Taxonomy, systematics, and biogeography of Ficus subsection Urostigma (Moraceae)

Chantarasuwan, B.

Summary & Conclusion

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Ficus subsect. *Urostigma* is a taxonomically notorious group, because of the very variable morphological characters, the wide range of distributions, its unsatisfactory systematic classification, and its problematic circumscription when compared with other subsections. Moreover, *Ficus amplissima* and *F. rumphii* were misplaced by Berg (2004), and this also had its impact on the morphological characters typical for the group. Therefore, the aims of thesis are: 1) To solve the problem of the classification, 2) To study the history, as well evolutionary as biogeographically, and 3) To establish the subsection's economic value.

Five research methods were used: Morphological characters, leaf anatomy, pollen morphology, molecular phylogeny, and historical biogeography. Seven topics are the result: 1) A revision was made based on morphology in which 27 species are recognized, but which also showed that morphology alone cannot solve all problems because of variation within the species. 2) Leaf anatomy displayed less variation in characters and anatomical characters proved to be useful for the classification of *Ficus*, especially in combination with morphology. 3) Pollen morphology appeared to be similar for all species and the characters can merely be used for generic recognition. 4) A new classification for subsection *Urostigma* is proposed in which the circumscription of the subsection and the species is the result of combining molecular phylogenetic information with morphology and leaf anatomy. 5) *Ficus cornelisiana*, a new species from Sino-Himalayan, was reported based on morphological and leaf anatomical evidence. 6) The historical biogeography was studied by using molecular dating and ancestral area reconstruction. 7) The use of some Thai species within subsect. *Urostigma* is reported, six of them are used as food, as ornamental, or the uses are related to religion or sacred purposes.

Which species can we morphologically distinguish in *Ficus* subsect. *Urostigma*? What are their diagnostic morphological characters? What is the extend of morphological overlap between the species?

Based on morphology, 27 species of *Ficus* subsection *Urostigma* were described in the revision of Chantarasuwan et al. (2013, see chapter 2). *Ficus cornelisiana* was later added as a new species based on morphology and leaf anatomy (Chantarasuwan et al., 2014, see chapter 6). A new classification based on morphology, leaf anatomy, and a molecular phylogeny (chapter 5) resulted in the reinstatement of *F. glabella* and *F. wigthiana* as species and the description of a new species, *F. pseudocaulocarpa*, distinct from *F. caulocarpa*. Thus in total 31 species are recognised as part of subsect. *Urostigma*. Morphologically the subsection is distinct by the presence of intermittent (seasonal) growth, shedding of the leaves during the dry season, articulated leaves in Asian-

Australian species, figs below the leaves and/or on spurs on the older branches, and staminate flowers mostly near the opening (ostiole) of the fig. However, none of these characters is always present or unique for the subsection. *Ficus verruculosa* is evergreen, while *F. religiosa* does not shed its leaves when growing conditions are everwet. Figs below the leaves or on are spur are also present in other sections such as Sect. *Americana* (e.g., *F. americana*), sect. *Galoglychia* (e.g., *F. bubu*). Staminate flowers near the ostiole is a rather good character, but some species of subsect. *Urostigma* show dispersed staminate flowers (*F. cornelisiana*, *F. densifolia*, *F. hookeriana*, *F. orthoneura*, and *F. prolixa*), while *F. arnottiana* shows staminate flowers mainly around the ostiole, but also a few dispersed when there are abundant staminate flowers. Dispersed staminate flowers are typical for other sections of subgen. *Urostigma*. The variation within species can be high, easily causing misidentifications if only morphology is used to recognise species. Hence morphology has to be combined with other characters.

Do the species of *Ficus* subsect. *Urostigma* differ in leaf anatomy? Does the leaf anatomy provide proper diagnostics for the recognition of species? Will leaf anatomy strengthen or improve morphological species circumscriptions?

The main leaf anatomical characters of *Ficus* subsection *Urostigma* (Moraceae) for the subsection recognition (Chantarasuwan et al., 2014, see chapter 3) are: The epidermis is mostly single-layered, but sometimes a multiple layer is present. The multiple epidermis comes in two forms: 1) The outer and inner epidermal cells are similar in shape and only gradually increasen in size from the periphery to the deeper layers (*F. arnottiana*, *F. wightiana*) or 2) the cells in the inner layer are much larger than those in the outer layer and both layers resemble an epidermis with a separate hypodermis (*F. cornelisiana*, *F. hookeriana* and *F. orthoneura*). "Enlarged lithocysts" mostly appear on the abaxial side of the lamina, except in *F. arnottiana*, which shows abundant enlarged lithocysts adaxially and very few abaxially. The anatomical variation within species is limited when compared with morphology. However, some species are not clearly identifiable with only leaf anatomy (*F. ingens* vs. *F. virens*, *F. prasinicarpa* vs. *F. pseudoconcinna*). Nevertheless, leaf anatomy in combination with morphology provides conclusive characters for species recognition.

Does pollen morphology show the same functionality as leaf anatomy in the characterisation of species?

