TAXONOMIC STUDIES IN SOME THYMELAEACEAE

by

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Abstract of thesis

Title of thesis: Taxonomic studies in some Thymelaeaceae.

The work deals mainly with the taxonomic and morphological investigation
of some Thymelaeaceae occurring in the Sud-Oriental, S. E. Asiatic
regions. It broadly falls into four parts:
1. Part A is a brief introductory section, defining scope and aims.
2. In parts B and C, morphological, anatomical and botanical
characters is surveyed. Descriptive studies on the structure, inflorescence, flower, seed distribution, fruit and seed, etc. Detailed
descriptions of

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combinations. The relationships of the genera discussed and an
evolutionary trends in the family pointed out.
3. Part D includes a taxonomic revision of Wikstroemia itself. The
classification proposed is purely phenetic in origin but is intended
to replace the existing one by Meissner (1857). Four sections, seven
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The thesis is illustrated by 13 figures, 9 plates, 10 maps and accompanied
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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, in-
florescence, 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, Dendrostellera, 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 <u>Stellera</u>, <u>Stelleropsis</u>, <u>Dendrostellera</u> and <u>Diarthron</u>, and would
certainly enlarge the genus <u>Diarthron</u> to include the C. and S. W. Asian species
of <u>Stelleropsis</u> and <u>Dendrostellera</u>. There appears to be no justification
in maintaining small, separate genera for species with hairy or glabrous/
pubescent perianths. The two genera <u>Daphne</u> and <u>Wikstroemia</u> 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 delimit-
ation and infra-generic classification.

Part D contains the general and systematic treatment of <u>Thymelaea</u>. 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   <u>TAXONOMIC EVIDENCE RELATING TO GENERA</u>

CHAPTER II   <u>EXTERNAL MORPHOLOGY</u>

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 <u>Materials and Methods</u>

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.

<u>Floral parts</u>: 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 I). 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 sub-
divisions (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
(Plate 1A), Passerina, Restella, Wikstroemia. Some are cold- (not nec-
essarily in winter) or drought-deciduous. Orshan's category of 'leaf
shedders' is not applicable in more mesic conditons.

2. <u>Frutescent chamaephytes</u>: 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. <u>Thymelaea</u> <u>subrepens</u>, with bowed-down, decumbent branches, and the cushion type, e.g. <u>T. granatensis</u>, which forms compact little clumps. <u>D. petraea</u> and <u>D. jasminea</u> 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. <u>Suffrutescent chamaephytes</u>: <u>Dendrostellera</u>, <u>Stellera</u>, <u>Stelleropsis</u>, <u>Thymelaea</u>. This category includes all herbaceous and suffruticose per- ennials 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 <u>Dendro- stellera</u>, the base or lower third of these stems usually become thick- ened 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' (suffruticose 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 _domin-
ating species_ in plant communities of three phytogeographical regions
of Palestine (1953).

A. Daphne giraldii. Shrub in early spring. Buds are the future leafy shoots of a year's growth. Cult. RBG, Edinburgh x 1/5.

B. Stellera chamaejasme. Plant in full flower, mid-summer. Fan-shaped tufted habit, with stems arising from woody rootstock. Cult. RBG, Edinburgh x 1/7.

PLATE 1

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 imbricately 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 protection during the resting season is from the imbricate, often incurved, 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. broteriana. The leaf shape in this shrub gives it its heath-like appearance.

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 dis-
tinction 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.

Pl. 2
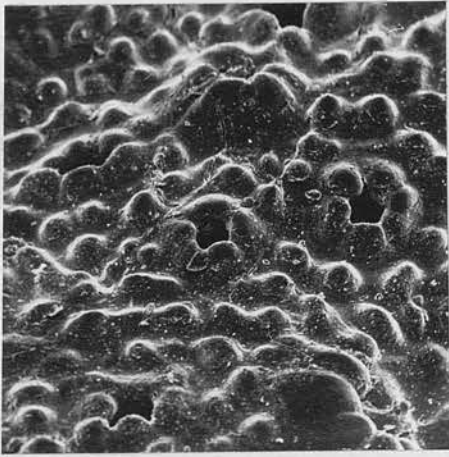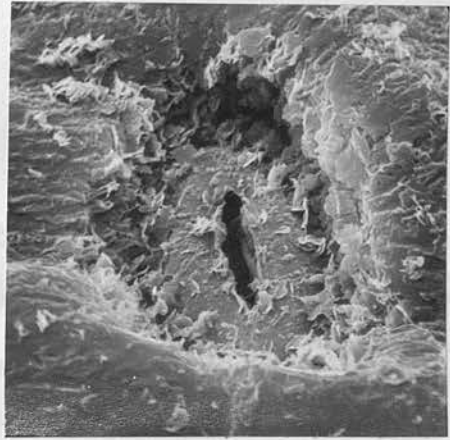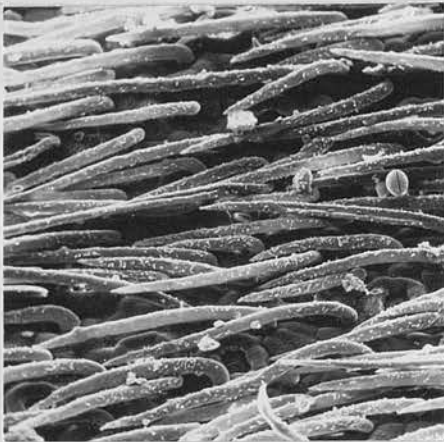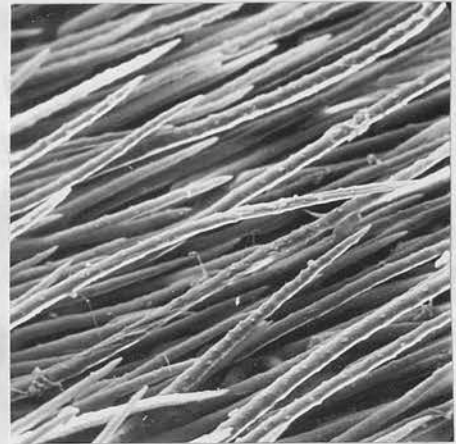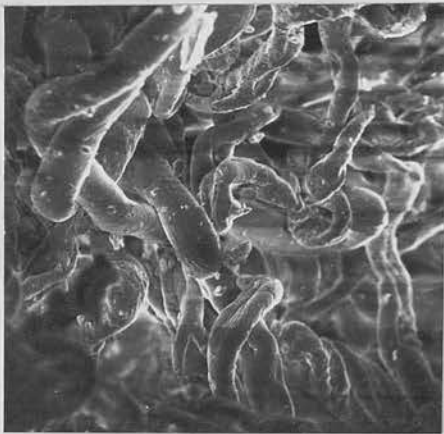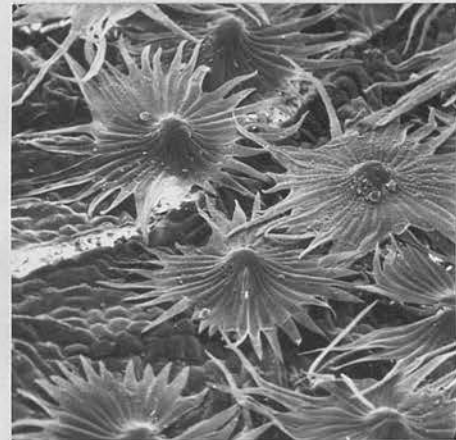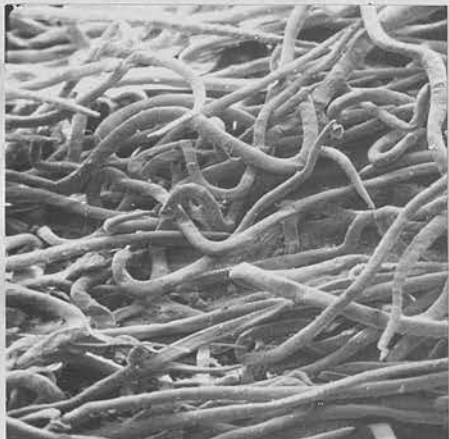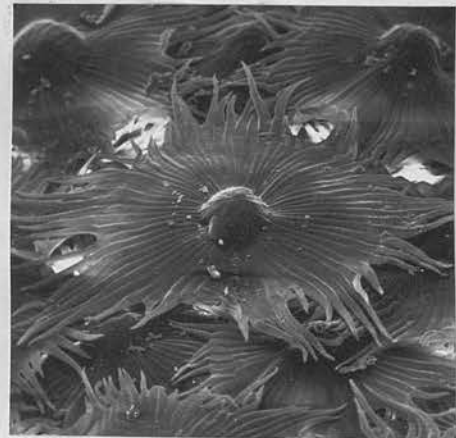
2.3. Inflorescence

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 descrip-
tively 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 chamae-phytes. The apex of each leafy shoot is terminated by an inflor-escence, 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.

Fig. | A-J. Inflorescence types. Inflorescence not terminating growing point of branch (Type I).

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.

