

# Lime-trees and Basswoods

A Biological Monograph of the Genus *Tilia*

DONALD PIGOTT



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## **Lime-trees and Basswoods**

A Biological Monograph of the Genus *Tilia*

Lime-trees (*Tilia* spp.) are widely distributed and locally important members of northern temperate broad-leaved forests. In marked contrast to the largely uniform morphology of the genus, described in the first two chapters, its taxonomic treatment has become increasingly confused and controversial, with over 100 species described.

Using extensive data from field studies of natural populations throughout the native distribution, this book clarifies the situation, proposing a revised taxonomy of 23 species and 14 subspecies. Detailed descriptions are provided for all recognised taxa and are accompanied by illustrations. Data from herbaria and cultivated trees are used to extend the analyses where appropriate and type specimens are included to ensure stable nomenclature. The distribution and general ecology is summarised for each species.

The final chapters are devoted to the geological history of the genus, the physiological and reproductive ecology of the most fully studied species and the association of lime-trees with human culture, including their utilisation and cultivation.

DONALD PIGOTT is a past director of the Cambridge University Botanic Garden and former Professor of Biology and Head of Department at the University of Lancaster. He has spent over 15 years extending his earlier studies of the genus *Tilia* to cover its full natural range from Japan and China, to Europe, eastern North America and Mexico.



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**To Margaret, Julia and Sheila**





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# Preface and acknowledgements

Lime-tree, basswood, duan, Linde, lípa, shinanoki, tilleul and many more: there are as many names as there are languages in the regions where this very distinctive tree is native, for it is surely one of the most easily recognised trees of the woods of the northern temperate zone and, until the advent of the car, one of the most loved and respected. Ever since Carl Linnaeus accepted the classical name *Tilia* for the genus, there has never been any confusion about its identity.

The same cannot be said of the species, however, of which the names, and the trees to which they refer, began with a confusion and have continued in much the same way up to the present day. Linnaeus himself was very familiar with the native lime-tree of southern Sweden that was, and still is, common in woods and meadows around his family home. It was also the tree from which his family had taken its name. Unfortunately, he did not distinguish it from the large tree that still grows at Uppsala University, from which he probably took the one specimen that he labelled *T. europaea*, and which remains in his herbarium in London. Thus the name that he surely intended for the widespread species for which we now use Miller's name, *T. cordata*, is, by the rules of nomenclature, applied to the hybrid of that species with *T. platyphyllos*. Even Miller's name, *T. cordata*, proves not to have priority, but it is so well established that a proposal to conserve it has been accepted. Indeed, a simple measure of the general confusion is that more than 200 names of species of *Tilia* have been published for what, in my opinion, is about a tenth of that number of species.

Before embarking on this project, I had discovered, as evidently Linnaeus had before me, that even with only two native species in Britain, and with both natural and planted hybrids between them, correct identification is not learnt easily or quickly. The reasons for this are discussed in later chapters but essentially the solution is to study whole trees, collect flowering or fruiting specimens for taxonomic purposes and, if possible, first study natural populations. To extend

this discipline over the whole native range of the genus has only been possible with generous financial grants and with co-operation and help from a very large number of people.

A long list of people's names has little to commend it, so I have placed them in their historical and geographical context, and start at the beginning. My lifelong fascination with plants, not just discovering their names but also how they work, stems directly from my mother, Helen Constance Pigott (née Lee), who encouraged me to grow plants, raise them from seeds and learn their names. A large tree grew in our rather marshy garden and, at an early age, I was with her on a visit to Kew Gardens (the Royal Botanic Gardens) when she identified it as *Acer negundo*, box elder (scarcely a recommendation for using English names). I thank her for sowing a seed that grew into my deep interest in trees and a delight in Kew.

As a boy, I had the good fortune to meet, by chance, Mr A.B. Jackson, whom I visited at Kew several times and accompanied on excursions. Then, as an undergraduate, I was taught by Dr H. Gilbert-Carter and took to heart his advice 'when entering a wood, first look up at what is above you' and I fell under the spell of Dr A.S. Watt. From Cambridge, using Babington's *Flora* (1860), I visited the White Wood at Gamlingay and there encountered *T. cordata* with *Convallaria majalis* (lily-of-the-valley), both species that I had not previously seen in the wild, and in a combination that later proved to be significant.

In 1951, I moved to the University of Sheffield and began research on the influence of climate and soils on the vegetation of the Derbyshire upland. While exploring the extensive woods in the limestone dales, in which ash (*Fraxinus excelsior*) predominates in the canopy and was regarded by Moss (1913) and Tansley (1939 pp. 427–8) as the 'natural climax dominant', I came across small populations of lime-trees, usually on cliffs, or steep, rocky outcrops. They invariably consisted of large and evidently old trees of *T. platyphyllos*, rarely *T. cordata*, and often hybrids between them, with no regeneration from seedlings. A field-layer of several unusual species, including *Convallaria majalis*, characterised the sites.

Further investigation provided evidence that these were probably relics of a much older woodland, largely destroyed by clearance and grazing, and then replaced by secondary woodland of ash. In that case, *T. platyphyllos* was surely native, even though the then current *Flora of the British Isles* (Clapham, Tutin and Warburg 1952) treated the species as doubtfully so. The absence of suitable deposits of peat or sediments nearby prevented the use of pollen analysis to confirm these hypotheses. I am much indebted to Professor A.R. Clapham for his support and keen interest in all my work throughout that period.

A brief spell in Cambridge and my move in 1964 to the then new University of Lancaster gave me the opportunity to investigate the causes of failure of regeneration, as it brought me within easy working distance of localities of *T. cordata*, both close to, and at, the north-western limit of its natural distribution. A preliminary study found that these populations, like those in Derbyshire, consisted of large, often very large, old trees with no apparent regeneration from seedlings. Large samples of fruits from several trees at Aughton near Lancaster proved each year to be almost completely sterile, and smaller samples from other sites in the Lake District were the same. A research project was designed to investigate the causes and I thank the Natural Environment Research Council for a sequence of grants to fund this work. I also thank both Mr J.S.R. Chard of the Forestry Commission for proposing that part of this work should be at Grizedale, and members of the staff there for their help. I am indebted to Mrs J.P. Huntley (née Paice) for her enthusiasm and wide range of skills as my research assistant, Mr W.A. Wood, my very able research technician, and Mr W. Blackledge, glass-house technician at Lancaster. Grants from NERC also supported me and Professor W.J. Davies in a joint project on shade tolerance and water relations of young plants of *T. cordata*, and me and my first wife, Margaret Pigott (née Beatson), in palynological studies at Cunswick Tarn, close to localities of *T. cordata* and *T. platyphyllos* (the latter now known to have been planted).

An opportunity to investigate regeneration of *T. cordata* in Poland arose in 1973, when Professor M.J. Dąbrowski suggested that I visit Białowieża. I thank the Royal Society and the Polish Academy of Sciences for financial help, Professor Dąbrowski for making the arrangements, and Ewa Kamin-ska for her assistance with fieldwork. The results were the stimulus for studies of regeneration in southern England and France, for which I thank the National Trust for permission to set up enclosures on their properties and Mr P.G. Collis and Dr J.P. Sankey for looking after the plots. In France, I thank the Université de Paris 12 and Professor C. Jacquot for permission to work at the laboratory at Fontainebleau, and the forest officers, first M. J. Gallon and then M. P. Pouvesle, for protecting my plots at the Forêt de Villefermoy for a period of 34 years.

A visit to the Institute at Vác-rátót in Hungary, arranged by the Royal Society and Hungarian Academy of Sciences, led to my association with Professor Fekete G., who took me on excursions to study *Tilia* and has since helped me in so many ways. I also thank Dr Géza K. of the Institute for his help with establishing a neotype of *T. tomentosa*.

The mechanism by which climate-controlled seed production in *T. cordata* that Jacqueline Huntley and I had discovered, attracted the attention of Professor D.M. Gates and, in 1978, I was invited to Ann Arbor University in Michigan. From this, a programme to study the ecology and taxonomy of *Tilia* in eastern America evolved, and I thank the Royal Society, the Waldorf Astor Foundation, the University of Cambridge and the Arnold Arboretum of Harvard University for generous financial assistance that over many years enabled me to make field collections in 14 states and work at Harvard. I thank Dr E.W. Wood for enabling me to work in the Harvard Herbaria and Ms G. Wade for help in the library. I thank Dr R.E. Cook for inviting me to work in the Arnold Arboretum and Ms S. Kelley, Ms S. Hardy Brown and Mr K.D. Port for their assistance and Jianhua Li for our co-operative project on the analysis of the DNA of diploid species of *Tilia*. During fieldwork in America, so many people have helped in various ways, but I am especially grateful to Mr A.K. Gholson (Florida, Georgia), Mr C. Ludwig (Virginia), Professor R.K. Peet (Carolinas) and Mr A.E. Radford (Carolinas), who arranged programmes and contacts, and accompanied me, or my wife and me, on fieldwork. I thank Dr G. Williams-Linera of the Instituto de Ecología at Jalapa for arranging a visit to the Sierra Madra Orientale in Mexico and Mr N.P. Pavón for his guidance in the field.

During a visit to the Soviet Union in 1983, which was primarily for the ecological study of deciduous, broad-leaved woodlands, under an arrangement between the Royal Society and Soviet Academy of Sciences for academic exchange, I was also able to visit the Main Botanic Garden in Moscow and the garden of the Ukrainian Academy of Sciences in Kiev. In both gardens, I was permitted to collect herbarium material of several species of *Tilia* from the Caucasus, the far east of Siberia and north China. I became aware, as I had in America, that there seemed to be very real problems in the taxonomic treatment of the genus. I thank Dr N.A. Kokhno and the staff of the gardens for their help and particularly Dr A. Kurdyuk, who subsequently sent me seed samples and literature.

In 1984, I moved to the University Botanic Garden in Cambridge and decided to consolidate and extend my interest in *Tilia* to the whole genus. So, I began to build up a collection to determine chromosome numbers and, I hoped, eventually for molecular analyses. For the next 10 years, Mrs J. Free was my research technician, and I thank her for the wide variety of laboratory work she undertook and especially for her skill in preparation of root-tip squashes and making most of the chromosome counts. I also thank Mr P. Kerley for his care of and

contribution to the living collection, and with Mr N. Villis for their help on collecting expeditions to the Caucasus and America. During this period and the years immediately after, my wife, Sheila Pigott (née Megaw), and I made a series of expeditions, primarily to collect herbarium material and, where possible, seed or scion wood of almost all the species of *Tilia* now accepted.

For several of these expeditions, I received financial assistance from the Royal Society and from corresponding academies, which included the Soviet and subsequently Russian Academy of Sciences, Chinese Academy of Sciences (Academia Sinica), China Association of Science and Technology, British Council, Japan, the Stanley Smith Horticultural Trust, and the University of Cambridge Travel Fund. For all this generous support I express my sincere gratitude.

Two expeditions were made to the Great and Little Caucasus and I thank Professor Dr M.A. Gogolishvili for inviting us to be based at the Central Botanic Gardens in Tbilisi in 1988, Miss M. Bestaeva, our interpreter, and Professor Dr N.G. Tarassashvili, both for his guidance in the field then, and for his and Mrs L. Tarassashvili's hospitality on a second expedition in 1990. A visit to the Crimea in 1992, specifically to study *T. dasystyla*, was arranged through the Botanical Society of the Russian Republic and we thank Dr V. Schatko and Miss I. Volkovskaya for their company and help throughout, and Dr V.N. Golubev for guiding us in the hills near Yalta.

In the summer of 1993, 10 weeks were spent in China visiting sites in Hebei, Sichuan, Yunnan and Guangdong. Two more visits of two to three weeks' duration were made to Sichuan and Hubei in 1995, and to Jiangxi in 1996. Studies of herbarium material, especially types, were made in Beijing, Chengdu, Guangzhou, Kunming, Lushan (Botanic Garden) and Nanchang (Agricultural University), and I thank the staff of all these herbaria for their help and for providing translation. From each city, several expeditions were arranged and I express my sincere thanks to those who accompanied us in the field, shared their expert knowledge with us and helped us in every way. I also thank our drivers and the many local people who guided us and acted as tree-climbers for collecting specimens. From so many, I must, however, select for special thanks Professor Fu De-zhi (Xiangshan, Beijing), Professor Hu Chi-ming (Guangzhou), Professor Lai Shu-shen (Lushan), Dr Liu Ni-an (Guangzhou), Professor Qin Hai-ning (Xiangshan, Beijing), Professor Ren Xian-wei (Beijing), Mr Tan Ce-ming (Jiujiang Forestry Institute), Dr Yang Guang-yao (Nanchang), Professor Yin Kai-pu (Chengdu), Professor Yu Zhi-xiong (Nanchang) and Professor Zhang Zhi-ming (Beijing).

I owe a special debt to Professor Tang Ya (Chengdu) and Dr Zhuge Ren (South-western Forestry University, Kunming), who are both specialists on *Tilia*, *Craigia* and *Burretiodendron* in China. They planned much of our programme, shared their knowledge with me and accompanied us in the field. I also acknowledge a large contribution made by Tang Ya to the data for my maps of the distribution of many of the Chinese species. In Guangzhou, I was invited to Zhongshan University by Professor Chang Hung-ta and I thank him for a long and valuable discussion of his taxonomic work on *Tilia*.

In 1998, my wife and I visited Japan and I thank Professor Y. Uedo of Chiba University for making all our arrangements and for asking a number of his colleagues to assist and guide us on a tour of northern Kyushu and southern Honshu that enabled me to study in the wild and collect from several populations of each of the Japanese species of *Tilia*. We are most grateful to Mr H. Shide (Ooita, Kyushu), Dr T. Sera (Hiroshima), Professor Emeritus T. Seki (Hiroshima, now at Hatsukaichi), Mr Y. Kurashige (Akagi, Gunma) and Mr K. Arai (Karuizawa, Nagano) for their guidance in the field. I was also able to work in three herbaria and I thank Drs F. Konta and N. Murakami for their help in the National Science Museum in Tokyo and Kyoto University, respectively, and Professor H. Ohba (Tokyo University) for his help in general and especially with a joint study of T. Nakai's specimens from Korea. We thank Miss S. Akimoto for her care and for acting as interpreter in Kyoto.

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From 1990 to 2007, I made frequent visits to the Royal Botanic Gardens of Kew and Edinburgh and to the Botany Department of the Natural History Museum, London. I am most grateful to the staff of their herbaria and libraries, and of the two gardens, for the very great help given to me. In particular, I thank at Kew, Ms S. Andrews, Dr M. Cheek, Mr M.J.E. Coode, Dr M.J. Lock, Mrs F. Ainsworth, Mr A. Hall, Ms Y. Harvey and Mrs S. White; at Edinburgh, Dr C. Alexander, Dr D. Harris, Ms H. Atkins, Ms R. Hourston, Ms H. Hoy, Mr J. Main, Mrs M. Main, Ms L.

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America. I am indebted to Dr. W. Pennington for [Figures 12.7](#) and [12.8](#), which were prepared as part of a joint project, and to Dr. P.R. Gomarova for the data in [Table 9.2](#).

More generally, I have received help in many ways and constant encouragement from Dr A. Coombes and from Dr R.K. Brummitt, who, in addition, has been my constant adviser on sources of information, especially nomenclature, and finally read and checked the full text. I thank them both for all their help.

Important publications on the taxonomy and ecology of lime-trees have been published in many different languages and, although French and German presented few problems, I am grateful for assistance from Mrs B. Lousa and Mrs G. Megaw for their help. For large numbers of translations, I am indebted to Mr C. King (Hungarian), Dr W. Linnard (Russian, Polish), Professor Hong Tao, Dr Li De-zhu (Chinese), Mrs C. Burgess (Chinese place names), Mr J.S. Moyes (Spanish),

Mr P.H. Oswald (Greek, Latin) and Mrs M. Parslow-Otsu (Chinese, Japanese). Translation of a different kind was achieved by my son-in-law, Dr M. Hoggard, who devised a program to convert Canon word processor files to Microsoft Word and helped in the preparation of the book in many ways.

During my early studies of *Tilia*, mainly in Britain and Europe, I worked with my first wife, Margaret, and, on fieldwork, I was accompanied by our daughter, Julia, and I thank them for their interest, contribution and support. Since 1985, I have travelled extensively for fieldwork in Europe, Asia and North America, and my wife, Sheila, has been my constant companion and field assistant, often in wild and remote places. She has also helped me and supported me during the years of writing and preparing this monograph, finally checking and correcting the whole text, for all of which I thank her sincerely.





*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.

