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Thyme

The genus *Thymus*

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For Rainer, Inma, Natalia, Angel and Rubén

1 The history, botany and taxonomy of the genus *Thymus*

Ramón Morales

INTRODUCTION

Within the Labiate family, with about 220 genera, the genus *Thymus* is one of the eight most important genera with regard to the number of species included, although this number varies depending on the taxonomical point of view. If we choose criteria to minimise variability, available data report 215 species for the genus, a number only exceeded by the genera *Salvia*, *Hyptis*, *Scutellaria*, *Stachys*, *Teucrium*, *Nepeta*, and *Plectranthus*.

The common English word 'thyme' has traditionally been used to name both the genus and its most commercially used species, *Thymus vulgaris*, sometimes leading to misunderstandings. Generally speaking, thyme is an aromatic plant used for medicinal and spice purposes almost everywhere in the world. The genus *Thymus* is very frequent in the Mediterranean region, where some species form a special type of bushy vegetation not more than 50 cm high, well adapted to hot and dry summer weather. The Spanish name for these vegetation communities, 'tomillares', include other Labiate species such as *Sideritis*, *Satureja*, *Salvia* or *Lavandula*, with similar climatic and edaphic patterns.

A common feature of these and many other aromatic plants is the presence of countless glandular hairs of different forms which contain volatile essential oils that evaporate when the glandular hairs are damaged. This way they produce an intensive fragrance that embraces the plant. It is probably due to the strong scent that humans have always been attracted to these plants and have exploited their essential oils for popular and industrial purposes.

HISTORICAL BACKGROUND

The history of *Thymus* before Linné

Several explanations exist concerning the origin of the name 'Thymus'. Some authors assume that the Latin name *Thymus* comes from the Greek word *thyo* (perfume). Another interpretation of its etymology considers the Greek word *thymos* (courage, strength). Originally 'thymus' described a group of aromatic plants with similar aspects which were used as stimulants of vital functions. Many popular names in the Romance languages are derived from the Latin name. The same occurs with the English name.

In his work about medicinal plants and poisons, Dioscorides (First century, translation of Laguna, 1555) writes about '*Thymo*'. Laguna however did not find there any *Thymus*

species, but a plant corresponding to the genus *Satureja*. On page 294 Laguna describes the *Serpol*, presenting two varieties, a cultivated and a wild one. The latter, *Zygis*, resembles a *Thymus* species. It is presented as an erect plant, whereas the former shows a creeping habit.

In his Natural History, Book 21, Chapter 10 (translation of Huerta, 1629), Plinio (First century) reports on *T. vulgaris* as follows: 'in the Narbonne province, the stony fields are full of thyme, and thousands of sheep come from very far provinces to feed on it'. Later (page 289) he speaks about two different varieties of thyme, a white and a black one, and he comments on their therapeutic attributes. In Chapter 62 of his first book, Clusius (1576) refers to *T. vulgaris* with his *Thymum durius sive Plinii*. The subsequent chapter 'De Serpyllo silvestri Zygi' includes a description of *T. zygis*, which is one of the most common species in Spain; and in Chapter 64 entitled 'De Tragorigano' he writes: 'Multis Hispaniae locis provenit solo arido petroso cum Stoechade permista', refering to *T. mastichina*, whose Spanish name is 'sarilla'. Some years later, in the book of icons of Lobelius (1581) five drawings of thyme are presented all being very difficult to identify.

In the beginning of the seventeenth century, like preceding authors, Dodonaeus (1616) also described two varieties saying: 'Thymo: unum cephaloton dictum, alterum durius'. Today we can be sure that with the first he refers to *Thymbra capitata* and with the second to *Thymus vulgaris*. His *Serpyllo vulgari* seems to be a *Thymus* species of the section *Serpyllum*. Furthermore, in his chapter 'De Serpyllo ex Dioscoride, Theophrasto et aliis', he comments on the different ideas about *Serpyllum* expressed by several authors. He describes *T. mastichina*, the first plant which he treats in his Chapter 18 on *Tragoriganum*, applying the criteria of Dioscorides. We can find in the work of Bauhin (1623) a few years later, that he divides *Thymus* into four parts: the first (*T. vulgaris folio tenuiore*), as well as the second (*T. vulgaris folio latiore*) seems to be *T. vulgaris*; the third is called *Thymus capitatus* (today *Thymbra capitata*), and the fourth is *Thymum inodorum*. Within his *Serpyllum* nine different varieties are considered; the last one, 'Serpyllum folio Thymi', has turned out to be identical with the *Zygis* of Dioscorides.

In the eighteenth century Barrelier (1714) presents a book of icons. Icon number 788 represents *T. moroderi* (Martínez, 1936) from 'the kingdom of Valencia'; icon number 780 shows *T. hyemalis* (Figure 1.1) and number 694, entitled *Marum hispanicum*, contains a drawing of *T. piperella*. In his list of names with short explanations Tournefort (1719) described six varieties of *T. lusitanicus*, four of them are *T. lotocephalus* and another is *T. moroderi* (Figure 1.2). Within *Thymbra* he considers '*Thymbra hispanica*', with *T. mastichina* and *T. zygis*.

The Linnean *Thymus*

It is very interesting to observe the changes made by Linné in his different works about the *Thymus* species. Most of his knowledge is based on experiences of former authors. In Hortus Cliffortianus (1737, pp. 305–306) he describes six species. Nowadays we know that two of them, the latter ones, do not refer to *Thymus* but to *Satureja* and *Acinos*. His No. 1, *T. erectus* turned out to be *T. vulgaris* (Figure 1.3), No. 2 *T. repens* is a species within the section *Serpyllum*, No. 3 is *Thymbra capitata*, and No. 4 *T. mastichina* (Figure 1.4). In his *Hortus Upsaliensis* (1748, pp. 160–161) only *T. vulgaris* and *T. mastichina* are mentioned. The reference work for the binomial

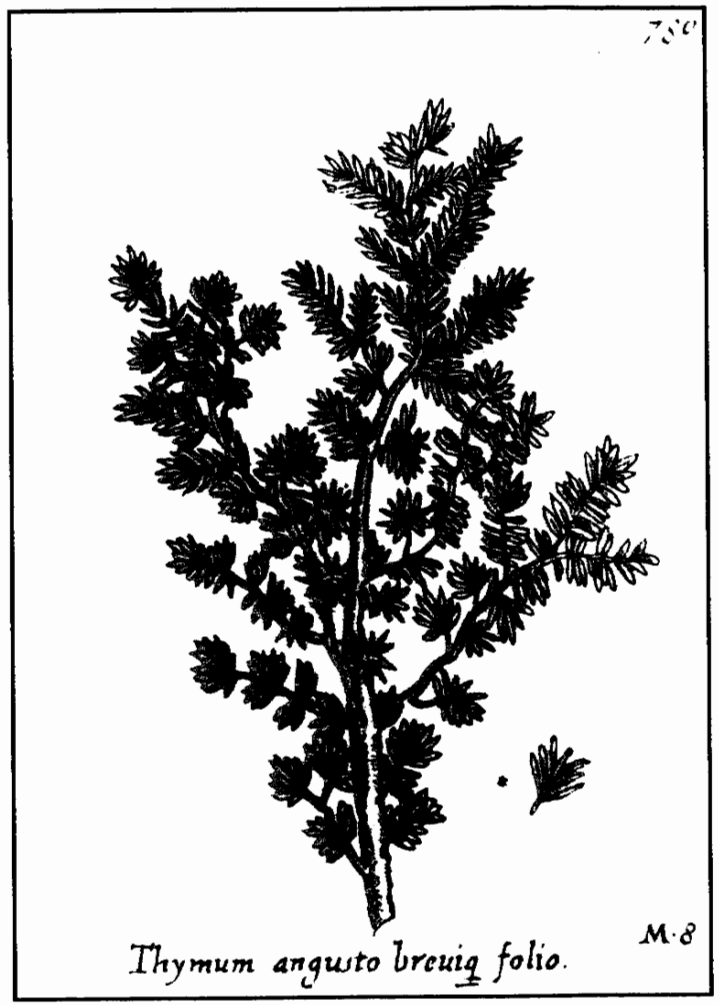

Figure 1.1 Drawings from Barrelier (1714) work, number 780 corresponds to *T. hyemalis*.

system of nomenclature in Botany '*Species Plantarum* 1st edition' (1753) includes the following eight species in *Thymus*: 1. *T. serpyllum*, 2. *T. vulgaris*, 3. *T. zygis*, 4. *T. acinos* (today *Acinos arvensis*), 5. *T. alpinus* (today *Acinos alpinus*), 6. *T. cephalotos* (today *T. lotocephalus*), 7. *T. villosus*, and 8. *T. pulegioides* (Figure 1.5). Within *Satureja* we find 4. *Satureja mastichina* (today *T. mastichina*).

In Genera Plantarum (1754, p. 257) Linnaeus lists in 646. *Thymus: Serpyllum, Acinos*, and *Mastichina*. *Species Plantarum* 2nd edition (1762, pp. 825–827) transferred *T. mastichina*, former *Satureja mastichina*, as number 8 into *Thymus*. In the 1st edition this number was

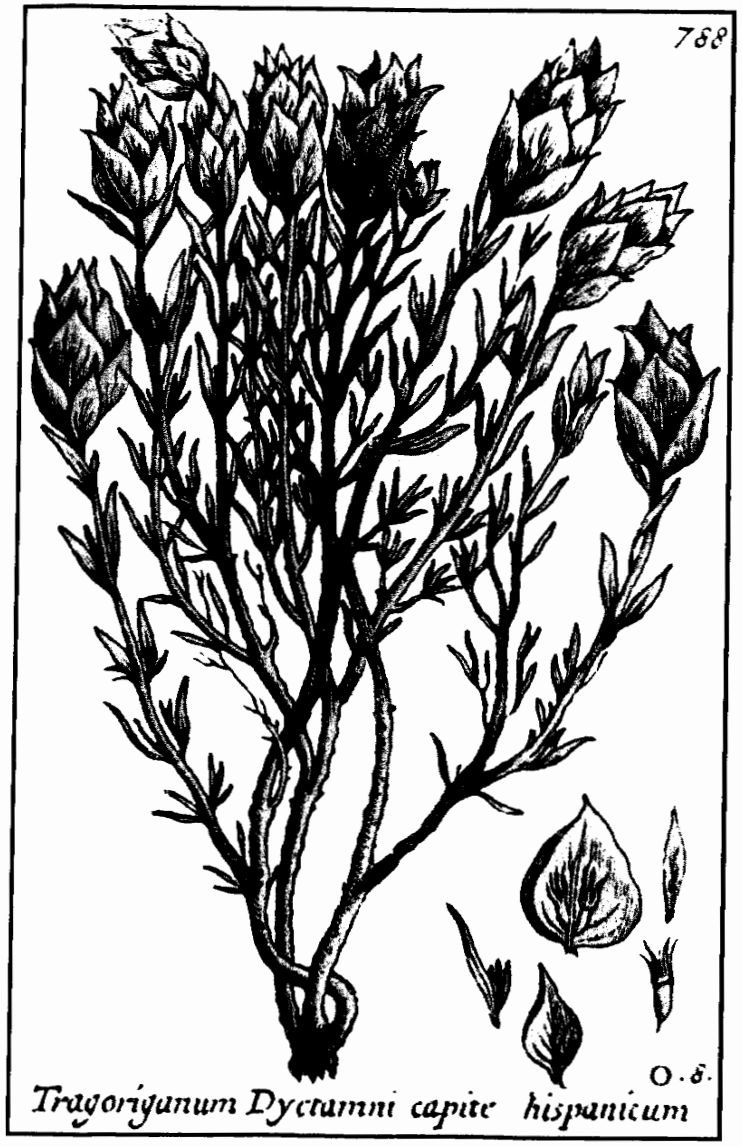

Figure 1.2 Drawings from Barrelier (1714) work, number 788 corresponds to *T. moroderi*.

established for *T. pulegioides*. This transfer Linnaeus commented on literally: 'Ambigit media inter Saturejam et Thymum, sed cum stamina delitescant in fundo corollae, et stylus corolla longior ad Thymum refero'. In *Systema Naturae* 2 (12th edition, 1767, P. 400) for the first time *T. piperella* appears.

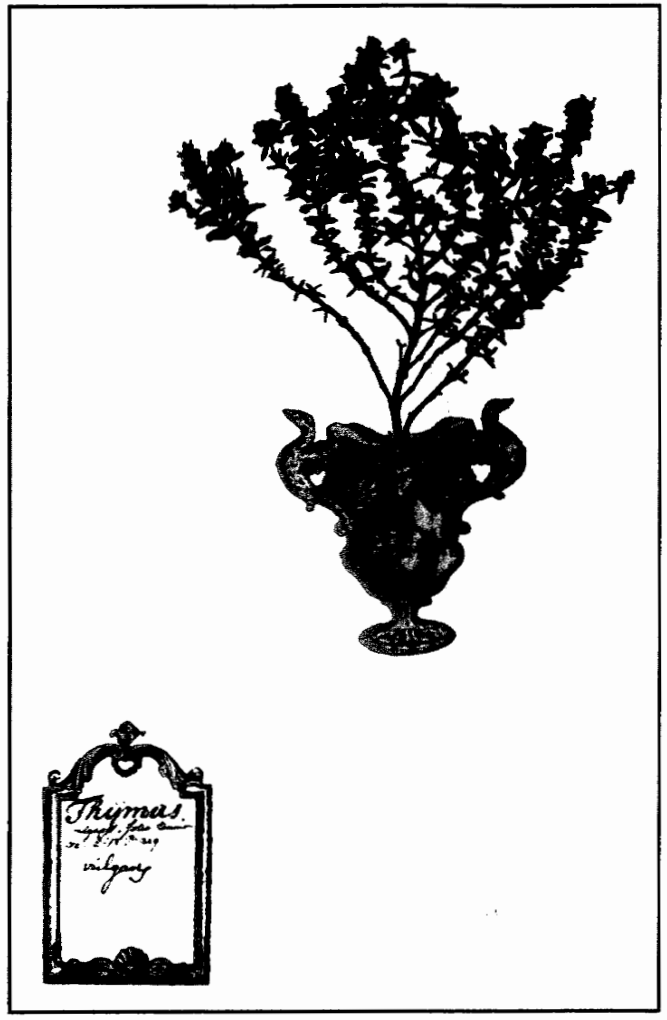

Figure 1.3 Typus of *T. vulgaris* in Linné (1737) Hortus Cliffortianus.