♀	flower sessile	ᴗ	morphologically distinct bract
♀	flower pedicellate	◊	leaf
▨	vegetative axis	↑	direction of vegetative growth
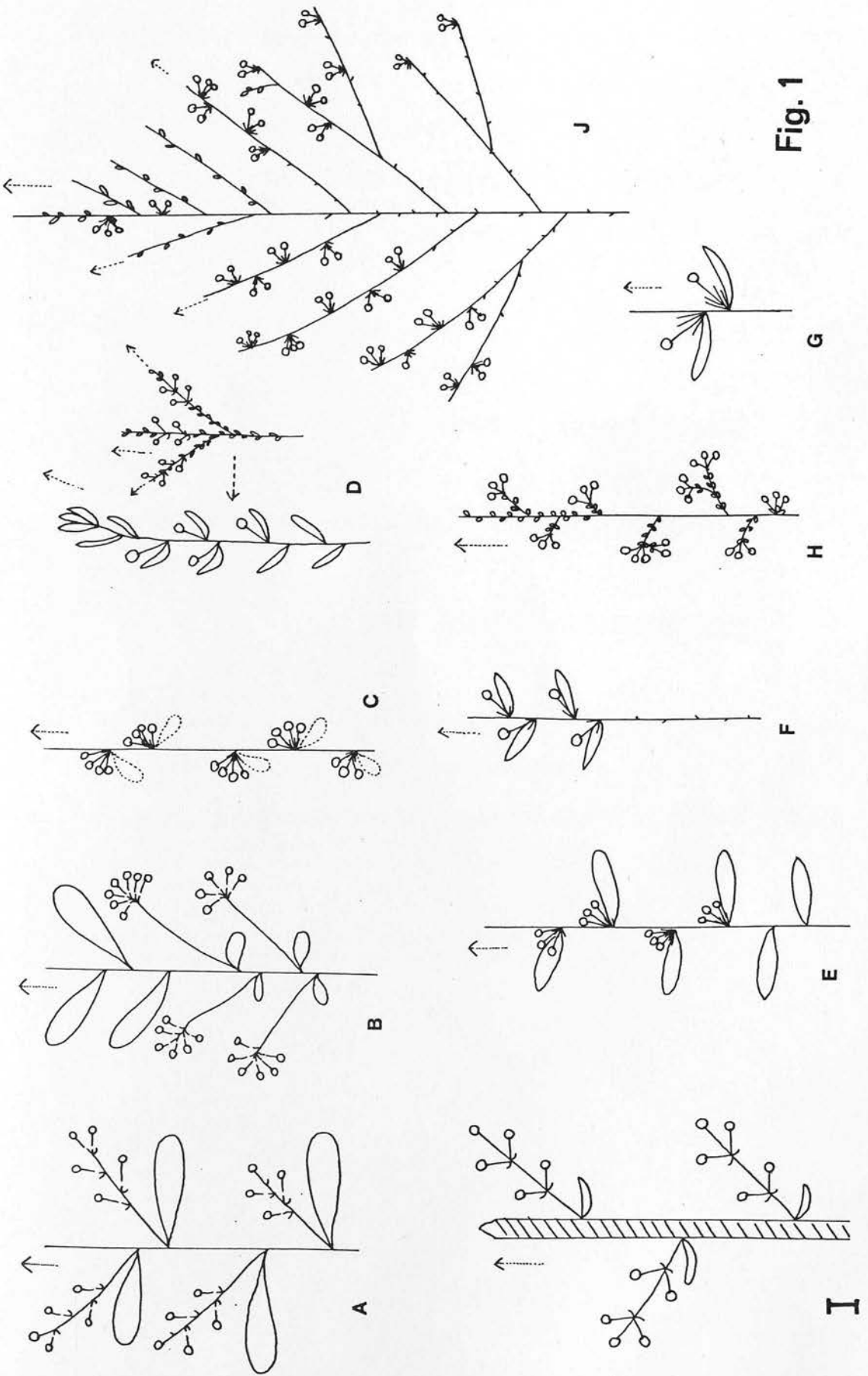
Fig. 1

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.

D, Da. *Daphne mucronata*. Subumbellate, axis later elongating.

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.
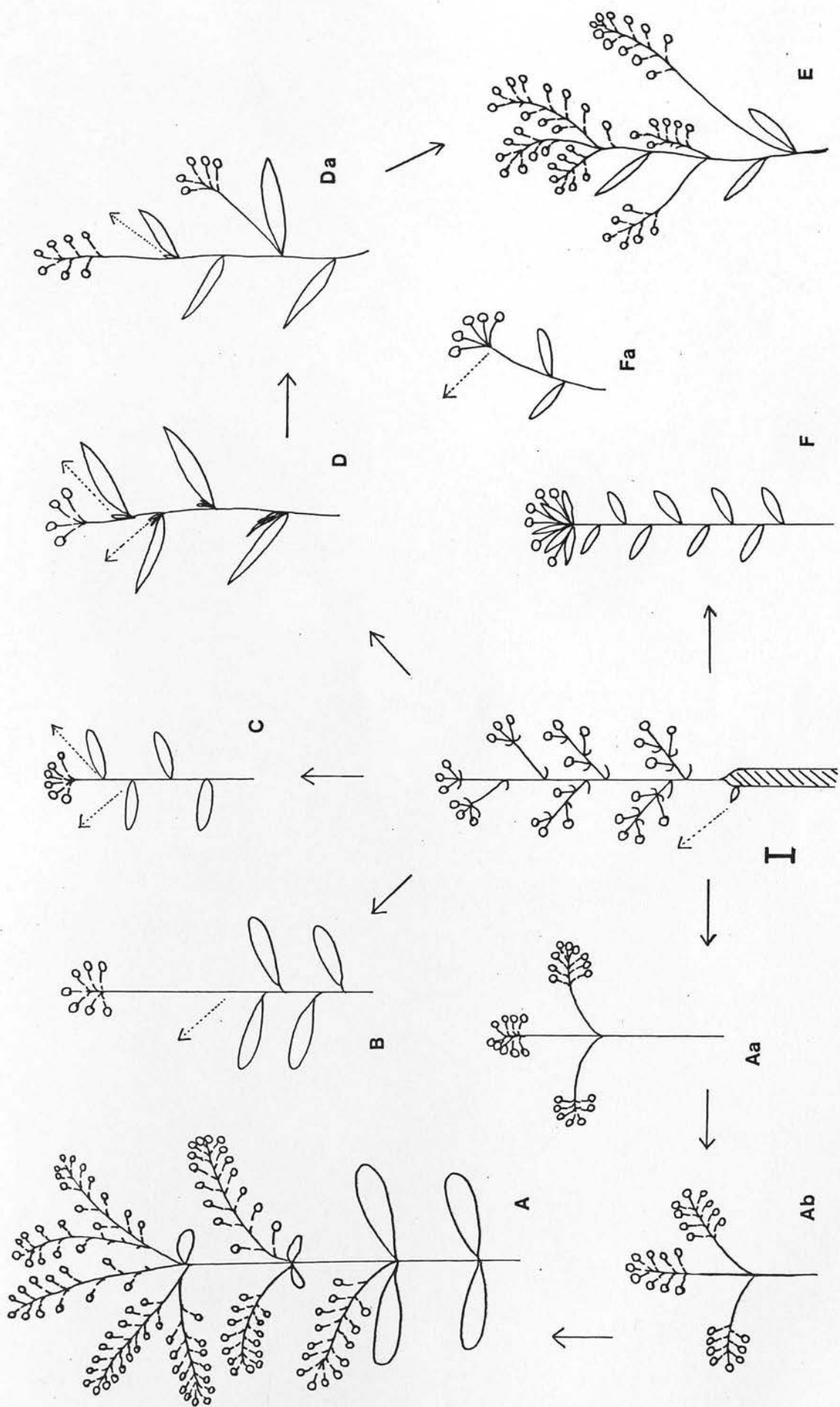
Fig. 2

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'.
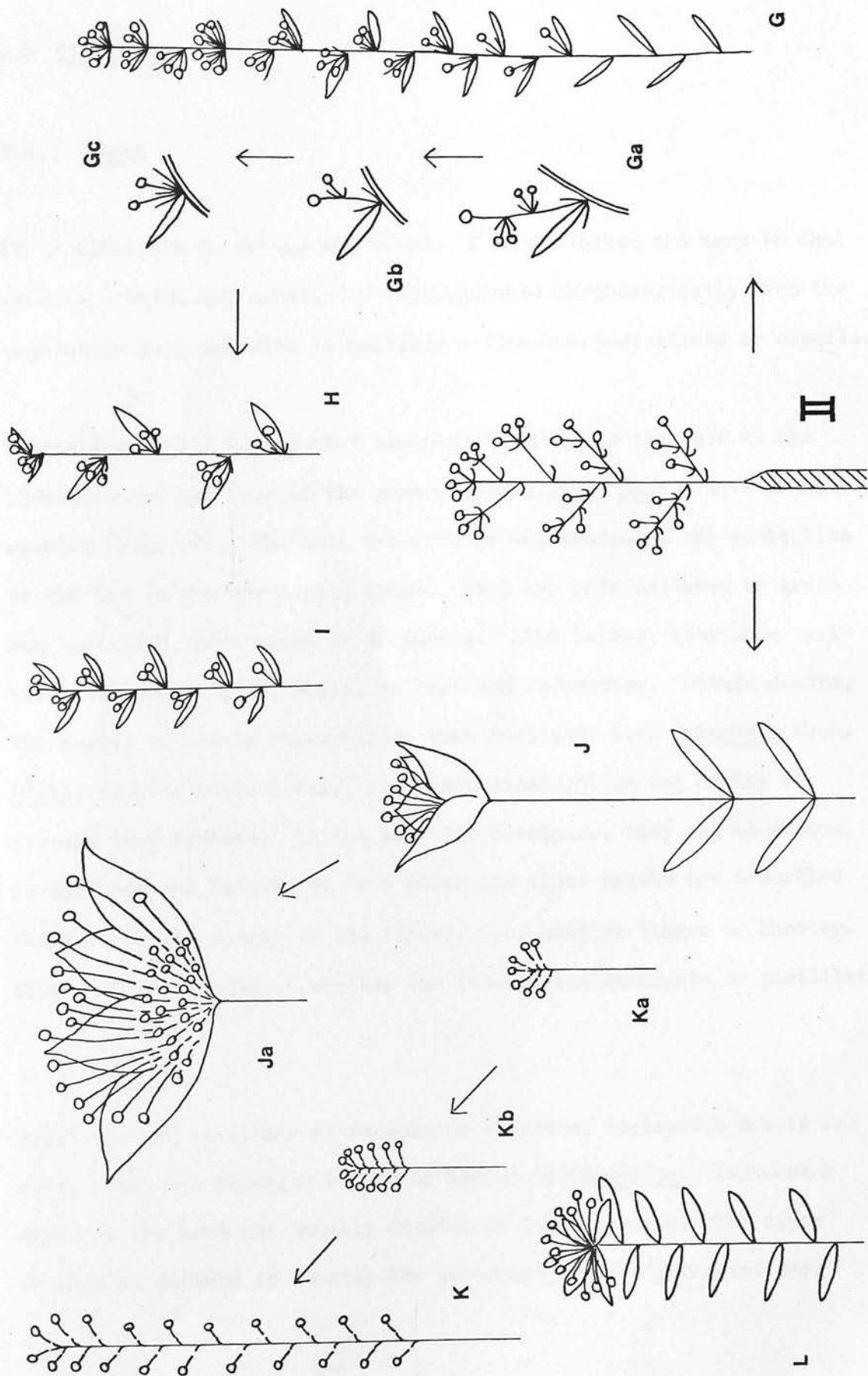
Fig. 3

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 vari-
ation 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 infundi-
buliform, pistillate flowers are shorter and urceolate. This is partly
correlated with the degree of spread of the perianth lobes and the in-
crease 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. 58Hb). 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 <u>Wikstroemia</u> 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 <u>Thymelaea hirsuta</u> and <u>T. procumbens</u>.