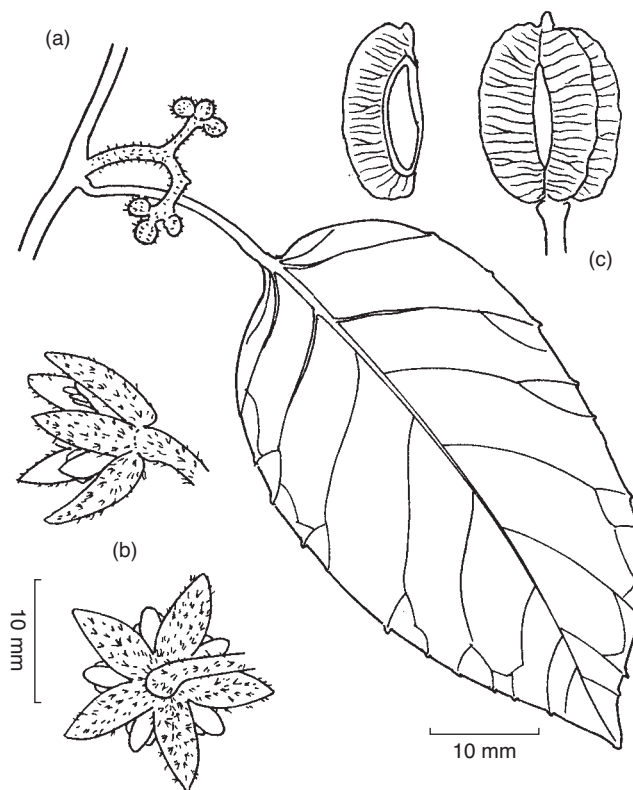
In the treatment of the Malvales by Cheek (in Heywood *et al.* 2007), the group of genera, including *Apeiba*, consisting of large trees, *Grewia*, with many species of shrub or small trees, *Sparmannia*, small shrubs, and the herbaceous genera *Corchorus* (jute) and *Triumfetta*, which in their flowers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

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



**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).

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, *Mortoni dendron* has already been shown to be another member.

# 2

## General morphology of *Tilia*

The species that make up the genus *Tilia* are remarkable for the uniformity of their general morphology and many features contribute to the ease with which the genus may be recognised. It is this overall uniformity which, by contrast, has made recognition of species difficult and resulted in much of the taxonomic confusion for which the genus is renowned.

This chapter describes the general morphology and provides a basis and terminology for the subsequent descriptions of the taxa.

### Tree form

Most species of *Tilia* have the potential to grow into large, long-lived trees that are stocky and broad-crowned when in the open (Figure 2.1a), and often 30–40 m tall and narrow-crowned when in woodland (Figure 2.2). There is great uniformity throughout the genus in the structural development of the tree but significant differences between species in the form of their crowns, which results from variation from the bottom to the top of the tree in rates of growth of branches and in frequency of branching.

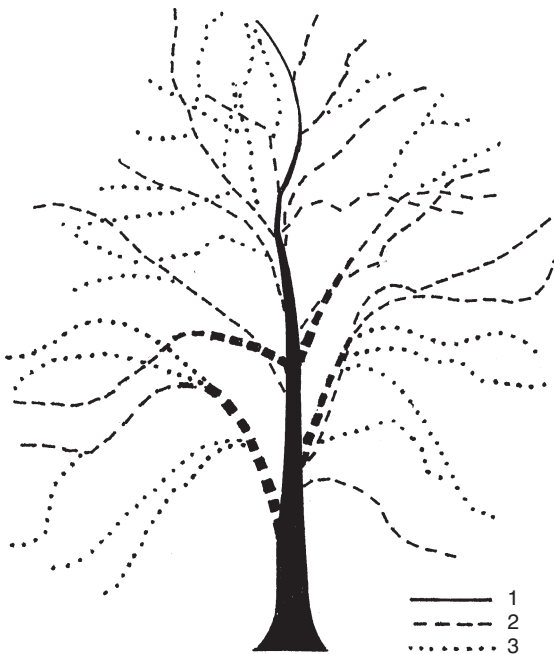
The main stem is orthotropic and usually remains dominant during the period of growth of a tree up into the canopy (Figure 2.1b). Branches form on the young sapling, even in shade, where, however, they are soon lost by abscission as the tree grows taller. The young tree develops a structure that is more or less the same in all species (Figure 2.3). In open, unshaded situations this consists of a vertical axis of the first order from which axes of the second order branch radially at angles of 40–80°. Branches of the third order are in two ranks and more or less horizontal. Growth in length of second order axes is initially slower than that of the primary axis to give a conical crown. In deep shade, axes of the second order also grow in two planes to form a flat, frond-like shoot that curves towards the horizontal (Figure 13.6).

Subsequent growth of the tree follows a pattern that was described by Ward (1909) and seems to be uniform for the genus (Figure 2.1b). A proportion of second order axes are promoted (the others are eventually lost) and grow at a rate that is only a little less than that of the primary axis. Similarly they retain their individuality to the periphery of the crown. A proportion of the third order axes do the same.

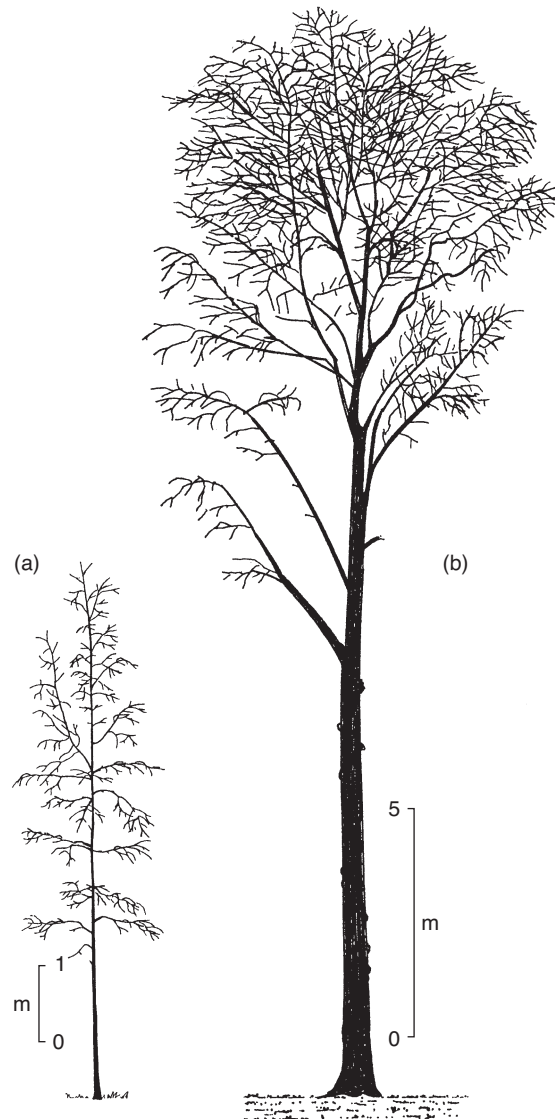
A remarkable feature of *Tilia* occurs in very old trees. On horizontal parts of the lowest branches, new vertical axes may arise that assume dominance and eventually produce a system of shoots resembling a whole tree. As the load increases the horizontal branches may sink down on to the ground and the whole structure can become rooted. Or events may be reversed and the terminal part of branches that touch the ground may root and produce a new vertical axis.

All species have the capacity to initiate new shoots from the base of the stem, or collar, immediately above the hypocotylar region. The morphology of the collar and its occurrence in *T. americana* is described by Del Tredici (2001). In most species, these sprouts are suppressed, so long as the primary axis remains uninjured and healthy. There are, however, a small proportion of individuals in some species (*T. americana*, *T. platyphyllos*, *T. cordata*, *T. tuan*) that produce basal shoots, even when there is no apparent damage to the main stem. The feature is most strongly developed in certain clones of hybrids (*T. × europaea*).

When mature trees are blown over, or when the main stem is broken or cut, dormant buds are activated, or new buds are initiated at the base, and these produce shoots capable of vigorous, orthotropic growth. Eventually a tree with several stems results (Figure 2.4). This process may occur naturally and is repeatable, so it seems able to bestow great longevity, perhaps even virtual immortality, on the individual tree (see Chapter 13). Trees of most species of *Tilia* with this structure have been noted throughout the range of the



**Figure 2.1** (a) Maiden tree of *Tilia platyphyllos* (160 years old, height 20 m, dbh 0.9 m) in an open situation at Cartmel, Lancashire. (b) Simplified plan of the same tree showing the primary axis (1), second order axes (2), that initially make an angle of  $20^{\circ}$ – $27^{\circ}$  to the vertical but diverge with increase of mass, and the main third order axes (3) which reach the canopy fringe (from photocopies of photographs).

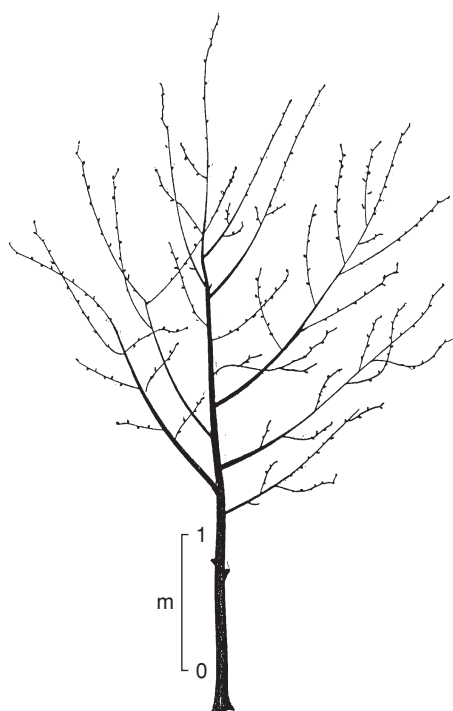


**Figure 2.2** (a) Young tree of *Tilia platyphyllos* (10–12 years old; dbh 0.06 m), shaded by *Larix decidua*, Alpes Maritimes, France. (b) Maiden tree of *T. tuan* growing in closed woodland at Xi-he reservation, Jiangxi, China (tracings of photographs).

genus in Japan, China, western Asia, Europe and eastern America.

## Bark

The anatomical structure of the bark of *Tilia* is quite characteristic and is described in [Chapter 3](#) (see pp. 28–31). It is uniform throughout the genus but the external morphology varies and there are significant differences between some species. The colour of the surface, when bark begins to form in the second year, changes from green to pale grey or brownish-grey. The outer bark is persistent and its thickness on the trunk and



**Figure 2.3** Tree of *Tilia dasystyla* subsp. *dasystyla* (9 years old), shaded on one side with the angle of the second order axes  $30^{\circ}$ – $40^{\circ}$  to the vertical on the shaded side and  $35^{\circ}$ – $60^{\circ}$  on the exposed side (from photograph).

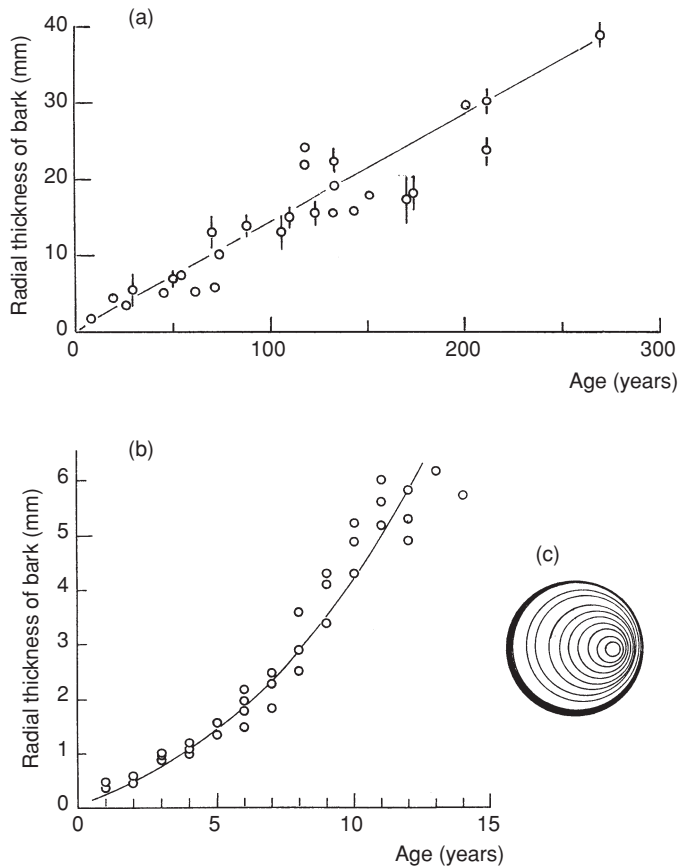
branches increases with age of the trunk (Figure 2.5a), and at a rate that is dependent on the radial growth of the whole stem. On vigorous branches, growth is faster than on those which are suppressed. If radial growth of a stem is not concentric, growth in thickness of bark is proportional to that of the wood on the same radius (Figure 2.5c). The outer surface is initially smooth, up to an age of 15–20 years and a thickness of both inner (phloem) and outer bark of up to 5–8 mm. At this stage, there are longitudinal rows of elliptical lenticels, each 1.0–1.5 mm long (Figure 2.6), and, as growth continues, cracks form down some of these lines of lenticels and shallow grooves begin to open. These run longitudinally and become wider and deeper to accommodate transverse stretching of the bark as the diameter of a stem increases.

In most species the ridges between the grooves are sinuous, remaining joined here and there to create an elongated mesh (Figure 2.6c and d) that is analogous to that of ‘expanded metal’ (Figure 2.6e and f). In a few species, such as *T. oliveri*, while the bark is still smooth the annual extensions of the shoots are marked by narrow ridges that form transverse rings around the stem and mark the annual increments in height or length.

With age, the longitudinal grooves deepen and either form narrow fissures, or remain open with relatively smooth or



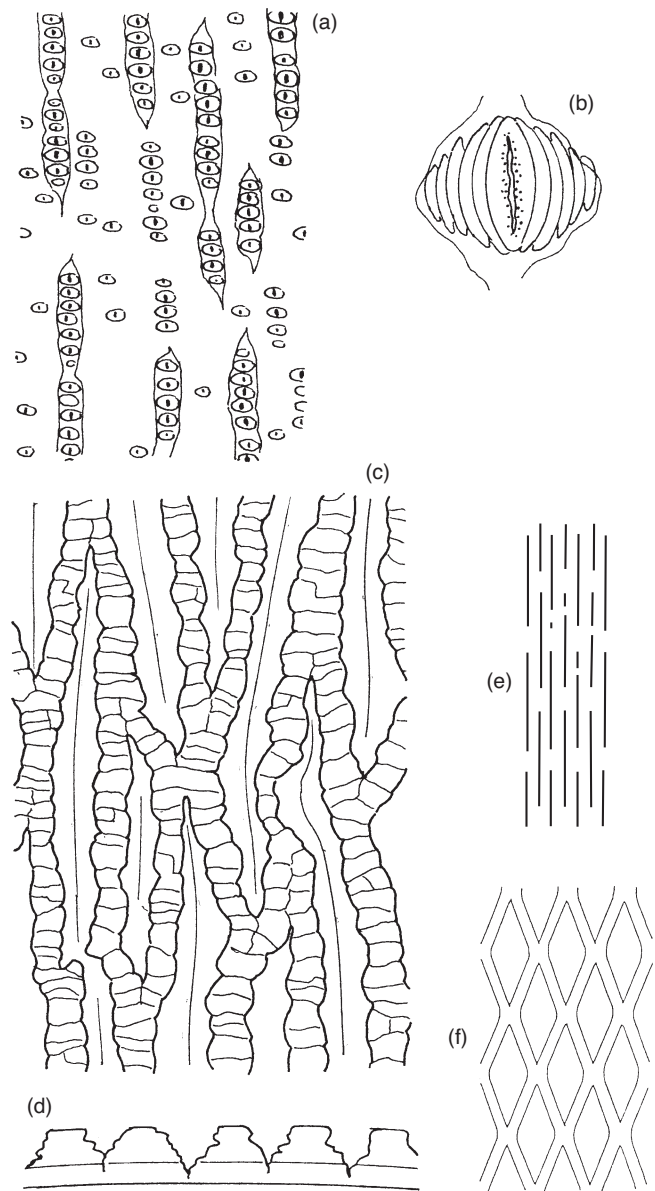
**Figure 2.4** Tree of *Tilia cordata* with six main stems, the oldest c. 90 years old, in a group up to 4.5 m across, Coniston, Lancashire, England (from photocopy of photograph).



**Figure 2.5** Growth in radial thickness of bark (periderm and phloem) on (a) 28 trees of *Tilia cordata* (mean and limits of 3–5 largest measurements for each tree) and (b) branches of *T. dasystyla* subsp. *caucasica*. (c) Radial growth of the bark is normally directly proportional to that of the wood on both trunks and branches.

slightly roughened margins. The intervening outer surface forms ridges varying in width between species from as narrow as 20 mm to as wide as 60 mm. In some species the surface of the ridges remains intact, but in others it becomes horizontally cracked as ridges deform, and in *T. chinensis* the rectangular pieces are gradually lost as loose flakes. In *T. kiusiana* the surface of the ridges erodes to form loose fibrous layers which can be peeled off. In most species, however, loss of material is by gradual erosion, and ridges become increasingly more prominent with age, as the bark increases in thickness to 10–16 mm at 100 years and 20–25 mm at 200 years (Figure 2.5a).

