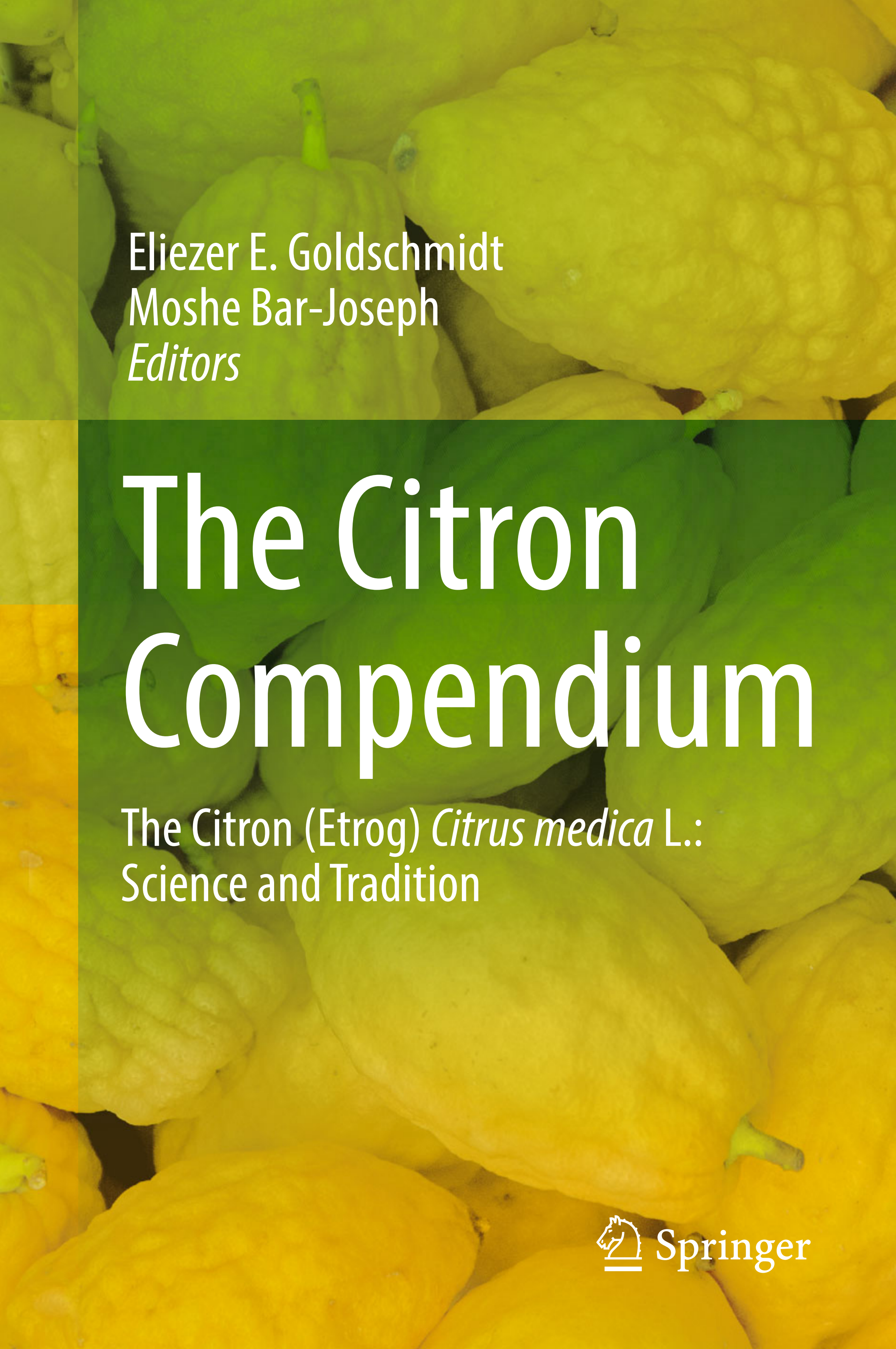

Eliezer E. Goldschmidt
Moshe Bar-Joseph
Editors

The Citron Compendium

The Citron (Etrog) *Citrus medica* L.: Science and Tradition

Springer

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Editors
Eliezer E. Goldschmidt
Institute of Plant Sciences and Genetics in Agriculture
The Hebrew University of Jerusalem
Rehovot, Israel

Moshe Bar-Joseph
The S. Tolkowsky Laboratory
The Volcani Institute, ARO
Rishon LeTsiyon, Israel

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Dedicated to
Ian J. Warrington
Emeritus Professor, Massey University,
Palmerston North, New Zealand

With appreciation and gratitude
for his outstanding editorial work
in the preparation of
The Citron Compendium

But the noble-hearted man has noble
purposes, and by these he will be guided
(Jes. 32, 8) BBE

Foreword

The Citron Compendium, co-edited by Eliezer E. Goldschmidt and Moshe Bar-Joseph, is an expanded revision from a Hebrew work published in 2018. It includes twenty-two chapters written by thirty authors covering citron history, cultivation, biology, genetics, diseases, and iconography; it will prove to be a classic compilation of the citron literature. Eliezer E. Goldschmidt is an eminent horticulturist and Hebrew scholar whom I have known for many years. Among his many achievements, he is a world authority on etrog, the Hebrew name for an ancient type of citron. Moshe Bar-Joseph is a world-renowned citrus pathologist specializing in plant virology and experienced in citron propagation for viroid diagnosis.

Citron (*Citrus medica* L.) is a large fragrant fruit with a bumpy rind and thick white albedo that is barely edible, yet it was highly esteemed in antiquity. As the epithet of its scientific name implies, it was deemed to have medical properties and was once considered an antidote for poisons. It was referred to as the Median (Persian) apple by Theophrastus in the fourth century BCE. In Europe, the sugar-infused albedo (candied citron) was a favorite of Christopher Columbus, and the citron was imported to the New World in his second voyage (1493). An unusual form of citron, whose fruit is segmented in fingered sections, and referred to as Buddha's hand, is a popular offering in Buddhist temples.

Citrus is native to Southeast Asia, and there are a number of indigenous species in Australia. *Citrus medica* (citron) along with *C. reticulata* (mandarin) and *C. maxima* (pummelo) are considered foundational species for citrus. The lemon genome derives mostly from citron; rough lemon, a hybrid of citron and mandarin, is a widely used citrus rootstock.

Although etrog is not native to the Middle East, it holds a key position in Jewish history. The citron was introduced to Israel after the return of Judeans from Babylonian captivity (586–516 BCE). The fruit now maintains a featured role in the week-long festival of Sukkot (Tabernacles), celebrated by worship and dining in huts (*sukkot*), commemorating the forty years that the Jewish people spent in the desert on their way to the Promised Land.

