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STUDIES IN THE THYMELAEACEAE II:* a revision of the genus Thymelaea

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ABSTRACT. In a taxonomic revision of the genus *Thymelaea* 4 sections, 7 subsections (5 new) and 30 species are recognized. Keys, important synonyms, descriptions and diagnoses are given, supplemented by distribution maps. Two taxa are raised to subspecific rank (*T. tinctoria* subsp. *nivalis* (Ramond) K. Tan, *T. virgata* subsp. *broussonetii* (Ball) K. Tan) and the infraspecific combinations *T. pubescens* subspp. *thesioides* (Lam.) K. Tan and *elliptica* (Boiss.) K. Tan are made. The infraspecific classification of *T. tartonraira* is completely reassessed, resulting in a new variety, subsp. *argentea* var. *linearifolia* K. Tan and a new combination, subsp. *tartonraira* var. *transiens* (Briq.) K. Tan. Vegetative structure, sex distribution and floral biology are also described. Diagnostic features of the related genera are tabulated.

CONTENTS

* Studies in the Thymelaeaceae I. *Notes R.B.G. Edinb.* 38:149–164.

DELIMITATION OF THE GENUS

It is well known that in the Thymelaeaceae generic limits are often arbitrary and based on tradition. Many genera are separated by only one diagnostic character. Peterson (cited in Ding Hou, 1960) states that 'limits in the African genera are in some cases so vague that it is easy to give a specific epithet but very difficult to come to a decision on the generic name'. In order to give a satisfactory definition of *Thymelaea* it is necessary to examine the genera most closely related to it: *Daphne, Wikstroemia* and *Restella* (see Table 1 for comparison of characters).

Daphne L. contains approximately 70 species. It is characterized by fleshy fruits which are naked at maturity, an annular hypogynous disc with entire margins, a perianth tube which does not separate into an upper and lower part after anthesis, and alternate leaves (although rare exceptions to most of these characters occur).

Wikstroemia Endl. with approximately 90 species is closely related to *Daphne*. It is often characterized by opposite or subopposite leaves and a hypogynous disc unequally divided into 2–5 segments. However, as a number of its species have characters previously considered to be diagnostic of *Daphne*—such as alternate leaves, a cup-shaped disc, an inflorescence axis not elongating in fruit, absence of bracts and a deciduous or persistent perianth—the status of *Wikstroemia* as a separate genus is open to question. At the moment both genera are maintained, but a study of the whole family, especially species of *Daphne* and *Wikstroemia* from the subtropics and E Asia, is necessary in order to circumscribe the genera.

Restella is a monotypic genus and its species, *R. albertii*, was first described under *Stellera* by Regel in 1886. Pobedimova (1941) transferred it to a new genus *Restella*, emphasising the persistence of the perianth (which remains entire without transverse splitting) and the much-branched shrubby habit, as contrasted with the suffrutescence of *Stellera*, as the main distinguishing characters. Domke (1932,34) united *Stellera* and *Wikstroemia* and thus made the new combination *Wikstroemia albertii* (Regel) Domke—even if this taxonomic decision were sound, *Stellera* L. (1753) has priority over *Wikstroemia* Endl. (1833). However, *Wikstroemia* is a fairly large and widespread genus showing considerable character variation and the characters regarded as diagnostic of *Restella* (inflorescence remaining subumbellate instead of becoming laxly racemose, persistent perianth and dry, non-fleshy fruit) also occur in *Wikstroemia*. Since there are no consistent and clear-cut differences between *Restella* and *Wikstroemia*, I suggest that *Restella* should not be re-established. Its merger with the earlier name *Wikstroemia* is therefore proposed and the previous inadvertent combination by Domke must be reinstated, although the reader must bear in mind that *Wikstroemia* and *Stellera* are two quite distinct genera.

Thymelaea is more closely related to *Daphne* than to the other neighbouring genera and can be distinguished from it by the persistent, rarely deciduous, perianth, the absence of a disc (or presence of only a very minute structure), the style often becoming subterminal in fruit, and the membranous, never fleshy or semi-coriaceous, pericarp (see Table 1).

The annual and woody members of *Thymelaea* are linked by an intermediate group of suffrutescent perennials which include the type of the

TABLE 1

Characters in *Thymelaea* and related genera

		Thymelaea	*Daphne*	*Wikstroemia*	*Restella*
1.	Annuals	+			
	Herbaceous or suffrutescent perennials	+			
	Shrubs	+	+	+	+
2.	Leaves alternate	+	+	+	+
	opposite		rarely	+	+
3.	Inflorescence axis elongating in fruit			+	
	not elongating	+	+	+	+
4.	Bracts present	+	+		
	absent	+	+	+	+
5.	Flowers unisexual	+		+	
	hermaphrodite	+	+	+	+
6.	Perianth persistent	+	rarely	+	+
	deciduous	rarely	+	+	
7.	Perianth lobes 4; stamens 8	+	+	+	+
	lobes 5; stamens 10			+	
8.	Hypogynous disc annular		+		
	cup-shaped		+	+	
	divided into 2–5 segments			+	+
	absent/rudimentary	+			
9.	Style terminal in fruit	rarely	+	+	+
	subterminal	+			
10.	Pericarp membranous at maturity	+		+	+
	semi-coriaceous		rarely	+	
	fleshy		+	+	
11.	Internal phloem fibres in stem present	+	+		
	absent	+	+	+	+
12.	Leaves amphistomatic	+	+	+	+
	epistomatic	+			
	hypostomatic		+	+	
13.	Sclereids present in leaf	+	+		
	absent		+	+	+

genus, *T. sanamunda* (L.) All. Despite the distinctness of the annual habit and the floral and vegetative characters associated with it, these cannot be used to warrant generic separation as some of the characters break down in the suffrutescent group. The maintenance of *Ligia* as a separate genus for the annuals by Fasano (1788) is thus not upheld, but the group (including some perennials) is reduced to sectional rank.

Thymelaea sect. *Ligia* is not closely allied to the genus *Diarthron* Turcz. *Thymelaea* always has a perianth which remains as a single unit in fruit, an inflorescence which does not elongate after anthesis, and in sect. *Ligia* two conspicuous bracts. *Diarthron*, on the other hand, has a perianth with a

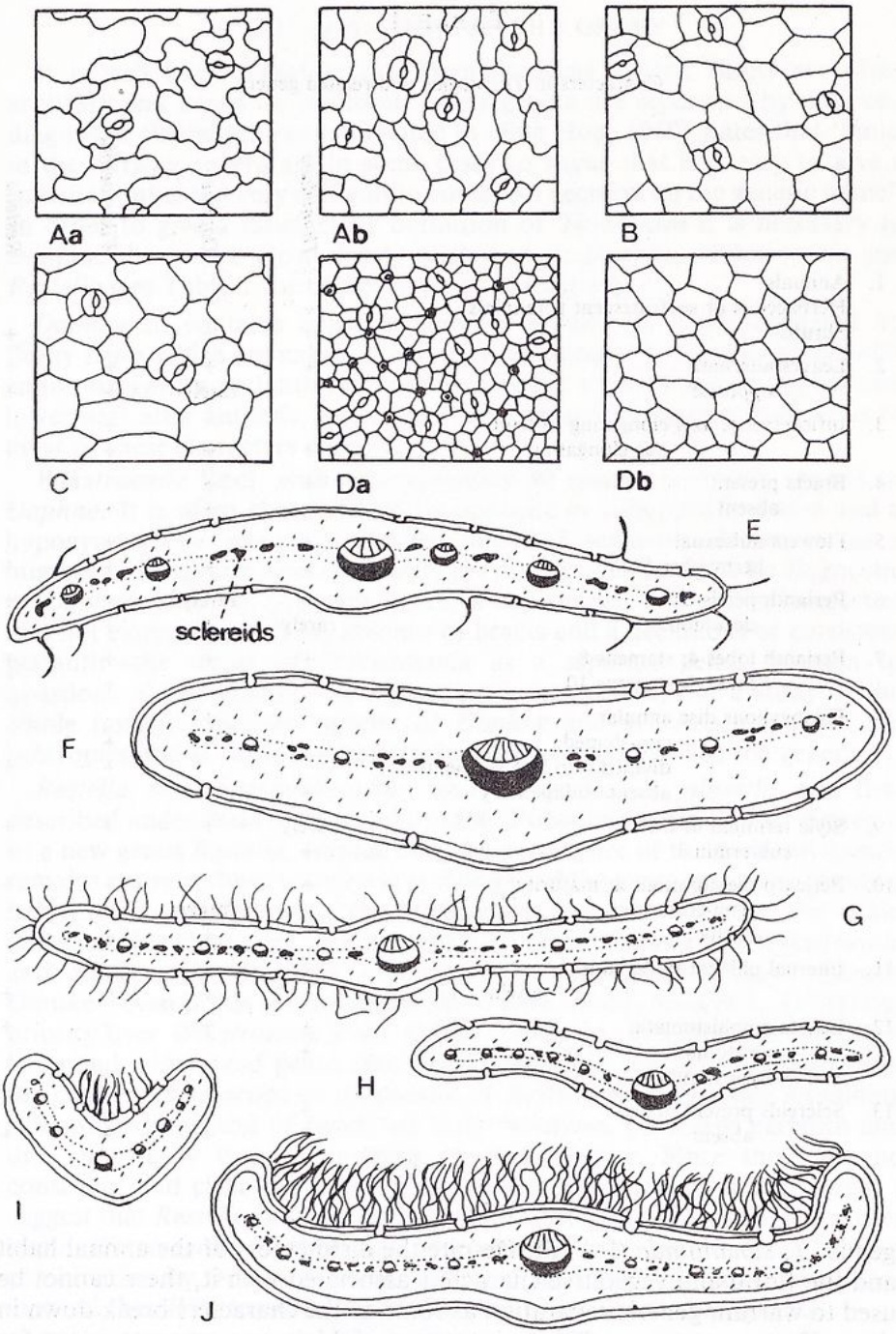

FIG. 1. A–D, leaf epidermal peels (× 410). A, *T. passerina*, anisocytic stomata: a, adaxial, b, abaxial; B, *T. sanamunda* & C, *T. villosa*, modified tetracytic, both adaxial; D, *T. lythroides*, anomocytic, from flowering shoot: a, adaxial, b, abaxial. E–H, amphistomatic leaves in T.S.: E, *T. villosa* (× 25); F, *T. tinctoria* subsp. *tinctoria* (× 25); G, *T. velutina* (× 28); H, *T. aucheri* (× 36). I & J, epistomatic leaves in T.S.: I, *T. broteriana* (× 36); J, *T. hirsuta* (× 28).

persistent basal half and deciduous upper portion and an ebracteate racemose inflorescence which elongates in the fruiting stage.

VEGETATIVE ANATOMY

Older literature on the anatomy of vegetative parts of *Thymelaea* has been summarized by Solereder (1908) and Metcalfe & Chalk (1950) though special mention should be made of the investigations of van Tieghem (1893), Supprian (1894) and Leandri (1930) which were based on the family as a whole throughout its geographical range. Of the three, Leandri's account is the most comprehensive and briefly mentions five species—*hirsuta, argentata* (as *T. nitida*), *dioica*, *pubescens* (as *T. elliptica*) and *passerina*. Further and more recent observations on *T. hirsuta* are provided by Fahn & Sarnat (1963, wood structure), Saleh & Sarg (1966, stem and leaves) and Fahn (1974). A comparatively detailed study on *T. tartonraira* has been made by Crouzet (1967). All other species have received little attention.

A comparative study of the anatomy of stem and leaf in all species of *Thymelaea* was carried out and the results for the most important diagnostic characters are summarized in Table 2. Notes on stomata and venation are given below and detailed information is given in Tan (1978).

LEAF STOMATA. Stomata are present in both epidermides (leaf amphistomatic, Figs 1 E–H) or are confined to the adaxial surface only (leaf epistomatic, Figs 1 I & J). Stomatal distribution is a specific and sectional character apparently uncorrelated with habitat. Only two species-groups are epistomatic: sect. *Piptochlamys* subsect. *Hirsutae* and three members of sect. *Chlamydanthus* subsect. *Coridifoliae*.

Three stomatal types based on the number of subsidiary cells as seen in surface view can be distinguished, viz. anomocytic (Fig. 1 D), anisocytic (Figs 1 Aa & Ab) (after Metcalfe & Chalk, 1950) and modified tetracytic (Figs 1 B & C). The latter have the stoma accompanied by four subsidiary cells of which one, parallel to the long axis of the pore, is longer or shorter than the guard cells and smaller than the other three. Hexacytic stomata (Tomlinson, 1969), as found in the genus *Daphne*, do not occur in *Thymelaea*. It is sometimes difficult to differentiate the anomocytic and the modified tetracytic types especially when the small subsidiary cell of the latter becomes enlarged. However, the surrounding cells of the tetracytic type usually have denser cytoplasmic contents. The anisocytic pattern is represented in the fruticose and suffrutescent members, with a gradual change over to the anisocytic condition in the annuals and herbaceous perennials. Stomata are sunken or flush with the epidermis, randomly oriented and distributed, though noticeably fewer over costae.

VENATION. In *Thymelaea*, venation is basically eucamptodromous, i.e. secondary veins are upturned, not terminating at margins. In *T. tartonraira* subsp. *tartonraira* var. *tartonraira* venation is near-actinodromous, basal reticulate, i.e. there are three or more primary veins from a basal initial point running ± parallel to the main vein, and then diverging radially towards, but not reaching the margin (Fig. 2 C). Development is considered as perfect, since the veins cover at least two-thirds of the lamina.

TABLE 2

Comparison of some anatomical characters of leaf and stem in *Thymelaea*

x = feature always present (well-developed)
s = feature sometimes present
\+ = feature moderately present
w = feature weakly developed
blank = absent

Species	Leaf: Stomatal distribution		Stomatal type			Anticlinal walls of epidermis: adaxial straight	adaxial undulate	abaxial straight	abaxial undulate	Sclereid distribution: throughout	Sclereid distribution: apical	Young stem: Indumentum	Young stem: Internal phloem fibres	Young stem: Stomata	Old Stem: Cork	Old Stem: Chlorenchyma	Old Stem: 2° phloem rays dilated	Old Stem: Internal phloem fibres
	amphistomatic	epistomatic	anomocytic	modified tetracytic	anisocytic													
Sect. *Piptochlamys*																		
Subsect. *Hirsutae*																		
1. T. lythroides		x	x	x		x		x		x	+	x	+		x		x	+
2. T. hirsuta		x		x		x		x		x	+	x	+		x		x	+
3. T. lanuginosa		x		x		x		x		x	w	x			x		x	
4. T. gattefossei		x		x		x		x		x	w	x	+		x		x	+
Subsect. *Argentatae*																		
5. T. argentata	x		x	x		x		x		x	+	x	x		x		x	x
6. T. virescens	x		x	x		x			x	x	+	x	x		x		x	x
7. T. putorioides	x		x	x	x	x		x		x	w	x	x		x			x
Subsect. *Sempervirentes*																		
8. T. microphylla	x		x	x		x		x		x	w	x	x	x	+	x		x
9. T. sempervirens	x		x	x		x		x		x	+		x	x	+	x		x
Sect. *Chlamydanthus*																		
Subsect. *Tartonraira*																		
10. T. tartonraira	x		x	x		x		x		x	+	s			x			
11. T. velutina	x		x	x		x		x		x	+	x			x			
12. T. dioica	x		x			x	s	s	x	w	w				x			
Subsect. *Coridifoliae*																		
13. T. tinctoria	x		x	x		x		x		x	+	x			x		x	
14. T. subrepens	x		x	x		x	s	x	s	x	w	x			x			
15. T. procumbens	x		x			x		x		x	w	x			x		x	
16. T. ruizii	x		x			x		x		w	w	x			x		x	
17. T. calycina		x	x			x		x		x	w	x			x		x	
18. T. coridifolia		x	x			x		x		x	w	x			x			
19. T. broteriana		x	x			x		x		x	w	x			x		x	
Sect. *Thymelaea*																		
Subsect. *Antiatlanticae*																		
20. T. antiatlantica	x		x	x		s	s	s	s	x	w	x	x	x	+			x
21. T. virgata	x			x		s	s	s	s	x	w	x	x	x	+	x		x

Subsect. *Sanamunda*																		
22. T. villosa	x		x	x		x		x		x	w	x			x			
23. T. pubescens	x		x	x			x		x	x	w	x	x	x	+	x		x
24. T. sanamunda	x		x	x		x		x		x	+	s	x	x	+	x		x
Sect. *Ligia*																		
25. T. cilicica	x			x	x		x		x	x	w		w	x		x		+
26. T. aucheri	x			x	x		x		x	x	w		x	x		x		x
27. T. passerina	x			x	x		x		x	x	x		x	x		x		x
28. T. gussonei	x			x	x		x		x	x	x	x	x	x		x		x
29. T. salsa	x			x	x		x		x	x	+			x		x		
30. T. mesopotamica	x			x	x		x		x	x	+	x		x		x		

Three venation types can be distinguished on divergence angle of secondary veins: (1) angle of lowest (lower) pair(s) of veins more acute than those above (Fig. 2 A); (2) angle of veins at apex or those in *upper* half of leaf less acute than the lower (Figs 2 B & C); (3) divergence angle nearly uniform (Fig. 2 D). Type 1 is characteristic of sect. *Ligia*; type 2 occurs mainly in sect. *Piptochlamys* and sect. *Chlamydanthus*, while all three types are present in sect. *Thymelaea*. Divergence angle and type and density of higher order reticulation are surprisingly constant characters for a given species, and not dependent on developmental stages or size at maturity.

Detailed studies of floral morphology and anatomy of Thymelaeaceae have been made as part of the present investigation. Much of the information, however, is not strictly relevant to the present revision and it has been decided to reserve it for a later publication. Embryology will also be dealt with in the same publication as will various other aspects.

SEX DISTRIBUTION

The sex distribution occurring in the species of *Thymelaea* is listed below.

1. All flowers hermaphrodite: *T. passerina*.

2. All flowers unisexual:

   A. Dioecious or near dioecious species (in the latter case with occasional flowers of the opposite sex present): *T. lythroides, T. gattefossei, T. velutina, T. dioica, T. tinctoria, T. subrepens, T. procumbens, T. ruizii, T. calycina, T. coridifolia, T. broteriana, T. antiatlantica, T. villosa, T. pubescens, T. sanamunda.*

   B. Monoecious species:
      i. Both pistillate and staminate flowers in the same cluster: *T. putorioides, T. microphylla, T. sempervirens.*
      ii. Pistillate and staminate flowers always in separate clusters: *T. cilicica, T. aucheri, T. salsa, T. mesopotamica.*

3. Both hermaphrodite and unisexual flowers occurring:
   A. Gynodioecious species, i.e. some plants with hermaphrodite flowers, others with pistillate flowers only: *T. lanuginosa, T. argentata**—in the latter female plants apparently flower later (June) than the hermaphrodites (late April and May).

* But see 3 E

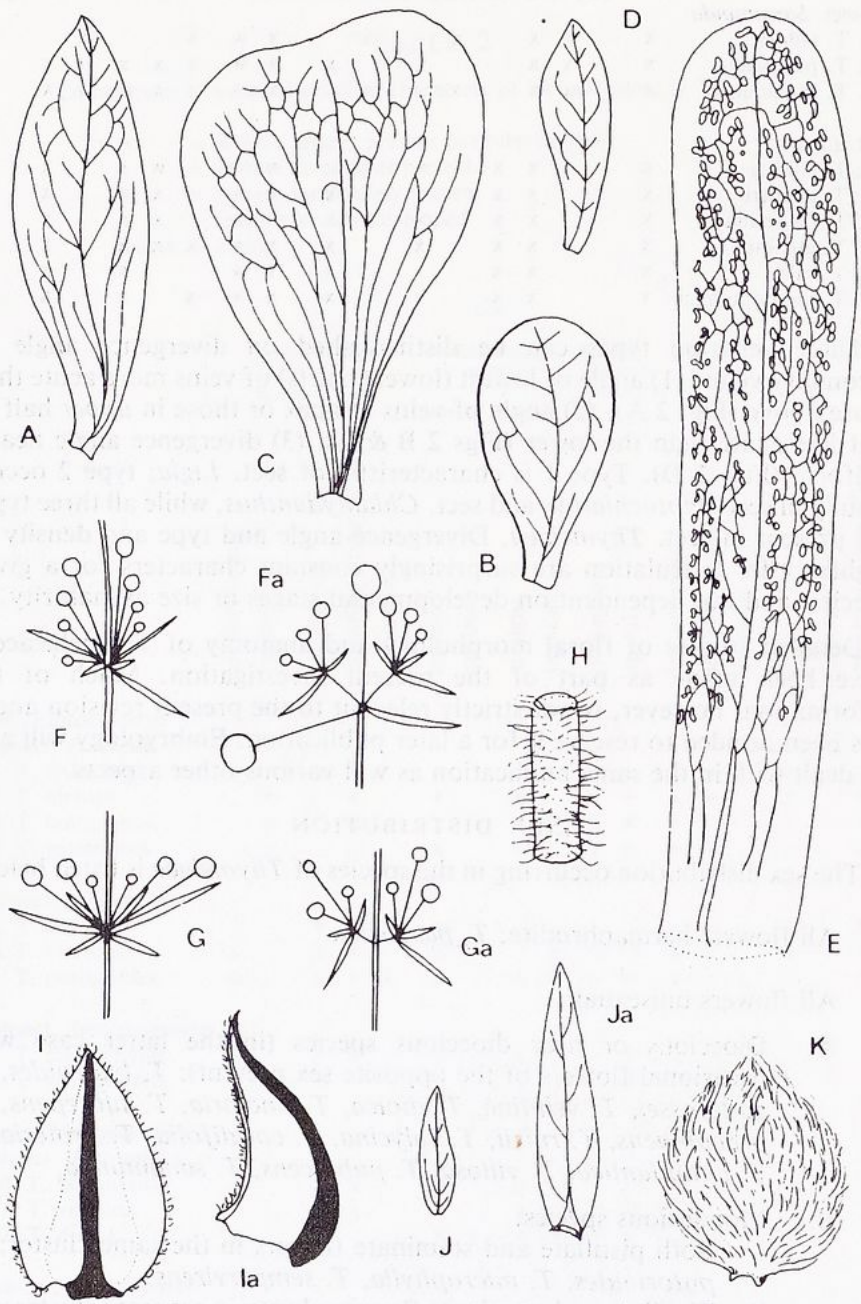

FIG. 2. A–D, cleared leaves to show secondary venation types (× 4·5): A, *T. sanamunda* (Type 1); B, *T. velutina* & C, *T. tartonraira* subsp. *tartonraira* var. *tartonraira* (both Type 2); D, *T. virescens* (Type 3). E, *T. tinctoria* subsp. *tinctoria*, showing sclereid distribution (× 45). F & G, *T. virgata* subsp. *virgata* (diagrammatic): F, flower cluster from lower part of inflorescence; Fa, the same dissected to show cymose arrangement, youngest flowers furthest from axis (axes elongated for clarification); G, cluster from near apex; Ga, the same dissected, youngest flowers nearest to axis. H, *T. pubescens* subsp. *elliptica*, stem hispid-pubescent (× 5). I & Ia, *T. tinctoria* subsp. *nivalis*, bract, abaxial and lateral views (× 20). J & Ja, *T. dioica* subsp. *dioica*, innermost and outermost bracts, abaxial view (× 10). K, *T. tartonraira* subsp. *tartonraira* var. *tartonraira*, inner bract, abaxial view (× 10).

B. Androdioecious species, i.e. some plants with hermaphrodite flowers, others with staminate only: *T. virescens, T. virgata.*

C. Trimonoecious species, i.e. with hermaphrodite, staminate and pistillate flowers on the same plant but the hermaphrodites and one of the sexes so rare that the plant is functionally dioecious: *T. hirsuta, T. tartonraira.*

D. Andromonoecious species, i.e. with hermaphrodite and staminate flowers in the same plant: *T. gussonei.*

E. Polygamous forms—some plants of *T. argentata* (already listed as a gynodioecious species) have 4–9 flowers in the same cluster of which 1 or 2 are pistillate and the rest hermaphrodite. Staminate flowers are rarer, occurring in separate clusters.