The phloem which forms the inner bark consists of concentric, alternate bands of conducting tissue and long-celled fibres with thick walls (see p. 28). In transverse section these are visible to the naked eye as triangular wedges between the expanded ends of the medullary rays and can be used to identify both roots and leafless shoots of the genus.

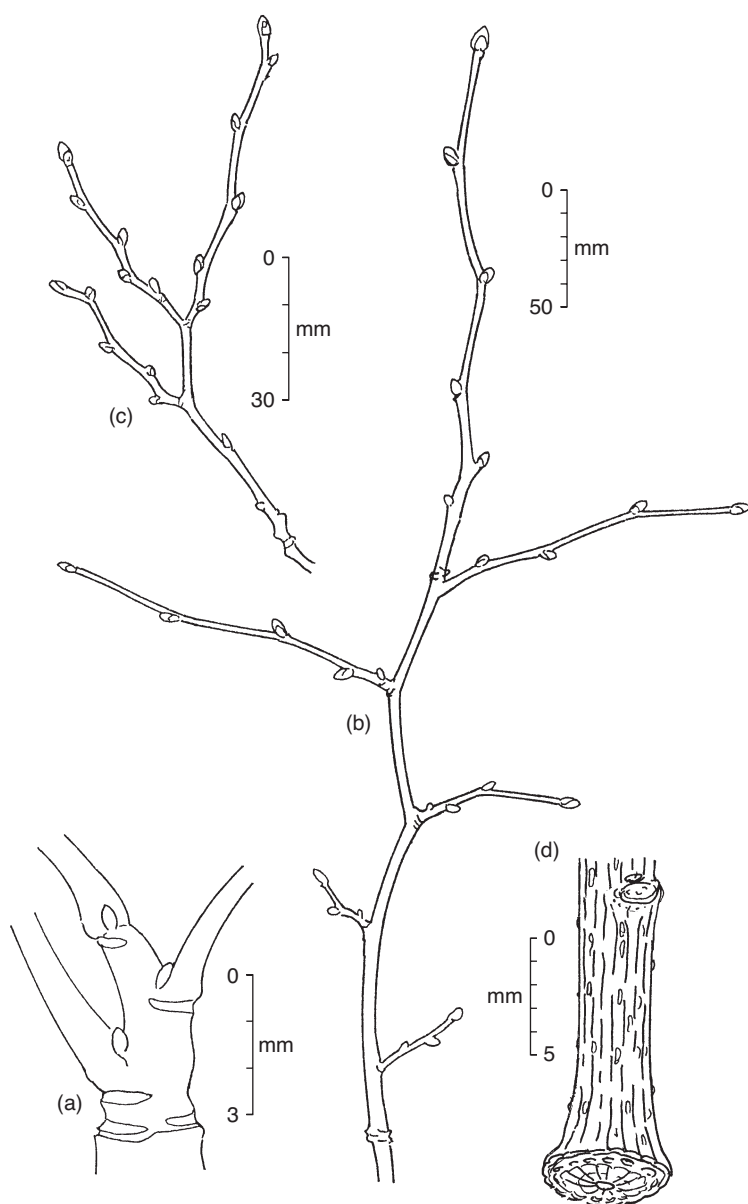


**Figure 2.6** Development of bark of *Tilia platyphyllos*. (a) Surface of bark on 11-year-old trunk with longitudinal rows of lenticels. (b) Lenticel enlarged. (c) Plan of surface. (d) Section of ridges and grooves (lines mark split at bottom of groove) of bark of 120-year-old tree. (e) metal sheet with vertical slots and (f) after lateral extension ('expanded metal').

## Twigs

Morphology of the twigs of the terminal shoots is broadly similar in all species of *Tilia* but varies in relation to the age of a tree, the position of shoots in the canopy and environmental conditions, particularly light intensity and exposure to wind.

The form of shoots in very young trees is described in Chapter 14. As trees grow larger, except in deep shade, the more or

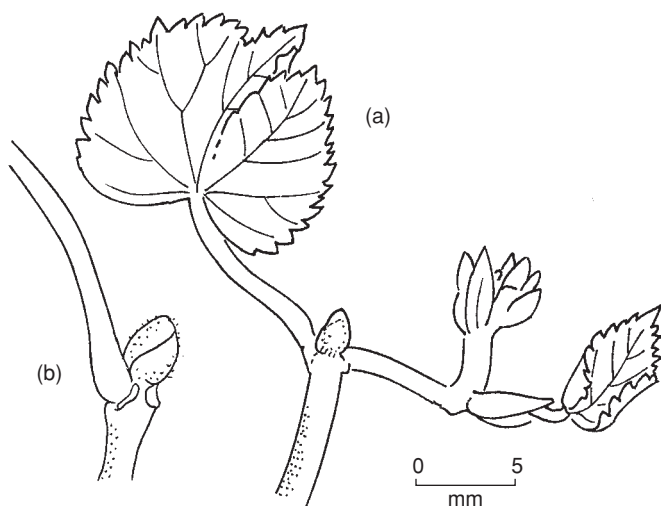


**Figure 2.7** Shoot of *Tilia cordata*. (a) Shortly after extension begins from bud. (b) From a lower branch with extension of long shoot of current year (c. 0.45 m) and development of intermediate- and short-shoots on long-shoots of previous year. (c) From fringe of canopy at 18 m above the ground with no clear hierarchy of shoots (each 35–50 mm long). (d) Base of dead 2-year-old twig showing transverse, basal abscission.

less horizontal, terminal shoots of the lateral branches develop a well-defined hierarchy of branching (Troll 1954, Pigott 1984). Each bud along the extended shoot of the previous year normally contains initials of three leaves (Figure 2.7a). After the buds open, the young shoots extend and these leaves expand. The new shoot in the terminal position (Figure 2.7b) continues

to grow, usually until June, producing a long-shoot with 8–15 internodes. The shoots from the two next buds below extend to an intermediate length, and the lowest buds, including those in axils of the three original leaves, form short-shoots or remain dormant. In the following year, the sequence repeats on the three longest shoots.

Growth of the uppermost, more or less vertical shoots at the periphery of the crown of old trees is less clearly organised and the long-shoots are usually no more than 30–60 mm long with 3–6 internodes (Figure 2.7c). Throughout development of the canopy there is self-pruning by transverse abscission (Figure 2.7d) of suppressed, usually shaded, shoots. These are shed and rarely decay and disintegrate *in situ*. Shoots that survive form an outer fringe of the canopy and support a large



**Figure 2.8** Apical part of shoot of *Tilia tomentosa* showing (a) the part about to wither and be lost leaving (b) a lateral bud in the terminal position (false or substitute terminal bud).

proportion of the foliage and inflorescences of the monolayer structure (Horn 1971).

Development of all twigs is sympodial: at midsummer, the apical portion withers and is lost to leave a lateral bud that continues growth in the following year (Figure 2.8). Activation of this substitute terminal bud in the same year to form a proleptic shoot (Späth 1912) ('Lammas shoot', 'Johannistriebe') is unusual for *Tilia* but can be induced by defoliation, either experimentally or naturally by predation by insect larvae, or by wet conditions following a midsummer drought (Pigott 1984).

Each year the hierarchy of branches is repeated (Figure 2.7b). The substitute 'terminal' bud again forms a long shoot, the second and third buds may form long-shoots or shoots of intermediate length that are shorter than the leader, and the lower buds form short-shoots. The short-shoots generally have three internodes, and do not develop further and are eventually lost. The structure develops more or less in one plane, even on the uppermost vertical shoots of young trees. This, coupled with torsion of the petioles of the leaves, results in the shoots being frond-like and permits formation of a tight leaf-mosaic.

Twigs of *Tilia* are always cylindrical and their diameter increases from tip to base, and varies in relation to position on the tree and between species. The epidermis of new shoots is transparent and the underlying cortex is green or flushed with red. Depending on species, the epidermis may be hairless, or covered with sparse or dense, simple or fasciculate hairs. The phellogen (p. 27) arises by division of cells immediately under the epidermis and, as the twig thickens, the epidermis

persists until it begins to become patchy in the late summer. Small, slightly raised, elliptical lenticels are scattered over the surface. In the second year, a thin, usually light greyish-brown bark develops, and the epidermal hairs are then lost from long-shoots but often persist on short-shoots.

## Vegetative buds

All the buds on twigs of *Tilia* are axillary and although phyllotaxis is spiral the leaves become distichous by torsion (p. 17). They vary in shape from ellipsoidal to ovoid, and from obtuse to acute at the apex. These and other differences are of taxonomic value and enable many species to be identified in the leafless state. The full range of variation is shown (Figure 2.9) so that the taxa may be easily compared. In some species only the two outer scales are exposed (Figure 2.9a) on dormant buds, in others three (Figure 2.9c and d), and there is variation between species in relative lengths of the exposed parts (compare Figure 2.9i, p and o) and whether or not the outer scale is swollen. The scales are often ciliate at the apex but the remainder of their exposed surface may be hairless, and often shining, or covered by varying densities of fasciculate hairs.

Dormant buds have two or three outer bud-scales (Figure 2.10) that enclose the leaf-initials, each of which has the blade folded between pairs of large stipules. The substitute terminal bud may enclose as many as seven leaf-initials that grow into a new long-shoot, while those buds that form short-shoots normally enclose three initials and only these expand with no further extension.

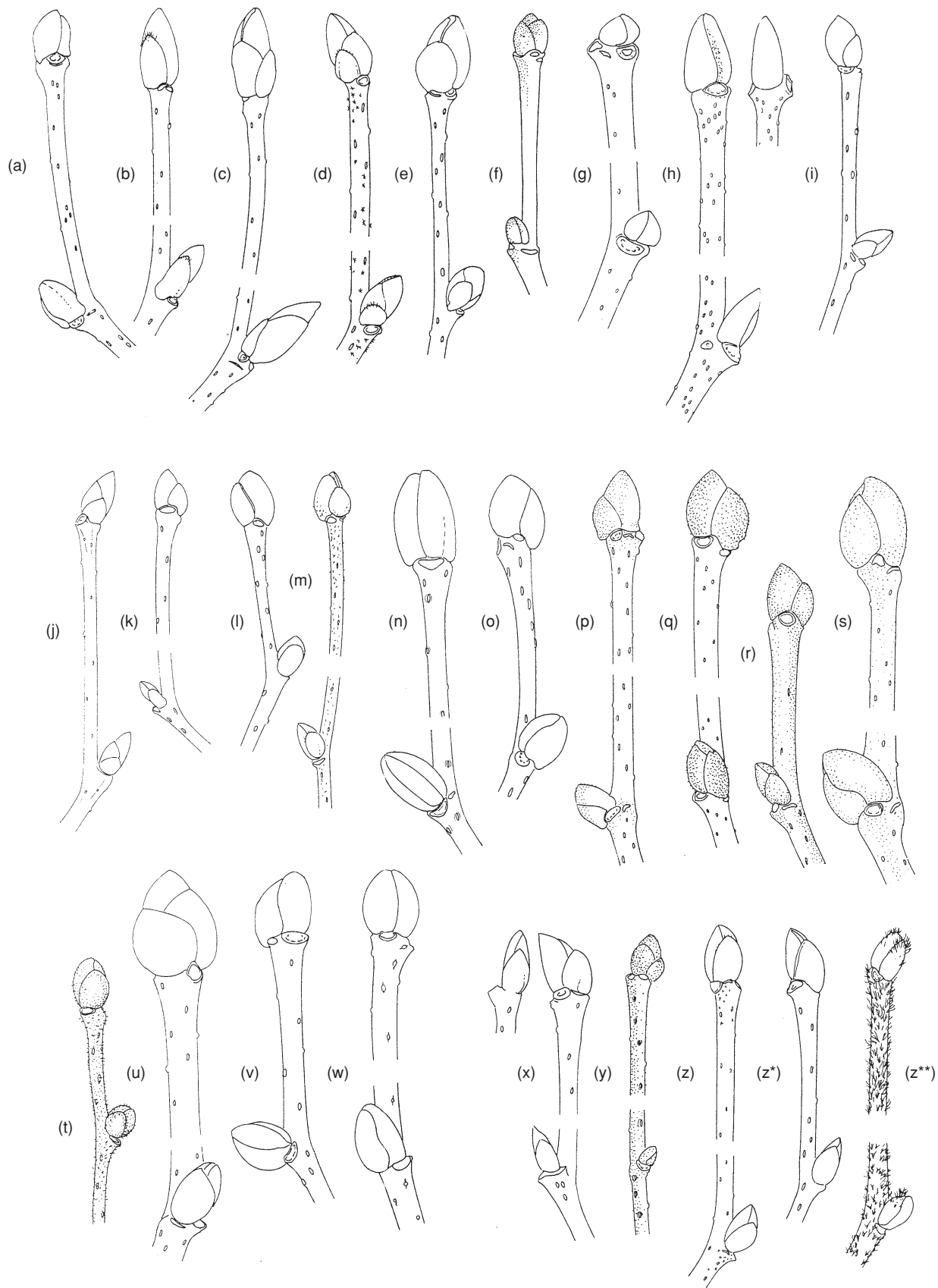
## Leaves

### General morphology of blades.

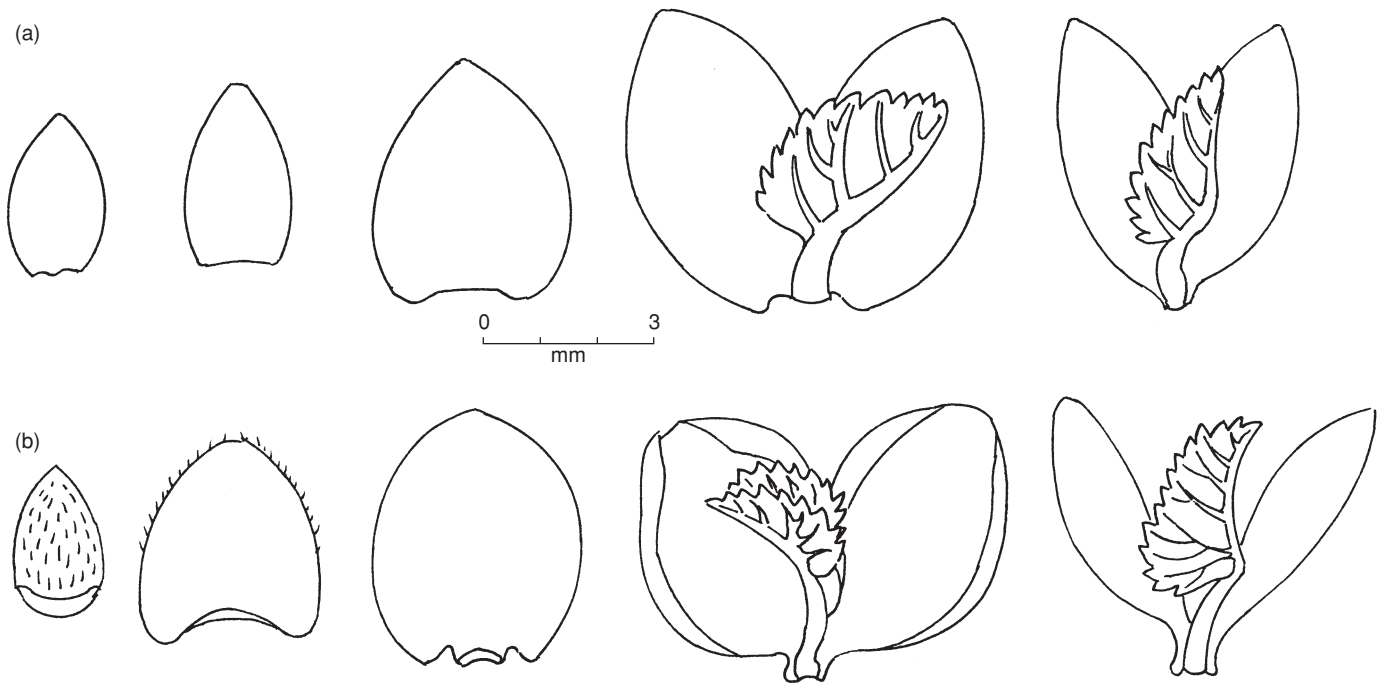
All species of *Tilia* are deciduous and their leaves are alternate, simple, petiolate, stipulate and have mesophytic, dorsiventral structure. The leaves are arranged spirally on the primary shoot of the seedling, but thereafter the distichous arrangement is universal and leaves are turned by torsion of the petiole so that the blade lies in the plane of the shoot: one edge, the forward edge, is towards the apex and the other, the rear edge, towards the base. Associated with this is a very distinctive asymmetry of the blade.