Four plants are commanded to be gathered in the celebration. These are defined in Leviticus 23:40 as *Pri etz hadar* (fruit of a goodly tree), *lulav* (palm fronds), *hadas* (myrtle leaves), and *arava* (willow). The fruit of a goodly tree was defined as etrog in the Mishnah, a rabbinical codification of Jewish law written in the third century. It was chosen, perhaps, for its unique appearance and divine fragrance. Etrog is depicted in second-century Bar Kokhba Revolt coins and in the sixth-century Beit Alpha synagogue in Israel.

Later rabbis would insist that the fruits had to be unblemished and borne on a non-grafted tree, undoubtedly derived from the prohibition of mixing species in Jewish law. Furthermore, the presence of a *pitam* (remnants of the stigma and style) was especially esteemed. The difficulties of obtaining these fruits on the appropriate date made the etrog a very expensive fruit in the Diaspora. Thus, the production of these fruits would become a very special horticultural skill for the Jewish market.

The chronicle of the etrog emphasizes the close connection of plants and the human experience. Plants, flowers, and fruits are revered in many cultures and become celebrated in legends, songs, and traditions. Many cultures formed a cultural bond between the plants that sustained them. Olive, wheat, rice, and maize were revered plants incorporated in the symbolism of many religions. Tree worship is ancient, and evergreen trees and wreaths symbolize eternal life in many cultures. Fruits are particularly esteemed. In the United States, the use of a carved pumpkin to make Jack-o'-lanterns in the celebration of Halloween has made pumpkin a symbolic fruit, and millions of homes use them as doorway decorations in the fall.

The unblemished etrog is the symbolic fruit of the Jewish people. *The fruit of the land shall be the pride and honor of the survivors of Israel* (Isa. 4:2).

Jules Janick
Distinguished Professor Emeritus
Purdue University
West Lafayette, IN, US

Preface

The present volume—*The Citron Compendium*—follows its predecessor, *The Etrog Citron: Tradition and Research*, which appeared in Hebrew.[1] To some extent, it is also a descendant of Tolkowsky's classic, *Hesperides*.[2] However, the present volume is not merely a translation of the Hebrew text; it is in fact an entirely revised and expanded edition. While the Hebrew edition was intended mostly for the traditional Jewish audience, the current volume is internationally and scientifically oriented, having in mind the broader citrus professional community. Led by this vision, we deleted some traditional sections, revised the previous chapters, and added a few new ones in an attempt to provide the most extensive coverage of the citron theme.

The citron (*Citrus medica* L.) is one of the forefathers of the citrus tribe and was probably the first to have reached the Near East and the Mediterranean. The citron fruit received great attention due to its unique appearance, fragrance, presumed medical qualities, and was subject to scientific investigations by classical botanists (Fig. 1).[3]

Over the last millennium, however, as other, juicy citrus varieties became available in Europe, the interest in the citron declined considerably. Thus, although the significance of citron as a citrus forefather was undisputable, attention has shifted mostly towards the etrog citron and its role in the Jewish Tabernacles festival (Sukkot), and its culture which was mainly intended for that religious purpose (with some tangential culinary uses). Presently, very few researchers concern themselves with the citron, with the exception of some viral pathologists, and the broader ramifications of this subject have not been compiled. The present volume is an attempt to fill this void. Bringing a full range of the citron's cultural, scientific, and historic aspects under

[1] Eliezer E. Goldschmidt and Moshe Bar-Joseph, *The Etrog Citron: Tradition and Research—Essays on the Scientific, Halachic and Historical Significance of the Etrog Citron* (Jerusalem: Mossad Harav Kook, 2018).

[2] Samuel Tolkowsky, *Hesperides: A History of the Culture and Use of Citrus Fruits* (London: John Bale, Sons and Curnow).

[3] Giovanni B. Ferrari, *Hesperides, Sive De Malorum Aureorum cultura et usu libri quatuor* (Rome: Hermanni Scheus,1646).

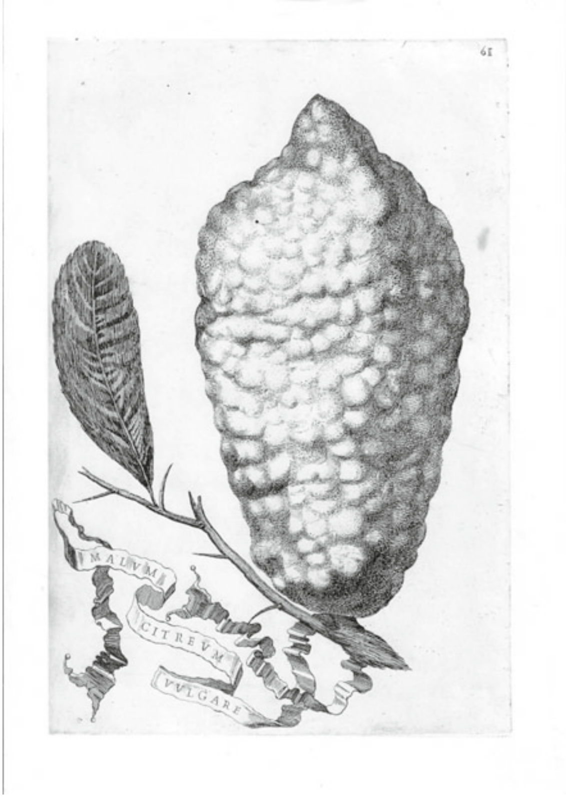

Fig. 1 Picture of citron fruit from the Hesperides of Ferrari (1646). (*Photo* E. E. Goldschmidt)

the same roof has been our dream, and this goal has now been achieved. The best professional experts have joined us for this international operation.

The Etrog Citron: An Appreciation

The etrog citron has become a Jewish symbol as much as the menorah (the seven-branched candelabrum), and has been depicted on coins, mosaics, floor tiles, and wall paintings in ancient synagogues in Israel and the Diaspora (Fig. 2).

Evidence of the great efforts expended by Jews of antiquity in observing the Four Species ritual (Lev. 23:40) is found in the "Four Species Letter" of Bar Kokhba, written on papyrus in 134 CE and discovered by Prof. Yigael Yadin:

To Yehuda bar Menasheh of Kiryat Arbiya (modern-day Arub, south of Jerusalem). I sent you two donkeys so that you can send them with two men to Yonatan bar Baaya and to Masbala, so that they can load palm fronds and etrogs to send to the camp for you. And you should send other people from your camp to bring myrtles and willows,

Fig. 2 Mosaic in the synagogue of Ma'on (Nirim; sixth century), showing two citron fruits on both sides of the sanctuary candelabrum (*Photo* Z. Radovan. The Israel Antiquities Authority)

and arrange them in sets and send them to the camp, because the army is very large. Peace unto you.[4]

Even now, despite the intervening centuries since the suppression of the Bar Kokhba Revolt by the Romans, it is thrillingly clear how much effort the revolt leader and his men expended in order to provide the Four Species and observe the Sukkot holiday, even during the most critical times of the failed revolt.

