilated, near the middle especially on one side (obviously to accomodate a copious nectar production), so that an adaptation to orniphophily is manifest. Since apparently all other essential diagnostic characters (including the chromosome number) agree with those of *Ipomoea,* I do not hesitate to refer *Mina lobata* to *Ipomoea,* more so because other species with adaptive specialisations of the corolla (such as the typically tube-blossomed *I. alba*) might as well by placed in separate genera. When such a segregation had been proposed, as in the case of *I. alba* (as *'Calonyction'*) the authorities did not recognise such seggregates and *'Mina'* would not be an exception.

In other genera the incidence of two or more syndrome types has not induced a dismemberment. In *Lonicera* (Caprifoliaceae) most species have a bilabiate corolla that is white to pink or party yellow and they are clearly melittophilous (with the exception of the red-flowered and almost certainly ornithopilous *L. ledebourii*) and some, with a relatively somewhat longer corolla tube, such as *L. periclymenum*) and some related species, tending towards sphingophily. *Lonicera sempervirens* has a red tube-blossom with long tube and a nearly actinomorphic spreading limb indicating ornithophily by humming birds (see Fig. 2, g-h). There has apparently been no reason to split *Lonicera* up into several genera (as has been done with *'Mina'* and *Ipomoea*) and this is clearly measuring by two standards.

Also at higher levels anthecological adaptations have obscured taxonomic relationships. *Tropaeolum* is adapted to ornithophily (and possibly also psycho-or sphingophily) when diurnal and yellow- to orange-flowered. The floral morphology orginially suggested a relationship with Geraniales, but I have repeatedly pointed out (Meeuse, 1986, 1987) that there are ample reasons to include the Tropaeolaceae in tne Capparales; the semmingly aberrant floral morphology is the result of the special syndromic adaptations. Another example is provided by the Thymeleaceae, which are predominantly monoclinous and often have tube-blossoms visited by long-tongued insects, but agree in other aspects with certain subfamilies of the Euphorbiaceae (Meeuse, 1990) which have 'open' flowers and are visited by various, mainly short - tongued insects (Meeuse *et al.*, 1989). The relationship, especially with the Crotonoidae, is apparent from especially the palynology, phytochemistry (recently substantiated by Hecker, in press) and embryology (Kapil & Bhatnagar, in press). Euphorbiaceae sensu mihi (1990) and Thymeleaceae must accordingly be included in the Euphorbiales in spite of their divergent anthecological evolution.

Secondary adaptations to anemophily (as in the *Artemisia* group of the Compositae) apparently have not led to misinterpretations of the tribal relationships because other features such as the organisation of the capitula and the stigma morphology point in the right direction.

Fruit and seed dispersal syndromes

In the evolution of dispersal syndromes, several convergencies and adaptive divergence have taken place. One of the most common differences between fruit types is dryness *versus* juiciness of the pericarp, the latter being in many, but certainly not in all cases, the primitive condition. Generally speaking juiciness is associated with endozoochory and dryness with various other modes of disperal, both biotic and abiotic. The same holds true for seeds if they act as the diaspores. In zoochorous ones the only general adaptation is the presence of a protective, hard layer in the fruit wall (endocarp) or the seed coat. The taxonomic significance of the condition in the seed coat has neatly been demonstrated by Corner (1976) and need not be discussed here. In all other types of dispersal additional adaptive features assist in the displacement of the diaspores *e. g*, wings or seed floss in anemochory, corky tissue or gas-filled cavities in dispersal by water, elaiosomes in myrmecochory, hooks, bristles or stickiness in epizoochorous taxa, etc. In more special cases no apparent or only indirect adaptations are discernible (*e. g.* in barochory, although the fibrous exocarp of *Cocos* and other palms and the spiny and though, resilient exocarp of *Durio* species act as shock-breakers; in cases of autochory structural features of the fruit wall are instrumental in the ejection of the seeds at maturity). Convergencies are manifold: one curious example is that of the mericarps of myrmecochorous Labiatae that have an edible part functioning in the same way as the elaiosome of seeds dispersed by ants. For the purpose of the present paper two antithetic syndrome features are important, *viz.*, fleshiness *versus* dryness (see above) and dehiscence *versus* indehiscence. As a rule of thumb one may accept that dehiscence is much more common in dry fruits than in fleshy or leathery ones. Another rule with rather numerous exceptions has already been mentioned: often dry (and also dehiscent) fruits are derived and juicy (and also indehiscent) ones more primitive. Theoretically at least, the transitions are understandable: the ovary wall is made up of living tissues and during fruit maturation the tissues may increase in size but remain soft, but an acceleration of the ageing process may turn the growing fruit wall or parts of it into a fibrous or sclerotised structure (as in seeds). Owing to differences in turgor pressure and/or a different tissue elasticity, the maturing septa of the ovary or other structures of a dry fruit may come under some tension during their development and their growth. The following desiccation causes the fruit to burst or split at maturity, the fruit wall falling apart and the seeds thus becoming shed or sometimes forcibly ejected. This occurs more readily when the carpels do not form continuous septa and the placentation is parietal or central. The explanation becomes more feasible if actual situations corroborate this hypothesis. At one time the species of

Momordica (Cucurbitaceae) with dry and dehiscent fruits were (as *Raphanocarpus*) distinguished from other species with soft fruits. Since all other important features indicate congenerity, *Raphanocarpus* is now considered, at best, a subgenus or section of *Momordica*.

There has been some disagreement as regards the most primitive type of seed coat. Corner's monumental word on seed characters (1976) is marred by the conviction that, in the Angiosperms, primitive seeds are arillate, which is unacceptable for two reasons: arils and arilloids are of various origin, and secondly, in view of conditions prevailing in archaic Flowering Plants such as Magnoliaceae, the most primitive adaptive feature is a sarcotesta, *i. e.*, a fleshy outer layer of the seed coat. Arils, arilloids, and other accessory organs of zoochorously dispersed seeds (such as caruncles and elaiosomes) are clearly secondary adaptations and their different origin from an integument, raphe, funicle or placenta etc. renders their taxonomic significance rather low. Incidentally, another seed character, apparently only found in angiosperms, is the presence of an operculum, *i. e.*, a local, preformed differentiation of the seed coat that comes off as a sort of a lid or plug when germination takes place. Opercula originate in different ways and are certainly not always homologous, but because they develop in different fashions they may be of considerable taxonomic significance (Bouman, pers comm.).

Whenever there is a diversity of dispersal strategies with in a taxon of at least the generic level, one must always be aware of the danger of evaluating a difference in adaptive chorological features as of important taxonomic weight. A relatively great number of special adaptive features in the family Labiatae involving especially calyx and mericarp characters: (Bouman & Meeuse, in press) should not be over-exploited in taxonomic classifications.

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