The persistence of the perianth after flowering appears to be related to the nature of the fruit. The fleshy berries of <u>Daphne</u> 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 membraneous base. In the latter case, the tube becomes constricted and deciduous above the ovary.

<u>Flower colour and odour</u>: 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 <u>Stellera chamaejasme</u> subsp. <u>chamaejasme</u>. 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 <u>Thymelaea</u> 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 exserted, 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).

n. Daphne giraldii. Tri-nucleate grains.
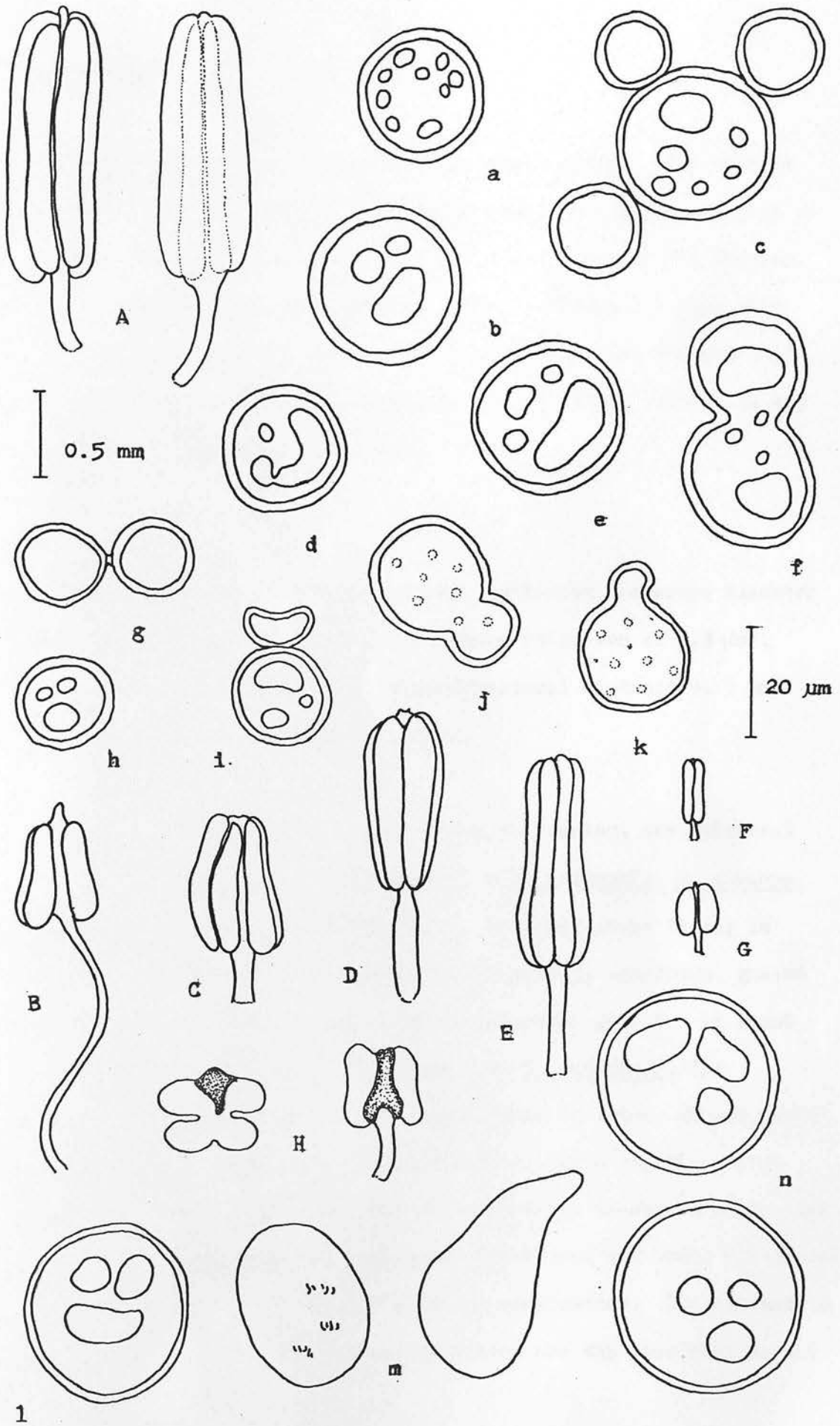
FIG. 4

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 dia-
meter 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 inter-
poral distance of 5 μm. Exine moderately thin to fairly thick (2
-6.5 μm) It is interesting to note that both P. ericoides 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.

TABLE 1 POLLEN CHARACTERS

SPECIES	EQUATORIAL DIAMETER (μm)				% ABORTIVE POLLEN (not stained)	% FERTILE POLLEN (stained)	% MISSHAPED GRAINS
	SMALL GRAINS		LARGE GRAINS				
	MEAN	RANGE	MEAN	RANGE			
Daphne arbuscula	20	16-22	27	25-30	12	88	10
D. blagayana	24	16-25	36	32-40	15	85	5
D. cneorum	22	20-25	30	28-32	18	82	15
D. giraldii	30	26-33	35	35-44	1	99	5
D. gnidium	23	22-25	33	30-35	7	93	5
D. laureola	30	26-32	46	42-47	3	97	5
D. longilobata	20	16-25	32	29-33	12	88	15
D. mezereum	20	18-25			5	95	5
D. odora	16	11-20	24	20-27	13	87	20
D. oleoides	26	22-29			5	95	5
D. rodriguezii	23	19-26			6	94	5
D. sericea	26	20-27	30	30-35	14	86	5
Thymelaea argentata	23	20-27			5	95	5
T. dioica subsp. dioica	26	22-30			18	82	5
T. hirsuta	23	20-26			10	90	2
T. lanuginosa	27	23-30			7	93	5
T. lythroides	26	26-28			10	90	5
T. microphylla	16	13-20	27	25-32	12	88	7
T. ruizii	27	22-30			10	90	5
T. sanamunda	22	20-27			5	95	5
T. tartonraira subsp.							
argentea var. argentea			22	18-25	15	85	5
tartonraira var. tartonraira	10	9-16	23	20-27	13	87	10
" var. transiens			20	18-25	10	90	5
valentina	16	10-16	20	20-25	15	85	5
T. thesioides subsp.							
thesioides	27	25-30	33	31-35	15	85	5
elliptica	20	18-22	27	25-30	13	87	5
T. tinctoria subsp. tinctoria	28	26-28	33	30-35	15	85	5
T. villosa	24	22-27			15	85	5
T. virescens	16	16-20	23	20-33	20	80	10
T. virgata subsp. broussonetii	16	13-18	23	20-25	15	85	5
Sect. Ligia							
T. aucheri	23	19-24	41	35-44	6	94	2
T. cilicica	22	18-22	35	30-44	24	76	10
T. gussonei	23	20-24	35	30-36	0	100	0
T. mesopotamica	18	16-20	33	30-41	12	88	0
T. passerina	25	20-25	39	33-44	0	100	0
T. salsa	22	19-22	35	29-36	11	89	0
Diarthron linifolium	23	20-26			15	85	2
D. vesiculosum	13	11-13	16	15-16	10	90	2
Passerina ericoides	20	20-27	33	30-36	7	93	5
P. filiformis	23	20-25	33	30-36	7	93	5
P. galpini	24	20-25	33	31-34	7	93	5
P. montana	28	25-30	33	30-36	7	93	10
P. paleacea	30	27-30	33	30-36	7	93	5
P. rigida	27	25-28	33	33-46	5	95	5
P. vulgaris	30	30-33	36	35-50	5	95	5
Pimelea spectabilis			56	46-75	15	85	5
Dendrostellera lessertii	13	11-16	23	20-25	15	85	7
D. stachyoides	13	13-16	20	18-22	20	80	10
Stellera chamaejasme	16	14-18	23	22-25	12	88	5
Stelleropsis antoninae	24	22-26			10	90	5
S. iranica	20	18-22	30	30-35	15	85	5

Discussion

The results indicate that pollen stainability in all, with the ex-
ception 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 (T. cilicica) 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 approx-
imately 50% of these were small grains. Abortive pollen was 24% and
there was also a high proportion of misshapen grains. Pollen di-
morphism 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. <u>Stellera chamaejasme</u>. Stigma shallowly furrowed / centrally depressed.

B. <u>Thymelaea sanamunda</u>. Style subterminal /sublateral.

C. <u>Dendrostellera lessertii</u>. Stigma conical-ovoid, covered with pollen.

D. <u>Thymelaea dioica</u>. Style terminal.

E. <u>Thymelaea cilicica</u>. At level of lower (inner) whorl of stamens. Pollen spheroidal, periporate, dimorphic, with small grains staining deeply.

F. <u>T. cilicica</u>. At level lower down in perianth tube.

All   x 155.

