TAXONOMIC STUDIES IN SOME THYMELAEACEAE

by

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TAXONOMIC STUDIES IN SOME THYMELAEACEAE
Abstract of thesis

Title of thesis: Taxonomic studies in some Thymelaeaceae.

The work deals mainly with the morphological and anatomical investigation of some Thymelaeaceae occurring in the Mediterranean, S. W. and C. Asiatic regions. It broadly falls into four parts.

1. Part A is a short introductory section, defining scope and aims.
2. In parts B and C, the variation in morphological and anatomical characters is surveyed. This includes studies on the stem, leaf, inflorescence, flower, sex-distribution, fruit and seed, etc. Synoptic descriptions of five genera are given. The species of Stelleropsis and Dendrostellera are transferred to Diarthron, involving fifteen new combinations. The relationships of the genera are discussed and evolutionary trends in the family pointed out.

3. Part D includes a taxonomic revision of Thymelaea itself. The classification proposed is purely phenetic in origin and is intended to replace the existing one by Brecher (1941). Four sections, seven subsections and thirty species are recognized. One new species, T. gattefossei, is described.

The thesis is illustrated by 65 figures, 9 plates, 18 maps and accompanied by two appendices, an index and cited references.
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PART A

INTRODUCTORY SECTION
CHAPTER 1 Introduction

1.1 Scope and aims

Eight genera, Daphne, Dendrostella, Diarthron, Restella, Stellera, Stelleropsis, Thymelaea and Wikstroemia, all of Thymelaeaceae subfamily Thymelaeoideae, occur in the Mediterranean, S.W. and C. Asiatic region. The first named can be distinguished from all others in the area, by fruits with succulent or semi-coriaceous pericarps.

Taxonomic classification in the family is often rather difficult because many of the traditionally accepted genera often have no well-defined limits. Peterson (1959) refers to this problem when revising the Thymelaeaceous genera of the African continent. To give an example, the only generic characters used to distinguish Arthrosolen C. A. Meyer, Gnidia L. and Lasiosiphon Fresen. are the number of calyx lobes and the presence or absence of petals (petaloid appendages). In my study I have referred to the same structures as the perianth, since in the eight genera examined there were no petals. However, floral anatomy showed that the perianth lobes are probably sepaloid in origin (see Sect. 4.1). To go back to the African muddle, the number of sepals and the presence or absence of petals were found not always to be constant. In view of this, Peterson finds it impossible to keep the genera separate but treated all three as Gnidia.

Clearly demarcated species which form complexes of their own but are closely related could be better treated as subgenera rather than genera. This makes the latter larger but more 'natural'. I have in mind several
groups like *Stellera*, *Stelleropsis*, *Dendrostella* and *Diarthron*, and would certainly enlarge the genus *Diarthron* to include the C. and S. W. Asian species of *Stelleropsis* and *Dendrostella*. There appears to be no justification in maintaining small, separate genera for species with hairy or glabrous/pubescent perianths. The two genera *Daphne* and *Wikstroemia* also cannot be easily separated when we move to the tropics. Since genera show 'tendencies' to merge into each other, in such cases, the treatment seems to be a matter of convenience. One of the aims of this study was to find the most suitable characters for generic delimitation.

The present work broadly falls into three parts. Parts B and C include a general treatment of the genera occurring in the area. Descriptive accounts are given, variation in morphological and anatomical characters surveyed with the intention of finding some useful information for generic delimitation and infra-generic classification.

Part D contains the general and systematic treatment of *Thymelaea*. This genus was suggested for investigation by my supervisors, especially from the point of view of stem and leaf anatomy. It was hoped that anatomical characters would be useful to reinforce taxonomic classification based on external morphology, especially for delimitating sections or distinguishing certain species. The main taxonomic source is Endlicher's (1848) account which was the first attempt to place all the then known species under two genera and two sections. Since then, the number of species has approximately doubled, mainly due to increased collecting particularly in N. Africa, Spain and the Middle East, thus rendering his treatment a little inadequate. Meissner's account in *de Candolle's Prodromus* (1857) and Brecher's (1941) more extensive revisions are useful references. In general, the latter's
major sections based on exomorphic characters have been accepted. In my study I have attempted to assign the heterogeneous group of species in Subsect. *Euthymelaea* (Lange) Brecher to further subsections, and to attempt to correlate anatomical characters with some exomorphic ones. Although the taxonomic history of a genus usually corresponds with the pioneering plant explorations of early collectors, it is surprising that since Endlicher's classification (130 years ago) only twice as many species have been known. This suggests that the genus is certainly not vigorously expanding and speciating. Davis (pers. comm., 1978) was unable to find any of the species during a recent visit to the Spanish Pyrenees. Species have mainly been known through various descriptions and citation in floristic works, e.g. Lapeyrouse (1813), Willkomm & Lange (1862). In the taxonomic revision, species limits, identification, distribution and their phenetic relationships are dealt with.

Since the temperate genera were considered to be already rather specialised groups, evolutionary trends that might have occurred in the family were sought from a study of the more primitive members. Six of them, *Gonystylus*, *Amyxa*, *Aëtoxylon*, *Aquilaria*, *Octolepis* and *Microsemma*, all with one exception, occurring in the S.E. Asian and W. Pacific basin, were studied at generic level.

*Passerina* L. is a fairly small genus (with c. 15-20 spp.) endemic to S. Africa. It has been included in the study mainly because most of the species in the area have come under this Linnean name at one time or other and several, in fact, were thus listed in herbaria. Its morphology, anatomy and floral biology also afford an interesting contrast to the other genera. The flowers are small, with exserted stamens, often compacted into showy
masses at or near the ends of slender, pendulous branches with linear subulate leaves. They are reported to be wind pollinated.

Herbarium studies have yielded much information but there are many other problems which remain to be investigated. For example, the cytology and phytochemistry of the genera is little known. That of Daphne, and to a lesser extent, Wikstroemia, are among the sparsely documented few. Cytological studies in this investigation were hampered by the lack of suitable material; such studies would be useful in understanding relationships between species. As regarding how this special topic is related to a wider field of knowledge, it is but a small contribution to our present knowledge and assessment of the family. It would be particularly useful if the entire family could be revised throughout its geographical range. This would result in better and more consistent generic treatments as well as giving some indications as to the affinities of the family.
PART B

TAXONOMIC EVIDENCE RELATING TO GENERA
PART B TAXONOMIC EVIDENCE RELATING TO GENERA

CHAPTER II EXTERNAL MORPHOLOGY

The diagnosis of a genus should ideally contain those characters whose states in the genus concerned best serve to distinguish it from related genera. It was found impossible to recognize genera on single characters alone and combinations of several characters had to be employed. This chapter is a descriptive account of the range of variation in morphology, relating to the nine genera investigated. Characters which were easily observed are selected and described. The taxonomic importance of these is evaluated when it is felt they may aid in elucidating generic relationships.

2.0 Materials and Methods

The work has been based mainly on the herbarium and living collections of the Royal Botanic Garden, Edinburgh. For studies on indumentum and pollen (including scanning electron microscopy), specific reference regarding the provenance of material examined, can be found in Appendix A. Materials and methods for studies on seed germination are described separately under Sect. 2.6. For examination of all plant parts other than those mentioned below, no special procedures were necessary except to select material wisely.

Floral parts: herbarium material was softened by gentle simmering in water for 2 - 5 minutes. A drop of liquid detergent (commercial Squezy) promoted rapid sinking. Flowers were examined under a
binocular dissecting microscope with low-power objectives (x 1.25 and x 5). Some were stained in leucobasic fuchsin (modified after Fuchs, 1963), dehydrated and mounted in Euparal, but this procedure was used mainly for anatomical studies.

**Pollen for light microscopy:** fresh or dried flowers were used. Herbarium samples were boiled in water for two minutes, centrifuged and strained through 60 mesh gauze. The pollen and debris were washed in glacial acetic acid, then acetolyzed according to the procedure outlined in Erdtman (1960). For each species, a total of 2 - 10 flowers from as many different collections was sampled (refer Appendix A). Untreated pollen was initially mounted in 10% lactic acid which caused crumpled grains to expand and resume their original size. However, further swelling in some samples, brought about a 8 - 15% increase in diameter, which calculation was obtained by comparing measurements of grains from fresh, recently dehisced anthers of the same species. To allow for comparable observations the grains were later all acetolyzed and mounted in the same medium — glycerol jelly stained with safranin. Slides were left inverted till the jelly set, so that the grains fell close to the coverslip. Semi-permanent slides thus made kept well for two years. A few permanent slides, as sources of future reference, were also prepared by sealing coverslips with paraffin wax. All size measurements given are the mean equatorial diameters (range included) of acetolyzed pollen, mostly from herbarium material, and are presented in micrometers (µm). Photomicrographs were taken on Ilford Pan F film, with a Leitz Dialux Microscope, using bright or dark field optics.
Method used to obtain percentages of fertile and abortive pollen: in living material examined, the upper anthers dehisce at approximately the same time as anthesis. The stigma in hermaphrodite flowers is covered with pollen at this stage or 1 - 2 days after. So, nearly mature flower buds were collected. The undehisced anthers were carefully dissected out in a drop of aceto-carmine (formula according to Belling, 1928). A coverslip was placed in position and the anthers gently tapped (not squashed) with the blunt end of a needle. The slide was passed through a spirit flame 5 - 6 times. A minimum total of 500 grains over various fields under High Power, was counted with the aid of an eyepiece grid. The number of grains which did not take up stain was noted. This represented abortive pollen in the sample and was expressed as a percentage (Table 1). When the source was herbarium material, judicious sampling of an inflorescence gave a good approximation of flower age.

Pollen for scanning electron microscopy (SEM): to avoid difficulties in obtaining undistorted images while examining pollen, the following procedure was carried out. The pollen was acetolyzed as described for light microscopy. When dried, the samples were folded up in filter papers. The aluminium stubs for the SEM were rubbed on wet carborundum paper, rinsed in water and dried, immediately before use. A very thin film of adhesive (commercial Durofix) was smeared on the surfaces of each stub. The stub was inverted so that the sticky surface lightly touched the filter paper bearing the pollen. It was examined under a low power microscope to ensure that sufficient pollen had adhered. The stub must not be pressed hard on to the paper in case surface detail will be destroyed or the pollen sink into the adhesive. All the stubs
were then 'spattered' with gold. I tried to view the specimens as soon as possible after coating, but think that some poorly defined images obtained on the screen were due to oxidation of stub or coating during the long interval between preparation and scanning. This was to some degree, unavoidable as the SEM instrument, as well as having to be booked in advance, had a heavy workload and tended to 'break down' on Mondays. While waiting to be examined, the specimen stubs were stuck on polystyrene sheets in dustproof boxes. The instrument used was a Cambridge Stereoscan with a range of x 50 to x 50,000 but only those magnifications at x 750 to x 20,000 were employed. Photomicrographs were taken over a 40-second exposure, when the image on the visual screen was satisfactory.

For SEM studies on seed surfaces, stem and leaf indumentum, a similar procedure was followed, except of course that the material was not acetolyzed. Severe 'charging' was the most common problem encountered; this was mainly due to bad electrical conductance. But to evaporate a thick coating of gold over the surface so as to cover each epidermal hair, thus ensuring better conductance, would mask detail and cause coating cracks during prolonged exposure to the electron beam. The use of the 'black level' to reduce light intensity was not employed at high magnifications as this would create a false impression of depth. Acetolysis of pollen definitely reduces poor definition, excessive contrast and glare. Surprisingly few grains underwent distortion or collapse (implosion or explosion) in the high vacuum of the coating chamber.
2.1 Vegetative Parts

2.1.1 Habit and life form

Following the plant life-form categories of Raunkiaer with revised subdivisions (Ellenberg & Mueller-Dombois, 1967), the great majority of species would be classified as woody or herbaceous perennials. The annual habit is shown by only six species. Raunkiaer's system (1934) is based mainly on the location of the renewal buds. This criterion is said to express the ability of the plant to endure the unfavourable season better than any other feature. In 1953, Orshan pointed out that in arid regions where water is the most decisive factor, classification of life-forms should be based instead on criteria expressing the hydro-ecological behaviour of the plants. Such criteria are provided by those parts of the plant which are seasonally renewed and/or seasonally lost. He has divided his four life-forms into two main groups: a) drought-escaping, i.e. annuals and 'whole-shoot shedders' and b) drought-enduring, i.e. 'branch-shedders' and 'leaf-shedders'. The categories embracing Orshan's modifications are thus presented below.

1. Nano (1-2 m tall) - or micro-phanerophytes (2-5 m tall): the renewal bud is at least 25 cm above ground. They are small trees with a single trunk (Pacific Wikstroemias) or caespitose shrubs in which the oldest shoots of the same order are branched from near the base, e.g. Daphne (Plate1A), Passerina, Restella, Wikstroemia. Some are cold- (not necessarily in winter) or drought-deciduous. Orshan's category of 'leaf shedders' is not applicable in more mesic conditions.
2. **Frutescent chamaephytes**: include most phrygana shrubs which would be referred to Orshan's 'branch shedders' but for the Thymelaeaceae would be included in his 'leaf shedders' category instead. They are caespitose dwarf shrubs not usually exceeding 1 m in height, 'woody' all the way to the branch tips and periodically shed their leaves only. The two most common growth forms encountered are the reptant, e.g. *Thymelaea* subrepens, with bowed-down, decumbent branches, and the cushion type, e.g. *T. granatensis*, which forms compact little clumps. *D. petraea* and *D. jasminæa* are two of the Daphnes with a prostrate habit. New plants can often be obtained successfully in cultivation by layering. In nature they often produce suckers or underground runners, thus achieving vegetative spread.

3. **Suffrutescent chamaephytes**: *Dendrostellera, Stellera, Stelleropsis, Thymelaea*. This category includes all herbaceous and suffruticose perennials that exhibit a periodic die-back during the unfavourable season. The latter group refers to those with a woody root-stock (which remains active) and numerous, virgate, herbaceous stems which die down at the end of each growing season (Orshan's 'branch shedders' if each stem is regarded as a branch). The shoot-crowding habit and tuft appearance of these genera are due in part to the degree of branching and the angle of ascent of the new shoots produced at the base (Plate 1B). In *Dendrostellera*, the base or lower third of these stems usually become thickened and lignified, although the upper portions remain herbaceous. In more favourable habitats or a wetter season, the height reached may be more than 50 cm, but if they do reach 100 cm, the shoots thin out rapidly. In contrast to the shrub habit, height differences are not as important. Instead, the degree of lignification and the habit of the shoot system
are more important.

Herbaceous chamaephytes are the non-woody, evergreen perennials that seldom grow taller than 30 cm ('whole-shoot shedders'). The stems die back periodically to a remnant shoot system all at once, i.e. almost like therophytes: *T. aucheri* and *T. cilicica* of *Thymelaea* Sect. *Ligia* are good examples.

4. *Annuals*: may be classified as small to medium-sized, with a height of 3 - 30 cm. They are single-stemmed (may branch) and live much shorter than a year, completing their life cycle within one favourable growing season and dying after seed production. The six species in this category are late spring or early summer flowering—*Diarthron* (2 spp.) and *Thymelaea* Sect. *Ligia* (4 spp.). Although considered to be more protected against drought because they pass the unfavourable season as seeds without vegetative organs, their geographical distribution is not restricted wholly to arid regions.

Among the genera examined, the 'branch shedders' (suffrutiocose perennials) inhabit more arid regions. 'Whole-shoot shedders' (herbaceous perennials) and 'leaf shedders' (frutescent chamaephytes) are found in more mesic conditions. This is in accordance with Orshan's analysis of the dominating species in plant communities of three phytogeographical regions of Palestine (1953).
A. *Daphne girdlidi*. Shrub in early spring. Buds are the future leafy shoots of a year's growth. Cult. RBG, Edinburgh x 1/5.

2.1.2 Root and stem

As herbarium specimens rarely show any roots, one has to rely on field notes or dig up seedlings and adult plants in the field, or grow them. Erosion exposing the soil profile shows that the roots of *Thymelaea hirsuta* and *T. tinctoria* have developed from a branched taproot system. In suffrutescent chamaephytes, root features recognisable above ground are restricted to the semi-subterranean, woody rootstock. In *Stellera chamaejasme*, the taproot increases in width during each growing season. A plant 10 inches tall may have a taproot 3 cm thick.

The outer cortex of the root is strong and pliable. From Theophrastus we learn that the root of *D. oleoides* was long, useful 'for binding, like withy'. That of *Stellera chamaejasme* was described by the Tibetan Lamas as being excellent for the manufacture of good quality paper.

Stems and branches are in general, slender and flexible. Young bark is reddish brown or light grey; older bark dark grey to purplish-black, thin or moderately thick, relatively smooth and never fissured. Like the root, it is so tough and pliant that specimens must be cut with knife or secateurs to avoid tearing it off in long strips (see Sect. 3.3). Such bark is useful for making rope and twine; *T. hirsuta* has been employed by the natives in Cyrenaica, *D. bholua* and *D. papyracea* by the Himalayan Jhamsuries for such purposes.

Internodes vary in length, depending on the leaf arrangement, whether lax or densely crowded. The position of the inflorescence affects the overall habit of the plant, being either apical, lateral on branches
or cauliflorous. Because it is fairly complex, it is referred to in
greater detail in Sect. 2.3. The inflorescence is a useful character
for delimiting certain genera, sections and species.

2.1.3 Leaf

Leaves are sessile or petiolate, alternate in all the genera except
Wikstroemia. A few Chinese Daphnes, namely D. aurantiaca and D. genkwa
have opposite, subopposite or alternate leaves. Young leaves are im-
bricately arranged and may remain so although leaves of a previous
year's growth or those on the lower branches or part of branches, may
have a strongly decumbent posture. This is a characteristic feature
of some species, e.g. Thymelaea virescens. In T. tinctoria and related
species, leaf-fall preceded by the formation of a thick abscission
layer results in a very conspicuous raised scar on the branches; I
refer to this scar as 'tuberculate'.

Leaves are evergreen or shed in times of cold or drought. Bud pro-
tection during the resting season is from the imbricate, often in-
curved, tightly adpressed leaves. Stipules are absent in all genera.

Most Mediterranean species have semi-sclerophyllous or sclerophyllous
leaves, i.e. they are not soft to the touch. In others, the leaves
are malacophyllous, i.e. they collapse when steamed, e.g. Daphne striata,
Stellera and related genera (see Sect. 3.1.2). Some become almost
subulate or narrowly cylindrical with inrolled margins, e.g. T. brot-
eriana. The leaf shape in this shrub gives it its heath-like appear-
ance.
Leaf size varies from the nanophyllous (<1 cm$^2$) to mesophyllous (<50 cm$^2$). Broad leaves are characteristic of the more mesophytic Daphnes of the Himalayan regions, where apparently, the same species is deciduous at higher altitudes but can be evergreen lower down, e.g. D. bholua. The leaves were found to be narrowest in Passerina and Thymelaea, with a range of 0.25 to 5 mm. Within an individual genus like Daphne, the width varies even more extensively.

Margins are always entire but have been found to be minutely toothed in D. rodriguezii, a rather rare endemic from Menorca. Leaves in adult plants of T. lythroides may show a difference in size and shape but this is not a constant feature in all specimens examined, and I cannot really refer to them as being seasonally dimorphic. They are persistent.

Scanning electron micrographs show that the epidermal cells are flat or raised (Plate 2A); the stomata are invariably sunken (Plate 2B). Cuticular waxes provide an astonishing array of patterns but this line of investigation could not be pursued for lack of time.
2.2 Indumentum

The nature of stem and leaf indumentum is a character of specific distinction and the presence or absence of it allows some infra-specific ranks to be recognised, e.g. *T. tartonraira* subsp. *thomasii*. Similarly, its presence or absence on perianth parts is taxonomically useful and aids in the identification of closely related species. However, one must always bear in mind the odd glabrous form occurring in species populations which are predominantly hairy.

In the majority of species, the young shoots, if initially pilose or tomentose, gradually become glabrescent. The hirsute or setose tuft surrounding the base of vegetative and floral buds usually remains.

The hairs are all unicellular, thin- to thick-walled and knee-shaped at the base. Some indumentum types are illustrated by scanning electron micrographs (Plate 2C-F), mostly the straight adpressed, villous and canescent-tomentose. Lepidote or stellate hairs, as found in the Elaeagnaceae (Plate 2G,H), a family considered to be related to the Thymelaeaceae, are absent.
PLATE 2. Scanning electron micrographs of stem and leaf surfaces.

A. Daphne oleoides. Adaxial leaf surface. Stomata under over-arching subsidiary cells. x 1375.

B. Thymelaea tartonraira subsp. thomasii. Adaxial leaf surface. Stoma sunken. x 6250.

C. Thymelaea tartonraira subsp. argentea var. argentea. Adaxial leaf surface. Hairs adpressed, straight (Indumentum described as silvery sericeous). Stomata sunken. x 575.

D. Thymelaea tartonraira subsp. tartonraira var. transiens. Adaxial leaf surface. From a specimen somewhat intermediate between var. tartonraira and var. transiens. x 650.

E. Thymelaea hirsuta. Adaxial leaf surface. Hairs curled and matted (Indumentum described as tomentose). x 3000.

F. Thymelaea virgata subsp. virgata. Stem surface. Hairs twisted (Indumentum described as villous). x 650.

G. Hippophae rhamnoides. Adaxial leaf surface. Lepidote or stellate hairs. x 600.

H. Elaeagnus angustifolia. Adaxial leaf surface with similar hairs. x 600.
2.3. Inflorescence

The consideration of the whole plant when in flower, not just the flower-bearing parts alone is necessary when studying the inflorescence. Workers have not always been consistent when referring to the latter structure. For example, in species of Thymelaea Sect. Ligia it is described as representing an axillary cyme but only the lateral flower clusters were considered. However, when the inflorescence of Wikstroemia chamaedaphne is described as paniculate (Blatter, 1929), the sterile shoot is recognised as well! Different levels of homology are referred to and keys based on such morphological statements do not reveal the structure of the inflorescence although they may be descriptively correct.

In the Thymelaeaceae the inflorescence is described as basically racemose (Airy-Shaw, 1973). Two main types are found in the taxa studied. The diagrammatic sketches (Figs. 1-3) are not meant to illustrate an evolutionary scheme but to show variations in the form of the inflorescence.

The first type (Figs. 1 & 2) can be represented as a free-growing shoot in which flower development does not terminate apical growth. With the formation of periderm and secondary xylem, the axis can become permanently woody. Flower clusters are lateral or if terminal, there is a growing point located below the inflorescence so that the latter is not truly terminal.

The second type (Fig. 3) is an apical inflorescence, the axis of
which becomes completely adapted to floriferous functions. It remains herbaceous to some extent or is deciduous. Little or no periderm and secondary xylem is formed. The shoot apex thus does not remain indefinite after having developed a number of flowers. In Diarthron, Dendrostellera and Stelleropsis, successive opening of the flowers is accompanied by an elongation of the axis but no further vegetative growth occurs at the inflorescence. Anatomical study of the floral axis in Diarthron vesiculosum shows that it is monopodial, i.e. not built up by the coalescence of separate branches.

The first type with the growing point at apex or located below inflorescence, because it is never terminated by a flower, belongs to the "polytelic" type of Troll (1964). If the inflorescence is later overtopped by a vegetative shoot, this shoot repeats the structure of the main axis and thus would be considered as a "paracladium" by Weberling (1965), whether it produces flowers or not.

The second type with the growing point abortive corresponds to the "monotelic" type of the above mentioned workers and gives rise to the overall "habit" of annuals and suffrutescent chamaephytes. The apex of each leafy shoot is terminated by an inflorescence, there are no other floral branches (paracladia) from each main axis. In this group are Diarthron, Stelleropsis and Dendrostellera which have the axis elongating during or after anthesis and without any floral bracts. Also Stellera which has the axis not elongating and the inflorescence umbellate by elimination of internodes, surrounded by leaf-like bracts. The
increase in number of flowers compensates for the decrease in ovule number; the dense arrangement and uniform orientation of the flowers is probably related to pollination ecology, forming an attraction unit.
A. *Daphne laureola*. Flowers pedicellate, bracteate.

B. *Daphne glomerata*. Subumbellate, ebracteate.

C. *Daphne mezereum*. Leaves deciduous before flowering.

D. *Passerina filiformis*. Branch leafy throughout, bracts coriaceous.

E. *Thymelaea tartonraira*. Bracts numerous.

F. *Thymelaea subrepens*. Bracts 2.

G. *Thymelaea dioica*. Bracts 2-6.

H. *Thymelaea argentata*. Flowers terminal on very short leafy branches.

J. *Thymelaea microphylla*. Flowers on very short branchlets or ramiflorous.
Fig. 2 A-Fa. Inflorescence types. Growing point located below, inflorescence not truly terminal (Type I).

A. *Wikstroemia chamaedaphne*. Paniculate.
Aa, Ab. Stages in development.

B. *Restella albertii*. Subumbellate, axis not elongating.

C. *Daphne oleoides*. Umbellate.


E. *Daphne gnidium*. Paniculate.

F. *Daphne arbuscula*. Umbellate. Leaves crowded at apex to become subtending bracts.
Fa. Bracts removed to show future direction of vegetative growth.
Fig. 3 G-L. Inflorescence types. Inflorescence terminating growing point (Type II).

G. **Thymelaea virgata**. Bracts numerous.

Ga-Gc. Probable stages in condensation of flower clusters.

H. **T. passerina**. Bracts 2.

I. **T. sanamunda**. Bracts absent.

J. **Pimelea cornucopiae**. Involucre cupular, 4-lobed.

Ja. Involucre dissected to show flower attachment.

K. **Dendrostellera lessertii**. Subumbellate, axis elongating during and after anthesis.

Ka, Kb. Stages in development.

L. **Stellera chamaejasme**. Umbellate, axis not elongating. Leaves crowded at apex to form 'involucre'.
2.4 The Flower

2.4.1 Bract

It is difficult to define the bract. I have limited the term to that structure which can usually be distinguished morphologically from the vegetative leaf and when it subtends a flower — pedicellate or sessile.

Skottsberg (1972) states that absence of bracts is the rule in the Thymelaeaceae but four of the genera investigated have bracts in some species (Figs. 1-3). The main function of the bracts is the protection of the bud in the developing stage. They are pale coloured or green and leaf-like, persistent or deciduous. Like leaves, they show variation in number, size, shape, texture and indumentum. Within genera, the number of bracts characterize some sections, e.g. *Thymelaea* Sect. *Ligia*, or even subsections. It is not dependent on the number of flowers they subtend. In the same inflorescence, they may be unequal in size and the lengths of both outer and inner bracts are described relative to the length of the flower, i.e. whether longer or shorter. This in turn depends on whether the flowers are staminate or pistillate.

Bract texture is either herbaceous or scarious; coriaceous bracts are rare. They are strongly ribbed or keeled in *Passerina*. Indumentum again is variable but usually consistent for a species. The upper or adaxial surface is usually the pubescent or more pubescent one.
2.4.2 Perianth

The visually attractive part of the flower is the undifferentiated perianth although anatomical studies show that the lobes, at least (also proposed by Gilg, 1894), have a sepalous origin. Petals are absent in the nine genera investigated. The nature of the perianth tube has been a subject of much controversy (for older literature, see Endlicher, 1833; Meissner, 1857; Gray, 1865; Eichler, 1877; Baillon, 1877; Bentham and Hooker, 1883; for more recent assertions, refer to Lecomte, 1914; Rendle, 1925; Johnson, 1931; Domke, 1934; Lawrence, 1951; Heinig, 1951). Shape, size and colour are easily recognized characters which could be correlated with others for purposes of identification, e.g. flowers of Daphne are large, compared to those of some other genera; they are pink or yellow and tubular. Hermaphrodite flowers are often of this shape, staminate flowers tend to be infundibuliform, pistillate flowers are shorter and urceolate. This is partly correlated with the degree of spread of the perianth lobes and the increase in size of a developing ovary.

Perianth lobes are generally oblong-obtuse to triangular-acute, with entire or irregularly-crenulate margins. Shape is a useful criterion for separating closely allied species. The two outer lobes are usually larger than the inner. Aestivation is the same as that in the leaves but as the flower is tetramerous, the term 'imbricate' must be used in the sense of just being overlapping, not necessarily like shingles or scales (see Fig. 58H). The number and position, whether spreading or connivent, are also helpful. All the genera examined have four lobes with the exception of Stellera which is either pentamerous or not
uncommonly hexamerous. Some species of *Wikstroemia* are reported to have five perianth lobes but this was not the case in the three species examined. Aberrant states like polytepaly and multiple stamens resulting from the fusion of two flowers, were found in *Thymelaea hirsuta* and *T. procumbens*.

The persistence of the perianth after flowering appears to be related to the nature of the fruit. The fleshy berries of *Daphne* are exposed at maturity, while the dry fruits of other genera are rarely naked but enclosed instead, either in the entire perianth tube or its membranous base. In the latter case, the tube becomes constricted and deciduous above the ovary.

**Flower colour and odour:** field notes and literature accounts may be at variance regarding the latter character in some species. This is because scent is not always apparent and production seems to be correlated to atmospheric conditions and time of day. The colour ranges from white, creamy or greenish-yellow to orange, dark purple or rose-pink, and this character must be treated with caution when inferring from herbarium material. A good case illustrating this is found in *Stellera chamaejasme* subsp. *chamaejasme*. Flowers have been described as 'yellow', but in the natural state they are magenta outside and waxy-white within. Somehow, on drying, every trace of purple is lost and even the herbarium sheets become stained a clear orange-yellow.

The same species of *Thymelaea* may have either yellow or purplish flowers, though not on the same plant. The magenta colour is due to the presence of pigment spots on the perianth tube or lobes, which commonly deepen
in intensity during development. Other than this, there was little variation in size or flowers of individual species, certainly much less than in leaves.

2.4.3 Stamens

Each flower has eight or ten stamens in two whorls of four; the number is proportionate to that of the perianth lobes. An exception is found in *Diarthron linifolium* where only the upper whorl is present. Although the presence of a single whorl is often considered the more advanced condition, no anatomical evidence was available to show that the second whorl of stamens as found in the other species *D. vesiculosum* had been lost by suppression or reduction. Neither was there any evidence that remnants of stamens have been transformed into an intra-staminal disc. The upper (outer) stamens are situated opposite the perianth lobes and the lower (inner) stamens alternate with them. Development is centripetal, i.e. the outer stamens develop before the inner.

Filaments are long and slender in *Passerina* but very short in the other genera. Those of the upper and lower whorl may be unequal or slightly unequal in length. The anthers are thus completely included, fully exerted, or the upper whorl is situated at the mouth of the tube. The majority of species have oblong, cylindrical, dorsifixed anthers (Fig. 4 A, Plate 3E), but there are some with anthers in which the width is equal to or greater than the length (Fig. 4H). Anthers are biloculate at anthesis, usually yellow in colour but some are bright orange. Maturation and dehiscence, etc. are covered in the account on floral biology (see Sect. 4.4.).
Fig. 4. Stamens and pollen grains. All drawn to respective scales shown.

A. *Daphne odora*. Stamen.
   a-k, various grains from various anthers. Tri-nucleate condition most common.

B. *Passerina vulgaris*. Stamen.

C. *Thymelaea dioica*. Stamen.

D. *Daphne alpina*. Stamen.

E. *Dendrostellera lessertii*. Stamen.

F. *Thymelaea aucheri*. Stamen.

G. *Thymelaea passerina*. Stamen.

H. *Thymelaea hirsuta*. Adaxial and view from above.

I. *Daphne longibolata*. Mature grains tri-nucleate. 5% of cells remain thin-walled (m).

2.4.3.1. Pollen

Material investigated: c. 60 species from eight genera. The methods employed are covered in Sect. 2.0. Excess pollen was dried and kept on filter paper in a specimen tube. This was later used for SEM studies. The pollen characters are summed up in Table 1, blanks ( ) mean that data are unavailable at the moment. The terminology used follows that of Erdtman (1969). Aperture number refers to the pores visible in any single view, i.e. equatorial or polar.

Daphne

Pollen grains periporate (9-14 apertures), spheroidal (average diameter 20-30 μm, range 11-47 μm), apertures circular (diameter c. 1.3 μm), covered with a granular membrane. Mean interporal distance c. 5 μm. Exine 1.5-4.4 μm thick, reticulate-pilate.

Grains which are irregularly shaped, being triangular, hemispherical or dumb-bell in form, occur most commonly in **D. arbuscula**, **D. cneorum**, **D. longilobata** and **D. odora** (see Table 1). They stain deeply in aceto-carmine or cotton-blue, similar to the normal, spheroidal grains and I did not include them in my count for abortive pollen. At least 5% of the pollen grains are of this type. In **D. arbuscula**, the cytoplasmic contents of the smaller grains (mean diameter, 20 μm) stain deeply. The larger ones (mean diameter, 27 μm) stain lightly. Some of the grains showed ridges, furrows or tri-radiate crests in polar view (Plate 2 A, B). In **D. giraldii** both large (35-44 μm) and small (26-33 μm) grains are produced in a 1:1 ratio from the same anther. In contrast to **D. arbuscula**, the small, thicker-walled grains are the ones that do not take up stain.
Mature flower buds of *D. odora* (cult. RBG, Edinburgh) often have stigmas completely covered with pollen grains, showing anther dehiscence occurred prior to, or very near anthesis. No pollen has been observed germinating on the stigmas. The cause of sterility in this species has been elucidated by Okura & Kono (1959). Tri-nucleate and poly-nucleate grains (Fig. 4 a-k, l-n; Plate 4D) are shed at anthesis but I have never found a binucleate grain in pollen samples.

**Thymelaea**

Pollen grains periporate (8-16 apertures), spheroidal (average diameter 20-27 µm, range 9-44 µm), apertures circular (diameter 2-2.5 µm), covered with membrane. Mean interporal distance c. 5 µm. Exine 1.0 - 5.8 µm thick, reticulate-pilate.

The proportion of misshapen grains is lower than in *Daphne*, c. 5%. Pollen dimorphism reached its peak in a perennial member of Sect. *Ligia* (*T. cilicica*), where the ratio of small to large grains is approximately 1:1 (Plate 3 E,F). Mean diameters of the grains were 22 µm and 35 µm. The smaller grains take up stain easily while the larger ones stain lighter, showing distinct apertures. The difference as viewed morphologically is a matter of overall size, since exine ornamentation (later confirmed by SEM) remains the same. However, the genetic constitution and physiological behaviour of the grains at germination are unknown. In other species of this section, 9 - 28% of the pollen is smaller than the rest. *T. gussonei* and *T. passerina* have 100% fertile pollen; *T. hirsuta*, *T. microphylla*, *T. passerina* and *T. tinctoria* were found to have trinucleate grains at anthesis.
Dendrostellera
Pollen grains periporate (8-9 apertures), spheroidal (average diameter 13-16 μm, range 11-25 μm), apertures appear circular. No size measurements or interporal distances available. Exine c. 3 μm thick, reticulate-pilate. Small, shrunken and furrowed grains were present. The proportion of non-stainable pollen is fairly high, varying from 15-20%.

Stellera
Pollen grains periporate (12 apertures?), spheroidal (average diameter of the two sizes, 16 μm, and 23 μm), apertures circular. Exine reticulate-pilate. Only one species was investigated.

Stelleropsis
Pollen grains periporate (12-16 apertures), spheroidal (average diameter 20-24 μm, range 18-35 μm), apertures circular (diameter c. 2.5 μm), covered with membrane. Mean interporal distance, c. 5 μm. Exine 1.5 - 2.5 μm thick, ornamented with small spinules. 10-15% of pollen were not stained, the proportion of misshapen grains is a uniform 5%.

Diarthron
Pollen grains periporate (13-18 apertures), spheroidal. Genus with only two species: D. linifolium (average diameter 23 μm) and D. vesiculosum (average diameter 13 μm, range 11-16 μm). Apertures circular (diameter c. 1.3 μm), covered with membrane. Mean interporal distance c. 4.5 μm. Exine 1.3 μm thick, pilate. Percentage of misshapen grains low, c. 2%. Note that D. linifolium which has half the number of stamens (only 4) has the larger sized grains.
Passerina
Pollen grains periporate (10-16 apertures), spheroidal (average diameter of small grains 25 μm, large grains 33 μm). Largest grains found in P. rigida and P. vulgaris (range 33-50 μm). Apertures circular (all uniformly 2.5 μm in diameter except in P. paleacea where they are c. 5 μm). Mean interporal distance c. 8 μm. Again, correlated with the larger apertures, P. paleacea has a reduced interporal distance of 5 μm. Exine moderately thin to fairly thick (2 -6.5 μm) It is interesting to note that both P. ericooides and P. rigida, the only two species with succulent pericarps, have thick exines.

Pimelea (an Australasian genus)
As a comparison, one species, P. spectabilis was examined. The high aperture number (20-24), large size (average diameter 56 μm, range 46-75 μm), thick exine (5 μm) with a characteristic stellate pattern when viewed under the light microscope, all point to its distinctness and warrant its separation from the Mediterranean, S.W. and C. Asian genera.
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<th>% FERTILE POLLEN (not stained)</th>
<th>% MISMAPE POLLEN GRAINS</th>
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Discussion

The results indicate that pollen stainability in all, with the exception of a perennial species of *Thymelaea Sect. Ligia*, was high — over 80%. There was always a proportion of misshapen grains, which because they stained in a similar manner as the normal grains, were not included in my count of abortive pollen. In the species mentioned, the flowers are unisexual and each sex can be easily identified by the shape of the perianth. This species has a very narrow distribution, being endemic to the Cilician Taurus.

The average pollen production of a staminate flower of *T. cilicica* was found to be c. 400 grains. It is interesting to note that approximately 50% of these were small grains. Abortive pollen was 24% and there was also a high proportion of misshapen grains. Pollen dimorphism is very obvious in preparations stained with leucobasic fuchsin; thus both types, especially when deposited on the stigma, are rapidly distinguished. However, no data were compiled and the reproductive system was not investigated in the absence of suitable material.

Population size, density, sex distribution, pollen production and viability are some of the factors affecting breeding. The dimorphic pollen in this species suggests that the present highly restricted distribution is perhaps associated with a less efficient reproductive system, since such a high percentage of the pollen is apparently abortive. An annual member of the same section, provides a sharp contrast—*T. passerina* is a widespread species of uncultivated land
and it has almost homomorphic pollen. 9% are small grains but none are abortive. Practically no misshapen grains were found. It also has the lowest output of pollen as compared with the other species, c. 240 per hermaphrodite flower.
PLATE 3. Flower clearings to show stigmas and dimorphic pollen.

A. Stellera chamaejasme. Stigma shallowly furrowed / centrally depressed.

B. Thymelaea sanamunda. Style subterminal /sublateral.

C. Dendrostellera lessertii. Stigma conical-ovoid, covered with pollen.

D. Thymelaea dioica. Style terminal.

E. Thymelaea cilicica. At level of lower (inner) whorl of stamens. Pollen spheroidal, pariporate, dimorphic, with small grains staining deeply.

F. T. cilicica. At level lower down in perianth tube.

All x 155.
PLATE 4. Photomicrographs of some pollen grains.

All x 4800

A. Daphne gnidium, with ridge on one face of grain.

B. Daphne cneorum with tri-radiate crest.

C. Pimelea spectabilis, grain large, apertures many.

D. Daphne odora, wall thick, polynucleate.
2.4.3.2. Pollen analysis using scanning electron microscopy

The major advance offered by the scanning electron microscope (SEM) is the extreme magnification and depth of focus possible in views of surface structure or ornamentation. Thymelaeaceous pollen has long been regarded as being very uniform as no previous workers have had the opportunity to include SEM work in their investigations. Surface features have been hitherto observed as more or less similar because of inadequate resolution by light microscopy (Erdtman, 1972).

Pollen of eight genera were examined. The species scanned are listed in Appendix A; those belonging to the genus Thymelaea were examined in greater detail. Preparative techniques are described in Sect. 2.0. The following are descriptions of some of the variations seen, the SE micrographs supplement them and make detailed descriptions unnecessary. Any measurements taken are from light microscopy. Although terminology is a controversial subject and difficult to apply exactly for the structures found, that used follows Erdtman (1969), further elaborated for SEM work by Hideux & Ferguson (1976).

**Observations**

Features observed include:

1. shape and form, ectoaperture configuration (number and arrangement).
2. sculptural elements such as verruculae, echinules, muri and lumina.
3. ectoaperture membranes which are attached only in semi- or nonacetolyzed grains.
4. fibrillar matrix which is destroyed in acetolyzed material.

The pollen grains are circular in polar view, spheroidal, small to medium sized (14-30 µm), periporate. Ectoapertures are fewer than 10 or more than 20, sharply or poorly defined, without annuli. They are circular or irregular in outline, with protuberances or granular membranes which are often blown out, presumably in the high vacuum of the coating chamber. Aperture membranes may be a means of protection against desiccation of the grain but their true function and development is unknown. Surfaces of fresh grains undergo a change in appearance after acetolysis, with the loss of acid-soluble matrix. There is a definite advantage in using acetolyzed pollen although the process of acetolysis removes all cellular contents, incipient pollen tubes or aperture membranes. It was found that treated pollen did not suffer serious coating cracks, severe distortion or wall collapse during prolonged exposure to the electron beam at high magnification. In addition, pore and exine structure were more clearly revealed. Six types (A-F) can be defined and are listed below.

Type A: tectum partial, heterogeneous. The basic structural pattern is a reticulate network consisting of processes in rings of five or six fused at base to form muri separated by distinct rounded lumina (the 'croton-pattern' of Erdtman, 1972). Each process (echinule) is triangular in cross-section, topped by a (rarely two) rounded wart-like protuberance (verrucule) so that the lateral view is broadly mammillate. The ridges (muri) are unusually distinct because the processes are widely separated (Plate 5F). This can be compared with a narrowly spaced grouping as found in Wikstroemia chamaedaphne (Plate 7E), which
micrograph was taken at even higher magnification. Each process stands where three lumina adjoin, the corners extend beyond the ridge towards the lumina. Examples are found in the following species.

Thymelaea Sect. Piptochlamys — T. lythroides, T. hirsuta (Plate 5F), T. microphylla.


Dendrostelligera lessertii (Plate 7D).

The aperture outline is sometimes slightly irregular though still sharply defined, and the processes spaced such that the ridges are still visible, e.g. in Thymelaea Sect. Chlamydanthus — T. broteriana (Plate 6H), T. tartonraira subsp. argentea (Plate 6B); Daphne gnidium (Plate 7A, B).

Type B: processes are broadly obtuse-triangular in cross-section, the lumina are small and crowded. Ridges are not well defined because of adjoining processes, e.g. in Daphne blagayana, Wikstroemia chamaedaphne (Plate 7E); Thymelaea Sect. Chlamydanthus — T. dioica (Plate 6F) and Sect. Piptochlamys — T. virescens (Plate 6E); Sect. Thymelaea — T. thesioides subsp. elliptica.

Type C: appears to characterize Thymelaea Sect. Ligia. Hexagonal groups and lumina are very distinct. Processes are adjoining and the wart-like protuberances not so distinct in the annual species — T. salsa (Plate 5C), T. gussonei, T. mesopotamica and T. passerina. They are more widely spaced and obtuse-conical in the two perennials, T. aucheri (Plate 5D) and T. cilicica. Both large and small grains of the former
have a similar exine pattern. Apertures are circular and 8 - 13 in polar or equatorial view. Pollen grains of *Stelleropsis iranica* (Plate 7F) and *Diarthron vesiculosum*, show a similar pattern. That of the C. Asiatic species, *Stellera chamaejasme*, is somewhat intermediate between Types B and C.

**Type D:** the 'warts' are more prominent, the lumina small and hexagonal units not distinct because of crowding, e.g. Sect. *Thymelaea* subsect. *Antiatlanticae*— *T. virgata* subsp. *virgata*.

**Type E:** no definite hexagonal groupings present; the processes are broad and rounded in cross-section, surmounted by large, obtuse 'warts', e.g. in Sect. *Chlamydanthus*— *T. velutina*, *T. subrepens*, Sect. *Thymelaea*— *T. villosa* (Plate 6 C,D).

**Type F:** this pattern is found in the genus *Passerina* (Plate 5A,B) and some of the Himalayan Daphnes, e.g. *D. papyracea* (Plate 6A). The grains are larger (30-50 μm) than in the other groups, their surfaces are minutely verrucate, i.e. the processes are small and never project beyond muri. Apertures are large and regularly distributed. Shallow concavities of acid-soluble matrix underlie lumina, these are lost in acetolyzed preparations.

**Discussion**

The pollen grains of various species are similar in many respects, thus supporting the homogeneity in the family, but they are not structurally identical. The general pattern is a 'reticulum' of hexagonal
units. *Chamydanthus* as circumscribed by Brecher (1941) is a very heterogeneous section. It is possible to subdivide it further into more natural groupings, based on the assessment of other characters (see Sect. 7.4.1) but not on the degree of variation in the pollen. On considering the possibility of grouping the species of *Thymelaea*, according to the type of processes and their spatial relationship in each hexagonal unit, the retention of *Ligia* as a distinct section within the genus is supported. The exine processes in species of Sect. *Piptochlamys* are much more widely spaced than they are in species of Sects. *Ligia* or *Thymelaea*. The wart-like protruberances are more prominent and conical in Sect. *Thymelaea* than in Sect. *Ligia*, but hexagonal units and lumina are always more distinct in the latter. These differences are, of course, easily overlooked in preparations of non-acetolized grains.

The exine structure, as exemplified by Type A, does not provide evidence in favour of the separation of *T. coridifolia*, *T. microphylla*, *T. lythroides* and *T. hirsuta* into the two different sections *Piptochlamys* and *Chlamydanthus*. A rather similar pattern is found in *Dendrostellera lessertii*. Bearing this in mind, it is possible that gross similarities point more to ecological adaptations than to generic or species relationships. Thus in assessing affinities of species, it is not yet clear how much weight should be attached to the similarities and differences noted between the pollen of individual species. Increase in size, sphericity and elaboration of ridges with spiny processes appear to be trends that culminate in the most advanced members of some families (Kuprianova, 1969), but the less verrucate structure of the exine in *Passerina* certainly could merely be a secondary adaptation to wind rather than insect pollination in the dry.
Karroo.

Whilst we have limited information on the pollen microstructure of the Penaeaceae and Elaeagnaceae, two families which have often been closely allied to the Thymelaeaceae (Lawrence, 1951), examination of the grains even in the light microscope, show how completely different they are.

The grains in *Penaeas mucronata* (Plate 7H) are 4-colporate but appear 8-grooved as the colpi alternate with four deep pseudocolpi. They are subspheroidal (32 x 28 μm) and octangularly rounded in polar view. Ora are circular or slightly lalongate. The exine is psilate without any distinctive pattern. In *Elaegnus angustifolia* (Plate 7G), the grains are 3-colporate, the colpi being very short, oblate (24 x 40 μm), goniothere with a very indistinct exine pattern. As each of these families has very few genera (Penaeaceae, 4; Elaeagnaceae, 1 according to Nelson, 1935), perhaps the pattern obtained from the limited sampling will hold good even when other species are examined.

**Conclusion**

Scanning electron microscopy shows that pollen of the eight genera, although very similar in gross morphology, has a more complex external pattern than previously described from light microscopy. It was found that, together with other external and anatomical characters, micromorphology can be correlated to allow classification of some species of *Thymelaeas* at sectional level. Dimorphic grains in *T. cilicica* have a similar exine pattern. The study also did not reveal any structural
similarities to pollen of either the Penaeaceae or the Elaeagnaceae, and does not support the idea that the families could have a common phylogenetic derivation from ancestral stock. Erdtman (1972) states that outside the Euphorbiaceae, pollen grains with a 'croton-pattern' have been found in the Buxaceae and the Thymelaeaceae. In the Euphorbiaceae the 'croton-pattern' is only found in the subfamily Crotonoideae — the 'Croton-type' is inaperturate and the less common 'Manihot type' has large apertures with indistinct outlines. The morphological similarity to the Thymelaeaceae may perhaps be considered as a parallel development.

In the context of the totality of characters, Thymelaeaceous pollen is not quite identical with any of the suggested allied relatives and there may be some justification for placing the family in a separate order, Thymelaeales, as proposed by Hutchinson (1948) instead of including it in an Order containing other families to which its affinities are very doubtful.
PLATE 5. Scanning electron micrographs of pollen. All showing wall detail except when indicated.

A. *Passerina montana*. Whole grain incompletely acetolysed. x 2150.

B. *P. montana*. Lumina shallow, still filled with cellulosic material. x 10,100.

C. *Thymelaeasalsa*. x 5750.

D. *T. aucheri*. x 4750.


F. *T. hirsuta*. x 5750.
SCANNING ELECTRON MICROGRAPHS OF POLLEN

PLATE 5
PLATE 6. Scanning electron micrographs of pollen. All showing wall detail except when indicated.

A. *Daphne papyracea*. Whole grain showing furrow. x 1000.


C. *T. velutina*. x 5750.

D. *T. villosa*. x 5750.

E. *T. virescens*. Whole grains. x 700.

F. *T. dioica* subsp. *dioica*. x 7850.

G. *T. broteriana*. Whole grain. x 2600.

H. *T. broteriana*. x 7850.
PLATE 7. Scanning electron micrographs of pollen. All showing wall detail except when indicated.