After Linnaeus

Brotero (1804) described a new species, *T. caespititius*. Also Hoffmannsegg and Link (1809), in their magnificent and big work about the Flora of Portugal, described some new species: *T. albicans*, *T. capitellatus*, *T. camphoratus*, and *T. sylvestris*. It was Bentham (1834) who, for the first time, divided the genus *Thymus* into sections: *Mastichina*, with *T. mastichina* and *T. tomentosus*; *Serpyllum* with *T. vulgaris*, *T. piperella*,

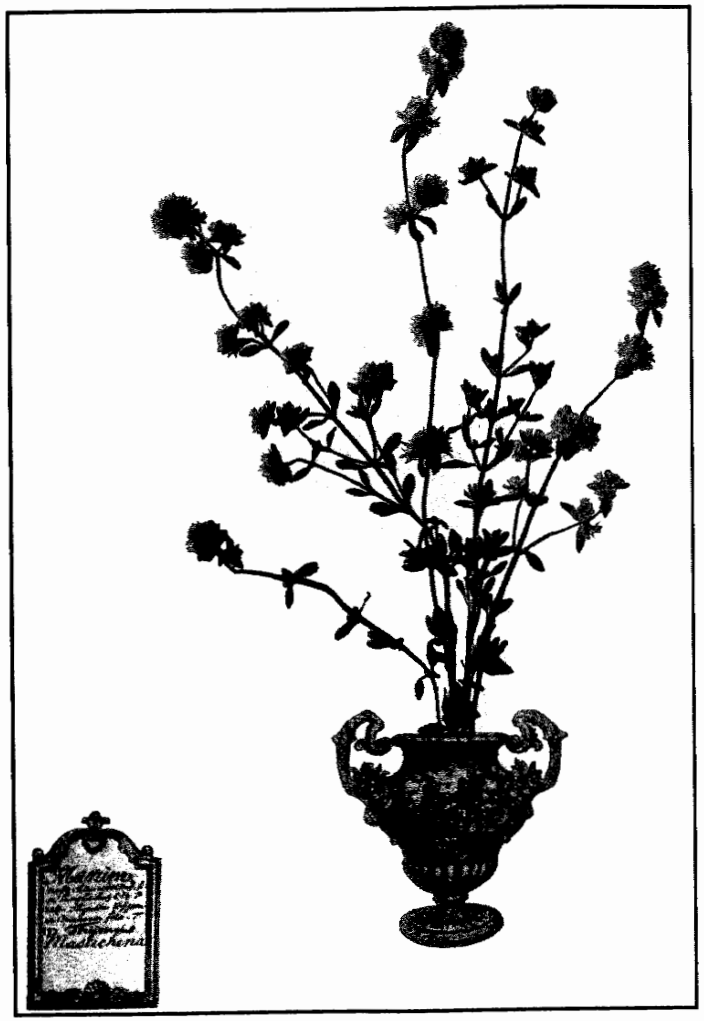

Figure 1.4 Typus of *T. mastichina* in *Linné (1737)* Hortus Cliffortianus.

T. villosus, *T. capitellatus*, and *T. capitatus*; and *Pseudothymbra*, with *T. cephalotos* (today *T. lotocephalus*).

Edmund Boissier (1839–1845), the famous Swiss botanist from Geneva, studied and described new *Thymus* species from the Iberian Peninsula, a result of years of research travelling through Spain. He also left valuable descriptions of *Thymus* species from the north of Africa (Figure 1.6) as well as from Greece and Turkey written down

Thymus repens, foliis planis, floribus verticillato-ſpicatis. *Hort. cliff.* 306. *Roy. lugdb.* 325.
Serpyllum vulgare minus. *Bauh. pin.* 220.
Serpyllum vulgare. *Dod. pempt.* 277.
β. Serpyllum vulgare majus. *Bauh. pin.* 220.
γ. Serpyllum vulgare minus, capitulis lanuginoſis. *Tournef. inſt.* 197. *It. gotl.* 219.
δ. Serpyllum anguſtifolium hirſutum. *Bauh. pin.* 220.
ε. Serpyllum foliis citri odore. *Bauh. pin.* 220.
Habitat in Europæ *aridis apricis.* ♄

2. THYMUS erectus, foliis revolutis ovatis, floribus verticillato-ſpicatis. *Hort. cliff.* 305. *Hort. upſ.* 160. *Mat. med.* 281. *Roy. lugdb.* 325. *Sauv. monſp* 148. *vulgaris.*
Thymus vulgaris, folio tenuiore. *Bauh. pin.* 219.
β. Thymus vulgaris, folio latiore. *Bauh. pin.* 219.
Thymum durius. *Dod. pempt.* 276.
Habitat in G. Narbonenſis, Hiſpaniæ *montoſis ſaxoſis.* ♄

3. THYMUS floribus verticillato-ſpicatis, caule ſuffruticoſo, foliis linearibus baſi ciliatis. *Lœſl.* *Zygis.*
Thymo vulgatiori rigidiori ſimile. *Bauh. hiſt.* 2. *p.* 271.
Thymum anguſto longioreque folio. *Barr. ic.* 777.
Serpyllum ſylveſtre Zygis dioſcoridis. *Cluſ. hiſt.* 358.
Serpyllum folio thymi. *Bauh. pin.* 220?
Habitat in Hiſpania.
Facies T. vulgaris, at Folia baſi ciliata.

4. THYMUS floribus verticillatis, pedunculis unifloris, caulibus erectis ſubramoſis, foliis acutis ſerratis. *Acinos.*
Fl. ſuec. 478.
Thymus caulibus vix ramoſis, foliis ovatis acutis, pedunculis plurimis unifloris. *Hort. cliff.* 306. *Roy. lugdb.* 325.
Clinopodium arvenſe, ocymi facie. *Bauh. pin.* 225.
Clinopodium vulgare. *Lob. ic.* 506.
Habitat in Europæ *glareoſis, cretaceis, ſiccis.* ⊙

5. THYMUS verticillis ſexfloris, foliis obtuſiuſculis concavis ſubſerratis. *alpinus.*
Clinopodium verticillis pauciforis in ſpicam congeſtis. *Hall. helv.* 653.
Clinopodium montanum. *Bauh. pin.* 225. *Bocc. muſ.* 2. *p.* 50. *t.* 45.
Acini pulchra ſpecies. *Bauh. hiſt.* 3. *p.* 620.

Ha-

Figure 1.5 Page from Linné (1753) Species Plantarum, where *T. vulgaris* and *T. zygis* are described.

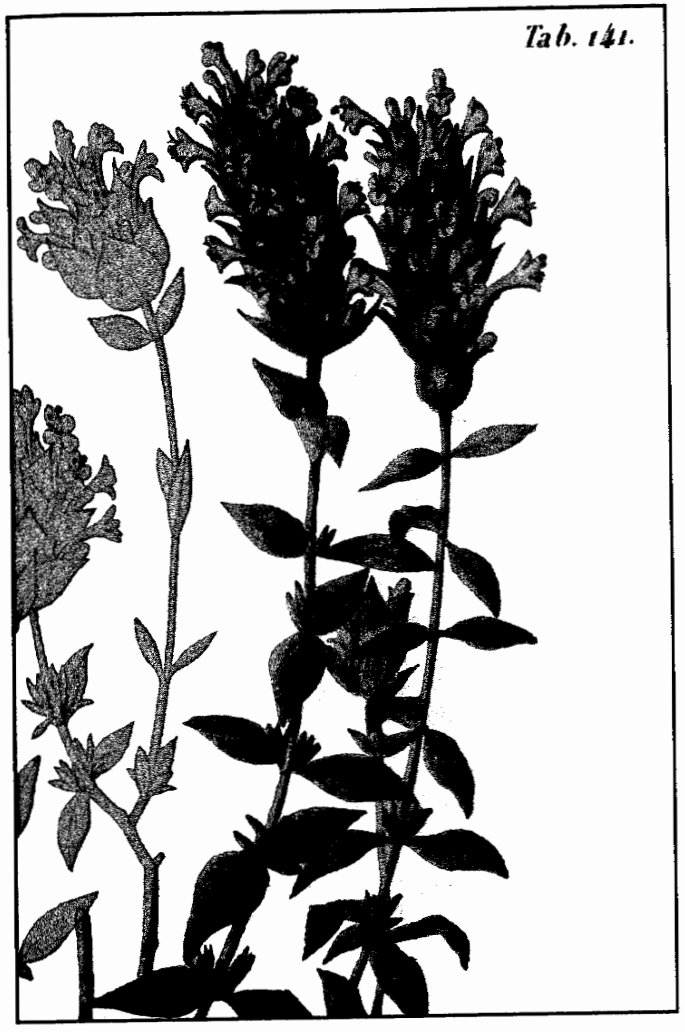

Figure 1.6 *T. broussonetii* (Boissier, 1839–1845, tab. 141).

in his *Flora Orientalis* (1867–1884). Fortunately various beautiful illustrations are available. In his *Elenchus* (1838) he describes *T. willdenowii*, *T. granatensis*, *T. longiflorus*, and *T. membranaceus*. In 1845, he created the section *Pseudothymbra* and later he described *T. carnosus*, *T. lusitanicus*, and *T. baeticus* to be a variety of *T. hirtus*.

Willkomm (1868), a German botanist and author of the *Prodromus Florae Hispanicae*, together with his Danish colleague Lange, stated that the genus comprises five sections: *Mastichina*, *Zygis*, *Piperella*, *Serpyllum*, and *Pseudothymbra*. The section *Serpyllum* includes

two groups: the first one with *T. chamaedrys*, *T. serpyllum*, and *T. herba-barona* and the second one with *T. bracteatus*, *T. serpylloides*, and *T. granatensis*.

Briquet (1897) edited the Labiatae in Engler's monumental work, and considers two sections, *Pseudothymbra* and *Serpyllum*, the latter with five subsections: *Bracteatae* (*T. capitellatus*, *T. villosus*, *T. algarbiensis*, *T. albicans*); *Serpylla*; *Piperellae* (*T. piperella*, *T. caespititius*, *T. origanoides*, *T. bovei*); *Vulgares* (*T. vulgaris*, *T. sabulicola*, *T. hyemalis*, *T. zygis*, *T. carnosus*, *T. hirtus*); and *Mastichinae* (*T. mastichina*, *T. tomentosus*, *T. welwitschii*, *T. fontanesii*).

Velenovsky (1906) focused on *Thymus* writing a monography on it. There he considered ten sections: *Coridothymus*; *Vulgares*; *Orientales*; *Anomali* (*T. antoninae*, *T. portae*); *Mastichina* (*T. fontanesii*); *Thymastra* (*T. algarbiensis*, *T. albicans*, *T. capitellatus*); *Pseudothymbra* with 2 groups (suffruticosi: *T. membranaceus*, *T. longiflorus*, *T. funkii*, and herbacei: *T. cephalotos*, *T. villosus*, and *T. granatensis*); *Piperella*; *Micantes*; and *Serpyllum* (includes *T. serpylloides*).

The most important Spanish author is Pau, whose interest in *Thymus* runs throughout his whole botanical work. In his important article published in 1929 entitled 'Introducción al estudio de los tomillos españoles', he analyzes the previous works of Linnaeus, Boissier, and Willkomm. In this article, many interesting details can be found. Further remarkable Spanish authors who worked in this genus were Huguet del Villar (1934), Vicioso (1974), and Elena-Rosselló (1976), and in recent years many contributions from Spanish authors are known.

Although Spain has always been a centre of the systematic, research on thyme, also outside the Iberian Peninsula several famous botanists were dedicated to *Thymus*. They are enumerated here in alphabetical order: Bonnet, Braun, Debray, Klokov, Lyka, Machule, Negre, Opiz, Podlech, Paulovsky, Ronniger, Roussine, Roux, Schmidt, Sennen. Two of them shall be emphasized: Ronniger, who left a very valuable herbarium (today in Vienna) and Jakko Jalas, a Finnish botanist, who edited the genus *Thymus* within the Flora Europaea (1972), Flora Iranica (1982), and the Flora of Turkey (1982).

Illustrations

A lot of old illustrations of *Thymus* are available, specially in the works of Hoffmannsegg and Link (1809), and Boissier (1838, 1839–1845, 1859). The early depictions were very primitive drawings like those of Laguna's translation (1555) of the Dioscorides or those of Barrellier (Figures 1.1 and 1.2). The herbariums from the seventeenth and the first half of the eighteenth century were bound like books and as we can see in the Linnean herbarium of the Hortus Cliffortianus, the plants were ornately arranged in vases (Figures 1.3 and 1.4). After Linnaeus, at the end of the 18th and in the 19th century, the drawings of plants spectacularly improved. Figure 1.7 shows beautifully coloured icons of *T. caespititius* with details of the calyx and the corolla. It is taken from the Portuguese Flora of Hoffmannsegg and Link. Another coloured icon showing *T. broussonetii* of North Africa is taken from Boissier's work (Figure 1.6). Although plant photography has reached a high standard, we must be aware that drawings can mediate more information on botanical details of plants than photographs. Therefore classification of plants can better be performed with drawings than with photographs.