The pollen morphology of the species within *Ficus* subsection *Urostigma* (Moraceae) (Chantarasuwan et al., 2014, see chapter 4) is largely similar to that of other sections. The main characters are: The grains are very small to small, mostly 2–porate with an ellipsoid or gibbous shape, or they are sometimes 3–porate and rarely 4–porate and then quadrangular in polar view. The pores are circular and 1.2–4.7 μm diam. The exine is less than 1 μm thick,

and the ornamentation is nearly always scabrate. The pollen morphology does not provide good characters to diagnose species or even the subsections.

What is the most likely phylogeny of *F.* subsect. *Urostigma*? How do the two species in section *Leucogyne, F. amplissima* and *F. rumphii*, fit in? How is *Ficus* subsect. *Urostigma* related to other subsections and sections within *Ficus* subgenus *Urostigma*?

The controversial classification of two species, *F. amplissima* and *F. rumphii*, forming former sect. *Leucogyne*, has been clarified. Based on morphology, leaf anatomy, and molecular phylogeny [chapter 5, but see also Rønsted et al. (2005, 2008), Cruaud et al. (2012)], evidence is presented to classify the two species in subsection Conosycea. The phylogenetic results also show *Ficus* subsect. *Urostigma* to be more close related with the dioecious figs (subgenera *Ficus*, *Sycidium*, *Sycomorus* and *Synoecia*) than with other members within subgen. *Urostigma* (sect. *Americana*, subsect. *Conosycea*, sect. *Galoglychia*, and sect. *Stilpnopyllum*). Morphological character states shared with other groups are the result of parallel evolution or reversals (homoplasy).

How can the phylogenetic results be translated into a classification? Are clades recognisable with the aid of morphology, leaf anatomy, and/or pollen morphology? How can we explain the evolutionary trends in morphology, leaf anatomy, and pollen morphology?

Changes in the environment (climate, geology) result in variability, homoplasy in characters and speciation. The variability and homoplasy in characters can obscure the phylogeny of a group. Molecular data, because of their multitude of characters, then help to reconstruct a phylogeny, and when combined with morphology and anatomy, clades in the phylogeny also become recognisable. The phylogeny clearly demonstrated the high levels of homoplasy in the morphology, not only within subsection *Urostigma*, but also among members of the various infrageneric groups. The phylogeny also helped to unravel or indicate cryptic species. Convergence in characters made it impossible to first separate *F. pseudocaulocarpa* and *F. caulocarpa*, because they were morphologically quite similar, but the molecular data clearly separated both entities in the phylogeny, which resulted in the description of a new species, *F. pseudocaulocarpa*.

Where and when did the major diversification events occur in the evolution of *Ficus* subsect. *Urostigma*? Which scenario results from the historical biogeography of the species? How can we explain the disjunction between the African and Asian-Australian species?

The origin of the subsection was probably on Madagascar at the end of the Paleocene or early-Eocene. Birds may be the main dispersal agent in the distribution of the figs from Madagascar to Africa in the Eocene. Probably the subsection reached Asia by rafting on India, because India has the first origin of the Asia species (*F. religiosa F. tsjakela* and *F. pseudocaulocarpa* mainly developed in India). All other species dispersed from India and widespread species even crossed Wallace's Line and even reached Micronesia and Australia (e.g., *F. glabella*, *F. geniculata* var. *insignis*, *F. virens*). *Ficus ingens*, an African species in the Asian clades, probably returned to Africa before the middle Miocene, when the Arabian land bridges were formed (Rögl, 1999) and when the climate was still warm and humid (Zachos et al., 2001).

Which species of *Ficus* subsect. *Urostigma* are used by man and for which purposes?

Species of *Ficus* subsect. *Urostigma* are commonly used as food and/or medicine around the world. In Thailand, the young syconium (fig) and young leaves of five species are used as food. *Ficus superba*, growing inshore, is consumed by people living in the south-eastern and peninsular part of Thailand; *F. caulocarpa*, *F. geniculata*, *F. glabella* and *F. subpisocarpa* are grown in home areas in the northern part for food. Seven species are utilised as sacred trees, *F. religiosa* is the most famous sacred tree in Hinduism and Buddhism. Six species are employed as ornamental plants.

Future studies

The taxonomic part of *Ficus* subsect. *Urostigma* is now clear, but some molecular work is still needed to prove the relationships of *F. cupulata* and *F. chiangraiensis*. The problematic variation within *F. virens* was only partly dissolved here, but more molecular data are needed to unravel this complex of cryptic species. Leaf anatomy appeared to be very suitable for species recognition in combination with morphology. Studying the leaf anatomy of other infrageneric groups of *Ficus* will also increase the taxonomic identification of their species. The functional ecology of the *Ficus* species was not studied. Figs are often very important as food tree for animals, quite often helping them to survive through the dry season (Berg & Corner, 2005; Berg et al., 2011; Shanahan et al., 2001; Harrison et al., 2012). The effect of deforestation and a changing climate on the species, its predators and its ecosystem should be studied to provide information for durable wildlife conservation.