The shape of the blade varies from almost orbicular, through suborbicular, to ovate, to almost deltoid (Figure 2.11a–d). The base varies from deeply cordate, through shallowly cordate to truncate and obliquely truncate. Almost all species have a degree of basal asymmetry, so that, when the leaf is cordate, the forward lobe is larger than the rear lobe. In some species the leaf has a forward lobe, as in a cordate leaf, and a cuneate or





**Figure 2.9** Over-wintering substitute terminal bud of (a) *Tilia cordata*, (b) *T. dasystyla* subsp. *caucasica*, (c) *T. × euchlora*, (d) *T. platyphyllos* subsp. *cordifolia*, (e) *T. × europaea* var. *europaea*, (f) *T. tomentosa*, (g) *T. endochrysea*, (h) *T. henryana*, (i) *T. amurensis*, (j) *T. japonica*, (k) *T. kiusiana*, (l) *T. mongolica*, (m) *T. paucicostata*, (n) *T. callidonta*, (o) *T. chinensis*, (p) *T. chingiana*, (q) *T. concinna*, (r) *T. mandshurica*, (s) *T. maximowicziana*, (t) *T. miqueliana*, (u) *T. nobilis*, (v) *T. oliveri*, (w) *T. tuan*, (x) *T. americana*, (y) *T. caroliniana* subsp. *caroliniana*, (z) *T. caroliniana* subsp. *floridana*, (z\*) *T. caroliniana* subsp. *heterophylla*, (z\*\*) *T. caroliniana* subsp. *occidentalis* (all except c and e from originally wild-collected trees).



**Figure 2.10** Dissection of opening buds of (a) *Tilia* × *europaea* var. *europaea* and (b) *T. concinna* showing the adaxial surface of the outer or basal bud-scale, the inner or second and third scales, and the first and third leaves and stipules.

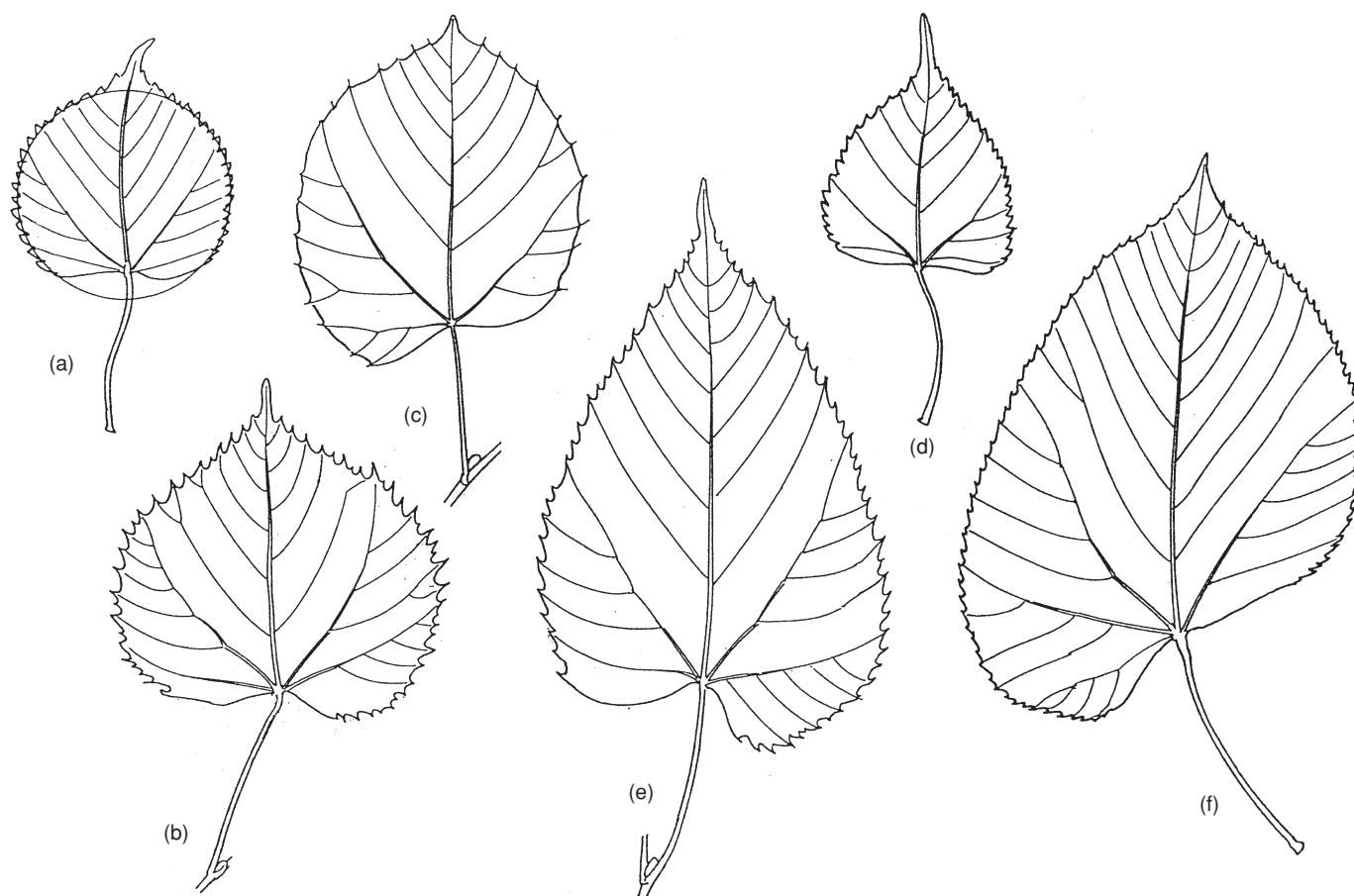
truncate rear lobe (Figure 2.11e): this shape may conveniently be described as ‘semi-cordate’. In obliquely truncate leaves the larger lobe is always forward. The apex of the leaf is often acuminate with a long narrow tip (Figure 2.11a, b and d), or it is a symmetrical triangular ‘tooth’, only a little larger than the neighbouring marginal teeth. For many trees of *T. cordata* the area of the orbicular ‘sun-leaves’ is almost exactly that of a circle with a diameter of its breadth because the area of the acumen is the same as that of the basal sinus (Figure 2.11a).

Venation appears as pinnate with 5–8 veins of the second order on each side of the main vein. These extend to the margin where they terminate in marginal teeth (Figure 2.12), but the basal pair of laterals meet at the top of the petiole with a third prominent vein that also extends to the margin of the forward lobe. This third vein has been regarded as vestigial of a palmate venation, which is common in Malvales. The extra vein relates to the basal asymmetry of the leaf and is a distinctive character of the genus *Tilia*, but many drawings are inaccurate in this respect. Veins of the third order form ladder-like ‘rungs’ between the second-order veins and are often described as transverse veins. Finally, each block is divided by veins of the third and fourth orders into small islets, in many of which small branches terminate.

In most species the margin of the leaf is entire at the base and dentate or serrate at the sides. Some taxa within the *T. tuan* complex have entire leaves but the juvenile leaves are serrate (Figure 2.13). The leaves of *T. endochrysea* have entire margins but are irregularly lobed. The form of the marginal teeth varies between species and is of taxonomic value (Figure 2.14) and, like the leaf buds, the differences are best appreciated by comparison. Every tooth is at the end of a vein. In adult leaves of *T. tuan* there are teeth only at the ends of main lateral veins in the upper part of the leaf, but in most species teeth are numerous and also at the ends of veins of the third and fourth order (Figure 2.12). The veins may end within the subacute apices of teeth, as in *T. cordata* (Figure 2.14a), but generally a vein forms an extended tip that varies between species in its length and whether or not there is green tissue forming a narrow wing up its sides (apiculate or mucronate). The forms of marginal teeth are not easily described by existing terminology and, because of their taxonomic value, they are shown as drawings and are here grouped into a series of types (Figure 2.14).

### Hairs

All species of *Tilia* have conspicuous differences between the upper (adaxial) and lower (abaxial) surfaces of the leaf-blade. These are most clearly developed on shoots that are situated on fully exposed parts of the canopy and have the potential to flower. Stomata are restricted to the lower surface of leaves. The upper surface is hairy in very young leaves of several species,



**Figure 2.11** Variation in leaf-shape. (a) Orbicular leaf of *Tilia cordata* with circumscribed circle of diameter equal to breadth (see text). (b) Orbicular blade of *T. dasystyla* subsp. *dasystyla*. (c) Suborbicular blade of *T. henryana*. (d) Deltoid (triangular) blade of *T. paucicostata* subsp. *dictyoneura*. (e) Ovate and cordate blade of *T. miqueliana*. (f) Ovate and semi-cordate/cuneate blade of *T. caroliniana* subsp. *heterophylla*.

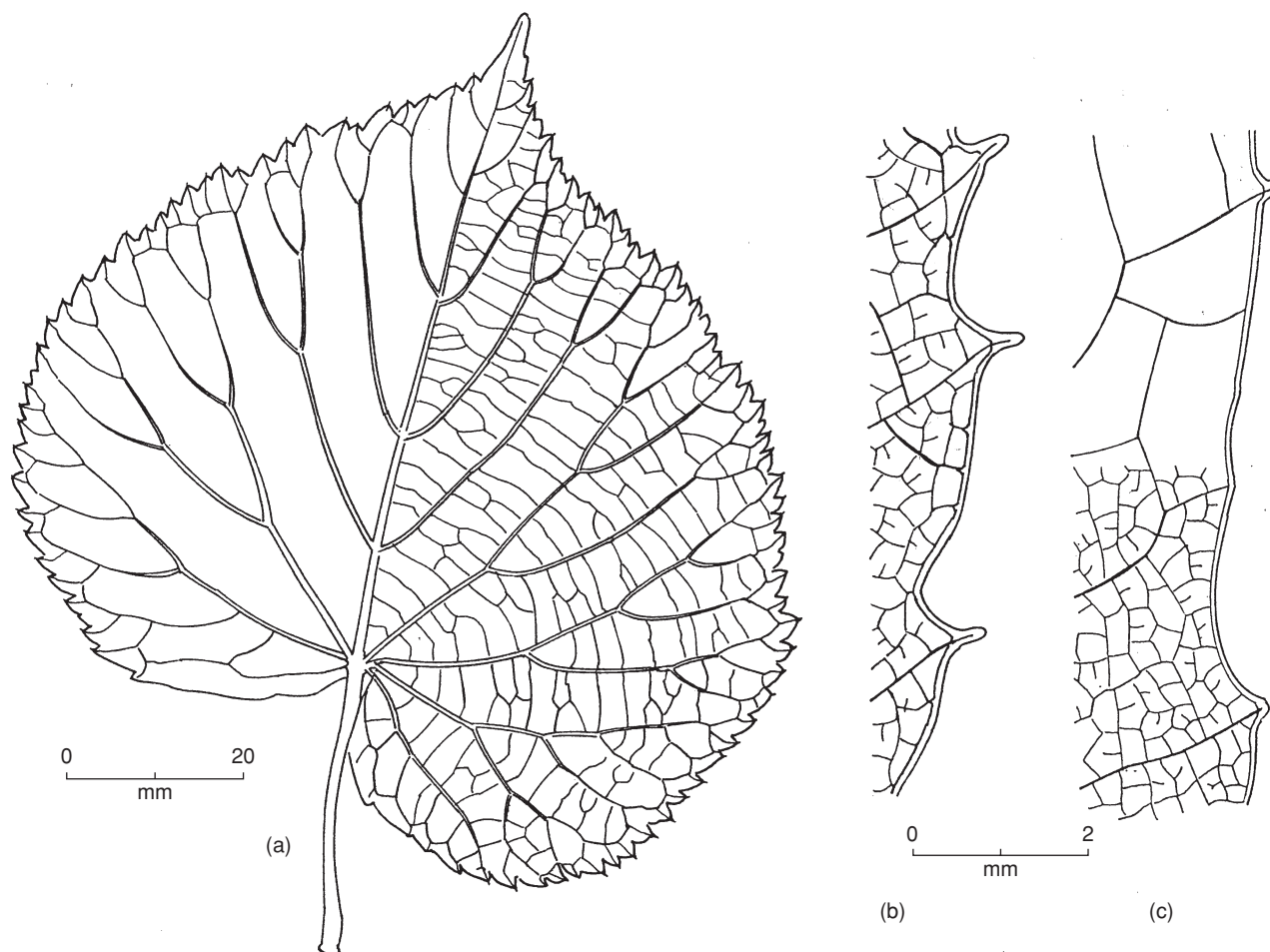
but these hairs are quite soon lost and then the surface is dark green and becomes hairless, or almost so, at maturity. The lower surface is much more variable; it is paler than the upper surface, generally greyish-green but conspicuously glaucous on the majority of trees of *T. cordata* and on some trees of *T. endochrysea*.

The presence of hairs, their type and distribution differ significantly between species and provide important taxonomic characters. Their persistence through the life of the leaf also varies: in *T. amurensis*, for example, the leaves may be densely hairy as they unfold but most hairs are lost during subsequent development. The hairs of *T. caroliniana* subsp. *occidentalis* are loosely attached, can be rubbed off and are easily eroded. A few species, such as *T. americana* and *T. paucicostata* subsp. *paucicostata*, are hairless or almost so, while others, such as *T.*

*cordata* and *T. mongolica*, are hairless except for small patches of fasciculate hairs (Figure 2.15) in the axils of main veins; these patches are sometimes referred to as barbae, or apodomatia because mites usually live amongst the hairs. The axillary hairs themselves are sometimes restricted to the sides of the veins or they extend over the veins and on to the intervening surface. There may also be adpressed double hairs along the veins (Figure 2.16).

A more or less uniform distribution of hairs over the whole lower surface occurs in many species. Several types of hair occur and their external morphology has been illustrated with scanning electron micrographs by Banerjee (1976) and by Hardin (1990), who have both discussed their taxonomic value. These types are illustrated diagrammatically in Figure 2.17. Details of their cellular structure are shown in the next chapter (pp. 34–35).

Hairs may be predominantly simple (Figure 2.17a), as in *T. platyphyllos* subsp. *cordifolia*. In many species they are fasciculate with 2–10 straight or gradually curved, unicellular arms, forming a tuft (Figure 2.15 and 2.17b), or stellate with 3–16, but frequently four or eight, unicellular arms that differ from fasciculate hairs by being abruptly bent almost at the base, so that



**Figure 2.12** Venation of (a) leaf of *Tilia platyphyllos* omitting the smallest veins bounding the islets, and margin of leaves of (b) *T. oliveri* and (c) *T. tuan* with veins bounding the islets, and terminal branches.

they radiate from a short pedicel formed by their joined bases (Figure 2.17c). The base may be tubular and secrete mucilage. Hairs of this type may be sparse, as in some individuals of *T. chinensis* and *T. tuan*, or so dense that they form a felt-like tomentum, obscuring the surface of the leaf as in *T. caroliniana* subsp. *heterophylla*, *T. mandshurica*, *T. maximowicziana*, *T. oliveri* and *T. tomentosa*. Hairs may be transparent initially but appear white when air-filled, or the sap within the cells may be red or reddish-brown and this colour persists when the hairs dry.

In addition to the relatively large hairs there are small, dark brown or reddish-brown, multicellular club-shaped (clavate) hairs (Figure 2.16) which, when present, are usually sparse and restricted to the lower parts of the main veins.