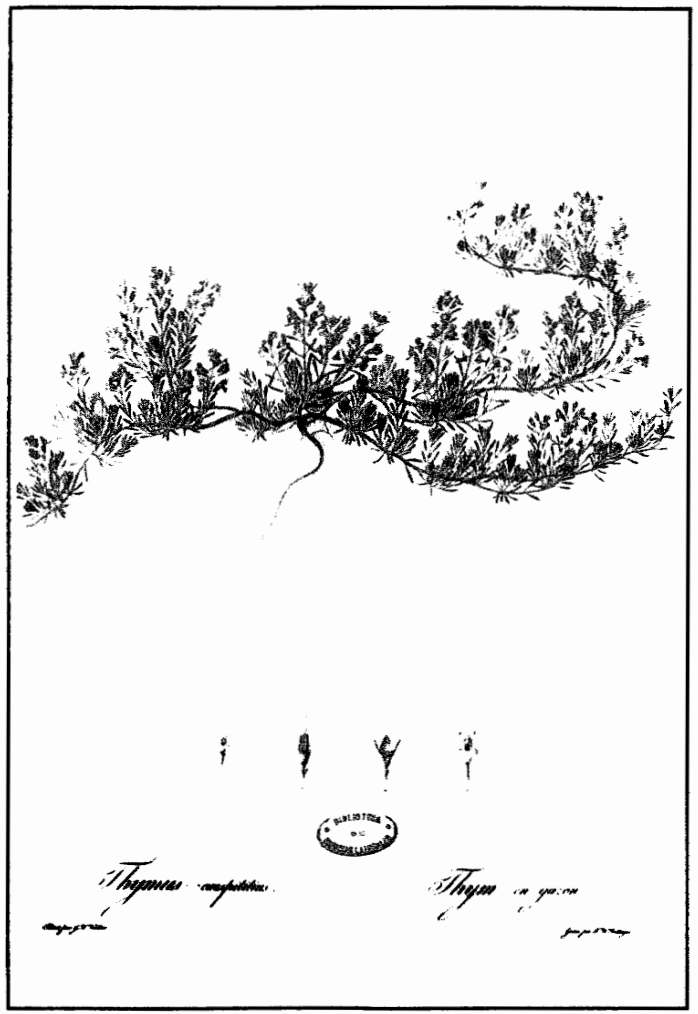

Figure 1.7 *T. caespititius* (Hoffmannsegg and Link, 1809).

BOTANY – THE MORPHOLOGY AND BIOLOGY OF *THYMUS*

Thymus plants are morphologically characterised by their habit or life-forms. We can differentiate two groups, on the one hand little bushy plants, usually below 50 cm, only sporadically up to 1 m, e.g. *T. baeticus* and *T. hyemalis* in the south and southeast of Spain. On the other hand there are creeping life-forms sometimes with rooting twigs. The latter is very common among the species belonging to the section *Serpyllum* or

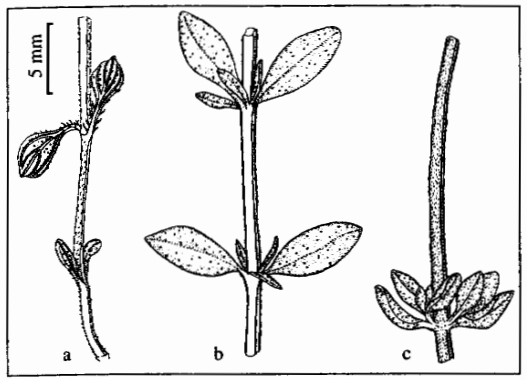

Figure 1.8 Stem morphology: (a) alelotrichous (*T. praecox*), (b) goniotrichous (*T. pulegioides*), (c) holotrichous (*T. piperella*).

Hyphodromi. *T. caespititius* is an exception with its caespitose habit which can have very long stems. Like most of the Lamiaceae, *Thymus* plants have quadrangular stems, the young being hirsute. The hairs can cover either all four faces of the stem (holotrichous) or only two faces alternating in each internode (alelotrichous). They also can be found only on the four ribs of the stems (goniotrichous). The function of the different types of hairs on the stems are not yet known. Figure 1.8 represents the different types of stems found within the genus, and Figures 1.17 to 1.23 show the plant morphology for different species of *Thymus*.

The leaves can be flat and more or less wide, or with revolute margins and almost acicular. All intermediates seem to be possible. The indumentum is very variable. Some species have leaves without hairs. The tector hairs in *Thymus* are always simple, but rarely single-celled. Leaves are very frequently ciliate at the margins, either at the whole margin or only at the base or on the petiole (Figure 1.9). The glandular trichomes are very important containing the essential oil. There exist two types of glandular trichomes: pedicellate glands with the upper cells full of essential oils, or big globose glands, typical of Lamiaceae, with some basal cells (Figure 1.10). Chapter 3 provides additional information on the anatomy and physiology of these glands.

The flowers grow more or less in clusters in the nodes. Few species have only two flowers per node (e.g. *T. antoninae*), but usually there are bigger clusters of flowers. Species with shorter internodes have globose and capituliform inflorescences. In these cases both leaves of the inflorescence node usually differentiate from the rest of the plant's leaves in form and size, and they are called bracts. This goes for *T. membranaceus*, *T. carnosus*, and other species belonging to the sections *Pseudothymbra* and *Thymus*. In some species the bracteoles can be extraordinarily long as in *T. satureioides*.

The calyx of thyme (2.5–8 mm) when dry plays an important role in the dispersion of the small fruits, or nuculas. Therefore its throat is closed by a hairy row and wind can take it over quite a big distance. The calyces of some species, like that of *T. mastichina*, have long ciliate teeth and seem to be a flying device like the pappus of the

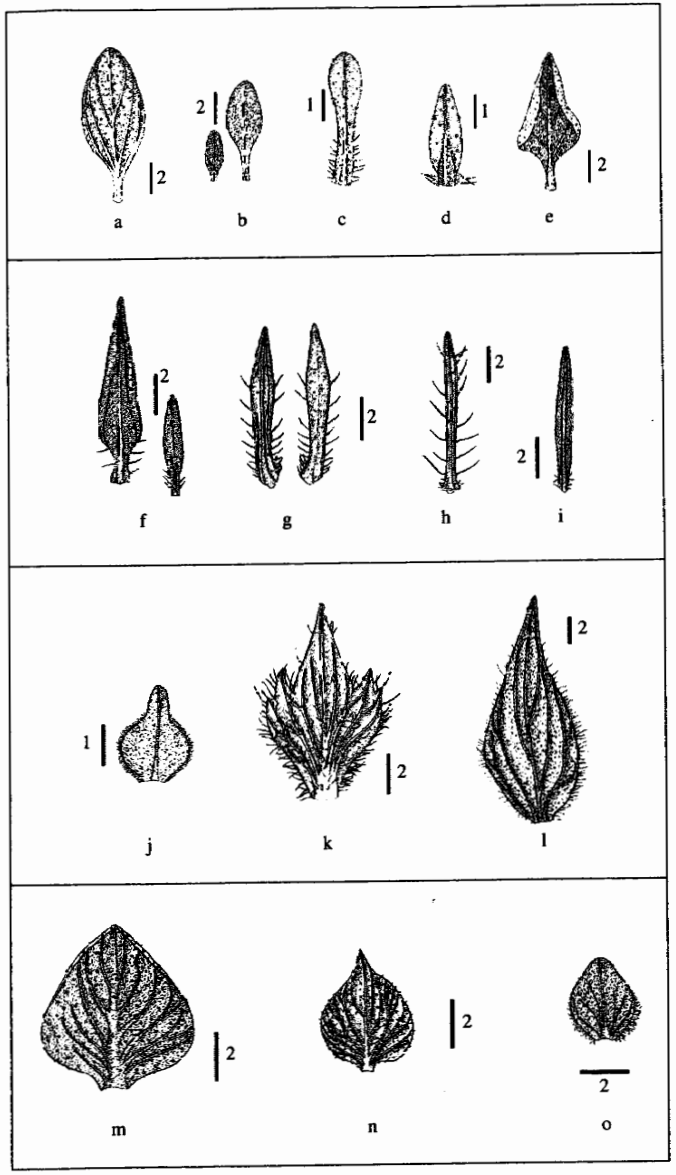

Figure 1.9 Leaf and bract morphology. **Leaves**: (a) *T. richardii*, (b) *T. albicans*, (c) *T. lacaitae*, (d) *T. hyemalis*, (e) *T. camphoratus*, (f) *T. longiflorus*, (g) *T. lotocephalus*, (h) *T. villosus*, (i) *T. zygis*. **Bracts**: (j) *T. lacaitae*, (k) *T. villosus*, (l) *T. lotocephalus*, (m) *T. camphoratus*, (n) *T. longiflorus*, (o) *T. albicans*.
Numbers beside the bars mean the length in mm.

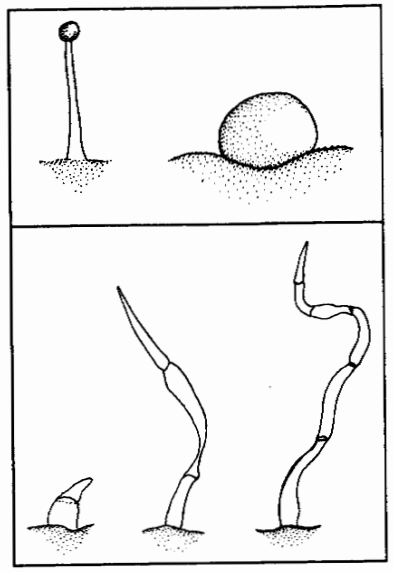

Figure 1.10 Morphology of essential oil glands (up) and hairs (down).

Asteraceae. Usually the calyx has five teeth; three upper and two lower, the latter always being longer and frequently curved upwards. They probably have to keep hold of the corolla's tube. The three upper teeth are shorter than the lower and sometimes reduced to one (*T. caespititius*). The corolla varies between 4 and 10 mm in length and finishes in one upper and three lower lobes, a typical structure to be pollinated by bees or similar insects. The production of pollen in the four stamens is low. Occasionally, the corolla can reach 2 cm like in *T. longiflorus*. Such long-tubed flowers are pollinated by insects with long trunks which can pollinate the flowers while they fly, like the flies of the *Bombilidae* family or crepuscular butterflies of the *Sphyngidae* and *Noctuidae* families do. Figure 1.11 presents examples of calyx and corolla morphology.

Thyme commonly presents gynodioecy, meaning that they produce two types of individuals, some with female flowers without stamens, and others with hermaphrodite flowers. It is proven that pollinators can pollinate female flowers faster than the hermaphrodites. The fruits are nutlets, up to four per flower, but usually some of them abort during early development. Seeds collected from wild populations germinate usually very easily and the seedlings grow relatively fast. Most of the species bloom in spring, others in summer like e.g. *T. serpyllum* or *T. praecox*. In the Mediterranean area, *T. vulgaris* subsp. *aestivus* and *T. piperella* flower in autumn, while *T. hyemalis* in winter. The latter inhabits the arid region of the southeast of the Iberian Peninsula.

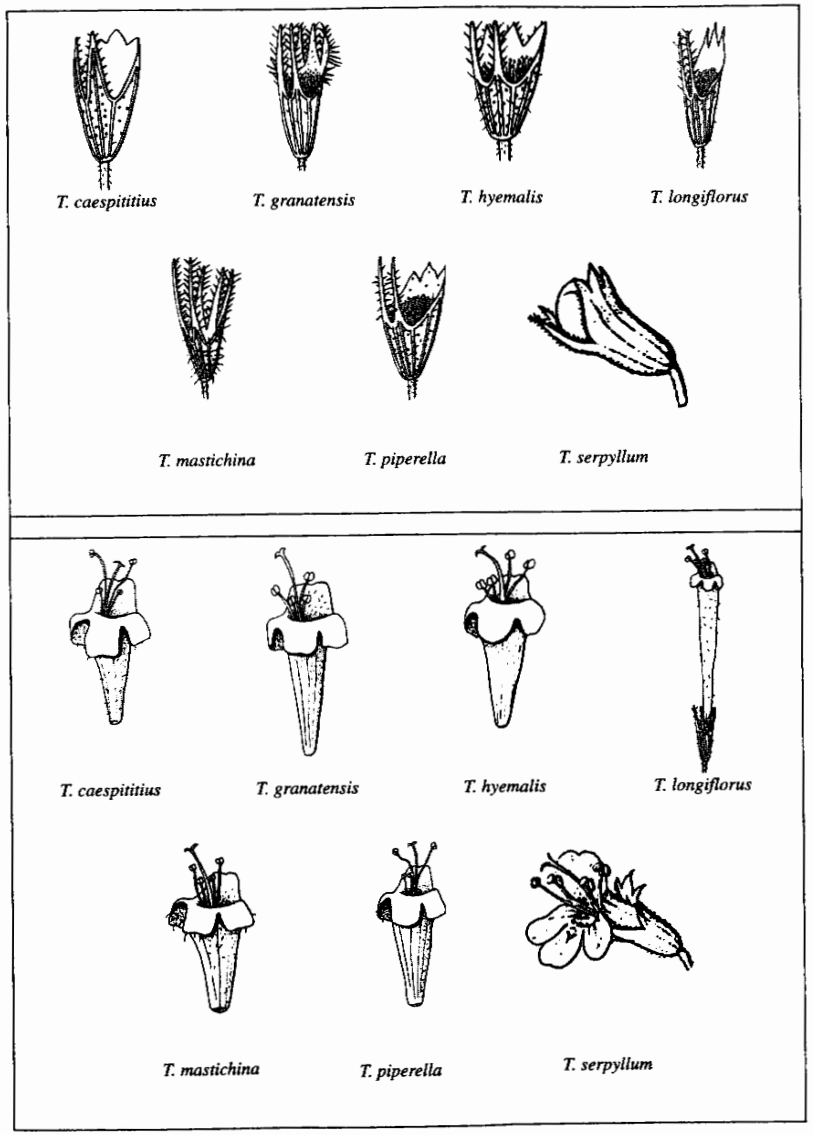

Figure 1.11 Morphology of calyx and corolla.

If we analyse some characteristics from the evolutionary point of view, flat leaves without hairs seem to be more primitive than leaves with revolute and hairy margins. The same occurs with spiciform inflorescences that present bracts similar to leaves. Globose inflorescences with special bracts seem to be more evolved. Woody species

with erect life-forms may be phylogenetically older than herbaceous species with only woody parts at the base. An interpretation of the evolutionary relationships among the different sections within the genus is shown in Figure 1.12.

ECOLOGICAL ASPECTS

Thymes are heliophylous plants and like the sun, a fact which reflects the ecology of the genus. *Thymus* plants frequently live on rocks or stones and it is very important that the soils are well drained. But different *Thymus* species require very different substrata, e.g.

