

## CECROPIACEAE A NEW FAMILY OF THE URTICALES

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### Summary

The problem of the correct position of the *Conocephaloideae*, a subfamily of the *Moraceae* in Engler's system, but transferred to the *Urticaceae* by Corner (1962), can be satisfactorily solved by assigning the rank of family to this taxon, to be named *Cecropiaceae*. Diagnoses of and a key to the six genera constituting this family (*Cecropia*, *Coussapoa*, *Musanga*, *Myrianthus*, *Poikilospermum*, and *Pourouma*) are given. The classification of the *Urticales* and the relationship between the *Cecropiaceae* and both *Moraceae* and *Urticaceae* are discussed. A key to the families of the *Urticales* is given.

### Cecropiaceae C.C. Berg fam. nov.

Type genus: *Cecropia* Loeffling

*Cecropieae* Gaudichaud in Freycinet, Voy. Uranie, Bot. 491, 506. 1830, as tribe of the *Urticeae* (= *Urticales*)

*Pouroumeae* Gaudichaud in Freycinet, Voy. Uranie, Bot. 491, 511. 1830, as tribe of the *Urticeae* (= *Urticales*); Trécul, Ann. Sci. Nat. Bot. III. 8: 77. 1847, as tribe of the *Artocarpeae* (= *Moraceae* s.l., p.p.); Miquel in Martius, Fl. Bras. 4 (1): 83, 122. 1853, as subtribe of the *Artocarpeae* (= *Moraceae* s.l., p.p.).

*Conocephaleae* Trécul, Ann. Sci. Nat. Bot. III. 8: 77. 1847, as tribe of the *Artocarpeae* (= *Moraceae* s.l., p.p.); Miquel in Martius, Fl. Bras. 4 (1): 83, 131. 1853, as subtribe of the *Artocarpeae* (= *Moraceae* s.l., p.p.); Bureau in De Candolle, Prodr. 17: 280, 283. 1873, as tribe of the *Artocarpaceae* (= *Moraceae* s.l., p.p.); Bentham & Hooker, Gen. Pl. 3 (1): 343. 1880, as tribe of the *Urticaceae* (= *Urticales*).

*Conocephaloideae* Engler in Engler & Prantl, Nat. Pflanzenfam. 3 (1): 93. 1889, as subfamily of the *Moraceae* sensu Engler, transferred to the *Urticaceae* by Corner, Gard. Bull. Singapore 19: 251. 1962.

For a historical review of the subdivisions of the *Urticales* the reader is referred to Chew Wee-Lek, Gard. Bull. Singapore 20 (1): 22. 1963.

Arbores vel frutices semper dioeci, radicibus aeriis vel gralliformibus; systema ductuum laticiferorum reductum, laticem haud exudans. Folia spiraliter disposita, integra vel plus minusve profunde palmato- vel radiato-incisa; stipulae connatae. Inflorescentiae cymoso-ramosae vel capitatae vel glomerulum digitatum spicarum effortantes. Flores staminati tepalis 4-2, liberis vel connatis; stamina 4-1, recta, interdum inflexa et gradatim porrigentia, sed non elastice eflectentia; pistillati tepalis 4-2, connatis; stigma ligulatum, capitato-penicillatum vel peltatum; ovulum (sub)orthotropum, basale vel subbasale; semen parvum vel magnum; embryo simplex, rectus; endospermum adest vel abest.

Terrestrial or hemi-epiphytic woody plants with aerial roots or stilt-roots and with a reduced system of latex tubes. Leaves spirally arranged, pinnately veined to subtriplinerved or to palmately veined in entire to palmately incised leaves or radially veined in peltate leaves; stipules fused, mostly fully amplexicaul; cystoliths present in *Poikilospermum*, lacking in the other genera. Plants strictly