In staminate flowers of *Thymelaea* a rudimentary, non-functional ovary is present in some species but completely absent in others. Gerber (1900) records the presence of staminodes in pistillate flowers of *T. hirsuta* but I have never observed staminodes in *Thymelaea.* I have observed 12 stamens inserted at different levels in *T. hirsuta* (Fig. 4 B) and 4 (half the full complement due to absence of the upper whorl) in *T. aucheri* from Lebanon. Nalepa (1900) described an Acarine parasite, *Eriophyses passerinae* (Eriophysidae) which has been suggested as responsible for the hypertrophy of stamens in *T. hirsuta.*

As shown above, dioecism occurs more frequently in *Thymelaea* than any other sex form.

FLORAL BIOLOGY, ETC.

As a corolla is absent the tubular perianth with its imbricate lobes has the dual function of protection and attraction. It persists in post-floral stages as a membranous envelope enclosing the fruit. The latter sometimes (in *T. lythroides*) or ultimately (*T. hirsuta*) becomes free of it on ripening. There is a tendency towards condensed grouping of flowers in axillary clusters, umbellate or subumbellate heads, presumably to make them more conspicuous to pollinators.

Nectar and scent are not obviously present though field notes mention *T. lanuginosa* as being 'sweetly fragrant'. Several species of small insect are often retained within the perianth tube at the time of collecting and pressing. Dissection of herbarium material sometimes show insects on the stigma itself. A few beetles have been identified with the help of the Entomology Section, Royal Scottish Museum, as species of *Cartodere* and *Macrophagus.* These would be of some value as pollinators, as would the tiny beetles observed to be frequent visitors to *T. hirsuta* and *T. tinctoria* in the field.

The flowers in sect. *Ligia* are rather small and insignificant with a greenish or pale yellow perianth. No insects were observed visiting cultivated material of *T. passerina* in the greenhouse, yet seed set is high. Presumably self-pollination occurs as the introrse anthers are situated above the stigma, and the stigmatic papillae are covered with pollen grains. The species is not apomictic: when the stamens were removed, the ovary did not develop.

Pollen grains are trinucleate when shed and those from the same anther often show a clear dimorphism which has never been recorded previously in the family. This phenomenon is particularly marked in *T. cilicica* (sect. *Ligia*), an endemic, monoecious, herbaceous perennial, in which the ratio of small grains (mean diam. 22 μm) to large grains (35 μm) is c. 1:1. The smaller grains are not immature or sterile; they take up stain strongly, while the larger grains stain more lightly. In other species of sect. *Ligia* 9–28% of the pollen is smaller than the rest. The proportion of smaller grains in the other three sections is 5–25%, the larger grains being approximately twice the diameter of the smaller ones. The significance of the pollen dimorphism is not understood; in some species it might be related to different types of pollen being specialized for pollination of hermaphrodite and female flowers—however, unlike the cases known in Plumbaginaceae, no obvious differences in the morphology of the stigmatic papillae of the two types of flowers have been observed, and further investigation is required.

Clearly occurrence of unisexual flowers, dioecism and an abundance of sex forms indicates that *Thymelaea* is a genus adapted to outbreeding. However, one species, *T. passerina*, which is a wide-ranging steppic annual provides a sharp contrast. It appears to be adapted to inbreeding and has tiny hermaphrodite flowers, almost homomorphic pollen, a mechanism ensuring occurrence of self-pollination (see p. 197), and a lower pollen output than occurs in other species—c. 240 grains per hermaphrodite flower, as opposed, for example, to c. 400 in the staminate flowers of *T. cilicica* belonging to the same section. Such an inbreeding genetic system is well-suited to an annual, colonizing species which has a higher requirement for immediate fitness than for long-term flexibility and also must be able to produce seed in isolated situations.

Cytology

T. microphylla (Reese, 1957), *T. tartonraira* subsp. *thomasii* (Contandriopoulos, 1964) and *T. passerina* (Kuzmanov, 1973; Majovsky *et al.*, 1974) are the only species for which chromosome numbers are available: all are diploids ($2n = 18$).

The majority of the genera in the Thymelaeaceae are still cytologically unknown, those studied (60 taxa in 10 genera, representing c. 10% of the family) all have a base number of $x = 9$ and exhibit little cytological diversity, consistent with the view that the family is a very natural one.

Distribution

The genus occurs only in the northern hemisphere of the Old World, and is mainly Mediterranean in distribution. Two-thirds of the species are narrow endemics, and of the 30 species recognized in this treatment, only 4 may be considered as widespread—*T. passerina, gussonei, hirsuta* and *tartonraira*. The main centres of morphological diversity lie in SW Europe and NW Africa where there is a total of 27 species. Lake Balkash and the Altai Mts are the localities furthest from these centres of distribution where *Thymelaea* species occur.

A brief account of the distribution pattern will now be given (distributions for all species are given in the maps). Sect. *Piptochlamys* subsect. *Hirsutae* has three of its four species endemic in Morocco and the

southernmost part of Spain. Subsect. *Argentatae* is represented in E and S Spain and NW Africa (Morocco to Tunisia), within latitudes 32° and 40° N. The ditypic subsect. *Sempervirentes* is restricted to N Africa, with one of its species confined to a single locality in Tunisia.

Sect. *Chlamydanthus* subsect. *Tartonraira* has one widespread, circum-Mediterranean species showing great variability in leaf form; another species is exclusive to the Balearics; while the third (*T. dioica*) has a rather disjunct distribution in the mountains of SE Spain, the Pyrenees and SW Alps. Subsect. *Coridifoliae* is a well-defined and natural group, unique in possessing solitary, axillary, unisexual flowers subtended by two small, non-green bracts. Within this group, *T. tinctoria* is the only species to show a wider distribution and even then is restricted to E Spain, the Pyrenees and S France. The others all occur in small areas in the mountains of N Spain, Portugal, and the Pyrenees, where rugged topography and the greatest possible diversity of habitats have provided niches favouring speciation and endemism.

The two subsections of sect. *Thymelaea* differ in their distribution as well as in a number of correlated characters. Subsect. *Antiatlanticae* is represented only in NW Africa, whilst subsect. *Sanamunda* with its three species is concentrated in S and E Spain, the Pyrenees, S France and the northernmost tip of Morocco.

Sect. *Ligia* includes six species, four of which are herbaceous annuals. Two of them, *T. salsa* and *T. mesopotamica*, occur in open, semi-arid habitats and appear to be peripheral developments of the common and wide-ranging *T. passerina*. The perennial members, *T. cilicica* and *T. aucheri*, which occur only in SW Asia, may be considered as providing a morphological link between sect. *Ligia* and sect. *Thymelaea*.

In conclusion 17 species, representing all four sections and more than half the total number of known species, occur in the Pyrenees and the Iberian Peninsula. The only section poorly developed in this area is sect. *Piptochlamys* which is represented by two species, *T. hirsuta* and *T. argentata*. In contrast, NW Africa contains 14 species, again representing all four sections. However, five of these species are also distributed in the Iberian Peninsula. But there is only a single member of sect. *Chlamydanthus* in NW Africa, namely *T. tartonraira*.

The revision that follows is based on the examination of c. 1300 herbarium specimens; none is cited but a list is provided at the end of the paper. The material selected for this list covers the range of the taxa and is easily accessible in herbaria; a great number of un-numbered collections especially of the more widely distributed *T. hirsuta, T. tartonraira* and *T. passerina* have not been included. In order to reduce the length of synonym citation, only the basionym and the more important synonyms are given, although other names have often been discovered to be applicable and typifiable. Type material of synonyms has been examined unless indicated by *n.v.*

SYSTEMATIC TREATMENT

Thymelaea Miller, Gard. Dict. Abr. ed. 4 (1754), **nom. cons.**, non Adanson, Fam. 2:285 (1763); from the Greek '*thymos*' and '*elaia*' referring to the thyme-like foliage and olive-like fruits.

Syn.: *Stellera* L., diss. Dassow, Nov. Pl. Gen. (1747), *p.p.*; Amoen. Acad. 1:126 (1749).
Daphne L., Sp. Pl., 356 (1753), *p.p.*
Passerina L., *op. cit.*, 559 (1753), *p.p.*
Sanamunda Adanson, Fam. 2:285 (1763).
Ligia Fasano in Atti Accad. Napoli 1:245 (1788); as '*Lygia*' *apud* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:356 (1843).
Sanamunda Necker, Elem. Bot. 2:179 (1791), sub *Daphne*.
Gastrilia Rafin., Fl. Tellur. 4:105 (1838), *p.p.*
Pausia Rafin., *loc. cit., p.p.*
Tartonia Rafin., Autikon Botanikon, 146 (1840).
Chlamydanthus C. A. Meyer, *op cit.*, 358 (1843).
Piptochlamys C. A. Meyer, *loc. cit.*
Stellera L. emend. Kuntze, Rev. Gen. Pl. 2:585 (1891).
Giardia Gerber in Bull. Soc. Bot. Fr. (sess. extr.):112 (1899).

Type species. *T. sanamunda* All. (syn. *Daphne thymelaea* L., *typ. cons.*). P. Miller described 40 species of which no. 17 is *D. thymelaea*.

Herbaceous annuals, suffrutescent perennials, or low shrubs with tenacious bark, often with tuberculate scars on branches. Leaves simple, entire, exstipulate, alternate, sessile or subsessile, herbaceous or coriaceous, adpressed-imbricate when young. Flowers hermaphrodite or unisexual, axillary or terminal, borne singly or in clusters. Bracts present or absent. Perianth actinomorphic, tubular, infundibular or narrowly urceolate, not constricted above ovary, petaloid, 4-lobed, persistent, rarely deciduous. Stamens 8, in 2 series, adnate to perianth, included or upper whorl semi-exserted. Hypogynous disc minute or absent. Ovary 1-locular, rudimentary in staminate flowers; style short, terminal or becoming subterminal; stigma capitate or discoid, minutely papillose. Fruit indehiscent, 1-seeded, dry.

A genus of 30 species occurring in S and C Europe (most numerous in Iberian peninsula), SW Asia and N Africa. One species is widespread, extending to C Asia.

Taxonomic revision: Brecher, Gy. (1941). A *Thymelaea*—génusz és fajai. *Index Horti Bot. Univ. Budapest.* 5:57–116 (in Hungarian).

HISTORY

The name 'thymelaea' was first used by C. Bauhin in his *Pinax* (1623) for some Mediterranean species of Thymelaeaceae. J. Pitton de Tournefort (1700) characterized but did not define the genus critically. He included species of *Daphne, Passerina* and *Gnidia* as well as those of other, at that time, supposedly related genera. Likewise some species comprising the genus were given binomials and described by Linnaeus under the genera *Daphne, Stellera* and *Passerina* in his *Species Plantarum* (1753). In 1754, the Tournefortian genus *Thymelaea* was validly published in the 4th edition of P. Miller's *Gardeners' Dictionary*.

Thymelaea as referred to by Adanson (1763) is synonymous with *Daphne*. *Ligia*, as circumscribed by Fasano in 1788, includes only the widespread annual, *Thymelaea passerina*. Later works often cite this erroneously as '*Lygia*'. Necker (1791) used *Sanamunda* for species of *Daphne* bearing tubular, not funnel-shaped, flowers and with eight fertile

stamens in two rows, thus including *Thymelaea*. *Tartonia* as coined by Rafinesque (1840) is derived from the name 'Tartonraira'; his concept of the genus was based on *Thymelaea hirsuta* (syn. *Tartonia ovatifolia* Rafin.) and *Thymelaea tartonraira sensu lato* (syn. *Tartonia obovata* Rafin. and *Tartonia cuneifolia* Rafin.) as the chief constituent species. *Chlamydanthus* and *Piptochlamys* were used by C. A. Meyer (*op. cit.*:358), the former to refer to species with persistent, the latter to those with deciduous, perianths.

In 1848, Endlicher separated the Linnaean genus *Passerina* to encompass those species from the S African Cape, whilst *Thymelaea* Endl. and *Ligia* (sphalm '*Lygia*') were limited to species from the Mediterranean region and temperate Asia. His infra-generic classification lists 16 species of *Thymelaea*, the two annual species having been relegated to *Ligia*. *Thymelaea* was divided into two sections, the first of which, sect. *Piptochlamys* (C. A. Meyer) Endl., was distinguished from the second virtually by its deciduous, in contrast to persistent, perianth. The second section, *Chlamydanthus* (C. A. Meyer) Endl. was subdivided into two groups, the first of which corresponds to *Tartonraira* C. A. Meyer. The second, named subsect. *Euthymelaea* Endl. was perhaps based on the suffrutescent habit of three of its species, although this was not stated. Three of Endlicher's 16 species were placed in 'dubiae sectionis'.

Considering the state of knowledge of the genus in Endlicher's time, his groupings are noteworthy. Indeed later classifications, e.g. those by Meissner (1857), Bentham & Hooker (1883) and Gilg (1894), are based on his system. Even the most recent account by Brecher (1941) is basically an elaboration of it, being an enumeration of additional species and complicated by his lumping of putative allies into an unwieldy group, subsect. *Euthymelaea* (Lange) Brecher. However, this more or less stable Endlicher-based classification has definitely aided further work because the sectional and subsectional nomenclature is not chaotic, synonyms being reduced to a minimum.

SYNOPSIS OF SECTIONS AND SPECIES

I. Sect. **Piptochlamys**
Subsect. **Hirsutae**
1. *T. lythroides*
2. *T. hirsuta*
3. *T. lanuginosa*
4. *T. gattefossei*
Subsect. **Argentatae**
5. *T. argentata*
6. *T. virescens*
6a. var. *glaberrima*
7. *T. putorioides*
7a. var. *rhodantha*
Subsect. **Sempervirentes**
8. *T. microphylla*
9. *T. sempervirens*

II. Sect. **Chlamydanthus**
Subsect. **Tartonraira**
10. *T. tartonraira*
10a. subsp. *tartonraira* var. *transiens*
10b. subsp. *argentea* var. *angustifolia*
10c. subsp. *argentea* var. *linearifolia*
10d. subsp. *angustifolia*
10e. subsp. *valentina*
10f. subsp. *thomasii*
11. *T. velutina*
12. *T. dioica*
12a. subsp. *granatensis*

Subsect. **Coridifoliae**
13. *T. tinctoria*
13a. subsp. *nivalis*
14. *T. subrepens*
15. *T. procumbens*
16. *T. ruizii*
17. *T. calycina*
18. *T. coridifolia*
19. *T. broteriana*

III. Sect. **Thymelaea**
Subsect. **Antiatlanticae**
20. *T. antiatlantica*
21. *T. virgata*
21a. subsp. *broussonetii*

Subsect. **Sanamunda**
22. *T. villosa*
23. *T. pubescens*
23a. subsp. *thesioides*
23b. subsp. *elliptica*
24. *T. sanamunda*
24a. var. *pubescens*

IV. Sect. **Ligia**
25. *T. cilicica*
26. *T. aucheri*
27. *T. passerina*
28. *T. gussonei*
29. *T. salsa*
30. *T. mesopotamica*

SECTIONAL CHARACTERS

Habit. Sections *Chlamydanthus* and *Piptochlamys* are woody shrubs; sect. *Thymelaea* consists of semi-shrubby or suffrutescent perennials, while sect. *Ligia* comprises both suffrutescent and annual members. The existence of perennials in the latter group forms a link with sect. *Thymelaea* and reinforces the view that sect. *Ligia* should not be reinstated as a separate genus.

Sex distribution. Members of sections *Chlamydanthus* and *Thymelaea* are always dioecious. In sections *Piptochlamys* and *Ligia*, hermaphrodite and/or unisexual flowers occur. Sex distribution in the genus is further complicated by the existence of trimonoecism, a state in which staminate and pistillate flowers occur on the same plant accompanied by a few true hermaphrodite flowers.

Flower position and number. Sect. *Piptochlamys* is the only section in which all species have flowers terminating leafy shoots. In the rest (*Chlamydanthus, Thymelaea, Ligia*) they are axillary.

Flowers are always clustered in sect. *Piptochlamys*. They are aggregated or solitary in the leaf axil, or very rarely paired, in sect. *Chlamydanthus*. Each of the two subsections of sect. *Thymelaea* shows the single, many- or few-flowered arrangement. Although the flowers in sect. *Ligia* may be secondarily solitary, more often than not they are in fascicles. These are actually condensed cymes and form a well-defined spicate conflorescence (aggregation of inflorescences).

Presence and number of bracts. This feature is useful for grouping some subsections; it is easily perceived in flowering material. Bracts are present or absent, leaf-like, herbaceous, reduced, coriaceous, semi-persistent or deciduous.

Pedicel. Flowers are always sessile in sections *Thymelaea* and *Ligia*. They may be sessile or shortly pedicellate in the other two sections.

Stomatal distribution. Leaves are either amphi- or epistomatic. The latter condition occurs only in sect. *Piptochlamys* subsect. *Hirsutae*, and a small

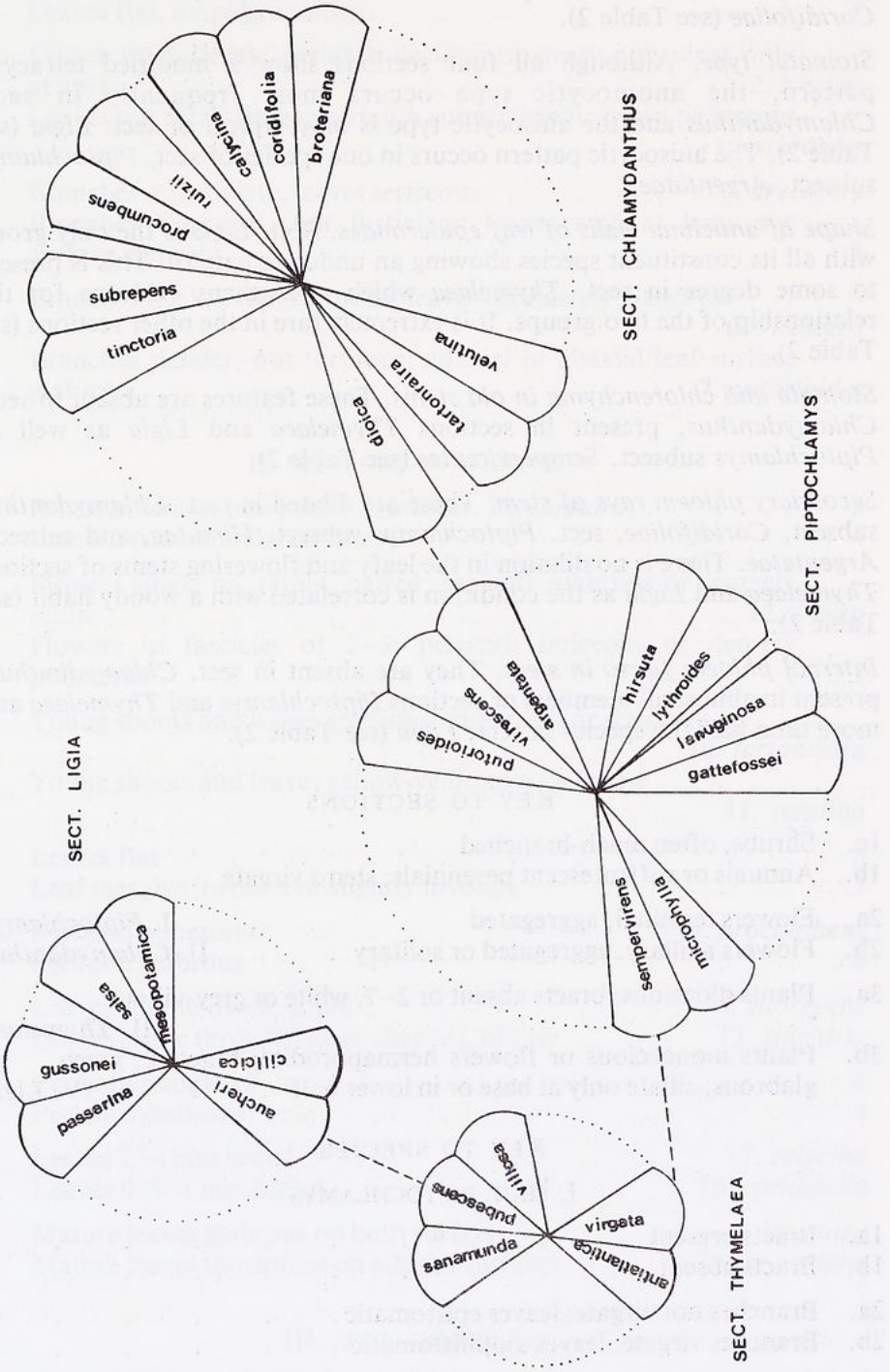

FIG. 3. Inferred overall relationships within the genus *Thymelaea*. The size of the circle denotes the relative size of the section (number of species). Closely related species are contiguous. The broken lines refer to sectional affinities.

group of closely related species within sect. *Chlamydanthus* subsect. *Coridifoliae* (see Table 2).

Stomatal type. Although all four sections show a modified tetracytic pattern, the anomocytic type occurs most frequently in sect. *Chlamydanthus* and the anisocytic type is only typical of sect. *Ligia* (see Table 2). The anisocytic pattern occurs in one species of sect. *Piptochlamys* subsect. *Argentatae.*

Shape of anticlinal walls of leaf epidermides. Sect. *Ligia* is the only group with all its constituent species showing an undulate pattern. This is present to some degree in sect. *Thymelaea* which strengthens evidence for the relationship of the two groups. It is extremely rare in the other sections (see Table 2).

Stomata and chlorenchyma in old stems. These features are absent in sect. *Chlamydanthus*, present in sections *Thymelaea* and *Ligia* as well as *Piptochlamys* subsect. *Sempervirentes* (see Table 2).

Secondary phloem rays of stem. These are dilated in sect. *Chlamydanthus* subsect. *Coridifoliae*, sect. *Piptochlamys* subsect. *Hirsutae*, and subsect. *Argentatae.* There is no dilation in the leafy and flowering stems of sections *Thymelaea* and *Ligia* as the condition is correlated with a woody habit (see Table 2).

Internal phloem fibres in stem. They are absent in sect. *Chlamydanthus*, present in almost all members of sections *Piptochlamys* and *Thymelaea* and more than half the species in sect. *Ligia* (see Table 2).