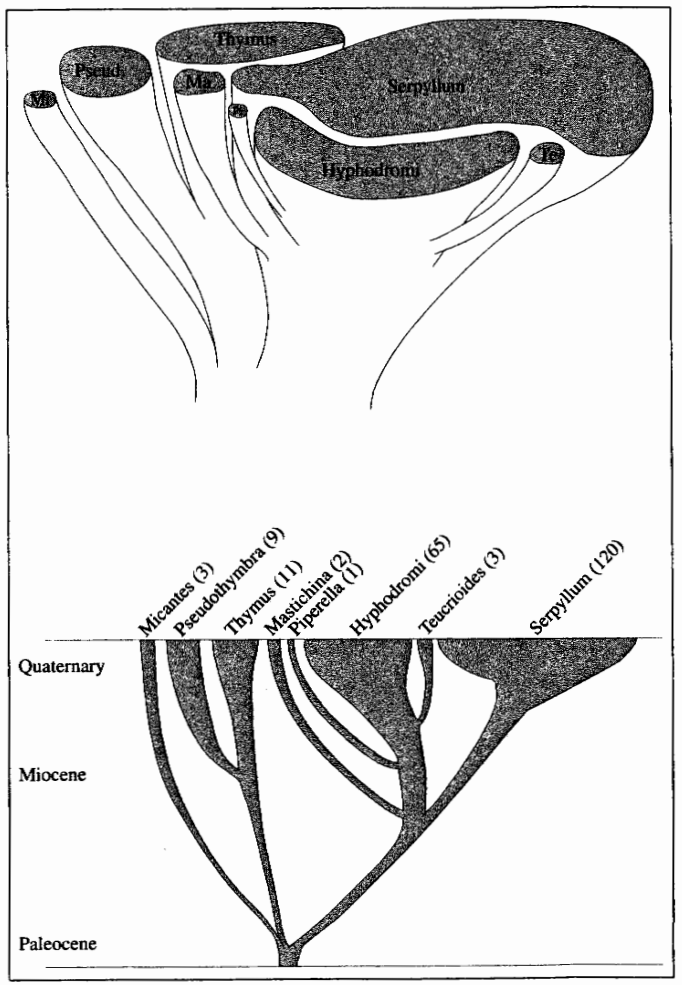

Figure 1.12 Evolutionary relationships in the genus *Thymus*. Number of species in brackets.

T. carnosus lives on sand dunes near the sea (Figure 1.13), *T. lacaitae* on gypsaceous soils, and *T. vulgaris* usually on calcareous soils.

Thymes are very resistant plants, which allows them to live under extreme climatic conditions concerning temperature and water supply. They do not avoid either cold or aridness. Dense and tomentose hairs as well as acicular leaves enable some species to support very dry conditions. The high production of essential oils can also be an adaptive characteristic for dry climate, because the volatile substances evaporate and produce a saturated atmosphere around the plant that makes the loss of water more difficult. Especially some species of the section *Serpyllum* can live in very cold climate, like *T. glacialis* in Siberia or *T. praecox* in Greenland. From an ecological point of view we can find the following correlation: bushy, woody, and erect plants are widely distributed in dry climates, whereas in more fresh and humid climates usually plants with flat leaves and woody only at the base are more common. The latter usually are herbaceous with creeping or lying stems. Such species mostly belong to the sections *Hyphodromi* and *Serpyllum*. The production of essential oils in this group is probably lower than in the first one.

SYSTEMATIC BOTANY

The genus *Thymus* is one of the most important genera of the Lamiaceae. It belongs to the tribe Mentheae within the subfamily Nepetoideae. The most related genera are *Origanum*, *Satureja*, *Micromeria* and *Thymbra*. *Thymus* is considered a well-defined genus, based on the morphological and chemical features of its species.

Figure 1.13 *T. carnosus* from Portugal.

General description

Perennial, subshrubs or shrubs, sometimes with herbaceous shape, but woody at the base, aromatic; stem erect to prostrate, sometimes caespititious and radicant, hairy in all the four sides, only in two alternating or only in the angles; leaves simple, entire or sometimes toothed, frequently revolute, glabrous or hairy, very variable in indumentum; inflorescence spiciform, interrupted in verticillasters or capituliform, bracts like the leaves or very different, lanceolate to broad ovate, usually coloured; flowers pedicellate or not, usually with little bracteoles (very small bracts at the pedicels' base); calyx two-lipped, sometimes nearly regular, more or less campanulate or cylindrical, ten-nerved; upper lip with three triangular teeth sometimes reduced to one, lower lip with two long triangular teeth curved upwards or widespread, throat barbate; corolla bilabiate, sometimes nearly regular, more or less tubular, sometimes with a very long tube, up to 20 mm, four-lobed, white, cream, pink or violet, frequently with clear spots in the throat or lower lobe; upper lobe more or less rounded, emarginate, straight, lower and lateral lobes rectangular to suborbicular, rounded, perpendicular to the tube; four stamens, sometimes reduced or not present (gynodioecy), inserted in the upper half of the tube, exserted or not; anthers with two parallel thecae; style apex branched; nutlets ovoid, smooth.

Biogeography

Thymus is widely distributed in the Old World (Figure 1.14). The Mediterranean region can be described as the centre of the genus – strictly speaking the West Mediterranean region. Only species of two sections occur outside the Mediterranean area. Seven sections are spread over the Iberian Peninsula and northwest Africa, five of them are endemic. In the Iberian Peninsula 35 species can be found, 24 of them endemic to the area. Two

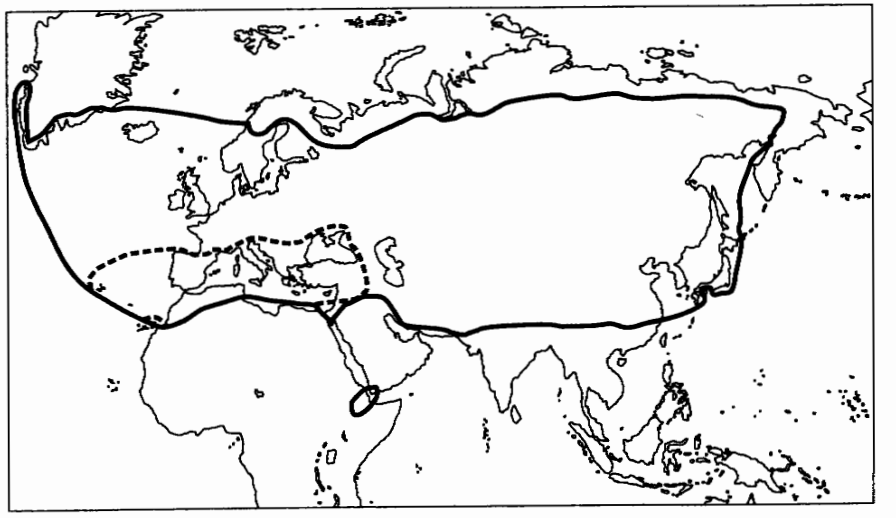

Figure 1.14 Distribution of the genus *Thymus* in the world. Dotted line represents all sections except sect. *Serpyllum* and sect. *Hyphodromi* subsect. *Serpyllastrum*.

species can be found in the Macaronesian region, one on the Canary Islands (*T. origanoides*) growing only at Riscos de Famara and surroundings, and the other one (*T. caespititius*) on Madeira and the Azores; the latter grows also in the western part of the Iberian Peninsula. Fifteen species (12 endemic) grow in northwest Africa, north of the Sahara desert (Morocco, Algeria, Tunis, and Libya), with only three of them also occurring in the Iberian Peninsula. Two species are common in the mountains of Ethiopia (*T. serrulatus*, *T. schimperi*) and one occurs in the southwest of the Arabian mountains (*T. laevigatus*). In Greece 18 species are recorded, 36 in Turkey and 17 in the Flora Iranica. Further eastwards *Thymus* can be found on the Sinai Peninsula (*T. bovei* and *T. decussatus*) and in the arid regions of West Asia up to the Himalayas reaching the limits of the tropical region up to East Asia and Japan. In China 11 species have been recorded. In the north it occurs in Siberia and northern Europe, the coasts of Greenland can be described as the most northern occurrence of *Thymus* (*T. praecox*). Introduced populations now growing wild are known to exist in regions as distant as Canada (*T. serpyllum* and *T. pulegioides*), Chile (*T. vulgaris*) or New Zealand (*T. pulegioides* and *T. vulgaris*).

We can suggest the origin of some taxa of the genus to be in the Mediterranean area, seeing that the sections *Serpyllum* and *Micantes* have been present there since the Paleocene. In the Miocene, some species of section *Thymus* and *Hyphodromi* developed. During the Quaternary the ancestors of the section *Serpyllum* and, to some extent, those within the section *Hyphodromi* have produced new speciation processes, colonizing all the ice-free land after the last Ice Age. These processes are not yet finished and may be the reason why all these species are difficult to be distinguished. We can assume that they are halfway in a process of speciation to produce clear species (Morales, 1989).

Pollen

The pollen grains of this genus have a very homogeneous morphology, both within the same species and among different taxa. According to Wunderlich (1967), it can be ascribed to the *Satureja* type. It has a radial isopolar symmetry and is usually hexacolpate (NPC 643) and three-celled. Octocolpate and tetracolpate grains are also known. The colpi are regularly disposed, and the mesocolpi usually are of the same width with one exception: the mesocolpi of *T. caespititius* are of varying wideness alternating a wider and a more narrow one. The pollen grains are more or less spheroidal and the index of Polar distance/Equatorial distance (P/E) varies between 0.9 and 1.3 (from prolate-spheroidal to oblate-spheroidal). The sizes of the pollen grains vary from 21 to 46 µm depending on the species and a correlation between ploidy level and size can be assumed. The ornamentation usually is suprareticulate, less frequently semitectate or reticulate. In the case of suprareticulate ornamentation, thick walls delimit in a lower level a net of narrower walls and pores. The wideness of walls and pores varies from one species to another, but it is homogeneous within each species. As an exception, pollen grains with cerebroid ornamentation can be found, which seems to be usual for tetracolpate pollen grains. Figure 1.15 illustrates the morphology of pollen grains from *T. hyemalis*.

Chromosomes

In the genus *Thymus* the chromosomes are very small. With 1–2 µm they appear like dots under the optical microscope. The following chromosome numbers are known: $2n = 24, 26, 28, 30, 32, 42, 48, 50, 52, 54, 56, 58, 60, 84$ and 90, corresponding to the

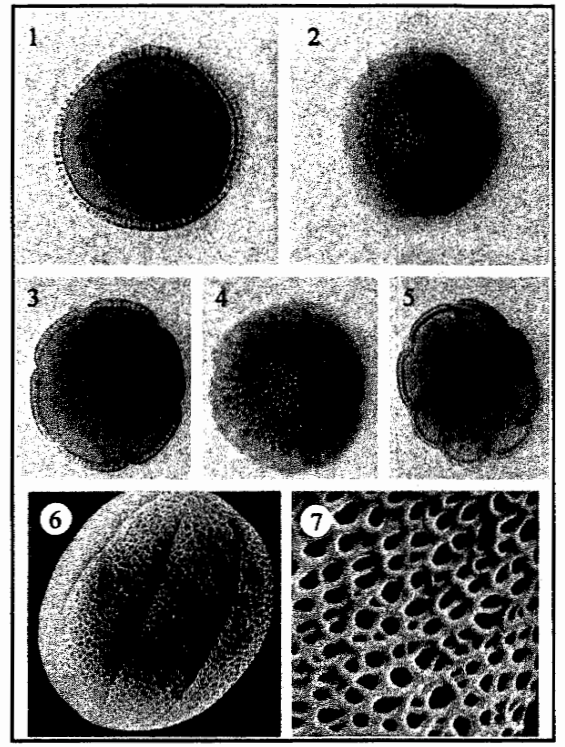

Figure 1.15 Pollen grains of *T. hyemalis* from Murcia (Spain). Images 1–5 are views from an optical microscope. Images 6 and 7 were obtained with a scanning electron microscope with a magnification of 1600x and 7000x respectively.

diploid, tetraploid and hexaploid levels. The secondary basic numbers $x = 14$ and $x = 15$ probably originate from a basic number $x = 7$. The most frequent numbers are $2n = 28$, 30, 56 and 60. Aneuploidy has been an important phenomenon during the evolution of this genus and is responsible for the other numbers. There are a lot of interesting cases of different levels within the same species. This is true for *T. mastichina* with $2n = 30$, 60; *T. vulgaris* $2n = 28$, 58; *T. zygis*, *T. leptophyllus*, *T. glabrescens*, *T. longicaulis*, *T. praecox* $2n = 28$, 56; *T. algeriensis* $2n = 30$, 56; *T. comptus* $2n = 26$, 52; *T. zygioides* $2n = 60$, 90; *T. longedentatus* $2n = 30$, 90; *T. striatus* and *T. herba-barona* $2n = 28$, 56, 84. The latter is most remarkable because the chromosome numbers studied in the West Mediterranean populations resulted to be $2n = 28$ in Majorca, $2n = 56$ in Corsica, and $2n = 84$ in Sardinia. Chromosomes from different *Thymus* species are shown in Figure 1.16.

Other features

In *Thymus* hybridization is very common where two or more species live together. Up to date 60 hybrids have been detected among the 35 species living in the Iberian

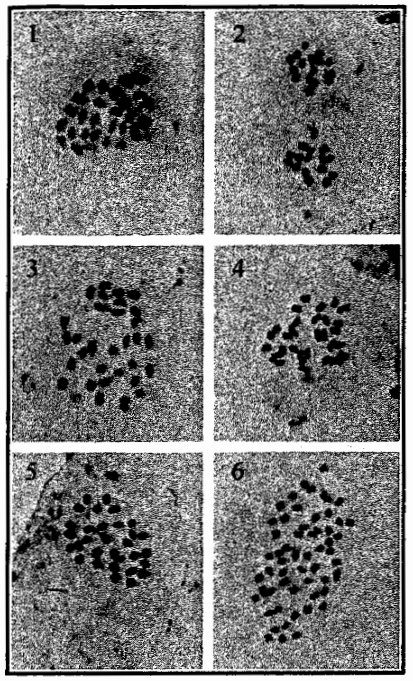

Figure 1.16 Chromosomes of some species of *Thymus*. (1): *T. mastigophorus*, 2n = 28 (Zaragoza, Spain). (2): *T. capitellatus*, n = 15 (Algarve, Portugal). (3): *T. camphoratus*, 2n = 30 (Alentejo, Portugal). (4): *T. camphoratus*, 2n = 30 (Algarve, Portugal). (5): *T. camphoratus*, 2n = 30 (Algarve, Portugal). (6): *T. carnosus*, 2n = 56 (Algarve, Portugal).