A

B

C

D

E

F

Pl. 3
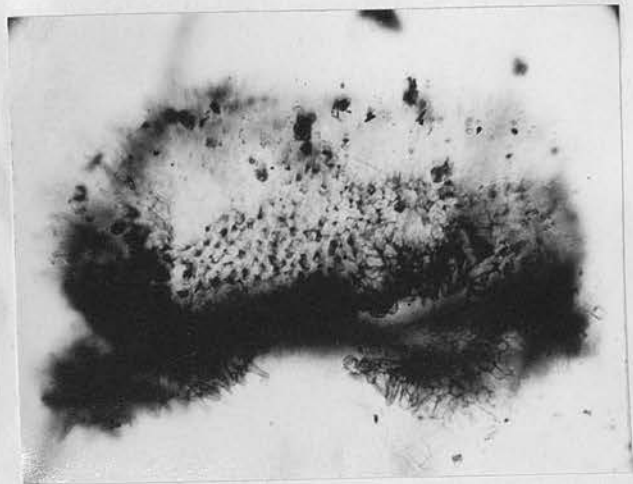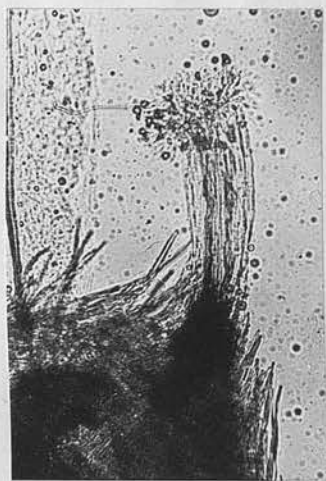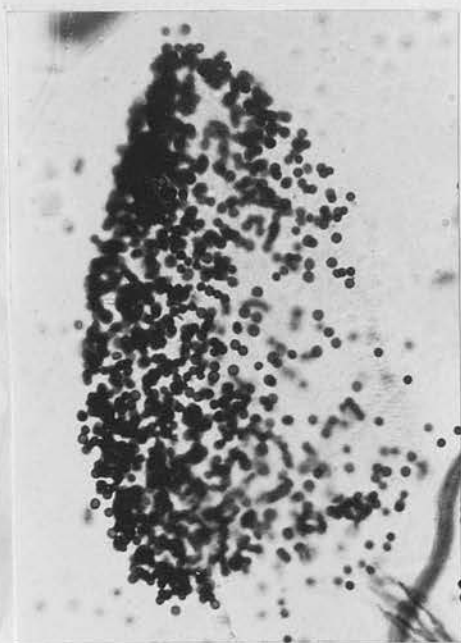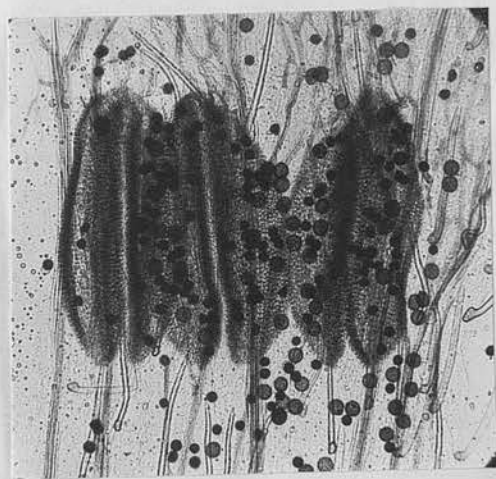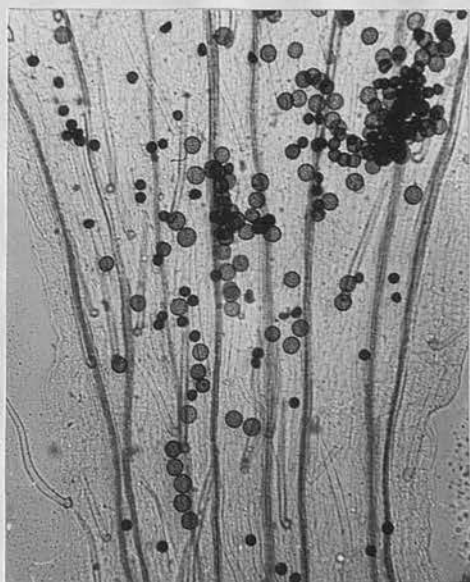
PLATE 4. Photomicrographs of some pollen grains.

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.
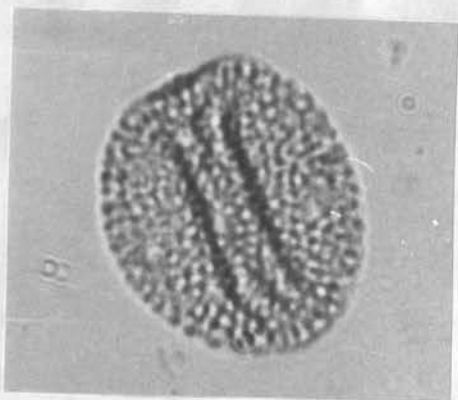
A
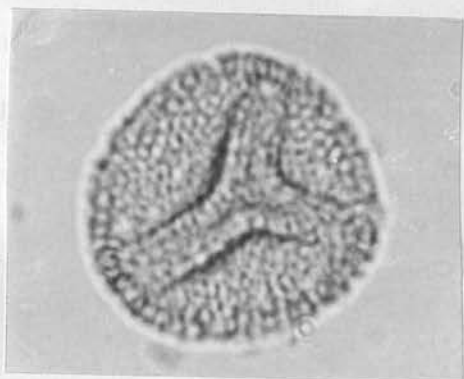
B
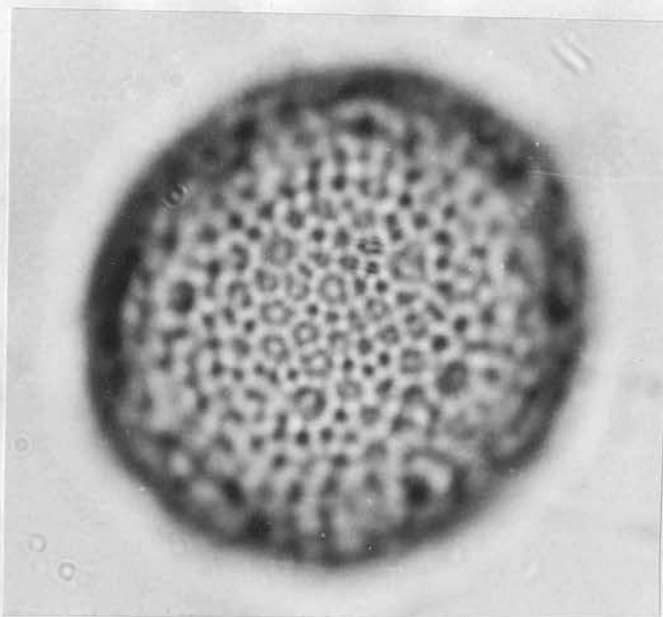
C

D

Pl. 4

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 5 F). This can be compared with a narrowly spaced grouping as found in Wikstroemia chamaedaphne (Plate 7 E), 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 5 F),
T. microphylla.
Thymelaea Sect. Chlamydanthus — T. coridifolia.
Dendrostellera 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 6 H), T. tartonraira subsp. argentea (Plate 6 B); 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 6 F) 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
5 C), T. gussonei, T. mesopotamica and T. passerina. They are more
widely spaced and obtuse-conical in the two perennials, T. aucheri
(Plate 5 D) 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 inter-
mediate between Types B and C.

Type D: the 'warts' are more prominent, the lumina small and hexa-
gonal 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 _Thymelaea_ 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 pro-
ject 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 struct-
urally 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-acetolyzed 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 relation-
ships. 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 <u>Penaea mucronata</u> (Plate 7 H) 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 <u>Elaeagnus angustifolia</u> (Plate 7G), the grains are 3-colporate, the colpi being very short, oblate (24 x 40 μm), goniotreme 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 <u>Thymelaea</u> at sectional level. Dimorphic grains in <u>T. cilicica</u> 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. Thymelaea salsa. x 5750.

D. T. aucheri. x 4750.

E. T. thesioides subsp. thesioides. x 5750.

F. T. hirsuta. x 5750.

A

B

C

D

E

F
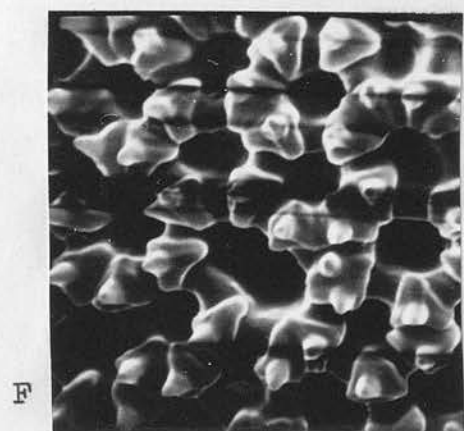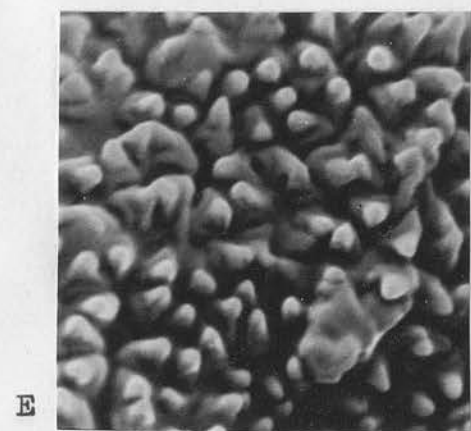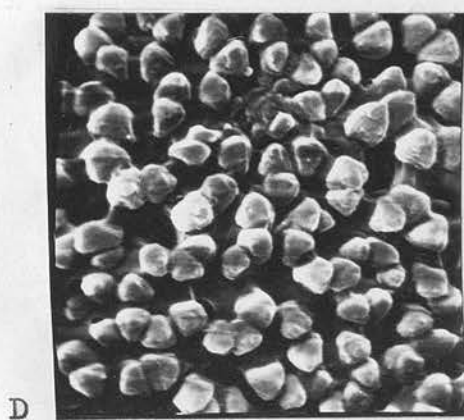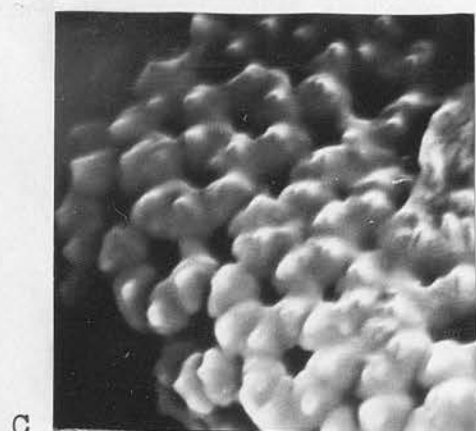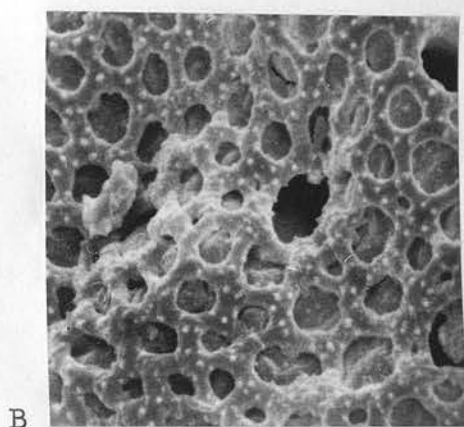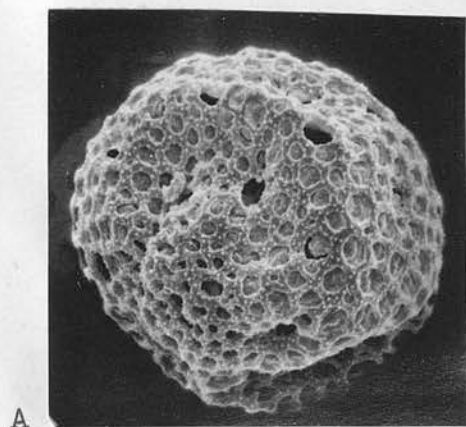
SCANNING ELECTRON
MICROGRAPHS
OF POLLEN

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.

