

**Some remarks on the classification  
and differentiation of Moraceae**

*by*

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## SOME REMARKS ON THE CLASSIFICATION AND DIFFERENTIATION OF MORACEAE

With the appearance in 1889 of Engler's treatment of the Urticales in "Die natürlichen Pflanzenfamilien" there came a pause in the interesting development of the classification of this group, which was defined, albeit somewhat vaguely, by A.L. de Jussieu in 1789 in his "Genera Plantarum" as the order Urticeae. Since the 1830's, many, including Gaudichaud, Trécul, Miquel, Bureau, Eichler, Baillon, and Bentham, have contributed to the establishment of the Engler system which until recently has been generally accepted. An important moment in this history was the appearance of Trécul's treatment of the then most problematical group, the "family" Artocarpeae. Trécul (1847) considered the "families" which at that time were distinguished within the "class" Urticineae, viz Moreae, Urticeae, Ulmeae, Celtideae, and Cannabineae, as being very closely related to the Artocarpeae. Along with the Conocephaleae, split off from the Artocarpeae, we find these "families" as tribes of the "class" Urticaceae in the "Genera Plantarum" of Bentham and Hooker (1880) and as subfamilies or families in Engler: the subfamilies Moroideae, Artocarpoideae, Conocephaloideae, and Cannaboideae in the family Moraceae, the subfamilies Ulmoideae and Celtoideae in the family Ulmaceae, and finally the family Urticaceae.

Since the end of the last century and until recently no revisions of any large groups of Moraceae and Urticaceae had appeared. But with the development of monographic taxonomic research the system has come out of its static situation, as can be seen from the study by Corner (1962). He proposed a new delimitation of the Moraceae and Urticaceae and another subdivision of the Moraceae *sensu stricto*.

### DELIMITATION MORACEAE-URTICACEAE

The Urticales, as far as the families Moraceae, Urticaceae, and Ulmaceae are concerned, form a clearly definable group within the Angiospermae. The relationships are very clear. Trécul emphasized this and Engler wrote: "Es gehören jedenfalls alle diese Familien zu einem Verwandtschaftskreis, der vielleicht auch als eine Familie angesehen werden könnte." (All these families certainly belong to a related group which could also perhaps be looked upon as one family). On the basis of morphological and anatomical characters the Moraceae and Urticaceae show a closer relationship to each other than either of the families does to the Ulmaceae (cf. Eichler, 1875; Tippe, 1938; Corner,

1962). Corner looks upon the recent representatives of both the Moraceae and the Urticaceae as relics of older groups derived from so-called Proto-Moraceae.

No exclusive characters can be found to delimit the Moraceae and the Urticaceae *sensu* Engler. The most important differentiating characters which have been used in this connection are: the presence or absence of latex, straight or inflexed stamens which later spring back elastically, and differences in the structure of the pistil and position of the ovule.

Moraceae have a system of latex tubes which, as far as is known, is limited in the Conocephaloideae to the bark, but which in other Moraceae also occurs in the wood, leaves, and inflorescences. However, a more or less extensive system of latex tubes has also been found (Guérin, 1923) in a few genera of the Urticaceae (*Ureva*, *Laportea*).

The characteristic inflexed stamens which on flowering spring back elastically also occur in a few groups of the Moraceae.

Herbs and trees occur in both families, although the Urticaceae are mainly herbaceous and the Moraceae mainly woody.

The occurrence of a basal ovule appears to be correlated with unbranched styles and apparently associated reductions in the vascular system of the pistil (cf. Bechtel, 1921). The type pistil with unbranched styles and a basal ovule is found in the Urticaceae and the Conocephaloideae. However, in these groups the ovule can also be in a sub-basal and even a lateral position, e.g. in *Pourouma* (cf. Chew Wee-Lek, 1963) and *Laportea* (cf. Eames, 1961). Nevertheless, also in the subfamilies of the Moraceae where an apical ovule is normal, the ovule may be placed sub-apically or laterally, e.g. *Castilla tunu*. In these subfamilies very often one of the two stigmas is more or less reduced and occasionally even completely missing. On the other hand, in the Urticaceae two stigmas are sometimes encountered, e.g. in *Phenax*. It is often mentioned that the pistil of the Moraceae is derived from two and that of the Urticaceae from one carpel. The reductions found in the vascular system and style of the pseudomonomerous pistils are insufficient grounds for assuming a difference in the number of carpels. Unfortunately, data are not available on the course of the vascular strands in the female flowers of Conocephaloideae, the group which in other respects as well occupies a more or less intermediate position.