Peninsula, as we can see in the appendix (Morales, 1995). Some chemical studies show the genus to be homogeneous, in the comparison with others such as *Teucrium* or *Sideritis* both chemically heterogeneous (Morales, 1986). These two features are the evidence to consider *Thymus* to be a good taxonomical genus, probably monophyletic. Within the genus genetic incompatibility between species does not seem to exist, which makes taxonomic studies in this genus very difficult, especially in some taxonomical groups e.g. in the section *Hyphodromi* and particularly in the section *Serpyllum*, where the concept of species is more difficult to apply. If we impose synoptocal criteria, probably a lot of forms, sometimes ecological forms, would be included as simple populations into a given taxon. But when using analytical criteria we risk overlooking existing species considered as natural units. In case of doubt I recommend synoptical criteria. At the species level, there are a lot of names, more than 1 000, many of them of course are synonyms.

Popular names

In the whole area of distribution, *Thymus* is usually well known and used by the population as spice, medicinal plant or source of essential oils. Therefore a big variety of

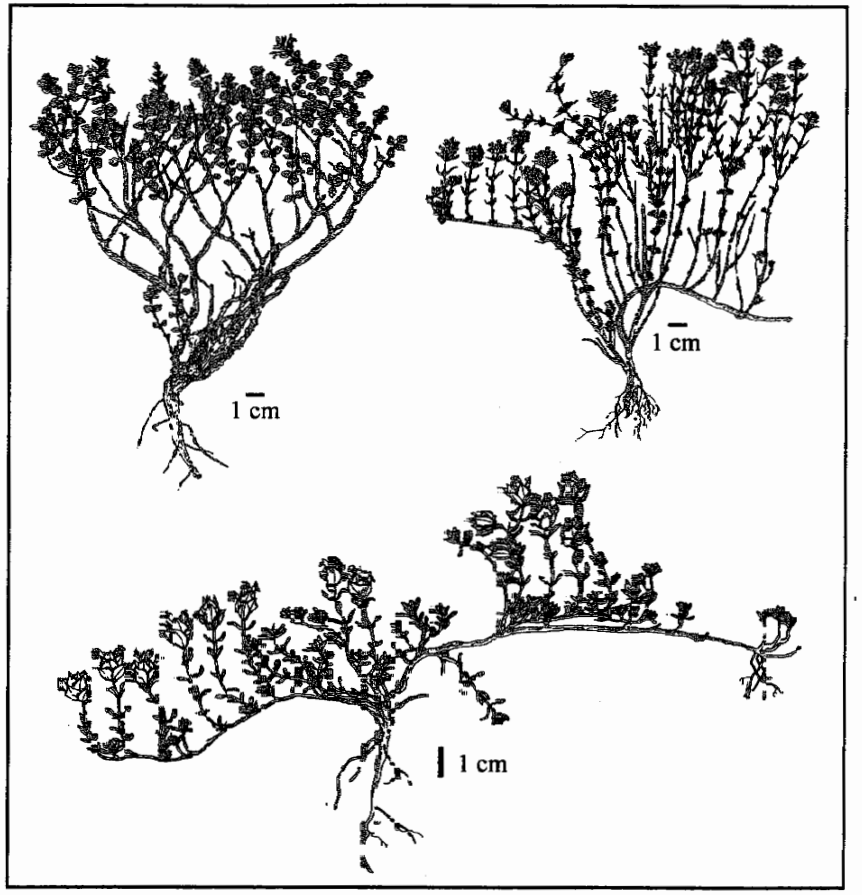

Figure 1.17 Plant habitus. (a) *T. piperella*, (b) *T. zygis*, (c) *T. granatensis*.

popular and vernacular names are known for the different species. If we begin in the west of its habitat *T. caespititius*, from the Azores, Madeira and the western part of the Iberian Peninsula has the portuguese names 'tomentelo' or 'tormentelo', and in Galicia 'tomelo do país', 'tomentelo do país' or 'tomillo'. The only species grown on the Canary Islands from this genus is *T. origanoides*, in the Riscos de Famara of Lanzarote island. An old name of this plant is 'tajosé'. 'Tomillo' is the popular name in other islands for *Thymus*-looking species of *Micromeria*. In continental Africa species of *Thymus* are found in Morocco, Algeria, Tunis and Libya. *T. algeriensis* is the most common in the four countries, and its popular names in arabic and berber languages are: 'azoukni', 'djertil', 'djoushshen', 'hamriya', 'hamzousha', 'khieta', 'mezoukesh', 'rebba', 'toushna'. *T. broussonetii* is named there 'zatar', 'za'atar el-hmir', 'za'ter el hmir', 'ze'itra', 'z'itra'. The Moroccan *T. maroccanus* has the name 'azukenni'. In the mountains of Ethiopia two *Thymus* species grow, *T. serrulatus* and *T. schimperi*, with the Abyssinian names for the first one: 'tausi',

Figure 1.18 T. mastichina (Spanish marjoram) very common in the Iberian Peninsula, from Central Spain.

'tazè', 'tenni', 'teschin', 'tessni', 'tesnè', 'thasne', and 'tessni', 'tosign', 'tosigne', 'tossign' or 'tossine' for the latter.

In Asia, in the Arabic Peninsula, the mountainous areas of Yemen are the southernmost localities in this continent, where *T. laevigatus* lives. It is named 'za'tar' or 'sa'tar'. In the far east in China the popular name of several species of thymes are 'bai li xiang' and the most used species, *T. quinquecostatus*, is called 'di jiao' or 'bian zhong'.

In the North of Europe *T. serpyllum* and other species of this group are widespread. The vernacular names in the nordic languages are 'timian' or 'timjan', 'stortimian' or 'backtimian'. And in Central Europe they are called 'Thymian', 'Feldthymian', 'Quendel', 'Kudelkraut', 'Kuttelkraut' in Germany; 'serpolet', 'piolet', 'piliolet', 'pignolet', 'pélevoué', 'pénévouet' in France; 'pepolino', 'sermollino selvatico' in Italy; 'erba pevarina', 'süsémbar' in Slavic (Puschlav); 'timian', 'masarón salvatg', 'pavradel', 'pavradella' in Rätorom. In English, the following names are known: 'thyme', 'wild thyme', 'penny mountain', 'hillwort', 'brotherwort', 'shepherds thyme', and in dutch 'tijm'.

In the different languages of the Iberian Peninsula, a lot of names are in use for the multitude of species of *Thymus* or 'tomillo' (Morales *et al.*, 1996):

T. baeticus: tomillo, tomillo basto, tomillo fino, tomillo gris, tomillo limonero.
T. granatensis: hierba luna, serpillo, serpol, tomillo, tomillo colorao, tomillo serpol.
T. hyemalis: tomillo, tomillo de invierno, tomillo fino, tomillo macho, tomillo morado, tomillo rojo.
T. lacaitae: tomillo lagartijero, tomillo de Aranjuez.
T. longiflorus: tomillo, tomillo real.

Figure 1.19 T. piperella from Valencia, Spain.

T. loscosii: ajedrea, tomillo sanjuanero.
T. lotocephalus: tomilho-cabeçudo.
T. mastichina: ajedrea de monte, almoradux, almoraú, amáraco, bela-luz, cantueso, escombrilla, marahú, marduix silvestre, mejorana, mejorana de monte, mejorana silvestre, mendaro, mendaroa, moraduix bord, salpurro, sarilla, tomilho-alvadio, tomillo, tomillo blanco, tomillo de las aceitunas, tomillo macho, tomillo salsero.
T. membranaceus: cantueso, escombrilla, mejorana, tomillo blanco, tomillo macho, tomillo terrero.
T. moroderi: cantahueso, cantueso, mejorana.

Figure 1.20 *T. membranaceus* from Murcia, Spain (Morales, 1986).

T. orospedanus: tomillo.
T. piperella L.: peberela, peberella, pebrella, pebrinella, piperesa, timó.
T. praecox: erva-ursa, farigola, farigoleta, folcó, herba de pastor, hierba luna, salia de pastor, samarilla, sarpoil, serpão, serpil, serpildo, serpilho, serpol, sérpol, serpolio, timó negre, tomillo de puerto, tomillo rastrero.
T. pulegioides: apiua, charpota, serpão glabro, serpol, te fino, te morado, té morau, tomelo, tomentelo, tomillo.
T. richardii: farigola de muntanya, farigola mascle, farigoleta, hierba luna, salsa de pastor, serfull, serpol, sèrpol, serpoll, timó negre, tomillo rojo.
T. serpylloides: samarilla, tomillo, tomillo de la sierra, tomillo de Sierra Nevada.
T. serpylloides subsp. *gadorensis*: samarilla, tomillo rojo, verbena.
T. villosus: azeitoneira, erva-azeitoneira, erva-das-azeitonas, tomilho-peludo, tomillo ansero.
T. vulgaris L.: arçã, arçanha, axedrea, boja, bojas, elar, elharr, ellbor, entremunsell, erle-bedarr, estremoncello, estremoncillo, estremonzillo, estremunsell, estremunzillo, ezkai, ezkaia, farigola, farigoleta, fariguala, forigola, frigola, frígola, friula, ispillu, lo timó, morquera, sajolida, senyorida, tem, timó, timó femella, timó mascle, timó normal, timón, timoncillo, timonet, timons, tomaní, tomelo, tomello, tomello vulgar, tomentelo, tomilho, tomilho-ordinário, tomilho-vulgar, tomilo, tomillo, tomillo ansero, tomillo blanco, tomillo borde, tomillo común, tomillo limonero, tomillo negrillo, tomillo royo, tomillo salsero, tomillo vulgar, tomillua, tomizo, tremoncillo, tremonsillo, tremontillo, tremonzillo, tumillo.
T. zygis: farigola salsera, morquera, paticas de mona, salsero salseta de pastó, serpão-do-monte, tomilhinha, tomillo, tomillo aceitunero, tomillo aceytunero, tomillo albar, tomillo ansero, tomillo blanco, tomillo del campo, tomillo español, tomillo fino, tomillo negrillo, tomillo risquero, tomillo rojo, tomillo salsero, tomillo sansero, tomillo sansero fino.

Figure 1.21 *T. vulgaris* (Hallier, 1884: 188, Tafel 1796).

T. zygis subsp. *gracilis*: tomillo, tomillo aceitunero, tomillo blanco, tomillo fino, tomillo rojo, tomillo salsero.

Sections of the genus *Thymus*

According to Jalas (1971), *Thymus* is divided into eight sections: *Micantes*, *Mastichina*, *Piperella*, *Teucrioides*, *Pseudothymbra*, *Thymus*, *Hyphodromi*, and *Serpyllum*. The sequence used here is that established by Jalas, but other ordinations would perhaps be more

Figure 1.22 T. lacaitae from Central Spain.

logical considering phylogenetic or evolutionary criteria. For distribution patterns of the sections and subsections see Morales (1997).

I. Sect. *Micantes*
II. Sect. *Mastichina*
III. Sect. *Piperella*
IV. Sect. *Teucrioides*
V. Sect. *Pseudothymbra*
  1. Subsect. *Pseudothymbra*
  2. Subsect. *Anomalae*
VI. Sect. *Thymus*
  1. Subsect. *Thymastra*
  2. Subsect. *Thymus*
VII. Sect. *Hyphodromi*
  1. Subsect. *Subbracteati*
  2. Subsect. *Serpyllastrum*
  3. Subsect. *Thymbropsis*
VIII. Sect. *Serpyllum*
  1. Subsect. *Insulares*
  2. Subsect. *Kotschyani*
  3. Subsect. *Pseudopiperellae*
  4. Subsect. *Isolepides*
  5. Subsect. *Alternantes*

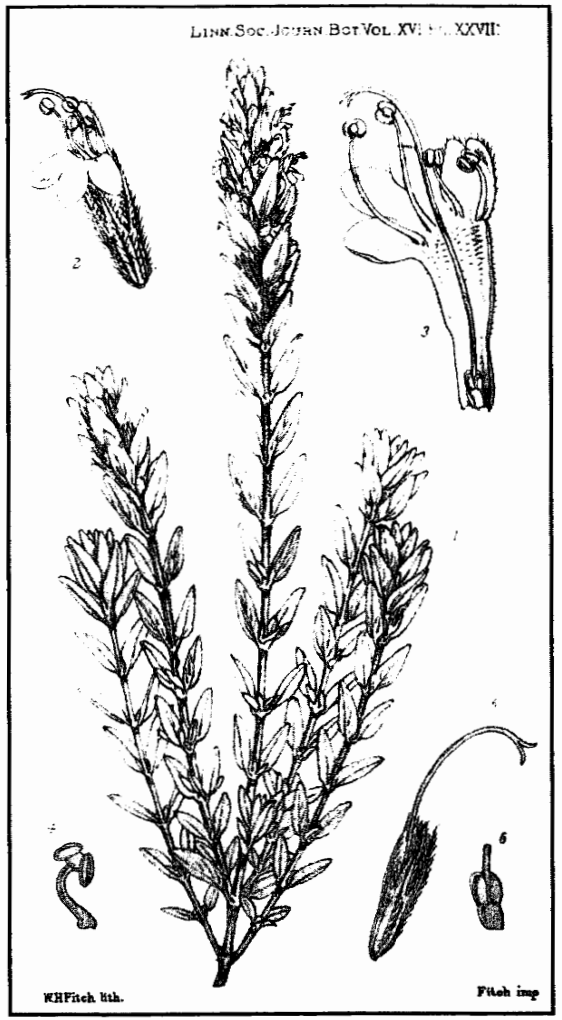

Figure 1.23 T. maroccanus (*Bot. J. Linn. Soc.*, 16: pl. 27).

6. Subsect. *Pseudomarginati*
7. Subsect. *Serpyllum*

I. Sect. *Micantes* Velen., Bei. Bot. Centr. 19(B2): 278 (1906)
Typus: *T. caespititius* Brot.
Erect plants (North-African species) or caespitose; stems holotrichous; leaves flat, glabrous, long oblong-obovate; inflorescence spiciform, sometimes dense; lateral upper teeth of calyx very short or reduced.

It comprises three species, two of them are North African woody species, that occur in Morocco: *T. satureioides* and *T. riatarum*. The former inhabits the High Atlas region, while *T. riatarum* is a prostrate plant and lives in the Rif mountains. The Ibero-Macaronesian species *T. caespititius* occurs in the northwest of the Iberian Peninsula and also in Madeira and Azores. If we take into account their plesiomorphic features, like flat, non-revolute and glabrous leaves, and their geographical distribution, this section seems to be very old.