Jumping from the immemorial past to our time, anyone who wishes to experience the excitement and affection that Jews feel towards the etrog citron should visit one of the Four Species markets that appear prior to Sukkot all over Israel and in centers of Jewish life around the world. There one can see thousands of citron fruits carefully displayed for sale, surrounded by customers from the widest range of socioeconomic and religious backgrounds, all intent on selecting the perfect and most beautiful fruit.

In previous generations, citrons were scarce even in the Land of Israel, and all the more so in the colder countries of the Diaspora. Those fruits that reached the market were so expensive that very few could afford them, and most people could only envy wealthy worshippers with their citrons. In recent years, citrons have again become available throughout Israel and the Diaspora, so that all who wish to purchase a citron can readily do so (Fig. 3).

[4] Yigael Yadin, *Bar Kokhba: The Rediscovery of the Legendary Hero of the Last Jewish Revolt Against Imperial Rome* (Jerusalem: Weidenfeld & Nicolson, 1971).

Fig. 3 Views of the Etrog market toward Sukkot (Collage by Dr. Yoel Fixler)

The Citron Compendium

The present volume with its twenty-two chapters is divided into four sections.

Part I, entitled "Citron Biology," contains a broad bio-historical and evolutionary analysis of the citron and the citrus tribe, citron phytochemistry, and an up-to-date account of citron genomics.

Part II, entitled "Cultivation and Production," covers a range of practical aspects of citron culture–horticulture, post-harvest, pests and diseases and, finally, detailed accounts on the history of citron culture in China, Calabria, Corsica, and the United States. A lovely description of the culinary use of citrons in the Mediterranean terminates this section.

Part III, entitled "Tradition," addresses religious and cultural aspects of the citron–Talmudic and mystic facets, and the significance of the citron in medicine, art, and literature.

Part IV, entitled “History,” traces the culture and commerce of citrons from antiquity, through the Middle Ages and up to modern times, paying special attention to the citron grafting controversy.

A pictorial album and a glossary complement this volume. Thus, with help of the Almighty, now we can congratulate the finished.

Finally, on a personal note, this is not our first encounter with the subject. The citron, with all its diverse aspects, has concerned us for many years. We trust that this volume will attract the interest of a wide range of scientists, horticulturists, historians, and intellectuals, and find a place of honor in the libraries of all those interested in the citron and its broader extensions.

Rehovot, Israel — Eliezer E. Goldschmidt
Rishon LeTsiyon, Israel — Moshe Bar-Joseph
May 21, 2023; Sivan 1, 5783

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The production of *The Citron Compendium* would not have been possible without the dedicated help of numerous colleagues and friends, many of whom acted voluntarily. The board of Mossad Harav Kook Publishing House, Jerusalem–R. Yehuda Leib Rafael, R. Natan David Shapira, and R. Yosef Eliyahu Movshovitz–generously permitted the use of chapters from their 2018 Hebrew edition of the book as a basis for the current English edition.

Zuzana Bernhart, our Springer Science Editor, accompanied the development of *The Citrus Compendium* from its earliest beginnings with personal attention and advice. Our senior colleague, Jules Janick, contributed a thoughtful foreword.

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Our colleague and friend, Moshe Huberman, was always there for us with unfailing, fullhearted assistance. Ellen Wachtel assisted in editing parts of the "Diseases" chapter.

R. Yeshaya Kirszenbaum and R. Elimelech Retman generously allowed us to use specimens from their etrog collection for the pictorial album. The photographs were taken by Yoel Fixler, who also designed the Etrog Market collage; Yiphat Kedem arranged the Pictorial Album; and Saar Zini prepared the map of the Mediterranean basin.

Our dedicated authors did not spare any effort in providing an intriguing coverage of their topic. Sadly, our colleague, Haim Aviv, author of Chap. 12, passed away during the preparation of this manuscript. The translators of the Hebrew chapters did their best in clarifying the meaning of the texts.

Shirley Zauer and Ian Warrington, our chapter editors, did a marvelous, endless job in the editing and styling of the entire manuscript.

Thanks are due also to Amudha Vijayarangan, Peggy Papandreou, Ineke Ravesloot and, in particular, Madanagopal Deenadayalan, who bore the major brunt of the publication.

Last but not least, we are ever-grateful to Leah Goldschmidt and Hannah Bar-Joseph, our life partners, who endured with us years of work on this volume and whose unfailing support and advice helped bring us to this point.

Eliezer E. Goldschmidt
Moshe Bar-Joseph

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Part I
Citron Biology

Chapter 1
The Biology of the Citron (*Citrus medica* L., Rutaceae-Aurantioideae-Aurantieae), its Hybrids and their Allies

David J. Mabberley

Abstract The biology of citrus is briefly reviewed, pointing up how surprisingly little is known of pollination and dispersal in wild species. The classification of the citron, *Citrus medica*, in modern science is set out in a historical context: its taxonomic relationships in the light of the evolution of the genus *Citrus* and the citron's role in the origin of major citrus crops as well as the importance of the etrog citron in the traditional Jewish Tabernacles festival are outlined. The global threat to the citron and all other citrus from the bacterial disease, *huanglongbing*, is explained. As an aid to understanding the much-confused citrological literature, the formal taxonomy of the citron is presented in an Appendix, complete with a nomenclatural account of those commercial crops which have citron in their make-up; for example, the Rangpur lime (a rough lemon) is *Citrus* × *otaitensis* (syn. *C.* × *volcameriana, C.* × *jambhiri*).

1.1 Introduction

The etrog is one of the most celebrated examples of the citron (Fig. 1.1), which is a species of *Citrus* (so, for example, one cultivar is written *Citrus medica* L. 'Etrog'; see Appendix)—and citrus-growing is the most important fruit industry of all in warm countries. In 2016, world production of citrus fruit was some 124 million tons, about half of which was oranges (UN Food and Agriculture Organization 2016) well over twice what it had been in the 1980s, though that in Israel had halved over this time and was estimated to be just some 525 thousand tons in 2020. Nonetheless, the Mediterranean region is very close in production to that of each of China and Brazil, the biggest producers—and three times that of USA, where yields have been falling since the 1990s.