A. Daphne gnidium. Whole grain, showing ridge on one face. x 2150.

B. D. gnidium. Detail of ridge. x 4750.

C. Dendrostellera lessertii. Whole grain. Apertures irregular, mostly shaped. x 2050.

D. D. lessertii. x 6000.

E. Wikstroemia chamaedaphne. Strangely enough, rather similar to the annual, Thymelaea salsa. x 8600.

F. Stelleropsis iranica. The two protuberances shown appear to be part of the grain and not debris. Also not blown-out opercular plugs. x 5050.

G. Elaeagnus angustifolia. Whole grain. x 1050.

H. Penaea mucronata. Whole grain. x 1450.
2.4.4 Hypogynous disc/scales

At the base of and surrounding the ovary is a disc which besides being annular or cupular is sometimes in the form of scales. In *Daphne* the disc is rather fleshy and nectar-producing (*D. x burkwoodii* was observed to have tube one-third filled with nectar on misty days), but in *Wikstroemia* consists of 2 - 5 linear structures which are free or joined at the base so that they form a deeply dissected collar. Some different shapes are illustrated Fig. 5); there is indeed a great variety of form.

The morphological nature of the disc has been the object of much argument. Endlicher (1833) describes them as 'squamae' in *Wikstroemia*. Bentham and Hooker (1883) likewise considers them as 'squamellae'. Gilg (1894) calls them 'receptacular effigurationen'. Johnson (1931) regards them as 'small processes growing out from the hypanthial wall'. They do not appear to be homologous to the petaloid structures found at the throat of the perianth in some African genera, and which I refer to, at the moment, as faucal scales. These are regarded by some as reduced petals and are totally absent in the nine genera surveyed. Domke (1934) makes a sharp distinction between these two types of scales and adds that the hypogynous ones do not correspond to a staminal tube. On the other hand, Heinig (1951) states that the disc is probably part of the androecium and not a modification of the receptacle as suggested by Gerber (1899).

I would consider the hypogynous disc or scales as a structure originally evolved for nectar production. Such a structure is common
in very many families with entomophilous flowers and few would quibble over their nature and function.
2.4.5 Gynoecium

In all genera, the ovary is 1-loculate and 1-ovulata. The shape is cylindrical-ovoid, subovoid or globose. It remains pubescent, hirsute, pilose or puberulous at the apex or becomes completely glabrous at maturity. The amount of indumentum on the top of the ovary is useful for species diagnosis. Staminate flowers in Thymelaea have a rudimentary ovary but I have not found any pistillate flowers with staminodes, in the material examined.

The style is very short in all the genera except Passerina, where it is long and exserted. When almost absent, the stigmas are often described as sessile. It remains terminal (Plate 3D) but in some species of Thymelaea it becomes subterminal/sublateral (Plate 3E). In Passerina it is characteristically lateral or sublateral. The style position seems to be a diagnostic feature for some species but it is also related to the maturity of the gynoecium, being 'laterally displaced' due to asymmetrical development in increase in size of ovary.

The stigma is conical-ovoid, discoid, globose or clavate. It may sometimes be shallowly bilobed or furrowed (Plate 3A). Joshi (1936) regards this as providing evidence for the bicarpellary nature of the gynoecium. The stigma is mop-like in Passerina. With the exception of this genus, the stigma in all other genera is positioned far down in the perianth tube, well below the level of the stamens. The papillose surface seems to be very efficient at catching pollen grains, as evidenced by the photo of the stigma in Dendrostellera lassetii at anthesis (Plate 3C).
2.5 Fruit and Seed

The fruit is the matured ovary. I have not broadened the term to include extracarpellary parts, e.g. perianth, that may be associated with it at maturity, as is the case in seven of the genera investigated. References in Floras to 'fruit ripening black' in these genera usually mean that the seedcoat turns black and the fruit appears this colour through the papery or membranous pericarp and perianth.

Daphne

The fruits are indehiscent, one-seeded berries, ovoid, globose or sub-globose, green ripening orange-red, scarlet (D. mezereum) or black (D. laureola). In D. alpina, they are almost dry-coriaceous. A few species have brownish-yellow (D. cneorum) or pale coloured fruits (D. blagayana). It must be emphasized that the fruit is not a drupe, to which it is commonly referred in descriptive works. This error arose because the hard seedcoat was mistaken for an endocarp, and has led to such dreadful ambiguities as 'drupa baccata' or 'bacca drupacea'. The pericarp is commonly glabrous (D. laureola) or adpressed-pubescent (D. alpina). The perianth splits at the base as the fruit matures, later becoming deciduous so that the fruit is exposed (Plate 8B). The average fruit production in some species, observed over one growing season, was fairly good, e.g. D. giraldii has 2.5 per flower cluster, i.e. a 35-40% of the maximum possible on the basis of an inflorescence of 6 - 7 flowers.

The seed is ovoid, ellipsoid or pyriform, covered by a moderately thick, pale, semitransparent, soft and almost smooth testa (outer seedcoat). The exotegmen (outer epidermis of the inner seedcoat) is thick, lignified
and a shiny blackish-brown. Although hard and crustaceous, it is brittle when dry. The endotegmen (inner epidermis of the inner seedcoat) is white or pale brown and membranous. Perisperm and endosperm are present, either copious or as a thin film round the embryo. Gilg (1894), Rendle (1925) and Domke (1934) all consider endosperm is generally absent or scanty, but the 'Nährgewebe' of Gilg refers to both endosperm plus perisperm. The cotyledons are thick, fleshy and plano-convex, turning dark-green in the light, the radicle and plumule are minute.

To avoid an unduly long presentation of facts, the descriptions of the following genera are written in a somewhat abbreviated form.

**Dendrostellera**

Fruit dry, indehiscent, one-seeded and enclosed by the sericeous-villous, persistent lower half of the perianth. The whole structure forms the dispersal unit. The pericarp is pubescent and villous-barbate at the apex. The seed is pyriform, greenish ripening to reddish-brown or black.

**Diarthron**

Fruit dry, one-seeded, enclosed in persistent lower half of perianth. Pericarp glabrous, membranous, green. Seed in both species ovoid, shiny black, c. 2 x 1 mm.

**Restella**

Fruit dry, indehiscent, one-seeded, ellipsoid, minutely pubescent, enclosed in persistent, membranous perianth. Seed pyriform, ripening
black.

Stellera

Fruit dry, indehiscent, one-seeded, enclosed in persistent lower half of perianth, pyriform, brown. Seed ripening black.

Stelleropsis

Fruit dry, indehiscent, one-seeded, enclosed in persistent lower half of perianth, ovoid, pubescent at apex, dark-green ripening blackish-brown. Seed pyriform, ripening shiny black.

Thymelaeae

Fruit dry, indehiscent, one-seeded, naked or enclosed in persistent perianth at maturity, ovoid or conical-pyriform. Pericarp thin, membranous or chartaceous, glabrous or pubescent, green ripening dark brown. Seed ovoid or pyriform, pendulously and laterally attached near apex of locule. Testa pellicular (skin-like), thin, semi-transparent as in Daphne. Exotegmen thick, hard, black, shallowly and regularly sculptured (Plate 8 C-E). Perisperm sometimes persistent. Endosperm absent or scanty, surrounding embryo. Embryo straight with radicle turned towards hilum. Cotyledons fleshy, plano-convex, almost filling entire seed. Radicle very short and pointed, plumule inconspicuous.

Wikstroemia

Fruit one-seeded berry or in the species investigated (W. chamaedaphne and W. salicifolia), dry, indehiscent, + exposed at maturity. Pericarp forming coriaceous envelope round pyriform seed. Perisperm and endosperm present.
In two species, fruits are ovoid, globose, indehiscent one-seeded berries. The rest have dry fruits which are either enclosed in the inflated, entire or split membranous base of the perianth or ultimately free from it on ripening. The pericarp is membranous and brownish-black in dry fruit; yellow-orange or scarlet in berries. The seed is ovoid with the microphyle at the end of a curved beak. Testa pellicular, thin and soft; the exotegmen hard, crustaceous and shiny black. Embryo is straight with fleshy, plano-convex cotyledons; perisperm and endosperm present.
PLATE 8

A. Thymelaea tinctoria subsp. tinctoria seedlings. Early thickening of tap roots indicated by arrows x 1/3.

B. Daphne longilobata. Perianth splits at base as fruit matures, later deciduous. x 1.

C. Thymelaea tartonraira subsp. argentea. Seed surface x 650.

D. Thymelaea gussonei. Seed surface x 1250.

E. Thymelaea virgata subsp. virgata. Seed surface x 1500.
2.6 Germination

The morphology of seedlings in species distributed in S.W. and C. Asia, W. Himalayas, N. Africa and the Mediterranean region of Europe has not been well documented, perhaps because most of the species, with the exception of Daphne, occur as weedy annuals, in steppeland or in association with and forming constituents of garigue and littoral scrub. Many species of Daphne are cultivated in gardens but there is a general lack of descriptive morphological studies, partly connected with the fact that seeds of this genus can take more than three years to germinate (Bisset, personal communication). However, well-ripened seeds of D. mezereum are reported to germinate readily in spring when sown the previous autumn (Miller, 1768). Carter (experiment quoted in Brickell and Mathew, 1976) found that maximum results were obtained when the testa is removed; also that seed from unripe fruits germinated better than those from ripened ones. This suggests that the presence of substances in the testa or sclerification of the tegmen during ripening play some inhibitory role during germination.

Materials and methods

1. Thymelaea passerina: two separate gatherings of seed were received from Israel and stored in the laboratory at approximately 25°C, until used. The first batch (nearly two years old) was sown in sandy clay under greenhouse conditions during April. The second batch (from undated collection, probably two to three months old) was kept in the laboratory. The seeds were removed from the enclosing perianth by gentle hand-rubbing. 5 - 10 seeds were placed in water-soaked blotting paper in covered Petri
Observations: the radicle is the first organ to emerge during germination. Following emergence, the tips of the seed-coat curl away from each other, exposing the cotyledons. The cotyledons are brought above ground, carrying the seedcoat up with them at their apices. The seedcoat is ultimately dropped. Cotyledons are unequal in size, being tightly adpressed for the first few days but unfold by forcing open the seedcoat in the second week. Root hairs form rapidly on the emerging radicle. Elongation is in a downward direction, up to 2 cm by the end of the second day. Lateral roots are produced within the first week. In laboratory conditions, root growth was poor and 70% of the seedlings died after a week. The first leaf emerged by the third to fourth week. The plants grew to maturity and flowered at ten weeks.

Seedling morphology of *T. passerina*: (Fig. 6): the two cotyledons are unequal initially but both reach the same size within a week. They are 2.5 - 3 x 1.52 - 2 mm, pale green on the lower surface and darker green above. They are slightly glaucous, oblong, obtusely rounded or shallowly retuse at apex, sessile, fleshy with indistinct midrib and indiscernible venation, long-persistent. The hypocotyl is erect, terete, thickened 1 mm below the cotyledons, glabrous, pale green and lies 16-20 mm above the soil. The young shoot is erect, glabrous and greenish, with the first internode 5 mm in length. Cataphylls are absent. The first leaves are opposite or sub-opposite, 2-3 mm long. They are glabrous throughout, simple, entire, lanceolate-oblong, obtusely rounded at the apex and exstipulate. They are also very shortly petiolate, produced by the
fourth week and long-persistent. Venation is pinnate whilst vernation is conduplicate induplicate, i.e. the lamina is folded lengthwise along the veins so that the halves of the upper surface lie together. The root is straight, penetrating 15-30 mm into the soil; the system reached 30 cm within 10 weeks.

2. Diarthron vesiculosum: nine year old seed (W. Pakistan: Lamond 1880) was sown under the same conditions. At the end of three weeks, 10% of the seeds germinated. The seedlings resemble those of T. passerina both in sequence of germination and external morphology. The cotyledons are equal in size and tightly adpressed in the first three days. The hypocotyl is pale green and glabrous, growing to 12 mm in length. Seedlings failed to become established but became constricted 1 mm below the cotyledons and died off at the end of the second week.

3. Daphne: seeds of D. alpina, D. caucasica, D. gnidium and D. longilobata were received from Botanic Gardens, not collected in the wild. They germinated after being kept in cold moist storage (0°C) for a month. Seed of certain other species, e.g. D. cneorum, did not show any signs of germination after six months.

Seedling morphology of D. longilobata (Fig. 7): the cotyledons are large, 8 x 5 mm, very fleshy, pale green and remain persistent for five weeks. Unlike that of T. passerina, the hypocotyl is short, only 4 - 8 mm long, and the young shoot rusty scabrous. Cataphylls are present in some 3 - 4 week old seedlings, usually caducous after two days (Fig. 7D). The first leaves are opposite, often unequal in size, shortly petiolate and sparsely ciliate at the apex. Either one or both
may be deeply lobed. They are also long-persistent. Vernation is conduplicate induplicate. The root system becomes well established by the tenth week with the number of laterals produced from the main root, gradually decreasing as they elongate. As in *D. g nidium*, *T. hirsuta* and *T. tinctoria*, whose seedlings were collected in the wild, the taproot of *D. longilobata* starts to thicken by the fifth month (Plate 8A).

Table 2.0 Some observed germination periods

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of germination (%)</th>
<th>Time course of germination (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Daphne alpina</strong></td>
<td>30</td>
<td>112</td>
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<tr>
<td><strong>Daphne caucasica</strong></td>
<td>30</td>
<td>43</td>
</tr>
<tr>
<td><strong>Daphne g nidium</strong></td>
<td>60</td>
<td>12</td>
</tr>
<tr>
<td><strong>Daphne longilobata</strong></td>
<td>30</td>
<td>15</td>
</tr>
<tr>
<td><strong>Diarthron vesiculosum</strong></td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td><strong>Thymelaea passerina</strong></td>
<td>60</td>
<td>42</td>
</tr>
<tr>
<td>(seed less than 3 mths old)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Thymelaea passerina</strong></td>
<td>50</td>
<td>13</td>
</tr>
<tr>
<td>(seed nearly 2 years old)</td>
<td></td>
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</tr>
</tbody>
</table>

Discussion

The dormancy characteristic of the six species successfully investigated is interesting. It is noted that nine year old seed of *Diarthron vesiculosum* was still able to germinate. Seed of *Thymelaea passerina* which was less than three months old took 42 days to germinate, but seed which had been stored for nearly two years since being collected, took only 13 days. However, the viability of the older seed was lower, only
50% of seed germinating as compared to 60% of the more recently collected seed. This dormancy could be a contributing factor to the success and spread of these annuals in open habitats. *T. passerina* has a relatively wide geographical range in Europe, N. and C. Asia, extending all the way to Lake Baikal. It has also been recorded as a weed of arable land in the United States and Australia.

Chilling tends to remove the dormant condition in seeds of *Daphne alpina*, *D. caucasica* and *D. longilobata*. In the natural habitat, the low temperature necessary could be correlated with climate due to geographical origin, e.g. extending to over 3000 metres above sea level. On the other hand, partial scarification or other physical means of pre-treatment does not appear to have any appreciable effect on germination. Barton (1965) reports that species from many families exhibit some form of dormancy imposed by seed coats, and this is probably true for *Daphne* as the thick inner seed coat would be relatively impermeable to moisture and gases as well as physically prevent expansion of the embryo. The fleshy pericarp might store a chemical inhibitor, thus partially accounting for the slow germination. As the fruits are bird-dispersed, passage through a bird's gut might aid in removing the inhibitory substance.

The germination of six species was successfully carried out (see Table 2); the sequence in seed germination of these species is uniform, with the radicle and cotyledons being the first organs to emerge.
Fig. 6. *Thymelaea passerina*

A. 2-day old seedling. Germination phanerocotylar; radicle emerges first.

Aa. Cotyledons unequal in size.

B. 1-week old. Root system well developed. Drawn with seedcoat removed.

C. At 4 weeks. 1st and 2nd leaves expanding.

D. At 9 weeks. Cotyledons still persistent.

E. At 14 weeks. Plant grown to flowering stage.
Thymelaea passerina seedlings

**Fig. 6**
Fig. 7. *Daphne longilobata*

A. 2-week old seedling. Hypocotyl short.

B. Cotyledons fleshy, first leaves unfolding. Drawn with seed-coat removed.

C. At $3\frac{1}{2}$ weeks. First leaves deeply lobed and equal in size. Cataphylls absent.

D. Another seedling at $3\frac{1}{2}$ weeks. First leaves entire or slightly cleft at apex, unequal in size. Cataphylls present.

E. Well established seedling at 14 weeks. First leaves still persistent.
A-D all drawn to same scale

Fig. 7

Daphne longilobata seedlings

2 weeks

3½ weeks

14 weeks
Of the nine genera, the most available information on character or range of variation in the anatomy of vegetative parts comes from Daphne (see Hamaya, 1955, 1959; Hara, 1957, 1961, 1962a & b; Greguss, 1959 and Fukuda, 1967). Most of the older literature has been comprehensively summarized by Solereder (1908) and Metcalfe & Chalk (1950) though special mention should be made of the anatomical investigations of van Tieghem (1893), Supprian (1894) and Leandri (1930) which were based on the family as a whole throughout its geographical range. From these publications we learn that internal phloem occurs in the stem of almost all genera. Leandri's account of Thymelaea dealt with four species - T. passerina, T. dioica, T. argentata and T. hirsuta. Further and more recent observations on T. hirsuta are provided by Fahn & Sarnat (1963), Saleh & Sarg (1966) and by Fahn (1967). Data on T. tartonraira is given by Crowzet (1967). Parsa (1934), Nechaysva et al. (1969) and Breckle (1971) have all independently made detailed studies on the stem and leaf anatomy of Diarthron vesiculosum. Thoday's (1921) observations on the anatomy and behaviour of two S. African species of Passerina record many features of diagnostic importance. The other genera have received comparatively little anatomical attention, with the exception of Stellera chamaejasme (Joshi, 1935). Seedling anatomy does not appear to have been documented for any single species. As this is often considered to be very conservative, it may have some taxonomic value at family or generic level.

Jonssonius (1950) points out some relationships of the Thymelaeaceae
in connection with his wood anatomical account of three members but these are all Javanese species and several taxonomists consider that one of them, *Gonystylus macrophyllus*, should not be included in the Thymelaeaceae at all. However Airy Shaw (1953, 1973) concludes otherwise.

3.0 Materials and Methods

Herbarium material was boiled for 2 - 5 minutes in water to soften tissues and expel air. This step was omitted for fresh material. Transverse sections were cut with a single-edged blade at the mid-laminar region of the leaf and at different distances along the stem. Sections were transferred to dilute safranin or phloroglucinol-HCl and mounted temporarily in 10% glycerol. Some leaves were sectioned at 12-15 μm using a rotary microtome after following standard TBA-dehydration and paraffin-embedding procedures. They were stained in Mayer's haemalum and erythrosin (Johansen, 1940). Epidermal peels were made from fresh or herbarium material treated with a 5-10% KOH solution for 1 - 48 hours. Whole leaves were cleared in 10% KOH and the lignified elements stained with basic fuchsin after the manner described by Fuchs (1963).

For seedling studies, young plants with intact whole root systems were fixed in formalin-acetic acid-70% alcohol (5:5:90). Transverse sections of the stem and primary root were made by hand; for the sake of convenience, the first and fourth leaves above the cotyledons were chosen and sectioned at the mid-laminar region.
3.1 Leaf

3.1.1 Stomata

An examination of the leaf epidermis was undertaken to find whether any characters could be used to support the separation of taxa at the generic, sectional or species level. It is well known that mature stomatal types have a diagnostic value and in many cases can be used as an indicator of natural taxonomic affinity. Van Cotthem (1970) points out that thorough investigations of the stomata of less well-known angiosperm families can probably provide much more information for comparison purposes. His own 1970 classification is based on stomata as seen in surface view only. Shape, structure and position in transverse section or ontogenetic studies have not been taken into account. Pant (1965) and Stace (1965) considered ontogenetic studies form a more valid base for taxonomic conclusions. Rao & Ramayya (1977) also recently showed that the anisocytic, anomocytic and tetracytic stomata in *Hibiscus* can be derived through more than one 'pathway', and that only the paracytic stoma is ontogenetically stable.

Approximately 80 species covering all the genera were examined. Stomata are present in both epidermides (leaf amphistomatic) or confined to one surface only (epi- or hypostomatic). Four types can be distinguished based on the number of subsidiary cells. They have been given the appropriate name following the definitions of the respective authors (Vesque, 1889; Metcalfe & Chalk, 1950; Metcalfe, 1961 and Tomlinson, 1969 (see Fig. 8 ).
Fig. 8. Stomatal types

- Anisocytic: after Metcalfe & Chalk, 1950
- Anomocytic: after Metcalfe & Chalk, 1950
- Cruciferous: after Vesque, 1889
- Modified tetracytic: after Metcalfe, 1961
- Hexacytic: after Tomlinson, 1969

Subsidiary cells shaded.
Type A: anomocytic (irregular-celled, ranunculaceous type): stoma surrounded by a limited number of cells that are indistinguishable in size or form from those of the remainder of the epidermis.

Type B: anisocytic (unequal-celled, cruciferous) type: stoma surrounded by 3 cells of which one is distinctly smaller than the other two.

Type C: modified tetracytic type: stoma accompanied by 4 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.

Type D: hexacytic type: stoma accompanied by 6 subsidiary cells consisting of 2 lateral pairs parallel to the long axis of pore and 2 polar (terminal) cells; the 2nd lateral pair being as long as the stomatal complex or the pair of polar cells as broad as the stomatal complex.

It was 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.

Development of stomata

This was followed only for two species, D. gnidium and T. passerina, and for both development may be classified as aperigenous (after Fryns-Claessens & Van Cotthem, 1973).
3.1.2. Sclereids

A survey of the form, structure and distribution of sclereid idioblasts in mature leaves was carried out. It is rather difficult to find any taxonomic significance or use for this character at the moment.

Sclereid idioblasts as seen in leaf transverse section, are mostly confined to the middle or lower third of the mesophyll. They are rarely branched, mostly irregular fusiform, shortly elongated and moderately thick-walled; in macerated preparations, rather similar to the vesiculose sclereids described by Bokhari (1970). The majority are terminally associated with vein endings. They are usually two, lying side by side although a cluster of three to several is not uncommon. Thus they appear very distinct in cleared preparations (Pl. 9 D-E). Their development begins at the apices and upper leaf margins and in some species, aggregate there without occurring at the base.

The frequency and distribution of such sclereids in the mesophyll contribute to some extent towards the sclerophyllous nature of the leaf.

3.1.3. Venation

Von Ettingshausen (1861) was the first to make a comprehensive systematic description of leaf architecture although his work never came into widespread use. In 1973 Hickey surveyed 135 dicotyledonous families and found that characters denoting shape and vein configuration had some taxonomic significance. He noted that in general, the small, coriaceous and entire leaves of xeric, arctic or alpine environments show relatively few of these characters. The types and orders of venation used in the
descriptions of leaf anatomy follow his system.

Primary (1°) and secondary (2°) veins determine the major classes such as pinnate, acro- or actinodromous. 1° veins are defined as the thickest veins of the leaf. They occur singly or as a medial vein accompanied by others (lateral primaries) of roughly equal thickness.

The divergence angle of 2° veins is categorized as follows:
Type 1: lowest (lower) pair(s) of 2° veins more acute than those above.
Type 2: veins in upper half of leaf more obtuse than those of lower half (my own addition to Hickey's classification).
Type 3: upper veins (those at apex) more obtuse than lower.
Type 4: divergence angle nearly uniform.

3.1.4. Descriptive accounts

I. THYMELAEA (Figs. 9-11, 14-19, 15, 28/Pl. 9 B & C).

In surface view: Glabrous or with indumentum varying from shortly puberulous to lanose. Hairs unicellular, bent at base, smooth or verruculose, short to long (reaching 600 μm in T. velutina), straight or crisp or twisted, thick- (Fig. 28A) or thin-walled (Fig. 18B), confined to adaxial and/or abaxial surface of the whole lamina. Hair-type characteristic of family but in Daphnopsis reported to be 2-armed (Metcalfe & Chalk, 1950). Cuticle of adaxial and/or abaxial surface smooth or ridged. Epidermal cells of both surfaces polygonal with straight to undulated anticlinal walls. Undulated walls present in Sect. Ligia and some species of Sect. Thymelaea. Cell walls sometimes strongly pitted. Adaxial cells in costal region flattened and elongated.
Stomata present in both epidermides (leaves amphistomatic) or confined to the adaxial surface (leaves epistomatic; Table 3). Mature stomatal pattern modified tetracytic (Fig. 9 E), anisocytic (Fig. 9 Da) or anomocytic (Figs. 9 H/Ha). Most species with combination of 2 different types. Ontogenetic stomatal type in T. passerina aperigenous. Venation basically eucamptodromous, i.e. 2° veins upturned, not terminating at the margins. In T. tartonraira subsp. tartonraira var. tartonraira, venation actinodromous, basal reticulate, rather similar to that of cotyledons of T. passerina. This means there are 3 or more 1° veins from a basal initial point running parallel to the main vein and then diverging radially (never converging) towards, but not reaching the margin (Fig. 15 C). Development considered as perfect, since the veins cover at least two-thirds of the lamina. Divergence angle of 2° veins Type 1 (Fig. 14 M), Type 2 (Fig. 15 M), Type 3 (Fig. 15 F) or Type 4 (Fig. 15 Na).

In transverse section: Lamina isobilateral or dorsiventral, 150-755 μm thick (Figs. 18 & 19 show leaves all drawn to same scale). The thinnest leaves are found in T. aucheri and T. salsa, both of Sect. Ligia. Cuticle and epidermis contribute to leaf thickness in T. tinctoria (Fig. 19 B). Adaxial cuticle 3-21 μm thick, abaxial 4-30 μm. Adaxial epidermal cells (14-90 μm) much larger to slightly smaller than abaxial cells (20-58 μm thick); small cells with thick outer tangential and radial walls, large often mucilaginous and with unspecified tannin-coloured contents. Stomata level or sunken, overarched by walls of epidermal or subsidiary cells. Mesophyll composed of (1)2-3(-4) layers of short to tall palisade cells on adaxial and/or abaxial side; spongy tissue loose to compact, parenchymatous. Midrib producing
shallowly grooved, flattened or raised adaxial and/or abaxial surfaces. Collenchyma rare. Vascular system simple, open, of one main bundle with massive abaxial un lignified sclerenchyma cap not extending to epidermis. Internal phloem absent. Vascular bundles at mid laminar region varying in number according to species. Leaf margin of compact chlorenchyma (Fig. 28E). Petiole + absent. Crystals solitary prismatic or fragmented sand, in adaxial and/or abaxial epidermis. Raphides and druses not observed. Sclereids present throughout leaf; those at apex and upper leaf margins weakly, moderately or well developed. (Figs. 16 & 17, 25 E).

II. DAPHNE (Figs. 11, 21-23, 25-28).

In surface view: Glabrous or with indumentum similar to that of Thymelaeae. Cuticle of adaxial and/or abaxial surface smooth, faintly striated or strongly ridged and furrowed. Epidermal cells of both surfaces polygonal; anticlinal walls straight, rarely undulated. Stomata confined to abaxial surface (leaves hypostomatic, Figs. 11 Ca, Da, Ea, etc.) but in some, e.g. D. rodriguezii, present in both epidermides (leaves amphistomatic, Figs. 11 I, Ia). Orientation and distribution random but sometimes in bands, fewer in costal region. Pattern modified tetracytic, anisocytic or anomocytic, very rarely hexacytic. Venation eucamptodromous, 1° veins straight; divergence angle of 2° veins Type 1 (Fig. 21 B), Type 2 (Fig. 23 B), Type 3 (Fig. 21 D) or Type 4 (Fig. 22 C). 3° veins often transverse ramified, e.g. in D. longilobata (Fig. 21 H) but in D. blagayana (Fig. 23 A), percurrent, i.e. with 3° veins from opposite 2° veins sometimes joining in a forked course, giving rise to 3° order ramifications. Relationship of 3° veins to midvein oblique, arrangement alternate (i.e. not joining each other
in a straight or curved path but with an angular discontinuity, occasionally alternate and opposite in almost equal proportions. 4° veins random or orthogonal reticulate. Marginal ultimate venation incomplete, with the veinlets ending freely adjacent to the margins. Areoles small (< 0.3 mm in diameter) to medium-sized (0.3 - 1 mm), development imperfect, arrangement random (without any preferred orientation), shape pentagonal or quadrangular. Veinlets simple or once-branched. 1° and 2° venation in D. x rosetii (Fig. 21 B) follows that of D. laureola subsp. philippi (Fig. 21 C), while the 3° and higher order pattern is closer to that of its other parent, D. cneorum (Fig. 21 A). The latter is very closely related to D. striata as evinced by its almost identical venation. Vein configuration of D. oleoides (from Greece) and D. sericea likewise indicate natural affinities; both species have been placed in the same section Daphnanthes C. A. Meyer, although in different subsections (Brickell & Mathew, 1976).

In transverse section: Lamina isobilateral or dorsiventral, 215 - 690 µm thick. Adaxial and abaxial cuticle 5-15 µm thick, sometimes with prominent cuticular projections (Figs. 28Ia, 27D). Adaxial epidermal cells (20-150 µm thick) often larger than abaxial cells (26-58 µm), sometimes appearing periclinaly subdivided because of hardened mucilage (Fig. 28I). Stomata sunken (Figs. 28G-H, Ia; 27D-E) or level with epidermis (Figs. 27I, 28F). Mesophyll of 2-3(-4) adaxial palisade layers; abaxial palisade absent or of 2-3 layers of short, cylindrical cells; spongy tissue loose to compact. Midrib producing flattened or shallowly depressed adaxial and flattened or raised abaxial surfaces. Two types as seen in t.s. illustrated in Figs. 21A & B.
Type A (the more common): vascular system simple, open, of a single bundle with well developed sclerenchyma cap not extending to epidermis. Internal phloem absent. Adaxial ground tissue composed of 2-3 palisade layers, collenchyma present on abaxial side.

Type B: vascular system of one large and two smaller lateral bundles without sclerenchyma caps. Internal phloem present. Ground tissue composed of parenchyma. Collenchyma absent.

Petiole vasculature not investigated in detail but similar to that of midrib’s in some species. Coarse crystal sand and raphides present in adaxial epidermis and palisade cells of D. laureola subsp. philippi (Fig. 30 E). Sclereids in some species well developed, distributed through leaf, e.g. D. petraea (Figs. 25 C, 27 C-Ca).

III. RESTELLA (Figs. 12, 27).
In surface view: Sparsely pilose on both surfaces, adaxial glabrescent. Hairs unicellular, smooth, straight, moderately long and thick-walled, bases slightly tuberculate. Epidermal cells polygonal with undulated anticlinal walls. Stomata present on both surfaces, randomly distributed and orientated, mainly anomocytic (Figs. 12 C, Ca). Venation eucamptodromous; 2° veins rarely distinct when dry, Type 2 (those in upper half more obtuse than in lower half). 3° veins ramified, branching into higher orders without rejoining 2°s. Marginal ultimate venation incomplete.

In transverse section: Lamina isobilateral, 145-150 µm thick. Cuticle very thin, only 1.45 µm thick on both surfaces. Adaxial epidermal
cells (c. 29 μm) slightly larger than abaxial cells (c. 22 μm thick). Stomata sunken to level of inner epidermal walls. Mucilage and tannin cells not conspicuous. Mesophyll of 2 layers of adaxial palisade (c. 44 μm thick) and 1 on abaxial side (c. 20 μm thick); spongy tissue compact. Midrib shallowly depressed on adaxial, raised on abaxial surface. Vascular system similar to *Wikstroemia chamaedaphne* but sclerenchyma cap not extending to abaxial epidermis. Internal phloem absent. Ground tissue parenchymatous, sometimes chlorenchymatous. Lateral bundles weakly developed, without vascular caps. Crystals and sclereids not observed.

A thin mesomorphic leaf with little sclerenchyma except in midrib region.

IV. **WIKSTROEMIA** (Figs. 13, 27) - based only on *W. chamaedaphne*. 
In surface view: Glabrous. Adaxial and abaxial epidermal cells small, polygonal; anticlinal walls straight (Figs. 13 I, Ia). Stomata in both epidermides, anomocytic or indistinct modified tetracytic. Venation eucamptodromous; 2° veins conspicuous in dried material, divergence angle Type 1 (lower pairs more acute than those above) or Type 4 (angle nearly uniform).

In transverse section: Lamina dorsiventral, c. 250 μm thick. Stomata sunken to inner walls of epidermis. Adaxial palisade 3-layered, abaxial 2. Midrib shallowly depressed on adaxial, prominently raised on abaxial surface. Sclerenchyma cap of midrib bundle well developed, extending to abaxial epidermis (Fig. 27 B). Internal phloem
absent (?). Crystals and sclereids not observed.

V. **STELLEROPSIS** (Figs. 13, 20, 29).

In surface view: Glabrous or sparsely pilose. Cuticle striated, adaxial and abaxial epidermal cells polygonal, anticlinal walls weakly undulated, straight in costal region. Stomata on both surfaces, modified tetracytic to indistinct anomocytic (Figs. 13 Ea, F). Venation eucamptodromous.

In transverse section: Lamina isobilateral, 285-340 \( \mu m \) thick. Adaxial and abaxial cuticle 5-8 \( \mu m \) thick, ridged over mucilage idioblasts (Fig. 29 B). Adaxial and abaxial epidermal cells 29-35 \( \mu m \) thick, stomata slightly sunken or level with inner epidermal walls. Palisade 2-layered on both sides, 55-70 \( \mu m \) thick. Midrib raised on both surfaces, vasculature similar to other genera but internal phloem present. Ground tissue parenchymatous on abaxial side. Smallest veins with little or no sclerenchyma. Crystals and sclereids absent.

VI. **DENDROSTELLERA** (Figs. 13, 20, 27; Pl. 9 A-Aa, E).

In surface view: Glabrous or with indumentum of varying density. Hairs unicellular, usually straight, moderately thick-walled. Cuticle often strongly ridged. Epidermal cells of both surfaces polygonal, anticlinal walls straight or weakly undulated. Large cells not uncommon near midrib. Stomata in both epidermides, randomly orientated. Pattern anisocytic (Fig. 13 Aa) or modified tetracytic, both types often occurring in the same species and even in the same leaf. Venation acrodromous, basal; development perfect, i.e. there are 3-5 1° or strongly developed 2° veins originating at the base of the leaf, running in convergent arches at least two-thirds of the distance to the apex (Figs. 24 A-F). Lateral
1° veins often are suprabasal branches on one side of the main vein (Figs. 24D, E). Divergence angle Type 4 (Fig. 24B). 4° and higher order veins very slender, minutely reticulate.

In transverse section: Lamina isobilateral or weakly dorsiventral, 300-420 μm thick. Adaxial and abaxial cuticles 5-12 μm thick, ridged between cells. Adaxial epidermal cells often large, mucilaginous (Fig. 27G), much bigger than or equal in size to abaxial cells. Stomata level on adaxial side but often sunken on abaxial in shallow epidermal crypts (Fig. 27H). Palisade 3-4 layered on each side; spongy tissue compact. Midrib flattened or raised on both surfaces. Vasculature simple, open, consisting of single bundle with well-developed sclerenchyma not extending to epidermis. Internal phloem absent. Ground tissue in midrib parenchymatous or of short palisade cells. Petiole with similar vascular pattern as midrib. Crystals not observed. Sclereids conspicuous or moderately developed at leaf apices and vein endings (Pl. 9 A-Aa, E).

VII. STELLERA (Figs. 13, 20, 29) - based on one species, S. chamaejasme.

In surface view: Glabrous. Adaxial cuticle often striated near veins. Adaxial and abaxial epidermal cells with straight, anticlinal walls (Figs. 13 G, H & Ha). Stomata on both surfaces in S. chamaejasme subsp. chamaejasme, confined to abaxial epidermis in subsp. angustifolia. Pattern anomocytic to complex modified tetracytic. Venation acrodromous, suprabasal (Fig. 19 A); divergence of 2° veins Type 4 (angle nearly uniform).
In transverse section: Lamina weakly isobilateral or dorsiventral, 170-180 μm thick. Adaxial and abaxial cuticle 5-6 μm thick, epidermal cells 20-30 μm thick. Stomata sunken to level of inner epidermal walls. Adaxial palisade 2-layered, c. 70 μm thick; on abaxial side absent or 1-layered, c. 45 μm thick. Midrib raised on both surfaces, supplied with open vascular bundle. Sclerenchyma cap not extending to epidermis; internal phloem absent. Ground tissue parenchymatous. Petiole vasculature at distal end similar to that of midrib but with 2 lateral bundles on either side. Crystals and sclereids absent.

The lesser amount of sclerenchyma fibres associated with vascular bundles as compared with leaf size and the absence of sclereids characterize the thin, mesomorphic leaves of this species.

VIII. DIARTHRON (Figs. 12, 25, 29; Pl. 9D).

In surface view: Glabrous. Cuticle smooth or striated. Adaxial epidermal cells with strongly undulated anticlinal walls (Figs. 12A, B), abaxial cells weakly undulated (Figs. 12Aa, Ba). Stomata in both epidermides, fewer on adaxial surface in D. linifolium, modified tetracytic. Venation eucamptodromous, divergence angle of 2° veins Type 1 in D. vesiculosum, closer to Type 4 in D. linifolium.

In transverse section: Lamina isobilateral in D. vesiculosum (228-235 μm thick), apparently dorsiventral in D. linifolium (205-210 μm thick). Adaxial and abaxial cuticles only 4-5 μm thick. Epidermal cells 14-22 μm, adaxial usually much larger. Stomata sunken to level of inner epidermal walls in D. vesiculosum (Figs. 29 Ca & Cb). Palisade 2-layered (c. 80 μm thick) on each side in D. vesiculosum, only...
1 (but 73 µm thick!) on adaxial side in D. linifolium. Midrib shallowly depressed on adaxial and slightly raised on abaxial surface. Vascular bundle single, simple, open. Sclerenchyma not extending to epidermis, internal phloem absent. Ground tissue palisade-like on adaxial side, on abaxial side parenchymatous. Lateral bundles from 2° veins not conspicuous (Figs. 29 C, D). Petiole very short, vasculature similar to midrib's. Crystals not present (?). Sclereids mainly aggregated at leaf apex (Pl. 9 D).

IX PASSERINA (Figs. 12, 30).

In surface view: Glabrous on abaxial side, hairs on adaxial surface unicellular, smooth, moderately long, dense, twisted and thin-walled. Cuticle smooth or faintly striated. Adaxial epidermal cells polygonal, anticlinal walls undulated (Fig. 12 D), straight on abaxial side (Fig. 12 Da). Stomata confined to adaxial epidermis, randomly distributed and orientated, anomocytic. Venation almost parallelodromous, i.e. 1° veins originating near each other at leaf base and running ± parallel to the apex.

In transverse section: Leaf shallowly to deeply grooved on adaxial side, the groove tomentose or lanuginose. Lamina dorsiventral. Adaxial cuticle thin, 0.5 - 7 µm, abaxial cuticle very much thicker, 11-23 µm. Adaxial epidermal cells squarish-rectangular and much smaller than abaxial; those of abaxial epidermis taller than wide (60-112 µm as seen in t.s.). Mucilage and tannin-coloured inclusions present; in some cells mucilage occupying nearly the entire lumen, compressing the tannin-coloured part to the outer wall. Stomata sunken to level of inner epidermal walls in young leaves but ± raised in mature leaves.
Palisade 1-2 layered, confined to margins and abaxial side only; spongy tissue loose, parenchymatous. Midrib not raised or impressed on either surface. Vascular bundles 3-9 in mid-laminar region, the number apparently constant for a given species. Bundle sheath parenchymatous, with or without tannin. Sclerenchyma in some species interrupting palisade, extending to abaxial epidermis, therefore hypodermal fibres present (a specific character for mature leaves regardless of whether plants are grown in full sun or shade). Young leaves of *P. vulgaris* do not have the sclerenchyma extensions, Figs. 30 D & Da. Petiole absent. Solitary prismatic or minute sand-like crystals infrequent in abaxial epidermis; raphides and druses absent. Sclereids absent.

A comparison between young and mature leaves of *P. vulgaris* was made and the observations tabulated below:

Young leaf (Figs. 30 Da & Db).

1. Leaf only slightly concave in t.s.
2. Indumentum conspicuous.
3. Stomata sunken at least to level of inner epidermal walls.
4. Tannin cells rare in abaxial epidermis.
5. Palisade 1-layered.
6. Palisade not interrupted by sclerenchyma.
8. Bundle-sheath cells without tannin.

Mature leaf (Fig. 30 D).

1. Leaf more deeply grooved.
Table 3. *Passerina*. Some anatomical characters of the leaf

<table>
<thead>
<tr>
<th>Species</th>
<th>P. filiformis</th>
<th>P. montana</th>
<th>P. paleacea</th>
<th>P. vulgaris (mature leaf)</th>
<th>P. vulgaris (young leaf)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of vascular bundles in mid-lamina</td>
<td>7</td>
<td>9</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>No. of palisade layers</td>
<td>1 (-2)</td>
<td>1-2</td>
<td>1-2</td>
<td>1-2</td>
<td>1</td>
</tr>
<tr>
<td>Tannin in bundle sheath</td>
<td>absent</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tannin in abaxial epidermis</td>
<td>absent</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Hypodermal fibres</td>
<td>absent</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Vascular bundle sclerenchyma</td>
<td>not interrupting</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
2. Indumentum present but less conspicuous.
3. Stomata raised or flush with outer epidermal walls.
4. Tannin and mucilage abundant in most abaxial epidermal cells.
5. Palisade often 2-layered.
6. Palisade interrupted by sclerenchyma.
7. Hypodermal fibres developing laterally.
8. Bundle-sheath cells with tannin.

In Passerina, sclerophylly is due to the increase in thickness of the cuticle and abaxial epidermis. The development of sclerenchyma extensions from the vascular bundle in some species contribute to leaf hardness as well. The deep-celled, tannin-filled, mucilaginous epidermis together with the thick cuticle, form a protective screen against solar intensity and drying winds. The epidermis is related to leaf closure during drought. Leaves are held vertically with the stomata located on the woolly involucrated adaxial side where transpiration rates may be less. In all species the stomata are confined to the adaxial surface, and in most species the stomata of mature leaves are slightly raised above the epidermis (Fig. 30 Aa). Thoday (1921) considers this might prevent mechanical closure of the pores during drought.

In P. paleacea and P. vulgaris, sclerenchyma fibres develop laterally from the larger vascular strands and ramify the mesophyll below the abaxial epidermis. They are un lignified, elongate by intrusive growth and are often forked at the tips. Thoday in his account of two S. African Passerinas referred to them as free-ending 'wandering' fibres.
Plate 9. Leaf clearings.

A. *Dendrostellera lessertii*. Upper third of leaf. Sclereids moderately developed at apex and at vein endings.


B. *Thymelaea ruizii*. Sclereids weakly developed at apex and throughout leaf.

C. *Thymelaea dioica*. Sclereids also weakly developed at apex.

D. *Diarthron vesiculosum*. Midrib slender, sclereids well developed, aggregated at apex.

E. *Dendrostellera stachyoides*. Midrib broad, sclereids conspicuous at apex and also throughout leaf.

A - C x 40.

D - E x 155.
Fig. 9. Thymelaea - leaf epidermal peels.

All drawn x 613.

Sect. Ligia A - Da.

A. T. aucheri upper.
B/Ba. T. cilicica upper/lower.
C/Ca. T. mesopotamica upper/lower.
Da. T. passerina lower.

Sect. Thymelaea E - Ia.

E. T. thesioides subsp. thesioides (narrow-leaved form) upper.
F/Fa. T. thesioides subsp. elliptica upper/lower. Unicellular hairs on both surfaces.
G/Ga. T. sanamunda upper/lower.
H/Ha. T. thesioides subsp. thesioides upper/lower. Ha is from costal region; cells elongated and with simple pits.
I/Ia. T. virgata subsp. virgata upper/lower.
Fig. 9
Fig. 10. Thymelaea - leaf epidermal peels.

All drawn x 613 except F.

I. *T. microphylla* upper.
F. *T. tinctoria* subsp. *tinctoria* upper (x 740).
Fig. 10
Fig. 11. Leaf epidermal peels. All drawn x 613 except Ha.

A/Aa. **T. lythroides** upper/lower. From leaf of flowering branch.
aa. **T. lythroides** lower. From leaf of young sterile shoot.
Ba. **Daphne longilobata** lower. Stomata in bands.
Ca. **Daphne sureil** lower.
D/Da. **D. papyracea** upper/lower.
Ea. **D. odora** lower.
F/Fa. **D. laureola** subsp. **philippi** upper/lower.
G/Ga. **D. gnidium** upper/lower.
Ha. **D. petraea** lower (x 740).
I/Ia. **D. rodriguezii** upper/lower.
Fig. 12. Leaf epidermal peels. All drawn x 788 except B (x 1250).

A/Aa. Diarthron vesiculosum upper/lower
B/Ba. Diarthron linifolium upper/lower
C/Ca. Restella albertii upper/lower. h.b. = hair base.
D/Da. Passerina montana upper/lower
Fig. 13. Leaf epidermal peels. All drawn x 613 except G.

A/Aa. Dendrostellera lessertii (glabrous form) upper/lower.
   l.e.c. = large epidermal cell, c.s.c. = common subsidiary cell.


Ea. Stelleroopsis magakjanii lower.

F. Stelleroopsis altaica upper.

G. Stellera chamaejasme subsp. angustifolia upper (x 740).

H/Ha. Stellera chamaejasme subsp. chamaejasme upper/lower.

I/la. Wikstroemia chamaedaphne upper/lower.
Fig. 14. Cleared leaves of Thymelaea as seen in surface view. All x 6.

A. T. ruizii. Narrowly elliptic, apex acute. 2° angle of divergence: Type 1 - lowest (lower) pair(s) of 2° veins more acute than pairs above.

B. T. dioica. Oblanceolate, apex ca. right-angled. Type 2 - veins of upper half more obtuse than those of lower half.

C. T. villosa. Narrowly elliptic, apex ca. right angled. Type 2.

Ca. T. villosa. Young leaf narrowly elliptic, apex acute. Type 1.

Sect. Thymelaea D - G.


F. T. virgata subsp. broussonetii. Very narrowly elliptic, apex acute. Type 3 - upper 2° veins more obtuse than lower.

G. T. thesioides subsp. thesioides. Narrowly oblanceolate, apex acute. Type 3.

Ga. Leaf from plant similar to D. Apex ca. right-angled. Type 1.

Sect. Ligia H - M.

H. T. cilicica. Narrowly elliptic, apex acute. Type 1.

I. T. gussonei. Very narrowly elliptic, apex acute. Type 2.

J. T. aucheri. Very narrowly elliptic, apex acute. Type 1.


M. T. mesopotamica. Elliptic, apex acute. Type 1.
Fig. 14
Fig. 15. Cleared leaves of *Thymelaea* as seen in surface view.

All x 6.

*T. tartonraira* sensu lato  A - F.

A. *subsp. valentina*. Oblanceolate, apex obtuse. Type 3.
B. *subsp. argentea* var. *linearifolia*. Narrowly oblanceolate, apex acute. Type 3.
C. *subsp. tartonraira* var. *tartonraira*. Wide obovate, apex emarginate. Type 3.
D. *subsp. tartonraira* var. *transiens*. Oblanceolate, apex ca. right-angled. Type 3.
E. *subsp. argentea* var. *argentea*. Oblanceolate, apex acute. Type 3.
F. *subsp. argentea* var. *argentea* - var. *linearifolia* intermediate. Oblanceolate, apex acute. Type 3.
G. *T. velutina*. Narrowly obovate, apex rounded. Type 3.
H. *T. microphylla*. Leaf from flowering branch wide elliptic, apex ca. right-angled. Type 4 - divergence angle nearly uniform.

I. *T. argentata*. Oblanceolate, apex acute. Type 3.
J. *T. tinctoria*. Lorate, apex obtuse. Type 2.
K. *T. lanuginosa*. Oblanceolate, apex acute. Type 2.
L. *T. virescens*. Oblanceolate, apex ca. right-angled. Type 4.
M. *T. subrepens*. Elliptic, apex acute. Type 2.
N. *T. lythroides*. Leaf from flowering branch elliptic, apex acute. Type 2.
O. *T. hirsuta*. Narrowly ovate, apex acute. Type 2.
Ob. *T. hirsuta*. Bract suborbiculate, apex acute. Type with 2° veins of upper half more acute than those of lower half.
Fig. 16. *Thymelaea tartonraira* sensu lato - leaf apex venation and sclereid distribution.

A, B, and C all x 34. Upper epidermal hairs all x 85.
Insects (Ab, Bb) x 170.
Free-ending phloem fibres present (+)
Free-ending phloem fibres absent (-)

A - Ab. subsp. valentina
A. Part of cleared leaf. Sclereids numerous. Vein reticulum formed from midrib lateral bundles.
Aa. Upper epidermal hairs short.
Ab. Enlarged portion of A. Free-ending phloem fibres present (+).

B - Bb. subsp. argentea var. linearifolia
B. Apex narrowly triangular-acute. Vein reticulum from midrib main bundle.
Ba. Upper epidermal hairs long.
Bb. Enlarged portion of B. Free-ending phloem fibres absent (-).