The differences in structure between the Moraceae and Urticaceae appear to be more or less gradual rather than essential. There are differences in the frequency of occurrence of certain features (inflexed stamens, herbs) and more or less clear morphological and anatomical series (latex-tube system, structure of the pistils, and position of the ovule).

In view of the above considerations, to maintain the Moraceae and Urticaceae as separate families within the Urticales is a dubious matter. The opinion of Eichler (1875), who considered then separately recognized families Urticaceae, Artocarpaceae, Moraceae, and Cannabinaceae as belonging to one family, is worth following. The close relationship between these groups of plants would then be shown to better advantage. Within the family Urticaceae *sensu lato* the subfamilies Urticoideae, Conocephaloideae, and Moroideae could be distinguished as reasonably well-defined entities. On the basis of the differences in the pistil Chew Wee-Lek transferred a number of genera of and Corner

all the genera of the Conocephaloideae to the Urticaceae. This simply transferred the problem but did not solve it.

### SUBDIVISION MORACEAE

In Engler's system the subfamilies Moroideae, Artocarpoideae, and Conocephaloideae were delimited chiefly by characters some of which were also used in delimiting the families Moraceae and Urticaceae, e.g. the nature of the stamens and position of the ovule. However, in drawing the limits at subfamily level differences in the nature of the stipules and the position of the leaves in bud were also used. Thus the Moroideae were distinguished particularly by the presence of inflexed stamens and the Conocephaloideae particularly by the basally placed ovule. In the Moraceae the stamens can be straight or inflexed before flowering, and in the latter case on flowering they can spring back elastically as in the Urticaceae. But it also occurs that before flowering the stamens are inflexed and on flowering they gradually become straight or remain more or less inflexed, e.g. in *Dorstenia* species. Such stamens must be distinguished from stamens which spring back elastically and throw out the pollen. Since that distinction is not made, *Dorstenia* has been incorrectly placed in the Moroideae. By utilizing the structure of the stamens for delimiting the Moroideae and the Artocarpoideae, genera agreeing in many features, such as *Sorocea* and *Trophis*, *Cudrania* and *Cardiogyne*, were placed in very different parts of the system. Surprising is the fact that stamens of the Urticaceae type occur in *Olmedia*. As a differential character, it seems that the structure of the stamens can only be used at subgenus to subtribe levels. The same is true for the stipules being amplexicaul and/or connate or not (cf. Jarrett, 1959, 1960). According to Corner, the leaves being plicate or not in the bud depends simply on the size of the leaf and cannot be used to distinguish Moroideae and Artocarpoideae, as Engler did.

The subdivision of the Moraceae in the Engler system is definitely unsatisfactory. The characters used were to a large extent determined historically. Significant is Engler's remark: "Bisher hat man ausschliesslich in erster Linie das Verhalten der Staubfaden berücksichtigt; es ist aber die Frage, ob dieses Merkmal phylogenetisch dieselbe Bedeutung hat, wie für Classificierung". (Up to now it has always been the behaviour of the stamens which has been considered first; it is, however, questionable whether phylogenetically this character has the same importance as for the classification). And this applies not only to the stamens.

It is therefore readily understandable that Corner (1962) through the study of several groups of the Moraceae arrived at a different subdivision of the Moraceae *sensu stricto*. This classification is based primarily on characters of the inflorescence, which in Engler's system were used for the subdivision of the subfamilies. Laying emphasis on the characters of these functional structures, which are of importance in connection with reproduction, is in my view correct. Corner distinguishes the following tribes: Ficeae, Moreae, Artocarpeae, Brosimeae, Dorstenieae, and Olmedieae. However, also in Corner's subdivision there are several weak points, so that it seems worthwhile making the attempt to arrive at a more acceptable and useful classification which does better justice to relationships and differences.

In view of the considerable variation in characters, the distribution of characters within the family, the occurrence of all kinds of transitions, and the many parallel developments and series, as with the subdivision of the Urticaceae *sensu lato* the emphasis will not fall on exclusive characters but more on correlations and frequencies in the occurrence of characters.

The Moraceae *sensu* Corner could be divided into four groups (tribes): Ficeae (as circumscribed and delimited by Corner), Olmedieae, Dorstenieae (incl. Brosimeae), and Moreae (incl. Artocarpeae).

#### OLMEDIEAE

Trees; leaves on the branches in 2 rows, stipules rarely connate; lacking uncinata hairs; inflorescences (in small groups) on shortened branches, unisexual, discoid, with involucre consisting of imbricate bracts, bracts never peltate; stamens straight or inflexed and only in *Olmedia* springing back elastically, rarely a pistillode; seeds large, without endosperm, vascular strands of the testa not limited to a thickened part of the testa, embryo longitudinal, cotyledons equal and thick, radicle apical; wood fibres always septate; cardiac glycosides present in several genera.