D. J. Mabberley (✉)
Wadham College, University of Oxford, Oxford OX1 3PN, UK
e-mail: David.Mabberley@botanicgardens.nsw.gov.au

School of Natural Sciences, Macquarie University and Australian Institute of Botanical Science (Royal Botanic Gardens and Domain Trust), Sydney, NSW 2000, Australia

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Fig. 1.1 *Citrus medica* (citron). (Reproduced from Henri Louis Duhamel du Monceau, *Traité des arbres et arbustes*, ed. 2, 7: t. 22 (1819))

1.2 The Family Rutaceae

Citrus and its allies form the most "natural" subfamily, subfam. Aurantioideae, of the family Rutaceae, which is found throughout the tropical and other warm parts of the world. The family Rutaceae (Kubitzki 2011; Mabberley 2017; Appelhans et al. 2021) is represented by some 2,000 or so species in about 155 genera especially well represented in the tropics. They are characterised by being aromatic trees and shrubs, rarely herbs. The scents are due to the presence of secretory cavities, which, in the leaves of most species, appear to the naked eye as transparent dots, often a good "field" character for family identification. Their leaves are usually pinnate or trifoliolate, more rarely simple blades, and their fruits are of a wide range of forms from those splitting open to fleshy ones such as berries or drupes.

The aromatic nature of the plants and the fleshy fruits of many are the basis of their interest to humans. Rue (*Ruta graveolens*) is a strongly flavoured herb in the Mediterranean, curry-leaf (*Bergera koenigii*) is an essential in curries in the East, and angostura (*Galipea* spp.) provides the bitters of a pink gin. The essential oils of *Agathosma* spp. from Africa are the source of *buchu* used in medicine and flavouring, while species of *Zanthoxylum* from Asia yield fruits sold as spices, notably *sansho*, one of the few condiments in Japanese cuisine.

Some Rutaceae provide timber such as satinwood (*Chloroxylon swietenia* from southern India and Sri Lanka) and sneezewood (*Ptaeroxylon obliquum* from Africa), but also other commercial timbers from tropical American species of *Amyris*, *Balfourodendron* and *Euxylophora*, besides Australian species of *Bouchardatia*, *Flindersia*, *Geijera* and *Halfordia.* Also from tropical America come the medicinal products known as *jaborandi* (*Pilocarpus* spp.) used in the treatment of glaucoma. Important constituents of commercial scent include extracts from species of *Boronia* (Australia) and, most importantly, *Citrus.*

Many Rutaceae are beautiful ornamentals, notable in northern-hemisphere gardens being the burning bush, *Dictamnus albus,* the Mexican *Choisya* species and hybrids, *Ptelea* spp. from North America, and *Orixa* , *Skimmia* and *Tetradium* spp. from temperate east Asia. Similarly, in the tropics and subtropics widely grown ornamentals include Cape chestnut (*Calodendrum capense*) from Africa, *Correa* spp. from Australia and species of *Atalantia*, *Euodia*, *Melicope*, *Murraya* and *Triphasia* from the Asia–Pacific region.

But, in terms of global commerce, it is the fruits of Rutaceae that are the most significant. Although the *bael* (*Aegle marmelos*), and species of *Clausena* and *Glycosmis* as well as the wood apple (*Limonia acidissima*), all from Asia, and the white sapote (*Casimiroa edulis*) of Mexico, are of local importance, it is only the fruits of *Citrus* that command world attention (Mabberley 2004).

Citrus and its closest allies (Rutaceae–subfam. Aurantioideae–tribe Aurantieae [Citreae]) are characterised by their fruits being berries having pulp derived from multicellular hairs within the ovary, becoming "pulp vesicles" within "segments" of a unique fruit type known as a hesperidium (Fig. 1.2), the rest of the subfamily (tribe Clauseneae) notably *Bergera*, *Clausena* and *Glycosmis* being without such. The name of the tough-coated hesperidium is an allusion to the mythological Golden Apples of the Hesperides (meaning daughters of the evening in Greek), said to lie beyond the Atlas Mountains of North Africa (Hammond and Scullard 1970). The mythological Hesperides sisters (variously three, four or seven), included Aegle and Hesperethusa, commemorated today in rutaceous generic names, the first for the *bael* fruit (*Aegle marmelos*) sacred to Hindus, the second now a synonym of *Naringi* (probably a rendering of the Hindi *nārangī* - see below), both referring to citrus allies. But the original Golden Apples of the Hesperides seem to have been quinces (*Cydonia oblonga*, Rosaceae), though, with the introduction of citrus fruits to the Mediterranean, the name was soon transferred to them.

1.3 The Genus *Citrus*

Citrons, oranges and lemons have been referred to the genus *Citrus* since the time of the eighteenth-century naturalist, Carl Linnaeus, who took up the classical name once used for the sweet-scented timber of *Tetraclinis articulata*, known to the Ancient Greeks as *thyon* and to the Romans as *citrus* (Meiggs 1982; they used *citreum* for what we now call citrus fruits), from the Greek kitros, meaning aromatic. Before Linnaeus's time, the fruits had been known as Aurantia (= gold) in Latin and, possibly then from French "*or*" (gold), comes "*orange"* in Old French, though the Arabic

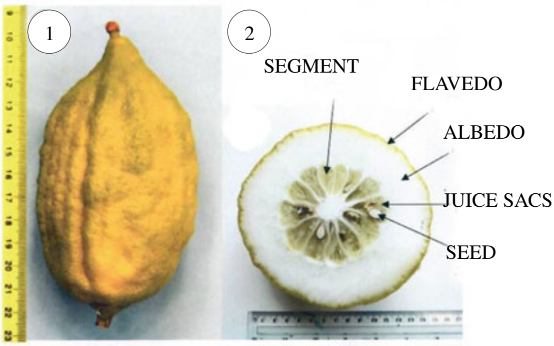

Fig. 1.2 The hesperidium of citron (*Citrus medica* L.)
1. A 'Calabria' etrog citron. Note the persistent style—'pitam', peduncle, bumpy rind, and essential oil glands in pits
2. Cross section of an etrog citron. Note rind components—flavedo and albedo; pulp segments containing juice sacs and seeds

word is *nāranj* from Hindi *nārangī* and Persian *nārang* which seems to be a more plausible origin (Mabberley 2004). Thence has come the name citron (*Citrus medica*), but confusingly the *citron* of France is the lemon (*Citrus* × *limon*), as is the *citroen* of The Netherlands and *Zitrone* of Germany. This is the result of the lemon and citron anciently being considered forms of the same thing and, in early texts, it is often difficult to determine which of the two is meant. It is very interesting to reflect on this, once the origin of the lemons is considered (see below), but Linnaeus in 1753, in face of considerable criticism, made the lemon a variety of the citron in his classification.