B. Thymelaea tartonraira subsp. argentea var. argentea. x 7100.

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.

A

B

C

D

E

F

G

H
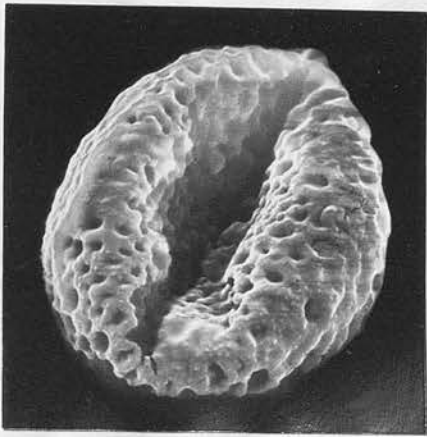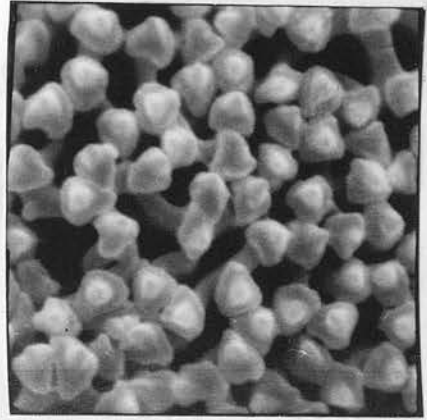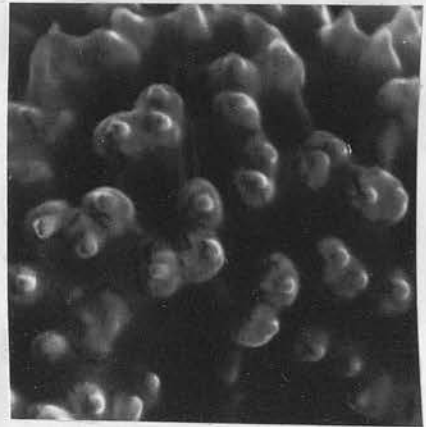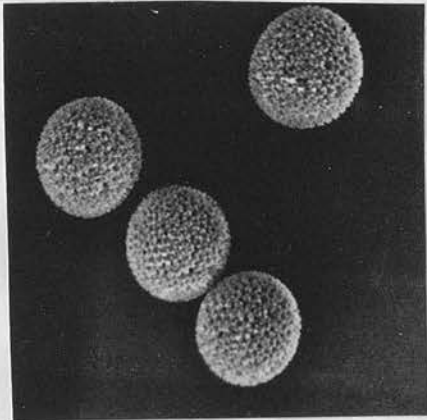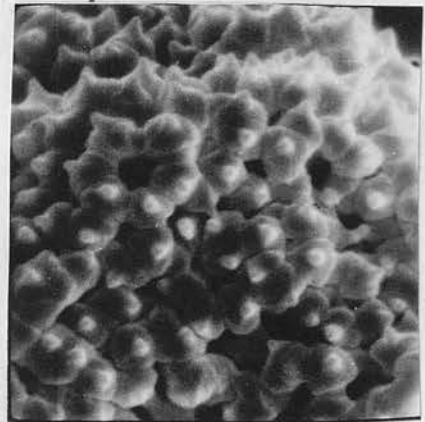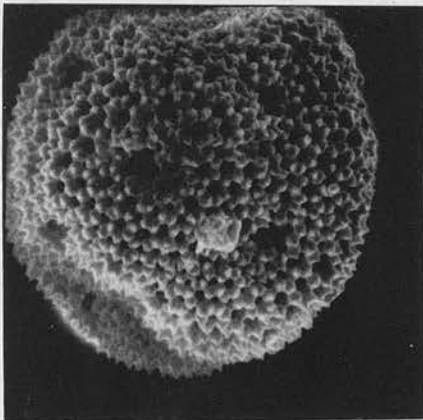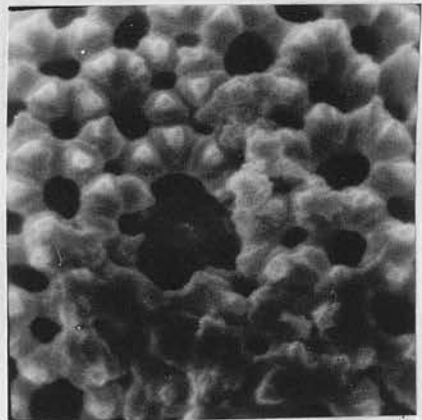
PLATE 6

PLATE **7**. Scanning electron micrographs of pollen. All showing
wall detail except when indicated.

A. <u>Daphne gnidium</u>. Whole grain, showing ridge on one face.
x 2150.

B. <u>D. gnidium</u>. Detail of ridge. x 4750.

C. <u>Dendrostellera lessertii</u>. Whole grain. Apertures irregular,
mostly   shaped. x 2050.

D. <u>D. lessertii</u>. x 6000.

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

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

G. <u>Elaeagnus angustifolia</u>. Whole grain. x 1050.

H. <u>Penaea mucronata</u>. Whole grain. x 1450.

PLATE 7
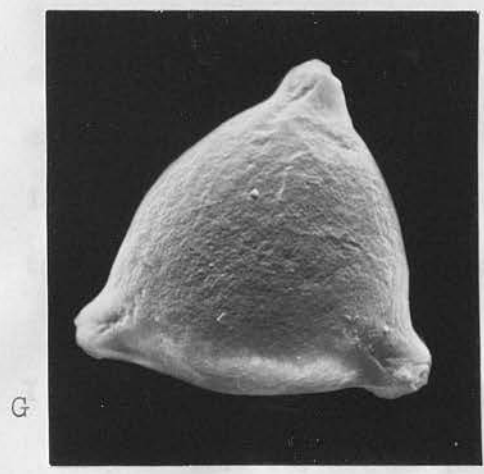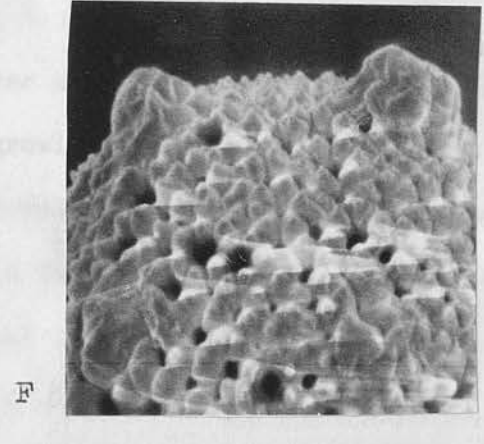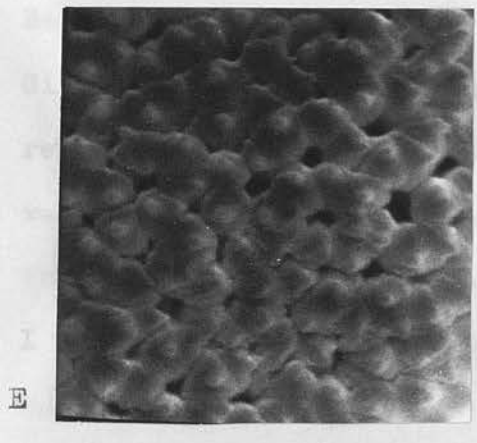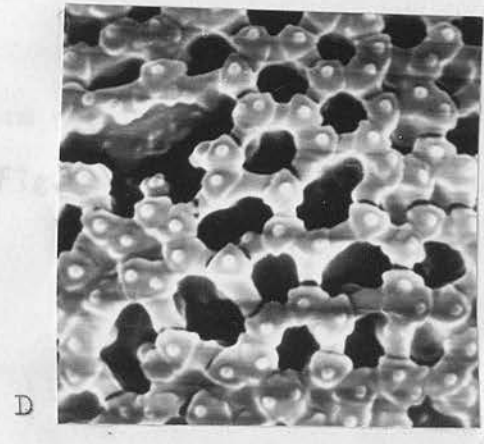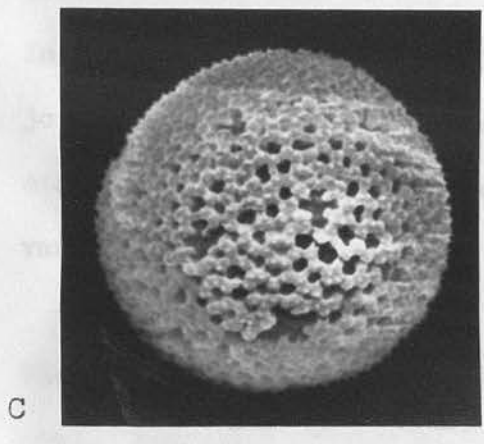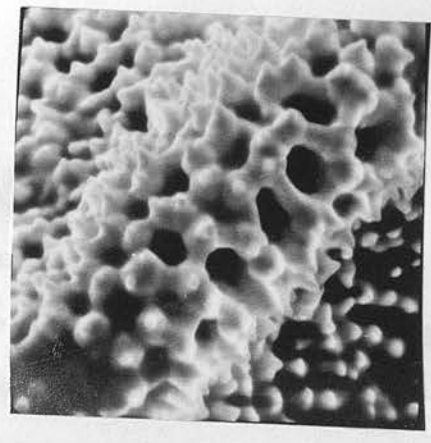
2.4.4 Hypogynous disc/scales

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 ob-
served 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 argu-
ment. 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 sur-
veyed. 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 recep-
tacle as suggested by Gerber (1899).