KEY TO SECTIONS

1a. Shrubs, often much-branched 2
1b. Annuals or suffrutescent perennials; stems virgate 3

2a. Flowers terminal, aggregated . . . . . I. *Piptochlamys*
2b. Flowers axillary, aggregated or solitary . . II. *Chlamydanthus*

3a. Plants dioecious; bracts absent or 2–7, white or grey-villous . III. *Thymelaea*
3b. Plants monoecious or flowers hermaphrodite; bracts 2, green, glabrous, ciliate only at base or in lower half . . IV. *Ligia*

KEY TO SPECIES

I. SECT. PIPTOCHLAMYS

1a. Bracts present 2
1b. Bracts absent 5

2a. Branches not virgate; leaves epistomatic 3
2b. Branches virgate; leaves amphistomatic 4

3a. Bracts 7–10, linear-lanceolate, 6–7 × 1·5 mm . 3. *lanuginosa*
3b. Bracts 3–5, ovate-lanceolate, 3·5–4 × 1·5 mm . 4. *gattefossei*

4a. Leaves sericeous, early-deciduous . . . . 8. *microphylla*
4b. Leaves glabrous, semi-persistent . . . . 9. *sempervirens*

5a. Leaves with involute or slightly involute margins, epistomatic . 6
5b. Leaves flat, amphistomatic 7

6a. Leaves thick-fleshy; perianth deciduous; ovary pubescent only at apex . . . . . 2. *hirsuta*
6b. Leaves not thick-fleshy; perianth subpersistent; ovary pubescent 1. *lythroides*

7a. Branches ± fastigiate; leaves sericeous . . . 5. *argentata*
7b. Branches divergent, not fastigiate; leaves with at least one surface glabrous 8

8a. Branches thick, often tortuous; leaves completely glabrous . 6. *virescens*
8b. Branches slender, not tortuous; adaxial or abaxial leaf surface glabrous . . . . . 7. *putorioides*

II. SECT. CHLAMYDANTHUS

1a. Bracts absent or more than 2 (subsect. *Tartonraira*) . . . 2
1b. Bracts 2 (subsect. *Coridifoliae*) 4

2a. Flowers single or, rarely, paired; perianth glabrous or sparsely pilose . . . . . 12. *dioica*
2b. Flowers in fascicles of 2–5; perianth sericeous or densely pubescent 3

3a. Young shoots and leaves glabrous, pubescent or sericeous . . 10. *tartonraira*
3b. Young shoots and leaves yellow-velutinous or lanate . . 11. *velutina*

4a. Leaves flat 5
4b. Leaf margins involute or slightly involute 7

5a. Perianth pubescent . . . . . 15. *procumbens*
5b. Perianth glabrous 6

6a. Leaves elliptic-ovate, acute . . . . . 14. *subrepens*
6b. Leaves lorate (broadly strap-shaped), obtuse . . 13. *tinctoria*

7a. Perianth pubescent 8
7b. Perianth glabrous 9

8a. Leaves 2–4 mm broad . . . . . 17. *calycina*
8b. Leaves 0·5–1 mm broad . . . . . 18. *coridifolia*

9a. Mature leaves glabrous on both surfaces . . . 16. *ruizii*
9b. Mature leaves tomentose on adaxial surfaces . . 19. *broteriana*

III. SECT. THYMELAEA

1a. Bracts absent (subsect. *Sanamunda*) 2
1b. Bracts present (subsect. *Antiatlanticae*) 4

2a. Young shoots hirtellous or white-pilose . . . . 22. *villosa*
2b. Young shoots not hirtellous 3

3a. Stems pubescent in upper leafy parts; perianth tube densely pubescent . . . . . 23. *pubescens*
3b. Stems glabrous or very sparsely pilose at tips; perianth tube glabrous or sparsely pilose . . . . . 24. *sanamunda*

4a. Stems white-villous or pilose in flowering parts; bracts 2–3 . . . . . 20. *antiatlantica*
4b. Stems grey-villous in part; bracts 5–7 . . . . . 21. *virgata*

IV. SECT. LIGIA

1a. Suffrutescent perennials; stems many 2
1b. Annuals; stem single 3

2a. Leaves narrowly elliptic, less than 1 cm long, margins never revolute . . . . . 25. *cilicica*
2b. Leaves linear-filiform, more than 1 cm long, margins usually revolute on drying . . . . . 26. *aucheri*

3a. Stems glabrous or very sparsely pilose at tips 4
3b. Stems hairy 5

4a. Flowers hermaphrodite; ovary hirsute-villous at apex . . . . . 27. *passerina*
4b. Flowers unisexual, very rarely hermaphrodite; ovary puberulous at apex . . . . . 29. *salsa*

5a. Leaves glabrous or with a few straight-adpressed hairs on abaxial surface . . . . . 28. *gussonei*
5b. Leaves greyish-pilose, with hairs crispate-spreading . 30. *mesopotamica*

SYNOPTIC DESCRIPTIONS OF SECTIONS AND SUBSECTIONS

I. Sect. **Piptochlamys** (C. A. Meyer) Endl., Gen. Pl. Suppl. 4(2):65 (1848).

Syn.: *Piptochlamys* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843), *pro gen.*
Sect. *Chlamydanthus* (C. A. Meyer) Endl., *loc. cit.* (1848), *p.p.*
Piptochlamys C. A. Meyer in Rouy, Fl. Fr. 12:126 (1910), *pro subgen.*

Monoecious, dioecious, or more rarely, trimonoecious shrubs. Flowers sessile or shortly pedicellate, in terminal fascicles. Bracts present or absent. Perianth persistent in fruit, semi-persistent or totally deciduous. Leaves epi- or amphistomatic; stomata anomocytic and/or modified tetracytic, very rarely anisocytic; anticlinal walls of adaxial and abaxial epidermides straight, very rarely undulate. Stem: stomata, chlorenchyma absent and cork well-developed, except in 2 species; secondary phloem rays dilated or not; internal phloem fibres present except in *T. lanuginosa*.
Type. *T. hirsuta* (L.)Endl., *loc. cit.* (1848).

Subsect. **Hirsutae** K. Tan, **subsect. nov.**

Bracteae 3–10 vel absentes. Folia epistomatica; stomata tetracytica modifacta aut rarissime anomocytica.

Stem: stomata and chlorenchyma absent; cork well-developed; internal phloem fibres present but not conspicuously prominent.
Type. *T. hirsuta* (L.)Endl., *loc. cit.* (1848).

Subsect. **Argentatae** K. Tan, **subsect. nov.**

Bracteae absentes. Folia amphistomatica; stomata aut anomocytica aut tetracytica modifacta, aut rarissime anisocytica.

Stem: stomata and chlorenchyma absent; cork well-developed; internal phloem fibres prominent.

Type. *T. argentata* (Lam.)Pau in Cavanillesia 5:44 (1932).

Subsect. **Sempervirentes** K. Tan, **subsect. nov.**

Bracteae 6–15. Folia amphistomatica; stomata aut anomocytica aut tetracytica modifacta.

Stem: stomata and chlorenchyma present; cork moderately well-developed; internal phloem fibres prominent.

Type. *T. sempervirens* Murb. in Acta Univ. Lund. 35(3):14 (1899).

II. Sect. **Chlamydanthus** (C. A. Meyer)Endl., Gen. Pl. Suppl. 4(2):65 (1848).

Syn.: *Chlamydanthus* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843), *p. pro gen.*
Subsect. *Fruticulosae* Meissn. in DC., Prodr. 14:554 (1857), *p.p.*
Subsect. *Euthymelaea* (Lange)Brecher in Index Horti. Bot. Univ. Budapest. 5:70 (1941), *p.p.*

Dioecious, rarely trimonoecious shrubs. Flowers sessile or shortly pedicellate, clustered or solitary in leaf axils. Bracts present or absent. Perianth persistent. Leaves amphi- or epistomatic; stomata modified tetracytic and/or anomocytic; anticlinal walls of adaxial and abaxial epidermides straight, very rarely undulate. Stem: stomata and chlorenchyma absent; cork well-developed; secondary phloem rays dilated or not; internal phloem fibres absent.

Type. *T. tartonraira* (L.)All., Fl. Pedem. 1:133 (1785).

Subsect. **Tartonraira** (C. A. Meyer)Endl., *loc. cit.* (1848), excl. spp.

Syn.: *Tartonraira* C. A. Meyer, *loc. cit.* (1843), *p. pro gen.*

Flowers clustered except in *T. dioica* where they may be solitary or paired. Bracts (5–)10–15 except in *T. dioica* where they are 3–8 or absent. Leaves amphistomatic. Stem: secondary phloem rays not dilated.

Type. *T. tartonraira* (L.)All., *loc. cit.* (1785).

Subsect. **Coridifoliae** K. Tan, **subsect. nov.**

Flores solitarii rarissime binatim semper bibracteis. Folia amphi- aut epistomatica.

Stem: secondary phloem rays usually dilated.

Type. *T. coridifolia* (Lam.)Endl., *op. cit.*, 66 (1848).

III. Sect. **Thymelaea**

Syn.: Subsect. *Euthymelaea* Endl., Gen. Pl. Suppl. 4(2):65 (1848), excl. *T. dioica.*
Subsect. *Suffrutescentes* Meissn. in DC., Prodr. 14:552 (1857), excl. *T. coridifolia.*
Subsect. *Sanamunda* (Lange)Brecher in Index Horti Bot. Univ. Budapest. 5:70 (1941).

Dioecious, semi-shrubby or suffrutescent perennials; stems virgate, simple or branched. Flowers sessile, clustered or solitary in leaf axils. Bracts present or absent. Perianth persistent. Leaves amphistomatic; stomata anomocytic and/or modified tetracytic; anticlinal walls of adaxial and abaxial epidermides straight or undulate. Stem: stomata and chlorenchyma usually present; cork moderately well-developed; secondary phloem rays not dilated. Internal phloem fibres present except in *T. villosa*.
Type. *T. sanamunda* All., Fl. Pedem. 1:132 (1785). Syn.: *Daphne thymelaea* L., Sp. Pl., 356 (1753).

Subsect. **Antiatlanticae** K. Tan, **subsect. nov.**
Plantae 20–60 cm altae. Flores raro solitarii plerumque 6–20 in fasciculis densis congestis. Bracteae 2–7, albae vel incano-villosae.
Type. *T. antiatlantica* Maire in Bull. Soc. Sci. Nat. Maroc 13:273 (1933).

Subsect. **Sanamunda** (Lange)Brecher, *loc. cit.* (1941), *p.p.*
Syn.: Sect. *Sanamunda* Lange in Willk. & Lange, Prodr. Fl. Hisp. 1:298 (1862), incl. *T. villosa*.
Plants rarely more than 20 cm tall. Flowers solitary or in fascicles of 2–3(–5). Bracts absent.
Type. *T. sanamunda* All., *loc. cit.* (1785).

IV. Sect. **Ligia** (Fasano)Meissn. in DC., Prodr. 14:551 (1857), as 'Sect. *Lygia*'.
Syn.: *Ligia* Fasano in Atti Accad. Napoli 1:245 (1788), *pro gen.*
Annuals or suffrutescent perennials; stems simple or branched. Monoecious or flowers hermaphrodite. Flowers sessile, solitary or 2–4(–7) in leaf axils. Bracts 2, green. Perianth persistent. Leaves amphistomatic; stomata anisocytic and modified tetracytic; anticlinal walls of adaxial and abaxial epidermides undulate. Stem: stomata and chlorenchyma present; cork absent; secondary phloem rays not dilated; internal phloem fibres present or absent.
Type. *T. passerina* (L.)Cosson & Germ., Syn. Fl. Env. Paris, ed. 2, 360 (1859).

Taxonomic account of species

Section Piptochlamys

Subsect. Hirsutae

1. T. lythroides Barr. & Murb. in Acta Univ. Lund. n.s. 2(1):69 (1906).
Ic.: Murb., *op. cit.*, t. 19, f. 1–6 (1906).
Erect dioecious or near dioecious shrub, 40–70 cm. Young shoots tomentose-villous. Leaves sessile, subcoriaceous, margins slightly involute, ovate or lanceolate, 4–12 × 2–3 mm (on young sterile shoots usually 7–20 × 1·5–2·5 mm); adaxial surface greyish-tomentose, abaxial surface green, glabrous. Flowers sessile, villous-tufted at base, in fascicles of 2–9 at ends of short branches. Bracts absent. Perianth subpersistent, 4–5 mm, yellow turning purplish-brown, villous-puberulous; lobes ovate, c. 1 mm, obtuse. Ovary 4 mm, pubescent; style terminal or subterminal. Mature fruit ovoid, c. 5 mm, pubescent.

Fl. and fr. Mar.–Jul., cultivated material Jan. Semi-arid, sandy, or non-calcareous soils with fairly high humus content; destroyed *Quercus* woods. Sea-level–150 m.
Type. [Morocco] in sylva Tamara, 12 & 13 iii 1887, *Grant* (holo. & iso. P—Hb. Cosson).
Distribution: endemic to W Morocco (Fig. 7).

Affinities of this species lie with *T. hirsuta* as the perianth does not usually persist when the fruits are mature. The leaves are sometimes dimorphic, those of young shoots often longer and narrowly lanceolate. Brecher (1941) retains it within sect. *Chlamydanthus* (C. A. Meyer)Endl. but transferring it to sect. *Piptochlamys* (C. A. Meyer)Endl. is more appropriate.

Barratte and Murbeck (*loc. cit.*, 1906) describe it as monoecious. The species is closer to being dioecious but female plants often have a few staminate flowers intermixed with the pistillate in the same flower fascicle.

2. T. hirsuta (L.)Endl., Gen. Pl. Suppl. 4(2):65 (1848).

Syn.: *Passerina hirsuta* L., Sp. Pl., 559 (1753), non Asso (1779) nec Brot. (1804).
P. metnân Forsskål, Fl. Aeg.-Arab., 81 (1775).
P. polygalaefolia Lapeyr., Hist. Abr. Pyr., 214 (1813), *p.p. excl. typ.*
Tartonia ovatifolia Rafin., Autikon Botanikon, 146 (1840).
Piptochlamys hirsuta (L.) C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843).
Chlamydanthus hirsutus (L.)Griseb., Spic. 2:547 (1845).
Thymelaea hirsuta (L.)Endl. var. *polygalaefolia* (Lapeyr.)Endl., Gen. Pl. Suppl. 4(2):65 (1848), *excl. typ.*
Passerina hirsuta L. var. *vestita* Gren. in Gren. & Godr., Fl. Fr. 3:63 (1855).
Thymelaea hirsuta (L.)Endl. var. *vulgaris* Meissn. in DC., Prodr. 14:557 (1857).
T. hirsuta (L.)Endl. var. *rotundifolia* Meissn., *loc. cit.*
T. hirsuta (L.)Endl. var. *angustifolia* Meissn., *loc. cit.*
T. hirsuta (L.)Endl. var. *microphylla* Reynier in Bull. Assoc. Pyrén. Échange Pl., (1904), *cit. n.v.* & in Bull. Soc. Bot. France 53 (sess. extr.):64 (1906).

Ic.: Sibth. & Sm., Fl. Graeca 4(2): t. 360 (1824); Holmboe, Veg. Cyprus 282, f. 113 (1914); Figs 4 A–E.

Trimonoecious shrub, 20–150 cm (rarely 2–3 m). Young and flowering shoots white-tomentose, older branches divergent, becoming pendent and glabrous. Leaves incurved or ± flat, sessile, thick-coriaceous, margins involute, orbicular-ovate or ovate-lanceolate, (2–)3–5(–8) × 1·5–3(–5) mm, obtuse or acute, adaxial surface white-tomentose or lanose, abaxial green, glabrous. Flowers sessile, villous tufted at base, 2–8 at ends of short branches. Bracts absent. Perianth deciduous, 3–4·5 mm, pale yellow, greyish-pubescent or white-tomentose; lobes ovate, 1–1·5 mm, obtuse. Ovary hirsute at apex; style remaining terminal. Fruit ovoid, c. 4 mm, minutely puberulous or glabrous.

Fl. Aug.–Jun. Fixed dunes, stony desert, cliff faces, limestone pavements, near salt lakes, garigue (*Pinus-Retama* association). Abundant and common in dry sunny places especially near sea. Sea level–1500 m.
Type. Described from Spain (Hb. Linn. specimen on left-hand side of sheet 504/4. The other specimen is *T. lythroides*).
Distribution: circum-Mediterranean. Europe, SW Asia and N Africa (Fig. 10).

As in *T. lythroides*, leaves can be slightly dimorphic; on full-grown shrubs, those on young sterile shoots may be narrowly ovate-lanceolate while those on flowering shoots and older branches are orbicular-ovate. Plants at edges of barley or wheat fields are more robust, sometimes with paler green leaves. Those growing in exposed, sterile soil, e.g. by the sea or in stony desert, tend to have much smaller and dull, dark-green leaves. Field studies also show that seedlings and young plants less than 20 cm tall initially produce lanceolate leaves (6–10 × 2–5 mm) on the main stem while those on lateral branches are ovate or ovate-lanceolate (2–4 × 1·5–3 mm). Mature shrubs do not show the type of leaf dimorphism present in young plants because the leaves no longer persist on the lower part of the main stem. Herbarium material, unless accompanied by field notes, may mislead one into thinking that a complete young plant taken just above soil level is part of a mature branch.

Meissner (*op. cit.*:557) describes his var. *angustifolia* as having leaves narrowly ovate-oblong or lanceolate, *acute*, concave on the upper surface and with the apices inflexed. Measurements were given as 6–8·5 × 2–3·5 mm. The specimens cited by Meissner from Marseilles (*Richard* 2) and Egypt (*Aucher* s.n.) are typical '*hirsuta*'. The remaining specimens (from Carthage, Pozzuoli (Italy), Sardinia, Sicily, etc.) do have a rather distinct 'angustifolia-appearance', but after studying a wide range of material from the whole Mediterranean, I am inclined to treat them as maritime forms (ecotypes or ecads). They can also be matched by specimens from S Spain. The flowers are often white-tomentose rather than yellow-pubescent, the branches occasionally more slender. The fact that both lanceolate-acute and orbicular-obtuse leaves can be found on the same plant and even on the same branch, further strengthens my conviction that no subspecies or varietal rank is necessary.

T. hirsuta var. *polygalaefolia* (Lapeyr.)Endl. has been described as 'foliis ovatis utrinque tomentosis, dorso demum glabratis' by Meissner, *loc. cit.* It is remarkable that there should be a variety with leaves white-tomentose on *both* surfaces and certainly extremely rare to have '*hirsuta*' leaves glabrous on the *adaxial surface*, no matter how long they persist. Examination of material originally named *Passerina polygalaefolia* by Lapeyrouse (*op. cit.*:214) proved that it is similar to typical *T. hirsuta* and in no way fits the above description. However, Lapeyrouse had listed the polynomials 'Thymelaea foliis kali lanuginosis salsis, Bauh. Pin., 463' and 'Thymelaea foliis Polygalae villosis, Tourn., Inst. R. Herb., 594' after his description. These are identical to those provided for *Daphne lanuginosa* Lam. in *Encyl.* 3:436 (1792). The confusion has arisen from the existence of two separate specimens mounted on the same sheet, P-Tourn. 5821. The specimen on the left (*D. lanuginosa*) is obviously the taxon Lapeyrouse was describing while referring to the other which is *T. hirsuta*.

Economic note: T. hirsuta is poisonous to livestock. In Cyrenaica it was formerly used as a substitute for *Imperata cylindrica* in dune fixation although liable to be removed by local inhabitants for fuel. Like most shrubby members of the Thymelaeaceae, the bark is strong and makes good twine; according to El-Ghonemy *et al.* (1974) it is a valuable potential cellulose and fibre plant.

3. T. lanuginosa (Lam.)Ceballos & Vicioso, Estud. Veg. Fl. Forest. Málaga, 235 (1935).

Syn.: *Daphne lanuginosa* Lam., Encycl. 3:436 (1792).
Passerina canescens Schousboe in Willd., Sp. Pl. 2:432 (1799).
Chlamydanthus canescens (Schousboe)C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843).
T. canescens (Schousboe)Endl., Gen. Pl. Suppl. 4(2):65 (1848).
P. kalifolia Pourret *apud* Willk. & Lange, Prodr. Fl. Hisp. 1:301 (1862), *pro syn.*
P. lanuginosa (Lam.)Pau in Mém. Mus. Ci. Nat. Barc. 1:67 (1922).

Ic.: Boiss., Voy. Bot. Espagne, t. 157a, f. 1–4 (1842); K. Tan in Notes R.B.G. Edinb. 35(3):346, f. 1F–Ka (1977).

Gynodioecious (hermaphrodite and pistillate flowers on separate plants) shrub, 50–100 cm. Branches flexuous, grey-lanuginose, older parts naked, glabrous. Leaves densely imbricate becoming patent, sessile, herbaceous, ovate or ovate-lanceolate, 2–4 × 1·5–2 mm (on young shoots sometimes lanceolate, 6–8 × 2 mm), obtuse or subacute, grey-lanuginose but to a lesser extent, and sometimes only on the basal half of abaxial surface. Flowers fragrant, shortly pedicellate, in fascicles of 7–10 at ends of short, densely leafy branches; very rarely staminate. Inflorescense bracts leaf-like, 7–10, linear-lanceolate, 6–7 × 1·5 mm, silvery or grey-lanose. Perianth 7–8·5 mm in hermaphrodite, 5·5–6 mm in pistillate flowers, yellow or silvery-lanose; lobes unequal, ovate, 1·5–2 mm, obtuse. Ovary pubescent; style becoming sub-terminal. Seed c. 2 mm.

Fl. Jan.–Jun.; fr. till Aug. Abandoned racecourse, scrub forest, sandy and dry rock soils near sea; rare in hills. Sea-level–15 m.

Type. [Spain] communiquée par M. de Jussieu (holo. P).

Distribution: S Spain, Gibraltar and Morocco (Fig. 7).

A species closely related to *T. gattefossei.*

4. T. gattefossei K. Tan in Notes R.B.G. Edinb. 35(3):345 (1977).

Ic.: Tan, *op. cit.*, 346, f. 1A–Ea.

Dioecious shrub with slender, grey-lanuginose branches. Leaves sessile, herbaceous, ovate, 4–5 × 2–3 mm, obtuse, grey-lanose, less so on abaxial surface. Flowers shortly pedicellate, apparently axillary but actually in fascicles of 9–14 at ends of very short branches. Inflorescence bracts leaf-like, 3–5, ovate-lanceolate, 3·5–4 × 1·5 mm, obtuse, grey-lanuginose. Staminate flowers 6 mm, silvery or grey-lanose; lobes broadly ovate, 1·5 mm, obtuse. Pistillate or hermaphrodite flowers unknown.

Fl. Jan.–Mar. Sandy plains, littoral region with *Chamaerops humilis* L.

Type. [Morocco] Chaouïa, chamaeropaie sur sable á Bouskoura, ii 1937, *Gattefossé* (holo. MPU).

Distribution: endemic to W Morocco (Fig. 8).

SUBSECT. ARGENTATAE

5. T. argentata (Lam.)Pau in Cavanillesia 5:44 (1932).

Syn.: *Daphne argentata* Lam., Encycl. 3:436 (1792).
D. nitida Vahl, Symb. 3:53 (1794).
Passerina nitida (Vahl)Desf., Fl. Atl. 1:331 (1798).
Chlamydanthus nitidus (Vahl)C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843).
T. nitida (Vahl)Endl., Gen. Pl. Suppl. 4(2):65 (1848).
P. segobricensis Pau in Not. Bot. Fl. Espan. 1:25 (1887).
Stellera nitida (Vahl)Kuntze, Rev. Gen. Pl. 2:585 (1891).
T. nitida (Vahl)Endl. var. *segobricensis* Pau in Willk., Suppl. Prodr. Fl. Hisp., 69 (1893).
T. virgata (Desf.)Endl. var. *microphylla* Willk., *loc. cit.* (1893), *pro syn.*
P. argentata (Lam.)Pau in Mém. Mus. Ci. Nat. Barcelona 1(1):67 (1922).

Ic.: Desf., Fl. Atl. 1: t. 94 (1798).

Erect gynodioecious shrub, 10–50 cm. Branches ± fastigiate, rarely divergent, pilose; flowering shoots short, sericeous, densely leafy. Leaves imbricate, sessile, subcoriaceous, oblanceolate or spathulate, 3–8 × 0·5–2 mm, obtuse or apiculate, adpressed-sericeous. Flowers hermaphrodite and pistillate, sessile, in terminal fascicles of 4–6(–9). Bracts absent. Hermaphrodite flowers 6–8 mm, pistillate 4–5 mm. Perianth greenish-yellow, sericeous; lobes ovate or oblong-lanceolate, c. 2 mm, obtuse. Ovary puberulous at apex; style becoming subterminal. Seed c. 3 mm.

Fl. Apr.–Jun. Calcareous rock, sandstone steppe, limestone pavement (with *Quercus* and *Stipa*), *Pinus halepensis-Tetraclinis articulata* scrub. 10–1500 m.

Type. [Spain] communiquée par M. Vahl (holo. P).

Distribution: Spain and N Africa (Fig. 7).

Ibéro-Maurétanian element. Although records are numerous from N Africa, the plant is not gregarious.

Many workers, e.g. Boissier (1842) have assumed the taxa *Daphne argentata* Lam. and *D. argentea* Sm. (syn. *T. tartonraira* subsp. *argentea* var. *angustifolia*) to be conspecific. When cited in synonymy, the former is often overlooked as a possible early synonym for an altogether different species. This error has been retained even in fairly recent works like *Fl. Europaea* (2:259, 1968) which lists *T. nitida* (Vahl)Endl. as the correct name for *T. argentata* (Lam.)Pau.

Pau (*loc. cit.*, 1922) distinguishes two forms—f. *segobricensis* with a perianth of 7 mm and f. *genuina* with one of 4 mm. I have found that flowers of f. *segobricensis* are usually hermaphrodite with a longer perianth, e.g. *Reverchon* 1898:254. Pistillate flowers are usually shorter and may occur either in the same cluster or on separate plants, e.g. *Davis* 58620. This may account for Pau's recognition of forms.

6. T. virescens Meissn. in DC., Prodr. 14:554 (1857).

Dwarf androdioecious shrub c. 20 cm (?). Leaves patent, soon decumbent and deciduous, sessile, subcoriaceous, spathulate-oblanceolate, 7–10 ×

2–3 mm (lower leaves much smaller, 3–5 × 0·75–1 mm), obtuse or apiculate, pale green, glabrous. Flowers hermaphrodite, very rarely staminate, sessile, in fascicles of (5–) 10–18 at ends of young branches. Bracts absent. Perianth 6–7 mm, purplish, sericeous; lobes ovate, 2 mm, obtuse. Ovary pubescent at apex; style becoming subterminal.

var. **virescens**

Syn.: *Passerina virescens* Cosson & Dur. in Munby, Cat. Pl. Alg., 30 (1866) et apud Bal., Pl. Alg. exsicc. no. 1007 (1853), *nom. nud.*
Stellera virescens (Meissn.)Kuntze, Rev. Gen. Pl. 2:585 (1891).