In this conception, the tribe comprises in addition to the 7 genera of the New World the genera *Antiaris* and *Mesogyne* of the Old World. The position of *Antiaropsis* and *Sparattosyce*, which Corner includes in the Olmedieae, is here left open. *Antiaris* and *Mesogyne* differ from the neotropical genera in characters of the inflorescence.

Septate wood fibres have been found in all Olmedieae (Tippo, 1938; Mennega, unpublished work), but they also occur outside this group, e.g. in *Prainea* and *Ficus religiosa* (Tippo, 1938).

So far, cardiac glycosides have been encountered in *Antiaris*, *Antiaropsis*, *Castilla elastica* (cf. Hegnauer, 1969), and in some species of *Naucleopsis* and *Maquira* (Bisset, personal communication), but also in *Streblus asper* (cf. Hegnauer, 1969). These substances are used both in Asia and South America for the preparation of dart poisons.

#### DORSTENIEAE

Trees, shrubs, or herbs (*Dorstenia*); leaves in 2 rows or in a spiral, stipules connate or not; uncinata hairs general; inflorescences solitary or in pairs, rarely in small groups on shortened branches, mostly bisexual, discoid to globose, involucre lacking or if present generally not consisting of several series of imbricate bracts, often peltate bracts in among the flowers; stamens straight or curved (but not springing back elastically), sometimes a distinct pistillode; seeds large or small, without endosperm, testa generally having a thickened part with vascular strands, embryo often not lying longitudinally in the seed, cotyledons often unequal; no septate wood fibres.

This tribe includes the neotropical genera *Brosimum*, *Trymatococcus*, and *Helianthostylis*, the genus *Dorstenia* which occurs in both Africa and America, and the African

genera *Scyphosyce*, *Trilepisium* (= *Bosqueia*), *Bosqueiopsis*, and *Utsetela*. In view of the many similarities, also in the pollen (cf. Erdtman, 1966), the genus *Craterogyne* can probably be included in *Dorstenia* (sect. or subgen. *Nothodorstenia*). The recently described *Dorstenia djettii* forms a clear link via *Craterogyne oligogyne* with the other *Craterogyne* species, via *Dorstenia elliptica* with other *Dorstenia* species, and via *Bosqueiopsis* with other genera of the tribe.

#### MOREAE

Trees or shrubs, climbing or not, or herbs (*Fatoua*) leaves in 2 rows or in a spiral, rarely opposite, stipules connate or not; uncinat hairs present or not; inflorescences cymosely branched, more often spicate or capitate, mostly unisexual, generally with bracts which are often peltate in among the flowers, sometimes sub-involucrate because of the presence of several (large) basal bracts; stamens straight or inflexed and then mostly springing back elastically, pistillodes general; seeds large or small, with or without endosperm, testa with or without a thickened part having vascular strands, embryos very diverse; occasionally septate wood fibres or cardiac glycosides.

This tribe can probably be subdivided fairly easily. Delimitation of the genera, however, appears to be less simple. The genus limits in the system and systems based thereon are unsatisfactory, probably as a consequence of the artificial subdivision of the Moraceae. But also the limits which Corner gives in his study on the classification of the Moraceae are unsatisfactory in a number of cases. Some of the genera distinguished by Corner, e.g. *Streblus*, tend in composition towards a subtribe, while others, e.g. *Maclura*, comprise species some of which exhibit more affinity with representatives of other genera than they do with each other.

In order to arrive at a justifiable genus delimitation within the Moreae, studies cannot be confined to representatives of one continent or of one flora area.

It is uncertain if *Hullettia* should be included in this tribe. *Poulsenia* occupies a rather isolated position within the whole.

#### GEOGRAPHICAL ASPECTS

In his monograph on African Moraceae, Engler (1898) suggested that the connections between the African and the American Moraceae are more numerous and more clear than those between the African and Indo-Malesian Moraceae. This appears to be true only for the Dorstenieae (incl. Brosimeae), which in their distribution are practically limited to Africa and America and of which the genus *Dorstenia* occurs in both continents. For the other groups the transatlantic connections are certainly less clear. Van Steenis (1962) drew attention to the trans-Pacific connections within the Olme-dieae, but these are not clear enough to serve as an example. The African representatives of the Moreae (incl. Artocarpeae) show the most relationships with those of the Indo-Malesian area, which in their turn exhibit connections with American representatives. Within the Conocephaloideae, the chiefly Malesian genus *Poikilospermum* and the

American genus *Coussapoa* appear to be most closely related to each other.