I would consider the hypogynous disc or scales as a structure origin-
ally 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-ovulate. The shape is
cylindrical-ovoid, subovoid or globose. It remains pubescent, hir-
sute, 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 it is almost absent, the stigmas are often des-
cribed as sessile. It remains terminal (Plate 3 D) but in some species
of Thymelaea it becomes subterminal/sublateral (Plate 3B). In Passerina
it is characteristically lateral or sublateral. The style position
seems to be a diagnostic feature for some species but it is also re-
lated 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 some-
times 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 lessertii 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 8 B). 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 membraneous. 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 endo-
sperm 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, membraneous, 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, membraneous 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.

Thymelaea

Fruit dry, indehiscent, one-seeded, naked or enclosed in persistent
perianth at maturity, ovoid or conical-pyriform. Pericarp thin, mem-
branous 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.

Passerina

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.

D. _Thymelaea gussonei_.
Seed surface x 1250.

E. _Thymelaea virgata_ subsp.
virgata. Seed surface x 1500.

B. _Daphne longilobata_. Perianth
splits at base as fruit matures,
later deciduous. x 1.
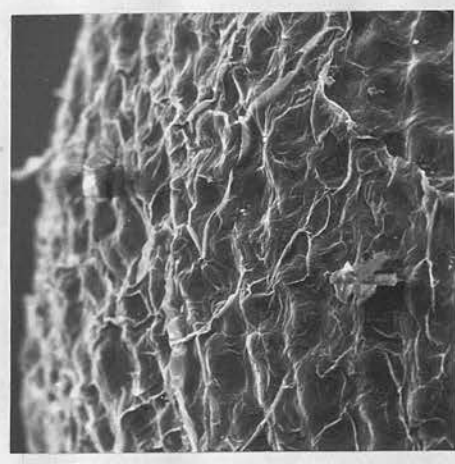
C. _Thymelaea tartonraira_ subsp.
argentea. Seed surface x 650.

PLATE 8 A. _Thymelaea tinctoria_ subsp.
tinctoria seedlings. Early thickening of
tap roots indicated by arrows x 1/3.

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

dishes. Germination was observed over a six week period, and stages recorded by drawings.

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. Roothairs 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, aften 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. gnidium, 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 8 A).

Table 2.0 Some observed germination periods

Species	Proportion of germination (%)	Time course of germination (days)
Daphne alpina	30	112
Daphne caucasica	30	43
Daphne gnidium	60	12
Daphne longilobata	30	15
Diarthron vesiculosum	10	21
Thymelaea passerina (seed less than 3 mths old)	60	42
Thymelaea passerina (seed nearly 2 years old)	50	13

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. <u>Thymelaea passerina</u>

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 seed-
       coat 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.
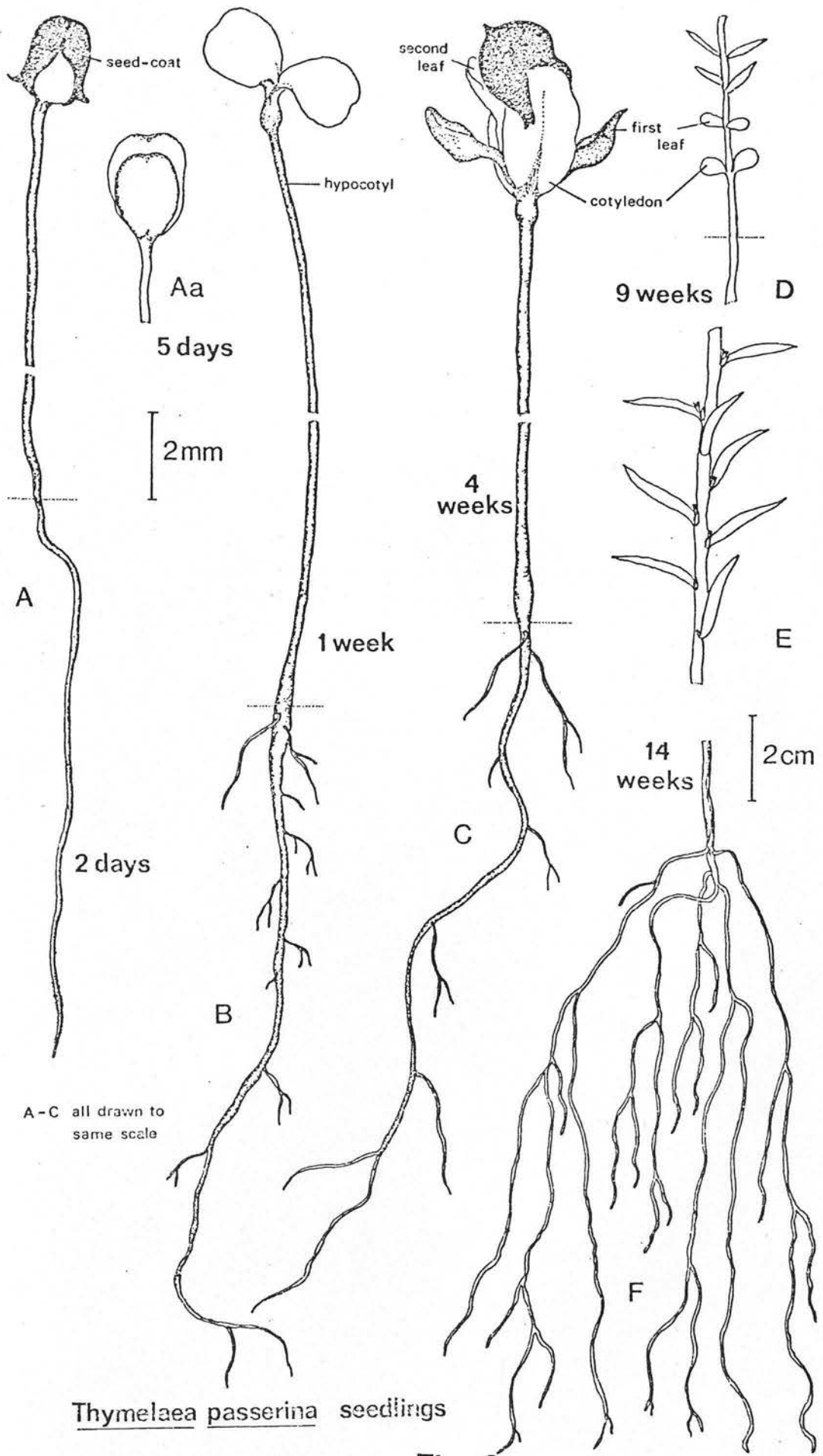
Thymelaea passerina seedlings

Fig. 6

Fig. 7. <u>Daphne longilobata</u>

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.

seed-coat

5 mm

hypocotyl

A

cotyledon

B

2 weeks

first leaf

first leaf

second leaf

first leaves

cataphyll

C

first leaves

D

1 cm

3½ weeks

A - D all drawn to same scale

E

14 weeks
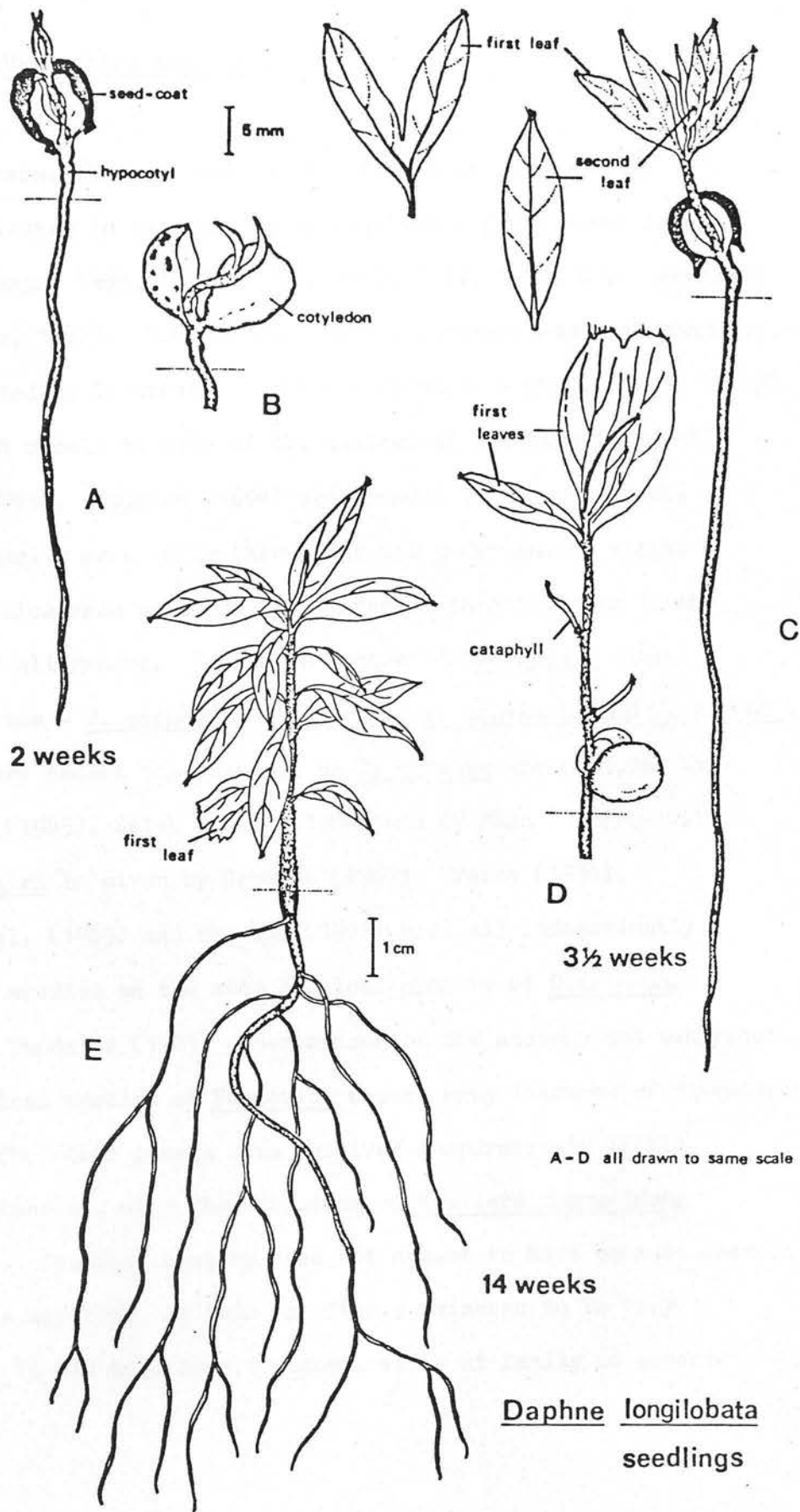
Daphne longilobata
seedlings

Fig. 7

CHAPTER III   Vegetative Anatomy

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 comprehen-
sively 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),
Nechayeva 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.