Branches thick, often tortuous, dusty-white; young shoots brown puberulous.

Fl. and fr. Apr.–Jul. Dry rocky ground. 1650–2200 m.

Type. [Algeria] ad fontes fl. Oued-Abdi et in sylvâ Lambèse, *Balansa* 1853:1007 (holo. G; iso. E, K).

Distribution: NW Africa (Fig. 8).

6a. var. **glaberrima** Batt. in Batt. & Trabut, Fl. Alg. 1(4):782 (1890).

All vegetative parts completely glabrous (not dusty-white puberulous).

Fl. Apr. *Cedrus libani* forest with *Quercus, Ilex, Hedera, Taxus*. 2000 m.

Type. [Algeria] Djebel Aïssa, *Battandier & Trabut* (holo. AL?), *n.v.*

Distribution: Morocco (Azrou to Ifrane, Figuig), Algeria (Djebel Bechar) (Fig. 8).

Only one collection has been examined. Affinities of this species are closest to *T. putorioides*.

7. T. putorioides Emb. & Maire in Bull. Soc. Hist. Nat. Afrique N. 23:214 (1932).

Syn.: *T. virescens* Lit. & Maire in Mém. Soc. Sci. Nat. Maroc 26:35 (1931), non Meissn. (1857).

Dwarf monoecious shrub; branches numerous, glabrous in older parts, pilose-pubescent at tips. Leaves spathulate, obtuse, greyish-green. Flowers terminal, (3–)5–7 at ends of very short shoots. Bracts absent. Perianth 6–7 mm, adpressed-pubescent; lobes triangular-ovate, 1·5–2 mm, obtuse or subacute. Ovary pubescent, villous at apex; style subterminal. Seed c. 3·5 mm.

var. **putorioides**

Syn.: *T. putorioides* Emb. & Maire var. *chlorantha* Emb. & Maire, *op. cit.*, 23:215 (1932).

Leaves spathulate-obovate, 5–9 × 1·5–3 mm; adaxial surface pubescent, abaxial becoming glabrous. Flowers yellow.

Fl. Jul. Mountains, calcareous rock. 1800 m.

Type. [Morocco] in rupibus calcareis secus amnem Tessaout, prope Aït-Alla, 1800 m, 28 vii 1926, *Maire* (holo. MPU).

Distribution: endemic to Grand Atlas, above Demnat (Fig. 8).

7a. var. **rhodantha** Emb. & Maire, *op. cit.* 23:215 (1932).

Differs from var. *putorioides* in having leaves spathulate-oblanceolate, 3–5 × 1–1·75 mm; adaxial surface glabrous, abaxial sparsely pilose, sparsely ciliate. Flowers purplish.

Fl. Aug. Calcareous rock. 3400 m.
Type. [Morocco] in rupibus montis Maaghal, 3400 m, 7 vii 1931, *Emberger* (holo. MPU).
Distribution: endemic to Grand Atlas (Mt. Maaghal = Ighil M. Goun).

Flower colour may perhaps be dependent on soil or altitude. The only specimens available for examination were the type material.

SUBSECT. SEMPERVIRENTES

8. T. microphylla Cosson & Dur. in Bull. Soc. Bot. France 3:744 (1856).
Syn.: *Passerina microphylla* Cosson & Dur. *apud* Bal., Pl. Alg. exsicc. no. 256 (1852), no. 826 (1853) & *apud* Kralik, Pl. Tun. exsicc. no. 333 (1854), *omnia nom. nud.*
T. microphylla Meissn. in DC., Prodr. 14:556 (1857).
Stellera microphylla (Cosson & Dur.)Kuntze, Rev. Gen. Pl. 2:585 (1891).
Ic.: Barr. in Cosson Illustr. Atl. 2:106, t. 166 (1897).

Erect monoecious shrub 20–150 cm. Branches virgate, soon naked; young shoots white-puberulous or sericeous. Leaves few, ± adpressed, sessile, sub-coriaceous, ovate, 1–2·5 × 0·5–1·5 mm (on young shoots often lanceolate, 4 × 1 mm), obtuse, sericeous. Flowers sessile, in fascicles of 2–5, ramiflorous or at ends of very short branchlets. Bracts leaf-like, imbricate, 8–15, ovate, sericeous. Staminate flowers 4–6 mm, pistillate 3–4 mm. Perianth pale yellow, densely sericeous; lobes ovate, 0·5–1 mm, obtuse. Ovary pubescent only at apex; style subterminal. 2n = 18.
Fl. Feb.–Jun. Low hills, fixed dunes (with *Artemisia, Stipa, Echichilon, Avena, Andropogon*), stony or rocky desert (hamada), sandy salines (*Tamarix* dominant), gypsaceous crusts. 20–1200 m.
Type. [Tunisia] in apricis Saharae totius, nempe a deserto Tunetano, *Kralik* Pl. Tun. 333 (holo. G, iso E).
Distribution: N Africa (Fig. 9).

This species, rather common in Algeria (High Plateau, Atlas Saharien and Sahara Septentrional), grows in steppe or rocky desert subject to wide temperature fluctuations both day and night. Oddly enough, it has been reported as *not* poisonous to livestock, whereas *T. hirsuta* growing nearby *is* antipastoral. It can be easily distinguished from all other species by its ± aphyllous branches and small leaves. The flowers appear to have their origin in the axils of early-deciduous leaves, but they are actually terminal at the ends of very short branchlets.

Its closest affinities within the genus appear to lie with the rare *T. sempervirens* from Tunisia and *T. putorioides* from the Grand Atlas.

9. T. sempervirens Murb. in Acta Univ. Lund. 35(3):14 (1899).
Ic.: Murb., *op. cit.* 15: f. 1; t. 12: f. 1–2 (1899).

Twice-branched monoecious shrub, c. 30 cm tall. Branches erect, glabrous. Leaves sessile, subcoriaceous, elliptic-lanceolate, 9–13 × 3·5–5 mm, acute or subacute, glaucous, glabrous. Flowers sessile, 7–20, apparently on branches of previous year's growth. Bracts 6–10, broadly ovate, 1 × 1·2 mm, obtuse, sericeous. Staminate flowers 6–7·5 mm, immature pistillate flowers 3·5–4 mm. Perianth adpressed-pubescent or

near-sericeous, tube greenish-yellow; lobes triangular-ovate, 1·5–2 mm, obtuse, purplish. Immature ovary villous-pubescent; style terminal.
Fl. Apr. Calcareous rock. 350 m.
Type. [Tunisia] Rochers calcaires du ravin qui descend du Ksar Sakket vers le caravansérail de Bir Saad, 19 (*in errore* 29) iv 1896, *Murbeck* (holo. LD).
Distribution: endemic to Tunisia. Recorded only from Bled Thala (Battandier, *Fl. Alg. Suppl.* 1910:82) and Ksar Sakket (Fig. 7).

A very rare species. P. H. Davis (pers. comm.) visited the type locality in April 1977 but was unable to find plants despite careful searching. Murbeck (*op. cit.*:14) states it is dioecious and that pistillate flowers are unknown, but I have found that the type gathering has both staminate and pistillate flowers. The bract number was also erroneously recorded as 2 instead of 6–10. The closest affinities of the species seem to be with *T. microphylla* which differs in having sericeous stems and smaller, sericeous, early-deciduous leaves.

The whole inflorescence has some resemblance to that in *T. virgata*. Murbeck drew attention to the similarity of *T. sempervirens* to members of subsect. *Sanamunda* (Lange)Brecher (this group formerly included *T. virgata* which is now separately placed in subsect. *Antiatlanticae* K. Tan).

Section Chlamydanthus

Subsect. Tartonraira

10. T. tartonraira (L.)All., Fl. Pedem. 1:133 (1785), as '*T. tarton-raira*'.
Trimonoecious, 20–60 cm shrub. Lower branches with tuberculate scars, young shoots densely leafy, ± glabrous or pubescent-sericeous. Leaves sessile, subcoriaceous, spathulate-obovate to narrowly linear-oblanceolate, obtuse or acute, ± glabrous and glaucous, adpressed-pubescent or sericeous on both surfaces, glabrescent. Flowers sessile, axillary, 2–5. Bracts imbricate, (5–)10–15, sericeous. Perianth 3–6 mm, pale yellow, pubescent or sericeous; lobes 1–2·5 mm, ovate, obtuse or acute. Ovary pubescent; style becoming subterminal.

Entirely Mediterranean, distribution extending from S Spain and Morocco to Cyprus. This is a common species with variation of a complex nature difficult to define. Aymonin (1971, 1974) gave a fairly recent account of some forms, pointing out the necessity of a revision throughout the geographical range. Diverse taxonomic treatments in the past have produced numerous synonyms. Webb & Ferguson (*Fl. Europaea* 2:259, 1968) recognise three subspecies in Europe: all the plants from Crete and mainland Greece correspond to *argentea* while the rest are treated as *tartonraira*, with the exception of *thomasii* which is endemic to Corsica. The infraspecific variation in Corsica itself has been analysed by Briquet & Litardière (1938). One might decline to recognise any infraspecific units in an extremely polymorphic species, but this appears to oversimplify the problem. Seven groups which are morphologically distinct and to a greater or lesser extent show a definite distributional pattern are dealt with here.

Flower and inflorescence characters cannot normally be used for distinguishing subspecies. The bracts subtending the flower fascicles show some difference in shape and amount of indumentum. They may be deltoid

to ovate, acute to obtuse, pubescent or sericeous (Fig. 3K). Although Rechinger (1943) uses 'bracteae subacutae' and 'bracteae obtusae' to differentiate *T. argentea* (Sm.)Endl. and *T. tartonraira* (L.)All., these correlations are not absolute. The hypogynous disc in staminate flowers may be entire or lobed. It is minute, occurring at the base of a rudimentary ovary less then 0·5 mm long and is therefore not an easy character to use. The chromosome number is only known for subsp. *thomasii* (2n = 18, Contandriopoulos, 1964).

KEY TO SUBSPECIES AND VARIETIES

1a. Leaves ± glabrous . . . . . 10f. subsp. *thomasii*
1b. Leaves pubescent or sericeous 2

2a. Leaves adpressed-pubescent; hairs only 0·1–0·2 mm long . . . . . 10e. subsp. *valentina*
2b. Leaves adpressed-pubescent or sericeous; hairs 0·2–0·7 mm long 3

3a. A compact shrub; leafy shoots c. 3 cm long, fastigiate (Sierra Nevada) . . . . . 10d. subsp. *angustifolia*
3b. Habit less compact; leafy shoots 5–10 cm long, not fastigiate . 4

4a. Leaves usually 2–4 times longer than broad (predominantly W Medit.) 5
4b. Leaves 4–12 times longer than broad (E Medit.) . . . 6

5a. Leaves spathulate-obovate, 4–6 (–9) mm broad . . . . . 10. subsp. *tartonraira* var. *tartonraira*
5b. Leaves spathulate-oblanceolate, 3–4(–5) mm broad . . . . . 10a. subsp. *tartonraira* var. *transiens*

6a. Leaves spathulate-oblanceolate, (2–)3–4 mm broad . . . . . 10b. subsp. *argentea* var. *angustifolia*
6b. Leaves narrowly linear-oblanceolate, c. 1·5 mm broad . . . . . 10c. subsp. *argentea* var. *linearifolia*

subsp. **tartonraira** var. **tartonraira**.

Syn.: *Daphne tartonraira* L., Sp. Pl., 356 (1753).
D. candicans Lam., Fl. Fr. 3:221 (1778).
D. osyroides [Vahl ex] Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 333 (1818).
Tartonia obovata Rafin., Autikon Botanikon, 146 (1840).
T. tartonraira (L.)All. subsp. *linnaei* Briq. var. *genuina* Lange emend. R. Lit. subvar. *normalis* R. Lit. in R. Lit., Prodr. Fl. Corse 3(1):4 (1938).

Leaves spathulate-obovate, 7–10(–15) × 4–6(–9) mm, often with a characteristic sericeous-yellow shine; veins rather more numerous than in other subspecies. Bracts ovate, 2·5 × 2mm. Perianth c. 6 mm, yellow-sericeous; lobes 2 mm. Disc in staminate flowers entire or crenate.
Fl. Dec.–May. Calcareous and granitic rock, sandy places by sea.
Type. Described from S France (Hb. Linn. 500/6).
Distribution: coastal France to Corsica and Sardinia with an outlier on the Ionian island of Cephalonia (easternmost occurrence, may possibly have been introduced) (Fig. 9).

10a. subsp. **tartonraira** var. **transiens** (Briq.)K. Tan, **comb. nov.**

Syn.: *Tartonia cuneifolia* Rafin., Autikon Botanikon, 146 (1840), *p.p.*
T. tartonraira (L.)All. var. *genuina* Lange subvar. *angustifolia* Reynier in Bull. Soc. Bot. Fr. (sess. extr.):70 (1906).
T. tartonraira (L.)All. f. *foliis angustioribus* Font-Quer in Iter Maroc no. 287 (1928).
T. tartonraira (L.)All. var. *angustifolia* R. Lit. & Maire in Mém. Soc. Sci. Nat. Maroc 26:35 (1931), non Meissn. (1857) nec Lange (1862).
T. tartonraira (L.)All. subsp. *linnaei* Briq. var. *genuina* Lange emend. R. Lit. subvar. *transiens* Briq. in R. Lit., Prodr. Fl. Corse 3(1):4 (1938).

Leaves spathulate-oblanceolate, 10–16(–25) × 3–4(–5) mm, adpressed-pubescent; veins fewer than in var. *tartonraira*. Bracts c. 12, 1·5–2·5 mm, outer deltoid or broadly ovate, obtuse; inner ovate, acute. Perianth 4·5–6 mm, pubescent; lobes 1–2·5 mm. Disc entire or deeply lobed.

Fl. Mar.–Jul. Calcareous rocky slopes and crusts (previous *Pinus halepensis* forest), maquis, *Lygeum-Artemisia* steppe, rare along coast. 900–1800 m.

Type. [Corsica] sommet du Pigno, sur le sentier de Farinola, *Mabille* 1866:171 (E, K).

Distribution: widespread in W Mediterranean; noticeably absent in Adriatic region and in N Africa, not further east than Tunisia. It grows at higher altitudes than var. *tartonraira* which is often coastal (Fig. 9).

Some specimens from Marseilles (ann. 1836b, *anon.*) and San Antioco off Sardinia (*Müller*, sheet III) are intermediate with var. *tartonraira*.

There being no legitimate epithet at varietal level, I have made the combination *T. tartonraira* subsp. *tartonraira* var. *transiens* (Briq.)K. Tan, using Briquet's appropriate earlier epithet.

10b. subsp. **argentea** (Sm.)Holmboe var. **angustifolia** (d'Urv.)Meissn. as '*T. tartonraira* var. *angustifolia*' in DC., Prodr. 14:556 (1857), non *P. tartonraira* var. *angustifolia* Boiss. (1842) nec *T. tartonraira* var. *angustifolia* (d'Urv.)Lange (1862) nec R. Lit. & Maire (1931).

Syn.: *Daphne argentea* Sm. in Sibth. & Sm., Prodr. Fl. Graec. 1:258 (1809).
D. tartonraira L. var. *angustifolia* (as '*angusti-folia*')d'Urv., Enum. Pl. Ins. Pont. Eux., 42 (1822).
Chlamydanthus argenteus (Sm.)C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843), *p.p.*
Thymelaea argentea (Sm.)Endl., Gen. Pl. Suppl. 4(2):65 (1948), *p.p.*
C. tartonraira (L.)C. A. Meyer var. *angustifolia* (d'Urv.) Raulin, L'île de Cret, Botanique, 849 (1869).
T. tartonraira (L.)All. var. *angustifolia* (d'Urv.)Boiss. (sphalm 'Cuv'), Fl. Or. 4:1053 (1879).
T. tartonraira (L.)All. subsp. *tartonraira* var *argentea* (Sm.)Shaw & Turrill in Kew Bull., 124 (1926).
T. tartonraira (L.)All. var. *candiliana* Beauv. & Top. in Bull. Soc. Bot. Gen. 28:134 (1938), *n.v.*

Ic.: Sibth. & Sm., Fl. Graeca 4: t. 355 (1824).

Leaves spathulate-oblanceolate, (5–)10–15(–20) × (2–)3–4 mm, adpressed-pubescent, yellowish, silvery or grey-sericeous. Flower clusters rather more numerous than in other subspecies. Bracts 10–12, 1·25–1·75 × 1 mm, obtuse or subacute. Perianth 4–6 mm, lobes 1–2 mm. Disc crenate.
Fl. Feb.–Oct. Dry stony hills, phrygana on marl (*Teucrium-Lavendula* dominant), in *Pinus brutia* forest. Sea-level–915 m.
Type. [Greece] In cacumine Insulae Scopeli, ad altitudinem 400 hexapodum crescit, ann. 1819, *Dumont d'Urville*. Syntypes. P-Tourn. 5825, *Sibthorp* (K, OXF).

Sibthorp collected several plants which are relevant to Smith's diagnosis; according to *Prodr. Fl. Graec.* 'in Salami et Samo, copiosius vero circa Corinthum'. The material at OXF bear the labels '*D. argentea* JES' and 'J. Sibthorp M.D.'; there are duplicates of Sibthorp's gatherings at K.

T. tartonraira subsp. *argentea* (sensu Holmboe) is a much longer and narrower-leaved 'variant' which I have treated below as a separate variety. Distribution: Aegean area, E Medit. element (Fig. 9).

10c. subsp. **argentea** (Sm.)Holmboe var. **linearifolia** K. Tan, **var. nov.**
Syn.: *T. tartonraira* (L.)All. subsp. *argentea* (Sm.)Holmboe, Veg. Cyprus 133 (1914), as '*T. tartonraira* subsp. *T. argentea*', *quoad typ. haud comb.*
Ic.: Holmboe, *op. cit.* 282: f. 122.

Proximum var. *angustifolia* a quo foliis peranguste linearibus-oblanceolatis, (10–)20–25 × c. 1·5 mm, incano- vel argenteo-sericeis differt. Bracteae 10–15, in plantis Cretae triangulato-acutis in illiis Cypriae plus ovato-obtusis.
Fl. Feb.–Jun. Dry igneous rock, limestone slopes, maquis on serpentine. Sea-level–830 m.
Type. [Cyprus] Mazoto, *Holmboe* 163 (C?).
Distribution: confined to SW Anatolia, Rodhos, Crete and Cyprus, the last two being the most southern and eastern part of subsp. *argentea's* range (Fig. 9).

The following specimens, all from W and SW Anatolia and islands, are intermediate between the two varieties, the leaves being 15–25 × 2–3 mm: *Lewejohann* Tu-74-066, *Davis* 41727, *Huber-Morath* 14248, *Runemark & Snogerup* 11434, *Tengwall* 84, *Forbes* 546.

Plants from Crete and Cyprus have a very distinct form. The extreme narrowness of the leaves (c. 1·5 mm) presents a case for taxonomic recognition as does the fact that the length:breadth ratio (leaves almost 8–12 times longer than wide) does not vary much throughout the range.

10d. subsp. **angustifolia** (Boiss.)Goday & Chueca in Anal. Real. Acad. Farm. 38(3):462 (1972).
Syn.: *Passerina tartonraira* (L.)DC. var. *angustifolia* Boiss., Voy. Bot. Espagne 2:555 (1842), non d'Urv. (1822) sub *Daphne*.
T. tartonraira (L.)All. var. *angustifolia* (d'Urv.)Lange in Willk. & Lange, Prodr. Fl. Hisp. 1:300 (1862), *excl. typ.*
Fl. Jun.–Jul. Calcareous mountains. 915–1981 m.

Type. [Spain] Sierra Nevada ad Cortijo de Rosales et Trevenque, S. Tejeda, vii 1837 (holo. G, iso. E).
Distribution: restricted to S Spain (Fig. 9).

This subspecies differs from subsp. *argentea* var. *linearifolia* mainly in its general habit, being a compact little shrub with thicker branches and very short (c. 3 cm, not 5–10 cm long) fastigiate leafy shoots crowded at the ends of older, naked branches; the leaves also differ being only near-sericeous, oblanceolate, 5–8(–14) × 1·5–2 mm, acute; the bracts are fewer, 5–7—apparently correlated with the general paucity of flower-clusters, but July when the type specimen was collected may be the end of the flowering season. Goday & Chueca (*loc. cit.*) state habitat and distributional differences as reasons for separating it from subsp. *argentea* in the E Mediterranean. Both subspecies do occur on calcareous soil but *angustifolia* is restricted to the high mountains of Granada. They may illustrate a case of convergence.

Daphne tomentosa Lam., Encycl. 3:436 (1792).
Syn.: *Passerina tomentosa* (Lam.)Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 332 (1818), *n.v.*

The real identity of *D. tomentosa* is of some interest. Lamarck describes it as 'Daphne floribus sessilibus axillaribus, foliis oblongis obtusis utrinque sericeo-tomentosis, N. . . . il croît dans le Levant.' Endlicher (1848) following Lamarck, mentions it as *T. tomentosa* from the Orient. Lamarck lists *D. tomentosa* immediately after *D. tartonraira* L. and in fact regards it as a variety of the latter with a similar habit but having longer and white-tomentose leaves. *D. tartonraira* L., as labelled in the Lamarck herbarium (*Encycl.* 3:436 no. 9), is the typical plant from Marseilles. It was perhaps this evidence that led Meissner (1857) and Brecher (1941) to equate the imperfectly described *D. tomentosa* Lam. tentatively with *T. tartonraira* subsp. *argentea*. Unfortunately no voucher specimen could be traced.

10e. subsp. **valentina** (Pau) O. Bolós & Vigo in Butl. Inst. Catal. Hist. Nat. 38(1):73 (1974).
Syn.: *Daphne myrtifolia* Poiret in Lam., Encycl. Bot. Suppl. 3:315 (1813).
Passerina tartonraira (L.)Schrader var. *valentina* Pau in Bol. Soc. Ibér. Ci. Nat. 25:72 (1926).
P. tartonraira var. *genuina* Lange f. *virescens* Pau, *loc. cit.*
P. tartonraira var. *angustifolia* d'Urv. f. *valentina* Pau, *loc. cit.*
T. tartonraira (L.)All. subsp. *linnaei* Briq. var. *genuina* Lange emend. R. Lit. subvar. *valentina* (Pau)R. Lit., Prodr. Fl. Corse 3(1):7 (1938).

Branches slender, graceful. Leaves spathulate-obovate, 5–10(–13) × 2–4 mm, obtuse, greyish-green, adpressed-pubescent (hairs very short, 0·1–0·2 mm). Flowers densely clustered along branches. Bracts c. 12, broadly ovate, 1·75 × 1·5 mm, outer obtuse, inner acute. Perianth 3–3·5 mm, lobes c. 1 mm. Disc entire.
Fl. Mar. Dry uncultivated hills, schistose rock. 150–200 m.
Type. [Spain] Valencia, near Alcira, ann. 1890, *Porta & Rigo* Iter hisp. II:101 (iso. E, K).
Distribution: confined to E Spain (Fig. 9).

Aymonin (1969) discovered that the obscure taxon, *Daphne myrtifolia* Poiret, is in fact a member of the *T. tartonraira* complex. Specimens in P-Hb. Poiret are marked 'Daphne, myrtifolia (n) encycl. suppl. Espagne' and with the polynomial 'Thymelaea hispanica foliis *myrthi* incanis'. The

latter is an exact duplicate of the text description by Tournefort (1700), 'Thymelaea hispanica, foliis myrti incanis. Tourn. Inst. R. Herb., 395' except for the orthographical error italicized. The type of this polynomial is from Valencia (P-Hb. Tourn. 5828), and identical to the plants collected by Porta and Rigo in 1890.

Pau (*op. cit.*:72) recognised the specimens of Porta and Rigo (originally distributed as *Passerina tartonraira* var. *calvescens* Gren. (syn. *T. tartonraira* subsp. *thomasii*) as sufficiently distinct to be described at varietal level (sub *Passerina*). He defined two forms which in my opinion do not deserve taxonomic recognition.