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dioecious, inflorescences unisexual, the staminate ones cymosely branched, the pistillate ones cymosely branched, capitate, spicate, subumbellate or both staminate and pistillate inflorescences forming a pedunculate digitate cluster of spikes enveloped by a caducous spathe. Staminate flowers with 4-2 free or fused tepals, stamens 4-1, straight in the bud, sometimes inflexed, but then straightening gradually at anthesis; a distinct pistillode mostly lacking. Pistillate flowers with a tubular, 4-2-lobed to 4-2-dentate perianth, ovary free, stigma 1, lingulate to capitate-penicillate to peltate, ovule (sub)orthotropous, basal or subbasal. Fruit small and free or large and either adnate to a fleshy fruiting perianth or free, endocarp crustaceous or woody, endosperm mostly present in small seeds, absent in large seeds, embryo small with flat cotyledons in small seeds, large and with thick cotyledons in large seeds. Light-demanding plants of more or less open vegetations.

#### THE GENERA OF THE CECROPIACEAE

##### *Cecropia* Loeffling

A genus of probably 70-80 species in tropical America, forming small to tall trees often with stilt-roots; stem and branches with hollow internodes; leaves large, lamina peltate, radially incised, with radial venation; inflorescences a pedunculate digitate cluster of spikes enveloped by a caducous spathe; perianth of staminate and pistillate flowers tubular; stamens 2; stigma capitate-penicillate or peltate, ovule basal; fruit a nutlet, endocarp crustaceous, tuberculate or smooth; endosperm present, cotyledons flat, radicle relatively long.

##### *Musanga* R. Brown

A genus of 2 species in tropical Africa forming trees with stilt-roots; stem and branches with hollow internodes; leaves large, lamina peltate, radially incised, with radial venation; staminate inflorescences repeatedly branched, bearing globose clusters of flowers on the ultimate dichotomies; perianth 2-lobed, stamen 1; pistillate inflorescence a clavate, more or less applanate spike; perianth tubular, stigma capitate-penicillate, ovule subbasal; fruit small, endocarp crustaceous, tuberculate; endosperm present, cotyledons flat, radicle relatively long.

##### *Coussapoa* Aublet

A genus of more than 50 species in tropical America. Usually hemi-epiphytic shrubs or trees with aerial roots or with stilt-roots if terrestrial; leaves with an entire lamina, pinnately veined to subtriplinerved to palmately veined; inflorescences cymosely branched with capitate clusters of flowers on the ultimate dichotomies, in pistillate inflorescences sometimes reduced to a single head; perianth of the staminate flower with 3, more or less connate tepals, stamens two, either free or entirely connate, or one; perianth of the pistillate flower tubular, stigma capitate-penicillate, ovule basal; fruit small, with a mucilaginous layer outside the verrucate crustaceous endocarp; endosperm scarce (or lacking?), cotyledons flat, radicle relatively long.

##### *Poikilospermum* Zipp. ex Miquel

A genus of 20 species in tropical Asia. Hemi-epiphytic scramblers with aerial roots; lamina entire, mostly pinnately veined, with punctiform or elongate cystoliths; stipules not (fully) amplexicaul. Inflorescences cymosely once or repeatedly branched, with capitate clusters of flowers on the ultimate dichotomies; perianth of the staminate flower with 4-2 free or basally connate tepals, stamens 4-2, straight or inflexed and straightening gradually at anthesis; perianth of the pistillate flower tubular, 4-lobed to 4-dentate, stigma ligulate to capitate-peltate, ovule basal; fruit small, with a mucilaginous layer outside the tuberculate crustaceous endocarp; endosperm scarce or lacking (?), cotyledons rather flat, radicle relatively long.

### *Myrianthus* Palisot de Beauvois

A genus of 7 species in tropical Africa. Usually medium-sized trees or shrubs with stilt-roots or sometimes lianas. Leaves with a simple, entire and pinnately veined or with a lobed and palmately veined lamina, or the lamina compound, with 3-7 leaflets; stipules sometimes not fully amplexicaul; staminate inflorescences repeatedly branched, bearing sessile flowers closely set on the ultimate dichotomies or down to more proximal dichotomies; perianth with 4(-3), free or basally connate tepals, stamens 4(-3), free or connate; pistillate inflorescences capitate; perianth tubular, 2-3-lobed, stigmas lingulate, ovule basal; fruit large, adnate to the enlarged fleshy perianth, endocarp woody; endosperm lacking, cotyledons thick, radicle short.