C - Ca. subsp. tartonraira var. transiens
C. Apex broadly triangular. Sclereids few (+).
Ca. Upper epidermal hairs moderately long.
Fig. 17. *Thymelaea tartonraira* sensu lato - leaf apex venation and sclereid distribution.

A, B and C all x 34. Upper epidermal hairs all x 85.

Insets (Ab, Bb) x 170.

Free-ending phloem fibres present (+)
Free-ending phloem fibres absent (-)

A - Aa. *subsp. argentea var. argentea*
A. Apex broadly triangular. Resembles var. *linearifolia* in having (-) and with
Aa. Upper epidermal hairs long.

B - Ba. *subsp. tartonraira var. tartonraira*
B. Apex broadly obtuse. Sclereid development maximum (-).
Ba. Upper epidermal hairs long.

C - Ca. *subsp. tartonraira var. tartonraira var. transiens* intermediate
C. Apex obtuse, resembles var. *transiens* in having (+) and intermediate in other aspects including
Ca. Upper epidermal hairs which are both long and short.
Fig. 18. T.S. of Thymelaea leaves. All drawn to scale shown (x 30).

Sect. Ligia A – E
A. T. aucheri. Leaf with tendency to become revolute on drying.
B. T. cilicica. Never revolute.
C. T. gussonei. Indumentum present, often disappearing with age. Collenchyma well developed at midrib.

Sect. Thymelaea F – K
F. T. thesioides subsp. thesioides. Narrow-leaved form.
G. T. sanamunda.
H. T. thesioides subsp. thesioides.
I. T. antiatlantica.
J. T. virgata subsp. virgata. Collenchyma at midrib.
K. T. villosa. Large sclereids in spongy mesophyll.
L. T. subrepens.
M. T. dioica.
N. T. virescens.
O. T. coridifolia. Stomata absent from abaxial surface.
P. T. ruizii.

Key to tissues
- xylem
- chlorenchyma
- phloem
- collenchyma
- sclerenchyma fibres and sclereids
Fig. 19. T.S. of *Thymelaea* leaves. All drawn to scale shown (x 30) except Ia.

**Sect. Chlamydanthus** A - F, I - Ia.

A. *T. calycina*. Stomata absent from abaxial surface.

B. *T. tinctoria* subsp. *tinctoria*. Cuticle and epidermis contribute to leaf thickness.

C. *T. velutina*.

D. *T. tartonraira* subsp. *tartonraira* var. *transiens*. Indumentum more developed on the abaxial surface.

E. *T. tartonraira* subsp. *argentea* var. *linearifolia*. Indumentum more developed on the adaxial surface.

F. *T. tartonraira* subsp. *thomasii*. Indumentum completely absent from both surfaces.

I. *T. broteriana*. Leaf folded to form groove. Stomata only on adaxial surface, none in section shown.

Ia. *T. broteriana*. Drawn on separate scale, x 70.

**Sect. Piptochlamys** G - L.

G. *T. argentata*.

H. *T. lanuginosa*. Stomata absent from abaxial surface.

J. *T. microphylla*.


Fig. 20. T.S. of leaves. All drawn to scale shown (x 44).

A. Dendrostellera lessertii.
B. Dendrostellera arenaria.
C. Diarthron linifolium. Palisade apparently restricted to adaxial side. Sclereids few.
D. Diarthron vesiculosum.
E. Stelleropsis magakjanii.
F. Stellera chamaejasme subsp. chamaejasme. Sclereids absent.
Fig. 2\l. Cleared leaves of Daphne as seen in surface view.

All x 6.

A. D. cneorum
B. D. rossetii nom. nud. (D. laureola subsp. philippi x cneorum)
C. D. laureola subsp. philippi
D. D. arbuscula
E. D. petraea
F. D. jasminea
G. D. odora (young leaf)
H. D. longilobata (lower half)
Fig. 22. Cleared leaves of Daphne as seen in surface view. x 6.

A. D. oleoides
B. D. stapfii
C. D. retusa
D. D. giraldii
Fig. 23. Cleared leaves of *Daphne* as seen in surface view.

x 6.

A. *D. blagayana*

B. *D. alpina*
Fig. 24. Cleared leaves of *Dendrostellera* as seen in surface view. All x 6.

A. *D. stachyoides*. Type 4 - divergence angle of 2° veins nearly uniform.

B-F. *D. lessertii* (a very polymorphic species). Type 4.

4° and higher order venation very finely reticulate. Sclereids moderately developed.
Fig. 24
Fig. 25. Leaf clearings and transverse sections.

Two types of midrib in Daphne - A & B. x 250.


3 leaf clearings C - E. Sclereids present. All x 62.5.

C. Daphne petraea. Type 3 - upper 2° veins more obtuse than lower.

D. Diarthron linifolium. Type 4 - divergence angle nearly uniform.

E. Thymelaea tinctoria. Type 2 - veins of upper half more obtuse than those of lower half.

palisade

sclerenchyma

xylem

collenchyma

phloem
Fig. 26. T.S. of Daphne leaves. All drawn to scale shown (x 44).

A. *D. altaica*. Palisade restricted to adaxial side.

B. *D. gnidium* var. *sericea*. Palisade on both sides.

C. *D. linearifolia*. s. cells = secretory/mucilage cells.

D. *D. mucronata*. s. cells fewer on abaxial surface. Sclereids numerous.

E. *D. jasmines*. Sclereids present.

F. *D. rodriguezii*. Palisade restricted to adaxial side. Stomata on both surfaces.
Fig. 27. T.S. of leaves.

A. Restella albertii.
B. Wikstroemia chamaedaphne.
C. Daphne petraea. Sclereids numerous. Stomata only on the abaxial surface. Palisade restricted to adaxial side.
Ca. Daphne petraea. Leaf section. Mucilage cells (stippled) in adaxial epidermis.
E. Daphne arbuscula. Abaxial epidermis. Stomata level with inner wall of epidermal cells.
G. Dendrostellera lessertii. Adaxial epidermis. Cells often large and mucilaginous.

A - C x 30, Ca x 350, D - H x 1400.
Fig. 28. T.S. of leaves.

A. *Thymelaea tartonraira* subsp. *argentea* var. *linearifolia*. Adaxial epidermis. Hairs thick-walled, straight. cu. = cuticle, h.b. = t.s. of hair (not through base).


g.c. = guard cell.


C. *T. tinctoria* subsp. *tinctoria*. Sclereids from leaf mesophyll.


D. *T. villosa*. Sclereids from leaf mesophyll. Walls thinner, lumina large.


F. *Daphne jasminea*. Abaxial epidermis. Stoma level with epidermis.

G. *D. rodriquezii*. Abaxial epidermis. Stoma sunken beyond inner wall of epidermal cells.

H. *D. gnidium* var. *sericea*. Abaxial epidermis. Stoma more sunken by increase in depth of epidermal cells.

I. *D. oleoides*. Adaxial epidermis. Cuticle smooth. s. cell = mucilage-filled part of epidermal cell.


A - D all drawn to scale shown, E on separate scale, F - Ia x 1400.
Fig. 28
Fig. 29. Leaf clearings and transverse sections.

A. **Stellera chamaejasme** subsp. **chamaejasme**. Whole leaf. Sclereids absent. x 6.

Aa. **S. chamaejasme** subsp. **chamaejasme**. Leaf in section. Epidermal cells large. Palisade 2-layered, restricted to the adaxial side. x 2100.

B. **Stelleropsis antoninae**. Adaxial epidermis. Stoma slightly sunken or level with inner wall. x 2100.

C. **Diarthron vesiculosum**. Sclereids at leaf apex. x 6.

D. **Diarthron linifolium**. Sclereids also present. x 6.

Ca. **Diarthron vesiculosum**. Adaxial epidermis and 2-layered palisade. Stoma level with inner wall. x 2100.

Cb. **D. vesiculosum**. Abaxial epidermis and 2-layered palisade. x 2100.
Fig. 30. T.S. of leaves. Hairs drawn detached from surfaces.


Aa. P. filiformis. Leaf near margin. Stomata raised above epidermis. Epidermal cells small on adaxial, large and deep on abaxial side. x 1000.


Db. P. vulgaris. Young leaf near margin. Stomata sunken or + level with inner walls of adaxial epidermis. x 1000.

E. Daphne laureola subsp. philippi. Leaf margin. Clustered raphides in adaxial epidermis and palisade cells. Mucilage cells not shown. x 800.

tannin-c. = tannin-containing cells.  st. = stoma.
hypo. = hypodermal.  u. epid. = upper (adaxial) epidermis.
3.2 Nodal anatomy

According to the number of leaf gaps present where the traces depart from the stele, the nodes are termed unilacunar. They all have a single trace (Figs. 31D, 32C, 33D, 350a). In some species of Daphne, the median trace has two laterals which continue as wing bundles throughout the petiole. I have not found any deviation from this type in all the genera mentioned.

In the light of known characters which show the family (as represented by temperate genera) to be a natural and advanced one, the simple unilacunar condition should not be regarded as relatively primitive. The nodal anatomy of other Thymelaeaceous genera should be studied and very likely it would be found that the single leaf gap present in these genera has been derived instead.

![Diagram](image)

unilacunar with one trace

unilacunar with median trace having two split laterals

**RECONSTRUCTION OF NODAL TYPE**
3.3 Stem

**I THYMELAEA** (Figs. 31 & 32).

The following descriptions apply as seen in transverse sections and cover the whole genus. Based on stem anatomical features, the species can be roughly divided into two main groups.

**Group A.** (Species numbering 20-30 in Table 5): Epidermis a single layer with fairly thick outer walls. Stomata present (Fig. 31 Ca.). Indumentum present and retained in some species, absent or gradually lost in others. Hairs unicellular and smooth-walled. Cork tissue absent or not well developed (only 2-4 layers). Photosynthetic tissue of 2-3(-4) chlorenchyma layers in most species (Fig. 31 A). Collenchyma absent. Cortex moderately wide and parenchymatous with temporary starch. Perivascular sclerenchyma composed of thick-walled, un lignified phloem fibres in an interrupted or complete ring, sometimes in scattered groups, less often in bands. 2° phloem rays not dilated. Vessels isolated or in radial groups. Tracheids moderately thick-walled; medullary rays 1-cell wide. Internal phloem well developed, directly adjacent to xylem. Internal phloem fibres grouped or scattered in stems of seven species (Figs. 31Aa, 32A). Pith cells large, isodiametric, walls uniformly thin, often becoming disorganized and loosely arranged in centre of older stems. Sclereids or crystals absent.

**Group B.** (Species numbering 1-19 in Table 5): Epidermis a single layer, often tannified. Stomata usually absent. Indumentum present in almost all species, more dense on young stems and leaf axils, disappearing from older twigs because of cork formation. Hairs unicellular
with smooth or verruculose outer walls. Cork superficial, arising in subepidermis; cells homogeneous, flattened-rectangular with thin walls, tannified but not lignified, up to 30 layers in young stems of T. dioica. Lenticels present on older twigs. Photosynthetic tissue absent except in T. microphylla and T. sempervirens. Primary cortex parenchymatous, cells crushed with increase in girth. Collenchyma absent. Phloem fibres un lignified, composed of thick-walled outer groups or moderately thick-walled inner groups; arrangement in 2-4 parallel tangential bands or an interrupted ring. 2° phloem in some species rather broad, appearing as triangular or fan-shaped groups; phloem rays often dilated in older stems, giving flared appearance in cross-section. 2° xylem well developed. Vessels small (mean tangential diameter <100 μm), solitary or in radial and oblique groups of twos and threes. Growth rings distinct in some species; wood tending to be ring- or semi-ring porous. Tracheids thick-walled with narrow lumen, with spiral thickenings in young stems. Xylem parenchyma sometimes sclerified. Medullary rays uniseriate, in T. hirsuta up to 4 cells wide. Internal phloem in young stems always present. Internal phloem fibres present in Sect. Piptochlamys, e.g. T. argentata (Fig. 32 D) and T. microphylla. Pith region usually small; cells compact, parenchymatous, sometimes thick-walled and lignified. Sclereids absent. Mucilage cells and solitary crystals or crystalloid bodies rarely present. Tannin idioblasts conspicuous in cortex of T. tinctoria (Fig. 32 E).

Cortical tissue of old stems often fracture from secondary phloem fibres during transverse sectioning. The nonseptate fibres with clavate or forked ends are visible to the naked eye as long silky threads when
a branch is torn off. They account for the flexible yet tenacious nature of the bark.

II **DAPHNE** (Fig. 33).

In transverse section: Indumentum absent or present. Hair type similar to that of leaves. Cork arising in subepidermis; cells flattened, thin-walled. Lenticels developing on older twigs. Primary cortex parenchymatous, outer region often collenchymatous (Fig. 33 A). Photosynthetic parenchyma in general absent or only present in very young shoots. Mucilage cells sometimes present. Sclereids or crystals absent. In D. tangutica, innermost cortical layer forming starch sheath (homologous with endodermis?). Phloem fibres thick- or moderately thick-walled, un lignified, arranged in continuous ring (Fig. 33 D), in tangential bands (Figs. 33 A, B) or at apices of distinct phloem groups (Fig. 33 C). Phloem rays often dilated in old wood. Vessels small, solitary or in multiples arranged in radial, oblique or tangential patterns. Growth rings often distinct. Wood diffuse or semi-ring porous. Medullary rays narrow, often uniseriate. Internal phloem present. Internal phloem fibres present (Figs. 33 A, C & D) or absent (Fig. 33 B). Pith cells compact, parenchymatous.

The number and arrangement of phloem fibres in *Daphne* have been found to be of specific diagnostic value by Vogl (1910). I have not examined a wide enough range of material to confirm or contradict this.

III. **RESTELLA** (Figs. 35 C-Ca).

In transverse section: As in *Daphne* but indumentum, cork and collenchyma all present. Chlorenchyma and starch sheath absent. Phloem rays
not dilated. Vessels small, arranged tangentially. Wood tending to be ring-porous. Internal phloem fibres absent.

IV. WIKSTROEMIA (Figs. 35 D-Da).
In transverse section: As in Restella but external phloem fibres in tangential bands/groups. Vessels larger, arranged in radial or oblique pattern.

V. STELLERA (Figs. 34A-Aa).
In transverse section: Indumentum and cork absent. Cuticle well developed, inner epidermal walls often thick, mucilaginous. Stomata more or less sunken. Outer cortex chlorenchymatous. Sclereids and crystals not observed. Starch sheath absent. Phloem fibres arranged in interrupted ring, never in parallel tangential bands. Phloem rays not dilated. Vessels inconspicuous. Internal phloem fibres absent. Pith wide relative to size of stem, cells parenchymatous, thin-walled. Joshi (1935) reports anomalous thickening in the old subterranean parts with concentric zones of xylem and phloem developing, separated by parenchyma. He also observed included phloem in the outer rings.

VI. STELLEROPSIS (Fig. 34B).
In transverse section: As in Stellera. Photosynthetic tissue well developed. External phloem fibres rather scanty, spaced apart in small groups.

VII. DENDROSTELLERA (Figs. 34C-Cb).
In transverse section: As in Stellera but indumentum present in young stem (Fig. 34Cb), disappearing with cork formation in old material.
(Fig. 34 C). Collenchyma and chlorenchyma absent. Phloem fibres at apices of phloem groups; rays not greatly dilated. Vessels solitary or in twos and threes. Old wood tending to be ring-porous. Rays uniseriate. Internal phloem in groups. Pith narrow, cells thicker-walled.

VIII. DIARTHRON (Figs. 35 A-B).
In transverse section: As in Stellera but collenchyma and prismatic crystals present in D. vesiculosum. Vessels radially or obliquely arranged. Pith narrow.

IX. PASSERINA (Figs. 35 E-F).
In transverse section: Indumentum present, hairs disappearing with cork formation. Collenchyma well developed or absent. Chlorenchyma and starch sheath absent. Mucilage and tannin cells occur frequently in cortex. Sclereids and crystals not observed. Phloem fibres un lignified, thick-walled, in a continuous or interrupted ring. Phloem rays not dilated. Vessels very small (less than 20 μm mean tangential diameter), obliquely or tangentially arranged. Internal phloem present. Internal phloem fibres absent. Pith cells often tannified.
Fig. 31. Thymelaea Sect. Ligia

A - Ac. T. passerina.

A. T.S. of stem. Internal phloem fibres present. x 30.

Aa. Section enlarged. x 70.

Ab. Cell detail of outer cortex. x 145.

Ac. T.S. of root. x 70.

B. T. mesopotamica. T.S. of stem. Internal phloem fibres absent. x 70.

C. T. salsa. T.S. of stem. Internal phloem fibres absent. x 70.


Fig. 32. *Thymelaea*. Stems in transverse section.


B. *T. hirsuta*. Internal phloem fibres moderately developed or scanty. x 30.


D. *T. argentata*. Epidermis tannified. Internal phloem fibres present. Pith cells both thin and thick-walled. x 30.

Da. *T. argentata*. Section enlarged. Vessels fewer, scattered. x 70.

Fig. 33. *Daphne*. Stems in transverse section. All x 70 except D.

A. *D. longilobata*. Internal phloem fibres present. Collenchyma well developed.

B. *D. mezereum*. Internal phloem fibres absent. Collenchyma absent, cork well developed.

C. *D. gnidium*. Internal phloem fibres present. Cork not yet developed.

D. *D. arbuscula*. Internal phloem fibres present. Sclerenchyma also occurring in outer cortex. x 30.
Fig. 34. T.S. of stems.


Aa. *Stellera chamaejasme* subsp. *chamaejasme*. Section enlarged. x 70.

B. *Stelleropsis antoninae*. Pith also large. Internal phloem in complete ring. Sclerenchyma not well developed. Chlorenchyma present. x 30.


Ca. *Dendrostellera lessertii*. Section enlarged. Wood tending to be ring-porous. x 70.


*Stellera, Stelleropsis and Dendrostellera* - internal phloem fibres absent.
Fig. 34
Fig. 35. T.S. of stems. All x 70 except Ca (x 30) and Da (x 145).

A. *Diarthron vesiculosum*. Collenchyma present.

B. *Diarthron linifolium*. Collenchyma absent.

C. *Restella albertii*. Vessels tending to be in tangential ring. Collenchyma and cork present.


E. *Passerina montana*. Vessels very small, not conspicuous.

F. *Passerina filiformis*. Cells at pith margin (near internal phloem) with tannin.

G. *Elaeagnus multiflora*. Lepidote scales present. Internal phloem absent.

*Diarthron*, *Restella*, *Passerina* and *Wikstroemia chamaedaphne*—internal phloem fibres absent.
A, pith
narrow rays

B
Ca

Da

narrow rays

pith

D

lenticel

tannin inclusions

E

F

tannin inclusions

G

stalks of peltate scales

Fig. 35
Wood anatomy in general has not been studied. Observations were based on older twigs (over 5 mm but less than 1 cm in diameter) and also taken from the account of the family by Metcalfe & Chalk (1950).

Growth rings vary from present and pronounced to entirely absent. In T. hirsuta there are no rings and the same type of wood is produced throughout the year (Fahn, 1967). This species grows in relatively dry soils but its root system reaches those levels containing a certain amount of moisture even in a dry summer. The cambium thus remains active throughout the year.

The following is a short description of the secondary xylem.

Wood relatively specialized with vessels small (<100 μm tangential diameter) to extremely small (Daphne longilobata and Passerina <25 μm); arrangement solitary and in oblique, radial or tangential groups; pattern often dendritic. Wood tending to be ring-porous. Vessel perforations characteristically simple, intervacular pitting in radially clustered vessels alternate. Axial parenchyma apotracheal and paratracheal, sometimes in terminal bands. Crystals absent. Vascular rays predominantly uniseriate, nearly homogeneous; cells procumbent or upright. Fibres with bordered pits, moderately to extremely short.

This type of wood occurs in a fairly large number of dicotyledonous families without necessarily indicating any natural affinities. For example, Janssonius (1950) considers the wood of three Javanese species to show certain similarities with the Simarubaceae, Euphorbiaceae...
or even the Meliaceae, Bignoniaceae, Tiliaceae and Rutaceae!
3.4 Seedling

Only six species representing three genera were available for study - insufficient for comparative purposes. One species, Daphne gnidium (Fig. 36), will be briefly described.

Cotyledons: Venation actinodromous, with 3-5 conspicuous primary veins in the lamina diverging radially from 2 vascular strands at the level of the node. Bailey (1956) in his survey of 99 dicotyledonous families found that many cotyledons were characterized by such a type of pseudo-palmate or palmate-parallel venation. Stomata absent in cotyledons of this species; in T. passerina, they are anomocytic but anisocytic or modified tetracytic in foliage leaves. Thoday (1921) examined the cotyledons of Passerina filiformis and found that unlike foliage leaves which are ingrooved, they are convex on the adaxial surface. Chlorenchyma is weakly developed and restricted to the adaxial not abaxial surface. The stomata, however, are similarly confined to the adaxial side, not raised or sunken. Mucilage cells are present in both epidermides.

Leaf: Venation in first foliage leaf eucamptodromous. Ultimate veinlets composed of tracheary cells not associated with sclereids. Stomata like in adult leaves, restricted to abaxial epidermis, anomocytic, slightly sunken (Fig. 36 D,E). Adaxial cuticle ridged and inserted between epidermal cells; abaxial cuticle usually striated and thicker especially in the region of a stoma. Secretory cells characteristic of adult leaves conspicuous even in the first leaves. Palisade compact, 1-layered, restricted to the adaxial side (dorsiventral) unlike adult leaves which have well developed palisade on both sides of the leaf (isobilateral).
Spongy parenchyma isodiametric in T.S. Midrib ground tissue parenchymatous. Vascular system simple. Sclerenchyma cap unlignified, not extending to the epidermis (Fig. 36 D).

The leaf structure in plants raised from seed in the greenhouse was compared with that of seedlings collected in a drier habitat in the wild. There were some differences. In the greenhouse material, the palisade tissue is still less compact, the cuticle thinner and the epidermal cells smaller in size. Stomata are sunken only to the level of the inner epidermal walls; there are fewer mucilage/secretory cells. The lateral bundles are uniformly small with sclerenchyma not well developed. Presumably these morphological modifications could be interpreted as adaptive responses to a more shaded and humid environment.

Stem: Nodes are unilacunar, a condition usually associated with exstipulate leaves. The hairs are similar to that of the adult plant - simple, unicellular, angled near the base and with moderately thick, verruculose outer walls (Fig. 36 B). Collenchyma is present, often in the form of a complete ring. Phloem fibres are unlignified and arranged in tangential bands. Internal phloem and associated fibres both occur; the former in a ring, the latter in scattered groups. Pith cells are compact and thick-walled.

Root: The upper region of the primary root is thickened as a result of an increase in the cortical parenchyma (Fig. 36 A). Starch is present in the large, thin-walled cells. Internal phloem and pith are both absent. (Fig. 36 C).
Fig. 36. Daphne gnidium

A. 16-week old seedling. Primary root thickened in upper region.

B. Transverse section of stem in region indicated by 'b'.
   Internal phloem fibres present. Hairs unicellular with verruculose walls.

C. Transverse section of root in region indicated by 'c'.
   Cortex wide. p.p. = primary phloem, s.p. = secondary phloem, s.x. = secondary xylem.

D. Transverse section of 4th leaf in midlaminar region.
   s. cell = secretory cell.

E. Detailed drawing of leaf section. Stoma on abaxial surface, slightly sunken.

A drawn to scale shown, B - E diagrammatic.
B. Starch bodies and cortical parenchyma are labeled. The periderm is indicated in the cross-section diagram.

Daphne gnidium - 4-mth-old seedling

Fig. 36
3.5 Discussion and conclusions

Taxonomic significance of characters with special reference to Thymelaea

1. Anticlinal walls of epidermis: from the anatomical study on Thymelaea, two distinct patterns emerge (see Table 4). In Sect. Ligia, the species of which are annuals or herbaceous perennials, the anticlinal walls are undulated. In Sect. Thymelaea, species of which are suffrutescent, both straight and undulated walls may occur in leaves of the same or separate plants. In response to the life cycle (an earlier, shorter and more rapid growth period), the anticlinal walls develop sinuous patterns in which dove-tailing in regions of maximum stress offers strength and rigidity and at the same time allows for cell wall extension and flexibility. Sect. Piptochlamys and Sect. Chlamydanthus, with evergreen sclerophyllous or leaf-shedding species the habit of which is influenced by the particularly long drought period prevailing in the Mediterranean, have straight anticlinal walls. Growth activity in these species is restricted to spring and early summer with water availability being the limiting factor.

2. Stomata: the occurrence of stomata on adaxial or abaxial leaf surfaces is a specific character not correlated with habitat. In Thymelaea, only 2 species-groups have stomata restricted to the adaxial surface; they are Sect. Piptochlamys subsect. Hirsutae and three members of Sect. Chlamydanthus subsect. Coridifoliae. In this genus, the anomocytic 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 randomly orientated and distributed, though noticeably fewer over costae. They are sunken or flush with the epidermis, but in mature leaves of *Passerina* the stomata are slightly raised above the leaf surface which unusual condition may perhaps be related to mechanical stress set up during drying. Thoday (1921) considers the raised position might prevent mechanical closure of the pores during drought. Stomata on stem: for *Thymelaea* this character has a clear correlation with the presence of chlorenchyma and absence or poor development of cork (see Table 5). Stomata are also present in the herbaceous stems of *Stellera*, *Stelleropsis* and *Diarthron*.

3. Leaf indumentum: the unicellular trichome is the only hair type ever found in leaves of all members of the family, although in *Daphnopsis*, a S. American genus, it has been reported to be bifurcate (Metcalfe & Chalk, 1950). The hairs are straight or highly twisted, thin- or thick-walled; the thickness of the wall and size of the lumen have no bearing on whether the indumentum is straight-adpressed or tomentose-lanose. Hairs may occur on the adaxial and/or abaxial surfaces, sometimes on the margins. Young leaves are conspicuously more pubescent. In mature glabrous leaves of *T. villosa* the slightly bulbous hairbases can be seen as dots with the naked eye.

4. Stem indumentum: this is a good diagnostic character only when dealing with young stems as it disappears gradually with cork formation in older twigs. Only 6 species of *Thymelaea* lack indumentum. In Sect. *Ligia*, its presence can be used to distinguish two species.
5. **Secondary (2°) phloem fibres in stem**: as seen in transverse section, these occur in scattered groups, a more or less complete ring, or in short, parallel, tangential bands. I could find no taxonomic correlations for Thymelaea although Vogl (1910) considers their arrangement diagnostic for species of *Daphne*. I did not investigate a wide enough range of material of *Daphne* to confirm this.

6. **Dilation of 2° phloem rays**: not occurring in annuals, herbaceous or suffrutescent perennials but prominent in *Thymelaea* Sect. *Piptochlamys* and Sect. *Chlamydanthus*. Also in old wood of *Daphne* and the lignified basal stems of *Dendrostellera*.

7. **Vessel distribution**: Leandri (1930) regarded this character in young stems up to 1 cm in diameter as having considerable taxonomic value, but I have found that his 4 classes often overlap in *Thymelaea* and *Daphne* with vessels being solitary, and in radial, oblique and tangential groups.

8. **Vascular rays**: the narrowness and near-homogeneous nature of the rays in the 2° xylem is characteristic of the family. If the development of only one type of ray (the uniseriate) with a homogeneous cell composition is considered as advanced from a phylogenetic viewpoint, then the Thymelaeaceae can be described as having a relatively specialized wood.

9. **Internal phloem**: this is present in the stem of all genera studied and seems to be a family character, thus useless for distinguishing genera or lower taxonomic levels. Some species have it occurring in
in scattered groups, others in complete rings.

10. **Internal phloem fibres**: its presence in the stems of some species has some diagnostic value. Old wood rarely shows this distinct character but not all young stems show it either. Internal phloem fibres are present in *Thymelaea* Sect. *Ligia*, Sect. *Thymelaea* and Sect. *Eptochlamys*. They have so far not been observed in Sect. *Chlamydanthus*. They are absent or present in *Daphne* and completely absent in *Restella*, *Wikstroemia*, *Stetteropsis*, *Diarthron*, *Stellera*, *Dendrostellera* and *Passerina*.

11. **Pith**: the pith region in *Stellera* and *Stelleropsis* is very broad when compared with that of other suffrutescent genera. This seems to be a character independent of the developmental stage, because the herbaceous or semi-herbaceous stems of *Diarthron*, *Dendrostellera*, *Thymelaea* Sect. *Ligia* and Sect. *Thymelaea* also die off or die down seasonally, but their pith regions are much smaller relative to stem size. Moreover, the cells of the latter genera often become crushed and disorganized in the early stages of secondary growth.

12. **Nodes**: in all genera these are unilacunar and only a single trace, which may have two laterals, enters the base of the leaf or petiole from the vascular cylinder of the stem. Unilacunar nodes are often associated with exstipulate leaves.

13. **Leaf midrib**: the primary vascular bundle is single or composed of a large median and two adjacent laterals. Abaxial sclerenchyma of un lignified phloem fibres is always well developed, forming a vascular
Bundle sheaths are invariably parenchymatous, surrounding the vascular tissues of the veins. In some species of *Passerina*, they are easily seen in t.s. because the cells are filled with tannin-coloured contents. Bundle sheath extensions are mostly parenchymatous, rarely collenchymatous but in some species of *Passerina* and *Wikstroemia*, sclerenchyma extends to the abaxial epidermis.

Vascular bundles are collateral in most species, but adaxial and abaxial phloem has been observed in *Stelleropsis magakjanii* and some but not all species of *Daphne*. This perhaps is a more diagnostic character but the condition of dried material did not allow evaluation with any certainty.

**14. Venation:** the following sums up the 1° venation types in the nine genera:

- **Eucamptodromous:** *Thymelaea, Daphne, Restella, Wikstroemia, Stelleropsis, Diarthron*

- **Actinodromous:** *Thymelaea tartonraira subsp. tartonraira var. tartonraira*

- **Acrodromous:** *Stellera, Dendrostellera*

- **Almost parallelodromous:** *Passerina*

The genus *Dendrostellera* can be very reliably recognized by its venation pattern. That in *Passerina* is masked by the indumentum and leaf thickness and can only be seen easily in leaf clearings. Details such as the divergence angle of 2° veins, type and density of higher order reticulation, are also surprisingly constant characters for a given species and not dependent on developmental stages or size at maturity.
15. Dorsiventrality of leaves: this is a specific or generic character as is the isobilateral condition; both types may be present in the same genus.

Leaves dorsiventral and isobilateral: *Thymelaea, Daphne*

Leaves isobilateral: *Restella, Stelleropsis, Diarthron vesiculosum*

Leaves dorsiventral: *Wikstroemia, Passerina, Diarthron linifolium (†)*

*Dendrostellera* and *Stellera* have isobilateral or weakly dorsiventral leaves.

16. Crystals: sand-like, in the form of raphides or prismatic crystals, not in idioblasts. However, in *Daphne laureola* subsp. *philippi* the raphides are grouped in the adaxial epidermis and palisade mesophyll. Druses are absent from all parts of the leaf, stem and wood. The presence or absence of crystals has no correlation with taxonomic relationships.

17. Tannin: leaf epidermal cells are often filled with tannin-coloured contents. Tannin idioblasts are also conspicuous in the outer cortex of stems of some species of *Thymelaea*, e.g. *T. tinctoria*. The occurrence of tannin in the abaxial epidermis and bundle sheath of *Passerina* has already been commented on (see Table 3).

18. Sclereids: foliar sclereids were found to be present in mature leaves of all 30 species of *Thymelaea*. They are vesiculose or tracheoidal, mostly terminal in distribution. As little information is available on sclereid characters in plants of the same species with reference
to edaphic conditions (De Roon, 1967; Rao, 1977), two species, *T. tartonraira* and *T. hirsuta*, which have a relatively wide geographical range in the Mediterranean, were studied in some detail with regard to occurrence and variation of sclereids.

For *T. hirsuta*, there was little correlation of morphology or anatomy with geographical distribution. For *T. tartonraira*, in which four subspecies can be distinguished, there is an increase in density and distribution of sclereids throughout the leaf and at the leaf apex in plants from coastal habitats. *T. tartonraira* subsp. *tartonraira* var. *transiens* from inland Morocco (Middle Atlas) had fewer sclereids per unit leaf area (Fig. 17 C) as compared with plants collected from Capri and Naples. Var. *tartonraira* and its various intermediates (Figs. 17 B & C) from the littoral region of S. France and the Mediterranean islands show maximum sclereid development. It is suggested that soil conditions, e.g. salt content, nitrogen deficiency and exposure to salt spray have modified leaf thickness and sclereid distribution.

**PASSERINA:** A special note should perhaps be added regarding this S. African genus. Some of the leaf anatomical characters are of diagnostic value. Figs. 30A - Db show transverse sections of some species; the observations are summarized in Table 3. Leaf outline in t.s. is of more limited value as several species characteristically exhibit a xeromorphic habit with the leaves inrolling because of water loss during the dry season. In herbarium material, the grooves are tightly closed so that the leaves are narrowly cylindrical, almost acicular. Thoday (1921) infers that leaf closure is due to tension
forces developing in the abaxial epidermis, the cells of which are very large compared to leaf size. Cells of the adaxial epidermis are significantly smaller.

The leaves are morphologically orientated in such a manner that absorption of solar radiation is minimized on the adaxial surface. Other features previously mentioned in the descriptive account of the genus are the deep-celled, tannin-filled, mucilaginous abaxial epidermis which being dark coloured would be a good absorber though poor conductor of radiation, the very thick cuticle which may be surface reflecting and the restriction of stomata to the woolly concave side.

Although stem and leaf anatomical studies yield much basic information which could be listed as an aim in itself, it is difficult to evaluate the taxonomic significance of some characters. Among the genera studied, Stellera, Stelleropsis, Dendrostellera and Diarthron are most similar regarding anatomical structure and these form a fairly closely related and natural group. Of the four, Diarthron and Stelleropsis, Stellera and Dendrostellera have more affinities with each other. It is noted that the second pair share a similar acrodromous venation with the $2^0$ veins exhibiting the same type of angle of divergence.

There have never been any comprehensive studies on Thymelaea itself which consider all parts of the vegetative anatomy. A comparative account devoted largely to the leaf and stem and based on all the known species is now given. It is summarized in Tables 4 & 5. The number of specimens studied forms a good representation of the
170

TABLE

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Some anatomical characters of the leaf.

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14. T. subrepens
15. T. procumbens
16. T. ruizii
17. T. calycina
18. T. coridifolia
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TABLE 5. *HYPERLAPA*. Some anatomical characters of the stem.

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<th>Old Stem</th>
<th>Internal phloem fibres</th>
<th>Stomata</th>
<th>Chlorenchyma</th>
<th>Internal phloem fibres</th>
<th>Cork</th>
<th>Phloem rays dilated</th>
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species and it was possible to detect and classify some species-groupings based on anatomy. The four sections and seven subsections distinguished show some modifications from the scheme proposed by Brecher in 1941, although the species comprising the last two sections are grouped in a similar manner as his first two.
CHAPTER IV  Floral anatomy and biology

4.0 Materials and methods

Flowers and fruits at various stages of maturity were collected and preserved in a fixative of formalin-glacial acetic acid - 70% alcohol (5:5:90). Herbarium material was also used. The species chosen for anatomical studies are enumerated in Appendix A. Hand sections of fruits and seeds were made with a razor blade, stained in 1% aqueous safranin (after Sass, 1958) and temporarily mounted in 50% glycerol. Some floral parts were cut at 10 - 15 μm and double-stained in Mayer's haemalum and erythrosin (Johansen, 1940). Whole flowers were also cleared with 10% KOH and the lignified elements stained in basic fuchsin (after Fuchs, 1963). This has the advantage over serial sections as the entire vasculature can be seen without reconstruction. However, it is necessary to examine transverse sections to establish the orientation of these bundles. Anther squashes were made in acetocarmine (following Darlington & LaCour, 1962) to obtain stages of microsporogenesis and observe maturation of pollen grains. Young ovules were dissected out in acetocarmine mixed with glycerol (1:1) and gradual pressure exerted on the coverslip to free the nucellus from the integuments. Other than these, no special techniques were used.
4.1 Flower

As described in Sect. 2.4, flowers of the nine genera investigated have a small and definite number of floral parts. In *Thymelaea*, the gynoecium is absent in the true staminate flower, rudimentary and non-functional in the partially staminate one. The flowers of the other genera are bisexual. The following account deals with the anatomical study of some floral parts. The detailed investigation of the inflorescence was not carried out in the absence of fresh material because this weakly lignified structure does not lend itself to anatomical study in the dry state.

Bract

Floral bracts are leaf-like in structure. In *Passerina* and some species of *Thymelaea*, stomata and thick cuticles are present on either or both surfaces. The mesophyll is either spongy or differentiated into palisade and spongy tissue, with the more compact palisade towards the abaxial side. Sclereids occur at the margin or at vein-endings (Fig. 37).

Pedicel

The pedicel receives a single large bundle from the inflorescence axis in those species with flowers initially grouped in umbellate or sub-umbellate clusters. Unlike the stem, the pedicel does not show much anatomical variation and appears to have little or no taxonomic importance. Joshi (1936) describes the structure in *Stellera chamaejaeme* in detail, commenting on its vasculature. He stated that the development of large intercellular air spaces in such a steppic-desert plant is rather unusual.
Perianth tube

The perianth tube is supplied with 8 vascular strands except in Stellera chamaejasme which is pentamerous (or hexamerous) and this has 10 (or 12) traces. Inverted bundles are absent in the perianth which is also referred to as the hypanthium in some floras, e.g. Fl. URSS Vol. 15 (1949), Fl. Europaea Vol. 2 (1968). According to Puri (1951), the absence of such bundles is evidence that the tube is a structure of appendicular origin. It may be regarded as formed by the fusion of the lower part of the staminal filaments with the base of the perianth.

In some genera there is the post-anthesis formation of an abscission layer which allows the separation of the withered upper portion from the lower half in an almost circumscissile manner.

Perianth lobes

The lobes resemble foliage leaves in their primary venation. The secondary veins of the midrib bundle join up with those of the two laterals (Fig. 39 A). The lateral strands of adjacent lobes fuse at a lower level of the perianth tube, usually at a point just before the vascular connection to the lower (inner) whorl of stamens. I see no reason why the perianth lobes should not be regarded as being of sepaloid origin as their structure is extremely sepal-like.

Transverse sections of the lobe show that it consists of an epidermis and 2 - 3 layers of undifferentiated parenchyma (Fig. 40F). Vesiculose sclereids (Bokhari, 1970) characterized by their more or less parenchymatous forms, unbranched or with rudimentary appendages, are present in Thymelaea and Diarthron (Fig. 39 A, Ab). As far as can be determined
from literature, this has not been previously recorded. The sclereids appear terminal on a topographical basis due to the juxtaposed development of vein endings. As they were present in all sections of *Thymelaea* without showing much difference in their morphology and distribution, no taxonomic significance was assigned to them. Most species of *Daphne*, however, have few or no sclereids in the perianth. The survey was by no means complete for the other genera, and it may perhaps be possible that examination of a wider range of material might reveal some variation which could be used in conjunction with other characters.

The outer epidermis of the perianth lobe may have a thin or, especially in species of a more arid habitat, e.g. *Dendrostellera*, *Passerina* (Fig. 40 F), a fairly thick, ridged and furrowed cuticle. Stomata and unicellular hairs which are either straight or crisped to some extent, resembling those on the external surface of the perianth tube, may be present (Fig. 39 Aa). In *Passerina montana* and *P. rigida*, the cells have tannin-coloured contents. According to Saunders (1933), the colour of the perianth results from anthocyanins in the cell sap. Flowers of *Stellera chamaejasme* have often been described as green or yellow (Hemsley, 1895, 1902) because flower heads stain herbarium sheets this colour on drying. But as observed in the natural state (Kashyap, 1930) and in cultivated material, they are distinctly purplish-red on the outside and white within. Some of the inner epidermal cells of the perianth lobes in *Daphne petraea* are much enlarged, presumably these contain volatile oils which contribute towards the characteristic fragrance.
Stamens

All species with the exception of Diarthron linifolium and Stellera chamaejasme have eight stamens in two alternating whorls of four each. The first mentioned species has only 4, the latter 10 or 12.

The stamens are adnate to the perianth tube. The anther is two-lobed and four-loculed (Fig. 40B). The filament has a single amphicribal bundle which terminates in the connective tissue between the two anther lobes. The vascular supply is continuous with the midrib or the fused bundles of the sepal, depending on whether it is the upper (outer) or lower (inner) whorl. Besides ground parenchyma, the only other distinctive feature is the fairly thick and cutinized outer epidermis, which may often have tannin-coloured contents (Fig. 40C). Stomata are absent from both filament and anther.

The outermost wall layer of the anther is the epidermis. In Passerina (Fig. 40D), the cells appear as thin-walled spherical projections. In most species of the other genera examined, only the epidermis and subepidermal layer (endothecium) remain when the pollen is mature. The latter is an unevenly thickened layer with strips of secondary wall material mainly on the walls not in contact with the epidermis. The tapetum in its later stages of development is composed of binucleate cells. In the mature anther the middle layer(s) and tapetal cells become crushed and disintegrated.

The development of the microsporangium (pollen sac) was only followed for Thymelaea passerina (see Sect. 4.3). Preparations of other species were of the older stages. According to Kausik (1940), all the wall
Fig. 38. Diagram of flower with hypogynous and faucal scales.

I have used the terms 'hypanthium' and 'sepal' to indicate the perianth tube and lobes since anatomical evidence currently favours this.

Fig. 5. Hypogynous Disc/Scales
layers in *Lasiosiphon erioccephalus*, are formed from the primary parietal layer except for the epidermis. Anther dehiscence is longitudinal and introrse or latrorse, preceded by the breakdown of tissue between locules of the same anther half. The cells in the region of the stomium are reduced to that of the epidermis alone, the endothecium being absent here. From the investigation stamen anatomy is so uniform it is unlikely to furnish any notable characters for distinguishing taxa of any rank.

**Hypogynous disc/scales**

Petaloid, fleshy-glandular, filiform or scale-like structures are present at the throat of the perianth tube in some African genera, e.g. *Dicranolepis, Gnidia, Lachnaea, Struthiola*. They alternate with the sepals and the outer whorl of stamens. Such scales are absent in the nine genera investigated. Joshi (1936) considers the disc-scale present at the base of the ovary in *Stellera chamaejasme* to represent a much reduced corolla because of its vascular supply from the receptacular stele (Fig. 200B).

From their studies, both Joshi (1936) and Kausik (1940) conclude that the Thymelaeaceae must have been derived from dichlamydeous ancestors, with the disc representing the missing corolla. I agree with the first proposition but think the second not very likely as the hypogynous disc is intrastaminal. *Gonystylus*, which is included in the Thymelaeaceae by some workers (Airy Shaw, 1947, 1973), does have 30 - 40 petaloid structures which are extrastaminal and thus not exactly in the same position as a hypogynous disc. These structures, and perhaps the faucal scales present in some genera (Fig. 38), should be regarded as petals or enations of the sepals, and for the latter, possibly of staminodal origin. Gerber
(1900) records that when flowers of *Thymelaea hirsuta* are parasitised, the stamens become transformed into 'leafy' structures but the hypogynous 'cupule plurilobée' remains as a disc.

**Gynoecium**

The gynoecium in the family is generally regarded as monocarpellary, but Joshi (1936) found anatomical evidence for a bicarpellary gynoecium in *Stellera chamaejasme*. Present findings in this species conform in all respects to his investigations and additional studies on the gynoecium in *Thymelaea* appear to support his views too.

In *Thymelaea*, four vascular bundles are symmetrically disposed in the stalk at the base of the ovary; when these bundles enter the ovary wall, three of them are located on the side where the ovule is attached (Fig. 39 Ba). Of these three bundles, part of the two larger ones supply the ovule (Fig. 39 B). The rest of the large bundles break up into four bundles, making with the addition of the other two smaller bundles, a total of six at the top of the ovary. Part of these bundles continue into the transmitting tissue of the style, disappearing near the stigma. The ovular supply goes to the base of the nucellus (Fig. 39 B) as Guerin (1916), Fuchs (1938), etc. have recorded in other members of the family.

Joshi (1936) states that there is no monocarpellary gynoecium with a bilateral symmetry and four traces, of which the two opposite and larger ones supply the ovule. Thus the gynoecium must be regarded as bicarpellary. The bilobed stigma was used as further evidence to support this interpretation. Each carpel would be theoretically
supplied with three traces of which the marginal traces of one would be fused with those of the other. The large vascular bundles would thus represent the fused marginals and the smaller ones, the midrib bundles of the carpels (Fig. 39 Ba). Gonystylus from S.E. Asia is 3-8-loculate whilst Peddiea from S. Africa has two locules, each with one ovule, in an apparently monocarpellate gynoecium.

**Obturator**

Fuchs (1938) in her embryological studies made reference to the 'obturator' which is regarded as a structure facilitating the growth and passage of the pollen tube into the ovule. In most families, this is a swelling of the placenta which grows towards the micropyle and fits like a hood over the nucellus, thus serving as a 'bridge' for the pollen tube (Maheswari, 1950). In the Thymelaeacae the obturator is a special tissue consisting of elongated cells at the base of the stylar canal which grows down towards the nucellus. Kausik (1940) also observed that the obturator in Lasiosiphon eriocephalus develops as part of the stylar tissue and not from the placenta or the funicle. Among some other families with such a functional device may be mentioned the Elaeagnaceae and Combretaceae. This tissue also develops in apparently unrelated families like the Euphorbiaceae, Rosaceae and Umbelliferae. As the origin of the obturator in the Thymelaeaceae is unique and unusual, so different from that known in the other families, its presence in these other groups need not signify taxonomic relationships.

**Stigma**

Most of the epidermal cells of the stigma become papillate and filled
with dense cytoplasm (Fig. 43 Bb). The nuclei are large and deep-staining. In Passerina, the papillae become much elongated to form epidermal hairs which give the 'mop-like' appearance of the stigma and at anthesis, occlude the throat of perianth tube (Fig. 40 A, E). The hairs drop off after pollination; presumably an age effect or fertilization has occurred.
Fig. 37. *Thymelaea tartonraira*. Clearings of upper (inner) bracts.

A. Subsp. *valentina*.

Aa. Unicellular hairs from adaxial surface.

B. Subsp. *argentea* var. *argentea*.

Bb. Epidermal hairs.

C. Subsp. *tartonraira* var. *transiens*.

Ca. Epidermal hairs.

Sclereids present at margin or at vein-endings.

Bracts all x 44; hairs x 110.
Fig. 37
Fig. 39.  Thymelaea tartonraira subsp. tartonraira var. transiens.

Floral anatomy.

A. Staminate flower. Part of perianth cleared to show sclereid distribution and vasculature in lobes. (x 44)

Aa. Unicellular hairs from lobe. (x 110)

Ab. Vesiculose sclereids from lobe. (x 220)

B. Pistillate flower. Gynoecium cleared to show vasculature. (x 44)

s.b. = small bundle (representing midrib bundle of carpel)

l.b. = large bundle (representing fused marginals)

o.b. = ovular bundle.

Ba. Gynoecium in t.s. (diagrammatic).
Fig. 40. *Passerina montana*. Floral anatomy. All as seen in transverse section.

A. Flower at level of 'mop-like' stigma. Vascular strands indicated in black.

B. Flower at the lower whorl of stamens. Filaments shown belong to upper whorl.

C. Filament with tannin-coloured cells. Part of epidermis enlarged to show angular thickenings between outer and radial walls.

D. Anther wall which consists of endothecium and epidermis alone.

E. Part of stigma with hyphal-like projections in transverse and longitudinal view.

F. Perianth-lobe which is anatomically sepal-like. Cuticle of outer surface ridged and furrowed.

A - C not drawn to scale; D - F drawn on scale shown.
4.2 Fruit and seed structure

Studies on the anatomy and development of the ovule and seed in some members of the Thymelaeaceae this century include contributions from Guérin (1916), Netolitzky (1926), Fuchs (1938), Kausik (1940) and Venkateswarlu (1945, 1947). The recent account by Corner (1976) is a noteworthy summary of existing knowledge of seed structure of this family, as well as providing further information based on an additional three species, each representing a separate genus. My own investigation has particular reference to Daphne and Thymelaea. Seeds of these two genera are ovoid-conical or pyriform and fairly small, ranging from 1 to 5 mm in length.

The fruit and seed structure of Daphne longilobata, previously unrecorded, will now be described. This serves as an example for the fleshy fruits of this genus. A common definition of the seed is 'fertilized ovule' and as most of the details of the developing ovule are to some extent similar to that of the maturing seed, they are also included in this section.

Daphne longilobata (Figs. 41 & 42).

Ovary superior, 1-carpellate, 1-loculate. Locule decreasing in size as seed develops so that at maturity, there is only a small air-filled gap with seed tightly adpressed to fruit wall (Fig. 41 B). Pericarp glabrous except at apex; fruit stalk short, covered with hairs similar to those on perianth. Vascular bundles 9 - 10 at base of fruit (Fig. 41 C), dividing into 25 - 30 strands which supply wall (Figs. 41 Ca, Cb). Wall consisting of pericarp alone, composed of 14 - 20 parenchymatous
layers measuring 1 - 1.5 mm in thickness at maturity (Fig. 42A).