Within the 'tartonraira-complex' the closest affinities of subsp. *valentina* are with subsp. *thomasii* (Duby)Briq. from Corsica. The former differs in having pubescent instead of glabrous young branches and leaves. From subsp. *tartonraira* var. *transiens* it can be generally distinguished by its more slender branches and its smaller, more numerous, greenish-glaucous leaves.

D. A. Webb (1967) adopted *D. myrtifolia* Poiret as the basionym for his combination *T. myrtifolia* (Poiret)D. A. Webb without examining the type material. It was used to indicate a species endemic to the Balearics (where *T. tartonraira* is absent) whose correct name should still be *T. velutina* (Pourret ex Camb.)Endl. This can be readily distinguished from *T. tartonraira* by the young stems and leaves which are yellow-velutinous or lanate instead of glabrous, adpressed-pubescent or sericeous.

10f. subsp. **thomasii** (Duby)Briq. in R. Lit., Prodr. Fl. Corse 3(1):5 (1938).
Syn.: *Passerina thomasii* Duby, Bot. Gall. 1:406 (1828).
T. thomasii (Duby)Endl., Gen. Pl. Suppl. 4(2):66 (1848).
T. tartonraira (L.)All. (as '*tartonrarina*') var. *thomasii* (Duby) Reichb., Ic. Fl. Germ. 11:13 (1849).
P. tartonraira var. *calvescens* Gren. in Gren. & Godr., Fl. Fr. 3:63 (1855).
T. tartonraira (L.)All. var. *calvescens* (Gren.)Meissn. in DC., Prodr. 14:556 (1857).
Daphne thomasii (Duby)Boullu in Ann. Soc. Linn. Lyon 24:73 (1899).
P. corsica [J. Gay ex] R. Lit., Prodr. Fl. Corse 3(1):6 (1938), *in adnot., pro syn.*
Ic.: Reichb., *op. cit.* t. 552, f. 1172 (1849).

Young branches almost glabrous. Leaves oblanceolate, 10–15 × 3 mm, glaucous, ± glabrous. Flower clusters few, scattered. Bracts 5–7. Perianth sparsely pubescent. Woods (1850) reports that the fruit is fleshy, but I have not seen any other such description. 2n = 18.
Fl. Mar.–May. Sandy or stony ground, maquis with *Cistus monspeliensis*.
Type. [Corsica] in montosis Corsicae, *Ph. Thomas* (iso. E, G).
Distribution: endemic to Corsica. Abundant and localized in the Asco valley, especially between Ponte-Leccia and Moltifao, Pont d'Asco, Olmi Capella, Pietrabello (Fig. 9).

Subspecific rank is appropriate for this taxon which is well characterized by its near glabrous nature and particularly local distribution. It was recorded from E Spain (Willk. & Lange, *Prodr. Fl. Hisp.* 1:301 & Willk.,

Suppl. Prodr., 69) but these specimens are in fact, not subsp. *thomasii* but subsp. *valentina* (Pau)O. Bolós & Vigo.

11. T. velutina (Pourret ex Camb.)Endl., Gen. Pl. Suppl. 4(2):66 (1848).

Syn.: *Passerina velutina* [Pourret ex]Camb., Enum. Pl. Balear., 183 (1827), reprint in Mém. Mus. Hist. Nat. (Paris) 14:304 (1827), non Boiss., Elenchus, 81 (1838).

T. velutina (Pourret ex Camb.)Meissn. in DC., Prodr. 14:555 (1857).

P. incana Pourret in Willk. & Lange, Prodr. Fl. Hisp. 1:300 (1862), *pro syn., n.v.*

Stellera velutina (Pourret ex Camb.)Kuntze, Rev. Gen. Pl. 2:585 (1891).

P. velutina [Pourret ex]Camb. f. *parvifolia* Knoche, Fl. Balear. 2:214 (1922), f. *folia acuminata* Knoche, *loc. cit.*

T. velutina (Pourret ex Camb.)Endl. var. *angustifolia* Willk. in Knoche, *loc. cit.*

T. myrtifolia (Poiret)D. A. Webb subsp. *montana* Malag., Las Subesp. y Variac. Geogr., 5 (1973). *T. myrtifolia* (Poiret)D. A. Webb, *comb. illegit.*

T. velutina (Pourret ex Camb.)Endl. subsp. *montana* (Malag.)Malag., Sinopsis Fl. Iberica (ed. 1), 149 (1975).

Dwarf dioecious shrub, young branches yellow-velutinous. Leaves sessile, subcoriaceous, spathulate or oblanceolate, 6–10 × 2·5–4 mm, obtuse, rarely subacute, yellow-velutinous or lanose. Flowers sessile, axillary, 2–3. Bracts imbricate, 10–15, ovate, c. 2 mm, subacute, lanose. Perianth 3–4 mm, yellow, velutinous-lanose; lobes ovate, 1–2 mm, obtuse. Mature ovary pubescent only at apex.

Fl. Feb.–Jul. Rocky shores, calcareous hills, with *Helichrysum angustifolium, Teucrium subspinosum, Astragalus balearicus, Rosmarinus officinalis.* Sea-level–1500 m.

Lectotype (provisional). [Majorca] in arenosis maritimis insulae Majoris prope Palmam vulgatissima, in montibus rarior, 30 iii 1825, *Cambessedes* (iso. P).

Distribution: endemic to Balearics (Fig. 8).

Records from Algeria and Morocco (Battandier, 1910:82; Jahandiez & Maire, 1932:511) possibly represent adventive cases and require verification. The presence of *T. velutina* in Tenerife (*fide* Meissn., 1857) is doubtful as it has never been mentioned in any of the Floras of the Canary Islands.

As mentioned previously, the combination *T. myrtifolia* (Poiret)D. A. Webb has been published in *Feddes Rep.* 74:28 (1967) and *Fl. Europaea* 2:559 (1968) as the correct name for this species. D. A. Webb based his name on what he thought was an earlier synonym, *Daphne myrtifolia* Poiret. This actually refers to a subspecies of *T. tartonraira* (L.)All. Knoche (1922), in recording the presence of *T. velutina* (sub *Passerina*) in the Balearics, admitted the affinities of the plant with *T. tartonraira*, but the dense yellow-velutinous or lanate indumentum covering the young stems and leaves suffice to distinguish it.

The type of *T. velutina* (Pourret ex Camb.)Endl. poses some problems. When Cambessedes validated Pourret's name in 1827, he did not list the

specimens named by Pourret as *P. velutina* (P-*Pourret* 466, MA-*Pourret* 1139, *fide* Aymonin, 1969). But his description tallies with the material—he further stated that plants were common near Palma. Although he did mention *P. velutina* Pourret as being in Hb. Desfontaines, this is erroneous as the specimen referred to is not *T. velutina* but *Daphne myrtifolia* Poiret. In view of this, one of his own collections, dated 30 iii 1825, has been chosen as a provisional lectotype.

Malagarriga (*loc. cit.*, 1973, 1975) distinguished his subsp. *montana* (based on *Sennen* 1275) as having sericeous branches, a later flowering period from June–July and as growing more inland on dry rocky ground. This was compared to the typical species which is more tomentose-velutinous, flowers earlier (from February to May) and is found along the coast. I have not seen his specimen but have examined material from montane and maritime regions. Except for the smaller size and frequently acute apices of the leaves in the montane material there is little appreciable difference to warrant separation as a subspecies.

12. T. dioica (Gouan)All., Auct. Fl. Pedem., 9 (1789).

Dioecious shrub. Leaves subsessile or with petioles 0·5 mm, subcoriaceous, spathulate or oblanceolate. Flowers sessile, solitary (rarely paired), fragrant, yellow. Bracts 0–8, lanceolate. Mature ovary pubescent. Seed c. 3 mm.

subsp. **dioica**

Syn.: *Daphne dioica* Gouan, Ill. Obs. Bot., 27 (1773).
Passerina dioica (Gouan)Ramond in Bull. Soc. Philom. (Paris) 41:131 (1800).
D. calicina Berger, Fl. Bas. Pyr. 2:211 (1803), non *D. calycina* Lam. (1792) nec Lapeyr. (1782).
P. empetrifolia Lapeyr., Hist. Abr. Pyr., 212 (1813).
Stellera dioica (Gouan)Kuntze, Rev. Gen. Pl. 2:585 (1891), 'dioeca' orth. mut.
'*P. geminiflora* Ramond' hb. ms. (E).

Ic.: Gouan, *op. cit.* t. 17, f. 1 (1773); Figs 3 J & Ja; Figs 4 F–H.

Erect shrub, 15–50 cm. Branches with tuberculate leaf scars, young shoots glabrous. Leaves spathulate or oblanceolate, (4–)6–12 × 1·3–3 mm, acute or obtuse, glabrous. Flowers glabrous. Bracts 6–8, outer 1·5 mm, innermost up to 3·5 mm, acute, sparsely ciliate, adaxial surface pubescent. Staminate flowers 6–9 mm; lobes triangular, 2·5–4 mm, subobtuse. Pistillate flowers 6–8 mm; lobes triangular, 2–3 × 0·6 mm, acute.

Fl. May–Jul.; fr. Aug.–Oct. Rocky screes, glacial ravines and fissures in alpine and subalpine zone, with *Saxifraga longifolia, Globularia repens, Bupleurum angulosum, Hypericum nummularium, Lonicera pyrenaica,* etc. 850–2550 m.

Type. [France] in apricis pyrenaicis eundo á pago S. Pauli de Fenouilhedes ad pagum St. Martin, ann. 1768, *Gouan* (K).

Distribution: W Pyrenees to SW Alps (Fig. 8).

12a. subsp. **granatensis** (Pau)Malag., Sinopsis Fl. Iberica (ed. 1), 149 (1975).

Syn.: *Passerina granatensis* Pau, Carta Bot. 1:7 (1904).
T. granatensis Lacaita in Bull. Soc. Bot. Genève, sér. 2(21):133 (1929), *nom. nud.*
T. granatensis [Pau ex]Lacaita in Cavanillesia 3:40 (1930).
T. dioica (Gouan)All. subsp. *granatensis* (Pau)Fernández Casas in Candollea 30:288 (1975).
'*P. spicata* L.' hb. m.s. (E).

Cushion-like plants less than 15 cm tall. Branches numerous, short and tortuous. Leaves oblanceolate, 2–3·5 × 0·5–1·25 mm, obtuse. Flowers usually sparsely pilose. Bracts 0 or 3–6, not more than 2·5 mm, non-ciliate, adaxial surface with a few hairs at base. Staminate flowers 4–6 mm; pistillate 3–5 mm, lobes ovate, 1·5–2 × 1·5 mm, obtuse.
Fl. Jun.; fr. Jul.–Aug. Ravines, escarpments, calcareous rock faces. 1524–2550 m.
Type. [Spain] Jaen, Sierra de Castril, lieux arides, sur calc., 1900 m, vi 1903, *Reverchon* (holo. G-Hb. Romieux, sub *T. coridifolia* Endl.).
Distribution: C and W Pyrenees, SE Spain (Sierra de Cazorla and adjacent ranges) (Fig. 8).

T. dioica with two distinct subspecies is common in the mountains of SW Europe and NW Italy. One is the typical plant of the SW Alps, the other, subsp. *granatensis*, is more rare, occurring in the Pyrenees and the mountains of SE Spain. Intermediates between the two are met with, e.g., above Ufsat towards Andorra, Ariege, 1 & 3 x 1849, *Ball*, which is more than 30 cm tall, but otherwise, is in all respects similar to the smaller plants from exposed situations in the Pyrenees. Subsp. *granatensis* can be generally distinguished by its more dwarf habit, smaller leaves, less numerous bracts, etc. It was initally identified as *T. coridifolia* (Lam.)Endl. by Pau (*loc. cit.*, 1904) but a locality so far south of the latter's known distribution in the Cantabrian Mts is extremely unusual and on further examination it proved to be related to *T. dioica* instead.

SUBSECT. CORIDIFOLIAE

13. T. tinctoria (Pourret)Endl., Gen. Pl. Suppl. 4(2):66 (1848).

Dioecious shrub. Branches glabrous, with tuberculate leaf scars; young shoots reddish-brown, crispate-pubescent at tips. Leaves sessile, coriaceous, lorate, obtuse, becoming entirely glabrous. Flowers sessile, solitary. Bracts ovate, concave. Staminate flowers 4–6(–10) mm; pistillate 4–5 mm. Perianth yellow, glabrous; lobes connivent in pistillate flowers, unequal, broadly ovate, 1–1·5 mm, obtuse. Upper stamens semi-exserted. Ovary crispate-pubescent at apex; style becoming subterminal. Seed 3–3·5 mm.

subsp. **tinctoria**
Syn.: *Passerina hirsuta* Asso, Syn. Stirp. Arag., 49 (1779), non L. (1753) nec Brot. (1804).
P. tinctoria Pourret, Chlor. Narb., 27 et in Mém. Acad. Sci. Toulouse 3:323 (1788).
Daphne vermiculata Vahl, Symb. 1:28 (1790).
P. orientalis Willd., Sp. Pl. 2(1):431 (1799), *p.p.*
P. imbricata Sennen in Ann. Soc. Linn. Lyon 70:69 (1923).
Ic.: Fig. 3 E; Figs 4 I & J.

Erect shrub up to 1 m tall. Leaves often remaining imbricate, (8–)10–16 × 2–3(–5) mm, *tomentose* on both surfaces when young.
Fl. Apr.–Sept. Screes, degraded calcareous rock, garigue. 450–1200 m.
Syntype. [Spain] P-Tourn. 5820.
Distribution: Portugal (?), NE and E Spain, S France (Fig. 8).

13a. subsp. **nivalis** (Ramond)K. Tan, **stat. nov.**
Syn.: *Daphne calycina* Lam., Encycl. 3:435 (1792), non Lapeyr. (1782) nec '*calicina*' Berger (1803).
Passerina nivalis Ramond in Bull. Soc. Philom. (Paris) 41:131, t. 9, f. 3 (1800).
Thymelaea nivalis (Ramond)Meissn. in DC., Prodr. 14:555 (1857).
T. tinctoria (Pourret)Endl. var. *nivalis* (Ramond)Lange, Pug. Hisp., 104 (1861).
Ic.: Lam., Tabl. Encycl., t. 290, f. 3 (1792); Bull. Alpine Gard. Soc. Gr. Brit. 39(2):124, photo (1971), as *T. nivalis*; Figs 3 I & Ia; Figs 4 K–M.

Similar to subsp. *tinctoria* but branches prostrate, leaves smaller and narrower (4–10 × 1–2 mm), often becoming deflexed, ciliate and sometimes puberulous on abaxial surface when young.
Fl. and fr. May–Jul. Semi-scree, limestone ridges, cropped turf in mountains. 914–2500 m.
Syntypes. [Spain, France] In summis alpibus Pyrenaeorum ad Port de Gavarnie; circa Mont Perdu, *Ramond* (P).
Distribution: endemic to C and W Pyrenees, rather rare (Fig. 8).

Morphology and distribution warrant recognition of this taxon as a subspecies. Although originally identified as, and showing strong affinities to *T. calycina* (Lapeyr.)Meissn., it is more closely related to *T. tinctoria*, partly on account of its amphistomatic, non-involute leaves and the absence of indumentum on perianth.

14. T. subrepens Lange in Dansk Vidensk, Selsk. Forh., 193 (1893).
Ic.: Lange, *op. cit.* t. 2: f. 1 (1893); Fig. 4 N.

Dwarf dioecious shrub 5–20 cm tall with long flexuous branches naked of leaves at base; young shoots and flowering branches villous-pubescent. Leaves subsessile, coriaceous, elliptic-ovate, 6–10 × 3–5 mm, acute, green, glabrous; young leaves sparsely pilose. Flowers sessile, solitary. Bracts ovate, 1 mm, obtuse. Pistillate flowers 4–5 mm, yellow, drying purplish-brown, glabrous; lobes ± connivent, unequal, ovate, 1·5–2 mm, obtuse. Ovary villous becoming pubescent at maturity. Seed c. 3 mm.
Fl. and fr. Mar.–Jun. *Pinus* forest, calcareous soil. 1500 m.
Type. [Spain] Sierra Valdemaca, near Cuenca, 30 v 1892, *Dieck* (holo. C).
Distribution: endemic to E Spain, rare (Fig. 8).

This species has affinities with *T. tinctoria*. Staminate flowers were not examined.

15. T. procumbens A. & R. Fernandes in Bol. Soc. Brot. ser. 2, 26:266 (1952).
Syn.: *T. coridifolia* (Lam.)Endl. subsp. *procumbens* (A. & R. Fernandes) Malag., Sinopsis Fl. Iberica (ed. 1), 148 (1975).
Ic.: Fernandes, *op. cit.*, t. 1 & 2 (1952).

Dioecious shrub with prostrate, spreading branches reaching 70 cm; old stems naked, with tuberculate scars; young shoots short, ascending, sericeous-villous, densely leafy. Leaves imbricate, becoming patent then decumbent, narrowly linear-lanceolate, 4–10 × 0·5–1·25 mm, acute, adpressed-pubescent or near-sericeous. Flowers sessile, solitary, greyish-pubescent. Bracts 1–2 mm. Staminate flowers 5–7 mm; pistillate 3·5–4·5 mm. Ovary villous-pubescent. Seed c. 3 mm.

Fl. Apr.–May; fr. Jun. Schistaceous rock (pH 5·8), ground layer of *Quercus pyrenaica* forest.

Type. [Portugal] Ribeira d'Arnes, pr. Sabugal, *Fernandes, Sousa & Matos* 4038 (holo. COI).

Distribution: endemic to E Portugal and W Spain (Fig. 8).

Three separate sheets of *Fernandes, Sousa & Matos* 4038 were examined. The first was a male plant, the second a female plant, and the third a predominantly male plant bearing pistillate flowers only on one small lateral branch. *Fernandes et al.* 3972 has some 6-merous staminate flowers and pistillate flowers with nine perianth lobes and two free ovaries. These specimens were collected in September and as suggested by Fernandes (*op. cit.*: 266), out-of-season flowering could have affected sex-expression.

The species can be readily distinguished from *T. coridifolia* by its prostrate habit and silvery-grey, not greenish-yellow, branches. According to Fernandes, it has a foetid odour which is absent in the related species. Its leaves are also broader and adpressed-pubescent or sericeous, never glabrous. The staminate flowers are always borne singly in the leaf axils and are much larger than in *T. coridifolia*, being 5–7 mm instead of 3–5 mm.

16. T. ruizii [Loscos ex] Casav. in Anal. Soc. Esp. Hist. Nat. 9:301 (1880).

Syn.: *T. calycina* (Lapeyr.)Meissn. var. *pilosa* Lange, Pug. Hisp., 104 (1861), *n.v.*

T. ruizii Loscos in Anal. R. Acad. Farm. 27(11):169 (1872), *nom. nud.* (?), *cit. n.v.*

T. ciliata Casav., *loc. cit.*, *pro syn.*

T. floribunda Boiss. in Willk., Ill. Fl. Hisp. Balear. 1:77 (1882), *pro syn.*

Passerina ruizii (Loscos)Font-Quer in Treb. Mus. Cienc. Nat. Barc. 5(5):28 (1924), *n.v.*

T. calycina (Lapeyr.)Meissn. subsp. *ruizii* (Loscos)Malag., Sinopsis Fl. Iberica (ed. 1), 149 (1975), *n.v.*

Ic.: Willk., Ill. Fl. Hisp. Balear. 1: t. 52 (1882)—but bracts wrongly positioned, they should be outside *inner* perianth lobes.

Dioecious shrub up to 35 cm; branches decumbent, spreading, young shoots grey-villous. Leaves sessile, subcoriaceous, lanceolate, 4–8(–12) × 1·5–2·5(–4) mm, obtuse, pale green or glaucescent, glabrous; young leaves imbricate, ciliate, grey-villous on abaxial surface. Flowers shortly pedicellate, solitary. Bracts ovate, 1·25 mm, obtuse, villous-pilose. Perianth 5–7 mm, yellow, glabrous; lobes ovate, 1·2–2 mm, obtuse, purplish. Ovary ovoid, pubescent.

Fl. and fr. Apr.–Oct. W aspect of cliff-faces, calcareous (amphibolitic) rock, dry exposed hill tops, alpine meadows. 1070–2300 m.

Type. [Spain] Picos de Europa, near Refugio Aliva, *Loscos* (*n.v.*).
Distribution: N Spain, NE Portugal (Fig. 8).

The distribution of *T. ruizii* follows the high ranges from Sierra de Cabrera in NE Portugal, along the Cordillera Cantabrica to the C Pyrenees. There is a more southerly extension from Logrono down to the mountains of Old Castille (Sierra de Guadarrama).

Closest affinities seem to be with *T. calycina* (Lapeyr.)Meissn. from which it can be distinguished by the amphistomatic leaves, villous bracts and glabrous perianth.

17. T. calycina (Lapeyr.)Meissn. in DC., Prodr. 14:555 (1857).

Syn.: *Daphne calycina* Lapeyr. in Mém. Acad. Sci. Toulouse 1:209, t. 15 (1782), non Lam. (1792) nec '*calicina*' Berger (1803).
Passerina calycina (Lapeyr.)DC. in Lam. & DC., Fl. Fr. 3:360 (1805).
P. tinctoria Pourret var. *angustifolia* Boiss., Voy. Bot. Espagne 2:556 (1842).
T. tinctoria (Pourret)Endl. var. *calycina* (Lapeyr.)Endl., Gen. Pl. Suppl. 4(2):66 (1848).

Ic.: Lapeyr., Fig. Fl. Pyr., t. 88 (1812).

Branched dioecious shrub 20–50 cm tall; young shoots grey-puberulous, leaf scars tuberculate. Leaves sessile, coriaceous, linear-lanceolate, 8–15 × 2–3 mm, subacute, margins slightly involute, glabrous; young leaves ciliate. Flowers shortly pedicellate, solitary. Bracts ovate, obtuse, non-ciliate. Perianth 4–6 mm, yellow, puberulous; lobes unequal, ovate, c. 1 mm, obtuse. Ovary pubescent.

Fl. May–Sept. Montane rock. 500–1500 m.

Syntypes. [France] Ariège, montagne de Bernadouze; Vallée de Vicdesso, *La Peyrouse* (*n.v.*).

Distribution: C Pyrenees, rare (Fig. 8).

Specimens from Huesca (Saumères near Benasque, 1000–1500 m, v 1831, *Endress*) should not be confused with material of *T. tinctoria* subsp. *nivalis* or *T. dioica* subsp. *dioica* from the same locality.

18. T. coridifolia (Lam.)Endl., Gen. Pl. Suppl. 4(2):66 (1848), *non sensu* Henriques (1885).

Syn.: *Daphne coridifolia* Lam., Encycl. 3:437 (1792).
Passerina coridifolia (Lam.)Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 354 (1818).
D. ericaefolia Vahl in Lange, Pug. Hisp., 103 (1861), *pro syn., n.v.*
P. cantabrica Pourret in Willk. & Lange, Prodr. Fl. Hisp. 1:299 (1862), *pro syn.*
T. dendrobryum Rothm. in Cavanillesia 7:116 (1935), *n.v.*
T. coridifolia (Lam.)Endl. subsp. *dendrobryum* (Rothm.)Malag., Sinopsis Fl. Iberica (ed. 1), 148 (1975).

Dwarf dioecious shrub with spreading, slender, flexuous branches 10–35 cm; young shoots pubescent. Leaves imbricate becoming patent, densely crowded at ends of branches, sessile, subcoriaceous, narrowly linear-lanceolate or subulate, 4–7 × 0·5–0·75 mm, subacute, ciliate, glabrous at

maturity, incurved on drying. Flowers sessile, 1–2, congested at ends of leafy shoots. Bracts ovate, 0·5 mm, ciliate, pubescent. Perianth 3–5 mm, pale yellow, pubescent; lobes ovate, 1–1·5 mm, obtuse. Ovary pubescent. Fl. May–Sept. Earthy screes, cattle trampled and grazed slopes, heathland, stony alpine pastures. 1200–2000 m.
Type. [Spain] ex Galicia (holo. P).
Distribution: endemic to N Spain (Galicia, Asturias to Navarra), not further east than 2° W (Fig. 8).