### *Pourouma* Aublet

A genus of probably more than 50 species in tropical America. Small or medium-sized trees, often with stilt-roots; lamina entire or palmately incised, venation pinnate to palmate; inflorescences repeatedly branched, the pistillate ones sometimes subumbellate; staminate flowers often pedicellate and mostly more or less densely glomerate on the ends of the ultimate dichotomies; perianth 4(-3)-lobed to 4(-3)-parted, stamens 4(-3), straight; pistillate flowers usually pedicellate; perianth tubular, entire to 4(-3)-lobed or 4(-3)-dentate, stigma (sub)peltate, ovule subbasal to almost lateral; fruit large, free from the enlarged, fleshy perianth, endocarp more or less woody; seed large, endosperm lacking, cotyledons thick, radicle short.

The 6 genera of the *Cecropiaceae* are two by two very similar in their ecology, habit, and characters of the fruit and seed. Most species of *Coussapoa* and *Poikilospermum* are hemi-epiphytes, the species of *Cecropia* and *Musanga* are mostly pioneer plants, and most species of *Pourouma* and *Myrianthus* are small or medium-sized trees of the lower stories of more or less open and disturbed forests.

*Poikilospermum* has been revised by Chew Wee-Lek, Gard. Bull. Singapore 20: 1-104. 1963; *Musanga* and *Myrianthus* have been revised by de Ruiter, Bull. Jard. Bot. Belg. 46: 471-510. 1976.

### KEY TO THE GENERA OF THE CECROPIACEAE

1. Leaves peltate, their incisions and venation radial.
  2. Both staminate and pistillate flowers in spikes arranged in digitate clusters enveloped by a spathe. *Cecropia*
  - 2'. Staminate flowers in capitules on the ultimate dichotomies of branched inflorescences, the pistillate flowers in a more or less applanate spike. *Musanga*
- 1'. Leaves entire to (sub)palmate.
  3. Fruits large (more than 1 cm long); terrestrial trees or shrubs.
    4. Pistillate flowers sessile in a capitate inflorescence; staminate flowers sessile. *Myrianthus*
    - 4'. Pistillate flowers pedicellate in branched (or subumbellate) inflorescences; staminate flowers often pedicellate. *Pourouma*
  - 3'. Fruits small (less than 5 mm long); mostly hemi-epiphytes.
    5. Stipules fully amplexicaul; cystoliths absent; stamens 2 or 1. *Coussapoa*
    - 5'. Stipules not fully amplexicaul; cystoliths present; stamens 4-2. *Poikilospermum*

### SUBDIVISION OF THE URTICALES

The order *Urticales* is a very natural and clear-cut group without distinct connections with other orders of the dicotyledonous Angiosperms.

The subdivisions of this order, the families *Moraceae*, *Ulmaceae*, and *Urticaceae* of Engler's system (1889), are, on the other hand, not as sharply distinct as

the order. The close relationships of the subdivisions of the *Urticales* have been emphasized by most botanists who studied the order or one of its subdivisions.

In Bentham & Hooker's *Genera Plantarum* (1880) the *Urticales* (as *Urticaceae*) were subdivided into 8 tribes: 1. *Ulmeae*, 2. *Celtideae*, 3. *Cannabineae*, 4. *Moreae*, 5. *Artocarpeae*, 6. *Conocephaleae*, 7. *Urticeae*, 8. *Thelygoneae*. The eighth tribe had to be removed from the *Urticales*. Tribes 1 and 2 became subfamilies of Engler's family *Ulmaceae*. The tribes 3, 4, 5 and 6 became subfamilies of the *Moraceae*, whereas the *Urticeae* constitute the *Urticaceae* in Engler's system which for a long time was generally adopted. The subfamily *Cannaboideae* is treated as the family *Cannabaceae* nowadays, and correctly so, as this taxon is quite distinct, even rather isolated within the *Urticales*.