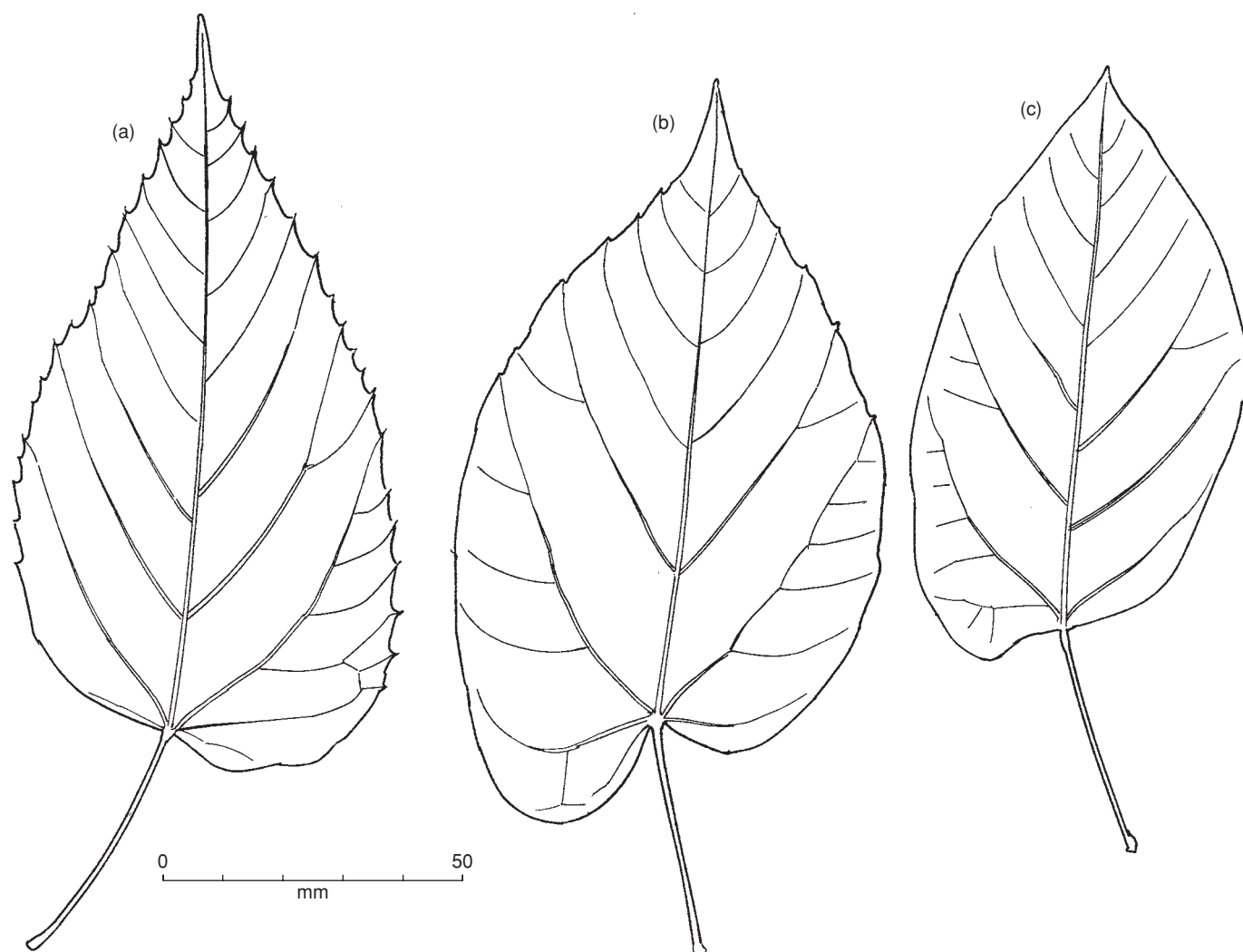
The statistical treatment by latent class analysis of the frequency distributions of the numbers of radiate arms and of their length is described in Chapter 11.

### Petioles

Leaves of all species have petioles that are almost circular in cross section, slender for most of their length and, in some species, swollen to form functional pulvini at both ends (Figure 2.18). The attachment to the stem is D-shaped with a semi-circle of five bundles but, along most of the petiole, these partly fuse to form a tube of vascular tissues with an inner system of medullary strands. Several species have been investigated and the arrangements of the vascular cylinder and strands are complicated and very variable, both within and between species. The taxonomic value of variation in petiole anatomy of *Tilia* has not been investigated. Species also differ in whether the petiolar surface is hairy or glabrous.

### Stipules

These are folded within the buds and expand as the leaves emerge (Figure 2.19). They are oblong or ovate with a broad base and have numerous parallel veins (Figure 2.20). Their texture is membranous and they are pale green or sometimes flushed red, often with adpressed hairs on the abaxial surface. In



**Figure 2.13** Heterophylly of *Tilia tuan* from Qing-chen-shan, Sichuan. Leaves from (a) exposed sprout on cut over tree, (b) partly shaded, non-flowering shoot at 3 m above the ground and (c) flowering shoot at 12 m above the ground.

most species there is a sequence from broad to narrow stipules along the extending shoot (Figure 2.20). As the leaves expand the stipules are normally lost by abscission, and usually within a matter of days after opening.

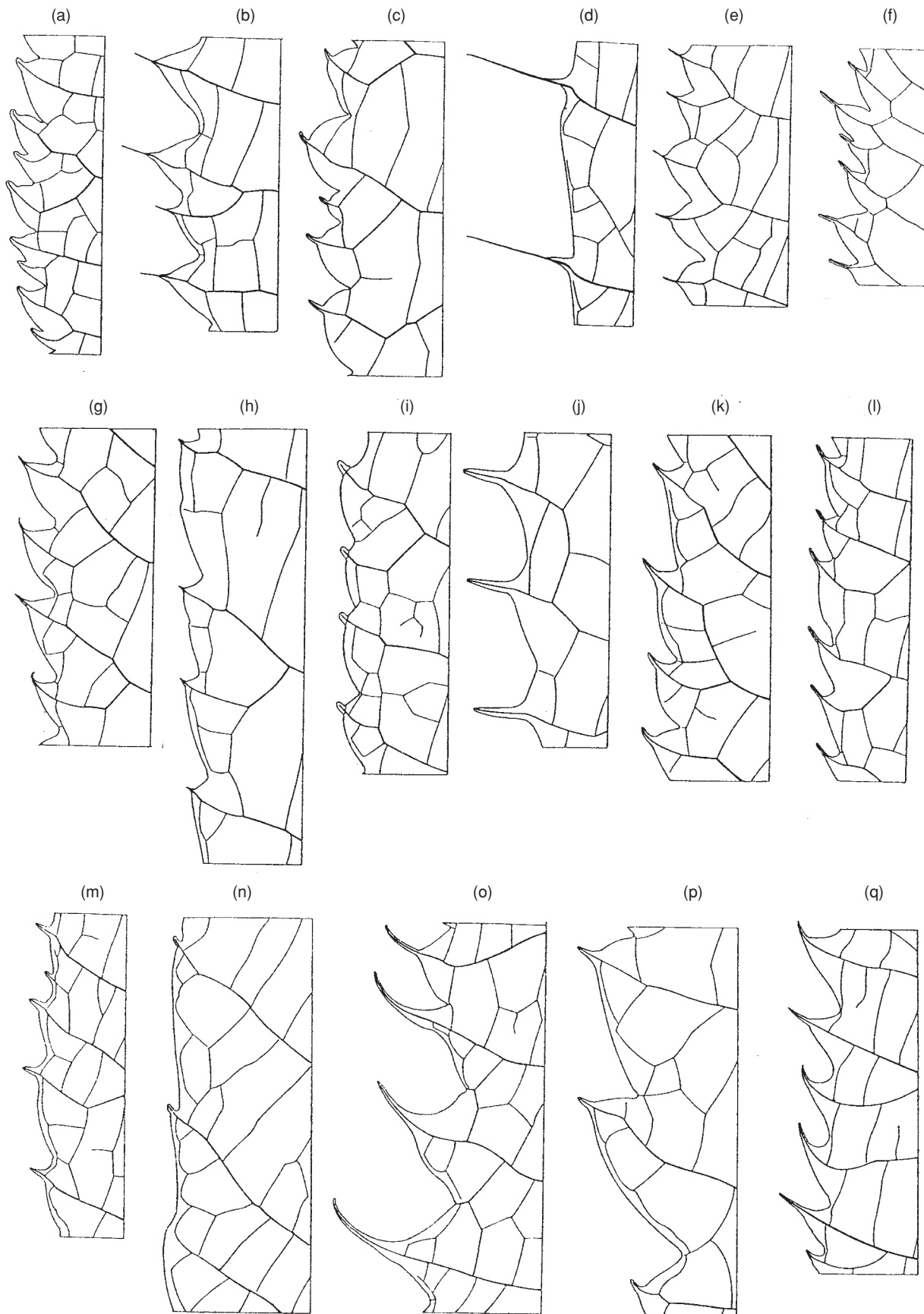
### Mucilage

Ducts, cavities and cells that contain mucilage are present in living tissues of all species. Composition of the mucilage is reviewed by Hegnauer (1973). Mucilage from the leaves of *T. cordata* yields uronic acid 38.5%, hexose 49% and methyl pentose 12.3%. In *T. tomentosa* the components are similar: galacturonic acid and the structurally related hexose, galactose, and

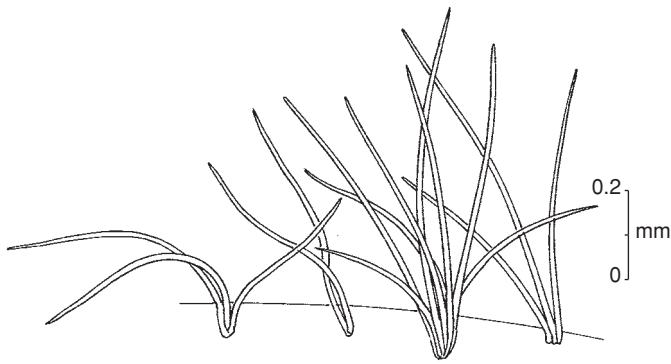
a pentose, arabinose, as well as the methyl pentose, rhamnose. Neither protein nor cellulose fibrils have been detected. Although hydrophilic and dispersing in water, the presence of this copious mucilage interferes with some methods of DNA extraction.

### Bracts

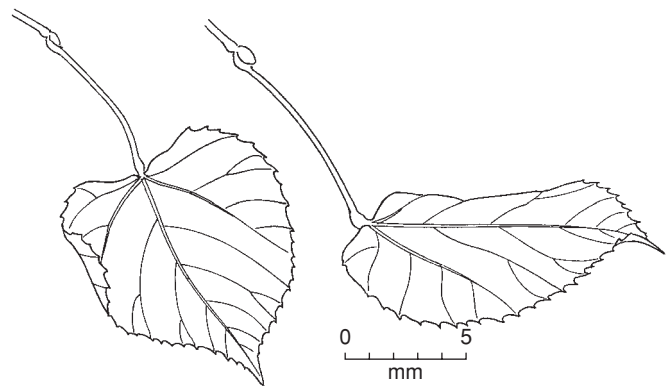
The tongue-like or paddle-shaped bract (Figure 2.21), of which the lower part is fused to the peduncle of a dichasial cyme, is a unique and unmistakable feature of both living and fossil members of the genus. The base of this combined structure is attached directly to the stem, not in the axil of a leaf, but immediately to one side and always above the leaf-base on the more or less horizontal flowering shoots (Figure 2.22). This anomalous arrangement makes it doubtful if the term bract is correctly applied: Troll (1957) used the term *Tragblatt* ('bearing (subtending) leaf') and applied the normal German term for



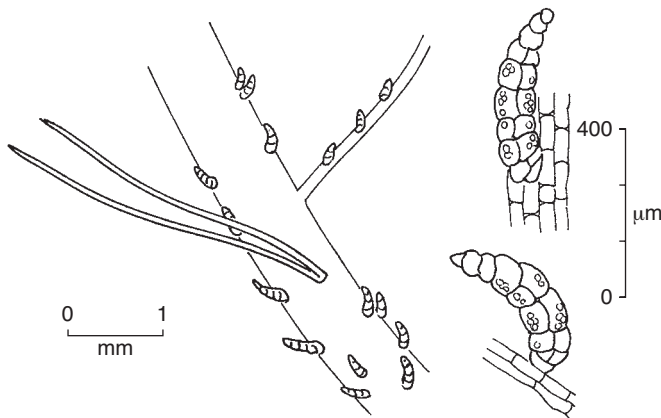
**Figure 2.14** Marginal teeth of unshaded leaves from flowering shoots of (a) *Tilia cordata*, (b) *T. dasystyla* subsp. *caucasica*, (c) *T. platyphyllos* subsp. *cordifolia*, (d) *T. henryana*, (e) *T. amurensis*, (f) *T. japonica*, (g) *T. paucicostata*, (h) *T. chinensis*, (i) *T. concinna*, (j) *T. mandshurica*, (k) *T. maximowicziana*, (l) *T. miqueliana*, (m) *T. oliveri*, (n) *T. tuan*, (o) *T. americana*, (p) *T. caroliniana* subsp. *caroliniana*, (q) *T. caroliniana* subsp. *heterophylla*.



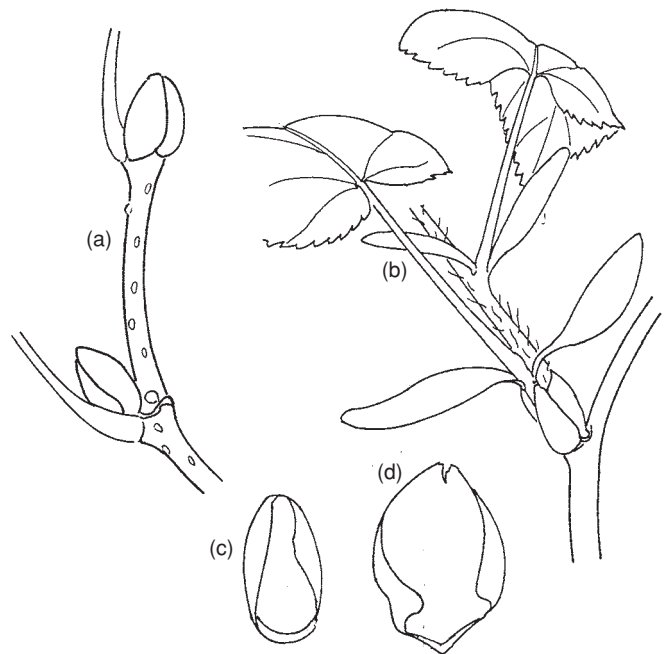
**Figure 2.15** Fasciculate hairs in the axils of the main veins on the lower surface of the leaf-blade of *Tilia cordata*; the number of arms varies from two to eight.



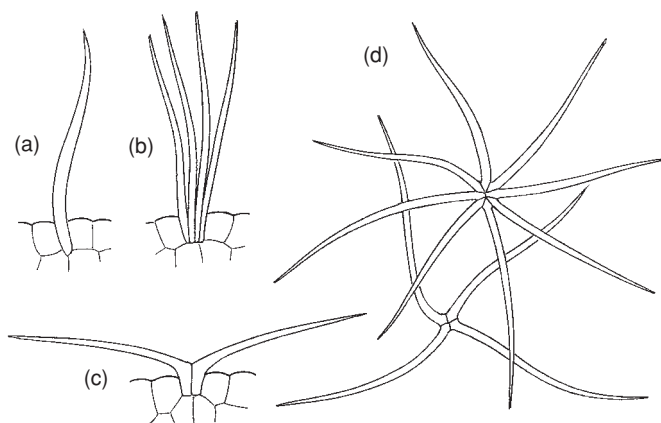
**Figure 2.18** Leaf of *Tilia oliveri* immediately after bending down a shoot and after adjustment by the pulvinus.



**Figure 2.16** Fusiform and fascicular hairs on the basal part of the main veins on the lower surface of the leaf of *Tilia* × *euchlora*.



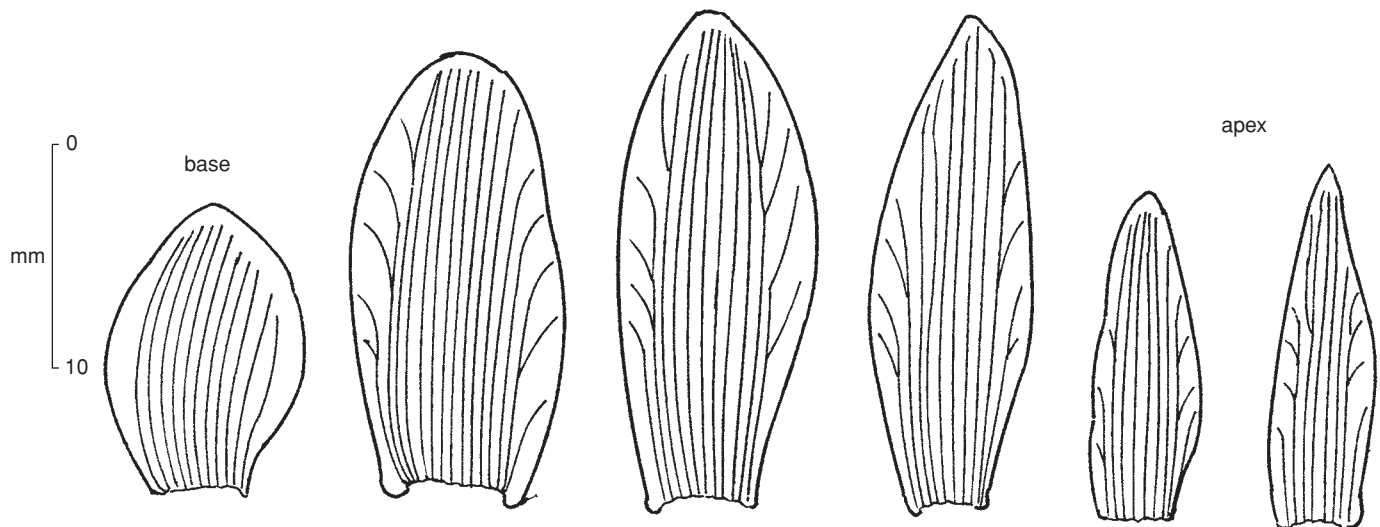
**Figure 2.19** (a) Over-wintered shoot with dormant buds of *T. chinensis*. (b) New shoot with bud-scales and stipules fully expanded shortly after opening of winter bud. (c and d) Detached bud-scales.