According to Dresser (1962), material he collected in the Picos de Europa is atypical in having curved, pubescent leaves thus differing from the description of *T. coridifolia* as originally published by Lamarck. But I have found the leaves of this species are ciliate, becoming glabrous at maturity and often incurved on drying. Although the type locality for *T. ruizii* is also near Refugio Aliva in the Picos de Europa, Dresser's specimens cannot be *T. ruizii* as the latter has a different habit and a glabrous perianth.

T. coridifolia is related to *T. broteriana*. In the Galician heathlands it is not grazed because of its toxic nature; this becomes obvious in summer, a time when most surrounding plants are closely cropped.

19. T. broteriana Coutinho in Bol. Soc. Brot. 24(1):145 (1909).
Syn.: *Passerina hirsuta* Brot., Fl. Lusit. 2:28 (1804), non L. (1753) nec Asso (1779).
T. coridifolia sensu Henriques in Bol. Soc. Brot. 3:191 (1885), non Endl. (1848).
P. broteriana (Coutinho)Sampaio, Herb. Port., 104 (1913).
T. coridifolia (Lam.)Endl. subsp. *broteriana* (Coutinho)Malag., Sinopsis Fl. Iberica (ed. 1), 148 (1975), as '*broterana*'.

Dwarf dioecious shrub, 15–40 cm. Branches flexuous, grey-tomentose becoming glabrous. Leaves densely crowded at ends of branches, sessile, coriaceous, linear-lanceolate but margins incurved thus appearing subulate, 2–9 × 0·5–0·75 mm, subobtuse, adaxial surface tomentose, abaxial glabrous. Flowers sessile, solitary. Bracts lanceolate, 1·5 mm, sparsely ciliate at base. Perianth 3·5–4 mm, pale yellow, glabrous; lobes triangular, c. 1·5 mm, acute. Ovary pubescent.
Fl. Jun.–Jul. Mountain heaths. c. 800 m.
Type. [Portugal] Serra do Gerez, *Brotero* (holo. COI).
Distribution: endemic to N and C Portugal (Fig. 8).

T. broteriana has affinities with *T. coridifolia* and *T. procumbens* from which it can be distinguished by its glabrous perianth and by the tomentose *adaxial* leaf surface. All three species have a rather restricted distribution.

Section Thymelaea

Subsect. Antiatlanticae

20. T. antiatlantica Maire in Bull. Soc. Sci. Nat. Maroc 13:273 (1933).
Syn.: *T. linifolia* Andr. in Index Horti Bot. Univ. Budapest. 3:78 (1938).

Suffrutescent dioecious perennial, 50–60 cm. Stems branched at base, flowering parts white-villous or pilose. Leaves narrowly lanceolate, (8–)10–15 × 2–3 mm, subobtuse, sericeous, later glabrescent. Flowers

axillary, sessile, 6–8. Bracts paired or one outer and two inner, white-villous. Perianth yellow, sericeous; lobes slightly unequal, ovate, obtuse. Ovary villous-pubescent at apex.
Fl. Mar.–Jun. In stony desert, dry mountain pastures. 800–1500 m.
Type. [Morocco] In pascuis lapidosis aridis Anti-Atlantis: prope Taliouine, 950 m, solo arenaceo, 16 v 1932, *Maire* (holo. MPU, iso. K).
Distribution: NW Africa (Fig. 7).

This is the only apparently Saharo-Sindian species of sect. *Thymelaea*. It has affinities with *T. virgata* from which it can be easily distinguished by its woody habit, narrower leaves and fewer bracts.

21. T. virgata (Desf.)Endl., Gen. Pl. Suppl. 4(2):66 (1848).

Predominantly androdioecious, perennial, 20–60 cm. Leaves elliptic-lanceolate, (10–)20–25(–40) × 2–5 mm, obtuse. Flowers rarely single, usually aggregated in glomerules of (3–)7–20. Bracts 5–7 (1 outer and 2–3 inner pairs), grey-villous. Perianth 5–8 mm, grey-sericeous, pale yellow within; lobes unequal, ovate, 1–2 mm, obtuse. Ovary villous-pubescent at apex. Seed 2·5 mm.

subsp. **virgata**
Syn.: *Passerina virgata* Desf., Fl. Atl. 1:331 (1798).
T. virgata (Desf.)Endl. var. *typica* Maire in Bull. Soc. Nat. Afr. Nord. 20:201 (1929).
Ic.: Desf., Fl. Atl. 1: t. 95 (1798); Figs 3 F–G.

Stems grey-villous from apex to lowermost leaves. Lowermost leaves glabrous, middle and upper ones grey-villous.
Fl. May–Jul. Stony scrubland (*Cistus* maquis), fallow pastures, limestone slopes and sandstone pavements, plateau wadis (with *Stipa, Lygeum, Artemisia*), on gypsaceous crusts overblown with sand. 1000–2100 m.
Type. [Algeria] In arvis incultis prope Tlemsen (holo. P-Hb. Desf.).
Distribution: NW Africa, S Spain (?) (Fig. 7).

The record from S Spain is without locality (*Cabrera* in Hb. Agardh, Hb. Liebmann, *n.v.*). According to Lange (1861), these specimens differ from the type material in Hb. Desf. and have thus been named var. *densiflora* Lange (*Pug. Pl. Hisp.* 101). They may be similar to Salzmann's Tanger specimens which have an unusually large number of flowers per glomerule. Plants collected by Bourgeau (*Pl. Espagne* 1851:1472) are not *T. virgata* but *T. pubescens* subsp. *elliptica*.

Subsp. *virgata* is not very common in Morocco, being habitually replaced by the following subspecies.

21a. subsp. **broussonetii** (Ball)K. Tan, **stat. nov.**
Syn.: *Passerina virgata* Desf. var., Fl. Atl. 1:331 (1798).
T. virgata (Desf.)Endl. var. *broussonetii* Ball in J. Linn. Soc. (Bot.) 16:654 (1878).

Similar to subsp. *virgata* but stems glabrous in lower half or at least near base; middle stem leaves green, glabrous, not grey-villous. Smell reported as foetid.

Fl. May–Jul.; fr. Aug. Abundant and common in uncultivated mountain pastures and valleys in *Cedrus atlantica* zone, basalt and schistose rock, miocene marne. 600–2650 m.
Type. [Morocco] ex Imp. Maroccano, *Broussonet*.
Distribution: NW Africa (Fig. 7).

The following specimens from Morocco are intermediates between the two subspecies in which the middle leaves are subglabrous and the stems villous-pubescent: Great Atlas, *Reading Univ./BM Exped.* 696; Middle Atlas, *Davis* 55131.

T. virgata is a W Mediterranean and Mauretanian steppe species. It is not known definitely to which subspecies var. *rodriguezii* Sennen & Mauricio (*nom. nud.* in *Cat. Fl. Rif. Or.*, 105 (1934)) should be referred, but it seems probable that it is subsp. *broussonetii*.

SUBSECT. SANAMUNDA

22. T. villosa (L.)Endl., Gen. Pl. Suppl. 4(2):66 (1848).
Syn.: *Daphne villosa* L., Sp. Pl. ed. 2, 510 (1762).
P. tingitana Salzm. *apud* Meissn. in DC., Prodr. 14:554 (1857), *pro syn.*
Ic.: Boiss., Voy. Bot. Espagne, t. 157b, f. 1–4 (1842); Figs 4 O & P.

Erect dioecious shrub or subshrub, 20–50 cm. Branches slender, young shoots hirtellous or white-pilose. Leaves laxly imbricate when young, subsessile or shortly petiolate, subcoriaceous, elliptic-lanceolate, (5–)7–11 × (1·5–)2·5–4 mm, acute or obtuse, long ciliate; abaxial surface pilose, old leaves glabrous, with scars from hair bases. Flowers axillary, sessile, solitary. Bracts absent. Perianth 6 mm, yellow, sparsely pilose; lobes lanceolate, 2–3 mm, obtuse, inner pair less hairy. Ovary pubescent at apex; style becoming subterminal. Seed c. 3 mm.
Fl. Mar.–Jun. A calcifuge. Open rocky slopes, forestry roads. Near sea-level–700 m.
Type. [Spain] *Alstroëmer* 235 (Hb. Linn. 500/5).
Distribution: S Portugal and Spain, Gibraltar, Morocco (Fig. 8).

A record from Escorial (ex Cutanda, 1861) is unlikely, that from Tenerife (*fide* Bory St-Vincent in Meissn., *loc. cit.*, 1857) doubtful.

23. T. pubescens (L.)Meissn. in DC., Prodr. 14:558 (1857), non var. *pubescens* Meissn., *op. cit.*, 553.

Suffrutescent dioecious perennial, 5–15 cm. Stems simple or sparingly branched at base, hairy at least in upper parts. Leaves herbaceous, narrowly elliptic, linear-lanceolate or linear-filiform. Flowers axillary, sessile, 1–3. Staminate flowers longer and pistillate often shorter than surrounding leaves. Perianth purplish or pale yellow, tube densely pubescent; lobes ovate or ovate-lanceolate, 0·5–1 mm wide, sparsely pilose. Ovary pubescent at apex. Seed c. 4 mm.

1a. Upper stem leaves ± glabrous when young . . subsp. *thesioides*
1b. Upper stem leaves white-pilose or pubescent when young . . 2

2a. Stems adpressed-pubescent, usually glabrous in lower parts . subsp. *pubescens*
2b. Stems hispid-pubescent throughout . . . subsp. *elliptica*

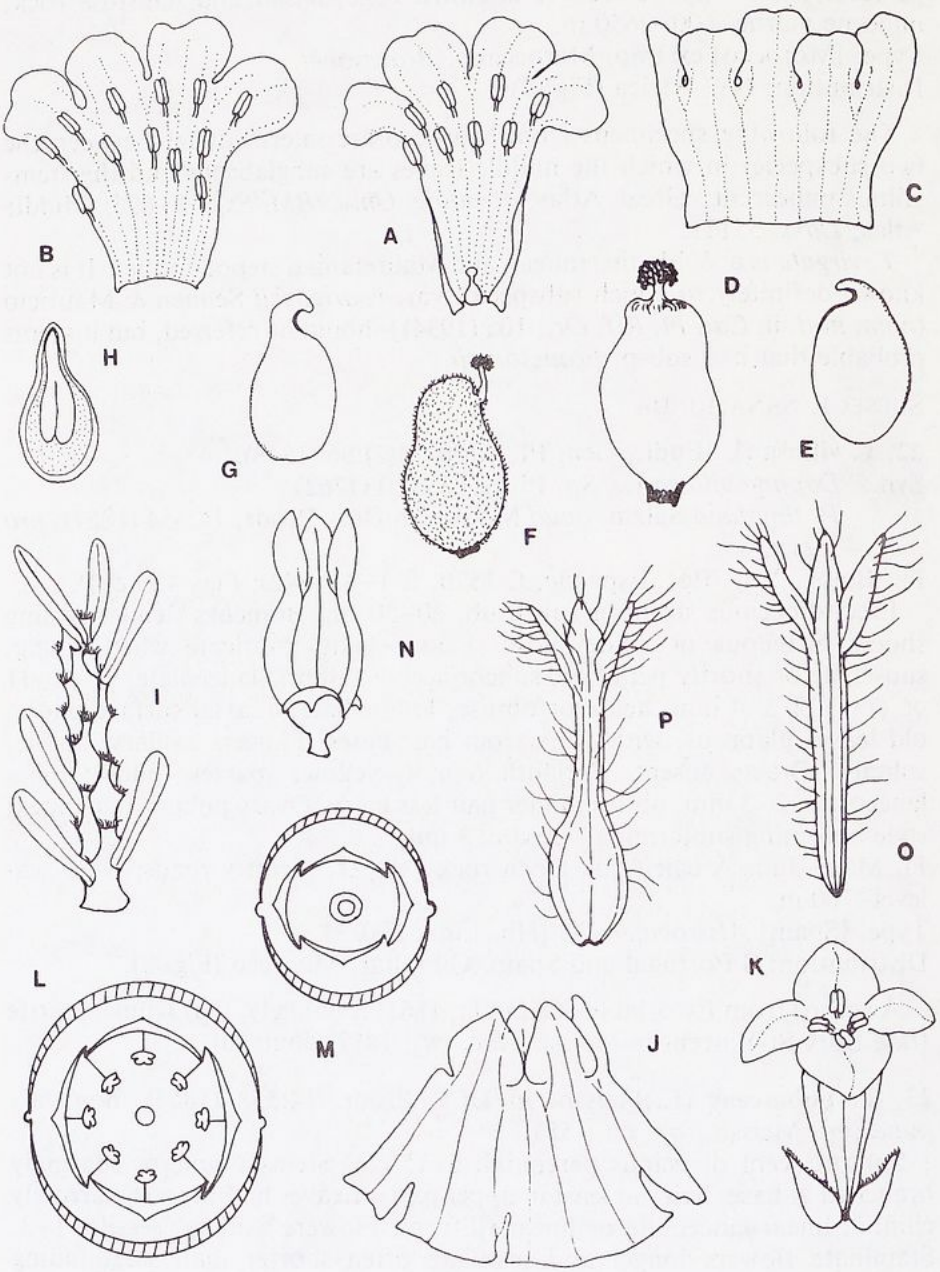

FIG. 4. A–E, *T. hirsuta*: A, staminate flower dissected; B, abnormal staminate flower with 12 stamens and no rudimentary ovary; C, pistillate flower dissected, gynoecium removed; D, fruit (style terminal); E, seed. F–H, *T. dioica* subsp. *dioica*: F, fruit (style subterminal); G, seed; H, seed in L.S. I & J, *T. tinctoria* subsp. *tinctoria*: I, part of stem with raised leaf scars; J, pistillate flower dissected, view from outside. K–M, *T. dioica* subsp. *nivalis*: K, staminate flower; L, floral diagram of staminate flower; M, floral diagram of pistillate flower. N, *T. subrepens*, pistillate flower. O & P, *T. villosa*: O, staminate; P, pistillate flower. I × 1⅓, O & P × 5⅓, all others × 6⅔.

subsp. **pubescens**

Syn.: *Daphne pubescens* L., Mant. 1:66 (1767), non Röhling (1812).
Passerina pubescens (L.)Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 332 (1818).
T. sanamunda All. subsp. *pubescens* (L.)Sagr. & Malag. in Lab. Bot. Sennen. Barc., 9 (1974).

Leaves (8–)10–20 × 1–3·5 mm, glabrous in lower parts of plant.
Fl. Jun.–Jul. Rocky slopes with oak and pine, metamorphic substrate. 600–700 m.
Type. 'habitat in Austria' (Hb. Linn. 500/4).
Distribution: Pyrenees, S and E Spain (Fig. 7).

This subspecies does not occur in Austria which Linnaeus (*loc. cit.*) cites as the country of origin. According to W. T. Stearn (pers. comm.), Linnaeus often ascribed an Austrian origin for specimens obtained from Jacquin.

One collection from the Sierra Nevada (ann. 1849, *Boissier & Reuter*) was found to have mature vegetative parts subglabrous except at stem tips.

23a. subsp. **thesioides** (Lam.)K. Tan, **comb. nov.**

Syn.: *Daphne thesioides* Lam., Encycl. 3:437 (1792).
P. linariaefolia Pourret *apud* Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 333 (1818), *pro syn.*
T. thesioides (Lam.)Endl., Gen. Pl. Suppl. 4(2):66 (1848).
D. humilis Vahl *apud* Willk. & Lange, Prodr. Fl. Hisp. 1:299 (1862), *pro syn.*
P. pubescens (L.)Loscos var. *virgata* Pau in Mem. Mus. Ci. Nat. Barc. (Bot.) 1(3):33 (1925).
T. pubescens (L.)Endl. var. *thesioides* (Lam.)D. A. Webb & Ferguson in Feddes Rep. 74 (1–2):28 (1967).
T. sanamunda All. subsp. *thesioides* (Lam.)Sagr. & Malag. in Lab. Bot. Sennen. Barc., 9 (1974).

Leaves conferted and smaller at base of stems or on sterile shoots, 6–13 × (0·5–)1–2·5 mm, acute.
Fl. May–Jun. Calcareous hills, Jurassic rock, *Pinus sylvestris* forest. 1000–1800 m.
Type. [Spain] communiquée par M. de Jussieu (iso. G.).

Orthography here and as originally published is 'theosioides' but Lamarck used 'thesioides' for plate accompanying description.
Distribution: Spain. Record from Ibiza, Balearics (Margalef, pers. comm.) not checked (Fig. 7).

23b. subsp. **elliptica** (Boiss.)K. Tan, **comb. nov.**

Syn.: *Passerina velutina* Boiss., Elenchus, 81 (1838), non [Pourret ex] Camb. (1827).
P. elliptica Boiss., Voy. Bot. Espagne 2:556 (1842).
T. elliptica (Boiss)Endl., Gen. Pl. Suppl. 4(2):66 (1848).
T. thesioides (Lam.)Endl. subsp. *elliptica* (Boiss.)Brecher in Index Horti Bot. Univ. Budapest. 5:84 (1941).
T. sanamunda All. subsp. *elliptica* (Boiss.)Sagr. & Malag. in Lab. Bot. Sennen. Barc., 9 (1974).

Ic.: Boiss., Voy. Bot. Espagne, t. 158 (1842); Fig. 3 H.

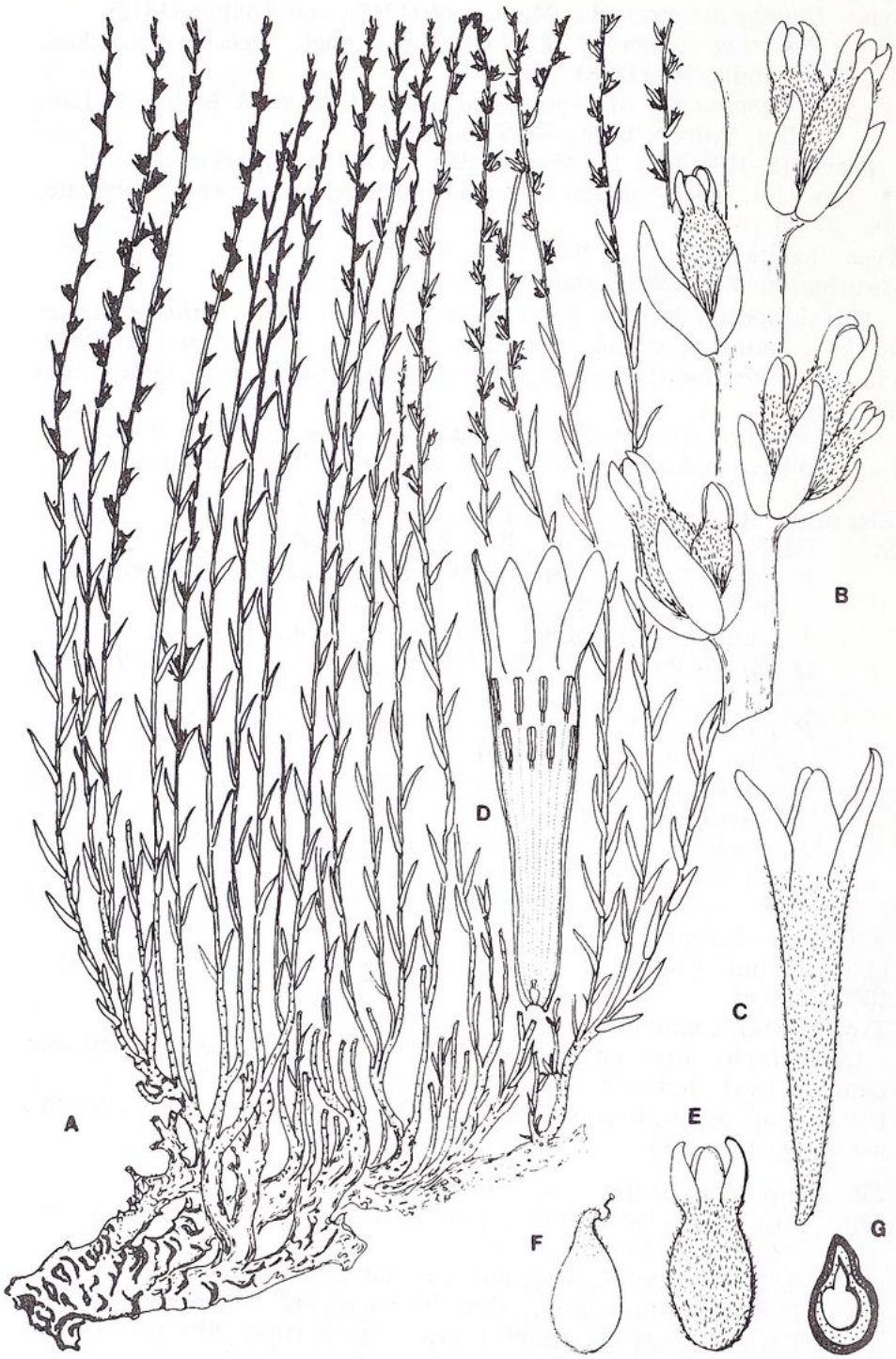

FIG. 5. *T. cilicica*: A, habit (× ⅔); B, part of flowering stem; C, staminate flower; D, the same dissected; E, pistillate flower; F, fruit; G, seed in L.S. (B–G × 6⅔).

Differs from subsp. *thesioides* in having leaves much broader (5–10 × 2–6 mm), acute or obtuse, white-pilose or pubescent when young.
Fl. Jun.–Jul. Mountains, calcareous rock. 1100–2743 m.
Type. [Spain] in aridis calcareis in Sierra Nevada, 1829–2134 m, vi 1837, *Boissier* (holo. G).
Distribution: endemic to S Spain (Fig. 7).

Passerina velutina Boiss. is a later homonym of *T. velutina* (Pourret ex Camb.)Endl. and thus cannot be used for the subspecific epithet.

24. T. sanamunda All., Fl. Pedem. 1:132 (1785).
Syn.: *Daphne thymelaea* L., Sp. Pl., 356 (1753).
Passerina thymelaea (L.)DC., in Lam. & DC., Fl. Fr. 6:366 (1815).
T. bauhinii Endl., Gen. Pl. Suppl. 4(2):66 (1848), cited in Int. Code of Bot. Nomencl. (1956:256) as type of genus.
T. cneorum Reichb., Ic. Fl. Germ. 11, t. 551 (1849).
P. sanamunda (All.)Bub., Fl. Pyr. 1:135 (1897).
Suffrutescent dioecious perennial, 3–30 cm. Stems glabrous or sparsely pilose at tips. Leaves oblong- or ovate-lanceolate, 7–18 × 2–8 mm, acute, glaucous, glabrous on both surfaces, sparsely ciliate. Flowers axillary, solitary near base and midway along stem, in fascicles of 2–3(–5) at tips. Perianth yellow, glabrous or sparsely pilose; lobes lanceolate, acute. Ovary puberulous at apex. Seed c. 3 mm.
Fl. May–Jul. Hills, stony mountains. 600–1800 m.
Type. Described from Spain and Montpellier (Hb. Linn. 500/3).
Distribution: Spain, S France and Italian Riviera. Record from N Africa (Meissner 1857:553) unlikely (Fig. 7).

24a. var. **pubescens** Meissn. in DC., Prodr. 14:553 (1857); Rouy, Fl. Fr. 12:123 (1910).
This variety based on specimens from S France (c. Frejus et Toulon) is unusual in having pilose-pubescent stems and leaves. I have only seen one collection (ann. 1831, *Berreymond* 10).

Section Ligia

25. T. cilicica Meissn. in DC., Prodr. 14:552 (1857).
Syn.: *Lygia multicaulis* Schott & Kotschy in Kotschy, Reise in den Cilicischen Taurus, 381 (1858).
L. cilicica (Meissn.)Boiss., Fl. Or. 4:1053 (1879).
Ic.: Fig. 5.
Suffrutescent monoecious perennial. Stems 15–40, up to 25 cm, slender, erect, simple or sparingly branched at base, green, glabrous, leaves subsessile, not clearly adpressed to stem, narrowly elliptic to linear, 6–10 × (1·5–)2–2·5 mm, acute, glabrous. Flowers in axillary clusters of 2–5. Subtending bracts 2, ovate to lanceolate, 2–5 mm. Staminate flowers 5–6 mm; pistillate 2–2·5 mm. Perianth densely pilose or sericeous in immature flowers, greenish-yellow; lobes reddish-brown.
Fl. Jul.–Aug. Calcareous screes, rocky slopes. 1150–2440 m.
Type. [Turkey C5 Içel] in montibus Ciliciae, c. Güllek Boghas (Cilicischer Engpass), 1158 m, *Kotschy* 234b (holo. G; iso. K, W).