Janssonius (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-HC1 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

modified tetracytic

after

anisocytic

cruciferous
|
after
Vesque, 1889

Metcalfe, 1961

hexacytic,
|
after
Tomlinson, 1969

anomocytic

after Metcalfe & Chalk,
1950
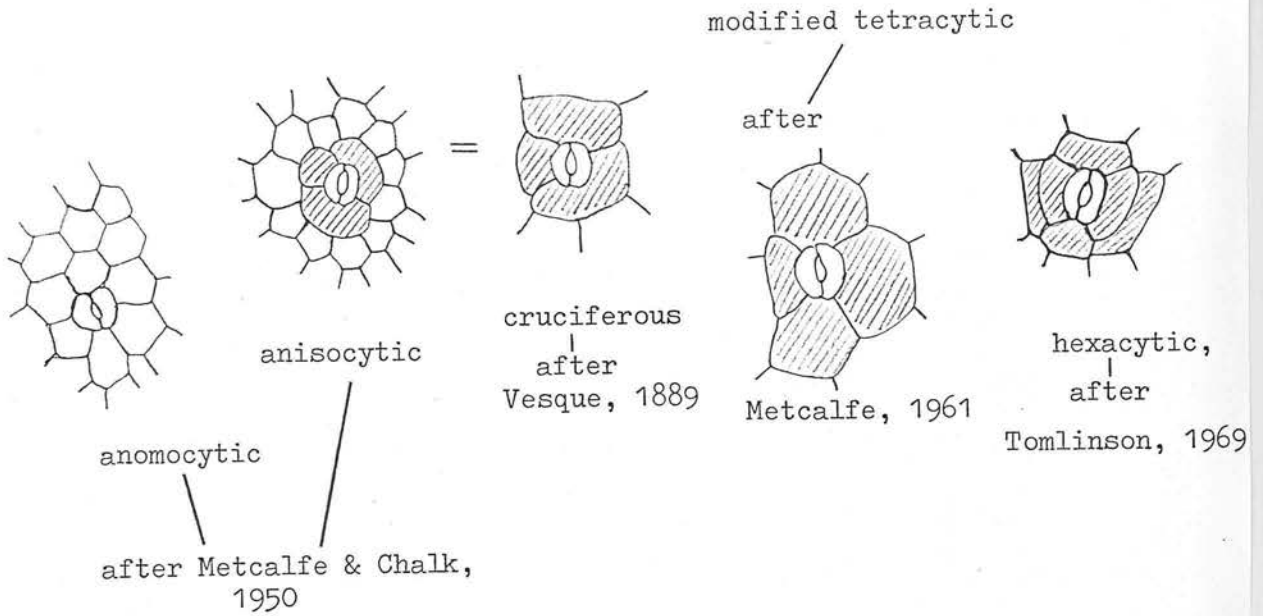
subsidiary cells shaded

Type A: anomocytic (irregular-celled, <u>ranunculaceous</u> 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, <u>cruciferous</u>) 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.

<u>Development of stomata</u>

This was followed only for two species, <u>D. gnidium</u> and <u>T. passerina</u>, 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 wide-
spread 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, 25,28/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. 28B), 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. 15C). 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 unlignified sclerenchyma cap not extending to epidermis. Internal phloem absent. Vascular bundles at midlaminar region varying in number according to species. Leaf margin of compact chlorenchyma (Fig. 28 E). 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 Thymelaea. 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 rossetii (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. 28 Ia, 27 D). Adaxial
epidermal cells (20-150 μm thick) often larger than abaxial cells
(26-58 μm), sometimes appearing periclinally subdivided because of
hardened mucilage (Fig. 28 I). Stomata sunken (Figs. 28 G-H, Ia; 27 D-E)
or level with epidermis (Figs. 27 F, 28 F). 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. 25 A & 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 out 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 eucampto-dromous; 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^os. 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 <u>Wikstroemia chamaedaphne</u> 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. <u>WIKSTROEMIA</u> (Figs. 13, 27) - based only on <u>W. chamaedaphne</u>.
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 μm thick. Adaxial and abaxial cuticle 5-8 μm thick, ridged over mucilage idioblasts (Fig. 29 B). Adaxial and abaxial epidermal cells 29-35 μm thick, stomata slightly sunken or level with inner epidermal walls. Palisade 2-layered on both sides, 55-70 μm 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. 24 D, 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. 27 G), 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. 27 H). 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. 29 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 <u>D. linifolium</u>. 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 2^0 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. 1^0 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.

7. Hypodermal fibres absent.

8. Bundle-sheath cells without tannin.

Mature leaf (Fig. 30 D).

1. Leaf more deeply grooved.

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Table 3. Passerina. Some anatomical characters of the leaf

			Species		
	P. filiformis	P. montana	P. paleacea	P. vulgaris (mature leaf)	P. vulgaris (young leaf)
No. of vascular bundles in mid-lamina	7	9	4	3	3
No. of palisade layers	1 (-2)	1-2	1-2	1-2	1
Tannin in bundle sheath absent	-	x	-	-	x
present	x	-	x	x	-
Tannin in abaxial epidermis absent	-	-	-	-	x
present	x	x	x	x	-
Hypodermal fibres absent	x	x	-	-	x
present	-	-	x	x	-
Vascular bundle sclerenchyma not interrupting palisade	x	x	-	-	x
interrupting palisade	-	-	x	x	-

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 invaginated 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 unlignified, 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. <u>Dendrostellera lessertii</u>. Upper third of leaf. Sclereids
moderately developed at apex and at vein endings.

Aa. <u>Dendrostellera lessertii</u>. Lower third of leaf.

B. <u>Thymelaea ruizii</u>. Sclereids weakly developed at apex and
throughout leaf.

C. <u>Thymelaea dioica</u>. Sclereids also weakly developed at apex.

D. <u>Diarthron vesiculosum</u>. Midrib slender, sclereids well
developed, aggregated at apex.

E. <u>Dendrostellera stachyoides</u>. Midrib broad, sclereids
conspicuous at apex and also throughout leaf.

A - C x 40.

D - E x 155.
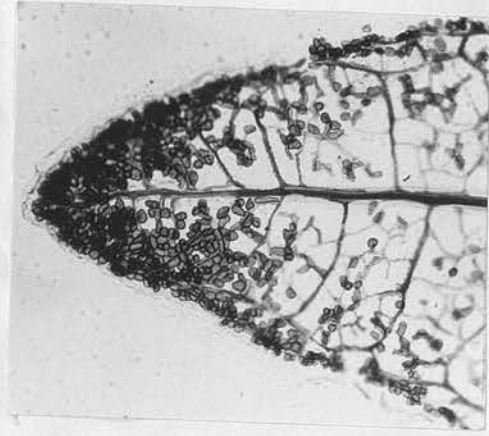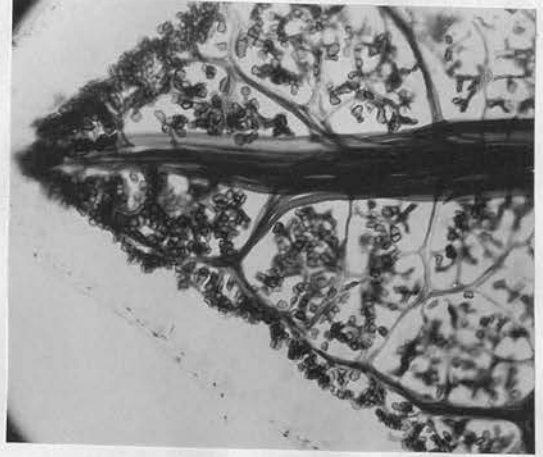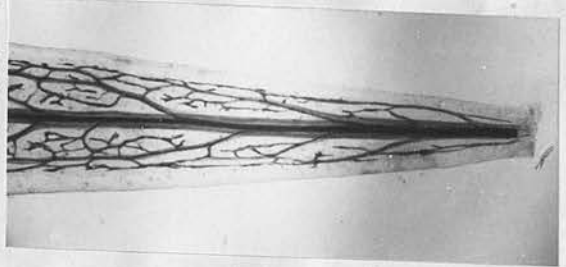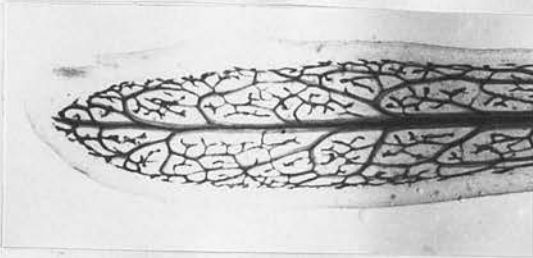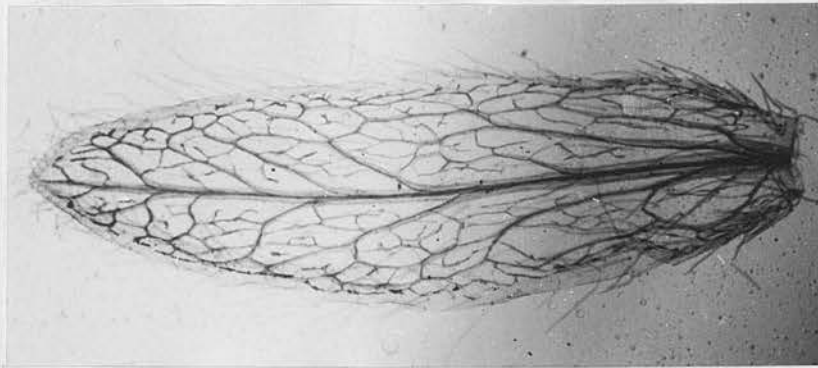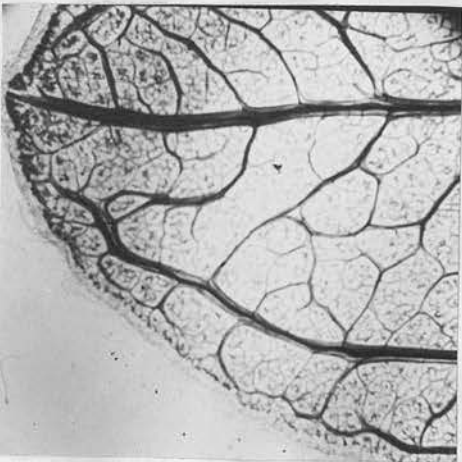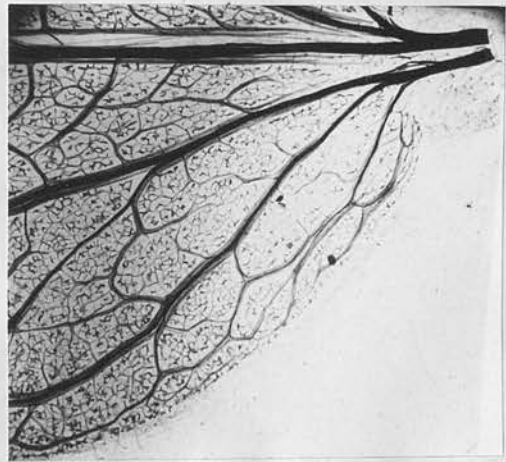
PI. 9

