1 Introduction: the Tiliaceae and genus *Tilia*

Tilia is the type genus of the family name Tiliaceae Juss. (1789), and T. × *europaea* L. the type of the generic name (Jarvis *et al.* 1993). Members of Tiliaceae have many morphological characters in common with those of Malvaceae Juss. (1789) and both families were placed in the order Malvales by Engler (1912). In Engler's treatment, Tiliaceae consisted mainly of trees and shrubs belonging to several genera, including a few herbaceous genera, almost all occurring in the warmer regions.

This treatment was revised by Engler and Diels (1936). The family was retained by Cronquist (1981) and consisted of about 50 genera and 700 species distributed in the tropics and warmer parts of the temperate zones in Asia, Africa, southern Europe and America. Several genera of trees, such as *Apeiba* in South America and *Tilia* itself, are of economic value for timber, and similarly the herbaceous genus, *Corchorus*, includes *C. olitorius* which is grown extensively in Bengal as the source of a brown fibre, jute, used for string, cloth ('hessian'), formerly carpet-backing and paper.

Significant characters that are shared by Tiliaceae and Malvaceae include the presence of mucilage, a general absence of secondary chemical constituents that are toxic to animals, some specialist feeders such as *Pyrrhocoris apterus* (L.) (Hemiptera), palmately lobed leaves (the leaves of *Tilia* are discussed on pp. 11–17) that bear soft, often fasciculate or stellate pubescence, and stipules that are free and often shed shortly after expanding. The flowers are actinomorphic and pentamerous, with valvate sepals and distinct petals; stamens are numerous and in two whorls (diplostemonous) and placentation of the ovules is always axile.

The two families are separated by floral characters. In Tiliaceae, as traditionally defined, the stamens are free or joined at the very base of the filaments to form five or ten groups, and each filament divides into two near its top and bears one half of a bilocular anther. Staminodes are present in some species. The ovary is syncarpous with five or more carpels but only one style and a stigma with a lobe above each carpel. In Tiliaceae, the ovules are anatropous. In Malvaceae, filaments of the stamens are fused into a tube but have separate apices that each bear a unilocular anther. Staminodes are absent. Each of five or more carpels supports a separate style, which together pass through the staminal tube so that the stigmas are exposed above the anthers. The ovules may be either anatropous or campylotropous.

Molecular studies comprising sequence analysis of DNA of two plastid genes (Bayer *et al.* 1999) show that, in general, the inclusion of most genera, including *Tilia*, traditionally placed in Malvales is correct. There is, however, clear evidence that some of the traditional families, including Tiliaceae, are heterogeneous and, for example, some genera in the family are more closely related to genera in the Sterculiaceae so that some reclassification is necessary.

The solution proposed by Bayer *et al.* (1999), and subsequently reaffirmed by the Angiosperm Phylogeny Group (APG II 2003), was to treat the groups (clades) defined by DNA analysis as subfamilies within a single greatly enlarged Malvaceae. Essentially, this converts an order to a family and creates subfamilies, which simply adds another layer of names. What rank the classes are given is largely an arbitrary decision. The retention of families, appropriately adjusted, within the order Malvales, as set out by Heywood *et al.* (2007) is simpler, retains taxonomic stability and is more useful for taxonomists and the many users of taxonomy.

In the treatment of the Malvales by Cheek (in Heywood *et al.* 2007), the group of genera, including *Apeiba*, consisting of large trees, *Grewia*, with many species of shrub or small trees, *Sparrmania*, small shrubs, and the herbaceous genera *Corchorus* (jute) and *Triumfetta*, which in their flowers or leaves often have a 'look' of *Tilia* and were formerly in Tiliaceae, are placed together in the Sparrmanniaceae.