The *Conocephaloideae* were transferred to the *Urticaceae* by Corner (1962). The *Moraceae* s. str., thus exclusive of the *Conocephaloideae*, but still comprising the tribes *Artocarpeae* and *Moreae* of Bentham and Hooker's system, appear to form a coherent group of plants, in which only *Ficus* L. does not show very clear connections with the other members of the family. But this genus is not so isolated as to disrupt the unity of the family.

Chew Wee-Lek (1963) suggested to transfer the microspermous genera *Cecropia*, *Coussapoa*, *Musanga*, and *Poikilospermum* to the *Urticaceae* and to leave the megaspermous genera *Pourouma* and *Myrianthus* in the *Moraceae*, thus breaking the unity of the *Conocephaloideae*.

For a student of the *Moraceae* the *Ulmaceae* look like a distinct and uniform taxon. However, the two subfamilies may be distinct enough to regard them as families, while the *Celtoideae* appear not to be profoundly distinct from the *Moraceae* (Grudzinskaya 1967).

#### COMPARISON OF CHARACTERS

The *Cecropiaceae* have several characters in common with the *Urticaceae*. The pistil with a single stigma and a basal or subbasal orthotropous ovule is urticaceous. This type of pistil can be regarded as derived from the type of pistil (with two stigmas and an apical anatropous ovule) characteristic of the *Moraceae* and *Ulmaceae* (cf. Bechtel 1921). In the former family transitions to the urticaceous type of pistil can be found in the rather common reduction of one of the two style branches and the occasional lateral position of the ovule (as in *Castilla tunu* Hemsl.).

As in the *Urticaceae*, the system of latex tubes is reduced (Renner 1907; Guérin 1923; Tippo 1938). The plants do not exude milky latex but a mucilaginous sap usually turning black upon exposure to the air. However, some true *Urticaceae*, e.g. *Pouzolzia* Gaud. and *Laportea* Gaud. (cf. Guérin 1923), may exude milky latex! Léandri (1948) did not find laticifers in the herbaceous *Fatoua madagascariensis* Léandri, which species, as well as *F. pilosa* Gaud., is in many features reminiscent of *Urticaceae*, but distinctly moraceous in its pistil and fruit.

The type of cystoliths as occurring in the *Urticaceae* can be found in *Poikilospermum* (Renner 1907; Chew Wee-Lek 1963), but is lacking in the other five genera of the *Cecropiaceae* (Renner 1907). Arachnoid hairs as found in the urticaceous genus *Boehmeria* Jacq. are common in the *Cecropiaceae*.

In contrast to the *Urticaceae*, the *Cecropiaceae* can be characterized as woody and do not even show tendencies towards a herbaceous habit (as the *Moraceae* do).

The urticaceous type of stamens, inflexed in the bud and bending outward abruptly and elastically at anthesis, does not occur in the *Cecropiaceae*. Only a few species of *Poikilospermum*, namely the members of subgenus *Poikilospermum*, have more or less inflexed stamens, which apparently straighten gradually at anthesis. It has to be noted that inflexed stamens straightening gradually at anthesis (or remain more or less inflexed during anthesis) should be regarded

as distinct from those bending outward elastically (cf. Berg 1973).

The difference between inflexed and straight stamens has played an important role in delimiting taxa at the rank of family, subfamily or tribe, although many students of (groups of) the *Urticales* expressed some doubt about the significance of this difference. Corner (1962) dropped the difference as taxonomically unimportant. Corner's broad genus *Maclura* Nutt. comprises as section the former genus *Cudrania* Tréc. differing from the other sections of that genus in having straight stamens instead of inflexed ones. Genera placed far from each other in previous systems because of the difference in stamens were put close together in Corner's classification of the *Moraceae*. It is clear that the difference in stamens has rather little significance in Corner's tribes *Artocarpeae* and *Moreae*, which can be united into a single tribe *Moreae* (cf. Berg 1973). In the *Moraceae* taxa with inflexed stamens are confined to this tribe (Berg 1977a). On the other hand, inflexed stamens (springing back at anthesis) are a characteristic feature of the *Urticaceae*. Moreover, the difference in the stamens can be regarded as important with regard to pollination. Inflexed stamens are distinctly connected with wind pollination; the *Urticaceae* — possibly with a few exceptions — depend on wind as pollinating agent.