The genus *Citrus*, as now understood (Zhang and Mabberley 2008; Kubitzki 2011; Mabberley 2013, 2022; Wearn and Mabberley 2016), comprises as few as 25 tree species growing naturally in the wild from South Australia northwards as far as China and extending east to New Caledonia and west to north-eastern India, but citrus fruits have now been introduced to most of the warm parts of the world, in many of which they have become naturalized so as to appear wild. The genus (Mabberley 1998, 2002, 2017, 2022; Ollitrault et al. 2020; Appelhans et al. 2021) now includes, once more, the formerly segregated genera, *Eremocitrus*, *Fortunella* (kumquats), *Microcitrus* and *Poncirus* (trifoliate orange). Contrary to information presented in books and on the Internet, most of them are not native in China and neighbouring territories, the region with the highest number of indigenous *Citrus* species being Australasa, where some of them are in commerce as "bush-tucker" and are also being hybridized with long established crop cultigens (Mabberley 2013), now apparently a matter of vital importance to the future of the citron (see below).

1.3.1 Morphology, Anatomy and Phytochemistry

Typical of tropical plants, *Citrus* buds are not surrounded with protective scales, but are almost naked (Bartholomew and Reed 1943). The dominance of the apical buds is especially strong in the citron (and the lemon). Lateral buds in the axes of the leaves are usually with the rudiments of a thorn (two in *C. inodora* of tropical Australia), especially in rapidly growing shoots. Because examples are known where in rapidly growing shoots of sweet orange 'Washington Navel' (older name 'Baia') such have borne not only leaves and "secondary" thorns, but also flowers and even fruits, they have been considered homologous with shoots (Shamel and Pomeroy 1918). The thorns are particularly large and tough in juvenile phases, much as in for example *Gleditsia* (Leguminosae; see Janzen and Martin 1982), suggestive of defences against large animals, which in mature trees might also be dispersal agents. The thorns are often a nuisance in orchards, causing injuries to pickers as well as to fruits subsequently infected with disease through punctures.

Bonavia (1888) concluded that the typical citrus leaf is derived from a compound one (Fig. 1.3) and illustrated citrus seedlings showing trifoliolate leaves (1890: t. 246). The apparently simple leaves are therefore unifoliolate, the trifoliolate *C. trifoliata* of China being an intermediate condition to that of the pinnate leaves in many Rutaceae.

With the exception of annually deciduous *Citrus trifoliata* and its hybrids, *Citrus* spp. are evergreen, the leaves persisting for up to two seasons or more (Bartholomew and Reed 1943; Primo-Millo and Agusti 2020). Stomata are produced during the early stages of lamina development and are found only on the abaxial (lower) surface, save a few sometimes on the upper side of the midvein. In lemons they are more numerous than in oranges (Reed 1931) and, in Aurantioideae as a whole, those from more tropical regions have the highest density, up to 500 per square millimetre,

Fig. 1.3 *Citrus* leaves in a reduction series when compared with other Rutaceae; (left to right) *Zanthoxylum simulans*, *Citrus trifoliata, Citrus* × *aurantium* (Sources: *Z. simulans* modified from https://plants.ces.ncsu.edu/plants/zanthoxylum-simulans/, Krzysztof Ziarnek, Kenraiz; *C. trifoliata* modified from https://plants.ces.ncsu.edu/plants/citrus-trifoliata/, Meneeke Bloem; *C.* × *aurantium* Sour Orange Group, Y. Yaniv with permission)

Citrus medica having one of the highest numbers of all, on average 673 per square millimetre (Hirano 1931), while a desert species, *C. glauca* (Australia), has as few as 167, on average.

The fragrance of citron and other citrus leaves and fruits is due to the release of essential oils when the tissues are bruised. The synthesis, secretion and accumulation of these oils are in the oil glands characteristic of the family Rutaceae. In oranges (Thomson et al. 1976), the young glands in leaves comprise a central group of polyhedral cells surrounded by layers of radially flattened ones. The oil chamber forms from the separation of the cell walls of the central ones, which become flattened as it increases in size through the secretion of oil from the central cells. The more-or-less spherical essential oil cavity in citrus fruit peel forms similarly, though formerly believed to be due to the disintegration of cells (Fahn 1974), such lysigenous development releasing the cells' contents into the cavity, but this is now known to be an artefact of specimen preparation techniques, in lemon at least (Turner et al. 1998). The acid oil droplets in juice vesicles of some species of *Citrus* 'subg. *Papeda*' make the fruits inedible to humans.

The biological function of the oil is not fully understood but it is likely to be concerned with deterrence of pests: indeed, the use of citrons and other citrus against the depredations of moths and other insects has long been known and exploited by humans. It is notable that it is only the stamens (Bartholomew and Reed 1943) that are free of the oil glands, such that they are unlikely to deter pollinators, which could damage tissues and release any such oil whilst collecting pollen. Interestingly, the stamens contain high concentrations of caffeine (which has insecticidal qualities), in the anthers and pollen almost as high as in coffee beans (Kretschmar and Baumann 1999). It has been shown that bees rewarded with caffeine are three times as likely to remember a learned floral scent as are those rewarded only with sucrose, so that it has been argued that there is selective advantage for the plant to produce enough caffeine to ensure pollinator fidelity but not enough to be repellent (Wright et al. 2013). Citrus also has the highest nectar concentrations known of the insect neurotransmitters, octopamine and tyramine, which at least in bumblebees interact with caffeine to affect floral preferences and sucrose responsiveness besides long-term memory (Muth et al. 2022). The fact that fruits hang so long on the tree and can be transported over long distances, while remaining "fresh", is testament to the efficacy of the pericarp components in deterring not only insects but also fungi and other pathogens. Insecticidal compounds include naringin used as a bittering agent instead of quinine in tonic water, though only half as bitter (ironically it has been chemically manipulated to a dihydrochalcone 500 times as sweet as sucrose and so related compounds are now being developed as commercial sweeteners in USA (Mabberley 2017).

Citrus oil comprises chiefly hydrocarbons, largely terpenes and sesquiterpenes. The terpene d-limonene makes up the largest proportion of oil in oranges and lemons, but citral is the characteristic one, lemon having many times more than do oranges. The different stereoisomers of limonene are responsible for the different tastes of oranges and lemons, for example. In citron (Bhuiyan et al. 2009) there are 19 components making up 99.9% of the oil in the leaves—eruclamide (28.43%), limonene

(18.36%) and citral (12.95%) being the main ones. The pericarp oil has 43 components making up 99.8%, mainly isolimonene (39.37%), citral (23.12%) and limonene (21.78%). The phytochemistry and pharmacological properties of *Citrus medica* extracts have been reviewed by Panara et al. (2012), who reported that the citron has analgesic, hypoglycaemic, anticholinesterase, anti-cancer, antibiotic, hypocholesterolemic, hypolipidemic, insulin secretagogue, anthelmintic, antimicrobial, anti-ulcer and oestrogenic properties.