II. Sect. ***Mastichina*** (Miller) Bentham, Lab. Gen. Sp.: 340 (1834)
Mastichina Miller, Gard. Dict. ed. 4 (2) (1754).
Typus: *T. mastichina* (L.) L.
Erect plants with holotrichous stems, leaves flat, lanceolate to obovate; inflorescence capituliform; calyx very hairy, teeth similar and subulate, with long cilia.

This section is endemic to the Iberian Peninsula, and comprises *T. mastichina*, with two subspecies, and *T. albicans*. *T. mastichina* subsp. *mastichina* is a very common plant in Spain and Portugal. The subspecies *donyanae* occurs only in the southwest of the Iberian Peninsula around the 'Coto de Doñana' and in some locations in the 'Algarve'. The other species, *T. albicans*, is also living in the southwestern pinewoods of *Pinus pinea*. *T. mastichina* subsp. *donyanae* and *T. albicans*, with 2n=30 chromosomes, are probably the origin of the tetraploid apoendemic *T. mastichina* subsp. *mastichina*, a modern taxon that has spread throughout the entire Iberian Peninsula.

III. Sect. ***Piperella*** Willk., Prodr. Fl. Hisp. 2: 404 (1868).
Typus: *T. piperella* L.
Erect or decumbent plants, with holotrichous stems and leaves obovate, flat and glabrous; flowers growing in lax verticillasters.

T. piperella is found at Valencia province and surroundings, and it is the unique species of this monotypic section, endemic to this region.

IV. Sect. ***Teucrioides*** Jalas, Bot. J. Linn. Soc. 64(2): 201 (1971).
Typus: *T. teucrioides* Boiss. and Spruner.
Plants usually decumbent with leaves revolute, ovate or triangular-ovate; flowers in verticillasters. Endemic to the Balkan Peninsula. It inhabits the mountains of Greece and Albania. Three species can be recognised within this section: *T. teucrioides*, *T. hartvigi*, and *T. leucospermus*, that have been studied by Hartvig (1987). Chromosome numbers of these species are not yet known.

V. Sect. ***Pseudothymbra*** Bentham, Lab. Gen. Sp.: 341 (1834).
Typus: *T. lotocephalus* G. López and R. Morales (*T. cephalotos* auct. non L.)
Erect plants with holotrichous stems and linear revolute leaves, usually hairy and with cilia at the base; inflorescence capituliform with broad bracts; corolla very long.

In this section are included nine Iberian-North-African species, usually with long corollas, up to 2 cm, and bracts rather different from the leaves and subglobose inflorescence, except in subsection *Anomalae*. The North-African species are *T. munbyanus*, common and very variable, extending from the Middle Atlas and the Rif Mountains as far as the Algerian mountains. A difficult species with two subspecies and hybrids with *T. algeriensis* and *T. willdenowii*. *T. bleicherianus* is only known from three locations, one in Algeria and two more in the north of Morocco. The other species of this section are all Iberian.

We recognize two subsections:

V1. Subsect. ***Pseudothymbra*** (Bentham) R. Morales, *Ruizia* 3: 146 (1986).
Inflorescence capituliform and bracts are very different from the leaves.

V2. Subsect. ***Anomalae*** (Rouy) R. Morales, *Ruizia* 3: 146 (1986).
T. sect. *Anomalae* Rouy, Bull. Soc. Bot. France 37: 166 (1890).
Typus: *T. antoninae* Rouy and Coincy
Flowers in verticillasters, bracts with similar appearance as the leaves.

VI. Sect. ***Thymus***
Erect or radicant plants with holotrichous stems, revolute leaves, usually hairy; flowers in spiciform or globose inflorescences.

Western Mediterranean section, with three most important species: *T. vulgaris*, *T. zygis* and *T. willdenowii*. The first usually occurs on basic soils and is distributed in northern Italy, south of France and east of Spain. *T. zygis* is a very common species in all the Iberian Peninsula and *T. willdenowii* is common in North Africa (Morocco and Algeria) and also grows only in Gibraltar area in the Iberian Peninsula.
We recognize two subsections:

VI1. Subsect. ***Thymastra*** (Nyman ex Velen.) R. Morales, *Ruizia* 3: 146 (1986).
T. sect. *Thymastra* Velen., Bei. Bot. Centr. 19(B2): 276 (1906).
Typus: *T. capitellatus* Hoffmanns. and Link.
Erect plants with triangular-ovate or lanceolate-ovate leaves, without cilia at the base; inflorescence more or less globose with bracts different from the leaves.

VI2. Subsect. ***Thymus***
Erect or subtended plants with leaves usually hairy, and ciliate or not at the base, with revolute margins and more or less linear, bracts broader than the leaves, but not very different.

VII. Sect. ***Hyphodromi*** (A. Kerner) Halácsy, Denkschr. Akad. Wiss. Wien 61: 252 (1894).
Typus: *T. bracteosus* Vis. ex Bentham.
Plants usually subtended and rooting; stems holotrichous; leaves flat or revolute, usually not hairy; inflorescence frequently capituliform with bracts different from the leaves.

This section extends throughout the Mediterranean area and comprises around 60 species. From the three subsections, *Subbracteati* is characterized by more or less revolute or convolute leaves and seems to be Oriental. Only one species occurs in North Africa, from Morocco to Libya: *T. algeriensis*. Another species occurs in Central Spain: *T. mastigophorus*. *T. spinulosus* occurs in Sicily and Italy, and *T. striatus* in the Italian and Balkan Peninsulas. Both species are very variable. *T. argaeus*, *T. brachychilus*, *T. cappadocicus*, *T. cherlerioides*, *T. convolutus*, *T. pulvinatus*, and *T. revolutus* occur in Turkey; *T. boissieri*, *T. comptus*, *T. dolopicus*, and *T. plasonii* in the Balkan Peninsula; *T. atticus*, *T. parnassicus*, and *T. leucotrichus* inhabit Turkey and the Balkan Peninsula. The last species also grows in Syria and in the Lebanon. *T. integer* is only found on the island of Cyprus. This species is probably not different from *T. leucotrichus*. *T. samius* occurs in the Aegean islands. *T. borysthenicus* and *T. pallasianus* occur north of the Black Sea, *T. persicus* south of the Caucasus, but only one location for this species is known.

We recognize three subsections:

VII1. Subsect. *Subbracteati* (Klokov) Jalas, Bot. J. Linn. Soc. 64(2): 205 (1971), emend.
T. sect. *Subbracteati* Klokov, Not. Syst. (Leningrad) 16: 315 (1954) pro parte.
Typus: *T. pallasianus* H. Braun.

VII2. Subsect. *Serpyllastrum* Huguet del Villar, Cavanillesia 6: 124 (1934).
Lectotypus: *T. bracteosus* Vis. ex Bentham.

VII3. Subsect. *Thymbropsis* Jalas ex R. Morales, Anales Jard. Bot. Madrid 45(2): 562 (1989).
Typus: *T. maroccanus* Ball.

Subsection *Serpyllastrum* is a group of species characterized by the presence of prostrate stems and flat leaves more or less wide. Five species from this section are living in Spain: *T. bracteatus*, *T. leptophyllus*, *T. fontqueri*, *T. granatensis* and *T. lacaitae*. It is also well represented in the East, but no species occur in Italy and North Africa. *T. aznavourii* and *T. bracteosus* occur in the Balkan Peninsula; *T. canoviridis*, *T. haussknechtii*, *T. pectinatus* and *T. spathulifolius* are found in Turkey. *T. zygioides* extends from the Balkan Peninsula as far as the Crimean Peninsula and also in Turkey. This species and the Spanish endemic *T. lacaitae* are morphologically very similar. There is also a group of species that occur only in the Caucasus: *T. dagestanicus*, *T. hadzhievii*, *T. helendzhicus*, *T. karjagnii*, *T. ladjanuricus*, *T. lipskyi*, *T. majkopiensis*, and *T. sosnowskyi*. Seven more species from Central Asia are considered inside this subsection: *T. cuneatus*, *T. eremita*, *T. incertus*, *T. irtyschensis*, *T. kirgisorum*, *T. nerczensis*, *T. petraeus*.

Subsection *Thymbropsis* includes the North African *T. broussonetii*, *T. maroccanus*, *T. lanceolatus*, *T. numidicus*, *T. pallescens*, and the two endemic species from Greece *T. laconicus* and *T. holosericeus*. Five more species from this section are found in Turkey: *T. cariensis*, *T. cilicicus*, *T. eigii*, *T. leucostomus*, and *T. sipyleus*. *T. syriacus* occurs in Lebanon, Syria and a location in northern Irak; *T. bovei* lives in the Sinai Peninsula, Israel, Jordan, Irak and Saudi Arabia; and *T. decussatus* in Sinai and Saudi Arabia. This group has predominantly North-African and East-Asian species.

VIII. Sect. *Serpyllum* (Miller) Bentham, Lab. Gen. Sp.: 340 (1834).
Serpyllum Miller, Gard. Dict. ed. 4 (3) (1754).
Woody plants or only woody at the base, but with herbaceous appearance, usually subtended and rooting, with holotrichous stems or hairy only in two opposite sides or in the angles (goniotrichous or alelotrichous), leaves flat and usually ciliate at the base, with distinct lateral veins; inflorescence spiciform or more or less globose.

In this section there are around 120 species. They occur throughout the area of the genus, except in Madeira and the Azores. We find in the species of *Serpyllum* the widest chromosomal variation. There are also woody species that grow in the mountains in arid areas like *T. origanoides* on Lanzarote (Canary Islands); *T. serrulatus* and *T. schimperi* in Ethiopia, *T. laevigatus* in the southwest of the Arabian Peninsula. Another group of species are more or less herbaceous and occur in the Mediterranean mountains, and all of Eurasia and also along the coasts of Greenland. The species of the last group seem to be younger in evolutionary terms and have probably been actively evolving since the last glaciation when this group colonized the new lands free of ice. This group is also

very difficult taxonomically and corresponds to the last three subsections. Few species of these subsections are present in the Mediterranean area. According to Jalas (1971), we divided this section into seven subsections.

Subsection *Insulares* comprises *T. willkommii*, an endemic species that occurs in the mountains of the provinces of Castellón and Tarragona (eastern Spain); *T. richardii*, with three subspecies: subsp. *richardii* from Majorca and Yugoslavia, subsp. *ebusitanus* from Ibiza and subsp. *nitidus* from Marettimo island near Sicily; the North-African *T. dreatensis* and *T. guyonii*, the Canary Island endemic *T. origanoides* and the endemic species to northwest Turkey *T. bornmuelleri*.

Subsection *Kotschyani* includes a lot of Asian species, but only *T. fallax* and *T. transcaucasicus* occur in Turkey. Other interesting species occurring outside the Mediterranean area are *T. laevigatus* from the mountains of Yemen or *T. schimperi* and *T. serrulatus* from the Ethiopian mountains.

Subsection *Pseudopiperellae* comprises *T. herba-barona* from Majorca, Corsica, and Sardinia (Mayol *et al.*, 1990) and *T. nitens* from the south of France.

Five species inhabiting the Balkan Peninsula belong to the **subsection *Isolepides***: *T. bulgaricus*, *T. glabrescens*, *T. longedentatus*, *T. pannonicusm*, and *T. sibthorpii*.

Subsection *Alternantes* includes *T. linearis* from the Himalaya mountains; the European *T. pulegioides*, *T. froelichianus*, *T. alpestris*, *T. oehmianus*, *T. bihoriensis*, and *T. comosus*.

Subsection *Pseudomarginati* includes the species *T. longicaulis* and *T. praecox*, very common in Europe and also in Turkey; *T. nervosus*, an endemic of the Pyrenees and the French Massif Central; *T. ocheus*, *T. stojanovii*, and *T. thracicus* from the Balkan Peninsula and the East Mediterranean region.

Subsection *Serpyllum* includes *T. quinquecostatus* from Japan, the European *T. serpyllum* and *T. talijevii* and other Russian species.

LIST OF *THYMUS* SPECIES OF THE WORLD

I propose at the moment the following list of species. There are 214 species and 36 subspecies more: 250 taxa. When known, the chromosome numbers and the countries are given (Ag=Algeria, Al=Albania, An=Asian Turkey, Az=Azores, Bl=Balearic Islands, Bu=Bulgaria, Co=Corsica, Cy=Cyprus, E=East Aegean Islands, Ga=France, Gr=Greece, Hs=Spain, It=Italy, Ju=former Jugoslavia, Li=Libya, LS=Lebanon and Syria, Lu=Portugal, Ma=Morocco, Ru=Romania, Sa=Sardinia, Si=Sicily, Tn=Tunis, Tu=European Turkey, URSS=former Soviet Union).