In order to reach justifiable hypotheses and theories regarding trans-oceanic connections, more insight into the distribution patterns and possible causes for them on the separate continents would seem to be essential. Unfortunately, the requisite knowledge, especially of the tropical flora, is very meagre for America. This is a fruitful and more or less untouched area of research from which important data could be obtained, which could also be of use in the interpretation of variation patterns within species and genera.

### MORPHOLOGICAL DIFFERENTIATION

Corner (1962) in his absorbing and stimulating study on the classification of the Moraceae wrote in connection with the enormous variation within the family, parallels in evolution, and with the fact that much of the data for this family have been taken only from the study of often scarce herbarium material: "Yet, the pieces of the puzzle are so strange, so splendidly different from the banalities of many other families, that the monography of the Moraceae is one of the most exciting chapters in angiosperm taxonomy. To relate a mulberry and a bread-fruit, one superficially the aggrandisement of the other, and add the little *Fatoua* calls for a working hypothesis of flowering-tree evolution. A concept of Proto-Moraceae is essential".

The survey which then follows of the differentiation in the various structures, based primarily on his knowledge of the Moraceae of Asia and Australasia, can already be supplemented by much new data from completed and current research on American and African Moraceae. All these data, which cannot be set out here in this short survey, have formed the basis for the above-proposed changes in the classification of Urticales and Moraceae *sensu stricto*. This new division can only be provisional, since the data are still relatively fragmentary. Although continued study of present-day herbarium material can give a survey of the morphological differentiation and correlations can be established, if necessary using mathematical methods, nevertheless in order to fit the pieces of the puzzle together in the best way it will be necessary to obtain some insight into the functional significance and consequences of the morphological differentiation. While this can be achieved to some extent by deduction from the available (but often scarce) data, the collection of new and other data from field studies will be of great importance. Further data on habitats and ontogeny could also be obtained in this way. Such an investigation, against the background of known morphological differentiation and supplemented by data on the anatomy and chemical constituents, is essential — rather than a concept of Proto-Moraceae which can hardly give a better insight into the relationships in this family. Nevertheless, general series occurring in other groups or general tendencies will have to be taken into account, bearing in mind that evolution is not just simply a question of natural selection (cf. Leppik, 1970).

Some remarks on phenomena, aspects, and characters which appear to be of importance for the taxonomy, but which received little or no attention in Corner's treatment, are discussed in the following paragraphs.

## INFLORESCENCE

The basic form of the inflorescence of the *Urticaceae sensu lato* is a repeatedly branched dichasium with male flowers and with female flowers which in the *Moraceae* are terminal, i.e. are situated in the basal part of the inflorescence. In addition, there is a tendency to dorsi-ventral flattening with the flowers directed adaxially. This construction can still generally be recognized in one or more characters in the representatives of this family (cf. Bernbeck, 1932). The inflorescences of *Cecropia*, a group of spikes which until the flowering is surrounded by a spathe resembling the stipules, from an exception. The sterile groove, which is found in the spicate inflorescences of various representatives of the *Moreae sensu lato* and for which Corner had no explanation, is probably connected with the adaxial orientation of the flowers, as is found in other types of inflorescences. The sterile grooves are normally to be found on the abaxial side of the inflorescences.

The position of the inflorescences in the *Urticaceae sensu lato* is very characteristic. In principle, the inflorescences are situated in pairs in the leaf axils — according to Eichler (1875) on basal buds of axillary shoots. This feature can even be observed on the shortened branches such as occur in the *Olmedieae* but also in other groups including *Clarisia*, *Dorstenia* (sect. *Nothodorstenia*), and *Treculia*. These shortened branches often bear scales resembling stipules which are probably homologous with the scales of the axillary resting buds in *Morus alba* studied by Cross (1936, 1937). Cauliflory, as it occurs in *Treculia africana*, for example, in which the female inflorescences are generally on older, already leafless, branches, is made possible by the presence of shortened branches. A closer study of the morphology and anatomy of leaves, axillary shoots, inflorescences, stipules, and cataphylls, and also their relations to each other, would appear to be of importance. From the results of such a study it may be possible to explain, for instance, the peculiar structure of the inflorescence of *Cecropia*.

Many inflorescences, especially those of representatives of *Dorstenieae* and *Olmedieae*; can be characterized as subpseudanth or sometimes even as pseudanth, e.g. in *Trilepisium* (= *Bosqueia*) in which the inflorescences resemble flowers such as those of some *Combretaceae* and in *Naucleopsis* with male inflorescences looking like flowers of *Ternstroemia*. Even where the inflorescences can hardly or not be called pseudanth, as in *Ficus* for example, in which the inflorescences are more like fruits, they can often be considered as functional units with regard to reproduction — pollination and later seed distribution.