Sclereids completely absent. Outer and inner epidermides cuticularized.
Fruit and stalk abscissing together with seed enclosed; separation
layer of cells formed at base of stalk.

Seedcoat
This is formed by two integuments which are clearly recognizable and
free from each other for the most part during development and remain
distinct even at maturity. In most seeds where there are two integuments,
the outer is often more massive than the inner, but this is not the
case in the Thymelaeaceae. The inner integument develops more rapidly
than and projects beyond the outer one, forming the micropyle. Part
of the outer integument grows and overarches it at a later stage (Fig.
43 C).

The testa (= outer integument) is composed of 5-6 parenchymatous cell
layers with the innermost (= endotesta, Corner 1976) containing tannin-
coloured matter (Fig. 42C). It forms a thin, easily removed covering
at maturity. Corner (1976) refers to such a structure as pellicular
(skin-like). The outer epidermis (=exotesta, Corner 1976) is glabrous,
without stomata, sometimes pigmented. Its cells are polygonal with
straight anticlinal walls as seen in surface view. As the testa is
non-indurated, it does not form the main protective coat in the ripe
seed and its slightly firm pulpiness may be regarded as an adaptation
for seed dispersal.

The tegmen (= inner integument) is much thicker than the testa and
is represented by a rather large and variable number of layers,
10 - 15 being the most common. The outer epidermis (= exotegmen, Corner 1976) is uniseriate and differentiates as a layer of closely packed, radially elongate, palisade-like cells which becomes lignified (Fig. 42D). The outer part (up to one-fifth of length) is highly refractive, forming a 'crystalline' zone. The lumen of each cell contains dark-coloured granules. At a later stage, it becomes nearly obliterated by thickenings developed on the radial walls. This epidermal layer forms the main mechanical tissue of the seedcoat and remains as a hard rigid lining for the mature embryo. It imparts the characteristic reddish-black shine to the ripe seed. The rest of the inner cell layers are of thin-walled, lacunose parenchyma. Some become compressed and structurally indistinct at maturity. The inner epidermis of the inner integument (= endotegmen, Corner, 1976) has subreticulate endothecial-like wall thickenings (Figs. 42D, Da).

Skottsberg (1972) refers to the seedcoat in Wikstroemia as 'hard, pitch black, covered by a thin, soft episperm'. He describes the 'episperm' as being 'semitransparent and peels off easily from the black and very lustrous custaceous but brittle cover'. Lecomte (1914) describes the seed cover of Wikstroemia longifoliva from China as having three layers - an external layer which is cellular and membranous, a middle layer with lignified cells elongated perpendicularly to the surface and an internal parenchymatous layer. Wawra (1875) refers to the external layer as the 'episperm'. Hamaya (1955) states that the 'testa is custaceous, black or blackish-brown; tegmen membranous, white or brown, adhered to the testa'. In actual fact, the testa is the thin pulpy external layer and the outer epidermis of the tegmen, the thick hard layer. A majority
of workers also mistake this hard palisade of the tegmen for an endocarp and erroneously refer to the fruit of Daphne as a drupe. However, Corner (1976) does refer to the fruit of Linostoma pauciflorum as a drupe because the innermost layer of the pericarp is of thick-walled cells (forming a weakly fibrous endocarp). In view of all these differences in opinion, I think it is preferable to refer to the fruits as dry or fleshy and not to use such terms as 'berry, drupe, baccate or drupaceous' for the latter nor 'nucule, nutlet, achene etc.' for the former.

Vasculature

The outer integument in Daphne longilobata is distinctly vascularized (Fig. 42 B) with the bundle extending from the funiculus to the chalazal region. The inner integument and nucellus share some tracheidal tissue. The presence of nucellar tracheids has also been reported in several other members of the Thymelaeaceae (Guérin, 1913, cited in Schnarf, 1931; Fuchs, 1938; Corner, 1976).

In his observations on the ovule of Myrica gale (Myricaceae), Kershaw (1909) regards the postchalazal branchings reaching almost to the micropyle as either representing the remains of an ancient nucellar vascular system or as an entirely new structure. Kausik (1940) describes a conducting strand of elongated cells in the chalazal region of the ovule in Lasiosiphon eriophalus and suggests its development might have arisen in response to the nutritive demands of the embryo-sac.
Nucellus

The nucellus is massive in the early stages and appears glandular as most of the cells are thin-walled, with large nuclei and filled with dense contents. It persists as a thin layer enveloping the embryo and endosperm with the apex projecting conically into the micropyle. The nucellar epidermis shows reticulate thickenings on its outer walls which are similar to those found on the inner epidermis of the inner integument. This suggests it is likely that the perisperm existing in the mature seed may have a dual origin, derived both from the nucellus and the inner integument. Both tissues also share a common vascular network. Cronquist (1968) states that perisperm is clearly an advanced feature with nutritive matter absorbed from there by the endosperm and passed on the the embryo during germination. Perisperm is often associated with embryo classified as 'peripheral' by Martin (1946).

Endosperm

The embryo does not occupy the entire volume of the seed and endosperm remains at the apices of the cotyledons in this species (Fig. 41B). As understood from the work of Hamaya (1955, 1963), endosperm is very poor or lacking in the genus Daphne. The majority of works refer to it as 'wanting or scanty'. The tissue in D. longilobata is composed of large thin-walled cells with oil globules (Fig. 42 Db) and is utilized during germination. There is little or no starch.

Embryo

Following the twelve categories of Martin (1946), the seeds of the nine genera studied can be described as having the embryo large,
axile, erect, spathulate with expanded cotyledons. *Wikstroemia* with
dry fruits show rather thin cotyledons as compared with the fleshy
ones of *Daphne*. A N. American species, *Dirca palustris*, is noted
by Martin (1946) to have the 'cotyledons investing', i.e. they over-
lap and cover the stalk for at least half of its length. Although
a normal embryo of *Daphne* has two cotyledons, tricotyly (the occurrence
of three cotyledons) is occasionally met with in cultivated plants,
e.g. *D. giraldii* and *D. longilobata*. All three cotyledons are well
developed and equal in size (Figs. 4†D, Da). Stomata are absent
in this species. The venation is near actinodromous with an odd number
of vascular traces at the cotyledonary node (Fig. 4†Db). Associated
polyspermy in *D. longilobata* and *D. odora*, a condition where there
are more than three nuclei in the pollen grain before germination,
has already been previously mentioned (see Sect. 2.4.3).

**Genera with dry indehiscent fruits**

With the exception of two species of *Passerina*, the other genera have
dry fruits. Their structure is similar to the described account
for *Daphne*, but the pericarp is composed of fewer cell layers and,
in *Thymelaea, Stellera* and *Dendrostellera*, supplied with only 4 - 6
main vascular bundles. It is thin, becoming dry and membraneous.
The testa in *Thymelaea* is 4-5 cells thick and similar to the pericarp
in structure. It often dries up on the hard tegmen at maturity.
Unicellular hairs (Fig. 43 E) and stomata (Fig. 4†Fa) are present
on the outer epidermis of the pericarp as well as on the testa (Fig.
4†Eda) in *Thymelaea hirsuta* and *T. lythroides*. Nucellar tracheids
are absent in *T. passerina*. The perisperm consists of only a few
cell layers in the mature seed. Endosperm is only obvious in young
ovules. It becomes nearly absorbed by the embryo when the seed matures and exists only as a very thin filmy layer (Figs. 43Da, 44Ac) or covering the apices of the cotyledons. Hence the genera with dry fruits are often described as 'exalbuminous'. As in other seeds where endosperm is almost absent, the embryo is large in relation to the seed as a whole. The cotyledons become fleshy, acting as food reserves and often photosynthetic, persistent for a long time during the seedling stage. Anomocytic stomata were present on the upper epidermides in most species of Thymelaea (Fig. 44Ba).

Conclusions

The relative constancy in seed structure in both the genera Daphne and Thymelaea gives some indication of their close relationship. The outer epidermis of the inner integument (exotegmen) is always palisade-like, thick-walled and lignified. It acts the protective function of the exo- or endotesta of seeds of other families and may also be assumed to be connected with a high degree of impermeability and thus the late germination of most seeds. In addition, the occurrence of reticulate or subreticulate thickenings on the walls of the endotegmen and cuticularization of the exotesta probably contribute to the impermeability of the seed coat as well.

Taxonomic significance of the seedcoat

The exotegmen is the most characteristic feature of seeds of Thymelaeaceae. Other families with such a similar palisade-like exotegmen are the Euphorbiaceae (subfamily Crotonoideae), Malvaceae, Sterculiaceae; Tiliaceae, Bixaceae, Passifloraceae and Piperaceae. Families where the mechanical tissue is also of exotegmic origin but fibrous instead
of palisade-like, include the Euphorbiaceae (subfamily Phyllanthoideae), Elaeocarpaceae, Celastraceae, Flacourtiaceae and Meliaceae. Gonystylus, included in the Thymelaeaceae by some (Airy Shaw, 1973), placed in a separate family, Gonystylaceae by others (Corner, 1976) has the mechanical layer intermediate between the fibriform exotegmen of the Elaeocarpaceae and the palisade-like exotegmen of the Thymelaeaceae. The family Elaeagnaceae, often considered related to Thymelaeaceae, has exotestal seeds, i.e. it is the outer epidermis of the testa which forms the rigid palisade. The Proteaceae has a fibrous exotegmen. This family has been stated to have affinities with the Thymelaeaceae (Hutchinson, 1967), the Elaeagnaceae (Takhtajan, 1966, 1969) or both (Cronquist, 1968). Seed structure of the Thymelaeaceae certainly does not suggest any affinities with the Elaeagnaceae. It would indicate some relationship with the Proteaceae if we regard the fibrous exotegmen and the palisade-like exotegmen to have a common origin.

The type of embryo in the Thymelaeaceae is distinctive of such a wide range of families with no close affinities that although seed structure is very conservative I am inclined to think the character has arisen several times independently. However, it does not occur in families considered to be primitive. Families putatively listed as having a similar embryo type include the Euphorbiaceae and Simaroubaceae. The Elaeagnaceae have the embryo partly investing.
Fig. 41. Daphne longilobata. Floral anatomy.

A. Dissected flower with ovary removed. Base of perianth splits as fruit develops, deciduous.

Aa. Young fruits.

A-Aa. Drawn to same scale.

B. L.S. young fruit. Note absence of hard endocarp and thus should not be termed a 'drupe'.

fr. wall = fruit wall (pericarp)
o. int. = outer integument (in mature seed becomes testa)
in. int. = inner integument (similarly becomes tegmen)
nuc. = nucellus (indicated by sparse dots)
end. = endosperm (indicated by close stippling)

C, Ca, Cb. Successive transverse sections from pedicel upwards at positions shown in B. Vascular tissue in black.

B-Cb. Drawn to same scale.

D. Lateral view of teratological embryo with three cotyledons.

Da. View from radicle end. cot. = cotyledon

Db. Cotyledon cleared to show venation.
Fig. 42. *Daphne longilobata*. Fruit and seed structure.

A. T.S. pericarp.

B. T.S. developing seed (diagrammatic). Nucellus persists in the mature seed as perisperm.

o. int. = outer integument

lig. = lignified layer

par. = parenchyma

in. int. = inner integument

v.s. = vascular strand in outer integument

C. T.S. outer integument. Inner epidermis with tannin-coloured contents.

Ca. Outer epidermis of outer integument in surface view.

D. T.S. inner integument. Outer epidermis is main mechanical layer consisting of a palisade of radially elongate cells.

Da. Inner epidermis of inner integument in surface view.

Reticulate thickenings present.

Db. T.S. perisperm and endosperm tissue.

All drawn to same scale except for B and Da.
Fig. 43. *Daphne x burkwoodii* and *Thymelaea hirsuta*. Floral anatomy. Drawings not to scale except where indicated.

A - C. *Daphne x burkwoodii* 'Somerset' (*D. caucasica* x *D. cneorum*).
A. Half flower.
B. Ovary with hypogynous disc in section.
Ba. View of stigma from above. Shape triangular, centre shallowly depressed.
C. L.S. ovary showing laterally attached, anatropous ovule with two integuments.
Aa - Ba drawn to same scale.

D - Ga. *Thymelaea hirsuta*
D. Unripe seed. Outer integument (o. int.) transparent, pellicular; inner integument (in. int.) thick, becoming hard and shiny black.
Da. Integuments removed showing embryo surrounded by membranous layer of endosperm and perisperm.
D - Da. on same scale.

E. Outer epidermis of pericarp in surface view. Unicellular hairs present.
F. Inner epidermis of outer integument in surface view. Cells rounded, thin-walled.
Fa. Outer epidermis of outer integument in surface view. Cells polygonal, slightly thick-walled.
G. Inner epidermis of inner integument in surface view. Sub-reticulate thickenings characteristic of this layer.
Fig. 44. *Thymelaea lythroides*. Fruit and seed structure.

A. Mature fruit. Pericarp forming dry, papery envelope round seed.

Aa. T.S. fruit stalk.

Ab. Seed in lateral view with testa removed. Micropyle faces placenta and is formed by the inner integument alone.

Ac. Seed with both coats removed.

B. Embryo in lateral and raphal-view.

Ba. Upper epidermis of cotyledon in surface view showing stomatal meristemoid - precursor divides into 2 guard cells (g.c.).

C. Endosperm cells from squash preparation.

D. Inner epidermis of inner integument in surface view.

Da. Outer epidermis of inner integument in t.s. Cells thick-walled and lignified, radially elongate.

E. Inner epidermis of outer integument in surface view.

Ea. Outer epidermis of outer integument in surface view.

Stomata and unicellular hairs present.

F. Inner epidermis of pericarp in surface view.


A, Ab & Ac on same scale; Ba - F on separate scale. Aa and B not drawn to scale.
4.3 Embryology: a review of present knowledge

The earliest embryological investigation on the Thymelaeaceae is by Brongiart in 1826 (cited by Fuchs, 1938) who drew attention to the conducting tissue at the base of the style (now referred to as an obturator). Since then, several contributions which relate to the embryology of the family have appeared from time to time. Early investigations on Daphne include that of Hofmeister (1849), Beauregard (1877), Vesque (1879), Prohaska (1883), Strasburger (1884, 1885), Osawa (1913) and Guérin (1915). Their observations have been independently summarized by Schnarf (1931) and Fuchs (1938) and need not be repeated here. Studies pertaining to the development of the embryo itself are much fewer. Those by Souéges (1942) on Daphne mezereum and Venkateswarlu (1947) on Daphne papyracea (as D. cannabina) are more recent and detailed. Within the other genera, Thymelaea passerina (as T. arvensis) and Wikstroemia salicifolia (as W. canescens) receive the same full treatment by Venkateswarlu (1945, 1947).

The following is not an exhaustive or critical account of the embryology of the family as I am only familiar, through my own research, with the structure and development of the anther and ovule of Thymelaea passerina. It is a summary of the more noteworthy features found in three genera investigated by other workers.

WIKSTROEMIA

In the genus Wikstroemia, only W. indica and W. salicifolia (as W. canescens) have been investigated (Winkler, 1904, 1906; Strasburger, 1909; Venkateswarlu, 1947).
Development of anther and pollen

The development of the tapetum, endothecium and spore mother cells follows a normal pattern. However, there is usually an increase in the number of tapetal nuclei after the microspore mother cells are formed (up to 4 in *W. salicifolia* and 2-6 in *W. indica*). These nuclei subsequently fuse. In completely mature anthers only the epidermis and endothecium remain, the middle layers being crushed. The pollen grains are tri-nucleate when shed. A number degenerate in the uni- or bi-nucleate stage. They either do not take up stain or the nuclei become irregularly shaped and the grains stain deeply. Large and small grains, irregularly shaped grains as well as multi-nucleate grains (polyspermy) occur. This has also been personally noted in *Thymelaea*, *Daphne*, etc. (see Sect. 2.4.3.1).

Development of ovule and embryo-sac

The two integuments each initially 3-4 cells thick, after fertilisation become 5-6 cells thick. The ovular strand ends at the base of the nucellus, tracheids are absent in the tissue itself. There is no hypostase. As the seed matures the whole nucellus becomes nearly absorbed except near the micropyle. The obturator composed of compact and protoplasmically dense cells, is formed from the base of the style.

The embryo-sac is contained in the upper part of the nucellus. The primary archesporium is subepidermal and divides periclinaly to form a primary parietal cell on the outside and a megaspore mother cell on the inside. The megaspore mother cell gives rise to a linear (or T-shaped) tetrad of megaspores. The chalazal megaspore is the
only functional one and develops into a uni-nucleate embryo-sac while the rest degenerate.

At the 8-nucleate stage there are three antipodal cells. These may divide to form an additional three cells. All disappear before fertilisation occurs. The early stages of endosperm development are unknown. The pro-embryo is 3-celled and both the terminal and basal cells take part in the formation of the mature embryo. An epiphyseal initial (which gives rise to the stem apex) and suspensor are present. This is characteristic of the Erodium variation of the Asterad type (Johansen, 1950). The plumule is differentiated only at a late stage. During the development of endosperm and embryo, the embryo-sac becomes greatly elongated throughout the length of the nucellus and crushes the tissue at the micropylar and chalazal end.

Abnormalities discovered include abortive ovules and embryo-sacs. Winkler (1906) reports a case of nucellar embryony in \textit{W. indica}, i.e. development of an embryo from a nucellar cell.

\textbf{THYMELAEAE}

The development of the embryo and embryo-sac of \textit{T. passerina} has already been followed in detail by Venkateswarlu (1945).

\textbf{Development of anther and pollen}

The anther is tetrasporangiate, its development is normal. Only a single middle layer is formed as compared to two in \textit{Daphne} and \textit{Wikstroemia}. The tapetal cells usually remain binucleate. In the
mature anther the epidermis becomes so thinned out that only the endothecium is prominent. This 'stretching' of the epidermis has also been personally observed in anthers of *Passerina montana*. The generative nucleus, which stains far more deeply, later divides into two so that the pollen grains are tri-nucleate when shed. Brewbaker (1967) lists the condition as characteristic for the family. However, grains with the unusually higher number of 4-5 nuclei also occur. From this it may be deduced that either the vegetative or the generative nuclei have undergone further divisions.

**Development of ovule and embryo-sac**

In the young ovule both integuments are usually 3 cells in thickness. After fertilization, the outer one becomes 4 cells thick whilst the inner, 5 cells thick. The obturator stated to be formed of compact hairs at the base of the style has not been personally observed in this species. It is absent in the mature seed and probably has disappeared after fertilisation.

The nucellus is not as massive as in *Daphne* or *Wikstroemia*. Thus the megaspore mother cell is less deep-seated. The nucellar cap is only 2-3 cells thick. Nucellar tracheids have also not been observed. In the mature seed, the nucellus remains only as a thin layer.

Venkateswarlu (1945) reports that the megaspore tetrad is linear and that the 3 antipodals in the early stages of the 8-nucleate embryo-sac later multiply, forming up to 25 or 30 cells. During endosperm formation the antipodal end of the embryo-sac elongates and the antipodal mass is left behind in the middle of the embryo-sac. The
presence of many antipodal cells in *T. passerina* was first recorded by Guérin (1915). Secondary multiplication and increase in the number of antipodals is however not unusual in many plants.

The endosperm remains free-nuclear for a long time before becoming cellular. It is vestigial in mature seeds. Embryo development conforms to the Erodium variation of the Asterad type, i.e. an epiphysial initial and suspensor are both present.

**DAPHNE**

Present knowledge of this genus stems mainly from studies on ten species, viz., *D. alpina*, *D. blagayana*, *D. cneorum*, *D. gnidium*, *D. kiusiana*, *D. laureola*, *D. mezereum*, *D. odorata*, *D. papyracea* and *D. pseudomezereum*. That on *D. papyracea* (as *D. cannabina*, Venkateswarlu, 1947) is the most detailed.

Development of anther and pollen agrees closely with that of *Wikstroemia*. The tapetal cells in *D. papyracea* remain binucleate at the time of microspore mother cell formation although increase in number of nuclei from 2 to 6 and their subsequent fusion have been observed in *D. cneorum* and *D. laureola*. Abortive pollen and variation in size and shape occur in several species (see Sect. 2.4.3.1). Osawa (1913) found that in *D. odorata*, a few chromosomes left behind in the cytoplasm during the first meiotic divisions of the pollen mother cells formed small nuclei. He concluded that irregular meiosis might be responsible for sterility in this species. He also observed that there were occasionally 5 - 7 large and small cells in a pollen tetrad.
Development of ovule and embryo-sac

In Daphne, the inner integument usually has more cell layers (10-15) than the outer (5-6). The structure and development of the ovule is similar to that of Wikstroemia. The young embryo-sac is more deep-seated than in Thymelaea or Wikstroemia. A hypostase of thick-walled cells is conspicuous at the base of the nucellus. The antipodal end of the embryo-sac touches the hypostase in late development.

The obturator in D. papyracea is not conical nor does it enter the micropyle. It thus differs in form from that of Wikstroemia and Thymelaea. However, the cells are similarly and compactly arranged. Those in Gnidia, Passerina and Peddiea are reported to be made up of loosely grouped hairs.

Linear and T-shaped megaspore tetrads are present in D. alpina, D. lauresola, D. odor a and D. papyracea. The three antipodal cells may form a further number of small cells which persist at fertilization. The number varies from remaining at 3 in D. alpina, 3-6 in D. odora to becoming numerous in D. blagayana, D. cneorum, D. kiusiana, D. lauresola, D. papyracea and D. pseudomezereum. The increase is by means of mitotic divisions and always originates from 3 cells.

The endosperm is initially free-nuclear; in later stages it becomes cellular. A small amount usually persists at the apex of the cotyledons. Embryo development appears to vary in different species. According to Souéges (1942), no epiphyseal initial nor suspensor is formed in D. mezereum which is characteristic of the Penaea variation of the Asterad type. In D. papyracea, Venkateswarlu (1947) observed both
features present. This is typical of the Erodium variation also met with in *Thymelaea passerina* and *Wikstroemia salicifolia*. Abortive ovules and embryo-sacs have also been discovered. One case of poly-embryony, i.e. development of an extra embryo in the ovule, has been recorded (Venkateswarlu, 1946).

**Discussion and conclusions**

Anther development is normal. Variation occurs in the number of middle layers formed. Most grains are tri-nucleate when shed. Megaspore tetrads are either linear or T-shaped. Increase in the number of antipodals before fertilisation is commonly met with. This feature occurs in a large number of unrelated families, e.g. Nyctaginaceae, Chenopodiaceae, Amaranthaceae. Endosperm formation is initially free-nuclear, becoming cellular in the later stages. It is either absorbed or nearly absorbed by the embryo in the mature seed. Some species of *Daphne*, e.g. *D. longilobata* may have quite a noticeable amount remaining at the apex of the cotyledons. Embryo development follows the Asterad type.

**Embryo development and its bearing on family relationships**

The following summary is taken from Johansen (1950) and Davis (1966), but many gaps in our knowledge of species and genera comprising the families are visibly apparent.

The embryo development in the Lythraceae, Sonneratiaceae and Myrtaceae follows the *Onagrad* type. The Combretaceae shows the Penaea variation of the Asterad type. That in the Proteaceae is apparently the Penaea variation too. Embryo development is still unknown in the Elaeagnaceae,
Flacourtiaceae or Bixaceae. The development in the Penaeaceae and Geissolomataceae has been assigned to the Penaea variation of the Asterad type. Our family Thymelaeaceae shows both the Erodium and Penaea variations.

Hutchinson's (1926) grouping of the Thymelaeaceae has in common the Asterad type of development. This is supposed to be the third most common type in dicotyledons. On embryogenical grounds alone the Thymelaeaceae do not seem to be convincingly related to any other family. The closest would be the Combretaceae, Geissolomataceae, Penaeaceae and Proteaceae! Our knowledge of the extent of variation within types in most families is still so unsatisfactory that until more information is available, this taxonomic character will remain considerably unexploited.
4.4 Review of floral biology

This is a synthesis of available information based on my own studies and culled from general reading. Herbarium material gives almost no obvious data except the period of flowering. However, a comment on the insect visitor presumed to be the pollinator, is occasionally made in field notes.

As mentioned previously a corolla is absent in the genera studied. The tubular perianth with imbricate lobes has the dual function of protection and attraction. Flowers of many species of Daphne are intensely fragrant, e.g. D. arbuscula, D. cneorum, D. odora, D. petraea, though Brickell & Mathew (1976) find atmospheric conditions and time of day to have an effect on scent production in D. oleoides and D. laureola. Nectar is present at the base of the ovary within the tube, but not in copious amounts.

In Daphne, the perianth is caducous when fertilization has not occurred, but when seed develops the perianth splits longitudinally at the base and falls off due to increase in ovary size. In Thymelaea, Wikstroemia and Restella, the entire perianth persists in post-floral stages as a membranous envelope enclosing the fruit which sometimes or ultimately becomes free of it on ripening. In the remaining genera (Dendrostellera, Diarthron, Stellera, Stelleropsis and some species of Passerina), abscission tissue develops above the ovary so that only the base of the tube persists in fruit, thus performing a semi-protective function.

There is a tendency towards condensed grouping of flowers in axillary
clusters, umbellate or subumbellate heads, suggesting that there may be some difficulty in 'attracting' enough insect pollinators. The spreading flat-topped inflorescences, tubular, attractively coloured, fragrant flowers with deep-seated nectar in Stellera and Daphne, indicate that long-tongued insects are potential visitors. I have noted butterflies (Aglais sp.) sunning on flower heads of D. cneorum in June (cultivated material); Davis (pers. comm. 1977) has observed them visiting D. gnidium in the field.

Nectar (if present) and scent is not obvious in Thymelaea though herbarium data for T. lanuginosa give it as 'sweetly fragrant'. Several small insects are retained within the perianth tube at the time of collecting and pressing. Dissection of herbarium material sometimes show them on the stigma itself. A few 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, likewise the tiny beetles observed to be frequent visitors to T. hirsuta and T. tinctoria in the field. As the latter is dioecious, pollen in a pistillate flower must have been transferred by insect agency from a separate plant.

The flowers in Diarthron and Thymelaea 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. As the anthers are situated above the stigma, dehiscence is introrse and the stigmatic papillae are covered with pollen grains, presumably self-pollination occurs. The species is not apomictic: when the stamens were removed, the ovary did not develop.
Flowers of *Passerina* are reported to be wind-pollinated. The pendulous, easily shaken branches with terminal inflorescences, 'mop-like' stigma, exserted anthers on long, slender filaments, are positive attributes suggesting this. Pollen is relatively smooth-coated and produced in quantities; the clump-forming habit also points to wind-pollination.

**Biology of pollen and stigma**

The stamens mature and the anthers dehisce introrsely and loculicidally from base to tip by gradual shrinking of the wall. All anthers dehisce more or less together in *Daphne blagayana*, *D. retusa* and *D. odora*, but in *Thymelaea passerina*, the period of anther dehiscence lasts two days, those from the upper (outer) whorl dehiscing first. The pollen grains are trinucleate when shed; after this the anthers wither. No germination of pollen within the flower has been observed. The stigma is receptive at approximately the same time as the anthers mature and for quite a long period as the pollen still remains attached. This perhaps gives the flower a chance of being self-pollinated. There is only one ovule in the ovary but the stigma is always covered with numerous pollen grains. The style is very short, almost absent. Although it is comparatively long in *Passerina*, the stigma is still well below the stamens when the latter are fully exserted, again perhaps a provision for selfing. The stigmatic surface is papillate which seems to be very efficient for trapping pollen and providing a suitable germination surface.

The number of pollen grains produced per anther was not counted in most of the species (see Sect. 2.4.3.1). It can be seen from Pl. 3 C, E & F to be rather high and that dimorphic pollen in the same flower occurs
to some degree in most species of *Thymelaea* (Table | ). The
dimorphism is a matter of size, the largest grains being twice the
diameter of the smallest ones. It is most distinct in the endemic,
monocious herbaceous perennial, *T. cilicica*, where the ratio reaches
1:1. In the other species the proportion of the smaller grains range
from 5 - 25%. The small grains are not immature or sterile; they
stain deeply with aceto-carmine and basic fuchsia. The large grains,
on the other hand, do not stain as deeply.

In monocious (e.g. *T. microphylla*) or gynodioecious species (e.g.
*T. argentata*), perhaps the large grains are for transference by
insect-pollinators to other plants and the small sized grains for
cross-pollination on the same plant (geitonogamy). Or perhaps the
large grains would germinate only on the stigma of the pistillate
flower and the small grains on that of the hermaphrodite. However,
an examination of stigma size, type of papillae and length of style
in pistillate and hermaphrodite flowers did not reveal any conspicuous
differences.

In *Daphne*, natural hybrids as well as those obtained in cultivation
occur but as far as is known, none are fertile. There are no reports
of fruit formation. Aborted ovaries, early withering stigmas and a
high proportion of small, misshapen grains, though not the underlying
basic cause of self-sterility, have been suggested to contribute
towards it (Osawa, 1913).

To sum up, it would seem that outbreeding by means of cross-fertilization
is the general rule in the nine genera we are concerned with. Flower
form, abundant pollen and nectar attractive to potential pollinators, self-sterility and sex distribution all seem to point to this. When the population is small and isolated, inbreeding probably occurs.

In *T. passerina* which is a wide-ranging steppic annual with tiny flowers, self-fertility coupled with self-pollination would be an advantage in habitats at the periphery of its range, acting as biological safeguards promoting seed set in environmental conditions where insects and other plants are scarce.
Sex distribution

The flowers in eight of the genera are consistently bisexual (hermaphrodite). The unisexual flower as found in *Thymelaea* is considered to be a derived state and the suppression of gynoecium development resulting in staminate flowers with rudimentary, non-functional ovaries gives weight to this view. Species of *Thymelaea* are described in literature as being polygamodioecious. This is said of a species which is functionally dioecious but with a few flowers of the opposite sex or a few hermaphrodite flowers on all plants at flowering time, and is true only for *T. argentata*, *T. hirsuta* and *T. tartonraira*. The sex distribution in various species of *Thymelaea* is listed below.

I. HERMAPHRODITE FLOWERS ONLY

* T. passerina

II. UNISEXUAL FLOWERS ONLY

(a) Dioecious or near dioecious species, i.e. with staminate and pistillate flowers on different plants

- *T. lythroides*
- *T. gattefossei*
- *T. velutina*
- *T. dioica*
- *T. tinctoria*
- *T. subrepens*
- *T. procumbens*
- *T. ruizii*
- *T. calycina*
- *T. coridifolia*
- *T. antiatlantica*
- *T. villosa*
- *T. thesioides*
- *T. sanamunda*

(b) Monoecious species, i.e. with staminate and pistillate flowers on same plant
i) Both types in the same flower cluster

T. putorioides
T. microphylla
T. sempervirens

ii) Both types not in the same flower cluster

T. cilicica
T. salsa
T. aucheri
T. mesopotamica

III. HERMAPHRODITE AND UNISEXUAL FLOWERS

(a) Gynodioecious species, i.e. some plants with hermaphrodite flowers, others with pistillate flowers

T. lanuginosa
T. argentata (the female plants flower later (June) than those bearing hermaphrodite flowers (late April and May)).

(b) Androdioecious species, i.e. some plants with hermaphrodite flowers, others with staminate flowers

T. virescens
T. virgata

(c) Trimonoecious species, i.e. with hermaphrodite, staminate and pistillate flowers in same plant but functionally dioecious

T. hirsuta
T. argentata (within the same cluster of 4-9 flowers, 1-2 are pistillate, the rest hermaphrodite. Staminate flowers are rarer, occurring in separate clusters).

T. tartonraira
(d) Andromonoecious species, i.e. with hermaphrodite and staminate flowers in same plant

T. gussonei
T. salsa and T. mesopotamica (rare).
From this compilation, in unisexual flowers, the dioecious state with staminate and pistillate flowers on separate plants is more common than the monocious. It is suggested that in the genus Thymelaea, dioecy and monoecy has separately evolved from hermaphroditism through gradual reduction of ovule fertility rather than from a dimorphic incompatibility system. Even in dioecious species, all staminate flowers retain the rudimentary ovary. If male fertility of these partially female-sterile hermaphrodites is greater than that of normal hermaphrodites, the latter will be ultimately eliminated, as has probably occurred for members of Group II.

Although it is very rare to find the true staminate flower, I have observed the presence of 12 stamens inserted at different levels on the perianth tube of T. hirsuta (Fig. 52f). In this case, the abortive ovary is completely absent. Gerber (1900) records staminodes in pistillate flowers of T. hirsuta but I have not seen this myself. In 1900, Natepa described an Acarine parasite, Eriophyes passerinae (Eriophyidae) which has been suggested as being responsible for the deformation of flowers of T. hirsuta in the environs of Marseilles. The stamens become 'leaf-like' by a hypertrophizing or castration effect.

In Group III, gynodioecy and androdioecy were found in equal proportions and the species comprising both groups show little tendency to evolve towards complete dioecy.

**Phenology**

With the exception of Thymelaea hirsuta, none of the species flower
throughout the year in the wild. The season is restricted and of fairly short duration, lasting not more than 2-6 weeks. Species are day-flowering either during winter and early spring (within the period of March and April), early summer (May - July) or late summer and autumn. In the Cape region of South Africa, the maximum flowering season for species of *Passerina* is 3-4 weeks mainly within September and December, which would be spring and early summer in the Southern Hemisphere. Cultivated hybrids of some Daphnes appear to have a semi-perpetual flowering habit, e.g. *D. x hybrida*, *D. x mantensiana*.

The flowering periods were determined from information on herbarium material and from reliable literature records. Although the peak flowering periods, dates of first flowering as well as those for the last flowers produced were also approximated from herbarium material and from some field observations, they were not tabulated. An individual plant usually has a comparatively short period in flower; the long time spread recorded for some species, e.g. *Thymelaea passerina* is a result of the geographical range, variation in altitude, exposure, etc., and also from climatic differences between one year and the next.

As in the wide-ranging *Daphne mezereum*, some of the large-leaved, deciduous Himalayan daphnes also come into flower at different seasons. At high altitudes (3300 m) *Daphne papyracea* flowers in April but at village level (ca. 1800 m), the peak flowering period is between late November and early December.

**Ecology of seed dispersal**

All species with dry fruits have a rather limited means of dispersal.
The growth form of the parent plant often restricts seed spread especially when it is of the compact cushiony or tufted type with no horizontally spreading branches or rhizomes. The diaspores themselves are light, easily blown by wind when ripe. Herbarium material floats in water; the pericarp, though not mucilaginous, absorbs moisture becoming smooth and slippery. It is suggested that rainwash especially down slopes or in shallow gullies, might be a means of dissemination. The fruits are not specially inflated (though in Diarthron the pericarp becomes slightly inflated and papery at maturity), nor equipped with hooks and spines to aid in long distance tumbling. The long silky hairs on the persistent basal half of the perianth in Dendrostellera may perhaps protect the diaspore against desiccation during the dry season or aid in seed germination by retaining a water-film when wetted. Although never observed or recorded, I think the conical-pyriform seeds of dry fruits with their hard yet brittle coats could easily be transported and cracked open by sparrow- or finch-like birds. However, the small size of the embryos within may not be a sufficiently attractive food-source, unless of course the entire seeds are swallowed to act as 'grinding stones in the gizzard'.

Petterson (1956) reports that the seed, not the fleshy pericarp of Daphne mezereum, is sought by greenfinches whereas blackbirds are more concerned with the flesh (Brickell & Mathew, 1976). Fruits of Daphne and two species of Passerina are succulent - red, black or pale-coloured at maturity. According to Halda (1972, cited by Brickell & Mathew), seed of D. arbuscula is freely produced in the wild and distributed by mice and birds. Dispersal by larger mammals (reports of 'horses and camels in Afghanistan violently sick after eating
ripe berries of *D. mucronata* is inadvertent and rare.

Each flower produces only one ovule. In most species flower congestion within an inflorescence not only increases the attractiveness but the number of flowers per plant and thereby the seed output. This compensates to some degree for the poor dispersal unit. By grouping reproductive organs, there is also the increased potential for extensive genetic recombination, as in the capitula of the Compositae and compound dichasia of some Rubiaceae.

In S. Africa, shrubs whose only method of regeneration is by seed are exterminated when veld fires are far too frequent to allow seedlings to reach flowering and fruiting stage. *Passerina* comes into this category and not being strikingly resistant to fires, has a slow recovery rate. Some species grow well on sterile or shifting sand dunes and these are left undisturbed by man, the dry habitats they occupy being considered unworthy of cultivation.
CHAPTER V. Review of cytological and phytochemical evidence; economic uses

5.1 Cytology

Chromosome morphology and number can suggest more natural groupings in some families, but in the Thymelaeaceae present information on the karyotype cannot be used to support or improve a classification. Previous to and during the earlier part of this century, cytological data were sometimes incorporated into embryological papers, but the bulk of the genera revised today are still cytologically unknown. The purpose of the present report is to summarize all available information from the work of earlier investigators. Chromosome numbers for over sixty taxa in eleven genera have been recorded (see Table 6). This forms approximately 12% of the family since more than five hundred species in fifty five genera are recognised (Airy-Shaw, 1973).

1. Daphne

The chromosome number \(2n = 18\) has been reported for 14 out of 15 investigated species of *Daphne* (excluding three hybrids). The lone exception is *D. odora* Thunb. for which counts of \(n = 14\), \(2n = 28\) (Hiraoka, 1958) and \(2n = 27\) (Okura & Kono, 1959) have been obtained. This species, native to China, is commonly cultivated in Europe for its showy and fragrant flowers. It is almost always sterile, very rarely producing seed. Plants in the Royal Botanic Garden, Edinburgh, have been badly attacked by virus with consequent fasciation of the inflorescences. Their flowers contain well-developed anthers and ovules but germination of pollen grains on stigmas has never been observed.
although the stigmas are often densely covered with self-pollen.
Plant sterility has sometimes been considered to be due to the influence of long cultivation in an unfavourable climate.

Osawa (1913) made a detailed study of the pollen grain and embryo-sac development in this species and concluded that the visibly abnormal later stages of pollen development together with degeneration of the embryo-sac was the cause of sterility. He believed that long cultivation or mutation had effected this since his determination (or rather mis-determination) of the chromosome number was different from that of closely related species.

Although hybridity may result in a very high proportion of mis-shapen and abortive pollen, defective pollen may also be due to the presence, among other factors, of a large number of unpaired chromosomes in the pollen mother cells at the first meiotic division. D. odora was thus discovered to be an allotriploid with $3x = 27$ (Okura & Kono, 1959).

A single chromosome count from the ovule of D. longilobata (Lecomte) Turrill has been personally obtained. As far as I know, this is a new determination. The somatic number of 18 is similar to that of many Daphnes in cultivation. The experimental method followed is briefly outlined here.

Flower buds (source of material listed in Appendix A), collected at the stage when anthers were still translucent, were placed in a freshly mixed solution of three parts absolute alcohol: one part glacial acetic acid and fixed overnight at $10^\circ C$ (cold tap in unheated lab.).
The ovule was dissected out, stained and squashed in acetic orcein, using the standard technique. Camera lucida drawings were made at an initial magnification of x 1850 (Fig. 45).

2. Pimelea
Cruickshank (1953) found that 14 species of the Australian genus Pimelea demonstrated a polyploid series, ranging from diploids to hexaploids. Some species were gynodioecious, i.e. with hermaphrodite and pistillate flowers on separate plants, others dioecious. A rather similar sex-distribution exists in some species of Thymelaea.

3. Wikstroemia
Apogamy has been reported in the pantropical genus Wikstroemia (Fagerlind, 1940). A number of species were found to have aborted pollen. Gupta & Gillett (1969) examined 13 Hawaiian species and found that with the exception of W. pulcherrima (2n = 36, in accord with Skottsberg's earlier observation in 1955), the rest had a uniform somatic number of 18. Chuang et al. (1962) found that W. indica from Taiwan also had 2n = 36. W. uva-ursi had separately determined counts of 2n = 18 and 72 (Skottsberg, 1955); the first of these was later confirmed by Gupta & Gillett in 1969.

4. Thymelaea
Thymelaea microphylla, T. passerina and T. tartonaira subsp. thomasii are the only species of Thymelaea worked out cytologically. The latter is endemic to the Asco valley in Corsica. Contandriopoulos (1964) determined it as a diploid (2n = 18) and regards it as possibly ancestral to subsp. tartonaira from coastal France. No cytological studies of
the other subspecies in the *T. tartonaira* complex have been made. It is possible that the diploid condition has spread over a relatively large area in the past and thus the Corsican diploid represents the remains of an older, now reduced population. But it is unwise to speculate about the factors involved in producing the present geographical distribution unless the karyotype details and ecology of more species are known. The direction and rate of evolution could have been modified by other influences.

Various species of *Thymelaea* in S.W. Europe and N.W. Africa appear to live under a kind of imposed endemism which perhaps prevented the sharing of gene-pools. This can also be linked with a rather inefficient dispersal mechanism. Habitat disturbances have probably resulted in the disappearances of species. Browicz (pers. comm., 1978) relates that natural populations of *Daphne cneorum* growing in perpetual shade under pine forest in many parts of Poland are now known to be sterile. After the forest is felled, the species reproduces by vegetative spread, forming a thick undergrowth. Flowering occurs but fruit and seed is seldom set. When the forest closes up so that the clearing comes under shade again, only the subterranean parts live on; the semi-dormant, denuded aerial parts are hardly visible. With a steady alternating cycle in the habitat, successful stabilization of any new chance mutant will clearly be limited.

For the few species of which karyotype details are available, there was found no steep gradient of size difference between the longest and shortest chromosomes (longest: shortest ratio c. 2). Marked structural heterozygosity in the chromosome complement would be indicated by
karyotype asymmetry. In conclusion, genera which have been cytologically studied have not exhibited the expected cytogenetic diversity. However, the Thymelaeaceae is generally conceded to be a very natural and advanced family. It is however interesting to note that Old World genera, e.g. Daphne, Dicranolepis, Drapetes, Edgeworthia, Thymelaea and Wikstroemia, have the same basic number, $x = 9$ as reported in a New World genus, Daphnopsis (Nevling, 1962a). Chromosome numbers as determined in the Elaeagnaceae and Penaeaceae (Table 7) are very different.
TABLE 6. Known chromosome numbers in the Thymelaeaceae.

Determinations made earlier than 1940 not listed unless not supplemented by later chromosome counts.

<table>
<thead>
<tr>
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<td>Osawa, 1913</td>
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<td>Loeve &amp; Kjellqvist, 1974</td>
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<td>* longilobata</td>
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<td>x burkwoodii</td>
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<tr>
<td>x hybrida</td>
<td>18</td>
<td>Nevling, 1966</td>
</tr>
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* newly determined by author
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<td>Subramanyam &amp; Kamble, 1967</td>
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<td><strong>PIMELEA</strong></td>
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<tr>
<td>drupacea</td>
<td>108 hexaploid</td>
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<td>glauca</td>
<td>36</td>
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<td><strong>WIKSTROEMIA</strong></td>
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<td>uva-ursi</td>
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<td>vacciniifolia</td>
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<td>1969</td>
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**TABLE 6 (contd.)** Known chromosome numbers in the Thymelaeeaeaceae.
TABLE 7. Known chromosome numbers in the Elaeagnaceae and Penaeaceae.

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<td>salicifolia</td>
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<td>ELAEAGNUS thunbergii</td>
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<td>PENAEB cneorum</td>
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<td>mucronata</td>
<td>20</td>
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</tr>
<tr>
<td>SALTERA sarcocolla</td>
<td>c.40</td>
<td>Dahlgren, 1968a</td>
</tr>
</tbody>
</table>

Fig. 45. Camera lucida drawing of mitotic chromosome complement. x 3700.

Daphne longilobata (Lecomte) Turrill

somatic metaphase, ovule. 2n = 18.

5 μm
5.2 Phytochemistry

As with several other disciplines, e.g. cytology and genetics, the main drawback is that only a few species have been analysed and one hesitates to generalize from such a limited basis. There is some information on the chemistry of the Thymelaeaceae and putatively allied families, for instance, Bate-Smith (1962), Gupta & Gillett (1969), the chemotaxonomic data compiled by Hegnauer (1973) and by Gibbs (1974). But insufficient is known at present for an assessment of their possible taxonomic or evolutionary significance. A more extensive investigation in this field will surely yield important information.

It is well known that phenolic compounds, alkaloids and glycosides have been used in recent years as an aid to plant identification (Harborne, 1966, 1971; Mears & Mabry, 1971; Bate-Smith, 1973, etc.). Relationships between groups circumscribed on morphological or anatomical grounds may thus be confirmed or denied. Almost identical glycoside patterns in critical taxa would certainly give a bearing on close relationships. Flavonoid variation can often be easily incorporated into the taxonomy of a group but this has been little studied with the exception of some work by Gupta & Gillett (1969) on Hawaiian Wikstroemias. A survey of the distribution of particular compounds at different taxonomic levels — family, generic and specific — should be profitable although time-consuming. Whether the subfamilies Thymelaeoideae, Aquilarioideae and Gonystyloideae have substances in common awaits discovery.

There is some chemical evidence supporting a relationship between the Elaeagnaceae and the Proteaceae, e.g. the seed-fats of the latter (Vickery,
1971) are remarkably similar to those of the former. These two families have been considered to be related to the Thymelaeaceae but nothing is known of the seed-fats of this family! With all proposed relationships, there should be similarities in the chemistry of at least one or two allies. Unfortunately, inadequate facts on which to base conclusions is the main limitation, and this 'most natural' family has not been easily placed in any family tree.

Phytochemical evidence to support the view that the Thymelaeaceae is a distinct and homogeneous group thus need to be gathered. But how much evidence is necessary to warrant placing it in an order of its own, excluding all other families, would be a problem requiring judgement as in orthodox taxonomy. To quote from Smith (1978), 'chemical characters can be profitably employed only when intelligently compared with all other evidence available .... in taxonomy all evidence is circumstantial'.

A brief survey of the chemistry of the family as known at present, will now be given.

1. Coumarins have been reported as characteristic.

Daphnin, regarded as an isomer of aesculin, is the most frequently occurring coumarin glycoside. It has been found to be present in

*D. alpina* L., *D. gnidium* L., *D. juliae* Kos.-Pol. (a var. of *D. cneorum* L.),

*D. kiusiana* Miq., *D. laureola* L., *D. mezereum* L., *D. papyracea* Wall. ex Steud. and *D. pontica* L. According to Asai, 1930 (cited in Dean, 1952), newly opened leaf buds of *D. odora* Thunb. have up to 27% dry weight of daphnin. It has also been found in *Gnidia polycephala* 'Gilg, Edgeworthia gardneri* Meissn., Wikstroemia ganpi* (Sieb. & Zucc.) Maxim.-
coumarins and phenolic glycosides were common in 11 Hawaiian species of *Wikstroemia* investigated by Gupta & Gillett (1969). The chromatographic evidence supported the separation of these species into two groups. Closely related species had strongly similar patterns, those morphologically different had dissimilar ones. All the species investigated were diploid with \( n = 9 \). The time of collecting, locality and sex (different plants bearing staminate, pistillate and hermaphrodite flowers) were stated to have no influence on the chromatographic patterns obtained.

*Daphnetin*, the yellow coloured aglycone of daphnin, has been found in *D. mezereum*, *D. pontica* and *Gnidia polycephala*. It is likewise present in the crotonoid members of Euphorbiaceae, a group which has been considered to have affinities with the Thymelaeaceae on grounds of pollen morphology, embryology and seed-coat development (Wunderlich, 1967).

*Daphnetin-\(\beta\)-glucoside* (according to Rindl, 1933 and 1934, not identical with daphnin) occurs in *D. juliae*, *D. mezereum*, *D. odora* and *Gnidia polycephala*.

*Daphnoretin* is found in *D. papyracea* and in seed of *D. mezereum*. It has also been isolated from the leaves of the S. American species, *Daphnopsis racemosa* Griseb.

*Daphnorin* (= Daphnoretin-7-\(\beta\)-glucoside) is present in the fleshy
pericarp of *D. mezereum*.

**Umbelliferone**, a coumarin widely distributed in several unrelated plant families, has been isolated from *D. mezereum* and *Gnidia polycephala*.

**Lasiocephalin** (a coumarin dimer with formula $C_{26}H_{14}O_6$) is named from the species investigated, *Lasiosiphon eriocephalus* Decne.

**Thymelol** in quantities of approximately 0.1% is reported from the root, stem, leaf and flower of *Thymelaea hirsuta* (L.) Endl. This apparently is similar to daphnoretin.

**Ellagic acid** a benzocoumarin, does not seem to occur in the Thymelaeaceae although it is widespread in supposedly allied families like the Elaeagnaceae and members of the Myrtales. However a wider survey is necessary to reveal if the restricted distribution is apparent or real.

2. **Flavonoid compounds**

The Thymelaeaceae have not really been studied for anthocyanins and anthocyanidins. Delphinidin glycosides are responsible for the flower colour in *Phaleria neumanii* F. Meull., *Pimelea longifolia* Sm. and *W. indica* (L.) C.A. Meyer. Leucoanthocyanins reported to be common in Drapetes and Pimelea are apparently rare in Daphne and Peddiea.