1.3.2 Pollination and Dispersal

When mature, a *Citrus* tree can produce more than 200,000 flowers annually—in tropical countries throughout the year, but especially in Spring, as in temperate ones. As few as 0.1%, but usually 1–5%, of the flowers mature as fruits (Agusti and Primo-Millo 2020). Floral initiation in the Mediterranean is promoted by low temperatures and short photoperiod, in the tropics by water stress engendered by seasonal drought (Southwick and Davenport 1986). Indeed, manipulation of water-supply can be used to extend the productive season and therefore commercial viability of lemon plantations (Davis and Albrigo 1994).

The flowers are generally strongly sweet-scented (though apparently scentless in the tropical Australian *C. inodora*), the fragrant oils from those of bitter oranges being the neroli of commerce (petitgrain oil being that extracted from the twigs and leaves). Neroli oil has antibacterial and fungicidal properties (Haj Ammar et al. 2012). The flowers are visited by a wide range of nectar-seeking insects, especially bees, the sought-after nectaries forming a prominent ring around the ovary base (Fahn 1974), though there are few reports of pollination studies in truly wild *Citrus* species. There are stomata with wide apertures on raised portions of the ring; both epidermal and parenchyma cells are capable of nectar secretion, the nectar being secreted into intercellular spaces and exuded by the stomata. Nonetheless, the citron is self-compatible and the flowers are largely cleistogamous, so that modern cultivars have high levels of homozygosity (Wu et al. 2018).

The epidermis of the developing corolla has papillose cells, the papillae being numerous near the apices and margins of the young petals (Ford 1942). The papillae overlap and interlock the petals to form a closed corolla. The opening of the flower is associated with the shrinking and plasmolysis of these papillose cells, while the stigma exudes a viscid secretion from long papillose unicellular epidermal hairs, which traps pollen; the stigma, at least in oranges, is receptive for up to eight days (Bartholomew and Reed 1943). Pollen grains, at least in pomelo, *Citrus maxima* (Banerji 1954), germinate at once and, indeed their viability is short, being reduced to 10% in 24 h and nil in 48 h. Functionally male flowers and those that set no fruit abscise at the base, though often the petals, stamens and pistils sometimes fall before that (Ford 1942). The nectary disc, the calyx and a small part of the flower stalk (pedicel) usually remain on the fruit until it is ripe and together they are known as the "button" of the fruit (Bartholomew and Reed 1943).

In navel oranges, pollination is required before seeds will develop even though those are not the products of cross-fertilization (pseudogamy; see below). The fruit develops from a syncarpous gynoecium with axile placentation (Fahn 1974), the developing fruit differentiating three more-or-less distinct strata of cells. The exocarp (flavedo) comprises small dense collenchyma cells, which contain chromoplasts, with essential oil cavities; the epidermis consists of very small thick-walled cells, on the surface resembling a cobbled effect, these cells containing chromoplasts and oil droplets. The mesocarp (albedo) comprises loosely-connected colourless cells; the endocarp is thin and comprises very elongated, thick-walled cells forming a compact tissue. The stalked spindle-shaped juice vesicles (almost spherical in the Australian *C. australasica* and the Chinese *C. mangshanensis* (Gmitter et al. 2020)), which fill the locules as the fruit ripens, develop from the cells of the inner epidermis and subepidermal layers. Each juice vesicle is covered with a layer of elongated cells, which enclose very large, extremely thin-walled juice-cells.

The vesicles adhere and, with the endocarp, make up a “segment”. The epidermis of a vesicle is covered with a thin cuticle, on top of which there are wax secretions which hold the vesicles together in the segment (Fahn et al. 1974). One problem in the canning industry is that this adhesion fails during processing. In *Citrus australasica*, the finger lime of eastern Australia, there appears to be no such adhesion and the individual vesicles burst out of the fruit when it is opened, such that they have been marketed as “citrus caviar” (Hardy et al. 2010).

In many citrus, especially in cultivation, one or more asexually produced embryos, besides sexually generated ones, can develop from the nucellus of the ovule. Being diploid, they are in effect clones of the mother plant. This is usually the cause of polyembryony, where seeds can yield two or more seedlings. At the beginning of the eighteenth century, the Dutch microscopist, Antoni van Leeuwenhoek showed that such citrus seeds often have several embryos, the first time the phenomenon of polyembryony was described (Fig. 1.4). Polyembryony is particularly common in the makrut (the lime-leaves of Thai cooking) or leech lime, *Citrus hystrix,* wild in Malesia but widely cultivated, and the calamondin, *C.* × *microcarpa.* Three to 12 embryos develop from the nucellus alongside the normal one, as was first described by the German cytologist, Edouard Strasburger in 1878 (Maheshawari 1950).

The fruits mature over a long period, those of ‘Valencia’ oranges (*Citrus* × *aurantium* Sweet Orange Group), for example, taking 12–14 months (Bain 1958) and therefore trees start flowering again before the previous season’s fruits are ripe. Bain recognised three phases of fruit development, the first “cell-division” period being of just a few weeks, in which the exocarp develops from the ovary wall, cells differentiate giving the exocarp and mesocarp, while the vesicles are formed in the carpels. The increase in fruit size in this phase is due mainly to the growth of the pericarp. In the second “cell enlargement” phase of around six months the tissues expand due to enlargement of cells, which differentiate, and the exocarp becomes yellow. The increase in fruit size is largely due to the growth of the carpels (segments), which leads to a thinning of the pericarp width. The final “maturation period” phase of over six months has a slowing of growth and anatomical change but the exocarp becomes orange.