**Figure 2.17** Section of leaf surface with (a) simple hair, (b) fasciculate hair and (c) stellate hair. (d) Leaf surface with four- and eight-armed stellate hairs.

a bract, Vorblatt, to the fugitive appendages in whose axils the branches of the cyme and the flowers arise (Figure 2.23).

In the majority of species the fully grown bract on the more or less horizontal flowering shoots is displaced slightly sideways and downwards, so that the abaxial surface remains on the upper side (Figure 2.22). The peduncle and cyme are on the adaxial surface and hang down, not only below the bract but also below the associated leaf, of which the petiole undergoes torsion through 90°, so that the adaxial surface faces up and the abaxial down: this is the opposite torsion to that of the bract. It is therefore confusing to refer to upper and lower surfaces of

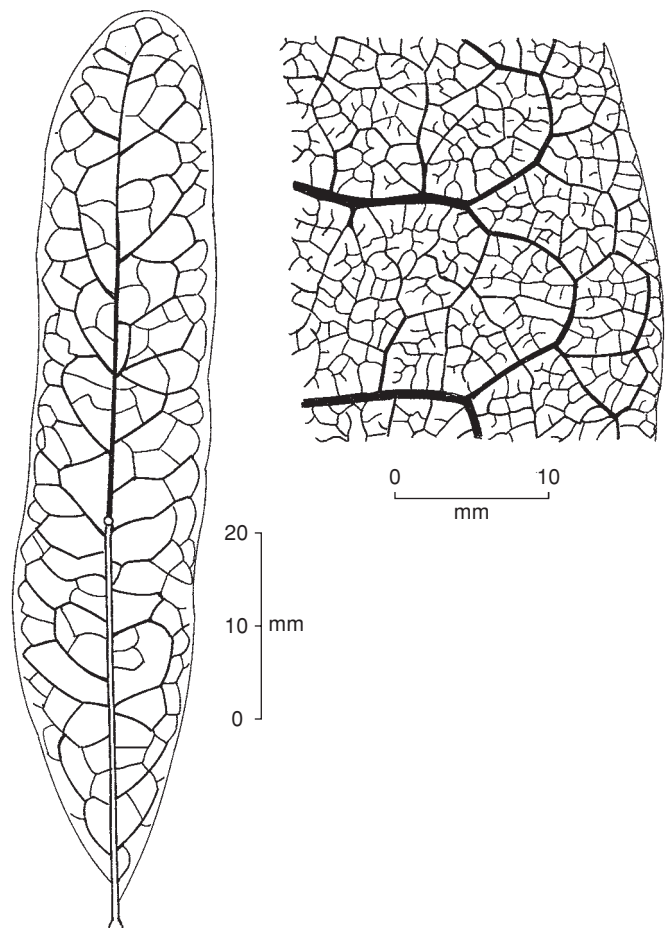


**Figure 2.20** Sequence of stipules (one of each pair) from the base to the apex of a long shoot of *Tilia oliveri*.

the bract. In two species, *T. cordata* and *T. mongolica*, the stalk of the bract is twisted and curves upwards and, while in flower, the inflorescence on the adaxial surface is lifted and held above the bract and associated leaf (Figure 8.2).

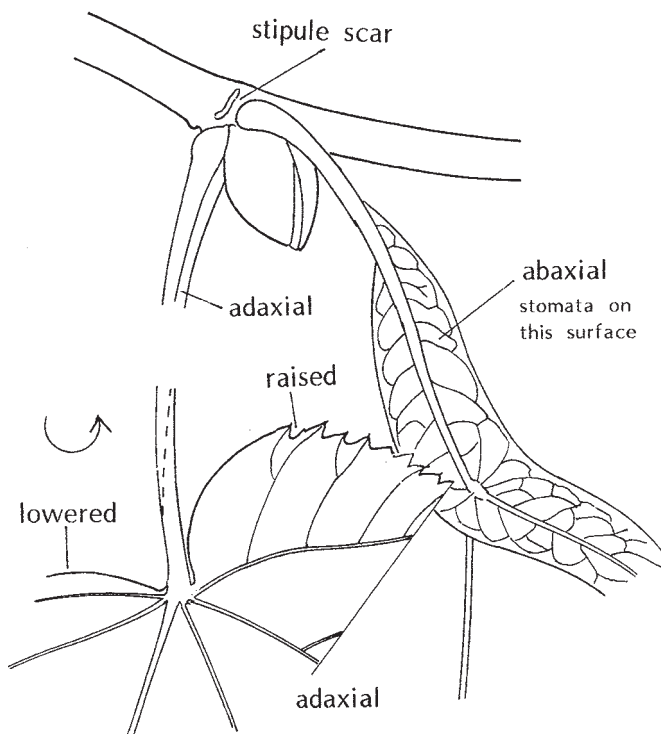
Bracts may be stalked or sessile and in all living species they are normally 50–150 mm long and 10–25 mm wide, and lanceolate, narrowly elliptical, oblong or oblanceolate, with entire margins and generally rounded at the apex. The texture is cartilaginous, the surface often waxy and the colour pale or yellowish-green, which contrasts with the darker green leaves. The cellular anatomy is described in the [Chapter 3](#) (pp. 35–38) and shows that their structure is essentially that of a thin leaf and clearly a photosynthetic organ with stomata on the abaxial surface and numerous chloroplasts in the mesophyll.

The venation is illustrated in [Figure 2.21](#): the midrib extends from the base to near the apex, where it often divides into fork-like branches. There is a single vascular cylinder in the basal stalk and no evidence of a fusion of two organs (Figure 3.21). A short distance above the base, a lateral branch vein on each side runs beside the main vein so that it appears as three parallel ridges. From the outer veins there are more or less regular pinnate branches which are cross-linked and looped round to join up near the margin. The distribution of hairs mirrors their distribution on the leaves. Species with almost glabrous leaves have glabrous bracts, and those with hairs on the abaxial or undersides of the leaves have similar densities of hairs on the abaxial or upper surfaces of the bracts.

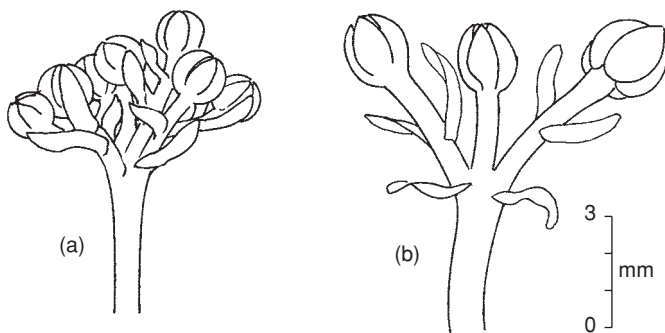


**Figure 2.21** Bract of *Tilia platyphyllos*. (a) Main and second and third order looped (anastomosing) veins and (b) reticulate venation with islets (traced from photographs of cleared bracts).





**Figure 2.22** Node of horizontal shoot of *Tilia platyphyllos*. At each node the bract stalk twists so that the abaxial surface is always upward and the inflorescence hangs down. The petiole of the leaf also twists so that the blade is horizontal with the adaxial surface upward.



**Figure 2.23** Early stage in development of cyme of (a) *Tilia cordata* and (b) *T. platyphyllos*, with bracteoles subtending either branches, or potential sites of branches

The bract, in addition to its photosynthetic function which may contribute carbohydrates to the developing fruit, appears to act, by its contrasting colour to the leaves, as an 'advertisement' for the flowers. The cartilaginous texture resists deformation as it dries and eventually provides a spinner-wing during dispersal of the fruits.

## Inflorescences

Although fused to the bract, the peduncle appears to remain a distinct central ridge along the midrib and in most species separates from it near the middle of the bract. The inflorescence is a dichasial cyme and, when there are more than three flowers, the cyme has branches which support the pedicels. If the branches are very short then the cyme may appear to be an umbel, as in *T. × europaea* var. *europaea* ('Pallida'), or it may be corymbose and compact. If the branches are long, the cyme is diffuse or divaricate. The number of flowers is related to the number of orders of branching and, if the cyme is regular, then the numbers increase in a progression where each addition is twice the previous addition: (1), 3, 7, 15, 31, 63, etc. (1 + 2 + 4 + 8 + 16 + 32...). In reality, occasional irregularities result from the omission or addition of an extra flower or branch so that these numbers show some variation.

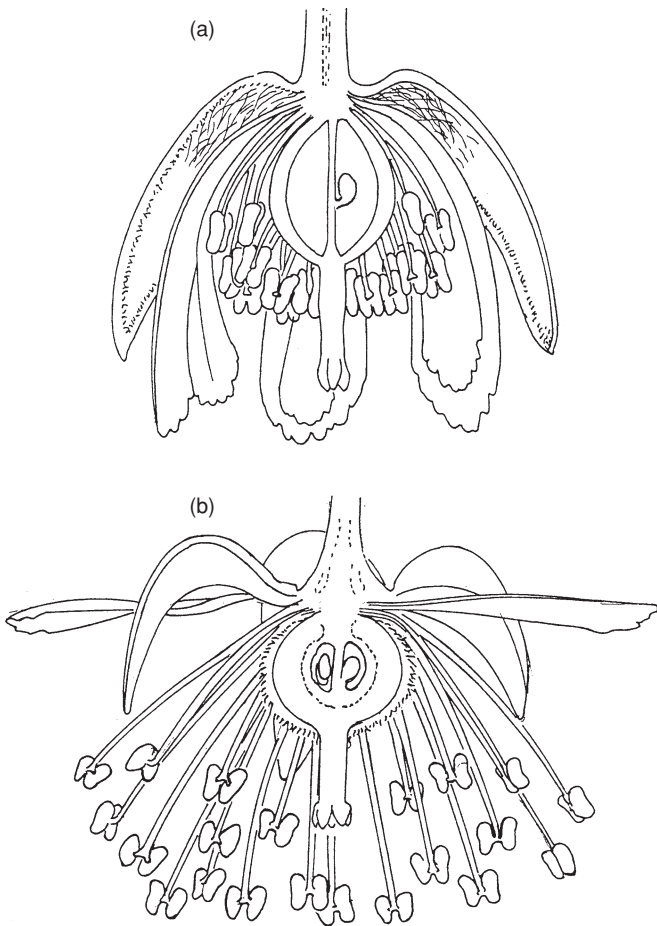
In the young inflorescence (Figure 2.23) each branch is in the axil of a very small bract, which, unlike the large bract, is soon lost. On each pedicel there are two small, narrow, triangular bracteoles but these are also soon lost by abscission to leave small scars. The peduncle, branches and pedicels may be glabrous or hairy, depending on the species.

## Flowers

The flowers are superficially uniform throughout the genus but are, in fact, of two main types (Figure 2.24), one with the perianth rotate, so that the petals are spreading, and the other with the perianth beaker-shaped with the petals almost perpendicular to the receptacle. The corolla is usually 10–15 mm in diameter.

The general arrangement of parts of the flower is summarised in floral diagrams (Figure 2.25). There are five valvate sepals, which are weakly united at the base. Each sepal is ovate, boat-shaped, pale to mid-green and either glabrous or with small stellate hairs on the abaxial surface and dense, white tomentum on the margin. At the base of the adaxial surface there is a patch of long hairs that cover a swollen cushion formed of columns of secretory cells of a nectary (Figure 14.3) (Frei 1955, p. 82). The flowers are strongly scented, a rich source of nectar and are primarily entomophilous with well-developed protandry. Alternating with the sepals are five petals that are longer and narrower than the sepals, ligulate with three longitudinal veins and with small irregular teeth (erose) at the apex. They vary in colour from pale to bright yellow.

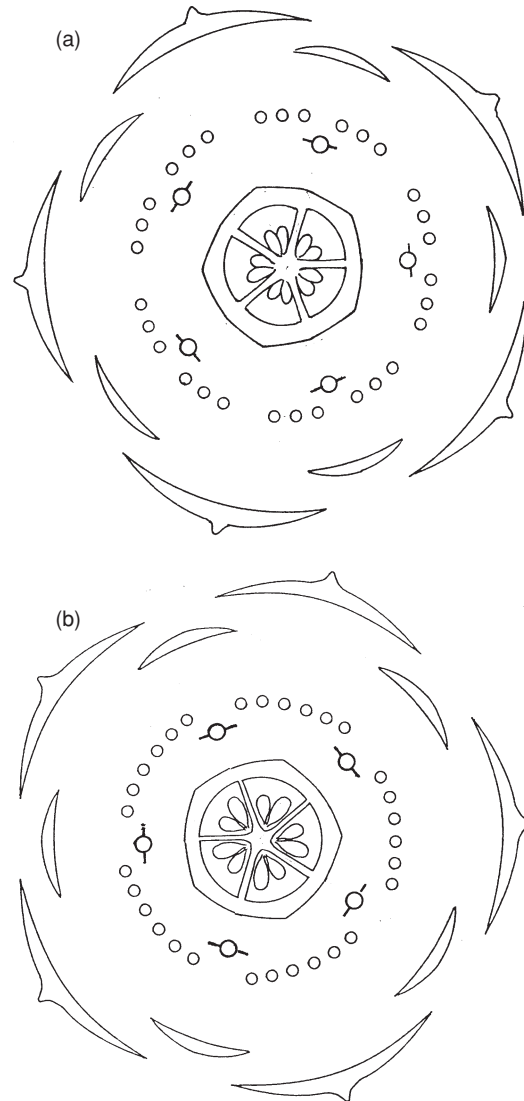
The flowers are diplostemonous with all, or all but five, of the stamens forming five groups in an outer whorl, and the



**Figure 2.24** Median section of flowers of (a) *Tilia chinensis* with staminodes and short, included stamens, and (b) *T. platyphyllos* without staminodes and long, exserted stamens.

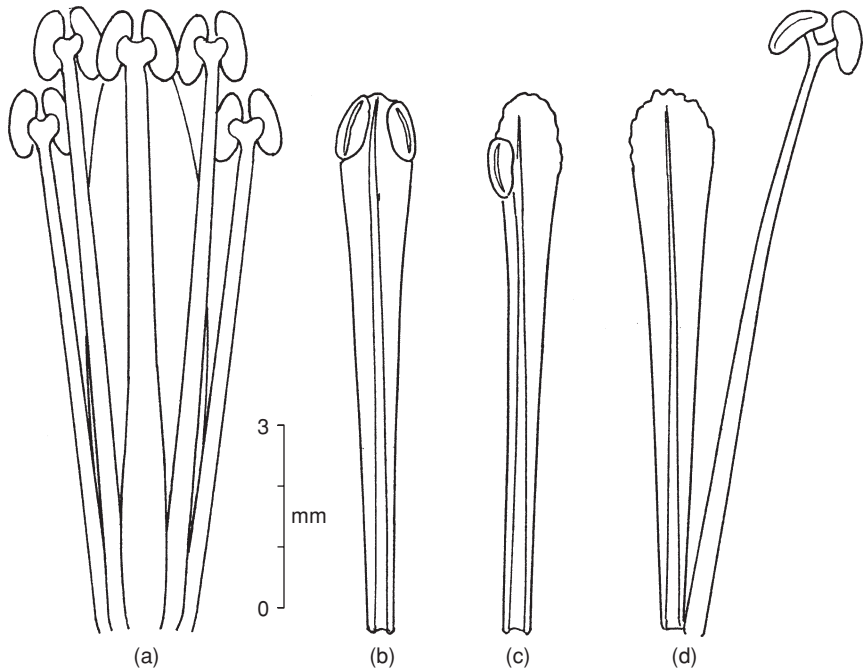
inner whorl consists of either five stamens or five staminodes (Figure 2.25a). From a study of the vascular traces, Saunders (1937) found that the five groups of the outer whorl originate on the alternate radii to the petals, but each separates into two half-groups that move tangentially during development towards adjacent half-groups. As a result the pairs of adjacent half-groups come to be on the same radii as the petals and partly ‘sandwiched’ between the petals and either the single stamens or the staminodes of the inner whorl (Figure 2.25b). This arrangement is clearly seen in the flowers of *T. cordata* (Figure 2.26a) or *T. kiusiana* (Figure 9.25). In *T. cordata*, from which staminodes are absent, the filaments of stamens of the inner whorl are significantly wider than those of the outer whorl (0.4 to 0.25 mm).