Wikstronin, another flavone glycoside, has been obtained from the root-bark of *W. indica* (Tseng & Chao, 1963). Flavones are no doubt numerous but no detailed investigation has ever been carried out in the family.
Genkwanin has been previously isolated from *Daphne genkwa* Sieb. & Zucc., linarin from *D. laureola*, hesperidin from *D. mezereum*, luteolin-7-glucoside from *D. oleoides* Schreb. and two unidentified glycosides from the root of *D. papyracea*.

3. Tannins

Although Dekker (cited in Hegnauer, 1973) states that tannin is absent or present only in very small quantities, the leaf and outer stem cortex of many species of *Daphne*, *Passerina* and *Thymelaea* investigated have cells with tannin-like inclusions. The presence of tannin would confer some protection against grazing animals. As early as 1911, Cook & Taubenhaus (cited by Rice, 1974) found that tannins were very inhibitory to parasitic fungi. Tannins are also of general occurrence in the *Elaeagnaceae*.

Investigations by Bate-Smith & Lerner (1954) and Bate-Smith (1956) show that there is an association between the occurrence of tannin and the woody habit. Bate-Smith and Metcalfe (1957) made a study of the distribution of tannins in higher plants and, on comparing their lists with the 'advancement indices' of Sporne (1954), they found that 'the capacity to synthesize tannins decreases as the advancement index numbers for the families go up. It thus seems that the capacity to synthesize tannins is a primitive character that tends to become lost with increasing phylogenetic specialization.'

4. Toxic constituents

It is well known that the root, stem, leaf, fruit and seed of many species in the family produce caustic, acrid substances of a resinous nature
which cause dermatitis, nausea and poisoning. The polyphenols and crotonols isolated from some Euphorbiaceae have a similar effect.

Vermeulen & Pieterse (1968) describes the isolation of a toxin with the formular $C_{37}H_{40}O_{3}$ from Gnidia polycephala. Gharbo et al. (1970) obtained a phytosterine from the leaves of Thymelaea hirsuta. This species is familiar as an antipastoral in Egypt. Cocarcinogens have been isolated from the Euphorbiaceae and Thymelaeaceae (Hecker, 1971). Three such toxic substances found in the latter are:

Daphnetoxin ($C_{27}H_{30}O_{3}$): of which 0.02% is present in the dried bark of D. mezererum and several other Daphne species. It is an ortho-benzoate-phorbol compound.

Mezerein ($C_{38}H_{38}O_{10}$): 0.1% in the seed of D. mezererum.

An acetate of 12-desoxyphorbol: has been found in Pimelea prostrata.

The presence of these substances would be of considerable selective value — reducing biotic threats by acting as deterrents against grazing or insect-attack.

5. Chelidonic acid
This has been detected in Daphne, Dirca, Gnidia, Lachnaca, Passerina, Pimelea, Stellera, Thymelaea and Wikstroemia, i.e. positive confirmations from leaves, flowers or fruits of 28% of the species investigated (152 spp.), representing 19 genera. The quantity of acid was found to be very variable.

\(\beta\)-sitosterin is the most frequently occurring sterine. In addition, 0.3% of free stearic acid has been found in leaves of *Daphne oleoides* and in the root of *Lasiosiphon meissnerianus* Endl.

The triterpenes, taraxerol, taraxeron and taraxerylacetate are listed as apparently exclusive to leaves of *D. papuacea* (Maiti et al., 1963, 1967).

According to Sisido et al. (1967) the flowers of *D. odora* produce 0.024% of ethereal oil, the composition of which includes 48 parts of linalool, 24 of citronella, 7 of \(\gamma\)-hexenol and 0.15 of wax.

Many Asiatic species, e.g. *Aquilaria agallocha* Roxb., *A. malaccensis* Lam., *Gonystylus bancanus* Baill. and *Wikstroemia tenuiramis* Miq., produce a scented heartwood called Aloe-wood, Eagle-wood or 'agaru' (see Sect. 5.3). Ethereal oils (agarol and agarospirrol, \(C_{15}H_{26}O\), agarofurans, \(C_{15}H_{24}O\) as well as unidentified sesquiterpenes, resin-acids and resin-esters have been extracted.

Paraffins (saturated alkanes) are the commonly occurring hydrocarbons in cuticular 'waxes' of leaves and stems. Wax-alcohols and ethyl esters of unsaturated fatty acids are documented in *Edgeworthia gardneri* and no doubt of general distribution in other taxa.

7. Various other compounds.

A. Carbohydrates: mucilage has been observed in the vegetative parts of *Daphne, Passerina, Pimelea* and also in the Elaeagnaceae and Malvales.
Mucilages are various acidic substances of a carbohydrate nature which swell in water, yielding simple sugars and uronic acids. Glucose, saccharose and starch have been detected but this is of such wide distribution in families that they are only of general interest. Maltose is said to occur in Lasiosiphon. Sugar alcohols and cyclitols (quebrachitol, sequoyitol) have not been observed.

B. Seed reserves: Earle & Jones (1962) included seeds of D. mezereum among their samples analysed for biochemical data. The protein content of seeds was found to be 24.4% and that of the pericarp 7.5%. Seed fat was an unusually high level, reaching 65.4%. The oil-content of the pericarp was only 6.0%. Seeds of Phaleria octandra (L.) Baill. also had 55% of oil. Starch was noticeably absent.

C. Mineral substances: Raphides reported to be absent in the family (Gibbs, 1974) have been personally observed in leaf sections of D. laureola subsp. philippi.

D. Alkaloids: the exact nature of those present in the seed (but not the fleshy pericarp) of Daphne mezereum has not been determined (Earle & Jones, 1962). Alkaloids have also been noted in Lasiosiphon and Phaleria. Indole-alkaloids (carboline and serotonin) have not been detected in the Thymelaeaceae though present in the Elaeagnaceae.

E. Saponins: have been reported in Wikstroemia ovata (Solis et al., 1938) and Dirca palustris L. They are said to be absent from Daphne, Linostoma and Pimelea as well as the Elaeagnaceae.
F. Pigments: the leaf and bark of *Phaleria capitata* Jack contain a bluish pigment which has been used to produce an indigo-dye. Carotenoids are present in the bark and fruits of *Daphne*, and no doubt in the scarlet and orange berries of other genera.
5.3 Economic uses

1. Ornamental

Many species, especially those of *Daphne*, have both fragrant and showy flowers, and as a result have been brought into cultivation.

2. Cordage-fibre

The strong, flexible and beautiful silvery bast fibres of several species are used in making ropes, twine and more rarely, woven into bags and clothes. In Japan and China, wood and bark of *Edgeworthia gardneri* and *Wikstroemia ganpi* produce an excellent quality paper-substitute. The roots of *Stellera chamaejasme*, being long, tough and pliant, have also been exploited by Tibetan Lamas for similar purposes. Several closely related Himalayan Daphnes—*D. bholua*, *D. papyracea* and *D. sureil*—are known locally as 'paper daphnes'. *Thymelaea hirsuta* has been investigated as a potential source of cellulosic material (El Ghonemy et al., 1977).

3. Scented wood, timber

The fragrant, resin-infiltrated wood of *Aquilaria* is only obtained from the centre of diseased and dying trees. Healthy wood is not durable, being soft, white and only useful for making tea-boxes and the like. When saturated with resin, it becomes very hard.

It is known commercially as Aloe-wood, Eagle-wood, or in Maly 'gaharu'. 'Garu' in Sanskrit mean heavy on account of the resin-impregnated wood. The Portuguese changed one of the Sanskrit names 'aguru' into 'paq d'aguila' which the French translated into 'bois d'aigle' and the

Early use in India was for fumigation of the body and surgical wounds. The main source was *Aquilaria agallocha* from the Assam hills (Dioscorides called Aloe wood 'agallochon', hence the specific epithet). The chief supply in the Malesian region comes from *A. malaccensis*, *A. hirta* Ridl. and to a lesser extent, from *Gonystylus bancanus*, *Wikstroemia polyantha* Merr. and *W. tenuiramis*. Scent and colour of the dead wood are the chief criteria for grading quality. The best kind sinks immediately in water. Because of its fragrant incense it was associated with religion and ceremonial purposes. In China and the Indo-malesian region it is burnt, often in funeral pyres, and poured out in libations. The Portuguese seized the Chinese trade in the latter half of the 16th century and also made religious objects (rosaries, crucifixes, etc.) from the wood.

*bancanus*  
*Gonystylus* yields an important timber, at one time exported in large quantities from Borneo.

4. Poison

The Thymelaeaceae is one of the few families in which the majority of genera have been said to be unpleasant and unpalatable to livestock. Hamaya (1959) reports the mixed-planting and establishment of *Edgeworthia* and *Wikstroemia* species at the edge of forest plantations to deter the removal of tree-bark by deer, rabbits and other rodents.

The toxic substances indentified so far are mentioned in Sect. 5.2. Effects of poisoning in humans include a caustic and burning sensation
in the mouth and stomach, followed by convulsions and, in cases of overdose, death. Even flowers of *Daphne mezereum* have been reported to have an acrid taste; deaths of young children caused by consuming fruits of this species have been documented. According to Linnaeus, six berries are fatal for a wolf; from field notes, one of *D. mucronata* makes camels very ill. The toxin isolated from *Gnidia polyccephala*, when administered to a guinea pig in a dosage of 11 mg per kg body weight, is sufficient to kill it within five hours (Vermeulen & Pieterse, 1968).

Hillebrand (1888) states that species of *Wikstroemia* known in Hawaii as 'Akia' or 'Akea' are employed for drugging fish because they contain an acrid principle. *Edgeworthia* is used in Nepal and at one time was imported into Malaya for this purpose.

5. Medicinal

The dried bark of stem and root of *Daphne gnidium* (Spurge Flax, chief source), *D. laureola* (Spurge Laurel) and *D. mezereum* (Spurge Olive) were formerly used in medicinal preparations and sold under the pharmaceutical name 'Mezereon' (Hare et al., 1905). Together with mercury or iodides, it was added to a compound decoction of sarsaparilla recommended for gout and 'sluggish blood'. Although still official in most pharmacopoeias (excluding the British Pharmaceutical Codex, 1973), it is now rarely employed. It was reputedly useful as an anthelmintic (being purgative), to cure cancer, syphilis and deaden toothache (having narcotic effect) or to clean up chronic skin ulcers (maintains discharge). Direct application on skin and mucous membranes produces immediate irritation and caustic blistering. Taken internally in overdose, it is an effective but dangerous emetic, 'provoking vomit and the forceful purging of phlegmatic humour and cholers'
Other medicinal prescriptions include the use of seeds of D. gniidium and D. laureola (which have 0.22% of an acrid resin) as abortifacients. In Japan, the fresh bark of D. genkwa infused in vinegar is applied externally to produce blisters. The burning sensation presumably blocks out or alleviates rheumatic pain. A decoction of the acrid root-bark of Wikstroemia indica (L.) C. A. Meyer is taken as a remedy for late stage schistosomiasis (Tseng & Chao, 1963). Garcia (1933) and Solis et al. (1938) also report that Filipinos chew leaves of W. ovata C. A. Meyer ex Meissn. for a cathartic effect.

The bark of Aquilaria cumingiana (Decne.) Ridl. is styptic. The root, wood and leaves of A. malaccensis are used in Malayan folk-medicine for the treatment of rheumatic pains, malaria, jaundice and dropsy. This and also the bark of W. ridleyi Gamble form one of the ingredients of an ointment for small-pox (Gard. Bull. S. S. 6:376(1930). The scented wood enters medicaments sold as stimulants, tonics or carminatives.

Additional note:
Recently, Kupchan & Baxter (1975) found that mezerein, in a dose of 50 mg per kg body weight, inhibited the progress of lymphocytic leukaemia in mice. The antileukaemic principle was isolated from seeds of Daphne mezereum.
PART C  GENERAL TAXONOMIC CONCLUSIONS

6.1 Generic and sectional concepts

It is difficult to give a categorical definition of the term 'genus' or 'section' but the groupings reached should be both practical and biologically sound. A revision of the genus from the species upwards would allow the recognition of species-groups which can be welded into higher natural units (Hedge, 1976; Davis, 1978). An extensive study of material throughout the generic range and a knowledge of distributional patterns would also make it easier to decide on the rank to be assigned to these groups.

The features selected for characterizing should be well-marked and permanent, not ordinarily subject to much variation. Thus a grouping should be easily recognised by the experienced and practised eye. The magnitude of intergeneric or intersectional discontinuities should be more or less equivalent and hence consistent, wherever they occur.

For the descriptive accounts in Sections 6.2 and 6.3, the generic concepts accepted have been based on 'received' ideas, from previous assessments by other taxonomists. As a result there are some small, narrowly defined genera. It seemed more convenient at first to adopt these familiar groupings. By maintaining them initially as separate genera, there is the additional advantage of being able to perceive 'relationships' with some ease later, i.e. if investigations encourage a revision of earlier opinions and the adoption of a broader concept.
6.2 Delimitation of genera

It is well known that in the family 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'. This unsatisfactory situation has led to the consequent merging of several genera. The morphological distinctions provided in the following paragraphs may help to define the taxa studied.

1. **DAPHNE** L., from Greek 'daphne', the laurel (*Laurus nobilis*). The leaves and fruits of many species have a superficial resemblance to laurel. Daphne was a nymph who became transformed into a laurel tree, thus escaping the attentions of the god Apollo.

Right from the start of this thesis, a comprehensive taxonomic treatment of the genus was never envisaged. Brickell & Mathew's (1976) account of *Daphne* provides much information especially on those species known or believed to be in cultivation or likely to attract horticultural interest. The five sections and six subsections provisionally recognised here, follow Keissler's 1898 treatment of Section *Daphnanthes*, modified by Brickell and Mathew (1976) in the light of new species from the Far East. This infra-generic classification has been accepted for the sake of convenience as no satisfactory taxonomic conclusions have yet been made.
DAPHNE L. (Several lesser known species from China are not treated here)

I. Sect. Mecynorhiza Spach
1. D. lecythoides Maxim. ex Regel
2. D. Rootina Maxim.
3. D. koehnei Regel
5. D. pseudomeynorhiza A. Gray

1. D. championii Benth.

III. Sect. Daphne
1. D. albomarginata Wall. ex Pobed.
2. D. alboflexa Laxm.
3. D. insulosa L. (type of genus)

IV. Sect. Erionolena (Blume) Meissn.
1. D. aurantiaca Diels
2. D. composita (L.) Gilg.

V. Sect. Daphnanthes C. A. Meyer
A. Subsect. Alpinac Keissl.
1. D. alpina L.
2. D. altaica Pallas
3. D. caucasica Pallas
4. D. giraldii Nitsche
5. D. sophia Kalenicz.
6. D. taurica Kotov

B. Subsect. Oleoides Keissl.
1. D. gnidioides Jaub. & Spach
2. D. jasminoides Sm.
3. D. kosmophyllum (Stoj.) Stoj.
4. D. lineariifolia Hart
5. D. malayana Blecic
6. D. mucronata Royle
8. D. rodriguezii Texidor

C. Subsect. Gnidiun (Spach) Gilg
1. D. gnidiun L.

D. Subsect. Cneorum Keissl.
1. D. arbuscula Celak.
3. D. petraea Leybold
4. D. striata Tratt.

E. Subsect. Daphnanthoides (Gilg) Keissl.
1. D. acutiloba Rehder
2. D. bholia Buch.-Ham. ex D. Don
3. D. grunbergiana H. Winkler
4. D. kiwiliana Miq.
5. D. longiloba (Lecomte) Turrill
6. D. luzonica Robinson
7. D. malyana Blecic
9. D. pauciflora Wall. ex Steud. emend Smith & Cave
10. D. sargass Smith & Cave (incl. D. chillogn Banerji)
11. D. taiwaniana (Masamune) Masamune
12. D. tanguita Maxim. (incl. D. retusa Hemsl.)

F. Subsect. Collinae Keissl.
1. D. blagayana Freyer
2. D. sericea Vahl (incl. D. collina Dickson ex Sm.)

TABLE 8. LIST OF DAPHNE SPECIES.
The genus contains approximately 70 species (fide several authors) of which the Asiatic ones are the least understood. It is characterized by succulent fruits naked at maturity (some species, e.g. *D. cneorum*, have semi-coriaceous fruits which are enclosed by the long-persistent perianth), an annular hypogynous disc with entire margins (though a few Asiatic species, e.g. *D. papyracea*, have a cup-shaped disc), perianth tube which does not separate into an upper or lower part after anthesis, and alternate leaves (some Chinese species, e.g. *D. aurantiaca* and *D. genkwa* have opposite leaves, or have the lower leaf pairs opposite and the upper alternate).

Fifty-two species which have been grouped into sections and subsections are listed on the facing page, and Table 9 shows the character variation in related genera.

2. **WIKSTROEMIA** Endl., named in honour of J. E. Wikstroem, a Swedish botanist of the 19th century.

*Wikstroemia*, which is closely related to *Daphne*, is often characterized by the presence of opposite or subopposite leaves and the hypogynous disc which is unequally divided into two to five segments. As several species share characters previously considered to be diagnostic of *Daphne*—such as alternate leaves, a cup-shaped disc, an inflorescence axis not elongating in fruit, the absence of bracts, 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. Domke (1934) proposed the subgenera *Euwikstroemia* (*Wikstroemia* s. str.) for the fleshy-fruited species and *Diplomorpha* for some of the dry-fruited ones.

3. **RESTELLA** Pobed., name obtained by anagrammatic rearrangement of the word 'Stellera'.

The sole species (*Restella albertii*) comprising this genus 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 remained entire without transverse splitting, and the much-branched shrubby habit as contrasted with the suffrutescent one of *Stellera*, to be the main distinguishing characters.

Domke (1932, 1934) united *Stellera* and *Wikstroemia* and thus made the new combination, *Wikstroemia albertii* (Regel) Domke. This is against the International Code of Botanical Nomenclature (1972: Art. 11) because, even if his taxonomical decision was sound, *Stellera* L. (1753) has priority over *Wikstroemia* Endl. (1883).

I can find no consistent and clear-cut differences between *Restella* and *Wikstroemia* (see Table 9). *Restella albertii* appears to be a perfectly good *Wikstroemia* from a different region. It must be stated that *Wikstroemia* is a fairly large and widely distributed genus and several characters, both leaf and floral, show variation throughout its range. Thus the features of an inflorescence remaining subumbellate instead of

<table>
<thead>
<tr>
<th>THYMELEAE</th>
<th>PAINTING</th>
<th>WURTHIAENA</th>
<th>HUSTYLLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Leaves alternate.</td>
<td>2. Alternate, rarely opposite.</td>
<td>2. Alternate, subopposite or opposite.</td>
<td>3. Not alternating.</td>
</tr>
<tr>
<td>3. Inflorescence axis not elongating in fruit.</td>
<td>3. Not elongating.</td>
<td>3. Not elongating or not elongating.</td>
<td>4. Absent.</td>
</tr>
<tr>
<td>5. Flowers unisexual or hermaphrodite.</td>
<td>5. Hermaphrodite or unisexual.</td>
<td>6. Persistent.</td>
<td>6. Persistent.</td>
</tr>
<tr>
<td>7. Perianth lobes 4; stamens 8.</td>
<td>7. Lobes 4; stamens 8.</td>
<td>8. Disc cup-shaped or equally divided into 2-5 segments.</td>
<td>8. Disc unequally divided into 2-5 segments.</td>
</tr>
<tr>
<td>18. Leaves amphitropic or epipetalous.</td>
<td>18. Eucamptodromous.</td>
<td>19. Type 1 or 4.</td>
<td>19. Type 1 or 4.</td>
</tr>
<tr>
<td>19. Stomata modified tetracytic, anisocytic or anomocytic.</td>
<td>19. Type 1 or 4.</td>
<td>20. Isobilateral or dorsiventral.</td>
<td>20. Isobilateral or dorsiventral.</td>
</tr>
<tr>
<td>20. Venation eucamptodromous, very rarely actinodromous.</td>
<td>20. Isobilateral or dorsiventral.</td>
<td>21. One main bundle with sclerenchyma not extending to epidermis or of one large and two small lateral bundles all without sclerenchyma.</td>
<td>21. One main bundle with sclerenchyma not extending to epidermis in species investigated.</td>
</tr>
<tr>
<td>26. Leaves isobilateral or dorsiventral.</td>
<td>26. Absent.</td>
<td>27. One main bundle with sclerenchyma extending to epidermis.</td>
<td>27. One main bundle with sclerenchyma extending to epidermis.</td>
</tr>
<tr>
<td>27. Venation eucamptodromous, very rarely actinodromous.</td>
<td>27. One main bundle with sclerenchyma extending to epidermis.</td>
<td>28. Absent.</td>
<td>28. Absent.</td>
</tr>
</tbody>
</table>
becoming laxly racemose, the persistent not deciduous perianth and a dry, non-fleshy fruit, which have been regarded as diagnostic of Restella, also occur in Wikstroemia.

To base a separation of the two genera on the expression of the aforementioned features seems to show a lack of taxonomic judgement. I suggest 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.

4. **Thymelaea** Miller, from Greek 'timos' - thyme and 'elea' - olive. referring to thyme-like habit and olive-like fruit.

A more extensive treatment of this genus is found in Chapter VII. It is more closely related to Daphne than to the other genera in the region and can be distinguished from the latter by the persistent, rarely deciduous perianth and the absence or presence of a very minute, annular hypogynous disc. The style often becomes subterminal in fruit and should there be some doubt as to whether a species with a deciduous perianth belongs to Thymelaea or Daphne, the pericarp in Thymelaea is always membraneous, never fleshy or semi-coriaceous. However, fruit succulence may be a doubtfully diagnostic character, as in the S. African genus Passerina two species, P. ericoides and P. rigida, have fleshy or semi-coriaceous berries while the rest of the species have dry fruits. It would thus appear that a character critical for one genus is not necessarily satisfactory for another.
<table>
<thead>
<tr>
<th>TABLE 10. Characters in Stellera and related genera</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>STELLERA</strong></td>
</tr>
<tr>
<td>1. Suffrutescent; stems unbranched, woody at base.</td>
</tr>
<tr>
<td>3. Inflorescence axis not elongating in fruit.</td>
</tr>
<tr>
<td>7. Perianth lobes 5-6; stamens 10/12.</td>
</tr>
<tr>
<td>15. Stomata anomocytic to complex modified tetracytic.</td>
</tr>
<tr>
<td>20. Vascular system of one main bundle in leaf with sclerenchyma not extending to epidermis.</td>
</tr>
</tbody>
</table>

Note: The table provides a comparison of characters in Stellera and related genera. The format is consistent with botanical classification and features such as leaf arrangement, flower structure, and vascular system characteristics.
The annual and woody members of *Thymelaea* are linked by an intermediate group of suffrutescent perennials which include the type of the genus, *T. sanamunda* (L.) All. Despite the distinctness of 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. Thus the maintenance of *Ligia* as a separate genus by Fasano (1789) for the annuals is not upheld. The group is reduced to sectional rank (see Chapter VII).

It is also not possible that *Thymelaea* Sect. *Ligia* is closely allied to *Diarthron* Turcz., another genus whose limits have partly been circumscribed as being annual. *Thymelaea* always has a perianth which remains entire 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 the upper portion of which becomes deciduous so that only the basal half persists and an ebracteate inflorescence which elongates in the fruiting stage.

The status of *Diarthron*, *Dendrostellera*, *Stelleropsis* and *Stellera* Members of the first three genera were compared with *Stellera*, mainly on the basis of morphological and a few anatomical features (see Table 10).

5. *Diarthron* Turcz., from Greek 'dis' - double and 'arthron' - joint, referring to the perianth which, after anthesis, separates into two parts.
Taxonomic views on the genus (C.A. Meyer, 1839; Meissner, 1857; Domke, 1934; Pobedimova, 1949; Webb and Ferguson, 1968; Breckle, 1971) up to the present, appear to be unanimous in recognising it as a small, distinct genus with only two species, both of which are annual herbs bearing a superficial resemblance to each other. D. vesiculosum has eight stamens like the other taxa in the region; D. linifolium, the type of the genus, has four.

6. **DENDROSTELLERA** Van-Tiegh., from Greek 'dendron' - tree and 'stellera' - generic name of plant; referring to the woody virgate stems.

Van Tieghem (1893) was the first to treat Dendrostellera as a genus separate from Stellera.

7. **STELLEROPSIS** Pobed.

Pobedimova (1949) noted the similarities of Stelleropsis to Stellera by the choice of the name for her new genus.

As far as I can establish (see Table 10), the morphological differences in Dendrostellera are the densely sericeous-villous lower half of the perianth, the conical, rarely ovoid stigma, and a more woody habit in some species. These characters cannot be regarded as sufficiently uniform and constant to warrant generic separation, as two species of Stelleropsis and one of Dendrostellera also have ovoid stigmas. Furthermore, the stems of both genera could be branched and woody not only at their bases but also up to the middle.
The only characters of *Stelleropsis* (with nine species from the steppe regions of C. and S.W. Asia) which have not been recorded in *Dendrostellera* (with 6 - 7 species inhabiting a similar area) appear to be the absence of long silky hairs on the lower half of the perianth and eucaumptral as opposed to acrodromous venation.

In view of the character-states listed in Table 10, a reduction of genera to subgenera is obviously necessary if their phenetic relationships lie more closely with each other than with the other genera of Thymelaeaceae. I suspect this may be in fact so and accordingly suggest that *Diarthron*, *Dendrostellera* and *Stelleropsis* be treated at subgeneric level. *Diarthron* s. str. is perhaps the most specialised genus but the name has priority over the other two under nomenclatural ruling.

A survey of *Thymelaea* had proved that habit differences do not make good generic characters because annuals, suffrutescent and shrubby perennials all can occur in one genus. To place *Dendrostellera* and *Stelleropsis* as sections of *Diarthron* is not so satisfactory, because the morphological gaps between them are of a different order to those I have used in distinguishing sections of the genus *Thymelaea*. In the latter, the sections were based on several well correlated characters and were produced to separate out groups of closely related species. As stated previously, consistency of treatment must be the chief consideration, the 'gaps' between the groups being (as far as possible) of a similar magnitude.

8. **STELLERA** L., after G. W. Steller, traveller and naturalist who died at thirty-seven.
Although undoubtedly allied to the 'Diarthon-Dendrostellera-Steller-opsis' complex, this genus can be easily distinguished by its inflorescence axis which never elongates during or after anthesis and the upper leaves which simulate involucral bracts. The flowers are 5-6-morous not 4-merous, and the hypogynous disc unilateral and ligulate.

Only the type of the genus, *S. chamaejasme* L. which has two subspecies, has been studied. I do not know if any other C. Asiatic taxa fit the above circumscription, but as the characters appear to be distinct and uniformly constant *Stellera* should be maintained as a separate and probably monotypic genus.
6.3 Distribution pattern of genera

The distribution pattern of a genus may give hints for reconstruction of its evolutionary history, especially when fossil records are scanty or lacking. Fossil Thymelaeaceae have been found in only four regions, as indicated in Map 4. They are Pimelea crassipes Heer in the Middle Sarmatian layer of E. Transcaucasia (Khatseba region), Daphne personiformis Weber in Tertiary deposits of Sakhalin (near Mgachi) and Daphne pollen found in late Quaternary deposits of the Ghab valley in N.W. Syria (Niklewski & van Zeist, 1970). A further reference from the Tertiary flora (Middle Miocene age) of the lower Rhine basin (Kreuzau) to Pimelea (Wayland, 1934) was simply based on the resemblance of the Kreuzau material to leaf remains first described by Heer (1856). Fossils, especially leaf remains are often of uncertain affinity. Pimelea, as known today, is primarily an Australian genus. However, from a qualitative study of leaf characters, Ferguson (1971) was able to suggest that the Rhine area had a fairly humid, warm-temperate or subtropical climate at the time of deposition. I think to refer a fossil leaf to living genera whose species are difficult to separate from one another on leaf characters alone, is to give a misleading picture of the distribution of a genus in the past. Perhaps the only record that could be relied on would be the pollen samples from N.W. Syria.

The main distribution pattern of each genus supplemented by maps, is now given. Thymelaea is excluded, it being covered in greater detail in Chapter VII.
1. **DAPHNE** (Maps 1–4)

The genus occurs in Europe, temperate and subtropical Asia, with a few species in N. Africa. The northern limit is occupied by *D. mezereum* and in E. Asia, by *D. kamtschatica*, both of Sect. *Mezereum*. The former reaches to the Arctic Circle in Norway and Fennoscandia. In the south, *D. composita* (belonging to Sect. *Eriosolena*) extends to W. Java; on the western side, the limit is reached with *D. laureola* (Sect. *Daphne*) in the Azores.

A total of seven sections and subsections occur in Europe, five in Asia. The maximum concentration of species are shown in Map 4. These centres of speciation are in the Caucasus, Yunnan, Formosa (Taiwan), the Alps and the S. and W. part of the Balkan Peninsula.

Sect. *Daphne* (Map 1) and the subsections Gnidium (Map 2), Oleoides, Collinae and Cneorum (Map 3) of Sect. *Daphnanthes*, all occur in Europe with Subsect. Oleoides having one species extending further through Iraq and Iran to W. Pakistan. *Daphnanthes* subsect. Alpinae (Map 2) has widespread disjunctions in the mountain regions of N. Italy, S.W. Russia and Crimea, Caucasus, E. of Lake Balkhash (Dzungaria-Tarbagatai region) and in China (W. Kansu and N. Shensi). Subsect. Daphnanthoides (Map 2) is wholly Asiatic, occurring mainly in the Himalayas, China, Japan, Formosa and also in high altitude moss-forest in N. Philippines.

Disjunctions are noted in Sect. *Mezereum* (Map 1). This could have arisen as a result of a contraction of a once formerly continuous area of distribution. The section is represented in Europe by only
one species, namely *D. mezereum*. Perhaps this particular species could have been one of the remnants of a more extensive previous flora. The bulk of the section is in the Far East.

Sect. *Eriosolena* (Map 1) is a ditypic section restricted to montane rain forests of Yunnan and S. E. Asia. Sect. *Genkwa* (Map 1) again is a very small section occurring in E. China, Formosa and S. Korea. The type species, *D. genkwa* although widely cultivated in Japan is not known to be native there.

2. **WIKSTROEMIA** (Map 5).

The distribution of only two species, *W. salicifolia* and *W. chamaedaphne*, will be mentioned. Only the former occurs at the easternmost limits of the region under study. It is found in E. Afghanistan, N. E. Pakistan, Kashmir, Kumaon, Nepal, Assam and Ceylon; in the latter area, above 1800 m in the Central Provinces. It does not occur in Yunnan or Kiangsi as has been listed by Peterson (1972). The specimen he cited as type 'in lapidosis totius Chinae borealis, Bunge' (holo. LE, photo!) is of the other species, *W. chamaedaphne*. This has a more easterly distribution in the Northern Chinese provinces of Hupeh, Shensi, Kansu, etc.

3. **RESTELLA** (Map 5).

Pobedimova (1941) considers this a monotypic genus endemic to the Tien-Shan, Pamir-Alai and Syr-Darya regions of Soviet Central Asia.

4. **DIARTHRON** (Map 6).

One species, *D. vesiculosum*, is a widespread weed in C. and S.W. Asia.
The other, *D. linifolium* (with only four stamens), is disjunct in E. Siberia, Mongolia and N. E. China. The Altai Mountains and Gobi Desert separate it geographically from the area of *D. vesiculorum*.

5. **DENDROSTELLERA** (Map 7).

Of the six to seven species often considered as comprising this genus (Pobedimova, 1953, 1954), only one, *D. lessertii*, is widespread in S. W. Asia. The others are endemic to certain localized areas in Soviet Central Asia.

6. **STELLEROPSIS** (Map 8).

Pobedimova (1949) divides nine species into two series, **Altaicae** Pobed. and **Turcomanicae** Pobed. The first group is restricted to Central Asia, the second to Turkmenia, E. Afghanistan, N. Iran and the Caucasus. The species have been assumed to have a narrow distribution though to what extent this is due to her species concept or to under-collecting, has not been assessed. The types of most species are in Leningrad.

I have only seen material of five species.

7. **STELLERA** (Map 6).

The genus *Stellera*, represented by *S. chamaejasme*, has been included because it occurs in the W. Himalayas. Its distribution is wholly Asiatic and widespread, ranging from N. India through Tibet, to Yunnan and Szechwan, to Hupeh, Manchuria, Mongolia and Lake Baikal.

8. **PASSERINA** (Map 9).

Thoday's 1924 revision of the genus *Passerina* includes fifteen species
all of which are restricted to the Cape Province of S. Africa. One species extends a little northwards to Rhodesia. As stated in the Introductory chapter, *Passerina* was only investigated because several species occurring in the area under study have previously been placed in *Passerina* although belonging to quite unrelated genera. Its specialised anatomy also provides an interesting contrast.
Map 1. Distribution of Daphne

- Sect. Mezereum
- Sect. Genkwa
- Sect. Daphne
- Sect. Eriosolena

Bartholomew's 'The Times' Projection
Map 3. Distribution of Daphne Sect. Daphnanthes

subsect. Oleoides
subsect. Collinae
subsect. Cneorum

52°N
4°
28°
Map 4. Distribution of the genus Daphne showing numbers of species in the different countries. Solid black lines indicate several centres of development (4-7 spp.). It would appear that there was an ancient centre from which wide migration occurred though there are no fossil records for the intervening areas.

Bartholomew's 'The Times' Projection
Map 5. Distribution of
Restella albertii
Wikstroemia chamaedaphne
Wikstroemia salicifolia

Lambert Azimuthal Equal-Area Projection
Map 6. Distribution of *Diarthron vesiculosum* ---

*Diarthron linifolium* ---

*Stellera chamaejasme* ---
Map 7. Distribution of the genus *Dendrostellera* showing number of species in the different areas.
Map 8. Distribution of *Stelleropsis*.

Lambert Azimuthal Equal-Area Projection
6.4 Key to genera

1. Perianth in fruit separating into deciduous upper part and persistent lower part
2. Perianth lobes 4; inflorescence axis elongating after anthesis
   5. DIARTHRON
2. Perianth lobes 5 - 6; inflorescence axis not elongating
   4. STELLERA
1. Perianth entire, wholly deciduous or persistent in fruit
3. Perianth persistent, rarely deciduous; pericarp membraneous at maturity
4. Hypogynous disc annular or absent
   3. THYMELAEA
4. Hypogynous disc cup-shaped or unequally divided into 2-5 segments
   2. WIKSTROEMIA
3. Perianth deciduous, rarely persistent; pericarp fleshy or semi-coriaceous
5. Hypogynous disc annular or cup-shaped
   1. DAPHNE
5. Hypogynous disc unequally divided into segments
   2. WIKSTROEMIA
6.5 Systematic description of Diarthron and its infra-generic groups


Incl. Dendrostellera Van Tiegh.

Stelleropsis Pobed.

Annuals, suffrutescent or suffruticose perennials. Stems virgate, simple or branched at base. Leaves alternate, petiolate or subsessile. Inflorescence terminal, subcapitate, becoming spicate or racemose; axis elongating in fruit. Bracts absent. Flowers shortly pedicellate. Perianth tubular, 4-lobed, upper part deciduous. Stamens 4 or 8. Hypogynous disc present or absent. Pericarp membraneous at maturity.

Key to subgenera and sections:

1. Herbaceous annuals; flowers 1.5 - 5 mm  I. Subgen. Diarthron
   2. Stamens 4
   2. Stamens 8

2. Suffrutescent or shrubby perennials; flowers 6 - 15 mm
   3. Lower half of perianth sericeous-villous
      II. Subgen. Dendrostellera
   3. Lower half of perianth glabrous or sparsely pubescent.
      III. Subgen. Stelleropsis
   4. Stems herbaceous, slightly woody at base; flowers pink, white within
      Sect. Altaica

4. Stems thick - woody at base or up to middle; flowers yellowish
   Sect. Turcomanica
I. Subgen. Diarthron

Annuals with slender, *+* dichotomously branched stems. Inflorescence becoming laxly racemose. Lower half of perianth slightly inflated-membranous in fruit. Stamens *4* or *8* included. Hypogynous disc absent. Ovary subsessile, glabrous; style terminal or becoming subterminal, short, stigma clavate. Ditypic.

Type: *Diarthron linifolium* Turcz., loc. cit. (1832).

A. Sect. Diarthron


Distribution: E. Asia - E. Siberia, China and Mongolia.

Type: *Diarthron linifolium* Turcz., loc. cit. (1832).


Distribution: European Russia, S. W. and C. Asia.

Type: *Diarthron vesiculosum* (Fisch. & C. A. Mey. ex Kar. & Kir.) C.A. Meyer, loc. cit. (1843).


Suffrutescent or suffruticose plants, stems branched at or near base.
Leaves herbaceous or subcoriaceous. Inflorescence axis and lower half of perianth densely sericeous-villous. Stamens 8, included or upper whorl semi-exserted. Hypogynous disc cup-shaped, margins entire or obliquely lobed. Ovary subsessile, villous or hirsute at apex; style terminal, short; stigma conical, rarely ovoid.

Distribution: C. and S. W. Asia.

Type: Diarthron lessertii (Wikstr.) H. K. Tan, comb. nov.


Other species: omnia comb. nov.

1. Diarthron stachyoides (Schrenk) H. K. Tan


2. Diarthron arenaria (Pobed.) H. K. Tan

Syn.: Dendrostellera arenaria Pobed. in Fl. URSS 15:689 (1949).

3. Diarthron linearifolia (Pobed.) H. K. Tan

Syn.: Dendrostellera linearifolia Pobed. in Fl. URSS 15:689 (1949).

4. Diarthron macrorhachis (Pobed.) H. K. Tan

Syn.: Dendrostellera macrorhachis Pobed. in Fl. URSS 15:690 (1949).

5. Diarthron turkmenorum (Pobed.) H. K. Tan

Syn.: Dendrostellera turkmenorum Pobed. in Fl. URSS 15:691 (1949).
III. Subgen. Stelleropsis (Pobed.) H. K. Tan, comb. et stat nov.


Suffrutescent perennials, stems simple or sparingly branched at base. Leaves herbaceous. Inflorescence axis and lower half of perianth not sericeous-villous. Stamens 8, included. Hypogynous disc oblique, margins entire, shallowly crenate or 3-lobed. Ovary stipitate or subsessile, villous-pilose at apex; style terminal, short, stigma ovoid or globose.


Type: Diarthron altaica (Thieb.) H. K. Tan

Other species: omnia comb. nov.

1. Diarthron tarbagataica (Pobed.) H. K. Tan


2. Diarthron issykkulensis (Pobed.) H. K. Tan

Syn.: Stelleropsis issykkulensis Pobed., op. cit. 152 (1949).

3. Diarthron tianschanica (Pobed.) H. K. Tan

Syn.: Stelleropsis tianschanica Pobed., op. cit. 153 (1949).
B. Sect. Turcomanica (Pobed.) H. K. Tan, stat. nov.

Syn.: Turcomanicae Pobed., op. cit. 155 (1949), pro ser.

Distribution: Turkmenia, N. and N. W. Iran, E. Afghanistan, Caucasus.

Type: Diarthron turcomanica (Czern.) H. K. Tan, comb. nov.


Other species: omnia comb. nov.

4. Diarthron antoninae (Pobed.) H. K. Tan

Syn.: Stelleropsis antoninae Pobed., op. cit. 157 (1949).

5. Diarthron iranica (Pobed.) H. K. Tan


6. Diarthron caucasica (Pobed.) H. K. Tan

Syn.: Stelleropsis caucasica Pobed., op. cit. 161 (1949).

7. Diarthron magakjanii (Sosn.) H. K. Tan

6.6 Generic relationships.

All the genera studied are native to Eurasia though Wikstroemia is more widespread, occurring in Fiji, Australia and Polynesia. Diarthron and Stellera are mainly Central and East Asiatic in distribution, Thymelaea basically in the Mediterranean area and South-west Asia.

Despite some morphological diversity, Diarthron, with its three subgenera Diarthron, Dendrostellera and Stelleropsis, is thought to be more closely related to Stellera than to any other genus in the N. hemisphere. The annual habit in Diarthron Subgen. Diarthron and Thymelaea Sect. Ligia certainly does not imply a common ancestry as the shortened life cycle evades the extreme effects of the summer drought and winter cold of steppe regions. The suffrutescent habit of Thymelaea Sect. Thymelaea, Stellera, Diarthron Subgen. Dendrostellera and Subgen. Stelleropsis is also an adaptation withstanding the severities of winter rather than resulting from the adverse effect of heavy grazing. Field notes accompanying herbarium material of Stellera chamaejasme L. state that 'it is so toxic and unpalatable that not even goats will touch it ...'.

Wikstroemia (including Restella) is related to Daphne. It may be argued that these two taxa should be treated as a single genus as the Asiatic species have a number of rather similar characters. I have kept them separate for this account so that Daphne as a genus may be reasonably restricted in content and circumscription.

In considering the relationships of Thymelaea to Daphne, there appear
to be sufficient morphological and anatomical characters as well as geographical distributions to distinguish them. The two genera will always be maintained and I think are unlikely to be merged even with further study. Although there is some character 'overlap' such as that of habit, leaf arrangement and persistency of perianth, there are also characters which, used in combination, display clear distinctions between them. It is noteworthy that Domke (1934) includes Thymelaea in the predominantly Southern hemisphere tribe Gnidieae. This contains several African genera. He placed Wikstroemia, Dendrostellera, Diarthron and Daphne in Tribe Daphneae which is mainly Northern hemisphere. I consider Thymelaea to be much more closely related to Daphne than to any other member of tribe Gnidieae. The following diagram is provided to show the phenetic relationships of these genera. It can be seen that the taxa with entire perianths show some character 'overlap'.
<table>
<thead>
<tr>
<th>Perianth entire</th>
<th>Perianth separating into upper and lower parts</th>
</tr>
</thead>
<tbody>
<tr>
<td>deciduous</td>
<td>Inflorescence axis not elongating in fruit</td>
</tr>
<tr>
<td>persistent</td>
<td>Inflorescence axis elongating in fruit</td>
</tr>
</tbody>
</table>

**Shrubs**
- DAPHNE
- WIKSTROEMIA
- THYMELAEA Sect.
  - PIPTOCHLAMY
  - Sect. CHLAMYDANTHUS

**Suffrutescent or herbaceous perennials**
- THYMELAEA Sect.
  - THYMELAEA
- THYMELAEA Sect. LIGIA

**Annuals**
- THYMELAEA Sect. STELLERA
- DIARTHRO Subgen. DENDROSTELLERA

Diagram to show phenetic relationships of the genera
6.7 Some primitive characters

The following features chosen to indicate lower levels of specialization characterize a great many families of living angiosperms regarded as 'primitive'. They have been taken from accounts by several workers (Bessey, 1915; Cronquist, 1968; Takhtajan, 1969; Pant & Kidwai, 1971; Smith, 1971, Stebbins, 1974, etc.).

1. Woody habit.

The woody or semi-woody habit as characteristic of all gymnosperms is regarded as primitive, the climbing perennial or herbaceous annual, derived. The early angiosperms were never tropical rain-forest giants but according to Hallier (1912), small, Cycad-like trees. Corner (1964) suggests they were pachycauls—fleshy, unbranched and monocarpic. Stebbins (1965, 1974) considered ancestral types to be shrubby, with a straggly habit rather similar to that of Daphne cneorum since shrubs occupying semi-arid habitats would be more subjected to strong selective pressures than trees. Concomitant with a loss in woodiness are a reduction in branching and the appearance of several to many stems near ground-level.

2. Leaves exstipulate, evergreen, alternate, simple, entire, pinnately nerved, coriaceous and with conduplicate vernation.

This string of characters has been based mainly on the leaf form of lower gymnosperms and many existing primitive angiosperms. We can never be entirely certain early angiosperms ever possessed such foliage. Protective indumentum, succulence and reduction in size of lamina are generally regarded as derived although the first feature may be secondarily
lost.

3. Paracytic stomata and sclerified leaf epidermis. 
Takhtajan (1967, 1969) concluded that the absence of subsidiary cells is derived rather than primitive because this condition is found more frequently in 'advanced' families. He also stated the mesogenous paracytic type as likely to be the most basic for angiosperms. Baranova (1962, 1972) regards wall thickening in leaf epidermal cells of tropical Magnolias as primitive; this structural feature is apparently absent in temperate species which include polyploids. Recently, Tucker (1977) has shown that sclerified epidermides also occur in five other tropical Magnoliaceous genera.

4. The multilacunar node with two traces in the central leaf gap. 
This hypothetical type has been suggested to be the primitive condition from which the tri- or unilacunar node has probably been derived, (Ozenda, 1949; Takhtajan, 1969).

5. Wood without xylem vessels, axial parenchyma or companion cells. 
Presence of heterogeneous and heterocellular rays.

6. Large, solitary, terminal, actinomorphic, hermaphrodite flowers with numerous parts spirally arranged upon an elongated receptacle. 
Based upon the Magnoliaceae and Ranunculaceae.

7. Undifferentiated perianth with a bract origin, as in Illicium and Paeonia.
8. Broad laminar stamens undifferentiated into filament and connective. Anthers narrowly linear, as in *Degeneria*.

9. Monocolpate pollen and plenty of it, as found in cycads and Order Magnoliales. Pollen was the first attractant for early pollinators—Coleoptera and primitive Hymenoptera; secretion of nectar a later development.

10. Stalked ovary with a moderate number of ovules; absence of style and a proper terminal stigma, as in *Drimys*.

11. Large, dehiscent fruits, aggregated in a follicetum, as in *Magnolia*.

12. Anatropous, bitegmic, crassinucellate ovules with a 'zig-zag micropyle' because these are characteristic of so many primitive families.

13. Large seeds with abundant endosperm and small undifferentiated embryos. Absence of dormancy.


The aril is generally interpreted as arising from the funicle. The fleshy or membranous arilloid is an elaboration of (or part of) the testa. It is not a third integument. The development of sarcotestal seeds in primitive early angiosperms was probably associated with animal dispersal.

The family Thymelaeaceae, as known by its temperate members, exhibit
few of the key characters previously listed. It would thus appear to
be a relatively advanced group. However, some less specialized genera
occur. They are all tropical and with one exception, with a geo-
ographical distribution in South East Asia and the West Pacific basin,
a region considered by many to be a centre of concentration (if not of
origin) of primitive angiosperms. A short account of these genera will
now be given.

6.7.1. Some primitive genera in the Thymelaeaceae

1. **GONYSTYLUS** Teysm. & Binn. (Fig. 46).
The genus *Gonystylus*, consisting of about twenty species, occurs in
the Malesian region (except E. Java and the Lesser Sunda Islands), with
one species, *G. macrophyllus* (Miq.) Airy Shaw, extending to the Nicobar,
Solomon and Fiji Islands (Map 9). The group has been revised in some
detail by Airy Shaw (1953).

The majority of species are tall to medium-sized trees (30 to more than
40 m), growing in primary rain-forest or fresh-water swamp. A few are
shrubs. Leaves are alternate, entire, extstipulate, chartaceous to very
coriaceous, glandular-punctate, and with very closely parallel secondary
veins. The inflorescence is paniculate with the lateral branches often
reduced to nodulose flower clusters. Bracts are minute and early decid-
uous. The flowers are long-pedicelled, hermaphrodite, with a persistent
cupular calyx of 5 thick, imbricate or subvalvate sepals and a distinct
corolla of 10 to 40 petaloid segments. The stamens are equal in
number to, or twice as many as, the petals. Filaments are free; the
anthers basifixed and hippocrepiform, i.e. horse-shoe shaped. The
similarity of pollen type (periporate, shed in tetrads) and hair type
(simple, unicellular trichomes) on vegetative and floral parts un-
doubtedly show it to be related to the family Thymelaeaceae. Light
microscopy indicates that the exine sculpturing is not quite similar
to that of Mediterranean, C. or S. W. Asian genera studied, and scanning
electron microscopy may well reveal critical features. The grains
have a tendency to burst when mounted in 10% lactic acid; the wall
is less than 1µm thick. The ovary is sessile, globose and usually 3 - 4,
rarely 5 - 8 loculate. A single, filiform, 'kinked' style is present.
G. areolatus Domke ex Airy Shaw, has additional small, clavate 'para-
styles'.

The fruit is a woody dehiscent capsule with one large seed developing
in each locule. Membranous arils originating from the fleshy funicles
have been reported in some species, e.g. G. velutinus Airy Shaw. Flowers
are likely to be insect-pollinated, although this has not been ob-
served. Hypogynous discs are absent. The capsular fruits with large,
glossy-black seeds, fleshy funicles and thin arils point to zoochorous
dispersal, although there have been no recorded observations.