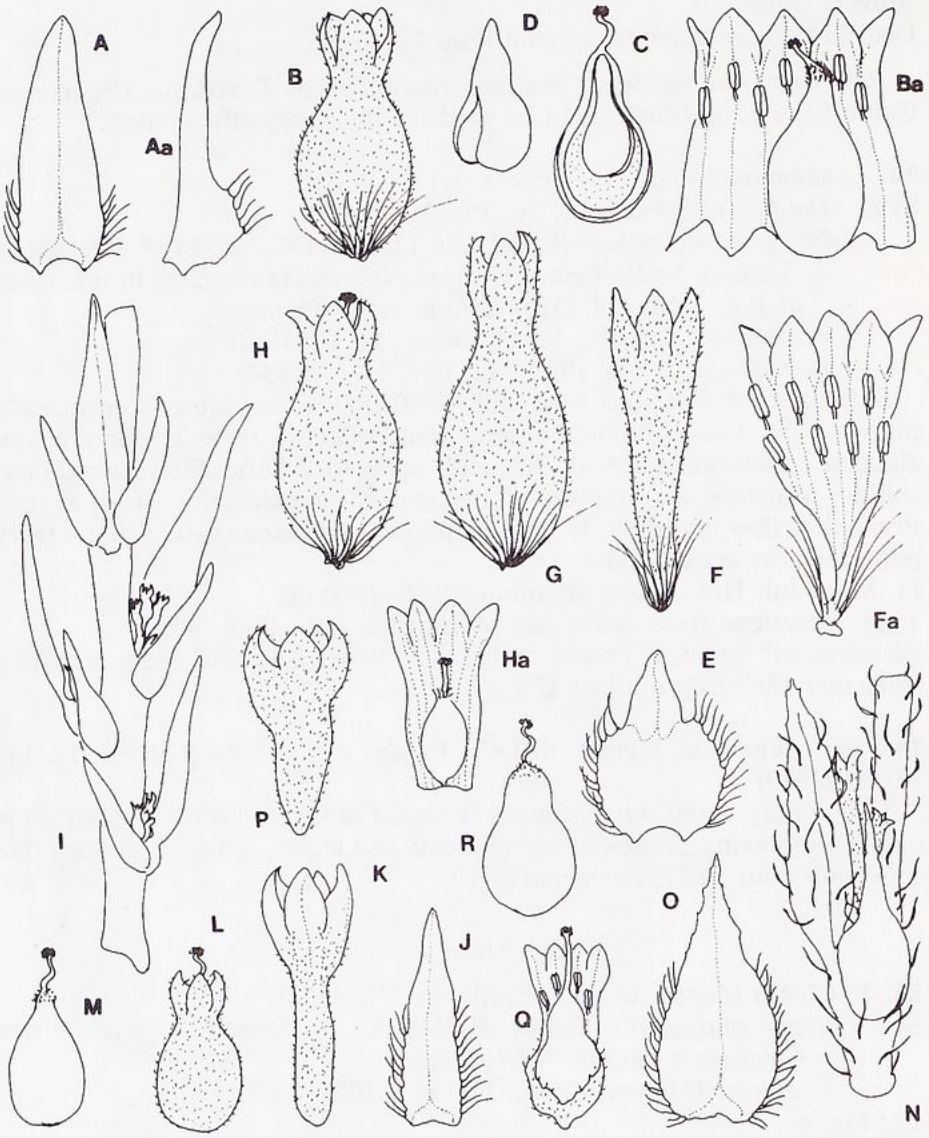

FIG. 6. A–D, *T. passerina*: A & Aa, bracts; B, flower; Ba, flower dissected; C, fruit in L.S.; D, embryo. E–H, *T. gussonei*: E, bract; F, staminate flower; Fa, staminate flower dissected; G, hermaphrodite flower; H, pistillate flower; Ha, immature pistillate flower dissected. I–M, *T. salsa*: I, part of flowering stem; J, bract; K, staminate flower; L, pistillate flower; M, fruit. N–R, *T. mesopotamica*: N, part of flowering stem; O, bract; P, pistillate flower; Q, hermaphrodite flower with only 4 stamens, 2 in each whorl; R, fruit. All bracts in adaxial view except Aa (lateral). All × 10 except I & N (× 6⅔).

Distribution: endemic to S Anatolia (Cilician Taurus) (Fig. 10). Related to *T. aucheri*.

26. T. aucheri Meissn. in DC., Prodr. 14:552 (1857).

Syn.: *Lygia aucheri* (Meissn.)Boiss., Fl. Or. 4:1052 (1879).
Passerina annua Aucher *apud* Meissn., *loc. cit.* (1857), *pro syn.*, non (Salisb.)Wikstr. (1818).
Stellera hedyotis Ehrenb. *apud* Meissn., *loc. cit., pro syn.*
Lygia amani Kotschy *apud* Boiss., *loc. cit.* (1879), *pro syn.*

Ic.: Mout., Nouv. Fl. Lib. Syr. 2: t. 248, f. 4 (1970).

Suffrutescent monoecious perennial. Stems as in *T. cilicica* but 10–18, 30–75 cm, glabrous or with tips minutely pubescent. Leaves subsessile, closely adpressed to stem on drying, linear-filiform, 8–20 × 1·5(–2·5) mm, acute, margins subrevolute, glabrous. Flowers in axillary clusters of 2–5. Subtending bracts 2, ovate, c. 1 mm. Staminate flowers 4–5 mm; pistillate 2·5–3 mm. Ovary hirsute at apex; style terminal or subterminal. Seed c. 3 mm.

Fl. Jul.–Sept. *Pinus* forest, sandstone, degraded slopes, in dry stream beds. 15–1460 m.

Selected syntypes. [Syria] ad Arissam, *Ehrenberg* (orig. B). [Turkey C5 Içel] in monte Tauro, prope portus Ciliciences, *Balansa* 1855:715 (holo. G; iso. E, W); Güllek Boghas, *Kotschy* 1836:426 (K, W).

Distribution: Syria, Lebanon, W Iran; disjunct in N and S Anatolia (Fig. 10).

Three separate sheets of *Kotschy* 1855:257 from Lebanon were examined. One was a teratological fasciated specimen with all stems fused into a solid structure c. 7 mm thick at widest (flowering) part.

The *Thymelaea passerina* complex comprises four taxa: *T. passerina* (L.)Cosson & Germ., *T. gussonei* Boreau, *T. salsa* Murb. and *T. mesopotamica* (Jeffrey) Peterson. Their geographical distributions are shown in Fig. 10. These four taxa are very similar, and their recognition relies on distributional and ecological attributes as well as on phenetic differences.

T. passerina is a weed of arable and wasteland, particularly widespread in early summer. Its leaves and flowers are consistently uniform in spite of a wide geographical and altitudinal range. It is the only species in sect. *Ligia* in which the occurrence of unisexual flowers is extremely rare. *T. gussonei* and *T. salsa* both have a more southerly distribution; the former in the Mediterranean, the latter restricted to NW Africa and S Spain. They also grow in more arid areas, often on dry and sandy soil. *T. salsa*, although very similar to *T. passerina*, can be distinguished from that species by its unisexual flowers, ± glabrous perianth lobes of the staminate flowers, and the glabrous or minutely puberulous apex of the ovary in the pistillate flowers. *T. mesopotamica* is restricted to the Mesopotamian region in Turkey, Iraq and Iran. It is generally smaller both in height and leaf than the other species, also all parts are crispate-pilose. The flowers are unisexual—only one or two imperfectly hermaphrodite flowers (without the full complement of stamens) have been observed.

It is rather difficult to decide how to treat this species-complex but since the constituents can be easily distinguished, it is perhaps preferable to

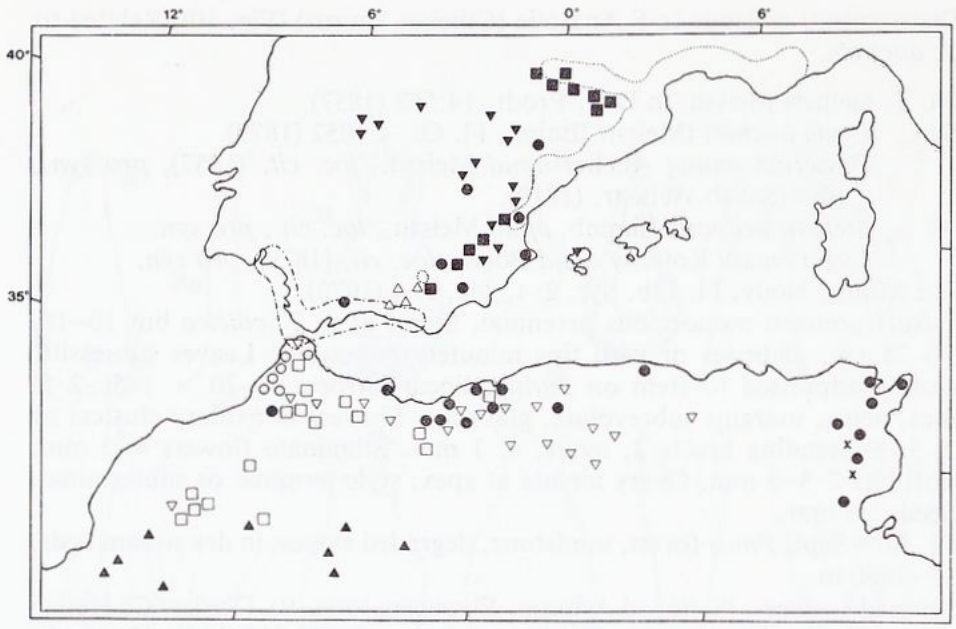

FIG. 7. Distribution of sect. *Piptochlamys:* ○ *T. lythroides;* ● *T. argentata;* × *T. sempervirens; T. lanuginosa,* line of dots and dashes. Sect. *Thymelaea:* ▲ *T. antiatlantica; T. virgata* subspp. ▽ *virgata* & □ *broussonetii; T. pubescens* subspp. ■ *pubescens,* ▼ *thesioides* & Δ *elliptica; T. sanamunda,* dotted line.

maintain all four as separate species rather than to regard them as subspecies of *T. passerina*.

The presence of two bracts and a superior ovary readily distinguishes sect. *Ligia* from *Thesium* in the Santalaceae; the latter bears a superficial resemblance to the *T. passerina* complex, and is often confused with it in herbaria.

27. T. passerina (L.)Cosson & Germ., Syn. Fl. Env. Paris, ed. 2, 360 (1859); Fl. Env. Paris, ed. 2, 586 (1861).

Syn.: *Stellera passerina* L., Sp. Pl., 559 (1753).
T. arvensis Lam., Fl. Fr. (ed. 1) 3:218 (1778).
Ligia passerina (L.)Fasano in Atti Accad. Napoli., 245 (1788).
S. annua Salisb., Prodr., 282 (1796).
Passerina stellera [Ramond ex] Lam. & DC., Fl. Fr. 3:361 (1805).

Ic.: Griffith, Ic. Pl. Asiat. t. 534 (1854) as *P. diarthronoides* Griffith; Nasir, Fl. W Pakistan 12:7, f. 2a–c (1971); Figs 6 A–D.

Erect annual. Stem (10–)15–60 cm, simple or strictly branched, green, glabrous or very sparsely pilose at tips. Leaves subsessile, linear-lanceolate, 5–20 × 1–2·5 mm, acute, glabrous, very rarely with a few hairs on abaxial surface. Flowers hermaphrodite, axillary, 1–5(–7). Subtending bracts 2, lanceolate, 2–3 mm, sparsely ciliate at base. Perianth 2·5–3 mm, adpressed-pubescent, greenish-yellow; lobes ovate, 0·5–1 mm, obtuse. Ovary hirsute at apex; style terminal. Seed 2–3 mm. 2n = 18.

Fl. late Apr.–Aug. Fallow fields and stony pastures, railway embankments, eroded slopes, dry river beds, salt-flats. Sea-level–2590 m.

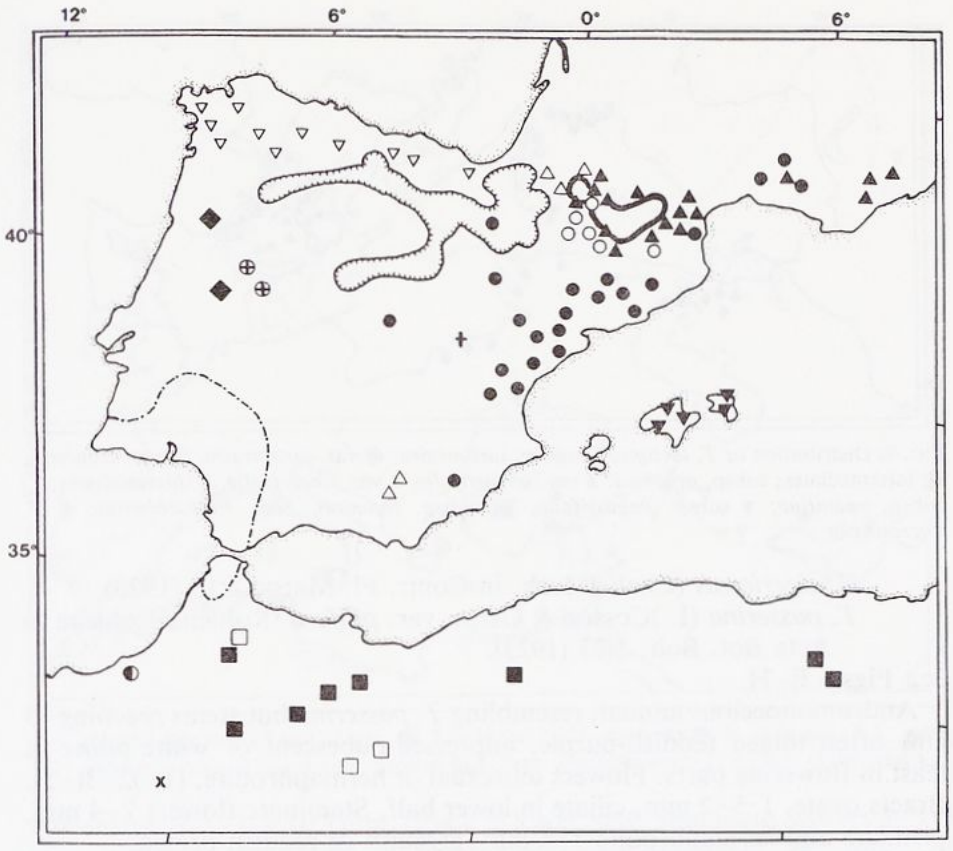

FIG. 8. Distribution of sect. *Piptochlamys:* ◐ *T. gattefossei; T. virescens* vars ■ *virescens,* □ *glaberrima;* × *T. putorioides.* Sect. *Chlamydanthus: T. dioica* subspp. ▲ *dioica* & Δ *granatensis;* ▼ *T. velutina; T. tinctoria* subspp. ● *tinctoria* & ○ *nivalis;* + *T. subrepens;* ⊕ *T. procumbens;* ▽ *T. coridifolia;* ◆ *T. broteriana; T. ruizii,* hatched line; *T. calycina,* continuous line. Sect. *Thymelaea: T. villosa,* line of dots and dashes.

Type. Described from Europe (Hb. Linn. 503/1).
Distribution: Widespread. C and S Europe, SW Asia, C Russia eastwards to C Asia. Introduced among fodder seed into Australia and N America. No records from S America or S Africa (Fig. 10).

28. T. gussonei Boreau in Mém. Soc. Acad. (Angers) 4:121 (1858) as '*T. gussoni*'.

Syn.: *Stellera pubescens* Guss., Fl. Sic. Prodr. 1:466 (1827), non *T. pubescens* (L.)Meissn. (1857).
Passerina annua (Salisb.)Wikstr. var.*pubescens* (Guss.)Ten., Syll. Fl. Nap., 565 (1831).
P. annua (Salisb.)Wikstr. var. *algeriensis* Chab. in Bull. Soc. Bot. Fr. 36:319 (1889).
T. passerina (L.)Lange var. *sericea* Coutinho, Fl. Port., ed. 1, 177 (1913); ed. 2, 213 (1939).
T. puberula Hand.-Mazz. in Ann. Naturh. Mus. (Wien) 27:86 (1913).

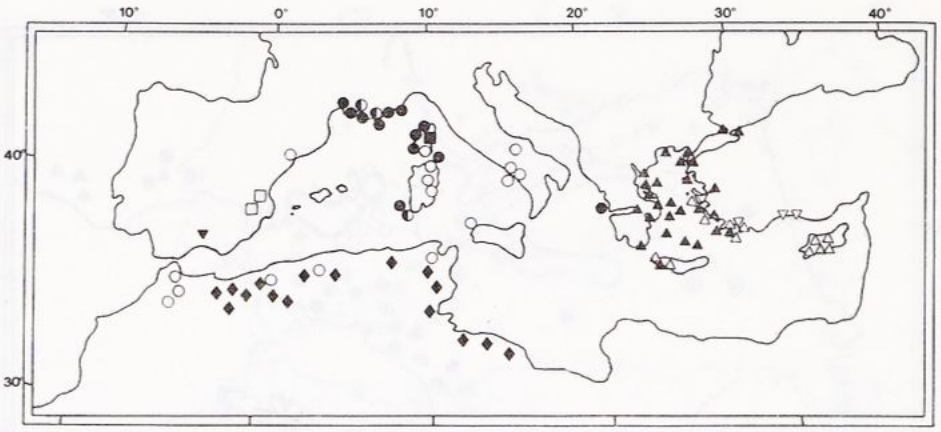

FIG. 9. Distribution of *T. tartonraira* subsp. *tartonraira:* ● var. *tartonraira,* ○ var. *transiens,* ◐ intermediates; subsp. *argentea:* ▲ var. *angustifolia,* Δ var. *linearifolia,* ∇ intermediates; □ subsp. *valentina;* ▼ subsp. *angustifolia;* ■ subsp. *thomasii. Sect. Piptochlamys:* ◆ *T. microphylla.*

T. algeriensis (Chab.)Murb. in Contr. Fl. Maroc 2:13 (1923).

T. passerina (L.)Cosson & Germ. var. *pilifera* (Rohlena)Rohlena in Acta Bot. Boh. 2:23 (1923).

Ic.: Figs 6 E–H.

Andromonoecious annual, resembling *T. passerina* but stems reaching 75 cm, often tinged reddish-purple, adpressed-pubescent or white-pilose at least in flowering parts. Flowers unisexual or hermaphrodite, (1–)2–3(–5). Bracts ovate, 1·5–2 mm, ciliate in lower half. Staminate flowers 2–4 mm, pistillate and hermaphrodite 3–5 mm, greenish or reddish-brown.

Fl. late Apr.–Sept. Dry fallow fields, sand dunes, calcareous and rocky slopes. Near sea-level–920 m.

Type [Sicily] in argillosis, inter segetes et post messen in arvis, Palermo, *Gussone.*

Distribution: S Europe, Turkey, Cyprus, W Syria, Algeria, Tunisia; recorded from Crimea (Fig. 10).

This species is more southern and restricted in distribution than *T. passerina*, the peak flowering period is a little later, August to September rather than April to June. The frequently reddish-purple stems of *T. gussonei* may be related to the arid soils on which it grows.

Two specimens (*Reverchon* 179, *Wheeler-Haines* 1216) were observed to be intermediate in character and may be of hybrid origin.

29. T. salsa Murb. in Lunds Univ. Årsskr. n.s. 19(1):11 (1923).

Syn.: *P. annua* (Salisb.)Wikstr. var. *salsa* Munby, Cat. Pl. Alg., 30 (1866), *nom. nud.*

T. passerina (L.)Lange var. *salsa* Munby in Lit. & Maire, Contr. Gr. Atlas, Mém. Soc. Sci. Nat. Maroc, 35 (1930), *nom. nud.*

Ic.: Murb., *op. cit*, 12: f. 2a–c (1923); Figs 6 I–M.

Monoecious annual. Stems erect, 10–45 cm, strictly branched, green or tinged reddish-purple, glabrescent or subglabrous at tips. Leaves linear-lanceolate, 6–10 × 1–2 mm, acute, glabrous. Flowers unisexual, axillary, 2–3(–5), usually in a cluster of a single pistillate with 2 staminates. Bracts 2,

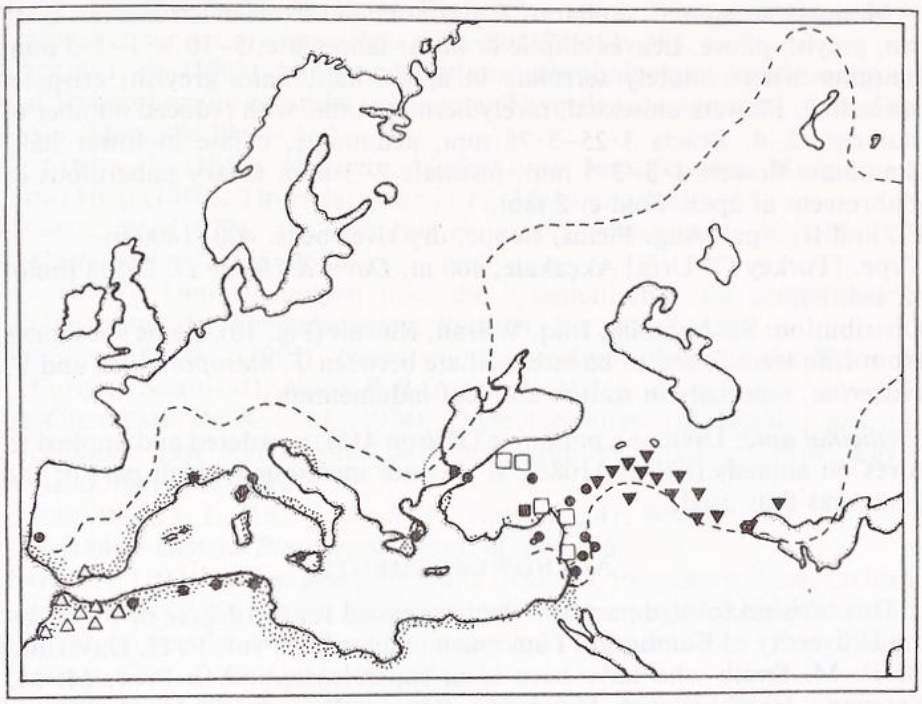

FIG. 10. Distribution of sect. *Ligia:* ■ *T. cilicica;* □ *T. aucheri;* ● *T. gussonei;* Δ *T. salsa;* ▼ *T. mesopotamica; T. passerina,* broken line. Sect. *Piptochlamys: T. hirsuta* (stippled area).

lanceolate, 2·5–3 × 0·5 mm, ciliate in lower half. Staminate flowers 3–3·5 mm, pistillate 1·75 mm. Perianth adpressed-pubescent but lobes of staminate flowers ± glabrous, greenish-yellow; lobes ovate, 0·5 mm. Ovary subglabrous or puberulous at apex; style terminal or subterminal. Seed 1·5–1·7 mm.
Fl. and fr. Apr.–Oct. Dry places, salt flats. 800–1300 m.
Type. [Algeria] Rel. *Maillefer* no. 1650 (LD).
Distribution: S Spain, Morocco and Algeria (Fig. 10).

Individuals with hermaphrodite flowers have been recorded by Murbeck (*op. cit.*: 11) but this state appears to be extremely rare and has not been observed in the material examined by me.

The affinities of *T. salsa* are with *T. mesopotamica* from which it can be distinguished by the glabrous stems and leaves, the smaller size of its bracts, pistillate flowers and fruits, and the ± glabrous perianth lobes of the staminate flowers. From *T. passerina*, the other glabrous annual species, it can be recognized by the occurrence of unisexual and not hermaphrodite flowers, the smaller size of the fruit when mature, the non-hirsute ovary apex, and the more ciliate nature of the subtending bracts.

30. T. mesopotamica (Jeffrey)Peterson in Rech. fil., Fl. Iranica 95:8 (1972).
Syn.: *T. arvensis* Lam. var. *pubescens* (Guss.)Meissn. in DC., Prodr. 14:552 (1857), *p.p. excl. typ.*
Ligia mesopotamica Jeffrey in Kew Bull. 22:469 (1968).
Ic.: Jeffrey, *op. cit.*, 470: f. 1; Figs 6 N–R.