The stamens in the half-groups are united at the base and there are five groups each of approximately 5–12 to give 25–60 stamens in a flower; the number depending on species and, to

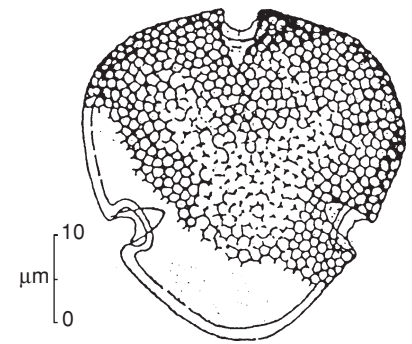


**Figure 2.25** Floral diagrams of a flower of *Tilia × europaea* at (a) an early stage of development with the outer whorl of 30 stamens in five groups on the radii of the sepals and the inner whorl of five stamens (or staminodes in other species) with slightly thicker filaments on the radii of the petals (diplostemony) and (b) after developmental regrouping of the outer whorl on each side of the inner stamens (after Saunders 1937).

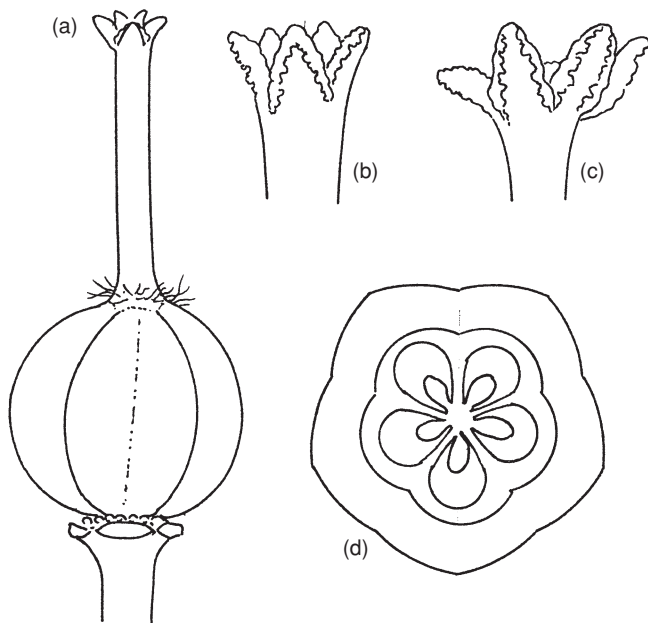
a limited extent, on individual trees. In general, the filaments are slender, white and may be longer or shorter than the petals. They are divided at the top into two short arms that hold the two separate pollen sacs of the anthers. These are initially yellow but change to orange as they age. They are extrorse (opening outwards by a longitudinal split). The pollen has three pores in short furrows (tricolporate) (Figure 2.27) with a distinctive reticulate pattern, which allows some of the species to be separately identified (Andrew 1971, Chung and Kim 1984). The



**Figure 2.26** (a) Adaxial aspect of a group of mature stamens of *Tilia cordata* with the single member of the inner whorl on the same radius as the petal and four stamens of the outer whorl. (b) Staminode with lateral pollen sacs in the position of a stamen of the inner whorl. (c) Staminode with one pollen sac. (d) Normal staminode and stamen. (b–d) All of *T. japonica*.



**Figure 2.27** Tricolporate pollen grain of *Tilia cordata* (from Pigott and Pigott 1959).



**Figure 2.28** (a) Ovary, style and stigma of *Tilia platyphyllos* with style fully grown and stigmatic lobes opening. (b–c) Opening of stigma. (d) Transverse section of ovary, 12 days after opening of flower, showing the ribs or ridges alternate with the septa between the loculi.

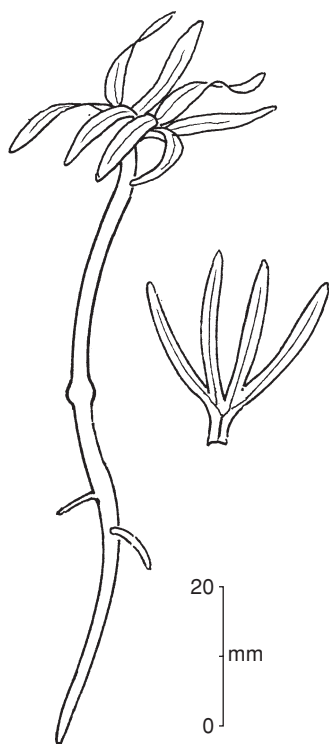
pollen grains tend to stick together in small clusters and readily become attached to insects.

In the majority of species there are five staminodes which are on the same radii as the petals and often curve over and lie close against them. The staminodes are generally like narrow spatulate petals (petaloid) but with a single longitudinal vein (Figure 2.26b). All species with beaker-shaped flowers and short stamens have staminodes but, of those with rotate perianths, some have staminodes (*T. japonica*, *T. mongolica*) and some do not (*T. cordata*, *T. dasystyla* and *T. platyphyllos*). In *T. amurensis*, normally without staminodes, a petaloid staminode may be present in a flower but very infrequently, and a small proportion of flowers can have 1–3 structures that seem to be wide filaments of stamens, often having one or two pollen sacs on the margin (Figure 9.14). Similar organs occur very rarely in *T. japonica* (Figure 2.26b).

In the centre of the flower is a spherical ovary consisting of five carpels (Figure 2.28a) which form five loculi in each of which there are two anatropous, bi-integumental ovules in axile placentation. The carpels are on the same radii as the sepals. The outer surface of the ovary is generally covered in white fasciculate hairs. On top of the ovary there is an erect style on which the stigma is initially closed, but after the style



**Figure 2.29** (a–d) Stages in germination of seed enclosed within fruit of *Tilia platyphyllos* (Surrey, England). Seedlings of (e) *T. chinensis*, (Yunnan, China), (f) *T. tuan* (Yunnan, China), (g) *T. caroliniana* subsp. *caroliniana* (North Carolina, United States), (h) *T. japonica* (Hokkaido, Japan) and (i) *T. mongolica* (Henan, China).



**Figure 2.30** Seedling of *Pterocarya stenoptera* from a tree in Tashkent that was from a native site in western China.

has elongated during the protandrous phase of flowering, five triangular stigmatic lobes curve back and receptive surfaces are exposed (Figure 2.28b).

### Fruits

After flowering, the floral parts are lost by abscission and the ovary develops into a spherical, ovoid or obovoid fruit. In many species of *Tilia* only a proportion of the fruits contain seeds and even the majority of fertile fruits (perhaps 90%) contain only one seed, about 9% contain two and 1% three. The seeds occupy 1–3 loculi, the others collapsing and becoming flattened against the ovary wall.

There are differences between species in the form of the ripe fruits. The fruits of *T. endochrysea* split along longitudinal lines of weakness down the middle of the outer carpel wall, releasing the seeds. In all other species the fruits are indehiscent and tear open during germination. The thickness of the dry fruit-wall varies from about 0.1–0.2 mm in *T. cordata*, *T. mongolica* and *T. paucicostata* to 0.8–1.0 mm in *T. chinensis* and *T. platyphyllos*, and whereas thin-walled fruits are easily broken, those that are thick-walled are strong enough to be virtually unbreakable between the fingers.

The strength of the wall results from thickening and lignification of the middle layer of tissue (Figure 3.25a) and on both sides there are tissues containing numerous druses, which are clusters of crystals of calcium oxalate. These two layers provide protection from some types of predation.

Differences of size, shape and surface ornamentation of the ripe fruits are of taxonomic value. In some species the fruits are smooth and without ribs, in others the fruits develop longitudinal ribs, which may not be apparent until the wall dries. Between the ribs the wall may be smooth or with mamillate ornamentation (small circular protuberances), and there is usually a dense covering of short, fasciculate or stellate hairs which in some species are of two sizes mixed together (Figure 3.25, 3.26). At maturity the hairs are generally brown.

## Seeds

The seeds are almost spherical but slightly narrowed at one end and flattened on one face (Figure 8.26). The seed-coat is

thin, dark brown or black and longitudinally finely striate. The endosperm is liquid during development but solid and translucent white at maturity. The embryo is embedded in endosperm with the pale green cotyledons characteristically folded (Figure 14.12d).

## Seedlings

Germination is epigeal (Figure 2.29a-c). The cotyledons are usually five-lobed but may be three- or seven-lobed. The striking difference in shape between the cotyledons and adult leaves is, in a sense, superficial, as, like the adult leaves, the veins at the base are palmate but those in the second pair of lobes are pinnate. The greater dissection of the cotyledons is not unique and a similar heterophylly of cotyledons occurs in *Pterocarya* (Figure 2.30). In a few species (*T. cordata*, *T. japonica*, *T. mongolica*) the lobes are short and rounded at the apex (Figure 2.29h), but in most species they are lanceolate and more or less acute at the apex (Figure 2.29d, e and f).

# Glossary of particular terms used in descriptions

## Tree

**collar** zone in the stem (immediately above the hypocotylar zone) from which buds arise and may form new shoots.

**coppice** to cut a tree at the base of the trunk and allow to regrow; also a tree so treated.

**crown** the structure formed by all the stem branches.

**dbh (diameter at breast height)** the diameter of the trunk at 1.3 m above the base; often measured as the circumference and divided by  $\pi$  (3.142).

**epicormic** on the trunk or stem: applied particularly to clusters of buds and sprouts.

**maiden** a tree that retains its original stem or trunk and has not fallen or been cut (coppiced) and regrown.

**stool** the persistent base of a coppiced tree.

## Bark and twig

**lenticel** small, open, blister-like structure on the surface of a young stem, becoming larger with a central slot and ridged on both sides (Figure 2.6a).

## Leaf

**acumen** narrow extension of the leaf apex (**acuminate** with such an extension).

**adpressed** applied to hairs which lie flat against a surface.

**apiculus** short extension of a vein to form a tip with a narrowing flange of green tissue on each side (Figure 2.14j,o) (**apiculate** with such a tip).

**axillary** situated in an axil, the angle between a stem or a vein and its branch.

**blade** distal part of leaf (lamina).

**ciliate** fringed with simple hairs along the margin.

**cordate** heart-shaped when applied to a leaf-blade and therefore with two rounded basal lobes when applied to the base of the blade.

**crenate** with rounded marginal teeth.

**cuneate** wedge-shaped, with straight margins divergent from the base.

**dentate** with triangular, acute, marginal teeth, often of uneven size, directed outwards.

**elliptic** shaped like an ellipse which is up to three times longer than broad and narrowed symmetrically to both ends.

**flat** with the surface in one plane and without depressions along the veins.

**glabrous** without hairs, hairless.

**glaucous** bluish-green, with a waxy bloom or a consequence of the fine structure of the cuticle.

**islet** small part of leaf-blade enclosed within a ring of veins.

**lanceolate** three to six times longer than broad and widest below the middle.

**mucronate** as applied to the marginal teeth of the leaf-blade, when the tip is abruptly narrowed and formed by only the emergent vein (Figure 2.14e).

**orbicular** circular or round with the length and breadth equal or almost so (*orbis* L. circle not a sphere).

**ovate** two to three times longer than broad and egg-shaped in outline with the broadest part towards the base.

**semi-cordate** with the base of the leaf on one side of the petiole cordate and the other truncate or cuneate.

**serrate** with sharp uniform teeth directed towards the apex.

**sinus** the re-entrant angle at the base of a cordate leaf or between lobes.

**suborbicular** as orbicular but the length a little longer than the breadth.

**sun-leaf** a leaf that developed more or less fully exposed to solar radiation.

### Hairs

**axillary groups** small groups of hairs, either on the sides of the raised veins and/or on the intervening surface in the axils of the veins (*barbae* or *domatia*).

**clavate** in *Tilia* small, multicellular, dark red, cylindrical hairs, narrowed at both ends.

**fasciculate** with several limbs joined at the base and forming a more or less erect tuft.

**simple** with a single, usually unicellular limb.

**stellate** star-like, with several arms that radiate outwards but join at the base.

### Inflorescence, flower and fruit

**beaker-shaped** with sepals and petals forming a short tube about twice as deep as wide (see rotate).

**bracteole** small, leaf-like structure on the flower stalk (**pedicel**), normally lost soon after extension in *Tilia* to leave a small scar.

**corymbose cyme** a cyme with flowers grouped into a dense, circular, flat or convex head.

**dichasium, dichasial cyme** with each axis of the inflorescence terminating in a flower below which in the lower part of the inflorescence there are normally two opposite branches.

**divaricate** with branches widely divergent.

**ellipsoid** applied to fruits which are elliptic in longitudinal section.

**erose** with small irregular indentations, applied to the apex of the petals of *Tilia*.

**ligulate** strap-shaped, applied to the petals of *Tilia*.

**loculus**, a compartment of the ovary or fruit of which there are normally five in *Tilia*.

**mamillate** surface feature of a fruit wall consisting of a mosaic of small circular swellings.

**oblanceolate** applied to bracts which are two to three times longer than broad and broadest towards the apex.

**oblong** applied to bracts with almost parallel sides.

**obovoid** as ovoid but the broadest part towards the apex.

**ovoid** applied to fruits which are egg-shaped with the broadest part towards the base.

**rotate** applied to a corolla which is circular and flat, or shallowly saucer-shaped.

**staminode** a small petal-like structure, apparently replacing a stamen.

# 3

## Cellular anatomy

This chapter describes the cellular structure of the tissues of the main vegetative organs, the root, stem, leaf and bract of *Tilia*. As in many other respects, the anatomical structure of the genus is distinctive and in some features unique but, at least in those species that have been investigated, there is general uniformity between them. Most of the detailed information that is presented here is based on studies of *T. americana*, *T. cordata*, *T. platyphyllos* and *T. tomentosa*.

Accounts of the anatomy of the wood of *Tilia* are available in many textbooks (Esau 1953) and more comprehensive accounts of the anatomy of European species in Kirchner, Loew and Schröter (1927), Cutler et al. (1987) and Cebrat (1991).

### Morphology of the root

The general structure of the root system of seedlings and of the adult trees is described in relation to their function in Chapter 13 and illustrated in Figure 13.14. The primary root of seedlings of *T. cordata* retains its dominance during the first year and in dry soils and light shade can reach a depth of 0.20–0.35 m by the end of the first summer. Growth is reduced in deep shade. A depth of 0.48 m was reported for growth in the first year of the primary root of *T. americana* in unshaded prairie and a similar reduction in deep shade (Holch 1931). Roots of young trees of *T. cordata* soon establish several laterals that grow almost vertically or obliquely down, and eventually become massive woody roots. There are numerous subsidiary laterals that terminate in densely branched, slender ‘feeding’ roots and in the upper horizon of the soil these also form tufts of mycorrhizae (Figure 13.19). Deeper roots branch less often, continue extension longer and mostly lack mycorrhizae.

### Cellular anatomy of extending roots

#### Primary tissues

Young roots of *Tilia* are cylindrical with a wide cortex and slender central stele (Figure 3.1a): those that continue to

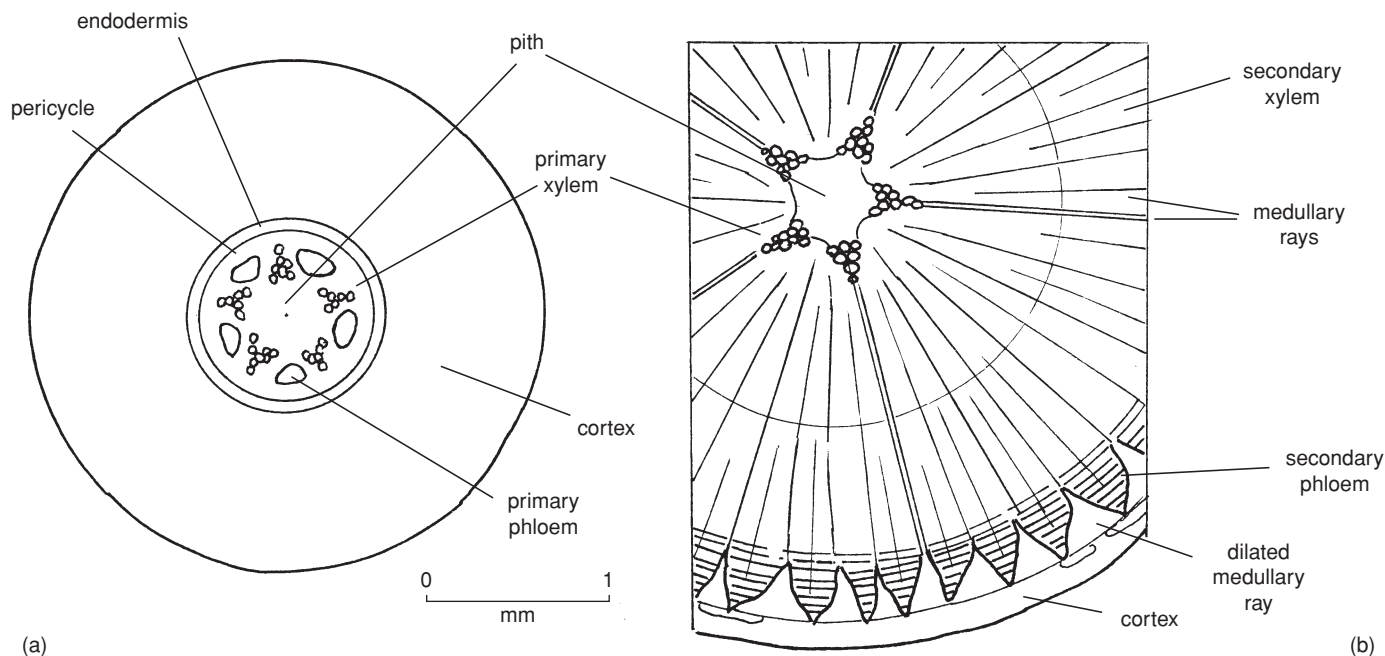
extend are usually pentarch, that is with five initial strands of xylem, according to Kirchner, Loew and Schröter (1927), but they may also often be hex- and heptarch (Figure 3.2). The xylem strands are initially composed of narrow elements and these predominate as centripetal differentiation proceeds and metaxylem forms a central cylinder. Strands of phloem alternate tangentially with the strands of protoxylem xylem and the vascular tissues are bounded by a ring of pericycle and endodermis. The first lateral roots are initiated at the endodermis and emerge through the cortex.