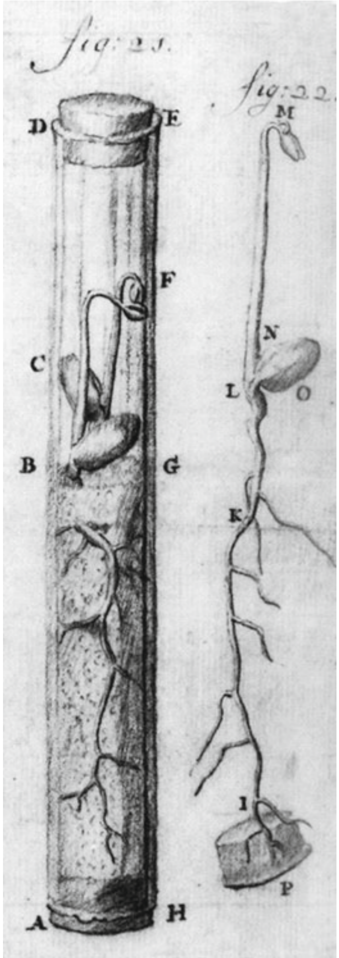

Fig. 1.4 Polyembryonous seed of citrus (left); red chalk drawing sent by Antoni van Leuwenhoek from The Netherlands to the Royal Society of London in [?]1719

The primordia of the all-important juice vesicles, in grapefruit (*Citrus* × *aurantium* Grapefruit Group) at least, are initiated two days before the flowers open, such that the main juice vesicle body is subtended by highly vacuolated stalk-cells attached to the carpel walls (Burns et al. 1992). They begin development immediately after fertilization; the epidermal cells first increase in length and then divide by anticlinal walls, the subepidermal eventually dividing in all planes, resulting in papillate processes extending into the locules (Banerji 1954). Between four and ten weeks after flower-opening, an oil cavity begins to develop and remains in place up to a year in the vesicle's development. These oils give the characteristic tastes to different citrus fruits.

The vesicles in the fruits hold a very large amount of water, up to 92% by weight, and this can be withdrawn to other tissues under stress in dry seasons (Bartholomew and Reed 1943). They also contain vitamins (particularly vitamin C), sugars and acids, principally citric, but also, in at least grapefruit, tartaric, malic and oxalic acids. The large, heavy, watery, long-lived fruits pose questions with regard to their dispersal. The fruits of tachibana in the mandarin complex (*C.* × *tachibana*) are taken by monkeys in Japan (Grimshaw and Bayton 2010) but also float (though killed by seawater) and are possibly spread by river waters as with pomelo (*Citrus maxima*) introduced in Fiji (Ridley 1930), though in Jamaica, citrus are dispersed by birds (Ridley 1930) and, in Madagascar, by lemurs, bush-pigs and humans (Humbert 1950). Indeed, the large, succulent vitamin- and sugar-rich fruits strongly suggest animal dispersal, the smaller species perhaps involving birds, but the very large fruits like the pomelo—and indeed the citron—are, on the whole, enigmatic.

In a similarly large fruit, of a similarly bee-pollinated species, the orchard apple (*Malus domestica*, Rosaceae), the original dispersal agents seem to have been bears, which also feed on the honey made by bees from nectar in the fruit-forests of the Tian Shan in western China (Juniper and Mabberley 2019), where the domestic apple originated. Could it be that bears are also efficacious dispersal agents for the larger-fruited bee-pollinated *Citrus* species? There seems to be little documentation of any such interaction, but a number of videos on the internet show bears very dextrously eating citrus fruits, ripping open the hesperidia with their claws, discarding the bitter pericarp and swallowing the endocarp, complete with the seeds. With different bear species across the range of the genus, perhaps they could be dispersal agents west of Wallace's Line, but what about east of it, for example in New Caledonia where there are no non-flying mammals? But it is also known from such films that elephants too not only relish citrus fruits, but also void apparently viable citrus seeds in their faeces. So, what dispersal syndrome is associated with the thick brightly-coloured pericarp of the citron? And why is that so different from that of its closest ally, *Citrus indica*? What is the ecological significance of the bitterness in citron and pomelo, yet the sweetness of mandarin and kumquat? There is much to be done on the basic natural history of wild citrus, not least citron and its allies.

1.3.3 Phylogeny

Molecular clock studies have led to the conclusion that the minimum age of the family Rutaceae is between late Eocene and late Palaeocene (Pfeil and Crisp 2008) though it could have diverged from other families much earlier (Heads 2012). Pfeil and Crisp give an age of "a maximum of 11.8 Ma" for the genus *Citrus*, when, as Heads argues, this is a minimum on the evidence presented, and their assertion that the progenitors of the eastern species of the genus therefore "must have arrived in New Caledonia by long distance dispersal" is fallacious. Heads uses the geographical breaks in the molecular clades with regional tectonics to argue that the main clades in Rutaceae originated in the Early Cretaceous, with what would be recognised as Rutaceae (but see Mabberley 1984) being even older.

The unravelling of the affinities between *Citrus* and other Aurantioideae genera is well advanced, but there is still resolution needed with respect to the placement of the Asiatic genera *Murraya* and *Merrillia* despite intensive recent DNA work (Bayer et al. 2009; Appelhans et al. 2021). It is remarkable that the largely Asiatic Aurantioideae, with some representatives in mainland Africa, are not native in Madagascar.

1.3.4 Palaeobotany and Archaeological Records

Wood fossils, which were referred to as two species of *Citrusoxylon*, are known from the Eocene of Paris over 41 M years ago (Privé-Gill 1981), while a species of '*Citroxylon*' is from the Miocene (5.3–23 M years ago) of Bavaria. Fossil leaves referred to *Citrus*, though these, like the last, could be referred to a number of allied genera if they were alive today, are known (Fischer and Butzmann 1998) from the Pliocene of Italy (*C. meletensis*), but also allegedly from the Palaeocene/Eocene of Guangdong (China—*C. nigra* ['niger']) and even the Cretaceous (Cenomanian) as well as Eocene of North America and possibly the Oligocene of the Caucasus (*Citrophyllum* spp.). Perhaps the most convincing is the late Miocene leaf fossil *Citrus linczangensis* from Yunnan (Xie et al. 2013). How this overall fossil record relates to the present distribution of modern *Citrus* species is unclear, but it is a common finding that many genera of plants currently restricted to the tropics and the subtropics of south-east Asia are represented by fossils in Europe.

The earliest archaeological evidence of citrus seeds is from the early second millennium BCE of northern India, while citrus wood charcoal of BCE 1400–1300 is claimed for Karnataka in south-west India (Pagnoux et al. 2013). Nothing in the Mediterranean is known before c. BCE 1200 where some mineralized seeds found in Hala Sultan Tekke in Cyprus are claimed to be citrus. More certain is citrus peel as evidenced by polymethoxyflavones (citrus-specific polyphenols) in organic residues in a wine-jug used as an offering for the dead and preserved in a cremation grave of the sixth-century BCE necropolis of Monte Siraï in southern Sardinia. This suggests that Phoenician settlers were responsible for the spread of plants from the eastern to western Mediterranean, as they were in southern Italy in the ninth century BCE, so closely linked with the Cypriot influence with regard to trading iron and associated technology.