In the context of the subject of this book, the most significant result of the molecular analyses is the separation of *Tilia* at the second division of the dendrogram from all other genera investigated, including those from traditional Tiliaceae. This implies separation from other Malvales at a very early stage in evolution, and is confirmed by the geological record (Chapter 12). Not only is *Tilia*-type pollen found in the Cretaceous and leaves, bracts and fruits of *Tilia* are present in the early Tertiary, but fossil parts closely matching species still living today occur in the middle Tertiary. All living species of *Tilia* are trees, and the slow rate of genetic change is surely linked to their longevity and to the length of up to 300 years of the regeneration cycle of trees when they occur in stable climax woodland (Chapters 13 and 14). This strengthens the case for retaining Tiliaceae even if it were to consist of a single genus.

The genus *Tilia* is morphologically unique: no other genus possesses the remarkable cymose inflorescence which is partly fused to a conspicuous oblong or elliptical bract.

The genus just enters the tropics in Vietnam and Mexico, but is otherwise exclusively in the temperate zone of the northern hemisphere, where it probably had a circum-boreal distribution in the Tertiary that is now interrupted by its absence from western North America, where it grew in the Tertiary, and westernmost China (Xingjang) and Central Asia. Although a very large number of species of *Tilia* have been described, evidence is presented here that there are probably no more than 24 taxa justifying the rank of species.

It is possible that other genera in the Malvales that have not yet been studied by molecular techniques will prove to be in the same clade. Two genera have been discussed in this respect, *Craigia*, which was originally placed in the Sterculiaceae by Smith and Evans (1921), contains two species, *C. yunnanensis* and *C. kwangsiensis*, that are both native in southern China, and are trees. The leaves of *C. yunnanensis* are symmetrical and ovate (Figure 1.1a), with conspicuous pinnate veins, but with two short veins in a palmate position at the base. The inflorescence is cymose but not attached to a subtending leaf or bract. The flowers are pentamerous with the stamens in groups on the same radii as the petals; the pollen is of *Tilia*-type and there are staminodes. The fruits (Figure 1.1c) have membranous wings in the same position as the ridges on the fruits of many species of *Tilia*; these split to release the seeds. The lower surface of the leaves, the inflorescence and the sepals are covered in dense fasciculate hairs. There are therefore many morphological features in common with *Tilia* and on this evidence it has been proposed that *Tilia* and *Craigia* should comprise Tiliaceae. Several Central American woody genera of 'old' Tiliaceae have yet to be studied using molecular techniques, but, of these, *Mortoniodendron* has already been shown to be another member.

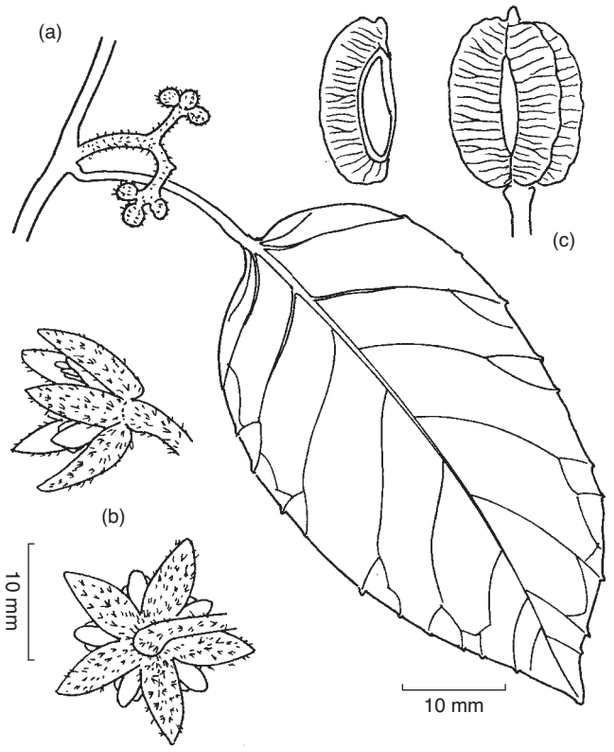

Figure 1.1 *Craigia yunnanensis* from the valley of the Longchuan Jiang, Yunnan, China. (a) leaf and inflorescence, (b) flower and (c) fruit and seed. Measured and drawn from type material collected by George Forrest (8253).