Apparent adaptations to wind pollination are missing in the *Cecropiaceae*, with the probable exception of *Cecropia*, which shows remarkable morphological adaptations to wind pollination (cf. Berg 1977b). These adaptations can only be expected in an urticalean group in which the stamens are basically straight.

While the *Urticaceae* are characterized by microsperry, both microsperrous and megaspermous genera occur in the *Cecropiaceae*.

Bisexual inflorescences and monoecious plants are rather common in both *Urticaceae* and *Moraceae*. But all species of the *Cecropiaceae* have unisexual inflorescences and are strictly dioecious.

The leaves are always spirally arranged in the *Cecropiaceae*, whereas the *Urticaceae* (and *Moraceae*) often bear their leaves in two rows (or less commonly opposite).

Formation of adventitious roots is a characteristic feature of the *Cecropiaceae*. These roots become stilt-roots in terrestrial taxa and aerial roots in hemiepiphytic genera.

The pollen grains of the *Cecropiaceae* do not deviate from the common urticalean type (Punt, personal communication).

The features of the secondary wood of the *Cecropiaceae* in some respects, like the presence of laticifers, resemble the *Moraceae* more closely than the *Urticaceae*. Considering the relative diversity of the wood characters of the *Moraceae*, the *Cecropiaceae* could be placed in the *Moraceae* on the basis of their wood structure (A.M.W. Mennega, personal communication).

## CONCLUSION

Corner's decision to remove the *Conocephaloideae* from the *Moraceae* was correct. But by placing this taxon in the *Urticaceae* he strongly reduced the uniformity and unity of this family.

The group of 6 genera which constituted the *Conocephaloideae* is quite distinct from the *Moraceae*, although it shows some, but not very pronounced, similarities to the *Moraceae* in vegetative characters. It is closely related to the *Urticaceae*, considering the similarities in the pistil and the reduced system of latex tubes. But it is not much closer to the *Urticaceae* than this family is to the *Moraceae*. Some genera of the *Moraceae*, like *Fatoua* and, to a lesser degree, the monotypic neotropical genus *Poulsenia* Eggers, show chiefly vegetative similarities and transitions to the *Urticaceae*.

The 6 genera appear to form a very natural, coherent group, which merits a rank equal to that of the *Moraceae* and the *Urticaceae*. To recognize the *Moraceae* s. str., the *Urticaceae* s. str., and the *Conocephaloideae* as subfamilies of a

broad family *Urticaceae* (cf. Berg 1973), would be an acceptable solution, but not a very practical one. It would certainly open the question whether the *Ulmaceae* could not also be inserted in such a broadly construed family, and consequently the limits of this family could co-incide with the limits of the order.

A better solution appears to be to return to Bentham and Hooker's subdivisions of the (*Urticaceae* =) *Urticales*, leaving however, the *Artocarpeae* and *Moreae* together in one family, the *Moraceae*, and the *Ulmaceae* and *Celtideae* provisionally in a single family. (cf. Grudzinskaya 1967).

#### KEY TO THE FAMILIES OF THE URTICALES

1. Ovule apical (to lateral) and anatropous; style usually bifid.
  2. Plants without latex; stamens straight.
    3. Arborescent plants. *Ulmaceae*
    - 3'. Herbaceous plants. *Cannabaceae*
  - 2' Plants with latex (except the herbaceous *Fatoua*); stamens straight or inflexed. *Moraceae*
- 1'. Ovule basal or subbasal, (sub)orthropous; style unbranched.
  4. Stamens straight in the bud, sometimes inflexed but not bending outward elastically; plants arborescent. *Cecropiaceae*
  - 4'. Stamens inflexed in the bud and bending outward elastically; plants herbaceous or woody. *Urticaceae*

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