2. AMYXA Van Tiegh. (Fig. 47).

A monotypic genus endemic to N. W. Borneo (Map 9). Medium-sized trees,
15 - 30 m tall. Leaves alternate, chartaceous, with fewer and less con-
spicuous secondary veins than in Gonystylus. Inflorescence a panicle
of cymes (thyrse-like). Bracts small, present on inflorescence branches.
Flowers smaller than in Gonystylus, long-pedicelled. Calyx cupular,
of 5 imbricate sepals. Corolla of 10, approximately paired, narrowly
oblong or deltoid petals. Stamens alternating with and equal in number
<table>
<thead>
<tr>
<th>Character</th>
<th>Aquilaria Lam.</th>
<th>Microsema Labill.</th>
<th>Octolepis Oliver</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Medium-sized trees or shrubs.</td>
<td>Shrubs or small trees.</td>
<td>Shrubs or small trees.</td>
</tr>
<tr>
<td>2.</td>
<td>Leaves alternate, chartaceous or sub-coriaceous, not glandular-punctate.</td>
<td>Alternate, coriaceous, not glandular-punctate.</td>
<td>Alternate, chartaceous, not glandular-punctate.</td>
</tr>
<tr>
<td>3.</td>
<td>Inflorescence subumbellate or paniculate, sometimes cauliflorous.</td>
<td>Flowers solitary in leaf axils.</td>
<td>Solitary or in fascicles at nodes.</td>
</tr>
<tr>
<td>4.</td>
<td>Bracts absent or minute.</td>
<td>Absent.</td>
<td>Absent or very minute.</td>
</tr>
<tr>
<td>5.</td>
<td>Pedicels usually shorter than calyx-tube.</td>
<td>Longer than calyx tube.</td>
<td>As long as or longer than calyx.</td>
</tr>
<tr>
<td>6.</td>
<td>Sepals imbricate, (4-)5(-6), persistent in fruit, pubescent on inner surface.</td>
<td>Imbricate, 4 or 5, persistent in fruit, densely sericeous in central part of inner surface.</td>
<td>Imbricate, 4 or 5, persistent in fruit, densely sericeous on outer surface, pubescent or subglabrous on inner surface, free to base or nearly so.</td>
</tr>
<tr>
<td>7.</td>
<td>Corolla of (8-)10(-12) lanceolate, ovate or rim-like petals, free or united.</td>
<td>10-13 semi-woody, oblong or linear-oblong petals, united only at base.</td>
<td>8-10 oblong or linear-oblong petals, united only at base.</td>
</tr>
<tr>
<td>11.</td>
<td>Ovule 1 per locule, pendulous, anatropous.</td>
<td>1 per locule, pendulous, anatropous.</td>
<td>1 per locule, pendulous, anatropous.</td>
</tr>
<tr>
<td>12.</td>
<td>Fruit a loculicidal, coriaceous or woody capsule.</td>
<td>Loculicidal, woody-coriaceous capsule.</td>
<td>Loculicidal, coriaceous capsule.</td>
</tr>
<tr>
<td>13.</td>
<td>Seed with caruncle-like appendage at the chalazal end, usually hanging out of fruit on a slender funicle.</td>
<td>With a caruncle-like thickening at the chalazal end.</td>
<td>With chalazal thickening.</td>
</tr>
</tbody>
</table>
to petals. Filaments free, anthers hippocrepiform. Hypogynous disc absent. Ovary sessile, 3-4-loculate. Style filiform, 'kinked'; para-styless 5-6, conspicuous. Fruit a thin-walled, beaked, dehiscent capsule. Seeds large, funicle thickened but not expanded into an aril.

3. **AETOXYLON** Airy Shaw

Another monotypic genus restricted to Borneo (Map 9). Airy Shaw (1950) separated this from Gonystylus and Amyxa by its opposite or subopposite leaves with rather indistinct lax venation, subumbellate inflorescence, valvate sepals and corolla which is reduced to a low, slightly fleshy annulus.

4. The characters in **AQUILARIA** Lam., **MICROSEMMA** Labill. and **OCTOLEPIS** Oliver are tabulated for easier reference (Table II). The geographical distribution is summarized in Map 9. **Aquilaria** (Fig. 49), comprising about 15 species, is Indo-malesian in distribution, occurring in S.E. and continental S.E. Asia. **Microsemma** (Fig. 48) is a small genus endemic to New Caledonia with an outly in N. Queensland. **Octolepis** (Fig. 50) which is more closely related to **Aquilaria** than to the other genera, is highly disjunct in the tropical Atlantic region of W. Africa.
Fig. 46. *Gonystylus macrophyllus* (Miq.) Airy Shaw

A. Leaf. Midrib channelled on adaxial surface. x 1.5.
   Aa. Section enlarged to show veins and glandular dots.
B. Part of inflorescence. x 1.
C. Half flower with sepals removed. x 10.
D. Stamen and two petaloid segments. x 10.
E. Stamen, abaxial view. x 12.
   Ea. Stamen, adaxial view. x 12.
F. Sepal. Outer surface densely pubescent, apical margin reflexed. x 5.
   Fa. Sepal. Inner surface densely sericeous. x 5.
G. Flower with sepals removed to show corolla of 30-40 petaloid segments and style with characteristic “kink”. x 5.
H. T.S. ovary. x 13.
I. Stigma. x 7.
J. Thick-walled, unicellular hair from ovary wall. x 100.
Fig. 47. *Amyxa pluricornis* (Radlk.) Domke

A. Flowering branch and detached leaf. x 1.
B. Flower. Sepals pubescent on outer surfaces. x 7.5.
C. Half-flower. Filiform style with characteristic 'kink'. x 10.
D. Sepals and narrowly deltoid-subulate petals. x 10.
E. View of flower from above, showing 'parastyles' on top of ovary. Sepals removed. x 10.
Fb. Stamen, adaxial view. x 20.
G. Detached 'parastyle'. x 30.
H. Globose, centrally depressed stigma in two views. x 30.
I. T. S. ovary. x 20.
J. Thin-walled, unicellular hair from ovary wall. x 180.
K. Mature fruit with single developed seed. From Ding Hou (1960).
Fig. 48 A - G. Microsemma sp.

A. Fruiting branch. x 0.3.
B. Fruit with persistent, semi-woody calyx. x 1.3.
C. View of calyx from pedicel end. x 1.3.
D, Da. Mature dehisced fruits. x 1.
E. Seed with caruncle-like appendage at chalazal end. x 2.
F. L.S. seed. Testa moderately thin, transparent; tegmen sclerified. x 3.5.
G. Embryo. Large oily endosperm stippled. x 6.5.

H - M. Microsemma francii Bonati

H. Flower with two sepals removed. Sepals hispid-villous on inner surface. x 5.
I, Ia. Thick, semi-woody petals. x 10.
J. Fascicle of stamens. x 6.
K. Two stamens with filaments fused along entire lengths. x 6.
L. Individual stamen, adaxial view. x 6.
M. Floral diagram.
Fig. 49 A - L excepting H. *Aquilaria grandiflora* Benth.

H. *Aquilaria malaccensis* Lam.

A. Flowering branch. x 3/4.
B. Flower. x 5.
D. Dimorphic pollen grains. x 650.
E. L. S. ovary. x 6.
F. Cuboidal stigma not centrally depressed (more common). x 50.
G. Petal. x 12.
Ga. Unicellular hair from petal margin. x 80.
H. Dehisced fruit. Seed hangs from thread-like funicle. x 1.3.
I. Leaf. Intra-marginal veins raised and thickened on abaxial surface. x 1.
J. Leaf, abaxial epidermis much enlarged. Cells thin-walled, stomata present.
K. Leaf, adaxial epidermis much enlarged. Cells thick-walled, stomata absent.
L. Floral diagram.
Fig. 50. *Octolepis casearia* Oliver

A. Flowering branch. Flowers cauliflorous, at but not in leaf axils. x $\frac{1}{2}$.

B. Half-opened flower. x 10.

C. Half-flower with ovary removed. x 10.

D. Detached sepal. Stamens alternate with petals. x 10.

E. Stamen. Filament sericeous-villous in lower half. x 20.

F. L.S. ovary. x 10.

G, Ga. Immature fruit split open to reveal single developed seed. x 10.

H. Floral diagram.
Fig. 50
Map 9. Distribution of some other genera studied.

- Passerina
- Gonystylus
- Amyxa (monotypic)
- Aëtoxylon (monotypic)
- Microsemma
- Octolepis
- Aquilaria

Bartholomew's 'The Times' Projection
6.8 Evolutionary trends and specializations

From these accounts, it is apparent that vegetative, floral and fruit characters in tropical and temperate members vary considerably and form the basis for defining genera. Several specializations can now be pointed out. To consider a relatively advanced temperate genus like Thymelaea alone, is to find only isolated states but no general trends. Hypotheses concerning advanced character-states in this family are based primarily upon comparison of the genera. The guiding principle has been that the evolution of characters has in most cases involved progressive reduction. Some of the specializations appear to have arisen independently several times, marking particular taxa rather than general trends. In the following list, advanced states are the first mentioned.

1. Development of opposite or subopposite leaves, as in Aëtoxylon, Phaleria, some species of Wikstroemia and Daphne, from the more primitive alternate position.

2. Leaves which are long persistent, glandular-punctate, strongly veined or heavily sclerified, as in Gonystylus, Aquilaria, Passerina and Thymelaea. Probably these specializations in leaf blade texture resist drought and damage during an extended life span. Correlated with the coriaceous condition is the orientation, the spreading being less advanced in relation to the erect and strictly adpressed.

3. The annual, herbaceous habit, as in Diarthron Subgen. Diarthron and Thymelaea Sect. Ligia. Entire plant body reduced to seed before
unfavourable season, thus evading the most extreme effects of drought, insolation or cold.

4. Umbellate, subumbellate or capitate inflorescences, as in Aëtoxylon, Octolepis, Stellera, Pimelea, which appear to represent simplification and condensation from the more primitive panicle (racemose) or thyrsoid type (cymose). However the post-anthesis elongation of the herbaceous inflorescence axis in Diarthron and related genera, is a secondary specialization aiding seed maturation and dispersal. For each diaspore to be accommodated on the plant, there must be a length-wise increase in the inflorescence axis. It should not be viewed in the same light as the curious, semi-woody racemes of Gonystylus augescens Ridl. which, with the apparent capacity to elongate almost indefinitely, is undoubtedly more primitive.

Associated with changes in the size of the inflorescence and its number of flowers is a shift from the terminal to the terminal and lateral position.

5. Unisexuality, reaching dioecism, as in Thymelaea and Solmsia.

6. Bracts which are large and persistent, forming an involucre, as in Pimelea cornucopiae and Stellera. Small, caducous bracts seem to be primitive in this family.

7. Small, sessile or subsessile flowers as in Thymelaea, Passerina, compared with the larger-flowered, long-pedicelled state.
8. 4-merous symmetry or a fixed, definite number of parts, as in Daphne, Thymelaea, Diarthron, Passerina, as opposed to the 5-merous condition and variability in number of floral parts.

9. Imbricate aestivation as in the temperate genera as compared to the valvate condition. A tightly overlapping calyx gives better protection to young floral organs against seasonal drought, cold and insect attack.

10. Tubular or infundibuliform calyx which is a specialization improving the concealment of nectar and pollen, as in the temperate genera. Primitive members have an open, cupular, or almost free calyx.

11. Calyx becoming corolline, i.e. with a more delicate petaloid structure and functioning as a corolla by being attractively coloured. Thick, coriaceous, hispid-villous sepals are present in primitive genera.

12. Associated with this is the loss of the corolla, as in all our Mediterranean, C. and S. W. Asian taxa. A good reduction series can be observed in three related tropical genera, Gonystylus, Amyxa and Aëtoxylon. The first named has 10 - 40 unpaired petals, the second 10 paired ones, and the last has the corolla reduced to a slightly fleshy ridge of tissue. This rim-like/annular structure is indeed the vestigial corolla, being extra-staminal and should not be confused with the intra-staminal hypogynous disc which is present in some other genera.
13. Persistence of the petaloid calyx, as in *Thymelaea*. This is a secondary specialization. Primitive genera also have persistent calyces, but the component sepals are always thick-coriaceous or semi-woody. The deciduous petaloid calyx as found in most species of *Daphne* is regarded as derived. The circumscissile condition in *Diarthron*, *Stellera* and *Passerina*, with the upper portion falling away from the persistent basal portion is a presumed specialization which has arisen independently in several other genera and does not indicate direct affinities. The remaining half of the calyx becomes inflated-membranous in *Diarthron vesiculosum* and *D. linifolium*, which may aid in dispersal. It is densely villous in *D. lessertii*. A suggested function is that the hairs retain moisture when wetted as they would be during germination (equivalent to wrapping up the seed in damp cotton wool).

14. Reduction in stamen number, e.g. from the rather numerous (40 – 80) in *Microsemma* and some species of *Gonystylus* to four in *Diarthron linifolium* (equalling number of sepals) or in *Pimelea prostrata*, culminating in two (equalling half the number of sepals!).

15. Attachment of stamens to calyx tube, as in *Daphne*, so that the anthers become, once again, included. The visible shortening of filaments, due to the adnation of their bases to the calyx tube, appears to be derived. Numerous free filaments on a broad, rather shallow receptacular axis are ideally suited for insect visitors in search of pollen. The vectors were probably large and beetle-like without sucking mouthparts. With the development of a tubular calyx in direct response to specialized relationships with slender-tongued pollinators, the anthers
became precisely positioned within, or exserted (e.g. *Daphne*, *Pimelea*).

Associated with this is the amassing of flowers into heads, firstly increasing their 'showiness', secondly resulting in the pollinator, once attracted, 'working' as many flowers as possible at one visit.

Exserted stamens in *Passerina* also point to wind pollination. The association of small flowers in dense clusters at the tips or near the tips of pendulous branches, the high pollen output which is sufficient to cause allergies in sensitive individuals, and the long, filiform style bearing an 'efficient' mop-like stigma which completely occludes the calyx throat, all form part of an easily recognized syndrome.

![Diagram of some possible stages in the evolution of an episepalous stamen, as seen from extant genera.](image)

Diagram of some possible stages in the evolution of an episepalous stamen, as seen from extant genera.

16. Development of introrse anthers as in *Daphne*, *Wikstroemia*, *Thymelaea*,
Diarthron and Stellera. This is considered to be derived, although primitive genera have introrse, extrorse and hippocrepiform anthers. Whether the introrse position as in most Magnoliaceae, or the extrorse as in Degeneriaceae, is more primitive has never been satisfactorily resolved. In the five genera previously mentioned, the stamens are episepalous with short filaments. It would thus be functionally effective to have the anthers facing inwards, releasing pollen to dust insects scrabbling around within the tube. Also, with the anthers situated above the stigma, introrse dehiscence would allow for selfing if the species is self-compatible, and there is an absence of insects.

Microsemma has numerous stamens with introrse anthers. In Amyxa, the anthers are decurrent along the back of the connective, whilst in Solmsia, regarded as the most advanced of the three, they show stages of becoming extrorse:\n
![Diagram of anther positions in Microsemma, Amyxa, and Solmsia]

Position of anthers in three 'primitive' genera

17. Development of the hypogynous disc.

The final stages of specialization seem to be the elaboration of an unequally divided (as in Wikstroemia) or unilateral disc (as in Stellera). It is inconspicuous (non-functional?) and sometimes secondarily lost in the annual species.
18. The uniloculate, uniovulate ovary as found in temperate genera presumably evolved from the multi (i.e. 3-8)-loculate and multi-ovulate conditions. The centrally depressed or bilobed stigma and degree of carpellary vascularization in Daphne suggest such a possibility. Joshi (1936) proposes a similar situation for Stellera.

19. Absence or extreme shortening of the style.
This has arisen independently in quite a number of unrelated genera, among which may be mentioned Aquilaria, Octolepis, Daphne, Wikstroemia and Stellera. The slender filiform style in Passerina, Thymelaea and Diarthron Subgen. Diarthron, seems to be secondarily derived; primitive genera have similar styles with a characteristic 'kink'.

20. Absence of 'parastyles'.
Parastyles are curious projections developing from the top of the ovary. They are found only in Amyxa and Gonystylus areolatus. Although situated at the base of the true style, they have no stigmatic surfaces and their probable function can only be guessed at.

21. Small, indehiscent one-seeded fruits as in Thymelaea, Stellera and Diarthron, as compared to the large, dehiscent several-seeded capsules of primitive genera.

22. Fleshy or coriaceous pericarps (Daphne, Wikstroemia), and from this a change to the dry and membraneous states (Thymelaea, Stellera, Diarthron) have probably originated from the thick, fibrous-woody condition (e.g. in Aquilaria, Microsema).

23. Small, conical or pyriform seeds as compared with large, rounded,
oblong-ovoid ones. The former approximate closely to the size and shape of the entire embryo within, the latter's shape is visibly determined by the thick, plano-convex cotyledons.

24. Absence of arils, fleshy funicles or thickened chalazal appendages, all or some of which are present in tropical genera and are probably related to endozoochory.
PART D

TAXONOMIC TREATMENT OF THE GENUS THYMELAEA
7.0 Description of genus

**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. Actually it is *Daphne* that has the succulent pericarp; the fruits of *Thymelaea* are always dry.


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

Type species: T. sanamunda All.

Syn: Daphne thymelaea L., type cons.

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


7.1 Historical survey

The name 'thymelaea' was first used by C. Bauhin in his Pinax (1623). J. Pitton de Tournefort (1700) characterized but did not define the genus critically. He included species of Daphne, Passerina and Gnidia as well as 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. & Tartonia cuneifolia Rafin.) as the chief constituent species. Chlamydanthus and Piptochlamys were used by C.A. Meyer (1843), 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 Fasano (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'. 
Lygia Fasano
1. L. passerina
2. L. pubescens

Thymelaea Endl.
1. T. hirsuta
2. T. tartonraira
3. T. argentea
4. T. canescens = T. lanuginosa
5. T. nitida = T. argentea
6. T. villosa
7. T. tomentosa (species obscura)
8. T. tinternia
9. T. virgata

10. T. bauhini = T. sanamunda
11. T. dioica
12. T. elliptica = T. thesioides subsp. elliptica
13. T. thesioides

Species dubiae sectionis.
14. T. coridifolia
15. T. velutina
16. T. thomasi = T. tartonraira subsp. thomasi

Sect. I. Lygia (Fasano) Meisen.
1. T. arvensis = T. passerina
2. T. cilicica
3. T. aucieri

Sect. II. Chlamydanthus (C.A. Meyer) Endl.
§ 1. Suffrutescentes Meissen.
4. T. virgata
5. T. sanamunda
6. T. thesioides
7. T. coridifolia

§ 2. Fruticulose Meissen.
8. T. villosa
9. T. nitida = T. argenteata
10. T. dioica
11. T. virgata
12. T. calycina
13. T. nivalis = T. tinternia subsp. nivalis
14. T. tinternia
15. T. velutina
16. T. tartonraira
17. T. microphylla
18. T. canescens = T. lanuginosa

19. T. hirsuta

Species obscurae.
20. T. orientalis
21. T. tomentosa
22. T. pubescens

The genus contains c. 20 spp.


Sect. I. Lygia (Fasano) Meisen.
3 spp. including T. passerina.

Sect. II. Chlamydanthus (C.A. Meyer) Meisen.
15 spp. including
T. virgata
T. thesioides
T. villosa
T. dioica
T. tinternia
T. tartonraira

1 sp. namely T. hirsuta
Brecher, Gy. - 1941 - A Thymelaea - gónusz és fajai -

I. Sect. Lyria (Fasano) Meissn.
1. T. passerina
2. T. aucheri
3. T. cilicica

1. Subsect. Sanamunda (Lange) Brecher
4. T. antialtantic
5. T. virgata
6. T. sanamunda
7. T. thesioides

2. Subsect. Euzympelaea (Lange) Brecher
8. T. villosa
9. T. subrepens
10. T. dioica
11. T. virescens
12. T. putorioides
13. T. coridifolia
14. T. ruizii
15. T. calycina
16. T. tinctoria
17. T. velutina
18. T. tartonraira
19. T. nitta = T. argentata

24. T. lythroides


1. T. lythroides
2. T. hirsuta (type of sect.)
3. T. lanuginosa
4. T. gattefoisii

Subsect. Argentatae H.K. Tan
5. T. argentata
6. T. virgata
7. T. putorioides

Subsect. Semprevirentes H.K. Tan
8. T. microphylla
9. T. semprevirens


10. T. tartonraira (type of sect.)
11. T. velutina
12. T. dioica

13. T. tinctoria
14. T. subrepens
15. T. procumbens
16. T. ruizii

Proposed Classification


1. T. lythroides
2. T. hirsuta (type of sect.)
3. T. lanuginosa

Subsect. Hirsutae H.K. Tan
1. T. passerina
2. T. aucheri
3. T. cilicica

IV. Sect. Ligia (Fasano) Meissn.

T. argentata
T. virecens
T. putorioides

Subsect. Euthymelaea (Lange) Brecher
1. T. antialtantic
2. T. sanamunda (type of sect.)

Subsect. Sanamunda (Lange) Brecher
22. T. villosa
23. T. thesioides
24. T. sanamunda (type of sect.)

T. calycina
T. coridifolia
T. broteriana

TABLE 12. PROPOSED INTRA-GENERIC CLASSIFICATION
AND PREVIOUS ONES COMPARED
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 (see Table 12), being an enumeration of additional species complicated by his lumping of putative allies into an unwieldy group, subsect. Euthymelaea (Lange) Brecher. However, this more or less stable classification has definitely aided further work because the sectional and subsectional nomenclature is not chaotic, synonyms being reduced to a minimum.

7.2 **Sectional characters** (see Tables 13 & 14).

The characters used in the classification are now listed; their taxonomic usefulness assessed.

1. **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 partly supports the view that Sect. Ligia should not be reinstated as a separate genus.

2. **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 polygamodioecism, a state in which staminate and pistillate flowers are on separate plants together
with a sprinkling of true hermaphrodite flowers.

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

Flowers are always clustered in Sect. *Piptochlamys*. They are aggregated or solitary in the leaf axil, very rarely paired in Sect. *Chlamydanthus*. Each of the two subsections of Sect. *Thymelaea* shows the single, unreduced 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).

4. 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.

5. Pedicel: flowers are always sessile in Sections *Thymelaea* and *Ligia*.

6. Perianth: the perianth is persistent in all species except two members of Sect. *Piptochlamys*.

7. Stomatal distribution: leaves are either amphi- or epistomatic. The latter condition occurs only in Sect. *Piptochlamys* subsect. *Hirsutae*, and a small group of closely related species within

8. Stomatal type: although all 4 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. It (the latter condition) is rare in Sect. Piptochlamys subsect. Argentatae.

9. Shape of anticlinal walls of leaf adaxial and abaxial epidermides: Sect. Ligia is the only group with all its constituent species showing an undulated 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.

10. 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.

11. Cork: the formation of cork tissue with the subsequent and gradual loss of the epidermis is characteristic of the shrubby members.

12. Secondary phloem rays of stem: these are dilated in Sect. Chlamydanthus subsect. Coridifolia, Sect. Piptochlamys subsect. Hirsutae and subsect. Argentatae; naturally not so in the leafy and flowering stems of Sections Thymelaea and Ligia as the condition is correlated with a woody habit.

13. Internal phloem fibres in stem: They are absent in Sect. Chlamydanthus, present in almost all members of Sections Piptochlamys and Thymelaea.
and half the species in Sect. *Ligia*. More pickled material of both old and young stems should be examined. This feature may be of greater importance than now apparent.
TABLE 3. THYMELAE: comparison of morphological characters.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>FLOWERS</th>
<th>LEAF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sex distribution</td>
<td>Position</td>
</tr>
<tr>
<td></td>
<td>hermaphrodite</td>
<td>pistillate</td>
</tr>
</tbody>
</table>
| Sect. Piptochlamea |         |         |         |         |         |       | 3.7
| Subsect. Hircuteae |         |         |         |         |         |       | 3.7
| 1. T. lythroides | x          | x      | x      | x      | x      | x      |         |         |
| 2. T. hirsuta  | x          | o      | x      | x      | x      | x      |         |         |
| 3. T. lanuginosa | x          | x      | x      | x      | x      | x      |         |         |
| 4. T. gattefoessii | x         | x      | x      | x      | x      | x      |         |         |
| Subsect. Argentatae |         |         |         |         |         |       | 3.7
| 5. T. argentea  |             | x      | o      | x      | x      | x      |         |         |
| 6. T. virescens | x          | o      | x      | x      | x      | x      |         |         |
| 7. T. patricoides | x          | x      | x      | x      |         |         |         |         |
| Subsect. Semprevirentes |         |         |         |         |         |       | 3.7
| 8. T. microphylla | x          | x      | x      | x      |         |         |         |         |
| 9. T. semprevirens | x          | x      | x      | x      |         |         |         |         |
| Sect. Chlamydanthus |         |         |         |         |         |       | 3.7
| Subsect. Tantonraira |         |         |         |         |         |       | 3.7
| 10. T. tantonraira | x          | o      | x      | x      | x      |         |         |         |
| 11. T. velutina | x          | x      | x      | x      |         |         |         |         |
| 12. T. dioica  | x          | x      |         |         |         |         |         |         |
| Subsect. Coridifoliae |         |         |         |         |         |       | 3.7
| 13. T. tinctoria | x          | x      | x      | x      |         |         |         |         |
| 14. T. subrepens | x          | x      | x      | x      |         |         |         |         |
| 15. T. procumbens | x          | x      | x      | x      |         |         |         |         |
| 16. T. ruizii  | x          | x      | x      | x      |         |         |         |         |
| 17. T. calycina | x          | x      | x      | x      |         |         |         |         |
| 18. T. coridifolia | x          | x      |         |         |         |         |         |         |
| 19. T. broteriana | x          | x      |         |         |         |         |         |         |
| Sect. Thymelae |         |         |         |         |         |       | 3.7
| Subsect. Antiatlanticae |         |         |         |         |         |       | 3.7
| 20. T. antiatlantica | x          | x      | x      | x      |         |         |         |         |
| 21. T. virgula | x          | x      | o      | x      |         |         |         |         |
| Subsect. Sanamunda |         |         |         |         |         |       | 3.7
| 22. T. villona | x          | x      | x      | x      |         |         |         |         |
| 23. T. thesioides | x          | x      | o      | o      | x      |         |         |         |
| 24. T. sanamunda | x          | x      | o      | o      | x      |         |         |         |
| Sect. Lixia |         |         |         |         |         |       | 3.7
| 25. T. ciliaris | x          | x      | x      | x      |         |         |         |         |
| 26. T. aucheri  | x          | x      | x      | x      |         |         |         |         |
| 27. T. papaverina | x          | x      | o      | x      | x      |         |         |         |
| 28. T. guessenii | o          | x      | o      | x      |         |         |         |         |
| 29. T. mallea | o          | x      | x      | x      |         |         |         |         |
| 30. T. mesopotamica | o          | x      | x      | x      |         |         |         |         |
### TABLE 14. THYMELAEA: comparison of sectional characters.

<table>
<thead>
<tr>
<th>PIPOCHLAUS</th>
<th>CHILAMBDANTHUS</th>
<th>THYMELAEA</th>
<th>LIGIA</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Monoecious; dioecious; more rarely polygamodioecious or flowers hermaphrodite.</td>
<td>2. Dioecious; rarely polygamodioecious.</td>
<td>2. Dioecious.</td>
<td>2. Monoecious; flowers hermaphrodite.</td>
</tr>
<tr>
<td>3. Terminal; aggregated.</td>
<td>3. Flowers axillary; aggregated or single.</td>
<td>3. Axillary; aggregated or single.</td>
<td>3. Axillary; aggregated, rarely single.</td>
</tr>
<tr>
<td>4. Absent, more than 2.</td>
<td>4. Bracts 2; more than 2.</td>
<td>4. Absent; more than 2.</td>
<td>4. 2.</td>
</tr>
<tr>
<td>5. Sessile; shortly pedicellate.</td>
<td>5. Flowers sessile, shortly pedicellate.</td>
<td>5. Sessile.</td>
<td>5. Sessile.</td>
</tr>
<tr>
<td>10. Absent except in 2 app.</td>
<td>10. Stomata and chlorenchyma absent from old stems.</td>
<td>10. Present or absent.</td>
<td>10. Present.</td>
</tr>
<tr>
<td>11. Well developed except in some 2 app.</td>
<td>11. Cork well developed.</td>
<td>11. Moderately well developed.</td>
<td>11. Absent.</td>
</tr>
<tr>
<td>13. Present except in 1 sp.</td>
<td>13. Internal phloem fibres absent from young or old stems.</td>
<td>13. Present except in 1 sp.</td>
<td>13. Present or absent.</td>
</tr>
</tbody>
</table>
7.3 **Species concept.**

A great deal has been written that is relevant to the title of this section. For our taxonomic purposes, the general concept adopted is a fairly straightforward morphological one. Following the proposals of Du Rietz (1930), correlated discontinuous variation in at least two taxonomic characters has been accepted as an adequate requirement for specific rank. For infraspecific taxa, distinct geographical distribution and one diagnostic character (which is of limited occurrence so that its use alone is sufficient to identify or characterize) have been used for the subspecies. Varietal rank has been seldom employed and is restricted for groups occupying a localized range and showing one or two characters whose differences are mostly quantitative and minor in degree of variation, e.g. *T. putorioides* var. *rhodantha*, *T. tartonraira* subsp. *argentea* var. *linearifolia*.

Among the species recognised, two groups are morphologically most distinct.

1. **Members of Sect. Chlamydanthus** subsect. *Coridifoliae* which are closely related and with a restricted distribution (endemic to the mountains of N. Spain). As far as is known, they are sexual taxa (dioecious) and probably non-hybridizing. They are very markedly distinct and pose no taxonomic problems.

2. **Members of Sect. Ligia** which are annual, monoecious or with hermaphrodite flowers. These are geographically separated discontinuous taxa with the rare occurrence of intermediates where they grow sympatrically. If sufficient information on the variation in their breeding systems were available and a strict biological concept applied—for these taxa, it might result in the lumping
into a polytypic, widely distributed species.

There is one species, *T. dioica*, which appears rather more difficult to relate to other species because it differs in a few rather striking characters. It has been placed in Sect. Chlamydraanthus, within subsect. Tartonairae, partly on account of its more numerous bracts (3-8) which may however be absent in one of its two subspecies. The general facies much resembles members of subsect. Coridifolii.

Presentation of data.

a) **Keys.** The key based on both vegetative and floral characters has been broken down into four groups which correspond to the sections. Separate keys to the species comprising each section are then given. Each has been constructed so that the species are arranged as far as possible, according to their overall similarity. It was not necessary to key out each species more than once.

b) **Descriptions.** All descriptions have been based on specimens seen. Unqualified measurements refer to length. Plant parts have been drawn for almost all species to supplement the descriptions and demonstrate variability or the lack of it in certain groups. Each drawing is not accompanied by a reference to the specimen from which the parts have been taken, e.g. the collector's number, unless only one specimen has been dissected. A list of abbreviations and usage of terms is given at the end of Sect. 7.6.

Information referring to flowering time, habitat and altitude has
mainly been condensed from herbarium sheets. A synopsis of infra-
generic taxa arranged in linear sequence, and also a classificatory
scheme showing inferred relationships (Fig. 51), are provided. Taxa
which are imperfectly known are referred to in observations under
their presumed allies.

c) Citation of specimens. Selection of specimens is more res-
trictive since they are supplemented by maps. As far as possible,
preference is given to recent and easily accessible herbarium
material. Those not listed in Brecher's (1941) revision are
usually cited. For the Turkish distribution, the grid system adopted
in Flora of Turkey, Vol. One (ed. Davis, 1965), has been followed --
one specimen per province per square being cited unless it has been
rarely collected.

d) Maps. All the species have been mapped. Each symbol used
represents a locality from which a specimen has been examined or
is a reliable literature record. For T. hirsuta the geographical
area covered is indicated by a broken boundary-line.
Fig. 51. Inferred overall relationships within the genus *Thymelaea*. The size of the circle (in cm) denotes the relative size of the section (number of species). Species closely related are contiguous. The broken lines (-----) refer to sectional affinities.
7.4 Synopsis of sections and species.

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<td><strong>Subsect. Hirsutae</strong></td>
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<td><strong>Subsect. Antiatlanticae</strong></td>
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<td>1. <em>T. lythroides</em></td>
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<td>20. <em>T. antiatlantica</em></td>
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<td>3. <em>T. lanuginosa</em></td>
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<td><strong>Subsect. Sanamunda</strong></td>
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<td>4. <em>T. gattefossei</em></td>
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<td>22. <em>T. villosa</em></td>
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<td><strong>Subsect. Argentatae</strong></td>
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<td>23. <em>T. thesioides</em></td>
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<td>5. <em>T. argentata</em></td>
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<td>24. <em>T. sanamunda</em></td>
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<td><strong>Subsect. Sempervirentes</strong></td>
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<td>14. <em>T. subrepens</em></td>
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<td>8. <em>T. microphylla</em></td>
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<td>15. <em>T. procumbens</em></td>
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<td>17. <em>T. calycina</em></td>
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<td>18. <em>T. coridifolia</em></td>
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<td>19. <em>T. broteriana</em></td>
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<td><strong>Subsect. Tartonraira</strong></td>
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<td>25. <em>T. cilicica</em></td>
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<td>11. <em>T. velutina</em></td>
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<td>27. <em>T. passerina</em></td>
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<tr>
<td><strong>Subsect. Coridifoliae</strong></td>
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<td>29. <em>T. salea</em></td>
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7.4.1 Synoptic descriptions of sections and subsections


Piptochlamys C.A. Meyer in Rouy, Fl. Fr. 12:126 (1910), pro subgen.

Monoecious, dioecious, or more rarely, polygamodioecious 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 undulated.

Stem: stomata, chlorenchyma absent and cork well developed, except in 2 species. Secondary phloem rays dilated or not so. Internal phloem fibres present except in T. lanuginosa.

Type: T. hirsuta (L.) Endl., loc. cit. (1848).

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

Bracts 3–10 or absent. Leaves epistomatic; stomata modified tetracytic.

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 H.K. Tan, subsect. nov.

Bracts absent. Leaves amphistomatic; stomata anomocytic, modified tetracytic, very rarely anisocytic.

Stem: stomata and chlorenchyma absent. Cork well developed. Internal phloem fibres prominent.

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

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

Bracts 6 - 15. Leaves amphistomatic; stomata anomocytic and modified tetracytic.

Stem: stomata and chlorenchyma present. Cork moderately developed. Internal phloem fibres prominent.

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


Dioecious, rarely polygamodioecious 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 undulated.

Stem: stomata and chlorenchyma absent. Cork well developed. Secondary phloem rays dilated or not so. Internal phloem fibres absent.

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


Flowers clustered except in *T. dioica* where they may be solitary or paired. Bracts (5-) 10 - 15 except in aforenamed species 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* H.K. Tan, subsect. nov.

Flowers solitary, very rarely paired. Bracts always 2. Leaves amphi- or epistomatic.

Stem: secondary phloem rays usually dilated.

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

III. Sect. *Thymelaea*


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 undulated. 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).


Subsect. **Antiatlanticae** H.K. Tan, subsect. nov.

Plants 20 - 60 cm tall. Flowers rarely solitary, usually in compact clusters of 6 - 20. Bracts 2 - 7, white or grey-villous.


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'.


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 undulated.

Stem: stomata and chlorenchyma present. Cork absent. Secondary phloem rays not dilated. Internal phloem fibres present or absent.

7.5 Key to sections

1. Shrubs, often much-branched
2. Flowers terminal, aggregated I. Piptochlamys
2. Flowers axillary, aggregated or solitary II. Chlamydanthus
1. Annuals or suffrutescent perennials; stems virgate
3. Plants dioecious; bracts absent or 2-7, white or grey-villous
   III. Thymelaea
3. Plants monoecious or flowers hermaphrodite; bracts 2, green, glabrous, ciliate only at base or in lower half IV. Ligia

Key to species

Sect. PIPTOCHLAMYS

1. Bracts present
   2. Branches not virgate; leaves epistomatic
      3. Bracts 7-10, linear-lanceolate, 6-7 x 1.5 mm
         3. lanuginosa
      3. Bracts 3-5, ovate-lanceolate, 3.5-4 x 1.5 mm
         4. gattefossei
   2. Branches virgate; leaves amphistomatic
      4. Leaves sericeous, early-deciduous 8. microphylla
      4. Leaves glabrous, semi-persistent 9. sempervirens

1. Bracts absent
5. Leaves with involute or slightly involute margins, epistomatic
6. Leaves thick-fleshy; perianth deciduous; ovary pubescent only at apex
   2. hirsuta
6. Leaves not thick-fleshy; perianth subpersistent; ovary pubescent
   1. lythroides
5. Leaves planar, amphistomatic

7. Branches + fastigiate; leaves sericeous 5. argentata
7. Branches divergent, not fastigiate; leaves with at least one surface glabrous

8. Branches thick, often tortuous, dusty-white; leaves completely glabrous 6. virescens
8. Branches slender, not tortuous nor dusty-white; adaxial or abaxial leaf surface glabrous 7. putorioides

II. Sect. CHLAMYDANTHUS

1. Bracts absent or more than 2 (subsect. Tartonraira)

2. Flowers single or rarely, paired; perianth glabrous or sparsely pilose 12. dioica
2. Flowers in fascicles of 2-5; perianth sericeous or densely pubescent
3. Young shoots and leaves glabrous, pubescent or sericeous 10. tartonraira
3. Young shoots and leaves yellow-velutinous or lanate 11. velutina

1. Bracts 2 (subsect. Coridifoliae)

4. Leaves planar
5. Perianth pubescent 15. procumbens
5. Perianth glabrous
6. Leaves lorate, obtuse 13. tinctoria
4. Leaf margins involute or slightly involute
7. Perianth pubescent
8. Leaves 2-4 mm broad
17. calycina
8. Leaves 0.5 - 1 mm broad
18. coridifolia
7. Perianth glabrous
9. Mature leaves glabrous on both surfaces
16. ruizii
9. Mature leaves tomentose on adaxial surfaces
19. broteriana

III. Sect. THYMELAEA

1. Bracts absent (subsect. Sanamunda)
2. Young shoots hirtellous or white-pilose
   22. villosa
2. Young shoots not hirtellous
3. Stems pubescent in leafy parts; perianth tube densely pubescent
   23. thesioides
3. Stems glabrous or very sparsely pilose at tips; perianth tube
   glabrous or sparsely pilose
   24. sanamunda
1. Bracts present (subsect. Antiatlanticae)
4. Stems white-villous or pilose in flowering parts; bracts
   2-3
   20. antiatlantica
4. Stems grey-villous in part; bracts 5-7
   21. virgata

IV. Sect. LIGIA

1. Suffrutescent perennials; stems many
2. Leaves narrowly elliptic, less than 1 cm long, margins never
   revolute
   25. cilicica
2. Leaves linear-filiform, more than 1 cm long, margins usually revolute on drying

1. Annuals; stem single

3. Stems glabrous or very sparsely pilose at tips

4. Flowers hermaphrodite; ovary hirsute-villous at apex

26. aucheri

4. Flowers unisexual, very rarely hermaphrodite; ovary puberulous at apex

27. passerina

29. salsa

3. Stems hairy

5. Leaves glabrous or with a few straight-adpressed hairs on abaxial surface

28. gussonei

5. Leaves greyish-pilose, with hairs crisped-spreading

30. mesopotamica
1. *T. lythroides* Barr. & Murb. in Acta Univ. Lund. n.s. 2(1); 69 (1906).

Loc.: Murb., loc. cit., t. 19, f. 1-6 (1906); Fig. 52A-Ca, map 10.

Dioecious or near dioecious erect shrub, 40 - 70 cm. Young shoots tomentose-villous. Leaves sessile, subcoriaceous, margins slightly involute, ovate or lanceolate, 4-12 x 2-3 mm (on young sterile shoots usually 7-20 x 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 scrub in open oakwood (with *Quercus suber*, *Galium viscosum*, *Daucus pumilis*, *Imperata cylindrica*, etc.), sea-level - 150 m.

Type: /Morocco/ in sylva Tamara, 12 & 13 iii 1887, Grant (P-Hb. Cosson, iso.!).

Distribution: endemic to W. Morocco.

Selected specimens:

Forest of Mamora, Irvine 3265! Jahandiez 1924: 225! Sidi Allal-el-Babraoui to Kenitra, 150 m, D. 54391! near Moulay-Bou-Salham, E. of lagoon, 10-50 m, D. 55584! Rabat to Tiflet, 150 m, Paunero et al. 1973/69! N. of Larache, c. sea-level, Archibald 799!
Affinities of this species seem to lie with *T. hirsuta* (L.) Endl. 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. *Chamydanthus* (C.A. Meyer) Endl. but to transfer it to Sect. *Piptochlamys* (C.A. Meyer) Endl. would be more appropriate.

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

Regeneration by seed is reported to be rare (Metro & Sauvage, 1955).


*P. metnan* Forsskål, Fl. Aeg.-Arab., 81 (1775).

*P. polygalaefolia* Lapeyr., Hist. Abr. Pyr., 214 (1813), photo:

*Tartonia ovatifolia* Rafin., Autikon Botanikon, 146 (1840).

*Piptochlamys hirsuta* (L.) C.A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:358 (1843), photo:

*Chlamydanthus hirsutus* (L.) Griseb., Spic. 2:547 (1845), photo:

*Thymelaea hirsuta* (L.) Endl. var. *polygalaefolia* (Lapeyr.) Endl., Gen. Pl. Suppl. 4 (2): 65 (1848), photo:

*Passerina hirsuta* L. var. *vestita* Gren. in Gren. & Godr., Fl. Fr. 3: 63 (1855), photo:

*Thymelaea hirsuta* (L.) Endl. var. *vulgaris* Meissn. in DC., Prodr. 14: 557 (1857), photo:

*Thymelaea hirsuta* (L.) Endl. var. *rotundifolia* Meissn., ibid., photo:

*Thymelaea hirsuta* (L.) Endl. var. *angustifolia* Meissn., ibid., photo:

*Stellera hirsuta* (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo:

*Giardia hirsuta* (L.) Gerber in Bull. Soc. Bot. France 46 (sess. extr.): 112 (1899), photo:


Ic: *Sibth. & Sm., Fl. Graeca* 4(2): t. 360 (1824); Holmboe, Veg. Cyprus 282, f. 113 (1914); Fig. 52 D - G, map 10.

Dioecious or polygamodioecious shrub, 20 - 150 cm (rarely 2 - 3 m).

Young and flowering shoots white-tomentose, older branches divergent,
becoming pendant and glabrous. Leaves incurved or + planar, sessile, thick-coriaceous, margins involute, orbicular-ovate or ovate-lanceolate, (2-3) -5(-8) x 1.5-3(-5) mm, obtuse or acute, adaxial surface white-tomentose or lanose, abaxial green, glabrous. Flowers sessile, villous tufted at base, in fascicles of 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. Upper stamens semi-exserted. 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.

Described from Spain (Hb. Linn. 504/4, photo!)


Selected specimens

As in *T. lythroides* Barr. & Murb., leaves can be slightly dimorphic. On full-grown shrubs (1-2 m tall), those on young sterile shoots may be narrowly ovate-lanceolate while those on flowering shoots and older branches are orbicular-ovate. This is probably related to seasonal fluctuations in available water. Plants on cultivated land, e.g. 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 produce lanceolate leaves (6-10 x 2-5 mm) on the main stem. Those on lateral branches are ovate or ovate-lanceolate (2-4 x 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 (1857: 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 x 2-3.5 mm. I have seen photos of the specimens cited and found that
the material from Marseilles (Richard 2) and Egypt (Aucher s.n.) are typical 'hirsuta'. The remaining specimens (from Carthage, Pozzuoli, Sardinia, Sicily, etc.) do have a rather distinct 'angustifolia'-appearance. 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 glabris' by Meissner, loc. cit. It is remarkable that there can 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. Again, examination of material thus named, proved that it is similar to the typical plant. Asso (1779) has used the name _Passerina hirsuta_ for _T. tinctoria_ (Pourret) Endl. The abaxial surface of leaves in this species is grey-puberulous and perhaps may account for any taxonomic confusion.

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 Boyko (1949, a valuable potential cellulose and fibre plant).
Málaga, 235 (1935), n.v.; T. lanuginosa (Lam.) Brecher in Index Hortic

Syn: Daphne lanuginosa Lam., Encycl. 3: 436 (1792), photo!
Passerina canescens Schousboe in Willd., Sp. Pl. 2: 432 (1799)!
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.

Stellera lanuginosa (Lam.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!
(1922), photo!

in Notes R.B.G. Edinb. 35 (3): 346, f. 1F-Ka (1977); map 10.

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 x 1.5-2 mm (on young shoots
sometimes lanceolate, 6-8 x 2 mm), obtuse or subacute, grey-lanuginose,
less so or only in basal half on abaxial surface. Flowers fragrant,
shortly pedicellate, in fascicles of 7-10 at ends of short, densely
leafy branches; very rarely staminate. Inflorescence bracts leaf-like,
7-10, linear-lanceolate, 6-7 x 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, 1.5-2mm, obtuse. Ovary pubescent;
style becoming subterminal. Seed c. 2 mm. Fl. Jan. - Jun.; fr. till
Aug. Abandoned race course, scrub forest, sandy and dry rocky soils near sea, rare in hills, sea-level - 15 m.

Type: /Spain/ communiquée par M. de Jussieu (holo. P, photo!).

Distribution: S. Spain, Gibraltar and Morocco.

Selected specimens

SPAIN. unloc., Schousboe s.n.: B-Hb. Willd. 7591, photo! (type of P. canescens). Hb. Pourret 2390, 6319 (type of P. kalifolia). Cadiz: Algeciras, 15 m, Stocken 271.64! Malaga: Estepona to Marbella, vi 1837, Boissier! GIBRALTAR. beach of St. Roch, 18 iv 1889, Dautez & Reverchon! old Spanish race course, 7 i 1858, anon.!: MOROCCO. Tanger, Schousboe s.n.:

A species closely related to T. gattefossei H.K. Tan.

Ic: Tan, op. cit.: 346, f. 1A - Ea; map 10.

Dioecious shrub with slender, grey-lanuginose branches. Leaves sessile, herbaceous, ovate, 4-5 x 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 x 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. Feb. - Mar. Sandy plains, littoral region with *Chamaerops humilis* L.

Type: [Morocco] Chaouia, chamaeropae sur sable a Bouskoura, ii 1937, *Gattefossé* (holo. MPU!).

Distribution: endemic to W. Morocco (refer Appendix B).
5. **T. argentata** (Lam.) Pau in Cavanillesia 5: 44 (1932).

Syn: **Daphne argentata** Lam., Encycl. 3: 436 (1792), photo!

**D. nitida** Vahl, Symb. 3: 53 (1794), photo!

**Passerina nitida** (Vahl) Desf., Fl. Atl. 1: 331 (1798), photo!


**Stellera nitida** (Vahl) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!


**T. virgata** (Desf.) Endl. var. **microphylla** Willk., loc. cit. (1893), pro syn.


Ic: Desf., Fl. Atl. 1: t. 94 (1798); Fig. 54 D–F, map 10.

Erect shrub, 10–50 cm. Branches + fastigiata, rarely divergent, pilose; flowering shoots short, sericeous, densely leafy. Leaves imbricate, sessile, subcoriaceous, ob lanceolate or spathulate, 3–8 x 0.5–2 mm, obtuse or apiculate, adpressed-sericeous. Flowers *hermaphroditic and pistillate, 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 ilex and Stipa tenacissima), Pinus halepensis – Tetraclinis articulata scrub, 10–1500 m.

* sessile, in terminal fascicles of 4–6 (–9). Glares absent. Hermaphroditic ...
Type: /Spain/ communiquée par M. Vahl (holo. P, photo!).

Distribution: Spain and N. Africa.

Selected specimens:

SPAIN. unloc. B - Hb. Willd. 7590, photo! Castellón: Segorbe, 350 m, 22 iv 1908, Pau (sub T. segobricensis nomen)! Valencia: Moxente, 13 vi 1852, Bourgeau! Malaga: Sierra de Mijas, Vicioso. MOROCCO. Taforalt, 300 m, 26 iv 1930, Faure! Melilla, Gandoger 80! ALGERIA. Gambetta, 12 vi 1907, Faure! Kabylie, 800 m, v 1898, Reverchon 254! Djebel Amour, 2 km N.W. of Aflou, 1450 - 1500 m, Davis 58597! c. 12 km from Aflou to Tiaret, 1300 m, Davis 58620! TUNISIA. Dj. Sidi Salem, Mornag to St.-Marie du Zit, 200 m, Davis 56982! Korbous, W. side of Cap Bon peninsula, 10-50m, Davis 56815! Dj. Ousselat, 39 km W. of Kairouan on C99 to Ousseltia, 310 m, Davis 57145!

Ibéro-Maurétanien element. Although records are numerous from N. Africa, the plant is not gregarious (Davis, pers. comm., 1977).

Many workers, e.g. Boissier (1839 - 1845) have assumed the taxa, Daphne argentata Lam. and D. argentea Sm. (syn: T. tartonraira subsp. argentea) 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 the flowers of f. segobricensis are usually shorter and may occur either in the same cluster or on separate plants, e.g. D. 58620. This would account for his recognition of forms.

* hermaphrodite with a longer perianth, e.g. *Pícneron* 1898: 254. Prostrate flowers are ........


*Stellera virescens* (Meissn.) Kuntze, Rev. Gen. Pl. 2: 585 (1891):

Ic: Fig. 58 J−L, map 10.

Dwarf shrub c. 20 cm (?). Branches thick, often tortuous, dusty-white; young shoots brown puberulous. Leaves patent, soon decumbent and deciduous, sessile, subcoriaceous, spatulate-oblancoolate, 7-10 x 2-3 mm (lower leaves much smaller, 3-4 x 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.