I. Sect. *Micantes* Velen.
T. caespititius Brot. 2n=30 Hs Lu Az Madeira
T. satureioides Cosson subsp. *satureioides* Ma
subsp. *commutatus* Batt. 2n=30 Ma
T. riatarum Humbert and Maire Ma

II. Sect. *Mastichina* (Miller) Bentham
T. mastichina (L.) L. subsp. *mastichina* 2n=56, 58, 60 Hs Lu

subsp. *donyanae* R. Morales 2n=30 Hs Lu
T. albicans Hoffmanns. and Link 2n=30 Hs Lu

III. Sect. *Piperella* Willk.
T. piperella L. 2n=28 Hs

IV. Sect. *Teucrioides* Jalas
T. teucrioides Boiss. and Spruner subsp. *teucrioides* Gr Al
subsp. *alpinus* Hartvig Gr
subsp. *candilicus* (Beauverd) Hartvig Gr
T. hartvigi R. Morales subsp. *hartvigi* Gr
subsp. *macrocalyx* (Hartvig) R. Morales Gr
T. leucospermus Hartvig Gr

V. Sect. *Pseudothymbra* Bentham

VI1. Subsect. *Pseudothymbra* (Bentham) R. Morales
T. lotocephalus G. López and R. Morales 2n=30 Lu
T. villosus L. subsp. *villosus* Lu
subsp. *lusitanicus* (Boiss.) Coutinho 2n=54 Lu Hs
subsp. *oretanicus* Hs
T. longiflorus Boiss. 2n=28 Hs
T. membranaceus Boiss. 2n=28 Hs
T. moroderi Pau ex Martínez 2n=28 32 Hs
T. munbyanus Boiss. and Reuter subsp. *munbyanus* Ma Ag
subsp. *coloratus* (Boiss. and Reuter) Greuter and Burdet Ma Ag
T. bleicherianus Pomel Ma Ag
T. funkii Cosson 2n=28 Hs

V2. Subsect. *Anomalae* (Rouy) R. Morales
T. antoninae Rouy and Coincy 2n=56 Hs

VI. Sect. *Thymus*

VI1. Subsect. *Thymastra* (Nyman ex Velen.) R. Morales
T. capitellatus Hoffmanns. and Link 2n=30 Lu
T. camphoratus Hoffmanns. and Link 2n=30 Lu

VI2. Subsect. *Thymus*
T. carnosus Boiss. 2n=56 Lu Hs
T. vulgaris L. subsp. *vulgaris* 2n=28, 30 Hs Ga It
subsp. *aestivus* (Willk.) O. Bolós and A. Bolós 2n=58, 60 Hs Bl
T. orospedanus Huguet del Villar 2n=28 Hs
T. hyemalis Lange subsp. *hyemalis* 2n=58 Hs
subsp. *millefloris* (Rivera and al.) R. Morales 2n=58 Hs
subsp. *fumanifolius* (Pau) R. Morales Ma Ag
T. zygis Loefl. ex L. subsp. *zygis* 2n=28 Hs Lu
subsp. *gracilis* (Boiss.) R. Morales 2n=28 Hs Ma
subsp. *sylvestris* (Hoffmanns. and Link) Coutinho 2n=56, 58 Hs Lu
T. baeticus Boiss. ex Lacaita 2n=58 Hs
T. willdenowii Boiss. 2n=30 Hs Ma Ag

T. loscosii Willk. 2n=54 Hs
T. serpylloides Bory subsp. *serpylloides* 2n=58 Hs
subsp. *gadorensis* (Pau) Jalas 2n=56, 58 Hs

VII. Sect. *Hyphodromi* (A. Kerner) Halácsy

VII1. Subsect. *Subbracteati* (Klokov) Jalas
T. algeriensis Boiss. and Reuter 2n=30, 56 Ma Ag Tn Li
T. argaeus Boiss. and Bal. An
T. atticus Celak. An Bu Gr Tu
T. boissieri Hal. Al Gr Ju
T. borysthenicus Klokov and Shost.
T. brachychilus Jalas An
T. cappadocicus Boiss. An
T. cherlerioides Vis. 2n=28 An
T. comptus Friv. 2n=26, 28, 52 Gr Tu
T. convolutus Klokov An
T. dolopicus Form. Gr
T. integer Griseb. Cy
T. leucotrichus Halácsy An Gr Ju LS
T. mastigophorus Lacaita 2n=28 Hs
T. pallasianus H. Braun subsp. *pallasianus* north to Black Sea
subsp. *brachyodon* (Borbás) Jalas
T. parnassicus Halácsy An Gr Ju
T. persicus (Ronniger ex Rech. fil.) Jalas IRAN
T. plasonii Adamovic Gr
T. pulvinatus Celak. An
T. revolutus Celak. An
T. spinulosus Ten. 2n=56 It Si
T. striatus Vahl 2n=26, 28, 42, 54, 56, 84 Al Bu It Gr Ju Tu

VII2. Subsect. *Serpyllastrum* Huguet del Villar
T. aznavourii Velen. Tu
T. bracteatus Lange ex Cutanda 2n=56, 58 Hs
T. bracteosus Vis. ex Bentham Ju
T. canoviridis Jalas An
T. cuneatus Klokov Central Asia
T. dagestanicus Klokov and Shost. 2n=28 Caucasus
T. eremita Klokov Central Asia
T. fontqueri (Jalas) Molero and Rovira 2n=56 Hs
T. *granatensis* Boiss. subsp. *granatensis* 2n=28 Hs
subsp. *micranthus* (Willk.) O. Bolós and Vigo Hs
T. hadzhievii Grossh. 2n=28 Caucasus
T. haussknechtii Velen. An
T. helendzhicus Klokov and Shost. Caucasus
T. incertus Klokov Central Asia
T. irtyschensis Klokov Altai
T. karjaginii Grossh. Caucasus
T. kirgisorum Dubjanski 2n=26 South of Russia and wide area until Siberia

T. lacaitae Pau 2n=28 Hs
T. landjanuricus Kem. Caucasus
T. leptophyllus Lange subsp. *leptophyllus* 2n=28 Hs
subsp. *paui* R. Morales 2n=56 Hs
subsp. *izcoi* (Rivas Martínez and al.) R. Morales Hs
T. lipskyi Klokov and Shost. Caucasus
T. majkopiensis Klokov and Shost. 2n=28 Caucasus
T. nerczensis Klokov N Mongolia
T. pectinatus Fisch. and Meyer An
T. petraeus Serg. Central Asia
T. samius Ronniger and Rech. fil. AE
T. sosnowskyi Grossh. 2n=60 Caucasus
T. sphatulifolius Hausskn. and Velen. An
T. zygioides Griseb. 2n=56, 60, 62, 90 An Bu Gr Ru Tu Crimea

VII3. Subsect. *Thymbropsis* Jalas ex R. Morales
T. bovei Bentham Sinai IJ Irak Saudi Arabia
T. broussonetii Boiss. subsp. *broussonetii* Ag Ma Tn
subsp. *hannonis* (Maire) R. Morales Ma
T. cariensis Hub.-Mor. and Jalas An
T. cilicicus Boiss. and Bal. An AE
T. decussatus Bentham Sinai Saudi Arabia
T. eigii (Zohary and Davis) Jalas An
T. holosericeus Celak. 2n=28 Gr
T. laconicus Jalas Gr
T. lanceolatus Desf. Ag
T. leucostomus Hausskn. and Velen. An
T. maroccanus Ball. subsp. *maroccanus* Ma
subsp. *rhombicus* Huguet del Villar Ma
T. numidicus Poiret Ag
T. pallescens de Noé (*T. fontanesii*) Ag
T. sipyleus Boiss. subsp. *sipyleus* An AE
subsp. *rosulans* (Borbás) Jalas
T. syriacus Boiss. An LS Iraq IRAN

VIII. Sect. *Serpyllum* (Miller) Bentham

VIII1. Subsect. *Insulares* Jalas
T. bornmuelleri Velen. An
T. dreatensis Batt. Ma Ag
T. guyonii De Noe Ag
T. origanoides Webb and Berthelot 2n=28 Canary Islands
T. richardii Pers. subsp. *richardii* 2n=28, 30 Bl Ju
subsp. *ebusitanus* (Font Quer) Jalas 2n=30 Bl
subsp. *nitidus* (Guss.) Jalas 2n=28 Si
T. willkommii Ronniger 2n=56 Hs

VIII2. Subsect. *Kotschyani* (Klokov) Jalas
T. ararati-minoris Klokov and Shost.
T. armeniacus Klokov

T. binervulatus Klokov and Shost.
T. carmanicus Jalas IRAN
T. collinus M. Bieb.
T. daenensis Celak. subsp. *daenensis* IRAN
subsp. *lancifolius* (Celak.) Jalas
T. desjatovae Ronniger
T. eriocalyx (Ronniger) Jalas IRAN
T. eriophorus Ronniger
T. fallax Fisch. and Meyer An IRAN
T. fedtschenkoi Ronniger IRAN
T. fominii Klokov and Shost.
T. guberlinensis Iljin
T. intercedens (H. Braun) Rech. fil.
T. kjapazi Grossh.
T. koeieanus Ronniger IRAN
T. kotschyanus Boiss. and Hohen. IRAN
T. laevigatus Vahl Yemen
T. migricus Klokov and Shost. IRAN
T. pubescens Boiss. and Kotschy ex Celak. IRAN
T. punctatus Vis.
T. roseus Schipcz.
T. schimperi Ronniger subsp. *schimperi* 2n=30 Ethiopia
subsp. *hedbergianus* Sebsebe Ethiopia
T. serrulatus Hochst. ex Bentham Ethiopia
T. squarrosus Fisch. and Meyer
T. transcaspicus Klokov IRAN
T. transcaucasicus Ronniger An IRAN
T. trautvetteri Klokov and Shost. IRAN
T. ziaratinus Klokov and Shost.

VIII3. Subsect. *Pseudopiperellae* Jalas
T. herba-barona Loisel. subsp. *herba-barona* 2n=56, 84 Co Sa
subsp. *bivalens* 2n=28 Bl
T. nitens Lamotte 2n=28 Ga

VIII4. Subsect. *Isolepides* (Borbás) Halácsy
T. bulgaricus (Dom and Podp.) Ronniger
T. coriifolius Ronniger
T. czernjaevii (*tschernjajevii*) Klokov and Shost.
T. dimorphus Klokov and Shost.
T. elisabethae Klokov and Shost.
T. glabrescens Willd. subsp. *glabrescens* 2n=28, 32, 56, 58
subsp. *decipiens* (H. Braun) Domin 2n=52
subsp. *urumovii* (Velen.) Jalas 2n=28, 56
T. karamarianicus Klokov and Shost.
T. klokovii (Ronniger) Shost.
T. latifolius (Bess.) Andr.
T. lavrenkoanus Klokov
T. longedentatus (Degen and Urum.) Ronniger 2n=30, 90 Gr

T. markhotensis Malejev
T. pannonicus All. 2n=28, 35 URSS, China
T. podolicus Klokov and Shost.
T. przewalskii Kom.
T. sibthorpii Bentham 2n=28
T. tiflisiensis Klokov and Shost.
T. turczaninovii Serg.

VIII5. Subsect. *Alternantes* Klokov
T. alpestris Tausch ex A. Kerner 2n=28
T. alternans Klokov
T. bihoriensis Jalas
T. buschianus Klokov and Shost.
T. caucasicus Willd. ex Ronniger
T. comosus Heuffel ex Griseb. and Schenk 2n=28, 58
T. disjunctus Klokov URSS, China
T. froelichianus Opiz 2n=56
T. komarovii Serg. 2n=24, 26
T. nummularius M. Bieb. IRAN
T. oehmianus Ronniger and Soska
T. pseudonummularius Klokov and Shost.
T. pseudopulegioides Klokov and Shost.
T. pulchellus C. A. Meyer
T. pulegioides L. 2n=28, 30
T. semiglaber Klokov

VIII6. Subsect. *Pseudomarginati* (Braun ex Borbás) Jalas
T. linearis Bentham subsp. *linearis* IRAN
subsp. *hedgei* Jalas
T. longicaulis C. Presl. subsp. *longicaulis* 2n=26, 28, 30, 50, 56, 58
subsp. *chaubardii* (Boiss. and Heldr. ex Reichenb. fil.) Jalas
T. nervosus Gay ex Willk. 2n=28 Ga Hs
T. ocheus Heldr. and Sart. ex Boiss. An Bu Gr Ju
T. praecox Opiz subsp. *praecox* 2n=24, 50, 54, 56, 58
subsp. *skorpilii* (Velen.) Jalas 2n=28, 56
subsp. *polytrichus* (A. Kerner ex Borbas) Jalas 2n=28, 50, 54, 55, 56
subsp. *britannicus* (Ronniger) Holub 2n=28, 50, 54, 56
subsp. *zygiformis* (H. Braun) Jalas
subsp. *grossheimii* (Ronniger) Jalas IRAN = T. caucasicus
T. pulcherrimus Schur subsp. *pulcherrimus* 2n=28, 56
subsp. *carpathicus* (Celak.) Mártonfi
T. stojanovii Degen. Bu Gr Ju
T. thracicus Velen. 2n=28, 56, 58 Al An Bu Gr Ju Tu

VIII7. Subsect. *Serpyllum*
T. alatauensis (Klokov and Shost.) Klokov
T. altaicus Klokov and Shost. URSS, China
T. amurensis Klokov URSS, China
T. arsenijevii Klokov
T. aschurbajevii Klokov

T. asiaticus Serg. 2n=26
T. bituminosus Klokov
T. bucharicus Klokov
T. cerebrifolius Klokov
T. chancoanus Klokov
T. crenulatus Klokov
T. curtus Klokov URSS, China
T. diminutus Klokov
T. diversifolius Klokov
T. eravinensis Serg.
T. eubajcalensis Klokov
T. extremus Klokov
T. flexilis Klokov
T. glacialis Klokov
T. iljinii Klokov and Shost.
T. inaequalis Klokov URSS, China
T. jenisseensis Iljin
T. mandschuricus Ronniger 2n=24 China
T. minussinensis Serg.
T. mongolicus Klokov URSS, China
T. narymensis Serg.
T. nervulosus Klokov URSS, China
T. ochotensis Klokov
T. oxyodontus Klokov 2n=24, 28
T. phyllopodus Klokov 2n=24
T. proximus Serg. URSS, China
T. quinquecostatus Celak. 2n=24, 26 China, Japan
T. reverdattoanus Serg.
T. schischkinii Serg.
T. seravshanicus Klokov
T. serpyllum L. subsp. *serpyllum* 2n=24, 26
subsp. *tanaensis* (Hyl.) Jalas 2n=24
T. sibiricus (Serg.) Klokov and Shost.
T. sokolovii Klokov
T. talijevii Klokov and Shost.
T. tonsilis Klokov
T. ussuriensis Klokov

Appendix

List of hybrids in the Iberian Peninsula. Hybridization occurs frequently in the Iberian Peninsula, where 60 hybrids have been detected and some of them described.