#### Secondary structure and anatomy of the roots

In roots that do not form mycorrhiza and continue to extend, a vascular cambium arises in the procambial tissue between the strands of protoxylem and of phloem. Secondary xylem differentiates centrifugally and the cambium and secondary phloem become circular in cross section (Figure 3.1b) as diameter increases. Superficially, the structures of the root and stem appear very similar, but in extension roots, as the cylinder of vascular tissues grows in diameter, the cells of the pericycle divide radially and its circumference increases. In contrast, the cortex of the root is eroded and eventually a cork cambium develops in the outer pericyclic tissue and a thin bark develops. Roots differ from stems in this respect, but stems may be most readily identified by the persistence of a clearly defined, undifferentiated central pith (Figure 3.3b), whereas in roots the central tissue is metaxylem.

The lateral branches that form mycorrhizae branch freely but remain short and secondary development is inhibited (Figure 13.19). The cortex is retained and becomes invaded and infested by fungal hyphae.

The tissues of the root of *T. × europaea* are described and well illustrated in Cutler et al. (1987, pp. 196–197). The secondary xylem (Figure 3.2) closely resembles that of stems and



**Figure 3.1** Plan of tissues in transverse section of extension root of *Tilia cordata* at (a) 1 month old with only primary tissues and (b) 27 months old.

has similar annual rings. As in stems, the phloem consists of alternate bands of fibres and conducting elements, which become triangular in section as the diameter increases with the expanded ends of the medullary rays between them. As already described, increase in diameter of the stele is accompanied by degeneration and loss of the primary cortex and a phellogen arises in the pericycle immediately inside the endodermis. This, as in the stem, primarily produces phellem, which tends to be thinner on roots than on stems of the same age, and is also accompanied by formation of lenticels.

## Anatomy of the stem

### Primary tissues

Stems of young shoots are cylindrical (Figure 3.3a), and, initially there is a wide cortex of which the outer tissue consists of collenchyma that contains chloroplasts and is green, although this is often masked by red anthocyanins in the epidermis. The procambium is cylindrical, and normally gives rise to about 16 bundles that form a circle in transverse sections of the internodes. These surround and bound an inner cylinder of pith, 80–100  $\mu\text{m}$  in diameter (Figure 3.3a).

Each bundle initially consists of a small strand of phloem outside the vascular cambium with an outer strand of fibres and an inner strand of sieve-tubes and companion cells. Inside

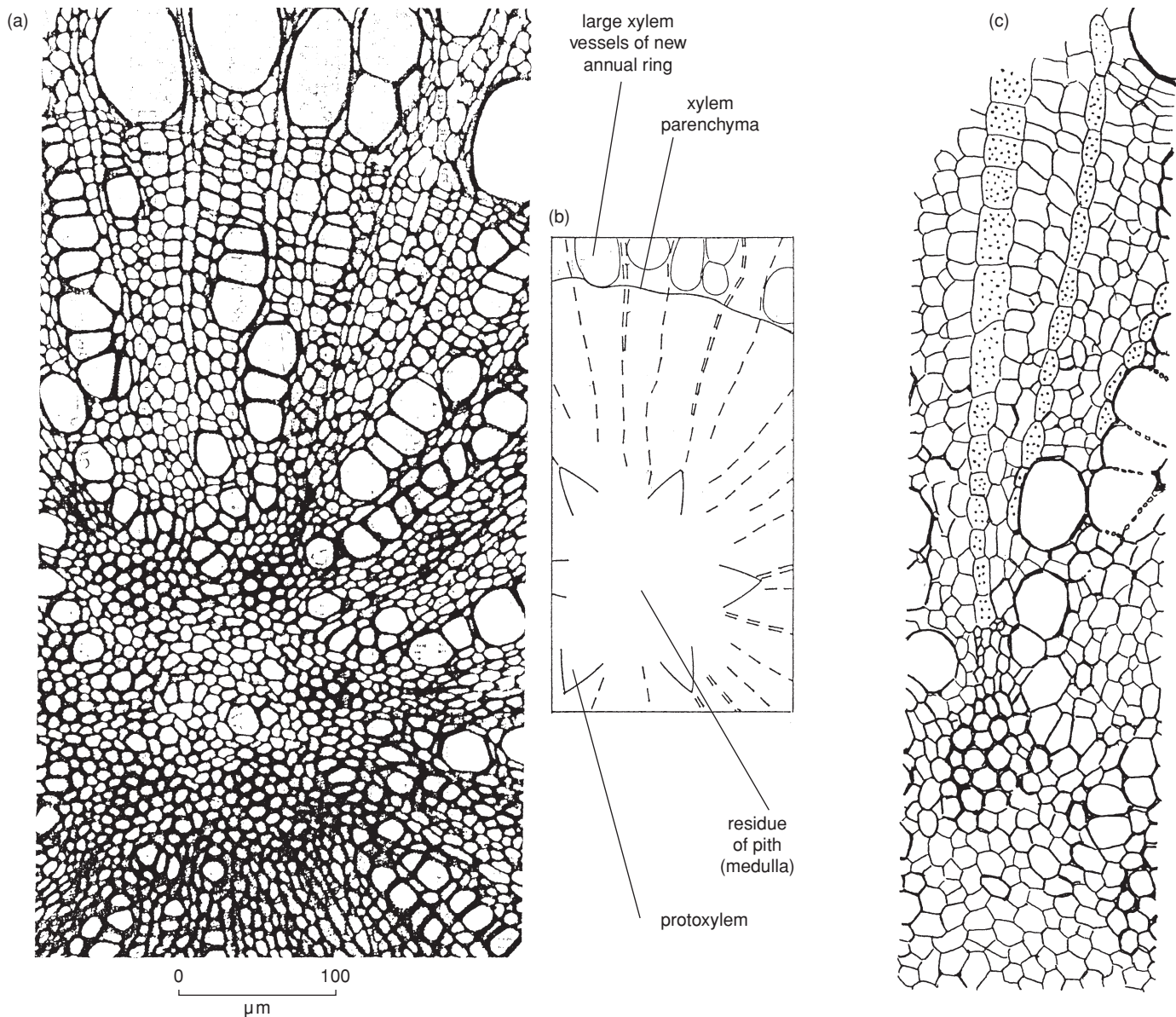
the cambium is a small strand of xylem formed of narrow vessels and parenchyma.

Cambial division and differentiation proceed rapidly to form a hollow cylinder of vascular tissue in the internodes. Immediately below each node, a gap on one side is associated with outward branching of a leaf-trace and on each side a small discontinuity corresponds with the development of the stipules (Figure 3.4a). Immediately above, a second trace develops into a cylinder in the axillary bud (Figure 3.4b and c) and will the following year become a branch.

The vascular cylinder of the young stem is traversed by 60–70 medullary rays (Figure 3.3b). Eight of these are two cells across tangentially, and subsequently widen to several cells across, and the rest remain one cell wide out to the point where they pass through the vascular cambium and expand tangentially in the phloem. Both primary xylem and phloem are similar in structure to their respective secondary tissues, so that the original bundles are not easily recognised, although there is a more or less continuous inner ring of vessels, 25–33  $\mu\text{m}$  in diameter, formed in the xylem at the start of growth in the second and each subsequent year (Figure 3.10). Secondary growth of the phloem during the spring and early summer consists of alternate tangential zones first of fibres and then of sieve-tubes and companion cells.

The epidermis may be almost uniform in structure, or it may include cells that are modified into simple hairs, or circular clusters of cells that form fasciculate or stellate hairs (Figure 2.17). The ordinary epidermal cells have a conspicuous outer





**Figure 3.2** Tissues at the centre of an extension root of *Tilia × europaea* with six strands of protoxylem: (a) photocopy of photograph by P. Gasson, (b) plan of tissues and (c) drawing of tissues along the radius of one protoxylem strand.

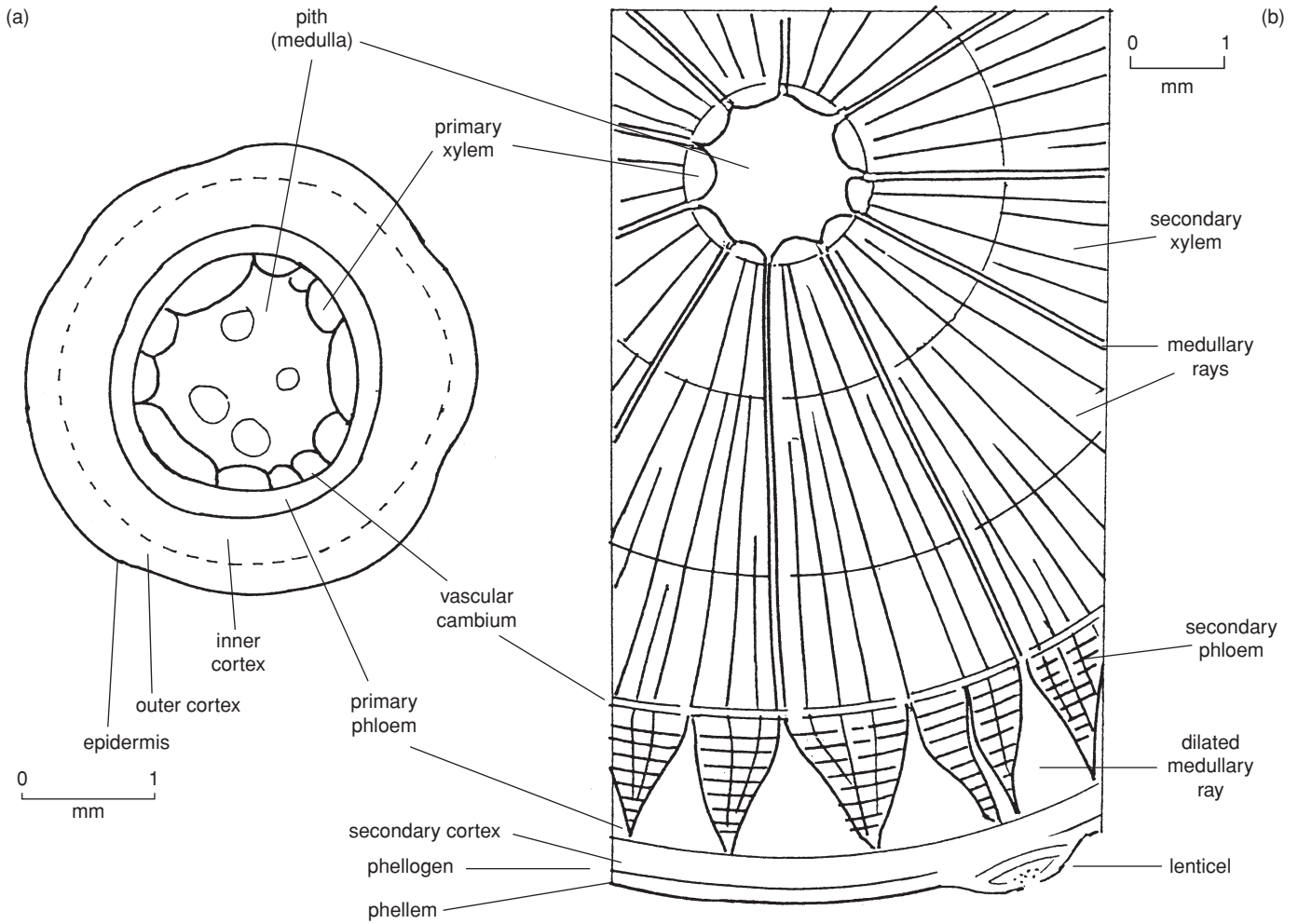
cuticle (Figure 3.5a) that is interrupted by the sparse, small, wart-like lenticels. Beneath the epidermis the collenchyma of the outer cortex grade into parenchyma of the inner cortex. About one cell in 20 contains a large druse of crystalline calcium oxalate.

During the first summer the phellogen arises by tangential divisions in the outermost layer of cells of the cortex, immediately under the epidermis (Figure 3.5a). Initially, the phellogen is discontinuous, so that only parts of the young stem develop

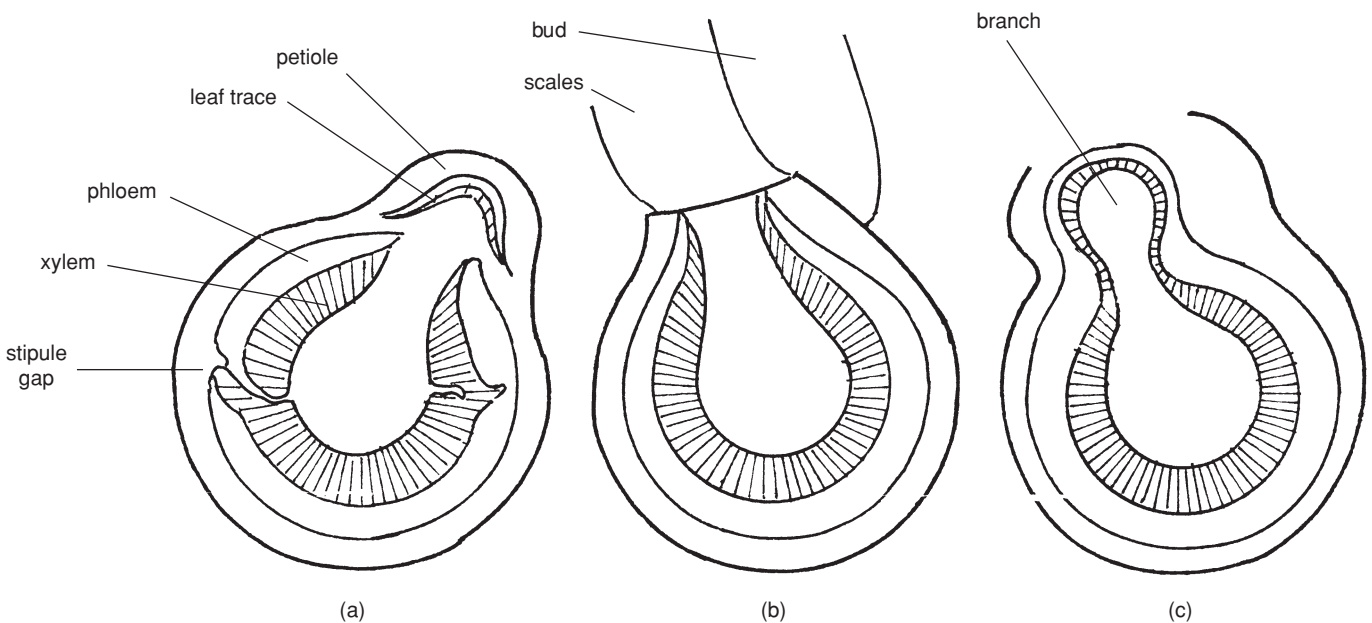
a thin layer of cork cells (phellem) and the epidermis persists but becomes suberised. Usually by the end of the first season the phellem is only three to five cells deep and secondary cortex (phelloderm) is absent (Figure 3.5b). These outer secondary tissues constitute the periderm.

### Secondary tissues of the stem

All tissues outside the vascular cambium, which are readily peeled off because of the fragility of the thin-walled cambial cells, are loosely referred to as bark. The outer bark is periderm and the inner bark is phloem. The bark of several species of *Tilia* has been utilised by people of many cultures as a source of relatively strong fibres (see Chapter 15).



**Figure 3.3** Plan of tissues in transverse section of internode of stem of *Tilia cordata* (a) 30 days after extension from bud and (b) at end of 4 months of growth in September.



**Figure 3.4** Transverse section of node of stem of *Tilia platyphyllos* at the level (a) of attachment of the leaf-petiole, (b) immediately below the axillary bud and (c) of the axillary bud that will eventually form a branch.