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

Type: *Algeria* ad fontes fl. Oued-Abdi et in sylvâ Lambēse, Balansa 1853: 1007 (holo. G−DC, photo! iso. E!).

Distribution: N.W. Africa.

Selected specimens

MOROCCO. Haute Moulouya, Itzer, 1650 m, Jahandiez 210!: Grand Atlas, plateau des Lacs, Emberger s.n.!

*T. virescens* var. *glaberrima* Batt. is a variety which, according to Battandier (Batt. & Trabut 1890: 782), differs in having all parts completely glabrous. Localities given include Figuig in Morocco.
Affinities of this species are closest to *T. putorioides* Emb. & Maire.


Monoecious dwarf 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.

a) var *putorioides*


Ic: Fig. 53 A - G; map 10.

Leaves spathulate-ovate, 5-9 x 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 annem Tessaout, prope Ait-Alla, 1800 m, 28 vii 1926, *Maire* (holo. MPU!).

Distribution: endemic to Grand Atlas, above Demnat.

b) var. *rhodantha* Emb. & Maire, op. cit. 23: 215 (1932). Ic: Fig. 53 H - J.
Differs from var. putorioides in having leaves spathulate-oblanceolate, 3-5 x 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: also 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 type material.

T. putorioides is related to T. virescens Meissn. and T. microphylla Cosson & Dur. From the former it can be distinguished by its more slender, graceful and pubescent branches which are not thick, tortuous and dusty-white; from the latter by its larger leaves and the absence of bracts.

Syn: *Passerina microphylla* Cosson & Dur. apud Bal., Pl. Alg. exsicc. no. 256 (1852); no. 826 (1853); et apud Kralik, Pl. Tun. exsicc. no. 333 (1854); omnia nom. nud.

*T. microphylla* Meissn. in DC., Prodr. 14: 556 (1857).


Ic: Barr. in Cosson Illustr. Atl. 2: 106, t. 166 (1897); Fig. 54 G - J, map 10.

Monoecious erect shrub 20 - 150 cm. Branches virgate, soon naked; young shoots white-puberulous or sericeous. Leaves few, ± adpressed, sessile, subcoriaceous, ovate, 1-2.5 x 0.5-1.5 mm (on young shoots often lanceolate, 4 x 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 sub-terminal. 2n = 18. Fl. Feb. - Jun. Low hills, fixed dunes (with *Stipa*, *Artemisia campestris*, *Echichilon fruticosum*, *Avena barbata*, *Andropogon laniger*), stony or rocky desert (hamada), sandy salines (Tamarix dominant), gypsaceous crusts, 20-1200 m.

Type: *Tunisia* in apricis Saharæ totius, nempe a deserto Tunetano, Kralik pl. Tun. 333 (G - DC, photo: iso. E!).

Distribution: N. Africa.
Selected specimens:

ALGERIA. ex Sahara Algeriens i juxta Biskra, ii 1880, Ball! Aghalesta to Djelfa, 28 iii 1873, Maw! 3 km S. of Hassi Bahbah, 800m, Davis 53286! Ain Sefra, 1100 m, 30 v 1934, Faure! TUNISIA. Oudref, iii 1907, Pitard! 10-20 km E. of Moulares, 400 m, Davis 61216! Djebel Ben Younes near Gafsa, 500 - 600 m, Murbeck s.n.! LIBYA. near Univ. of Libya (Tripoli), 100 m, Davis 49481! Tripoli to Sabrātah, 20 m, Davis 49795! Taubert 117!

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 (L.) Endl. 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 Murb. from Tunisia and T. putorioides Emb. & Maire from the Grand Atlas.

F. Murb., op. cit. 15: f. 1; t. 12: f. 1-2 (1899);
map 10.

Monoeious twice-branched shrub, c. 30 cm tall. Branches erect, glabrous. Leaves sessile, subcoriaceous; elliptic-lanceolate, 9-13 x 3.5-5 mm, acute or subacute, glaucous, glabrous. Flowers sessile, in fascicles of 7-20, apparently on branches of previous year's growth. Bracts 6-10, broadly ovate, 1 x 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. LD1).

Distribution: endemic to Tunisia. Recorded only from Bled Thala (Battandier, Fl. Alg. Suppl. 1910: 82) and Ksar Sakket.

A very rare species. P.H. Davis (pers. comm.) visited the type locality in April 1977 but was unable to find it despite careful searching. Murbeck (1899) states it is dioecious and that pistillate flowers are unknown but I have found that the type gathering has both staminate and immature 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 Cosson & Dur. This differs in having
sericeous stems and smaller, sericeous, early-deciduous leaves.

The general inflorescence has some resemblance to that in *T. virgata* (Desf.) Endl. Murbeck drew attention to the similarity with members of Subsect. *Sanamunda* (Lange) Brecher. This group formerly included *T. virgata*, now separately placed in Subsect. *Antiatlanticae* H. K. Tan.
Thymelaea tartonraira (L.) All. is a common Mediterranean species with variation of a complex nature difficult to define. Aymonin (1971, 1974) gave a fairly recent account of the various forms, pointing out the necessity of a revision throughout the geographical range. Diverse taxonomic treatments in the past have produced numerous synonyms. D. A. 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 infra-specific variation in Corsica itself has been analysed by Briquet & R. Litardière (1938). One might decline to recognise any infraspecific units in an extremely polymorphic species, but this appears to oversimplify the problem. In my opinion, the morphological variation observed in this species is best expressed following a broad concept, in terms of closely allied subspecies sometimes connected by intermediate variants. Six groups which are morphologically distinct and to a greater or lesser extent showing a distributional pattern are dealt with here.

Characters

Within this species flower 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; also the hypogynous disc in staminate flowers may be entire or lobed. Although Rechinger (1943) uses 'bracteae subacutae' and 'bracteae obtusae' to differentiate between T. argentea (Sm.) Endl. and T. tartonraira (L.) All., these correlations are not absolute. The disc is minute, occurring
at the base of a rudimentary ovary less than 0.5 mm long; it is not an easy character to work with. The chromosome number is only known for subsp. thomasi (2n = 18, Contandriopoulos, 1964).

10. T. tartonraira (L.) All., Fl. Pedem. 1: 133 (1785), as 'T. tarton-raira'.

Dioecious, rarely polygamodioecious, 20-60 cm shrub. Lower branches with tuberculate scars, young shoots densely leafy, + glabrous or pubescent-sericeous. Leaves sessile, subcoriaceous, spatulate-oblongolate, obtuse or acute, ± glabrous and glaucous, adpressed-ovovate to narrowly linear/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.

Key to subspecies and varieties:

1. Leaves + glabrous
   6. subsp. thomasi

1. Leaves pubescent or sericeous

2. Leaves adpressed-pubescent; hairs only 0.1-0.2 mm long
   5. subsp. valentina

2. Leaves adpressed-pubescent or sericeous; hairs 0.2-0.7 mm long

3. Leaves usually 2-4 times longer than broad (predominantly W. Medit.)
4. Leaves spathulate-obovate, 4-6(-9) mm broad
   1. subsp. tartonraira var. tartonraira
4. Leaves spathulate-oblanceolate, 3-4(-5) mm broad
   2. subsp. tartonraira var. transiens
3. Leaves 4-12 times longer than broad (predominantly E. Medit.)
5. Leaves spathulate-oblanceolate, (2-)3-4 mm broad
   3. subsp. argentea var. argentea
5. Leaves narrowly linear-oblanceolate, c. 1.5 mm broad
   4. subsp. argentea var. linearifolia

1. subsp. tartonraira var. tartonraira.

Syn: Daphne tarton raira L., Sp. Pl., 356 (1753), photo!
D. candidans Lam., Fl. Fr. 3: 221 (1778).
Passerina tartonraira (L.) Schrader [as 'P. tartonreira'] in Neues J. Bot. 4: 39 (1810), photo!

Tartonia obovata Rafin., Autikon Botanikon, 146 (1840).
Thymelaea tartonraira (L.) Meissn. in DC., Prodr. 14: 556 (1857), s. str.
Stellera tartonraira (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!
Thymelaea tartonraira (L.) All. var. typica Fiori in Fiori & Paol., Fl. Anal. Ital. 1: 284 (1898), photo!

Thymelaea tartonraira (L.) All. subsp. linnaei Briq. var. genuina Lange emend. R. Lit. in R. Lit., loc. cit. (1938).

Thymelaea tartonraira (L.) All. subsp. linnaei Briq. var. genuina Lange emend. R. Lit. subvar. normalis R. Lit., op. cit., 4 (1938).

Ic: Fig. 55 H – I; map 11.

Leaves spatulate-obovate, 7-10(-15) x 4-6(-9) mm, often with a characteristic sericeous-yellow shine; veins rather more numerous than in other subspecies. Bracts ovate, 2.5 x 2 mm. 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.

Described from S. France (Hb. Linn. 500/6, photo!).

Distribution: coastal France to Corsica and Sardinia with an outlier on the Ionian island of Cephalonia. The last mentioned appears to be the easternmost occurrence of a predominantly W. Mediterranean taxon and may possibly have been introduced.

Selected specimens

S. FRANCE. unloc. Hb. Linn. 500/7, photo! P-Hb. Tournefort 5824, photo! Mont Redon near Marseilles, Balls s.n.! ann. 1827 (ex Hb. Henslow)! xii 1830, Woods! Martigues, Requien s.n.! ix 1891, Antheman! CORSICA. Bastia, i 1848, Requien! SARDINIA. San Antioco,
Muller s.n. (Sheets I & II): W. GREECE. Cephalonia, Assos, Davis 11291

2. subsp. tartonraira var. transiens (Briq.) H. K. Tan, comb. nov.


Thymelaea tartonraira (L.) All var. genuina Lange subvar. angustifolia Reynier in Bull. Soc. Bot. Fr. (sess. extr.): 70 (1906).

Thymelaea tartonraira (L.) All. f. foliis angustioribus Font-Quer in Ier Maroc. no. 287 (1928).

Thymelaea tartonraira (L.) All. var. angustioribus Font-Quer in Ier Maroc. 26: 35 (1931), non Meissn. (1857), photo: nec Lange (1862).


Ic: Fig. 55 D - Fa, map 11.

Leaves spathulate-oblong-ellate, 10-16(-25) x 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, maquis, steppes (Lygeum and Artemisia herba-alba predominant), calcareous crusts (previous Pinus halepensis forest) rare along coast, 900 - 1800 m.
Type: /Corsica/ sommet du Pigno, sur le sentier de Farinola, Mabille 1866: 171 (K! E!).

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 established in littoral zones. 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.) H. K. Tan, using Briquet's appropriate earlier epithet.

Selected specimens

SPAIN. unloc. Hb. Willd. 7584 (as Passerina orientales Willd.) photo!
S. FRANCE Hb. Willd. 7540, photo! CORSICA. Orianda, 9 iii 1920, Aylies! ITALY. Capri, iv 1874, Ball! Mt. San Angeli, vi 1841, Ball! Naples, ann. 1845 (ex Hb. Alexander)! Salerno to Amalfi, 23 iv 1902, White! SARDINIA. Mt. Tului near Dorgali, 21 v 1884, Forsyth-Major! SICILY. Marettimo, Ross 1900: 278! MOROCCO. S. outskirts of Ifrane, 1150 m, Alexander & Kupicha 320! Dayet-Achlef, Maire!
ALGERIA. 10 km S.W. of Djelfa, 1250 m, Davis 53304! Maw s.n.! 30 km from Sebdou to El-Aricha, 900 - 1000 m, Davis 51461!

3. subsp. argentea (Sm.) Holmboe var. angustifolia (d'Urv.) H.K. Tan, comb. nov.
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), photo!


T. tartonraira (L.) All. var. angustifolia (d'Urv.) Meissn., in DC., Prodr. 14: 556 (1857), photo! non Lange (1862) nec R. Lit. & Maire (1931).

Chlamydanthus tartonraira (L.) C. A. Meyer var. angustifolia (d'Urv.) Raulin, L'ile de Cret, Botanique, 849 (1869), photo!

T. tartonraira (L.) All var. angustifolia (d'Urv.) Boiss. (sphalm 'Cuv'), Fl. Or. 4: 1053 (1879), photo!

T. tartonraira (L.) All. subsp. tartonraira var. argentea (Sm.) Shaw & Turrill in Kew Bull., 124 (1926):


Ic: Sibth. & Sm., Fl. Graeca 4: t. 355 (1824); map 11.

Leaves spathulate-oblanceolate, (5-)10-15(-20) x (2-)3-4 mm, adpressed-pubescent, yellow, silvery or grey-sericeous. Flower clusters rather more numerous than in other subspecies. Bracts 10-12, 1.25 - 1.75 x 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 - Lavandula dominant), in Pinus brutia forest, sea-level to 915 m.

Syntypes: [Greece] Samos, Sibthorp (Hb. Linn. 500/16a, photo!). Other specimens without locality; according to Prodr. Fl. Graec. 'in Salami et Samo, copiosius vero circa Corinthum' (K! OXF, photo!).
Sibthorp collected several plants which are relevant to Smith's diagnosis in the Prodromus. The only material at Oxford is a sheet containing four flowering branches and bearing the labels 'D. argentea JES' and 'J. Sibthorp M.D.'. There are duplicates of Sibthorp's gatherings at Kew.

According to Aymonin (1971) d'Urville's type material (Skopelos, 400 m, ann 1819, d'Urville; syntype P - Hb. Tournefort 5825, photo!) is similar to Sibthorp's specimen. T. tartonraira subsp. argentea (sensu Holmboe) is a much longer and narrow-leaved 'variant' which I have treated as a separate variety as explained later.

Distribution: endemic to the E. Mediterranean, in Aegean area.

Selected specimens:

GREECE. Kassandra, Mattfield 5412; Mt Hymettus, 400 m, Zerlentis 639; 300-500 m, Davis 591 Mt. Kerata above Eleusin, ann, 1885, Haussknecht! Attika, x 1867, Ball! Peloponnesi, ii 1836, Kotschy!

AEGEAN ISLANDS. Crete: Palaikhora, 915 m, Davis 1151 Euboea: Mt. Kandili, 800 m, 23 vi 1935, Beauverd (type of var. candiliana) Khios: above Karies, 400 m, K. H. & F. Rechinger 5401! Samos: Tigani, 0 - 50 m, Runemark et al. 19945! Lipsos: the N Aspra Nisia, N. island, Runemark & Bothmer 46447! Kalimnos: Forsyth-Major 349!

Kos: between Pili and Kardamona, Rechinger 7968! Nisiro: Papatsou 495. Sifnos: Mt. Prophetis Elias, Gathorne-Hardy 86! Rodhos: San Stefani, Fischer, s.n. Records from other islands have not been verified but more likely to be of var. argentea rather than var. linearifolia.

TURKEY (N. W. Turkey, W. Anatolia). A1 (A) Çanakkale:
18 km S. of Çanakkale, Huber-Morath 17469! A₁ (E) Çanakkale:
Ariburnu, A. & T. Baytop 12.611! B₁ Çanakkale: plains of Troy, tomb
of Ajax, Clarke s.n. ! Izmir: Ilica, 3 km E. of Çeşme, Aleva & Regel
4824! C. Aydin: 3 km from Didyma, 10m, Bocquet 2653!

4. subsp. argentea (Sm.) Holmboe var. linearifolia H. K. Tan, var.
   nov.
Syn: Thymelaea 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: Fig. 55 A – Cb, map III.

Leaves narrowly linear-oblanceolate, (10-)20-25 x c. 1.5 mm, greyish
or silvery-sericeous. Bracts 10-15, triangular-acute in Cretan plants,
rock, limestone slopes, maquis on serpentine, sea-level to 830 m.

Type: /Cyprus/ Mazoto, Holmboe 163 (C?).

Distribution: confined to S.W. Anatolia, Rodhos, Crete and Cyprus,
the last two being the most southern and eastern part of subsp.
argentea's range.

Selected specimens:

AEGEAN ISLANDS. Crete: above Paliokhora at Kephalá, c. 130 m,
Davis 1221! Selinos, Omalos, 24 v 1884, Reverchon! Mt. Sfákia,
Sieber s.n. ! Rodhos: iii 1944, Fink! W. slope of mt. Paradíscou,
100 - 250 m, Kjellqvist & Snogerup 22042! TURKEY (S.W. Anatolia).

C2 Muğla: Marmaris to Emecik, 200 m, Davis 25326! C3 Antalya: Kayran (N.W. Antalya) Bozakman & Fitz 1811 CYPRUS. Akanthou, 160 - 330 m, Davis 2029! Komi Kebir to Dhavlos, 100 - 330 m, Davis 2452! Lefkara, 12 viii 1898, Postian! Lefkara to Vavatsinia, c. 830 m, Davis 1899! Pisuri, Deflera 11351! 11361! 4 xi 1901, Warburg! Kotschy s.n.!
Aucher 1879! mt near Kantara, 7 iv 1880, Sintenis & Rigo!

The following specimens, all from W. and S.W. Turkey and islands, are intermediate between the two varieties, argentea and linearifolia, the leaves being 15-25 x 2-3 mm.

A1(E) Çanakkale: S.S.W. Çanakkale, c. 2 km S. of Güzelyali, Lewejchann Tu - 74 - 066! C1 Izmir: Samsun Dağ above Güzelçamlı, 800 m, Davis 417271 C3 Antalya: Antalya to Serik, Huber-Morath 142481! Ikaria: 3 km N. of Praya, 450 m, Runemark & Snogerup 11434! Rodhos: Sibthorp s.n. (sub. D. dioica)!

The 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 its range.


T. tartonraira (L.) All var. angustifolia (d'Urv.) Lange in Willk. & Lange, Prodr. Fl. Hisp. 1: 300 (1862), excl. typ.

Goday & Chueca (1972) have named some Spanish plants subsp. angustifolia (basionym Boissier's not d'Urville's) stating habitat and distributional differences as reasons for separating them from subsp. argentea in the E. Mediterranean. The plants also occur on calcareous soil but are restricted to the high mountains of Granada. They may illustrate a case of convergence. Material collected by Boissier, labelled 'in montibus Regn. Granat., 915-1981 m, vii 1837' (G, photo: iso. E!), with oblanceolate (10-14 x 2 mm) acute leaves is nearly identical to a specimen of subsp. argentea var. linearfolia from Crete (Davis 1221!).

I have only seen two other separate collections from the Sierra Nevada, viz. Cerro de Trevenque, 22 vii 1851, Bourgeau: Cerro Tesoro and la Cortijuela, 1524 - 1829 m, 26 vi 1851, Ball: These differ from subsp. argentea var. linearfolia mainly in their general habit, being compact little shrubs with thicker branches and very short (c. 3 cm, not 5-10 cm long) fastigate leafy shoots crowded at the ends of older, naked branches; the leaves are adpressed-pubescent or only near-sericeous, oblanceolate, 5-8 x 1.5-2 mm, acute; the bracts fewer, 5-7, apparently correlated with the general paucity of flower-clusters, but July may be the end of the flowering season.

The Spanish material from 'Sierra Nevada ad Cortijo de Rosales et Trevenque, S. Tejeda' used by Boissier to designate his var. angustifolia should be examined before the status of these high mountain variants
Daphne tomentosa Lam., Encycl. 3: 436 (1792).


Of some interest is the real identity of *D. tomentosa*. Lamarck describes it as 'Daphne floribus sessilibus axillaribus, foliis oblongis obtusis utrinque sericeo-tomentosis, N.' Endlicher (1848) following Lamarck, summarizes 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 longer and white-tomentose leaves. *D. tartonraira* L., as labelled in the Lamarck herbarium (Encycl. 3: 436 no. 9, photo:) is the typical plant from Marseilles. It was perhaps this evidence that led Meissner (1857) and Brecher (1941) to tentatively equate the imperfectly described *D. tomentosa* Lam. with *T. tartonraira* subsp. argentea. Unfortunately the voucher specimen designated 'il croit dans le Levant' could not be traced.


Syn: Daphne myrtifolia Poiret in Lam., Encycl. Bot. Suppl. 3: 315 (1813), photo:


P. tartonraira var. *genuina* Lange f. *virescens* Pau, ibid.!

P. tartonraira var. *angustifolia* d'Urv. f. *valentina* Pau, ibid.!

Thymelaea tartonraira (L.) All. subsp. *linnaei* Briq. var. *genuina*

Ic: Fig. 55 G - Gb; map 11.

Branches slender, graceful. Leaves spathulate-obovate, 5-10(-13) x 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 x 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:).

Distribution: confined to E. Spain.

Selected specimens:

Aymonin (1969) discovered that the obscure taxon, Daphne myrtifolia Poiret, is in fact a member of the T. tartonraira complex. Specimens in 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 myrthi incana. Tourn. Inst. R. Herb., 395' except for the orthographical error underlined. The type
of this polynomial is from Valencia (P - Hb. Tournefort 5828, photol) and identical to the plants collected by Porta and Rigo in 1890.

Pau (1926) recognized these specimens (originally distributed as Passerina tartonraira var. calvescens Gren. (syn. T. tartonraira subsp. thomassii) 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. thomassii (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 (Feddes Rep. 74: 28, 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 (from 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.


Syn: Passerina thomassii Duby, Bot. Gall. 1: 406 (1828)

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), photo.

T. tartonraira (L.) All. var. calvescens (Gren.) Meissn. in DC., Prodr. 14: 556 (1857), photo.


Ic: Reichb., op. cit. t. 552, f. 1172 (1849): map 11.

Young branches almost glabrous. Leaves oblanceolate, 10-15 x 3 mm, glaucous, + glabrous. Flower clusters few, scattered. Bracts 5-7.

Perianth sparsely pubescent. Woods (1850) reports that the fruit is fleshy. I have not seen any other such descriptions. 2n = 18. Fl. Mar. - May. Sandy or stony ground, in maquis with Cistus monspeliensis L.

Type: Corsica? in montosis Corsicae, Ph. Thomas (iso. E!).

Distribution: endemic to Corsica. Abundant and localized in the Asco valley, especially between Ponte-Leccia and Moltifao, Pont d'Asco, Olmi Capella, Pietrabello.

Selected specimens:

inter Ponte d'Asco et Ponte Leccia, ann. 1823, Ph. Thomas, photo!
prope Guissano, sphalm 'Giussano', ann. 1823, Ph. Thomas.

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.


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

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


Ic: Fig. 54A - C, map 10.

Dioecious dwarf shrub, young branches yellow-velutinous. Leaves sessile, subcoriaceous, spatulate or oblanceolate, 6-10 x 2.5-4 mm, obtuse, rarely subacute, yellow-velutinous or lanose. Flowers sessile, axillary, 2-3. Bracts imbricate, 10-15, ovate, c. 2mm, 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, s.l. – 1500 m.

Provisional lectotype: /Balearice7 in arenosis maritimis insulae Majoris prope Palmam vulgatissima, in montibus varior, 30 iii 1825, Cambessedes (iso. P!).

Distribution: endemic to Balearics. Records from Algeria and Morocco (Battandier, 1910: 82; Johandiez-Maire, 1932(2): 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 Canary Floras.

Selected specimens:
MALLORCA. Alcudia, Willkomm s.n.: Puig de Torella, v & vi 1881, Boissier! Bougeau 1869: 2792: Rabassa, 8 iv 1919, Bianor! Palma, 15 v 1913, Bianor! Soller, 0 – 1500 m, 5 vi 1911, Bianor! MENORCA. Puerto Fornells, 10 – 40 m, 27 iv 1885, Porta & Rigo!

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. According to Aymonin (1969) material named *Passerina velutina* by Pourret is in Paris (Hb. Pourret 466) and Madrid (Hb. Pourret 1139). When Cambessedes validated Pourret's name in 1827, he did not list any specimens. But his description tallies with Pourret's material and he further states that plants were common near Palma. *P. velutina* Pourret was mentioned as being in Hb. Desfontaines but this is erroneous as the specimen referred to is not *T. velutina* but *Daphne myrtifolia* Poiret. In view of this, one of his collections dated 30 iii 1825, has been chosen as a provisional lectotype.

Malagarriga (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, flowering earlier from February to May and 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 first group, there is little appreciable difference to warrant separation as a subspecies.

Dioecious shrub. Leaves subsessile or with petioles 0.5 mm, subcoriaceous, spatulate 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);
*Daphne calycina* 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), 'dioecia' orth. mut.;
'P. geminiflora' Ramond' m.s. E;
_Ic: Gouan, op. cit. t. 17, f.1 (1773); Fig. 56 A - F; map 12._

Erect shrub, 15-50 cm. Branches with tuberculate leaf scars, young shoots glabrous. Leaves spatulate or oblanceolate, (4-)6-12 x 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 6-8 mm; lobes triangular, 2-3 x 0.6 mm, acute. *Fl. May - Jul; fr. Aug.-Oct.* Alpine and subalpine zone, rocky scree, glacial ravines and fissures, with *Saxifraga longifolia, Globularia repens, Bupleureum angulosum, Hypericum*...
nummularium, Lonicera pyrenaica, etc., 850-2550 m.

Type: /France/ in apricus pyrenaicus eundo á pago S. Pauli de Fenouilhèdes ad pagum St. Martin, ann. 1768, Gouan (holo. K!).

Distribution: W. Pyrenees to S. W. Alps.

Selected specimens:


Val de Caros, 20 vii 1860, Ball! Col de Tende, Bordère s.n.: Hort s.n.!


Syn: Passerina granatensis Pau, Carta Bot. 1: 7 (1904)!


T. granatensis Pau ex Lacaita in Cavanillesia 3: 40 (1930)!

'P. spicata L.' m.s. E!

Ic: Fig. 56 G - H; map 12 .
Cushion-like plants less than 15 cm tall. Branches numerous, short and tortuous. Leaves oblanceolate, 2-3.5 x 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 x 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, S. E. Spain (Sierra de Cazorla and adjacent ranges).

**Selected specimens:**

**SPAIN.** Jaen: Sierra de Cabrilla, 'Las Empanadas', 2150 m, 16 vi 1928, Lacaita! FRANCE. Basses-Pyr.: Pic de Ger, 1829 - 2550 m, 22 vi 1861, Ball! Col de Tortes, 1524 - 1981 m, 26 vi 1861, Ball! Hautes-Pyr.: Mt. Né, near Bagnères de Bigorre, Woods s.n.: vi 1865, Bordère! viii 1839 & 1871, Bentham!

**Thymelaea dioica** is common in the mountains of S. W. Europe and N. W. Italy. There are two distinct subspecies. One is the typical plant of the S. W. Alps, the other is more rare, occurring in the Pyrenees and the mountains of S. E. Spain. Intermediate between the two are met with e.g., above Ufsat towards Andorra, Ariège, 13 3 x 1849, Ball! which grows to a height of more than 30 cm, but otherwise, 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 initially identified as *Thymelaea coridifolia* (Lam.) Endl. by Pau (1904) but one locality of *T. coridifolia* so far south of its known distribution in the Cantabrian Mts. would be extremely unusual. On further examination it proved to be related to *T. dioica* instead.

This species has a unique combination of characters, intermediate between Subsect. *Tartonraira* and Subsect. *Coridifoliace*. The latter is characterized by the presence of only two floral bracts.

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*


*Daphne vermiculata* Vahl, Symb. 1: 28 (1790).


IC: Fig. 57 C – Eb; map 12.

Erect shrub up to 1 m tall. Leaves often remaining imbricate, (8–)10-16 x 2-3(-5) mm, tomentose on both surfaces when young. Fl. Apr.
- Sep. Screes, degraded calcareous rock, garigue (Quercus valentina, Q. coccifera, Carex humilis, Erica multiflora, Rosmarinus officinalis, Bupleurum fruticosum, Fumana and Helianthemum spp.), 450 - 1200 m.

Type: described from Spain, Pourret (MA?).

Distribution: Portugal(?), N.E. and E. Spain, S. France.

Selected specimens:

SPAIN. unloc. P - Hb. Tournefort 5820, photo: Lerida: near Oliana, 800 m, K. & L. Tan 651; Barcelona: Centellas to S. Feliu de Codinas, 792 m, K. & L. Tan 1291; Montserrat, 800 - 1000 m, K. & L. Tan 1341; La Panadella, 800 m, Heywood 31; 2 km from Igualada to Santa Coloma de Queralt, 366 m, K. & L. Tan 1581; Valencia: Sierra de Segorbe, 500 m, Reverchon 1891: 5961; Benicarlo, Sennen 7931; Castellon de la Plana, ii & iv 1909, iiii & iv 1909 - 1917, Sennen! Chulilla to Requena, 366 m, K. & L. Tan 2721; Murcia: ann. 1837, Boissier!

subsp. nivalis (Ramond) H. K. Tan, stat. nov.


Thymelaea nivalis (Ramond) Meissn. in DC., Prodr. 14: 555 (1857):

T. tinctoria (Pourret) Endl. var. nivalis (Ramond) Lange, Pug. Hisp., 104 (1861), n.v.

Ic: Lam., Tabl. Encycl., t. 290, f. 3 (1792); Bull. Alpine Gard. Soc. Gr. Brit. 39 (2): 124, photo (1971), as T. nivalis; Fig. 57 F - L;
Similar to subsp. tinctoria but branches prostrate, leaves smaller and narrower (4–10 x 1–2 mm), often becoming deflexed, ciliate and sometimes puberulous on abaxial surface when young. Fl. and r. May–Jul.

Semi-scare, limestone ridge, cropped turf in mountains, 914–2500 m.

Syntypes: Spain, France In summis alpibus Pyrenaorum ad Port de Gavarnie et circa Mont Perdu, Ramond (P!).

Distribution: endemic to C. and W. Pyrenees, rather rare.

Selected specimens:


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

Ic: Lange, op. cit. t. II, f. 1 (1893); Fig. 58 A - E; map 12.

Dioecious dwarf 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 x 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, photo!).

Distribution: endemic to E. Spain, rare.

Selected specimens:

Teruel: Sierra del Pinar d'Albarracin, 1500 m, iv 1895; iii & iv 1896, Reverchon! Orihuela del Tremedal, 1500 m, v 1895, Reverchon!

Affinities with *T. tinctoria* (Pourret) Endl. Staminate flowers not examined.


Ic: Fernandes, op. cit. t. I & II (1952); map 12.

Dioecious shrub with prostrate, spreading branches reaching 70 cm; old stems naked, with tuberculate leaf scars; young shoots short, ascending, sericeous-villous, densely leafy. Leaves imbricate, becoming patent then decumbent, narrowly linear-lanceolate, 4-10 x 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.

Selected specimens:


Three separate sheets of Fernandes, Sousa & Matos 4038 were examined. The first was of a male plant, the second, a female plant and the third, a predominantly male plant bearing pistillate flowers on one
small side branch. Fernandes et al. 3970 and 3971 are of sterile material. No. 3972 had some 6-merous flowers and pistillate flowers with nine perianth lobes and two free ovaries. These specimens were collected in September and as suggested by Fernandes (1952), out-of-season flowering could have affected sex-expression.

The species can be readily distinguished from T. coridifolia (Lam.) Endl. by its prostrate habit and silvery-grey not greenish-yellow branches. According to Fernandes, it has a foetid odour absent in the related species. Its leaves are also broader, adpressed-pubescent or sericeous, never glabrous. The staminate flowers are always borne singly in the leaf axils and much larger than in T. coridifolia, being 5-7 mm instead of 3-5 mm.
104 (1861) n.v.
*T. ciliata* Casav. in Restaur. farm. 27(11): 169 (1872), pro syn. (?),
n.v.
*T. floribunda* Boiss. in Willk., Ill. Fl. Hisp. Balear. 1: 77 (1882),
pro syn.!
*Daphne pilosa* (Lange) Font-Quer, ibid.
*P. calycina* (Lapeyr.) DC. var. *pilosa* (Lange) Font-Quer, ibid.
*T. calycina* (Lapeyr.) Meissn. subsp. *ruizii* (Loscos) Malag. in Lab.
Ic: Willk., Ill Fl. Hisp. Balear. 1: t. 52 (1882) but bracts wrongly
positioned, should be outside inner perianth lobes; Fig. 58 H - Ia;
map 12.

Dioecious shrub up to 35 cm; branches decumbent, spreading, young
shoots grey-villous. Leaves sessile, subcoriaceous, lanceolate,
4-8(-12) x 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. Upper stamens semi-exserted. Ovary ovoid,
(amphibolitic) rock, dry exposed hill tops, alpine meadow, 1070-2300 m.
Type: /Spain/ Picos de Europa, near Refugio Aliva, Loscos.

Distribution: N. Spain, N. E. Portugal.

Selected specimens:

PORTUGAL. Trás-os-Montes e Alto Douro: above Paçó, near Vinhais, 1070 m, Silva & Teles 8733. SPAIN. Santander: near La Colladuna and Cuetos de Juan Toribis, 1800-1900 m, Harrold & McBeath 561. Picos de Europa, vii 1879, Boissier! near Puerto de Aliva, 1800 m, 12 vii 1879, Levier! Navarra: near Caparroso, iii 1882, Casaviella. Logrono: near Haro, 17 iv 1907, Elias! Fonzaleche (Rioja), Elias LISE 33891. Logrono/Soria: between Viniegra de Arriba and Montenegro de Cameros (Sierra de Urbion), 1700 m, Dresser 605! 699!

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

Its 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.
Passerina calycina (Lapeyr.) DC. in Lam & DC., Fl. Fr. 3: 360 (1805), photo!
T. calycina (Lapeyr.) Meissn. var. glabra Lange, Fug. Hisp., 104 (1861), n.v.
Stellera calycina (Lapeyr.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

Ic: Lapeyr., Fig. Fl. Pyr., t. 88 (1812); Fig. 57A - B: map 12.

Dioecious branched shrub 20-50 cm tall; young shoots grey-puberulous, leaf scars tuberculate. Leaves sessile, coriaceous, linear-lanceolate, 8-15 x 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.
Mountains, calcareous rock, 500 - 1500 m.

Syntypes: [France] Ariège, montagne de Bernadouze; Vallée de Vicedeso, La Peyrouse (G, photo!).

Distribution: C. Pyrenees, rare.
Selected specimens:

SPAIN. Huesca: Saumères near Benasque, 1000 - 1500 m, v 1831, Endress!
(not to be confused with material of T. tinctoria subsp. nivalis or or T. dioica subsp. dioica from the same locality).

Syn: *Daphne coridifolia* Lam., *Encycl.* 3: 437 (1792), photo!

*Passerina coridifolia* (Lam.) Wikstr. in *Kungl. Svenska Vet.-Akad. Handl.*, 354 (1818), photo!

*D. ericaefolia* Wahl in *Lange, Pug. Hisp.*, 103 (1861), pro syn.;

*n.v.*


Ic: Fig. 58 F - Ga; map 12.

Dioecious dwarf 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 x 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 - Sep.* Earthy screes, cattle trampled and grazed slopes, heathland, stony alpine pastures, 1200 – 2000 m.

Type: *Spain* ex Galica (holo. P - Hb. Juss., photo!)

Distribution: endemic to N. Spain (Galicia, Asturias to Navarra),
not further east than $2^\circ W$.

Selected specimens:
Leon: Puerto del Ponton, Cordillera Cantabrica near Picos de Europa, 1750 - 1800 m, **Dresser** 1066: Picón de la Bana, Sierra Cabrera, 8 viii 1933, **Rothmaler**; la Garganta near Santa Eulalia de Oscos, 9 v 1960, **Lainz**
Burgos: Castro Valnera, 1200 m, vii 1928, **Loso**

According to **Dresser** (Notes RBG Edinb. 24:11), material collected by him in Picos de Europa is atypical in having curved, pubescent leaves which thus differs from most herbarium material and the description of **T. coridifolia** as originally published. But the leaves of this species are ciliate, becoming glabrous at maturity and often incurved on drying. Although the type locality for **T. ruizii Loscos** is also near Refugio Aliva in Picos de Europa, **Dresser's** specimens certainly cannot be **T. ruizii** as the latter has a different habit and a glabrous perianth.

**T. coridifolia** growing in the Galican heathlands is not grazed by animals because of its toxic nature. This becomes more obvious in the summer, a time when most surrounding plants become closely cropped.

Related to **T. broteriana** Coutinho.

Syn: *Passerina hirsuta* Brot., Fl. Lusit. 2: 28 (1804), non L. (1753),
photo: nec Asso (1779), photo:

*T. coridifolia* sensu Henriques in Bol. Soc. Brot. 3: 191 (1885):
non Endl. (1848), photo:

*P. broteriana* (Coutinho) Sampaio, Herb. Port., 104 (1913).

*T. coridifolia* (Lam.) Endl. subsp. *broteriana* (Coutinho) Malag. in

Map 12.

Dioecious dwarf 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 x 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. COII).

Distribution: endemic to N. and C. Portugal.

Selected specimens:

N. Portugal: Serra do Gerez, near Curral and Vidueiro, vi 1885,
Aarão F. de Lacerda! Vidoal e Borrageiro, Henriques! Moller 880!

C. Portugal: Sierra de Alpedrinha and S. de Arrabida, R. da Cunha!
Affinities with *T. coridifolia* (Lam.) Endl. and *T. procumbens* A. & R. Fernandes 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.

**Syn:** *T. linifolia* Andr. in Index Horti. Bot. Univ. Budapest. 3: 78 (1938).

**Ic:** Fig. 59 A - Cb; map 13.


**Type:** *Morocco* In pascuis lapidosis aridis Anti-Atlantis: prope Taliouine, 950 m, solo arenaceo, 16 v 1932, Maire (holo. MPU! iso. KI).

Distribution: N. W. Africa.

**Selected specimens:**


This is the only apparently Saharo-Sindian species of Sect. *Thymelaea*, having affinities with *T. virgata* (Desf.) Endl. from which it can be easily distinguished by its woody habit, narrower leaves and fewer bracts.

Predominantly androdioecious, perennial, 20-60 cm. Leaves elliptic-lanceolate, (10-)20-25(-40) x 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), photo!


Ic: Desf., *Fl. Atl.* 1: t. 95 (1798); Fig. 60 A-E, 59 D-Ga; map 13.

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 with *Quercus ilex*, sandstone pavements, plateau wadis (with *Stipa, Lygeum, Artemisia*), steppe with gypsaceous crust overblown with sand, 1000 - 2100 m.

Type: [Algeria] In arvis incultis prope Tlemsen (holo. P - Hb. Desf. photo!).
Distribution: N. W. Africa, S. Spain (?).

Selected specimens:

MOROCCO. Tanger, Ball s.n.: vi 1912, Pitard: ann. 1825, Salzmann.

ALGERIA. Tlemcen, vi 1849, Munby! Bourgeau 1856: 27; vii 1877, Warion! ca. Saida, Balansa 1852: 257; Djebel Amour, Davis 58692!

Tiaret to Aflou, S. of Ain Deneb, Davis 58521! between Ain Deneb and Hassian-Ed-Dih, Davis 58574! Layoune to Kemisti (S. of Teniet-el-Had), Davis 58539! Chott-ech-Chergui between Bouktoub and le Kreider, Davis 58773! 3 km S. of Hassi-Bahbah, Davis 53279: Terny, 18 vii 1935, Faure!

S. SPAIN. unloc., Cabrera (in Hb. Agardh, Hb. Liebmann, n.v.). According to Lange (1861), these specimens differ from the type material in Hb. Desfontainoses 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. thesioides (Lam.) Endl. subsp. elliptica (Boiss.) Brecher.

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

subsp. broussonetii (Ball) H. K. Tan, stat. nov.


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 meadows between Cedrus atlantica zone, sandstone gullies with Dyris, etc, on limestone slopes, basalt and schistose rock, miocene marne, 600 – 2650 m.

Type: /Morocco/ ex Imp. Maroccano, Broussonet (K?)

Distribution: N. W. Africa.

Selected specimens:

MOROCCO. Great Atlas: Bou Gamez, Spence 210! Middle Atlas: between Azrou and Timhadite, Paunero et al. 1940/69! S. side of Immouzer, Davis 55053! Mischliffen (above Ifrane), Davis 55105! Ketama-Jebla-Targuist junction, Davis 54928! Azgour, Balls 2812! Dayet Achlef, Jahandiez 462! Jebel Azourki, Davis 55233!

Intermediate between subsp. virgata and subsp. broussonetii in which the middle leaves are subglabrous and stems villous-pubescent, are met with in the following specimens from Morocco.

Great Atlas: 7 km above Asni on track to Oukaimeden (31° 20' N., 7° 55' W.), 1800 m, Reading Univ./BM Exped. 696!

Middle Atlas: Ifrane, on way to Ras-el-Mar, 1700 m, Davis 55131!

Thymelaea virgata is a W. Mediterranean and Mauretanian steppe species. It is not known to which subspecies var. rodriguezii Sennen & Mauricio (nom. nud. in Cat. Fl. Rif. Or., 105 (1934)) should be referred.
Dioecious erect 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 x (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, photo).

Distribution: S. Portugal and Spain, Gibraltar, Morocco.
Selected specimens:

PORTUGAL. Algarve, anon.: Welwitsch 403: Sierra de Monchique,
Bourgeau 1853: 2025: SPAIN. unloc., P - Hb. Tournefort 5811, photo:
B - Hb. Willd. 7539, photo: Cadiz: San Roque, Willkomm 1844: 670:
Schott s.n.: Carbonera, Porta & Rigo s.n.: Algeciras, Sierra above
Rio de la Miel, Gibbs 81.5: S. de Palma, Reverchon 1887: 108: Las
Navas, 305 m, Allen 7677: GIBRALTAR. unloc., P - Hb. Juss., photo:
an. 1837, Boissier: MOROCCO. Tanger, Schousboe s.n.: iii 1912,
Pitard: ann. 1849, Boissier & Reuter: ann. 1835, Salzmann: Djebel
Kebir, ann. 1887, Ball!

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

Dioecious suffrutescent perennial, 5-15 cm. Stems simple or sparingly branched at base; leafy parts pubescent. Leaves herbaceous, narrowly elliptic, linear-lanceolate or linear-filiform. Flowers axillary, sessile, 1-3. Staminate longer, pistillate often shorter than surrounding leaves. Perianth purplish or pale yellow, tube densely pubescent; lobes ovate or lanceolate-ovate, 0.5-1 mm wide, sparsely pilose. Ovary pubescent at apex. Seed c. 4 mm.

subsp. *thesioides*

Syn: *Daphne thesioides* Lam., *Encycl.* 3: 437 (1792), photo:

*Passerina thesioides* (Lam.) Wikstr. in *Kungl. Svenska Vet.-Akad. Handl.*, 333 (1818), photo:

*P. linariaefolia* Pourret apud Wikstr., *ibid.*, pro syn.

*Chlamydanthus thesioides* (Lam.) C.A. Meyer in *Bull. Phys.-Math. Acad. (Pétersb.)* 1: 359 (1843), photo:


*Ic.* Lam., *Tabl. Encycl.* 2(1): t. 290 f. 4 (1792); *Fig.* 61 A-F; map 13.
Leaves conflated and smaller at base of stems or on sterile shoots, (6-)8-15 x 1-2 mm, acute, + glabrous when young. Fl. May - Jul. Calcareous hills, Jurassic rock, Pinus sylvestris forest, 1000 - 1800 m.

Type: /Spain/ communiqué par M. de Jussieu (iso. G - DC, photo!).

Orthography here and as originally published is 'theosïoides' but Lamarck used 'thesioides' for plate accompanying description. All later workers accept 'thesioides', crediting it to mean 'thesium-like'.

Distribution: Spain. Record from Balearics (Ibiza, Margalef, pers. comm., 1976) not checked.

Selected specimens:


Teruel: Royuela, 1400 m, vi 1894, Reverchon! Salamanca: Tesos de la Flecha, 28 v 1957, Lainz! Cuenca: Cuenca, New Castille, Huxley 17!

Valencia: Sierra de Sacañet, 1000 m, Reverchon 1891: 601! Alicante: Orihuela, Reverchon s.n.!

Affinities with T. sanamunda All. which has glabrous stems, broader leaves and a glabrous or sparsely pilose perianth tube. Plants from the far end of its range, e.g. Jaca near C. Pyrenees, resemble T. sanamunda in their taller habit.

T. pubescens (L.) Meissn. in DC., Prodr. 14: 558 (1857) non var.
The description of *Daphne pubescens* by Linnaeus (1767) is close to *T. thesioides* (Lam.) Endl. However, the specimen referred to (Hb. Linn. 500.4, photo!) is not very representative; it suggests a narrow-leaved *T. sanamunda* instead. *D. pubescens* L. was described with 'habitat in Austria. D. Jacquin.' If *T. thesioides* is synonymous with *D. pubescens*, this is not likely on distributional grounds. (Map 13). Wikstroem (1818) notes that Linnaeus might have meant 'habitat in Asturia' in which case he could be referring to *T. coridifolia* (Lam.) Endl. Linnaeus' species may be closely related to and perhaps not specifically distinct from *T. thesioides*, in the absence of flowers and without a detailed examination of material, I have not named it.


Syn: *Passerina velutina* Boiss., Elenchus, 81 (1838); non Pourret ex Camb. (1827)!


*T. thesioides* (Lam.) Endl. var. *aragonensis* Rouy apud Magnier, Scrinia
Fl. Sel., 86 (1885), n.v.
T. thesioides (Lam.) Endl. var. elliptica (Boiss.) Meissn. in DC.,
Prodr. 14: 553 (1857);
Stellera elliptica (Boiss.) Kuntze, Rev. Gen. Pl. 2: 585 (1891);
P. aragonensis Rouy, Fl. Fr. 12: 123 (1910), pro 'race'.
(Bot.) 1(3): 33 (1925).
T. thesioides (Lam.) Endl. var. catalaunica Vayreda in Cavanillesia
4: 58 (1931).
T. sanamunda All. subsp. elliptica (Boiss.) Sagr. & Malag. in Lab.
Bot. Sennen. Barc., 9 (1974);
Ic: Boiss., Voy. Bot. Espagne, t. 158 (1839 - 1845); Fig. 61 G;
map 13.

Differs from subsp. thesioides in having leaves much broader (5-10 x
2-6 mm), acute or obtuse, white-pilose or pubescent when young. Fl.

Type: /Spain/ in aridis calcareis in Sierra Nevada, 1829 - 2134 m,
vi 1837, Boissier (holo. G - DC, photo! iso. K! E!).

Distribution: Pyrenees, S. and E. Spain. This has a slightly different
distribution pattern running almost at right angles to that of subsp.
thesioides.

Selected specimens:
SPAIN. unloc., P Hb. Tournefort 5839, photo! Huesca: Torla, vi
1879, Francois! Valencia: Sierra de Chiva, Willkomm s.n.! Albacete:
Sierra de Alcaraz, Porta & Rigo s.n.: Jaen: Sierra de Segura, Reverchon s.n.: Granada: Sierra de Sagra and S. de Baza, Bourgeau 1851: 1472: Sierra Nevada, ann. 1849, Boissier & Reuter (stems and mature leaves sub-glabrous but habit and flowers typical subsp. elliptica)! 2134 m, 27 vi 1851, Ball! Cartijuela, ann. 1851, Bourgeau! Cerro di Trevenque, Campo 1852: 89!: Sierra de Cuarto, ann. 1903, Reverchon! Sierra di Alfacar, Huter et al. 1879: 870!: Almeria: Sierra de Maria, ann. 1899, Reverchon!

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

Syn: *Daphne thymelaea* L., Sp. Pl., 356 (1753), photo!

*Passerina thymelaea* (L.) DC. in Lam. & DC., Fl. Fr. 6: 366 (1815), photo!


*Stellera thymelaea* (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

*P. sanamunda* (All.) Bub., Fl. Pyr. 1: 135 (1897).


Ic: Fig. 60F - J; map 13.

Dioecious suffrutescent perennial, 3-30 cm. Stems glabrous or sparsely pilose at tips. Leaves oblong- or ovate-lanceolate, 7-18 x 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, photo!).

Distribution: Spain, S. France and Italian Rivera. Record from N. Africa (Meissner 1897: 553) unlikely.
Selected specimens:

SPAIN. unloc. P - Hb. Tournefort 5818, photo: B - Hb. Willd. 7535, photo! Huesca: between Jaca and San Juan de la Peña, Willkomm s.n. !
Catalonia: Oriols to Figueras, Thomas 1825: 387! 512! Valencia:
Valencia, Boissier s.n.: Sierra de Guadarrama, 4 vii 1854, Bourgeau!
FRANCE. Basses-Alpes: Sausses, 13 v 1885, Reverchon 33! Herault:
Pas-du-Loup near Beziers, 5 vi 1862, Cossou! Aude: near Narbonne, 
v 1846, Irat! Pyr.-or.: Villefranche, vii 1839, Rugel! Walker-Arnott & Bentham 872! Font di Compe, Thomas 1825: 572!

Although the perianth is glabrous in the Spanish plants, it is usually pilose in those from the Spanish or French Pyrenees where T. thesioides (Lam.) Endl., a closely related species with a densely pubescent perianth, is found.

Specimens from S. France (circa Frejus et Toulon, ex Meissner, loc. cit. 1857; Rouy, Fl. Fr. 12: 123 (1910)) have been described as var. pubescens Meissn. (ibid., 1857). This apparently differs in having leaves which are sparsely pilose on both surfaces but I have not seen the material.

Syn: Ligia (as Lygia) multicaulis Schott & Kotschy in Kotschy, Reise in den ciliicischen Taurus, 381 (1858).
Ligia (as Lygia) ciliicica (Meissn.) Boiss., Fl. Or. 4: 1053 (1879).