As regards various characters of the inflorescences, partly parallel morphological series and tendencies can be observed, for larger and smaller groups, e.g. richly flowering — poorly flowering (thus in fact many stamens and/or pistils — few stamens and/or pistils), bisexual — unisexual, free flowers (pseudo-apocarpy) — united flowers (pseudo-syncarpy), flowers situated on the receptacle (pistils) — flowers sunk in the receptacle (pistils). Some of these series appear to be a recapitulation of series generally accepted for flowers of *Angiospermae* as a whole. In this respect, the *Moraceae* show similarities with the *Compositae*, for which Leppik (1970) has demonstrated a recapitulation of series for the inflorescences.

Corner (1949, 1962) pointed out the close similarities between the infructescences of *Artocarpus* and the fruits of *Durio zibethinus*, the characters of which, according to Corner, must be considered as primitive. For the Moraceae more examples can be given of infructescence and inflorescence characters which are analogous to so-called primitive characters of fruits and flowers. A question is what significance should be attached to this secondary occurrence of "primitive" characters.

#### TRANSFERENCE OF FUNCTION

For the neotropical Olmedieae and Brosimeae it has been described how the protecting function of the perianth for the young stamens can be taken over by other structures. An elegant example of the transference of this protecting function is given by the inflorescence of *Trilepisium*. Here the perianth is missing and the stamens are surrounded by a membranaceous part of the receptacle. The delicate inflorescence is enclosed in its entirety by modified, leathery stipules until the stamens are ripe.

In most Moraceae the testa is very thin and the protecting function is taken over by the endocarp. In *Dorstenia*, but also in *Sloetia* and *Sloetiopsis* (incl. *Neosloetiopsis*), the outermost part of the fruit wall becomes fleshy and more or less thickened at the base. When this part of the fruit wall wears open, the endocarp body is pushed out or even ejected. In *Coussapoa* and *Poikilospermum* (cf. Chew Wee-Lek, 1963), in which the young plants are usually epiphytic, the endocarp body, which is provided with small projections, together with the surrounding slime from the slimy mesocarp is pushed out by the perianth. Finally, another example of the transference of function: while, for example, in *Dorstenia* the endocarp is surrounded by a fleshy exocarp, in other genera a fleshy, often coloured, perianth surrounds the endocarp and in yet other genera it is the receptacle which is fleshy and often coloured.

#### DIMORPHISM

An aspect which is worth attention is the occurrence of differences between juvenile and adult plants. This dimorphism is particularly related to features of the leaf: phyllotaxy, shape, indumentum, leaf edge, etc. With many species, groups or species, or genera, the differences between juvenile and adult specimens is very slight. However, there are also species in which these differences are very striking, e.g. *Chlorophora excelsa* and *Brosimum parinarioides*. In both these species there are on the lower surface of the leaf of adult specimens on the veins which surround the areoles horizontal hairs which more or less close off the areoles and thus form "stomatal crypts". The indumentum of the leaves of juvenile specimens does not resemble that of adult specimens at all. The juvenile characters appear to remain for some considerable time and are still found on fairly tall trees. Moreover, the juvenile characters can also be encountered on watershoots of adult specimens. In *Bagassa* two species are distinguished on the basis of leaf characters (shape, thickness, indumentum, incisions in the leaf edge). Very probably, here specimens with juvenile characters are assigned to one species and specimens with adult characters to the other. In *Castilla elastica* and *Antiaris toxicaria* subspecies

can be distinguished on the basis of leaf characters, among other things; the leaves of juvenile specimens, however, are very uniform. The dimorphism of leaves in *Pourouma* and *Myrianthus* species is probably also connected with the age of the plant. In groups where uncinata hairs are present, these often occur more frequently in juvenile specimens than in adult specimens. In groups where the leaves are placed in two rows on the branches, the leaves in juvenile specimens may be placed spirally or in two rows right from the very beginning.

Possibly, there is also a connection between the occurrence of great differences between juvenile and adult specimens and the degree of differentiation in the indumentum of the leaf. A closer study of this dimorphism could contribute to a better insight into variation patterns and relationships.

#### SEED

Regarding embryo characters, Corner (1962) noted that they have little value for the classification since they cannot be placed in a satisfactory scheme. Experience shows that the seed characters, including those of the embryo, are of importance for the taxonomy, but not in all groups. Relationships between species and genera also find expression in seed characters. Besides the presence or absence of endosperm and the shape and position of the embryo, testa characters such as the vascularization and the presence or absence of a thickened part near the hilum are important.

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