T. baeticus Boiss. ex Lacaita x *T. hyemalis* Lange
T. x indalicus Blanca, Cueto, Gutiérrez and Martínez, Folia Geobot. Phytotax 28: 138 fig. 1 (VIII-1993)
T. x garcia-martinoi Sánchez Gómez and Sáez in Saéz, Sánchez Gómez and Morales, Anales Jard. Bot. Madrid 51(1): 158 (XII-1993)

T. baeticus Boiss. ex Lacaita x *T. mastichina* (L.) L. subsp. *mastichina*
T. x arundanus Willk., Oesterr. Bot. Z. 41: 52 (1891), pro sp.
T. x fontquerianus Pau, Mem. Mus. Ci. Nat. Barcelona, Ser. Bot. 1(1): 61 (1922)

T. baeticus Boiss. ex Lacaita x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x arcanus G. López and R. Morales, Anales Jard. Bot. Madrid 41(1): 94 (1984)

T. bracteatus Lange ex Cutanda x *T. mastichina* (L.) L. subsp. *mastichina*
T. x bractichina R. Morales, Anales Jard. Bot. Madrid 43(1): 39 (1986)
T. x pectinatus R. Morales, Anales Jard. Bot. Madrid 41(1): 94 (1984) non Fischer and Meyer, nom. illeg.
T. x rivas-molinae Mateo and M. B. Crespo, Rivasgodaya 7: 130 (1993)
T. x sennenii Pau var. *leucodonthus* Pau, Bol. Soc. Aragonesa Ci. Nat. 15: 160 (1916), nom. inval.
T. x sennenii auct. non Pau

T. bracteatus Lange ex Cutanda x *T. pulegioides* L.

T. bracteatus Lange ex Cutanda x *T. zygis* Loefl. ex L. subsp. *zygis*
T. x borzygis Mateo and M. B. Crespo, Thaiszia, Kosice 3(1): 7 fig. 2 (1993)

T. caespititius Brot. x *T. mastichina* (L.) L. subsp. *mastichina*
T. x henriquesii Pau, Brotéria, Sér. Bot. 22: 121 (1926)

T. camphoratus Hoffmanns. and Link x *T. mastichina* (L.) L. subsp. *mastichina*
T. x ramonianus Paiva and Salgueiro, Anales Jard. Bot. Madrid 52(1): 114 fig. 2 (1994)

T. carnosus Boiss. x *T. mastichina* (L.) L. subsp. *mastichina*
T. x welwitschii Boiss., Diagn. Pl. Orient. 3(4): 9 (1859), pro sp.
T. noeanus Rouy, Bull. Soc. Bot. France 52: 507 (1905)

T. funkii Cosson x *T. vulgaris* L. subsp. *vulgaris*
T. x lainzii Sánchez Gómez, Fernández Jiménez and Sáez in Sánchez Gómez and Fernández Jiménez, Anales Jard. Bot. Madrid 54

T. funkii Cosson x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x paradoxus Rouy, Bull. Soc. Bot. France 20: 78 (1883)

T. granatensis Boiss. subsp. *granatensis* x *T. longiflorus* Boiss.
T. x almijarensis Ruiz de la Torre and Ruiz del Castillo, Ecología 6: 103 fig. 2(1992), pro sp.

T. granatensis Boiss. subsp. *granatensis* x *T. serpylloides* subsp. *gadorensis* (Pau) Jalas

T. granatensis Boiss. subsp. *granatensis* x *T. orospedanus* Huguet del Villar
T. x mariae Socorro, Arrébola and Espinar, Lagascalia 16(1): 121 (1991)

T. hyemalis Lange x *T. mastichina* (L.) L. subsp. *mastichina*
T. x mastichinalis Sánchez Gómez and Sáez in Sáez, Sánchez Gómez and Morales, Anales Jard. Bot. Madrid 51(1): 158 (1993)

T. hyemalis Lange x *T. moroderi* Pau ex Martínez
T. x diazii Alcaraz, Rivas Martínez and Sánchez Gómez, Itinera Geobot. 2: 118 (1989)

T. hyemalis Lange x *T. vulgaris* subsp. *aestivus* (Reuter ex Willk.) O. Bolós and A. Bolós

T. hyemalis Lange x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x enicensis Blanca, Cueto, Gutiérrez and Martínez, Folia Geobot. Phytotax. 28(2): 138 fig. 2 (VIII-1993)

T. x sorianoi Sáez and Sánchez Gómez in Sáez, Sánchez Gómez and Morales, Anales Jard. Bot. Madrid 51(1): 158 (XII-1993)

T. lacaitae Pau x T. vulgaris L. subsp. *vulgaris*
T. x armuniae R. Morales, Anales Jard. Bot. Madrid 41(1): 94 (1984)

T. lacaitae Pau x *T. zygis* subsp. *sylvestris* (Hoffmanns. and Link) Coutinho
T. x arcuatus R. Morales, Anales Jard. Bot. Madrid 41(1): 93 (1984)

T. leptophyllus subsp. *izcoi* (Rivas Martínez, Molina and Navarro) R. Morales x *T. mastichina* (L.) L. subsp. *mastichina*
T. x celtibericus Pau, Mem. Real. Soc. Esp. Hist Nat. 15: 71 (1929)

T. leptophyllus subsp. *izcoi* (Rivas Martínez, Molina and Navarro) R. Morales x *T. vulgaris* L. subsp. *vulgaris*
T. x moralesii nothosubsp. *navarroi* (Mateo and M. B. Crespo) R. Morales, Anales Jard. Bot. Madrid 53(2): 208 (1995)
T. x navarroi Mateo and M. B. Crespo, Rivasgodaya 7: 132 (1993)

T. leptophyllus Lange subsp. *leptophyllus* x *T. mastichina* (L.) L. subsp. *mastichina*
T. x celtibericus nothosubsp. *bonichensis* (Mateo and M. B. Crespo) R. Morales, Anales Jard. Bot. Madrid 53(2): 202 (1995)
T. x bonichensis Mateo and M. B. Crespo, Thaiszia, Kosice 3(1): 5 fig. 1 (1993)

T. leptophyllus Lange subsp. *leptophyllus* x *T. vulgaris* L. subsp. *vulgaris*
T. x moralesii nothosubsp. *cistetorum* Mateo and M. B. Crespo, Anales Jard. Bot. Madrid 49(2): 288 (1992)

T. leptophyllus Lange subsp. *leptophyllus* x *T. zygis* Loefl. ex L. subsp. *zygis*
T. x xilocae Mateo and M. B. Crespo, Anales Jard. Bot. Madrid 49(2): 289 (1992)

T. leptophyllus subsp. *paui* R. Morales x *T. pulegioides* L.
T. x benitoi Mateo, Mercadal and Pisco, Bot. Complutensis 20: 70 fig. 1 (1996)

T. leptophyllus subsp. *paui* R. Morales x *T. vulgaris* L. subsp. *vulgaris*
T. x moralesii Mateo and M. B. Crespo in Mateo, Cat. Fl. Teruel: 234 (1990)

T. longiflorus Boiss. x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x ruiz-latorrei C. Vicioso in Ruiz del Castillo, Anales Inst. Nac. Invest. Agrar., Ser. Rec. Nat. 1: 31 lam. 16 (1974), pro sp.

T. loscosii Willk. x *T. mastichina* (L.) L. subsp. *mastichina*
T. x riojanus Uribe-Echebarría, Est. Mus. Ci. Nat. Alava 5: 67 fig. 1 (1990)

T. loscosii Willk. x *T. vulgaris* L. subsp. *vulgaris*
T. x rubioi Font Quer, Treb. Mus. Ci. Nat. Barcelona, Ser. Bot. 3: 215 (1920)

T. lotocephalus G. López and R. Morales x *T. mastichina* subsp. *donyanae* R. Morales
T. x mourae Paiva and Salgueiro, Anales Jard. Bot. Madrid 52(1): 114 fig. 1 (1994)

T. mastichina (L.) L. subsp. *mastichina* x *T. mastigophorus* Lacaita
T. x ibericus Sennen and Pau in Sennen, Bull. Acad. Int. Géogr. Bot. 18 (229): 461 (1908)

T. mastichina (L.) L. subsp. *mastichina* x T. *orospedanus* Huguet del Villar
T. x mixtus Pau, Carta Bot. 3: 7 (1906)

T. mastichina (L.) L. subsp. *mastichina* x *T. praecox* subsp. *britannicus* (Ronniger) Holub
T. x genesianus Galán Cela, Anales Jard. Bot. Madrid 45(2): 562 fig. 1 (1989)

T. mastichina (L.) L. subsp. *mastichina* x *T. pulegioides* L.
T. x sennenii Pau, Bol. Soc. Aragonesa Ci. Nat. 6: 29 (1907)
T. jovinieni Sennen and Pau in Pau, op. cit.

T. mastichina (L.) L. subsp. *mastichina* x *T. serpylloides* subsp. *gadorensis* (Pau) Jalas
T. x hieronymi Sennen, Diagn. Nouv. Pl. Espagne Maroc: 92 (1936)

T. mastichina (L.) L. subsp. *mastichina* x *T. serpylloides* Bory subsp. *serpylloides*
T. x hieronymi nothosubsp. *hurtadoi* (Socorro, Molero Mesa, Casares and Pérez Raya) R. Morales, Anales Jard. Bot. Madrid 43(1): 39 (1986)
T. x hurtadoi Socorro, Molero Mesa, Casares and Pérez Raya, Trab. Dep. Bot. Univ. Granada 6: 109 (1981)

T. mastichina (L.) L. subsp. *mastichina* x *T. villosus* subsp. *lusitanicus* (Boiss.) Coutinho
T. x toletanus Ladero, Anales Inst. Bot. Cavanilles 27: 97 fig. 6 (1970)

T. mastichina (L.) L. subsp. *mastichina* x *T. vulgaris* L. subsp. *vulgaris*
T. x eliasii Sennen and Pau in Sennen, Bol. Soc. Ibérica Ci. Nat. 32: 79 (1933); in Pau, Cavanillesia 4: 55 (1931), nom. inval.

T. mastichina (L.) L. subsp. *mastichina* x *T. zygis* subsp. *sylvestris* (Hoffmanns. and Link) Coutinho
T. x brachychaetus (Willk.) Coutinho, Bol. Soc. Brot. 23: 79 (1907), pro var.

T. mastichina var. *brachychaetus* Willk. in Willk. and Lange, Prodr. Fl. Hispan. 2: 400 (1968)
T. x mixtus var. *toletanus* Pau, Bol. Soc. Aragonesa Ci. Nat. 15: 160 (1916)

T. mastichina (L.) L. subsp. *mastichina* x *T. zygis* Loefl. ex L. subsp. *zygis*

T. mastigophorus Lacaita x *T. vulgaris* L. subsp. *vulgaris*
T. x severianoi Uribe-Echebarría, Est. Mus. Ci. Nat. Alava 5: 69 figs. 3a y 4b (1990)

T. mastigophorus Lacaita x *T. zygis* Loefl. ex L. subsp. *zygis*
T. x zygophorus R. Morales, Anales Jard. Bot. Madrid 41(1): 93 (1984)

T. membranaceus Boiss. x *T. moroderi* Pau ex Martínez

T. membranaceus Boiss. x *T. orospedanus* Huguet del Villar
T. x beltranii Socorro, Espinar and Arrébola, Lagascalia 17(1): 186 (1993)

T. membranaceus Boiss. x *T. vulgaris* L. subsp. *vulgaris*
T. x guerrae Sáez and Sánchez Gómez in Sáez, Sánchez Gómez and Morales, Anales Jard. Bot. Madrid 51(1): 157 (1993)

T. membranaceus Boiss. x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x almeriensis G. López and R. Morales, Anales Jard. Bot. Madrid 41(1): 94 (1984)

T. moroderi Pau ex Martínez x *T. vulgaris* L. subp. *vulgaris*
T. x carrionii Sáez and Sánchez Gómez in Sáez, Sánchez Gómez and Morales, Anales Jard. Bot. Madrid 51(1): 157 (1993)

T. moroderi Pau ex Martínez x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x martinezii Pau ex Martínez, Mem. Real Soc. Esp. Hist. Nat. 14: 467 fig. 7 (1934), pro sp.

T. funkii var. *martinezii* (Pau ex Martínez) C. Vicioso, Anales Inst. Nac. Invest. Agrar., Ser. Rec. Nat. 1: 19 (1974)
T. capitatus Lag., Elench. Pl.: 18 (1816), non (L.) Hoffmanns. and Link (typus: MA 106457)
T. villosus sensu Willk., Suppl. Prodr. Fl. Hispan.: 146 (1893)

T. orospedanus Huguet del Villar x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x jimenezii Socorro, Arrébola and Espinar, Lagascalia 16(1): 122 (1991)

T. piperella L. x *T. vulgaris* subsp. *aestivus* (Reuter ex Willk.) O. Bolós and A. Bolós
T. x josephi-angeli Mansanet and Aguilella, Mediterránea, Ser. Biol. 8: 84 (1985)

T. piperella L. x *T. vulgaris* L. subsp. *vulgaris*
T. x josephi-angeli nothosubsp. *edetanus* Mateo, M. B. Crespo and Laguna, Anales Jard. Bot. Madrid 49(1): 140 fig. 1 (1991)

T. pulegioides L. x *T. vulgaris* L. subsp. *vulgaris*
T. x carolipaui Mateo and M. B. Crespo in Mateo, Cat. Fl. Teruel: 232 (1990)

T. pulegioides L. x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales

T. pulegioides L. x *T. zygis* Loefl. ex L. subsp. *zygis*
T. x viciosoi Pau ex R. Morales, Anales Jard. Bot. Madrid 53(2): 210 (1995)
T. x viciosoi (Pau) R. Morales, Anales Jard. Bot. Madrid 43(1): 41 (1986), comb. inval.
T. bracteatus f. *viciosoi* Pau, Bol. Soc. Aragonesa Ci. Nat. 15: 159 (1916), nom. inval.

T. serpylloides subsp. *gadorensis* x *T. vulgaris* subsp. *aestivus*
T. x aitanae nothosubsp. *dominguezii* (Socorro and Arrébola) R. Morales, Anales Jard. Bot. Madrid 53(2): 200 (1995)
T. x dominguezii Socorro and Arrébola, Lagascalia 17(2): 355 (1995)

T. serpylloides subsp. *gadorensis* x *T. vulgaris* subsp. *vulgaris*
T. x aitanae Mateo, M. B. Crespo and Laguna, Anales Jard. Bot. Madrid 49(1): 142 fig. 3 (1991)

T. serpylloides subsp. *gadorensis* (Pau) Jalas x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x pastoris Socorro and Arrebola, Lagascalia 17(2): 353 (1995)

T. vulgaris L. subsp. *vulgaris* x *T. zygis* Loefl. ex L. subsp. *zygis*
T. x monrealensis Pau ex R. Morales, Anales Jard. Bot. Madrid 41(1): 93 (1984)
T. x monrealensis Pau, Mem. Real Soc. Esp. Hist. Nat. 15: 71 (1929), nom. inval. sine descr.

T. vulgaris L. subsp. *vulgaris* x *T. zygis* subsp. *gracilis* (Boiss.) R. Morales
T. x monrealensis nothosubsp. *garcia-vallejoi* Sánchez Gómez, Alcaraz and Sáez, Anales Jard. Bot. Madrid 49(2): 289 (1992)

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