Other first-millennium evidence comes from Cuma near Naples, the site of the city of Cumae (Kyme), one of the earliest Greek colonies in Italy. The amount of *Citrus* pollen there is remarkable, bearing in mind that *Citrus* species are insect-pollinated, suggesting that the trees must have been intensively cultivated locally. Pollen is recorded from many other younger sites. By the Roman period there is citrus wood from near Pompeii in which city there are frescoes and mosaics depicting citrus trees (Andrews 1961), even though certainly they were being cultivated by the beginning of the first century CE, and possibly much earlier. However, neither Columella, *De re rustica* (first century CE), nor the earlier Varro in *Res rustica* and Cato in *De agricultura* mention citrus-growing, suggesting it was not widely practised in Italy, though Pliny wrote of the exotic ‘malus Assyria’ and Palladius has ‘citreum’ in his late fourth- or early fifth-century CE *Opus agriculturae* and mentions a ‘citretum’ where the ‘citreum’ were grown under a tegumentum (roof) to protect them from cold. Perhaps this was a proto-orangery.

Moreover, recent investigations (Pagnoux et al. 2013) have revealed mineralised and carbonised citron seeds in the pre-Roman Samnites levels under the Temple of Venus in Pompeii, as well as seeds and peel, perhaps of lemon, in central Rome from c. CE 100. Both finds suggest that citrus fruit was precious and used in sacred ceremonies.

1.4 The Citron, *Citrus medica*

Of the 25 or so wild species of *Citrus* known today (Mabberley 2022), the citron, *Citrus medica,* was the first known to Western science, brought from Asia to the Mediterranean, probably via Persia (Ramón-Laca 2003; Wearn and Mabberley 2016) and is traditionally associated with Alexander the Great’s imperial push into modern-day India.

But in CE 228, at Naukratis (Nikratj, near today’s Kom Gi’eif), a city on the western branch of the Nile, 72 km SE of the later capital of Ptolemaic Egypt, Alexandria, the first and, for much of its early history, the only permanent Greek colony permitted in Egypt, the Greek rhetorician and grammarian (remembered now as the first writer on patents), Athenaeus of Naukratis could write (Needham 1986),

> I am in a position to assure you that Hegesander the Delphian [? post BCE 283-239] nowhere mentions the citron, for I read through the whole of his “memorials” with the express purpose of finding out.

However, Theophrastus (Hort 1916), who effectively wrote up the results of Alexander’s expedition (Stearn 1977), gave a good description about BCE 309.

> And in general the lands of the East and South appear to have peculiar plants, as they have peculiar animals; for instance, Media and Persia have, among many others, that which is called the ‘Median’ or ‘Persian apple’ (citron). This tree has a leaf like and almost identical with that of the andrachne [*Arbutus andrachne*], but it has thorns like those of the pear or white-thorn [*Crataegus* sp.], which however are smooth and very sharp and strong. The ‘apple’ is not eaten, but is very fragrant, as also is the leaf of the tree; and if the ‘apple’ is placed among clothes, it keeps them from being moth-eaten. It is also useful when one has drunk deadly poison; for being given in wine it upsets the stomach and brings up the poison; also for producing sweetness of breath; for, if one boils the inner part of the ‘apple’ in a sauce, or squeezes it into the mouth in some other medium, and then inhales it, it makes the breath sweet.
>
> The seed is taken from the fruit and sown in spring in carefully tilled beds, and is then watered every fourth or fifth day. And, when it is growing vigorously, it is transplanted, also in spring, to a new soft well-watered place, where the soil is not too fine; for such places it loves. And it bears its ‘apples’ at all seasons; for when it has been gathered, the flower of others is on the tree and it is ripening others…It is also sown, like date-palms, in pots with a hole in them.

Indeed, unlike most citrus grown in the Mediterranean where they flower in spring, the citron is notable for its continuous flowering and fruiting, but also other rain-forest features such as nearly naked buds, making it more susceptible to frost than most citrus (Isaac 1959). By comparison with other *Citrus* species, it is a rather small tree or shrub and has large simple serrate leaves without a winged petiole typical of oranges, with fruits to 30 cm long weighing more than 2 kg. Georg Rumpf in seventeenth-century Ambon, Indonesia (Beekman 2011) described a particularly large-fruited form later to be called *Citrus papaya*, so resembling the large fruits of payaya (*Carica papaya,* Caricaceae), pointing out that.

> its peel is…very good for confections [i.e., "candied peel" as still used today].... One scrapes off the outer greenishness, soaks the rest in water for several days, then it is boiled with sugar….this is mostly done by the Chinese and Europeans.

However, Theophrastus's use of 'melon Persicon' became confused with other things including the peach (Andrews 1961), which confusion survives today in the Latin name for the peach, *Prunus persica*, originally a Chinese plant.

Theophrastus also noted in his *Enquiry into Plants* (Hort 1916),

> And they say that in the citron those flowers which have a kind of distaff [i.e. pistil] growing in the middle are fruitful, but those that have not are sterile

a clear allusion to sex (monoecy) in plants nearly 2000 years before Camerarius (1691) or Bobart, the northern Europeans usually attributed with drawing attention to sex in plants.

Theophrastus called the citron the Apple of the Medes—and Pliny the Elder took this forward in his *Naturalis Historae* (12: 7) of CE 77–79. 'Malus', originally used for the domestic apple, *Malus domestica* (*M. pumila*), was thereby expanded in a kind of carpological classification that now seems faintly absurd (cf. Greene 1983), though perfectly logical then, to take in other fruits as they were introduced from the east, with 'Malus Armenaica' for the apricot (*Prunus armenaica*) and 'M. Persica' for the peach (*P. persica*) for example. 'Malus arantia [sic]' was used for the orange (*Citrus* × *aurantium*), 'M. limonia' for the lemon (*C.* × *limon*) and so, via the great early western botanist, Pietro Andrea Matthioli (his *Commentaries*: 244, 248 (1565)) the Latinized name for the citron, 'Malus medica' came to Gaspard Bauhin (his *Pinax*: 435 (1671)), who was to be quoted by Linnaeus (1753), in whose *Species Plantarum*, the starting-point for today's plant nomenclature—where he coined the binomial *Citrus medica* L., though, bearing in mind its well-known medicinal uses, one cannot rule out some punning wordplay here (Fig. 1.5).

It is likely that citron fruits, brought back from Persia, had been for sale in Greek markets long before Theophrastus's work. The way he wrote suggests that his readers would have been familiar with the fruit, though he seems emphatic that the trees were then only known to him as growing in Persia. Indeed, recent excavations in Israel suggest strongly that the Persians introduced citron to the Holy Land, probably in the fifth century when the Jewish "temple state" was instituted. The Ramat Rahel site (Lipschits et al. 2012) on a hill above modern Jerusalem has revealed a palace from the period of the Persian occupation, complete with an elaborate irrigated garden.