Monoecious annual, similar to *T. passerina* but stems much shorter, 6–35 cm, greyish-pilose. Leaves elliptic or linear-lanceolate, 5–10 × 1–1·5 mm, margins often remotely serrulate in apical half, hairs greyish, crispate-spreading. Flowers unisexual, rarely hermaphodite with reduced number of stamens, 2–4. Bracts 3·25–3·75 mm, acuminate, ciliate in lower half. Staminate flowers 1·5–3·5 mm, pistillate 2–3 mm. Ovary puberulous or glabrescent at apex. Seed c. 2 mm.
Fl. and fr. Apr.–Aug. Fields, steppe, dry river beds. 400–1400 m.
Type. [Turkey C7 Urfa] Akçakale, 400 m, *Davis & Hedge D.* 28108 (holo. K, iso. E).
Distribution: SE Anatolia, Iraq, W Iran, Kuwait (Fig. 10). Some specimens from Iraq were found to be intermediate between *T. mesopotamica* and *T. passerina*, especially in stature and leaf indumentum.

Medicinal note: Used as a purgative (*Wilson* 413), powdered and applied to sores on animals (*Gillett* 11088). It was not mentioned which part of the plant was thus used.

ACKNOWLEDGMENTS

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LIST OF SELECTED EXSICCATAE

The name of the collector is followed by the number or date (or locality) of the collection, then the herbarium symbol and lastly the number of the species in parentheses (see synopsis, pp. 201–202). int. = intermediate between.

Aberdeen Univ. Amanus Exped., D1/307, J1/587, E (27); L1/766, E (26)
Aitchison, 668, E (27)
Al-Rawi, 11515, E (27); 14334, 20628, 20783, 21493, 22858, 22999, 27902, K (30); 21630, 22816, 23076, E, K (int. 27 & 30)
Al-Rawi & Gillett, 7149, 7399, E, K (30)
Alava, 10759, E (30)
Alava & Bocquet, 5283, E (27)
Alava & Regel, 4824, E (10b)
Alerido, 18 v 1926, holo. *P. oscilans*, K (1)
Alexander & Kupicha, 320, E (10a)
Alinoğlu, 23, 39, E (27)
Allen, B. M., 7677, E (22); 9868, E (2)
Alpay, 519, Hub.-Mor. BASEL (27); 525, Hub.-Mor. BASEL (2)
Archibald, 799, E, K (1); iv 1962, E (2); ii 1966, E, K (2)
Aucher-Eloy, 1879, 2819, K (10c); 2521, K (2); 2892, K (28); 2932, E (28)
Autheman, 10 iv 1879, K (10); ix 1891, E (10)
Aylies, 9 iii 1920, BM (10a)
Aznavour, 25 ix 1893, 15 viii 1897, G (28); 8 x 1893, 6 vii 1897, 1909, G (27)

B–Hb. Willd. 7535 (24). 7536 (12a); 7537 (17); 7538, 7586, holo. *P. orientalis* (13); 7539 (22); 7540 (10a); 7542 (23a); 7581 (2); 7589 (21); 7590 (5); 7591, holo. *P. canescens* (3)—all seen as microfiche
Baccarini *et al.*, 15 iv 1905, E (2)
Backhouse's coll., vi 1882, K (12)
Balansa, B., 1852:255, K (5); 257, E (21); 978, E (27); 1853:1007, iso. *T. virescens* var. *virescens*, E, K (6); 1854:322, W (10b); 1854:373, BM, E, K, W (10b); 1855:715, W (26)
Baldacci, 222, E (27); 25 vi 1893, BM (2)
Ball, J., 1 & 3 x 1849, E, K (int. 12 & 12a); 26 vi 1851, E, K (10e); 26 vi 1851a, 27 vi 1851, E, K (23b); 20 vii 1860, E (12); 22 vi 1861, E (12a); 14 viii 1861, E (13a); x 1867, E (10b); ann. 1887, E, K (22); 914a, v 1842, 9 xi 1854, x 1867, iv 1874, 1877:58, E (2); ii 1880, E (8); vi 1841, iv 1874, E (10a); Pannoniâ, Riva di Garda, E (27); Barga, E (28); Tanger, E (21)
Balls, E. K., 2812, E, K (21a); Marseilles, E (10)
Bauer & Spitzenberger, 1628, W (10b)
Bauer *et al.*, 2269, W (10b)
Bayliss, 115, E (30)
Baytop, A., 8235, ISTE (2); 14765, ISTE (10b)
Baytop, A. & T., 12611, E, ISTE (10b); 36544, ISTE (int. 10b & 10c); 30983, 33619, ISTE (27); 31 xii 1973, ISTE (2)
Bean, 16 iii 1912, E, K (13a)
Beauverd, 23 vi 1935, holo. *T. tartonraira* var. *candiliana*, G. (10b), *n.v.*
Becker, vi 1867, E (13a)
Bentham, viii 1839 & 1871, E (12a); s.n., E, K (28)
Berreymond, ann. 1831, K (24a)

Bianor, 15 ix 1910, E (2); 5 vi 1911, 15 v 1913, 8 iv 1919, E (11)
Billot, C., 4 iii 1862, K (10)
Birand, H., 20 viii 1955, ANK (2); 11 v 1956, ANK (10c)
Blanche, s.n., E (26)
Bocquet, 2653, G (10b)
Boissier, E., ann. 1837, Murcia, E (13); ann. 1837, Gibraltar, E (22); ann. 1837, S. Nevada, E, G (27); vi 1837, Marbella, E (3); vii 1837, holo. *P. tartonraira* var. *angustifolia*, G, iso. E, K (10d); Elenchus no. 172, holo. *P. velutina*, G, iso. E, K (23b); vii 1879, iso. *T. floribunda*, E, K (16); v & vi 1881, E (11); mt Torbol, E, G (26); Valencia, E (24)
Boissier, E. & Reuter, G. F., ann. 1849, Oran, K (5); ann. 1849, S. Nevada, E (23); ann. 1849, Tanger, E, K (22); S. de Ronda, E (29)
Bordère, P., vi 1860, E (13a); vi 1865, E (12a); vii 1868, E, K (12); vi 1869, K (16); vi 1869 as *P. elyptica*, vi 1873, vi 1874, vi 1876, E, K, P (23); vii 1879, K (int. 12 & 12a); Broto, E (27)
Borel, s.n., E (27)
Bornmüller, 12326, E (2)
Boujean, s.n., K (12)
Boulos, 5475, 6241, BM (2)
Bourgeau, 1847:182, K (24); 1847:183, K (12); 1848:335, K (10); 1851:1472, E, K, P (23b); 1851:1473, E, K (10d); 15 x 1851, 1853:2024, ii 1880, E (2); 13 vi 1852, E (5); 1853:2025, E, P (22); 4 vii 1854, E (24); 1856:27, E, K (21); 1860:242, E, K, W (int. 10b & 10c); 1869:2792, E (11); 1870:143, BM, E, K, LD, W (10c)
Bové, iv 1839, K (5); ix 1839, K (28)
Bozakman & Fitz, 181, W (10c)
Bramwell *et al.*, 71, K (1)
Britton, 63, BM (2)
Brummitt, 12838, K (16)
Brummitt & Chater, 245, K (18)
Buchinger, 12 vi 1802, K (22)
Burtt, B. L., 617, E (27)
Buttler, K. P., 15659, 15861, Buttler–MUNICH (27)
Buttler & Erben, 17232, 20310, Buttler–MUNICH (27)

Callier, 267, E (27)
Cannon, 4175, BM (2)
Campo, P. del, 1852:87, 1852:89, E, K (23); 20 vi 1859, K (23b)
Casaviella, iii 1882, iv 1888, K (16)
Casey, 960, E (28)
Chapel, ann. 1837, E (2)
Chapman, E., 342, 553, K (10c); 346, 420, K (2); 676, K (28); 9328, K (30); 26350, K (int. 27 & 30)
Charpin & Greuter, 8405, E (12)
Charrel, 17 vi 1891, E (27)
Chase, W., H.743, K (5)
Chesney, 189, E (27)
Choulette, Frag. Fl. Alg. 183, syntype *T. algeriensis*, E, K (28)
Church, ann. 1819, K (10)
Clarke, Troy, BM (10b); 28553, BM, E (27)
Cosson, 5 vi 1862, E, P (24)
Creswell, 12, E (27)
Cunha, R. da, s.n. COI (19)
Curle, 38, E (2)

Darrah, 614, E (26)
Dautez & Reverchon, 18 iv 1889, E (3)
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Deflers, 1135, 1136, K (10c)
Delacour, 2 iii 1862, K (10); s.n., E (27)
Dickson, 126, K (30)
Dinsmore, 15335, E (2)
Dresser, 605, 699, E (16); 1066, E (18)
Drummond, 14372, E (27)
Duchartre, s.n. K (12)
Dufour, Arag. no. 1693, K (23a)
Duthie, 12093, 15487, E, K (27)

Elias, 33891, 17 iv 1907, LISE (16)
Ellman & Hubbard, 831, K (23b)
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Enberger, Grand Atlas, MPU (6)
Endress, vi 1829, K (12); vii 1830, E, K (12); ann. 1831, Pyr. centr., E, K (17); ann. 1831, Pyr. occid., K (12a); v 1831, E (12 & 13a)
Faure, 30 v 1907, LD (29); 12 vi 1907, 26 iv 1930, E (5); v 1909, E (2); ix 1929, K (29); 17 vi 1930, K (5); 30 v 1934, E (8); 18 vii 1935, E (21); Oran, E (28)
Feinbrun, s.n., E (27)
Feinbrun & Zohary, 75, BM, E (2)
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Fischer, C., Rhodos, M (10b)
Fitz & Spitzenberger, 93, M, W (2)

Foggie, 384, E (10c)
Forbes, 546, K (int. 10b & 10c); xii 1841, E, K (2)
Forskål, 532, holo. *P. metnan*, C (2)
Forsyth-Major, 57, E (10b); 349, E, K (10b); 21 v 1884, E (10a)
François, vi 1869, K (23)
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Frödin, 207, W (28)

Gaillardot, s.n., E (26); Doumar, E (28)
Gandoger, 80, E (5); vi 1904, K (15); 21 vii 1894, K (16); Rhône, E (27)
Gathorne-Hardy, 86, 467, E (10b)
Gattefossé, 2 iv 1935, K (1); 1 viii 1935, K (21a); 1 i 1936, K (4)
Gay, J. Hb., ii 1822, K (12); 3 ix 1823, K (17)
Genneou, ARI 1394, K (10c)
Gibbs, 27.63, E (2); 81.5, E (22)
Gibbs & Dominguez, 85.1, E, K (23a)
Gillett, 8200, 11088, K (30); 15871, K (2); 12407, E (27)
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Grant, 1887:5, K (1); 12 & 13 iii 1887, iso *T. lythroides*, P (1); Oued Mehedouma, K (29)
Greuter, 7692, E, W (2)
Grenier, ann. 1839, K (int. 12 & 12a)
Gross, s.n., K (27)
Grundl, s.n., E (27)
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Guiol, 1733, BM (10b)
Guirao, 5 iii 1855, E, K (10e)

Haffner, s.n., E (27)
Hakim, 14, holo. *T. puberula*, W (28)
Halbaek, 59a, K (2); 1262, E (30)
Handel-Mazzetti, 403, W (28)
Hardy, 30 ii 1945, BM (2)
Harrold & McBeath, 56, E (16); 308, E (13a)
Hart, ann. 1883–84, Petra, Beersheba, BM (2)
Haussknecht, 23 vi 1865, W (26); 1885, BM, E (10b)
Hedenborg, ann. 1854, LD, W (int. 10b & 10c); s.n., Rhodos, W (2)
Hedge, 17.54, E (2)
Heer, s.n., E (27)
Heldreich, 659, E (27); 18 iii 1841, K (10)
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Henriques, s.n., BM (19)
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Hirmer, M., 27 iv 1933, M (10b)
Hohenacker, s.n., G (26)
Hooker, Hb., 16 vii 1859, K (12); 1867:40, 69, K (13a); iv 1871, K (22); v 1871, K (29)
Hort, L., Valle di Venda, E (27); s.n., E (12)
Huber-Morath, 5379, 14248, Hub.-Mor. BASEL (int. 10b & 10c); 17469, Hub.-Mor. BASEL (10b)
Huet du Pavillon, s.n., E (28)
Hunting Aero Survey, 1955:87b, E (2)
Hurst, ann. 1875, Ramleh, BM, K (2)
Huter *et al.*, 1879:869, K (10d); 1879:870, E, K (23b)
Huxley, 17, E (23a)

Irat, v 1846, E (24)
Irvine, 3265, E (1)

Jahandiez, 1924:225, E (1); 462, E, K (21a); 946, K (29); 1925:210, E, K (6)
Jlić, s.n., E (27)
Johnston, s.n., E (27)
Jordan, Hb., Bouches-du-Rhone, K (10)

Karamanoğlu, 308, 29 iv 1961, ANK (10c)
Karelin & Kiriloff, 1845:1935, E (27)
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Kjellqvist & Snogerup, 22042, LD (10c)
Koelz, 11579, E (27)
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Kotte, 25 vi 1932, ANK, M (27)
Kralik, Pl. Tunet. 1894:332, syntype *T. algeriensis*, E, K (28); Pl. Tunet. 1894:333, iso. *T. microphylla*, E (8)

Lacaita, 471, holo. *T. granatensis*, K (12a); 16 vi 1928, E (12a); 1928:670, K (18)
Lacerda, A. F., vi 1885, E (19)
Lacibe, M., 5 viii 1939, K (12)
Lainz, 28 v 1957, E, K (23a); 9 v 1960, K (18)
Lalis, xii 1828, v 1830, K (10)
Lambert & Thorp, 532, E (27)
Lange, J., 184, syntype *P. cantabrica*, K (18); 29 viii 1854, K (23a)
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Lascelles, A. G. & M. E., iii 1901, K (10c); iii 1902, K (2)
Laukkonen, P., 58, K (2)
Léveillé, s.n., E (27)
Levier, 12 vii 1879, E, K (16); s.n., E (27)
Lewejohann, TU-74-066, E (int. 10b & 10c)
Lindberg, H., 30 vi 1939, K (10c)
Lindsay, 1353, E (27)
Lloyd, s.n., K (int. 10 & 10a)
Lojacono, 194, E (28)
Loso, vii 1928, E (18)
Lowne, ann. 1864, Acre, K (2); ann. 1864, Beersheba, BM, K (2)

Mabille, P., 10 v 1866, E, K (10a); 1867:269, E, K (28)
Macdonald, 13, K (2)
McNeill, 817, E, K (2)
Macreight, vi 1831, E (12); ann. 1832, K (12)
Maillard, A., 28 v 1857, K (10)
Maire, R., 25 iii 1937, K, MPU (20); 1937:107, K (20)
Mardochée, Ida Oubahil, Adrar Mgora, K (20)
Maw, G., 28 iii 1873, E, K (8); Djelfa, E (10a)
Meebold, v 1928, K (12)
Mavromoustakis, G. A., 12, 18, 18b, K (10c)
Meikle, 2648, K (10c); 2913, K (2)
Meister, 1162, E (27)
Melville, 7015, K (2)
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Meyers, 156, E (28)
Meyers & Dinsmore, B.1054, E (27); B.5054, E (28); 3335, 7335, E (2)
Moller, 1890:880, E, K (19)
Moloney, 6682, E (27)
Money-Coutts, 61009, BM, E (13a); 11 iv 1962, BM (10b)
Mouterde, s.n., E (28)
Müller, s.n., E, K (10)
Munby, ann. 1844, K (5); x 1847, x 1848, K (28); vi 1849, E, K (21); 1851:68, holo. *P. salina*, K (29); Mitidja, le Figuier, E, K (28)
Murbeck, Gafsa, E, LD (8)
Murray, vi 1807, BM, K (19)

Neyraut, 30 viii 1903, P (12)
Nilsson, 26 vii 1883, LD (29)
Noë, v 1944, ANK (2)
Nyárády, s.n., E (27)

Orphanides, 1850:270, BM, E (2)
Oxijuk, s.n., E (27)

P– Hb. Juss. 3975 (10d); P– Hb. Lam. Encycl. 3:436 no. 9 (10); P– Hb. Tourn. 5811 (22); 5818 (24); 5819 (13a); 5820 (13); 5821, left-hand side (3); 5821, right-hand side of sheet (2); 5824 (10); 5825 (10b); 5827 (2); 5828 (10c)—all seen as microfiche
Pampanini, 5346, BM (2)
Pampanini & Pichi-Sermolli, 5355, K (2)
Parlatore, s.n., E (28)
Pau, 22 iv 1908, holo. *T. segobricensis*, E (5)
Paunero *et al.*, 1940:69, E, K (21a); 1973:69, E (1)
Perret, iv 1874, E (2)
Peyron, s.n., E (26)
Piaget, Hb., 14 iv, K (10)
Pichler, v 1876, BM (10b); s.n., E (27)
Pinard, C., 29 iv 1880, K (12); 13 v 1884, K (10)
Pirotta, 896.1, E (2)
Pitard, 1452, 1453, 1454, K (29); 1455, K (4); iii 1907, E (8); iii 1912, E, K (22); vi 1912, E, K (21); 2 v 1913, K (22)
Planchon, 8 iv 1857, K (10)
Podlech, 11670, 11967, E (27)
Pohl, 7452, E (27)
Polunin, 6019, E (27); 6676, K (2)
Poore, 521, E (30)
Porta & Rigo, 27 iv 1885, E (11); 1890:101, 1891:63, E, K (10e); 1891:132, K (23a); 1891:185, K (23); s.n., E (22)
Post, B., 12 v 1878, iv 1886, BM (2); 13 vi 1882, G (30)
Post, B. & G., 24, E (27)
Postian, 12 viii 1898, BM (10c)
Pourret, 124, FI (10e); 2390, 6319, syntypes *P. kalifolia*, MAF (3)
Price, 1306, 1314, K (12)
Probyn, F. M., ann. 1950, Messoria, K (2); ann. 1950, Troodos, K (10c)

Ramley, 5 iv 1870, E (2)
Reading Univ./BM Exped., 696, BM, E (21a)
Rechinger, K. H., 43, 7634, 12932, BM(2); 3576, K, LD (10b); 5401, E, K, LD (10b); 7968, BM, E (10b); 9653, E (30); 15273, W (27); 18207, K, W (10b); 57417, G (27)
Regel, s.n., E (27)
Reichenbach, fil., K (12)
Rein & Fritsch, vi 1872, K (29); Casablanca, E (2)
Requien, ann. 1820, K (10); i 1848, E (10)
Retz, 29392, K (12)
Reuter, Geneva, E (27)
Reverchon, 1 & 6 iv 1881, E (2); 24 v 1884, E, W (10c); 1885:33, E (24); iv 1895, v 1895, iii & iv 1896, E (14); 1886:138, E (12); 1887:108, E (22); 1891:596, E (13); 1891:601, 1894:601, Orihuela, E, K (23a); v 1898, E (5); 179, E (int. 27 & 28); Basses Alpes, E (27)
Rigo, s.n., E (27)
Ripley, H. D., 1933:6, K (23b)
Rogers, 1931:5453, K (2)
Romain, 1649, E (2); viii 1849, E, K, LD (29)
Ross, 1900:278, E, K (10)
Rothmaler, W., 8 viii 1933, holo. *T. dendrobryum*, JE (18), *n.v.*
Rugel, vi 1837, K (12); vi 1839, E (12); vii 1839, E (24)
Rugels, v 1839, K (10)
Runemark & Bothmer, 46447, E, LD (10b)
Runemark & Snogerup, 11434, 19945, LD (int. 10b & 10c); 12553, LD (10c)

Salzmann, viii 1821, K (10); ann. 1825, E, K (21); viii 1825, holo. *P. tingitana*, K (22); ann. 1835, E, K (22)
Sandwith, 3312, 4785, K (27); 5199, 5232, 5897, K (16); 5382, 5707, K (23a); 4773, 5545, 6307, K (23)

Sardagnay, M., 6 vi 1883, K (10)
Sauvage, 8667, K (1)
Scheppig, s.n., E (27)
Schilbersky, s.n., E (27)
Schlosser, s.n., E (27)
Schoenefeld, s.n., E (27)
Schott, s.n., E (22)
Schousboe, 121, K (22); Tanger, holo. *P. ciliata*, E, K (22); Hispania, Gibraltar, syntypes *P. canescens*, C (3)
Schultz, vi 1860, K (10); v 1888, K (12)
Scott-Elliott, 3549, E (2)
Sennen, 793, E (13)
Shuttlesworth, 26 iv 1863, BM, K (10)
Sibthorp, no 882, syntype *T. tartonraira* subsp. *argentea* var. *angustifolia*, K, OXF (10b); Rhodos, sub *D. dioica*, E, K, W (int. 10b & 10c); Samos, Hb. Linn. 500/16a (10c)
Sieber, s.n., E (10c)
Siehe, W., 1898:249, 372, Z (27)
Silva & Teles, 8733, LISE (16)
Simon, C., 6 vii 1955, LD (27)
Simpson, 460, 2244, 4162, K (2)
Sintenis, P., 1883:267, BM, E, K, LD, Z (10b); 1883:795, E (27); 1883:685, 1890:2611, 1892:4708, viii 1892, LD (27); 1888:17, LD (2); 1888:188, 1304, 1401, 1624, 1624b, LD (30)
Sintenis & Bornmüller, 1891:1568, LD (27)
Sintenis & Rigo, 1880:10, BM, K, W (10c); 1880:86, K (2)
Smith, G. E., s.n., E (27)
Socalski, 287, E (27)
Soligman, R., 48, K (10a)
Somerville, 63, E (2)
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Sorger, 62-97-15, 68-2-104 (27); 1979:17 (6a); 1979:24 (1), all at Hb. Sorger, WIEN
Spence, 210, E (21a)
Stapf, 518, E (30)
Stewart, 26434, E (27)
Stocken, 271/64, E (3)
Syngrassides, 495, 1749, K (2); 496, 1479, K (10c)

Täckholm *et al.*, ann. 1963, Sollum, K (2)
Tan, K., 65, 129, 134, 158, 272, E (13); 373, E (2)
Taubert, 117, E (8)
Tengwall, 69, K (2); 84, K (int. 10b & 10c)
Thompson, 16 iv 1870, 2 xi 1878, 29 v 1884, E (2)
Tholin, A., 8 iii 1879, K (10)
Thomas, P., ann. 1823, Corsica, K (10f); 1825:387, 572, E (24); Cagliari, E (2)
Timbal-Lagrave & Marçais, vi 1885, E (13a)
Tobey, 1152, E (27)
Todaro, 255, E (28); 358, K (10)
Townsend, T.34, K (24); 71/46, K (10c)
Tricker, s.n., E (27)
Trethewy, 28, 233, 234, K (1)
Turrill, 681, E (27)

Unar, 1543, E (27)
Uotila, 19581, E, Hub.-Mor. BASEL (27)
Uscher, 9 iii 1937, K (2)
Uslu, T., 3433, ANK, Hub.-Mor. BASEL (27)

Vaccari, A., 118, K (10c); 1442, K (10); s.n., E (27)

Walker, 809, 899, BM (10b)
Walker-Arnott, 555, K (12); 652, 871, E (12)
Walker-Arnott & Bentham, 77, E (2); 872, E, K (24); 1529, E (13a); s.n., E (12)
Wall, E., 23, Hub.-Mor. BASEL (27)
Wängsjö, E. & G., 2733, LD (27)
Walther, 3390, LD (10b)
Warburg, 4 xi 1901, BM (10c)
Warion, 950, K (29); vii 1877, E (21)
Webster & Nasir, 6287, E (27)
Welwitsch, F., 403, E (22)
Wendelbo, 2041, E (30)
Wheeler-Haines, 368, 718, 910, 1595, E (30); 1216, 1580, E (27); 1216b, E (int. 27 & 28)
White, 23 iv 1902, E (10a)
Whiting, 1335, E (2)
Wiesbauer, s.n., E (27)
Willkomm, H. M., 298, E (2); 1844:670, E (22); 847, K (22); 1844:1147, S. de Chiva, E, K (23); 20 viii 1845, COI (29); Jaca, E (24); Alcudia, E (11)
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Yurdakulol, E., 99, ANK, Hub.-Mor. BASEL (26)

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