Monoecious suffrutescent 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 x (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.


Type: /Turkey C5 Icel/ in montibus Giliicicis, c. Gulek Boghas (Ciliciischer Engpass), 1158 m, Kotschy 234b (holo. G - DC, photo: iso. W! K!).

Distribution: endemic to S. Turkey (Cilician Taurus).

Selected specimens:
C5 Icel: Taurus, Kotschy 53! Arpalik gorge, Kotschy 154! near Karli Boghas and Gizyl Deppe, Bulgar Dağ, 1830 - 2440 m, Kotschy 1853: 48!
178a!)
Nigde: Ala Dağ, Narpiz Gorge, 2338 m, Wood & Gibson 183! Demirkasik, Findlay 129!

E. Mediterranean (mt.) element. Related to T. aucheri Meissn.

**Syn:** *Ligia* (as *Lygia*) *aucheri* (Meissn.) Boiss., Fl. Or. 4: 1052 (1879).

Passerina annua Aucher apud Meissn., loc. cit. (1857), pro syn., photo: non (Salisb.) Wikstr. (1818).

Stellera hedyotis Ehrenb. apud Meissn., ibid., pro syn.


**Ic:** Fig. 63; map 14tb.

Monoecious suffrutescent perennial. Stems as in *T. cilicica* but 10-18, 30-75 cm, glabrous or with tips minutely pubescent. Leaves subsessile, closely appressed 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. Perianth adpressed-pubescent, greenish-brown, lobes reddish. Ovary hirsute at apex; style terminal or subterminal.

Seed c. 3 mm. Fl. Jul. - Sep. Pinus forest, sandstone hills, degraded slopes, in dry stream beds, 15 - 1460 m.

Syntypes: /Syria/ od Arissam, Ehrenberg (orig. B); /Turkey C5 Içe1 in monte Tauro, prope portus Ciliciences, Balansa 1855: 715 (G - DC, photo: WI E1), Kotschy 1836: 426 (WI K1).

Distribution: Syria, Lebanon, W. Iran; disjunct in N. and S. Anatolia.

Selected specimens:

TURKEY. A4 Zonguldak: Karabük to Kel Tepe, 850 m, Davis 38848.
Kastamonu: W. of Kastamonu, 800 m, Davis 38754! C5 Adana: S. end of Ülükisla Pass, 914 m, Findlay 238! C6 Hatay: Tolos Dağ, Kara Gaja, 305 m, Kotschy 1862: 107 (type of L. amani)! W. Amanus, 8-10 km N. of Iskenderum, 15 m, Aberdeen Univ. Amanus Exped. L1 766! above Yeşilkent, 305 m, Darrah 614 (leaves atypically broad)! Gaziantep: near Tullugo, Aintab (Gaziantep), 305 & 610 m, 23 vi 1865, Haussknecht!

SYRIA. Aleppo, Peyron s.n.: LEBANON. Barghoutié near Saida, Gaillardot s.n.: above Sidone, Blanche s.n.: Becherre, above Mar Tserkis, 1460 m, Kotschy 1855: 257! mt Torbol above Tripoli, Boissier s.n.: IRAN. Shiraz, Hohenacker s.n.: v 1842, Kotschy 443, photo!

Three separate sheets of Kotschy 1855: 257 from Lebanon were examined. One had a specimen with all stems fused into a solid structure ca. 7 mm thick at widest (flowering) part.
The *Thymelaea passerina* complex comprises 4 taxa:

- and *T. mesopotamica* (Jeffrey) Peterson. Their geographical distributions are shown in Map 14. These 4 taxa are very similar, and their recognition relies on distributional and ecological attributes as on phenetic differences. Tables 15 & 16 give a comparison of some of their morphological features and those of intermediates encountered.

*T. passerina* is the most widespread member, occurring in uncultivated fallow or arable land with an altitude ranging from 0 - 2590 m. Its leaves and flowers are consistently uniform in spite of a wide geographical and altitudinal range. It is the only species in which unisexual flowers have rarely been noted.

*T. gussonei* and *T. salsa* both have a more southerly distribution; the former in the Mediterranean, the latter restricted to N. W. 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 by its unisexual flowers, the + glabrous perianth lobes of the staminate flower and the glabrous or minutely puberulous apex of the ovary in the pistillate flower.

*T. mesopotamica* is restricted to the Mesopotamian region in Turkey, Iraq and Iran. It is generally smaller both in height and leaf, also all parts are crispsate-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 they can be rather easily distinguished, it is perhaps preferable to maintain all four as separate species rather than to regard them as subspecies of *T. passerina*.


   Syn: **Stellera passerina** L., *Sp. Pl.*, 559 (1753), photo!
   **Thymelaea arvensis** Lam., *Fl. Fr. (ed. 1)* 3: 218 (1778).
   **Ligia passerina** (L.) Fasano in *Atti Accad. Napoli.*, 245 (1788), photo!

   **S. annua** Salisb., *Prodr.*, 282 (1796).


   **P. annua** (Salisb.) Wikstr. in *Kungl. Svenska Vet.-Akad. Handl.*, 320 (1818), non Aucher apud Meissn. (1857), photo!

   **P. stellera** Cosson & Germ., *Fl. Env. Paris*, ed. 1, 478 (1845).


   **T. passerina** (L.) Lange in *Willk. & Lange, Prodr. Fl. Hisp.* 1: 298 (1862), photo!

   **P. arvensis** (Lam.) Ball in *J. Linn. Soc. (Bot.)* 16: 653 (1878).

   **T. passerina var. genuina** Strobl., *Fl. Nebrod. in Flora (Regensb.)* 64: 566 (1881).

   **P. passerina** (L.) Huth in *Helios* 11: 135 (1893), photo!

   **Daphne passerina** (L.) Krause in *Sturm, Fl. Deutschland*, ed. 2, 7: 142 (1902), photo!

   *Ic: Griffith, Ic. Pl. Asiat. t. 534 (1854); Nasir, Fl. W. Pakistan 12: 7, f. 2a-c (1971); Fig. 64 A - Ca; map 14a.*
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 x 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, 20 - 2590 m.

Described from Europe (Hb. Linn. 503/1, phot.).

Distribution: Widespread. C. and S. Europe, S. W. Asia, C. Russia eastwards to C. Asia. Introduced among fodder-seed into S. Australia (Moloney 6682!) and N. America, Iowa (Pohl 74521). No records from S. America or S. Africa.

Selected specimens:

SPAIN. Huesca: Broto, Borders s.n.: N.N.E. of Ainsa, 550 m, Sandwith 4785.
Granada: Sierra Nevada, ann. 1837, Boissier: FRANCE.
Gap near Romette, Borel s.n.: Étampes, Schoenfeld s.n.: near Cahors, Sandwith 3312.
Basses Alpes, Reverchon s.n.: Rhone, Gandoger s.n.:
Vaucluse, Avignon, Delacour s.n.: GERMANY. Saarbrücken, Sonder s.n.:
Falkenberg, Scheppig s.n.: SWITZERLAND. Jura plateau near Deindorf, 460 m, Meister 1162:
Geneva, Reuter s.n.: Zurich, Heer s.n.: Neustadt, Haffner s.n.: CZECHOSLOVAKIA. Moravia, dist. Břeclav, 320 m, Unar 1543.
HUNGARY. near N. Hérosöl and Vám, Schilberszky s.n.: Homokmegy,
Wiesbaur s.n.: Pannonia, near Budam, Ball s.n.: Dorugh near Strigonium, Grundl s.n.: RUMANIA, near Istria and Šarić, 50 m, Nyárády s.n.: ITALY. Taurin, Valle di Venda, Hort s.n.: Florence, Levier s.n.: Verona, near Castione, 180 - 240 m, Rigo s.n.: Venetia, Porto Sabbione to Cavallino, Vaccari s.n.: near Riva di Garda, Ball s.n.: YUGOSLAVIA. Schlosser s.n.: Dalmatia, near Spalato (Split), Pichler s.n.: near Fiume (Rijeka), G. E. Smith s.n.: ALBANIA. Renci, (Renx), Baldacci 222: BULGARIA. Vlase, Jlić s.n.: near Dragoman, 720 m, Turrill 681: GREECE. Parnetha near Dekeleia, Heldreich 659:

Aznavour 1909: 17 vi 1891, Charrel: TURKEY. Widespread in Anatolia but absent in Mesopotamia. A2 (A) Istanbul: Bostandjiq to Erenköy, 6 vii 1897, Aznavour: A2 (E) Istanbul: Makriköy, 8 x 1893, Aznavour: A2 Sakarya: Adapazari, near Geyve, 100 m, Davis 36309: A5 Sinop: Boyabat, 350 m, Davis 38041: Samsun: Lâdik Istasyon, Karadag Grid, 1000 m, Tobey 1152: A8 Çoruh (Artvin): above Artvin, 850 m, Davis 30020: A9 Kars: river Aras, 30-38 km W. of Tuzlu towards Kagizman, 1100 m, Rechinger 57417: B2 Manisa: Salihli to Turgutlu, 120 m, Buttler & Erben 17232: B4 Ankara: Atatürk Orman Çiftliği, near Dolap Dere, Alinoğlu 23: 39: Niğde: Tuz Golü N. W. of Ülükışla, 900 - 950 m, Davis 32818: B5 Kayseri: Plain of Césarée (Kayseri), 1107 m, Balansa 978: Everek (Develi), 1800 m, Siehe 249: B6 Malatya: Derendeh (Darende) to Kavak Aghatch (Akçadag), G. & B. Post 24: Sivas: Sivas to Suşehri, 1310 m, Buttler 15659: B7 Erzincan: between Selepur and Erzincan, 1250 m, 6 vii 1955, Simon: Tunceli: Partek to Hozat, 1100 m, Davis 31014: B8 Siirt: Silvan to Kurtalan, Davis 22115: B9 Agri: c. 10 km E. of Agri, 1650 m, Uotila 19581: Bitlis: Hısan, E. of Bitlis, 1372 m, Kotschy 480: Van: 5 km N. of Şatak, 1500-2000 m, Davis, 23197: C2 Muğla: 1 km W. of Muğla, 660 m,
Lambert & Thorp 532: Denizli: Pamukkale, Alava & Bocquet 5283:

Antalya: Sivri Dağ, 610 m, Tricker s.n.: C4 Konya: Kaşınhan, Davis 14767: C5 Adana: 5 km N. of Toros Dağ, 225 m, Aberdeen Univ. Amanus Exped. D1 307: C6 Hatay: Nur Dağ, 1.6 km N. of Kaypak, 800 m, Aberdeen Univ. Amanus Exped. J1 587: CYPRUS. above Mia Milea grazings, Merton 2965: PALESTINE. Esdraelon Plain, near Balfouria, Feinbrun s.n.: Jerusalem, 800 m, Meyers & Dinsmore B. 1054: SYRIA. Chesney 189: Aleppo, Kotschy s.n.! IRAQ. Sersarh, 1067 m, Wheeler-Haines 1216: Sikreen, 1067 m, Wheeler-Haines 1580: Aqra to Mosul, Rawi 11515: Gunda shar-Darband, 1500 m, Gillett 12407: IRAN. Fars, near Shiraz, Kotschy 443b: Ispili, Prov. Yehlah (Gilan) Lindsay 1353:

AFGHANISTAN. Kataghan, Prov. Takhar, Khost-o-Fereng, Podlech 11967:

Prov. Baghl, Andarab Valley, Darrah-i-Kasan, 1800 m, Podlech 11670:

Kabul, Mama Khel, 1200 m, Koelz 11579: Logar, Johnston s.n.: Kurram Valley, near Shálizán cantonments, Aitchison 668: W. PAKISTAN: Mardan, near Zaida, Topi to Jahangua, Burtt 617: Kurrum Valley, Duthie 15487:

Gilgit, Chalt Nagar, 1829 m, Stewart 26434: Karakoram, 1450 m, Polunin 6019: N.W.INDIA: Kashmir, Gandarbal, Drummond 14372: Ramoo, 1829 m, Clarke 28553: Balthistan, Indus Valley near Katzara, Duthie 12093:

Hushe River, N. of Saling, 2355-2591 m, Webster & Nasir 6287: Phandu, 305 m, Deane 111: Abogni, Deane s.n.: Hazara, Duthie s.n.: U.S.S.R.:


Lewpatoriya, Léveillé s.n.:
A weed of arable and wasteland, particularly widespread in early summer. It is the only species in Sect. Ligia in which unisexual flowers have rarely been noted (an exception being Wängsjö 2733! collected at 1050 m in June from Antalya in Turkey. This has staminate as well as hermaphrodite flowers, rather resembling the state of T. salsa Murb.).

Syn: Stellera pubescens Guss., Fl. Sic. Prodr. 1: 466 (1827), non
Thymelaea pubescens (L.) Meissn. (1857).

Passerina annua (Salisb.) Wikstr. var. pubescens (Guss.) Ten., Syll.
Fl. Nap., 565 (1831).

(1818).

Ligia (as Lygia) pubescens (Guss.) C. A. Meyer in Bull. Phys.-Math.
Acad. (Pétersb.) 1: 356 (1843).

T. arvensis Lam. var. pubescens (Guss.) Meissn. in DC., Prodr. 14:
552 (1857).

T. passerina var. pubescens (Guss.) Ces., Pass. & Gib., Comp. Fl. Ital.,
257 (1874).

P. gussonei (Boreau) Boullu in Bull. Soc. Bot. Fr. 24 (sess. extra) 66:
100 (1877), as 'P. gussoni'.

P. annua (Salisb.) Wikstr. var. algeriensis Chab. in Bull. Soc. Bot.
Fr. 36: 319 (1889).

17: 54 (1903).

T. passerina (L.) Lange var. sericea Coutinho, Fl. Port., ed. 1, 177
(1913); ed. 2, 213 (1939).


T. passerina (L.) Cosson & Germ. var. pilifera (Rohlena) Rohlena in

Ligia (as Lygia) passerina (L.) Pasano f. pilifera (Rohlena) Hayek,

Ic: Fig. 64 D - J; map 14 b.
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. - Sep. Dry fallow fields, sand dunes, calcareous and rocky slopes, near sea-level to 920 m.

Type: /Sicily/ in argillosis, inter segetes et p st messem in ar is, Palermo, Gussone.

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

Selected specimens:


Adiyaman/Urfa: Kjachta, Karamubara, 650 m, Handel-Mazzati 403: C 8

Mardin: Botan Su, 5 km W. of Tilo, 750 m, Frödin 207: CYPRUS. Kyrenia, Casey 960: Mia Milea, 160 m, Chapman 676: SYRIA. near Doumar, Gaillardot s.n.: Haleb (Aleppo), 400 m, Hakim 14 (type of *T. puberula*!).

ALGERIA: Oran, Le Figueur, Munby s.n.: Faure s.n.: Fragm. Fl. Alg. 183, Choulette! Mitidja, Munby s.n.: Tunisia: Zaghouan, Kralik 332:
<table>
<thead>
<tr>
<th></th>
<th>T. passerina</th>
<th>T. gussonei</th>
<th>Spain: Reverchon 179</th>
<th>Iraq: Wheeler-Haines 1216</th>
</tr>
</thead>
<tbody>
<tr>
<td>flowers</td>
<td>hermaphrodite</td>
<td>hermaphrodite and unisexual</td>
<td>unisexual</td>
<td>unisexual</td>
</tr>
<tr>
<td>ovary apex</td>
<td>hirsute</td>
<td>hirsute</td>
<td>hirsute</td>
<td>hirsute</td>
</tr>
<tr>
<td>bracts 3 mm long</td>
<td>1.5 - 2 mm</td>
<td>1.5 mm</td>
<td>1 mm</td>
<td>ciliate in lower half</td>
</tr>
<tr>
<td>sparsely ciliate at base</td>
<td>ciliate in lower half</td>
<td>ciliate in lower half</td>
<td>ciliate in lower half</td>
<td></td>
</tr>
<tr>
<td>stem glabrous</td>
<td>with straight-adpressed hairs</td>
<td>glabrous</td>
<td>glabrous</td>
<td></td>
</tr>
</tbody>
</table>

Table 15. T. passerina and T. gussonei. Comparison of some morphological features.
LEBANON. Aucher 2932! PALESTINE. Jerusalem, 800 m, Meyers 156!
El Reina (Nazareth), Davis 4719! Kefr Yasif, 85 m, Meyers & Dinsmore
B. 5054!

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

Two specimens were observed to be intermediate in character and may be
of hybrid origin (see facing page).
29. **T. salsa** Murb. in Lunds Univ. Årsskr. n.s. 19(1): 11 (1923).


Ic: Murb., op. cit., 12: f. 2a-c; Fig. 65 A - E; map 14b.

Annual. Stems erect, 10-45 cm, strictly branched, green or tinged reddish-purple, glabrescent or subglabrous at tips. Leaves linear-lanceolate, 6-10 x 1-2 mm, acute, glabrous. Flowers unisexual (hermaphrodite reported), axillary, 2-3(-5), usually single pistillate with staminate pair. Bracts 2, lanceolate, 2.5-3 x 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.

Selected specimens:

**SPAIN.** Jaen: near Jaen, 20 viii 1845, Willkomm! Granada: Sierra Nevada, El Pulchye, vii 1883, Nilsson; Serrania de Ronda, Boissier & Reuter s.n.: MOROCCO. Oued Mehedouma, Grant s.n.: Guicer, Pitard 1452! Dar Chafai, Pitard 1453! Nechra ben Abbou, Pitard 1454!

Reraja, Urical, vi 1872, Rein & Fritsch! Grand Atlas, Mzuda, v
1871, *Hooker fil.* Moyen Atlas, El Ramman, 1100 m, Jahandiez 946; halfway between Fez and Imouzzer, 800 m, Davis 55019b! ALGERIA. Oran, Plain Eghris near Mascara, viii 1849, Romain! 'Le Sénia to le Figuier', x 1851, Munby! along road to Setka and Senia, vi - vii 1883, Debeaux! Bossuet vicinity, 1300 m, ix 1929, Faure! Sidi-bel-Abbès, Warion 950!

Individuals with hermaphrodite flowers have been recorded by Murbeck (1923) but this state appears to be extremely rare and has not been observed in the material examined.

Its affinities are with *T. mesopotamica* (Jeffrey) Peterson from which it can be distinguished by the glabrous stem and leaves; the smaller size of its bracts, pistillate flowers and fruits and the + glabrous perianth lobes of the staminate flowers.

From *T. passerina* (L.) Cosson & Germ., 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.


**Loc:** Jeffrey, *op. cit.*, 470: f. 1; Fig. 65 F - L; map 14 a.

Annual, similar to *T. passerina* but stems much shorter, 6-35 cm, greyish-pilose. Leaves elliptic or linear-lanceolate, 5-10 x 1-1.5 mm, margins often remotely serrulate in apical half, hairs greyish, crisped-spreadng. Flowers unisexual, rarely hermaphrodite 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. late Apr. - Aug.* Fields, steppe, dry river beds, s.l. - 1400 m.

**Type:** [Turkey C7 Urfa] Akçakale, 400 m, *Davis* 28108 & Hedge (holo. K! iso. E!).

**Distribution:** Turkey, Iraq, W. Iran, Kuwait.

**Selected specimens:**

<table>
<thead>
<tr>
<th>T. passerina</th>
<th>T. mesopotamica</th>
<th>Rawi &amp; Chapman specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>flowers hermaphrodite</td>
<td>polygamous</td>
<td>polygamous</td>
</tr>
<tr>
<td>♂ (8 stamens) 2.5-3 mm</td>
<td>♂ (4 stamens, upper) 3.5 mm</td>
<td>♂ 4 mm</td>
</tr>
<tr>
<td>♂ and ♀ 2.5-3 mm</td>
<td>♀ 4 mm</td>
<td>♂ 3 mm</td>
</tr>
<tr>
<td>♀ 2-3.5 mm</td>
<td>♀ 3 mm</td>
<td>♀ 4 mm</td>
</tr>
<tr>
<td>ovary apex hirsute</td>
<td>puberulous or glabrescent</td>
<td>puberulous or glabrescent</td>
</tr>
<tr>
<td>bracts 3 mm,</td>
<td>3.25-3.5 mm,</td>
<td>3 mm,</td>
</tr>
<tr>
<td>sparsely ciliate at base,</td>
<td>ciliate in lower half,</td>
<td>ciliate in lower half,</td>
</tr>
<tr>
<td>lanceolate</td>
<td>ovate-lanceolate</td>
<td>ovate-lanceolate</td>
</tr>
<tr>
<td>stem glabrous</td>
<td>greyish-pilose</td>
<td>greyish-pilose</td>
</tr>
<tr>
<td>leaves glabrous</td>
<td>greyish-pilose</td>
<td>glabrous</td>
</tr>
<tr>
<td>height 15-60 cm</td>
<td>6-35 cm</td>
<td>45 cm</td>
</tr>
<tr>
<td>pollen homomorphic</td>
<td>nearly homomorphic</td>
<td>dimorphic &lt; 95%</td>
</tr>
</tbody>
</table>

Table 16. T. passerina and T. mesopotamica. Comparison of some morphological features.
13425: Jarmo, near Chamchamal, 762 m, W-Haines 368: Helbaek 1262: Kotschy 353: 389: S. Desert near Zulsir, c. 15 m, Rawi 14334: Koma Sank Police Station, c. 180 m, Rawi 20628: Mandali, 10 km E., Rechinger 9653: 25 km E. of Badra, Rawi 20783: 5 km S.W. of Dagoog, 170 m, Rawi 22858: Kirkuk to Sulaimaniya, Rawi 21493: 7 km N.E. of Kirkuk, Rawi 27902: 4 km E. of Wadi Thirthar, on pipeline, c. 150 m, Rawi & Gillett 7149: Kifri, 250 m, Rawi & Gillett 7399: N.E. of Sar Qal’a in valley of Narin Chai, 366 m, Poore 521: Sikreen near Sersarh, 914 m, W-Haines 1595: Zab near Eski Kellek, 300 m, Gillett 8200: Balad Sinja-Tal Afar, 335 m, Guest 4169: Qarydrah, Bayliss 115: Iskof Thindiwan-Atrush, 600 m, Chapman 9328: Bikhair Mt. near Zakho, 700 - 800 m, Rawi 22999: Jebel Sinjar, 700 - 1100 m, Gillett 11088: Jirga Jaran hills S. of Arbil, Uvarov, s.n.: IRAN. Luristan, S. of Kuh-e-Dasht, c. 1300 m, Wendelbo 2041: Fars, near Chenar Rah Dar, Stapf 518: road to Kharameh, 25 km from Shiraz, Alava 10759: KUWAIT. Falaicha islands, Wilson 413: Arafjan, Dickson 126:

The following specimens from Iraq (Rawi 21630: 22816: 23076: Chapman 263501) were found to be intermediate between T. mesopotamica and T. passerina, especially regarding stature and leaf indumentum (see facing page).

Medicinal uses: as a purgative (Wilson 4131), powdered and applied to sores on animals (Gillett 11088!). It was not mentioned which part of the plant was used.
### Abbreviations excluding those of authorities, books, journals or herbaria

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>anon.</td>
<td>collector unknown</td>
</tr>
<tr>
<td>c. or ca.</td>
<td>circa (about)</td>
</tr>
<tr>
<td>cm</td>
<td>centimetre(s)</td>
</tr>
<tr>
<td>comb. illegit.</td>
<td>combinatio illegitima</td>
</tr>
<tr>
<td>comb. nov.</td>
<td>combinatio nova</td>
</tr>
<tr>
<td>E.</td>
<td>East</td>
</tr>
<tr>
<td>e.g.</td>
<td>exempli gratia (for instance)</td>
</tr>
<tr>
<td>et al.</td>
<td>et alii (and other people)</td>
</tr>
<tr>
<td>excl.</td>
<td>excluding</td>
</tr>
<tr>
<td>f./fig.</td>
<td>figure</td>
</tr>
<tr>
<td>Fl. &amp; fr.</td>
<td>flowering and fruiting period (in months)</td>
</tr>
<tr>
<td>holo.</td>
<td>holotypus</td>
</tr>
<tr>
<td>Ic.</td>
<td>Icon (illustration)</td>
</tr>
<tr>
<td>ibid.</td>
<td>in the same place</td>
</tr>
<tr>
<td>incl.</td>
<td>including</td>
</tr>
<tr>
<td>iso.</td>
<td>isotypus</td>
</tr>
<tr>
<td>km</td>
<td>kilometre(s)</td>
</tr>
<tr>
<td>loc. cit.</td>
<td>on the page previously cited</td>
</tr>
<tr>
<td>m</td>
<td>metre(s)</td>
</tr>
<tr>
<td>mm</td>
<td>millimetre(s)</td>
</tr>
<tr>
<td>mt.</td>
<td>mountain</td>
</tr>
<tr>
<td>N.</td>
<td>North</td>
</tr>
<tr>
<td>nom. nud.</td>
<td>nomen nudum</td>
</tr>
<tr>
<td>n.v.</td>
<td>non vidi (refers to publication not seen)</td>
</tr>
<tr>
<td>obs.</td>
<td>observed</td>
</tr>
</tbody>
</table>
op. cit. in the work previously cited
p. page
photo! photograph of specimen seen
p.p. pro parte (in part)
pro gen. pro genus (as a genus)
pro syn. pro synonymum (as a synonym)
Pyr.-or. Pyrénées-Orientales
S. South
sect. nov. sectio nova
s.l. sea level
s.n. sine numero (without a number)
s. str. sensu stricto
t. plate
typ. cons. typus conservandus (type to be conserved)
unloc. unlocalised
W. West
+ more or less
x 'times' (e.g. 3 x 4 mm = 3 mm long by 4 mm wide)

An exclamation mark (!) following a cited specimen shows that the specimen has been seen; following a synonym it indicates that type material (in the broad sense) of the synonymous taxon has been seen.
7.7 Geographical distribution

The genus *Thymelaea* occurs only in the Old World. It is mainly a Mediterranean group, distributed over a moderately wide range in the Northern hemisphere. Map 18 shows the number of species present in different countries. Two-thirds are narrow endemics, i.e. confined to relatively small areas or with a restricted range of distribution within a floristic area. If we consider species restricted to geographical areas, e.g. S.W. Europe and N.W. Africa, the number of endemics would be even higher. Out of the 30 species recognized in this work, only four may be considered as widespread - *T. passerina*, *T. gussonei*, *T. hirsuta* and *T. tartonraira*. The main centre of morphological diversity lies within the two W. Mediterranean areas specified above. These two areas have a total of 27 species. There appears to be a small secondary centre in the Southern part of the Balkan peninsula, S. and W. Turkey and the northern regions of the Near East. Lake Balkash and the Altai Mts. are the most eastern extremities and furthest from the main centre of distribution.

A brief account of the distribution pattern will now be given.
Sect. *Piptochlamys subsect Hirsutae* (Map 16) has 3 of its 4 species endemic to Morocco and the southernmost part of Spain. Subsect. *Argentatae* (Map 15) is represented in E. and S. Spain and N.W. Africa (Morocco to Tunisia), within latitudes 32° and 40° N. The ditypic Subsect. *Sempervirentes* (Map 15) is restricted to N. Africa, with one of its species confined to a single locality in Tunisia.

Sect. *Chlamydanthus* has been divided into 2 subsections. The first
of these, subsect. Taronraira (Map 15) has one widespread, circum-
Mediterranean species showing great variability in leaf form;
another is exclusive to the Balearics; the third (T. dioica, Map
17), has a rather unusual distribution in the mountains of S.E.
Spain, the Pyrenees and S.W. Alps. Sect. Chlamydanthus subsect.
Coridifoliae (Map 17) is a well-defined and natural group, unique
in possessing solitary unisexual flowers subtended by two small,
non-green bracts in the leaf axils. With the exception of T. tinctoria
(the only one to show a wider distribution and even then, restricted
to E. Spain, the Pyrenees and S. France), the evolution of such
characters is apparently confined to the sierras of N. Spain and
Portugal, the W. and C. Pyrenees. Rugged topography and the greatest
possible diversity of habitats in these mountain ranges have provided
niches favouring speciation and endemism.

As regards Sect. Thymelaea (Map 16) its two subsections differ
in their distribution as well as in a number of correlated characters.
Subsect. Antiatlanticae is represented only in N.W. Africa, while
Subsect. Sanamunda has its 3 species concentrated in the northermost
tip of Morocco, S. and E. Spain, the Pyrenees and S. France.

Sect. Ligia (Map 18) includes 6 species, 4 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 widely distributed T. passerina. The perennial members,
T. cilicica and T. aucheri, which occur only in S.W. Asia, may be
considered as providing a morphological link between Sect. Ligia
and Sect. Thymelaea. T. passerina is the most wide-ranging species
and also unique in Sect. Ligia in having little development of unisexual flowers. It is self-fertile. (In the genus Thymelaea, flowers are unisexual by abortion, dioecy being more common than hermaphroditism).

In conclusion, 17 species representing all 4 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. argentata* and *T. hirsuta*. In contrast, N.W. Africa contains 14 species, again representing all 4 sections. However, 5 of these species are also distributed in the Iberian peninsula. But there is only a single member of Sect. Chlamydanthus in N.W. Africa, namely *T. tartonraira*.

If the number of sections, subsections and species in an area indicates the degree of morphological diversity in a genus, then maximum speciation has occurred probably in S.W. Europe and N.W. Africa. This does not mean, however, that the area has necessarily been the centre of origin.
Map 10. Distribution of Sect. Piptochlamys

- T. lythroides
- T. hirsuta (inset map)
- T. lanuginosefossa
- T. argenteata
- T. virescens var. virescens
- T. microphylla (inset map)
- T. microphylla var. alberrima
- T. putorioides
- T. microphylla var. virescens
- T. microphylla var. glaberrima
- T. putorioides
- T. microphylla var. virescens
- T. semprevirens
- T. velutina

Distribution of Sect. Chlamydanthus
Map II. Distribution of T. tartonraira.

- O subsp. tartonraira var. tartonraira
- O subsp. tartonraira var. transiens
- O intermediates between var. tartonraira and var. transiens
- ■ subsp. valentina
- ▽ subsp. argentea var. argentea
- ◀ subsp. argentea var. linearifolia
- ♦ intermediates between var. argentea and var. linearifolia
- ★ subsp. thomasi

- T. antiatlantica
- T. virgata subsp. virgata
- T. virgata subsp. broussonetii
- intermediates between subsp. virgata and subsp. broussonetii
- T. villosa
- T. thesioides subsp. thesioides
- T. thesioides subsp. elliptica
- T. sanamunda

See Map 14b for legend.

Lambert Azimuthal Equal Area Projection
Map 14b. Distribution of Sect. Ligia (in part).

- T. cilicica
- T. aucheri
- T. passerina
- T. gussonei
- T. salsa
- T. mesopotamica
- Intermediate between T. mesopotamica and T. passerina

Miller's Prolated Stereographic Projection
Map 15. Distribution of Sect. Piptochlamys

- subsection Argentatae (3 spp.)
- subsection Sempervirentes (2 spp.)
- Sect. Chlamydanthus subsection Tartonraira (2 spp. excluding T. dioica)

Sect. *Thymelaea* subsect. *Antiatlanticae* (2 spp.)

subsect. *Sanamunda* (3 spp.)

Miller's Prolated Stereographic Projection
Map 17. Distribution of:

Sect. Chlamydanthus subsect. Coridifoliæ (7 spp.)

T. dioica which is placed in Sect. Chlamydanthus subsect. Torboëaica

Map 18. Distribution of Sect. Ligia (6 spp.). The range is greatly extended by T. passerina. Also showing number of species of the genus Thymelaeö in different areas. Centre of development indicated by thick solid line.
Fig. 52A - Ca Thymelaea lythroides

A. Flowering branch. x 1.
B. Two pistillate flowers.
Ba. Fruit.
C. Leaf from young shoot, adaxial view. Margins slightly inrolled.
Ca. Leaf from flowering branch, adaxial view.

D - G Thymelaea hirsuta

D. Tip of flowering branch with staminate and pistillate clusters. x 2.
E. Fascicle of pistillate flowers. Perianth not persistent in fruit. x 5.
Ea. Pistillate flower.
Eb. The same, view from above.
Ec. Pistillate flower dissected, with gynoecium removed.
Ed. Fruit and seed.
F. Staminate flower.
Fa. Staminate flower dissected.
Fb. Stamen, much enlarged.
Fc. Abnormal staminate flower without rudimentary ovary but with twelve stamens.
G. Leaf, adaxial view.

All x 10 except when indicated.
Fig. 53. *Thymelaea putorioides*

A - G var. *putorioides* (3 get. 1926, Muirc)

A. Branch with leafy shoots. x 1.
B. Young leaf, adaxial view. Surface pubescent.
C. Mature leaf.
D. Staminate flower.
E. Staminate flower dissected.
F. Pistillate flower.
G. Mature ovary; style subterminal.
E-G x 10.

H - J var. *rhodantha* (7 get. 1931, Emberger)

H. Branch with young shoot. x 10.
I. Young leaf, abaxial view. Surface sparsely pilose.
J. Mature leaf, adaxial view. Surface glabrous.
I-J x 15.
Fig. 54 A - C. *Thymelaea velutina*

A. Staminate flower.
Aa. Staminate flower dissected.
B. Pistillate flower.
Ba. Ovary.
Bb. Seed.
C. Leaf, abaxial view. x 5.

D - F. *Thymelaea argentata*

D. Flowering branch. x 1.
E. Hermaphrodite flower.
Ea. Hermaphrodite flower dissected; ovary immature.
Eb. Fruit.
F. Leaf, abaxial view.

G - J. *Thymelaea microphylla*

G. Part of flowering branch. x 1.
H. Leaf, adaxial view.
Ha. Bract, adaxial view.
I. Pistillate flower dissected.
J. Staminate flower dissected.

All x 10 except when indicated.
Fig. 55. *Thymelaea tartonraira* All x 10 or x 20.

A - Cb. *subsp. argentea var. linearifolia*

A. Staminate flower. x 10 (scale shown beside H).

Aa. Rudimentary ovary with hypogynous disc. x 20.

B. Immature pistillate flowers.

Ba. Bract, abaxial view.

Bb. Pistillate flower dissected, ovary immature.

C. Fruit.

Ca. Seed.

Cb. Embryo.

D - Fa. *subsp. tartonraira var. transiens*

D. Staminate flower.

Da. Staminate flower dissected.

Db. Rudimentary ovary from staminate flower. Hypogynous disc lobed. x 20 (scale shown beside Dc).

Dc. Stamen. x 20.

E. Bracts in bud stage. Not drawn to scale.

Ea. Outer (lower) bract, abaxial view.

Eb. Middle bract, abaxial view.

Ec. Inner (upper) bract, abaxial view.

F. Pistillate flower.

Fa. Fruit.

G - Gb. *subsp. valentina*

G. Pistillate flower.

Ga. Immature ovary.

Gb. Fruit.

H - I *subsp. tartonraira var. tartonraira*

H. Staminate flower.

Ha. Rudimentary ovary of staminate flower. x 20.

Hb. Upper bract, abaxial view.

I. Floral diagram of staminate flower.
Fig. 55
Fig. 56. *Thymelaea dioica*

A - F subsp. *dioica*

A. Part of stem showing axillary flower subtended by six bracts.

B. Bracts 1 - 6, abaxial surface glabrous.

Ba. Bract, sparsely ciliate; adaxial surface pubescent.

C. Young leaf, abaxial view.

Ca. Mature leaf, abaxial view.

D. Pistillate flower; tube and inner surface of lobes puberulous.

Da. Pistillate flower; tube occasionally with a few hairs at base, none on lobes. Latter twice as long, half as broad as in D.

E. Fruit.

Ea. Seed, entire and in L.S.

Eb. Embryo, cotyledons fleshy.

F. Staminate flower with rudimentary ovary.

G - I subsp. *granatensis*

G. Two bracts; abaxial surface glabrous, adaxial with a few hairs at base. Non ciliate.

H. Staminate flower dissected, drawn in part. Perianth tube shorter, rudimentary ovary small than in F.

I. Mature leaves, abaxial view. Less than 5.5 mm in length, cf. Ca.

All x 10.
Fig. 57 A - B. *Thymelaea calycina*

A. Staminate flower, bud stage.

Aa. Staminate flower, from a different view. Bracts are outside and opposite inner perianth lobes.

B. Leaf, adaxial view. Margins slightly involute. x 5.

C - Eb. *Thymelaea tinctoria* subsp. *tinctoria*

C. Part of stem showing raised leaf-scars. x 2.

D. Young leaf, abaxial view. Both surfaces tomentose. x 5.


E. Staminate flower; upper stamens semi-exserted.

Es. Rudimentary ovary from staminate flower.

Eb. Bract, adaxial view.

F - L *Thymelaea tinctoria* subsp. *nivalis*

F. Staminate flower.

G. Young leaf, adaxial view. Margins ciliate but both surfaces glabrous. x 5.

Ga. Older leaf, adaxial view. Marginal hairs disappear at maturity. x 5.

H. Pistillate flower.

Ha. Pistillate flower dissected, view from outside. Perianth lobes connivent.

I. Mature ovary, style subterminal.

J. Stigma.

K. Floral diagram of pistillate flower. Bracts shaded.

L. Bract in two views. Abaxial surface keeled. x 20.

All x 10 except when indicated. Leaf margins from D and G show crispate hairs much enlarged.
Fig 58A – E Thymelaea subrepens

A. Female plant, flowering branch.
B. Leaf, adaxial view.
C. Two bracts, sometimes differing in shape.
D. Pistillate flower.
E. Style terminal in immature ovary, becoming subterminal in mature stage.

F – Ga. Thymelaea coridifolia

F. Leaf, abaxial view.
G. Staminate flower dissected.

H – Ia. Thymelaea ruizii

H. Staminate flower.
Ha. Bract, abaxial view.
Hb. Floral diagram of staminate flower. Note bracts are positioned opposite the smaller, inner perianth lobes.
I. Young leaf, abaxial surface villous.

J – L Thymelaea virescens

J. Part of flowering branch.
K. Hermaphrodite flower with immature ovary.
L. Leaf, adaxial view.

All x 10 except A and J which are drawn to scale shown.
Fig. 59 A - Cb. Thymelaea antiatlantica

A. Male plant, flowering stems. x 1.
B. Staminate flower dissected.
C. Outermost bract, adaxial view.
Ca. Outermost bract, abaxial view.
Cb. Innermost bract, abaxial view.

D - Ga. Thymelaea virgata subsp. virgata

D. Part of flowering stem.
Da. Staminate flower.
Db. Rudimentary ovary of staminate flower. x 10.
E. Leaf, abaxial view.
F. Inflorescence at lower part of flowering stem: 8 flowers subtended by 7 bracts. Diagrammatic.
Fa. Same inflorescence dissected to show cymose arrangement.
Youngest flowers situated away from main axis.
G. Inflorescence near tip of flowering stem: 6 flowers subtended by 6 bracts. Diagrammatic.
Ga. Same inflorescence dissected to show cymose arrangement.
Youngest flowers situated towards main axis.

All drawn x 5 except when indicated.
Fig. 6OA - E. Thymelaea virgata subsp. virgata

A. Staminate flower.
Aa. Staminate flower dissected.
B. Hermaphrodite flower.
Ba. Hermaphrodite flower dissected.
C. Ovary. Style terminal, becoming subterminal at maturity.
Ca. Seed.
D. Bract, adaxial view.
E. Part of flowering stem. Flowers in clusters of 7-20, subtended by 5 bracts. x 2.

F - J. Thymelaea sanamunda

F. Staminate flower.
G. Pistillate flower.
H. Mature ovary, style subterminal.
Ha. Immature ovary, style terminal.
I. Leaf from flowering stem, abaxial view. Glabrous.
J. Leaf from base of flowering stem, abaxial view. Ciliate.

K - N. Thymelaea villosa

K. Staminate flower.
Ka. Stamen.
Kb. Rudimentary ovary from staminate flower.
L. Pistillate flower.
Lb. Immature ovary, style terminal.
Lc. Seed.
Ld. Embryo.
M. Young leaf, abaxial view. Villous-pilose.
N. Mature leaf, abaxial view. Glabrescent, with scars from hair bases.

All x 8 except E.
Fig. 61. *Thymelaea thesioides*

A - F. subsp. *thesioides*

A. Male plant, flowering stems.
B. Staminate flower with rudimentary ovary.
C. Female plant, single flowering stem.
D. Pistillate flower.
E., Ea. Fruit and seed.
F. Leaf, abaxial view.

Subsp. *elliptica*

G. Leaf, abaxial view.

A and C x 1. The rest drawn to scale shown.
Fig. 61
A. Habit. x 1.
B. Part of flowering stem. x 7.
C. Leaf, abaxial view. x 4.
D. Immature staminate flower. x 10.
E. Staminate flower dissected, rudimentary ovary present. x 10.
F. Dimorphic pollen grains.
G. Unicellular hairs from perianth.

F - G not drawn to scale.
Fig. 63. *Thymelaea aucheri*

A. Habit. x 1.

B. Parts of stem showing staminate and pistillate flowers. x 10.

C. Leaf, adaxial view; margins not revolute before drying. x 2.

D. Pistillate flower. x 10.

E. Mature ovary. x 10.

F. Seed. x 10

G. Dehisced anther. x 100. Dimorphic pollen grains not drawn to scale.
Fig. 64 A - Ca. Thymelaea passerina

A. Bracts, adaxial and lateral views.
B. Flower.
C. Flower dissected.
Ca. Immature ovary.

D - J. Thymelaea gussonei

D. Bract, adaxial view.
E. Staminate flower.
Ea. Staminate flower dissected.
F. Hermaphrodite flower.
G. Pistillate flower.
Ga. Immature pistillate flower.
H. Stigma (not drawn to scale).
I. Unicellular hair from perianth (not to scale).
J. Part of flowering stem; hairs straight, adpressed. x 3.

K - N. T. passerina - T. gussonei intermediate

K. Bract. x 30.
L. Staminate flower. x 20.
M. Pistillate flower dissected. x 20.
N. Part of flowering stem. x 5.

All x 15 except when indicated.
Fig. 64
Fig. 65 A - E. Thymelaea salsa

A. Part of flowering stem. x 10.
B. Bract, adaxial view. Lower half ciliate.
C. Staminate flower.
D. Pistillate flower.
Da. Immature pistillate flower, dissected.
E. Mature ovary, puberulous at apex.

F - L. Thymelaea mesopotamica

F. Part of flowering stem; hairs crisped-spreading. x 10.
G. Bract, adaxial view.
H. Staminate flower.
I. Hermaphrodite flower with only 4 stamens, 2 from each whorl.
J. Mature ovary.
K. Fruit in longitudinal median section.
L. Embryo.

M - Na. T. passerina - T. mesopotamica intermediate

M. Hermaphrodite flower with only 4 stamens, all from outer whorl.

All x 15 except A and F.
APPENDIX A

Provenance of species and materials examined for anatomical studies. Species in Thymelaea arranged in some taxonomic order as adopted in main body of thesis.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Voucher / Specimen No.</th>
<th>Locality / Geographical Origin</th>
<th>Parts Studied</th>
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<tbody>
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<td>DAPHNE mezereum</td>
<td>cul. RBG, Edinburgh</td>
<td>Italy : Cortina d'Ampezzo</td>
<td>st, 1f, fls, fr, sd</td>
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<td></td>
<td>cul. G. Taylor’s garden</td>
<td></td>
<td>st, 1f, fls, p</td>
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<td>Pyrenees</td>
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<td>Pannerot et al. 1973/69</td>
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# chromosome count

<p>| st = stem | p = pollen | sd = seed |
| lf = leaf | pS = pollen for SEM | sdl = seedling |
| fis = flowers | fr = fruit |</p>
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<td>and other material from similar localities</td>
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A NEW THYMELAEAE FROM MOROCCO

H. K. Tan
A NEW THYMELAEAE FROM MOROCCO

H. K. TAN

ABSTRACT. A new species, Thymelaea gattefossei H. K. Tan (Thymelaeaceae), is described from W Morocco; it is related to T. lanuginosa (Lam.) Brecher.

Thymelaea gattefossei H. K. Tan, sp. nov. (figs. 1A—Ea, 2).
Affinis T. lanuginosae (Lam.) Brecher sed foliis latioribus, bracteis ovato-lanceolatis (haud linearibus) differt.

Frutex dioecius, 50-100 cm altus (?), ramis gracilibus flexuosis, junearibus incano-lanuginosis, interne denudatis et glabrescentibus. Folia sessilia, herbacea, late ovato-lanceolata, 4-5 x 2-3 mm, obtusa, utrinque dense incano-lanata, subtus minus tomentosa, imbricata, deinde patula. Inflorescentia: flores (staminati) 9-14 in fasciculos congestos ad apicem ramularum valde abbreviatorum I-2 foliorum aggregati, brevissime pedicellati, argenteo vel flavido incano-lanati. Bracteae 3-5, ovato-lanceolatae, obtusae, 4 x 1.5 mm, incano-lanuginosae. Flores staminati anguste infundibuliformes, 6 mm longi, intus glabri; lobae 1.5 mm longae, late ovatae, obtusae; ovarium rudimentarium disco hypogyno minuto provisum. Flores pistillati et hermaphroditii ignoti. Fl. Febr.-Mar.

Sandy plains with Chamaerops humilis L., littoral region. MOROCCO. Chaouia, chamaeropaie sur sable á Bouskoura, Février 1937, Gattefossé [holo. MPU; as T. canescens (Schousb.) Endl.]. Chaouia littoral, SE Casablanca, 23 iii 1937, Maire Iter marocc. 28 (MPU).

Recent study of herbarium material collected 40 years ago has led me to recognise a new species, T. gattefossei, which is closely related to T. lanuginosa (Lam.) Brecher (fig. F-Ka) from S Spain, Gibraltar and Tanger. They share a similar branching habit and greyish indumentum. Brecher (1941) cites the localities of Ain Saierni and Bouskoura for specimens of T. lanuginosa collected by Gattefossé in 1937 but did not examine the material. Plants from Bouznika, coll. Pitard (Jahandiez & Maire, 1932), Oued Bouskoura (Pitard, 1913) and Nouassèr, also collected by Gattefossé, have all been named T. canescens (Schousb.) Endl. (an earlier synonym of T. lanuginosa). Judging from their distribution, I would expect these records to refer to the new species. The differences between the two are tabulated here:

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<td>Inflorescence</td>
<td>At end of very short branchlets with 1-2 leaves so that the fascicles appear ± axillary.</td>
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<td>Flowers</td>
<td>At end of short, densely leafy branchlets so that the fascicles are obviously terminal.</td>
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<td>9-14 (staminate); bracts 3-5, ovate-lanceolate, 3.5-4 x 1.5-2 mm.</td>
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<td>7-10; bracts 7-10, linear-lanceolate, 6-7 x 1.5 mm.</td>
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* Botany Dept., Univ. of Edinburgh, at Royal Botanic Garden, Edinburgh EH3 5LR.
A NEW THYMELAEEA FROM MOROCCO

THE TOTAL DISTRIBUTION OF Thymelaea lanuginosa (based on checked herbarium specimens) and T. gattefossei.

Sex distribution

T. gattefossei
Staminate or pistillate.

T. lanuginosa
Hermaphrodite or pistillate, rarely staminate.

Perianth

T. gattefossei
Narrowly infundibuliform, 6 mm (staminate)

T. lanuginosa
Tubular, 7-8.5 mm (hermaphrodite), 5.5-6 mm (pistillate)

Leaf

4-5 x 2-3 mm

The distribution of the new species is apparently restricted to W Morocco, being known only from gatherings near the type locality. According to Sauvage (1961), the flora of the geographical sector of Chaouïa and Rabat has more affinity with the Lusitanian than the Iberian flora, with the existence of many interesting endemic species.

Fig. 1. A-Ea, Thymelaea gattefossei H. K. Tan: A, flowering shoot (x 8); B, part of flowering shoot, enlarged (x 3.5); Ba, leaves and bracts removed to show inflorescences (x 3.5); C, bract (adaxial surface); D, flower bud; Da, dissected staminate flower; E, leaf (adaxial surface); Ea, leaf (abaxial surface). F-Ka, Thymelaea lanuginosa (Lam.) Brecher: F, flowering shoot (x 1.5); G, terminal inflorescence with subtending bracts (x 2); H, bract (abaxial surface); I, immature hermaphrodite flower; Ia, immature ovary; J, dissected hermaphrodite flower; Ja, seed; K, leaf (adaxial surface); Ka, leaf (abaxial surface). All drawn to scale shown (x 7) except when indicated.
NOTES FROM THE ROYAL BOTANIC GARDEN

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Acknowledgments

I am grateful to Dr P. H. Davis for advice and comment in the preparation of this account. I also wish to thank the authorities at Institut de Botanique, Université de Montpellier (MPU) for the loan of specimens.
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WORKS CITED


88. __________ (1971). Terpenoid and other low-molecular weight substances of systematic interest in the Leguminosae. In: Harborne, J.B. et al. (eds.) Chemotaxonomy of the Leguminosae,


144. ________ (1964b). In: IOPB chromosome number reports II. Taxon 13: 201-209.


170. Roussi, A. (1965). Observations on the cytology and variation of
European and Asiatic populations of *Hippophae rhamnoides*.