Fig. 9. <u>Thymelaea</u> — leaf epidermal peels.

All drawn x 613.

Sect. <u>Ligia</u> A – Da.

A.   <u>T. aucheri</u> upper.

B/Ba.   <u>T. cilicica</u> upper/lower.

C/Ca.   <u>T. mesopotamica</u> upper/lower.

Da.   <u>T. passerina</u> lower.

Sect. Thymelaea E – Ia.

E.   <u>T. thesioides</u> subsp. <u>thesioides</u> (narrow-leaved form)
            upper.

F/Fa.   <u>T. thesioides</u> subsp. <u>elliptica</u> upper/lower. Unicellular
            hairs on both surfaces.

G/Ga.   <u>T. sanamunda</u> upper/lower.

H/Ha.   <u>T. thesioides</u> subsp. <u>thesioides</u> upper/lower. Ha is from
   costal region; cells elongated and with simple pits.

I/Ia.   <u>T. virgata</u> subsp. <u>virgata</u> upper/lower.

A B Ba C Ca Da E F Fa G Ga H Ha I Ia
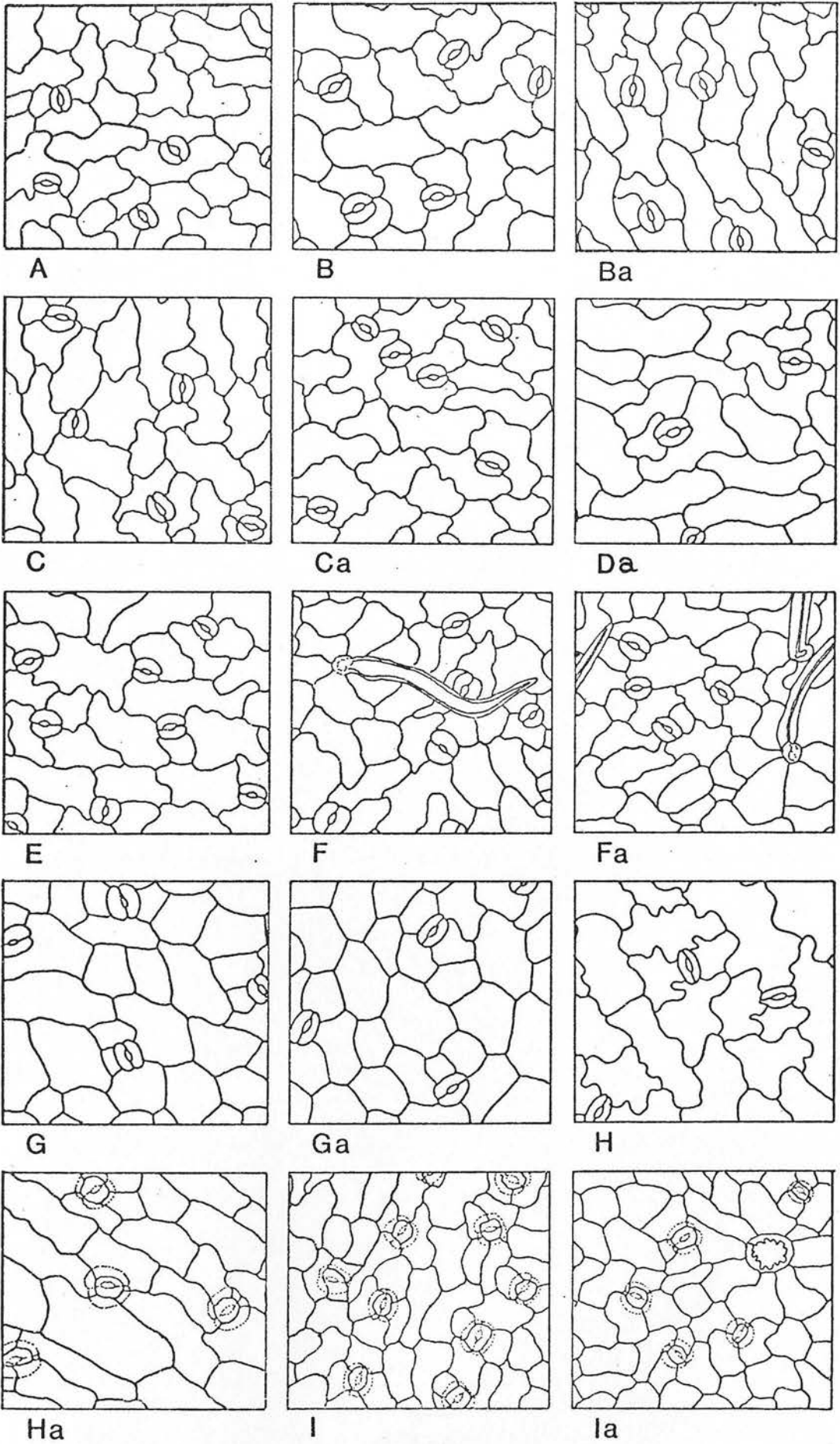
Fig. 9

Fig. 10. Thymelaea - leaf epidermal peels.

All drawn x 613 except F.

A/Aa.   T. villosa upper/lower.

B/Ba.   T. subrepens upper/lower.

C/Ca.   T. virescens upper/lower.

Ga.   T. tartonraira subsp. tartonraira var. tartonraira lower.

H/Ha.   T. tartonraira subsp. thomasii upper/lower.

I.   T. microphylla upper.

Da.   T. coridifolia lower.

E/Ea.   T. calycina upper/lower.

F.   T. tinctoria subsp. tinctoria upper (x 740).

Ja.   T. hirsuta lower.
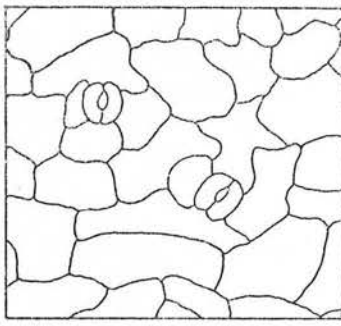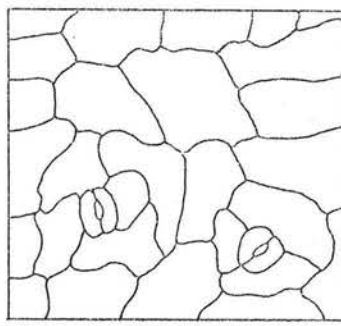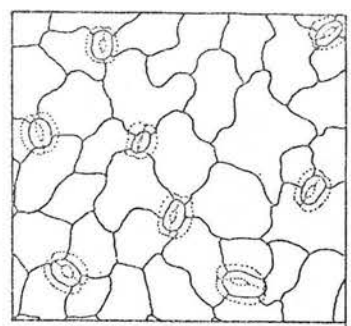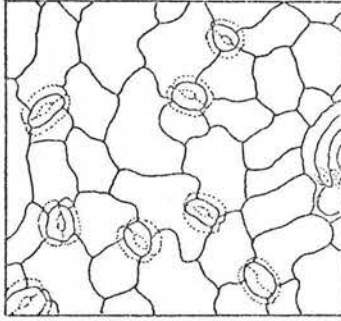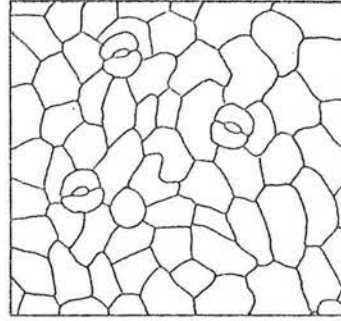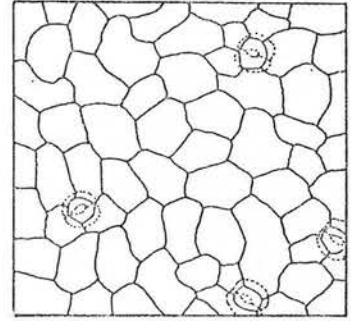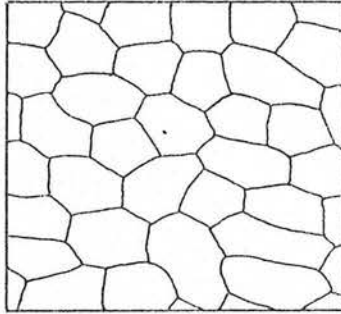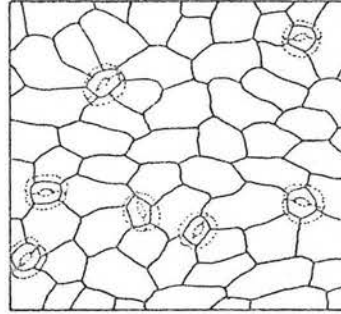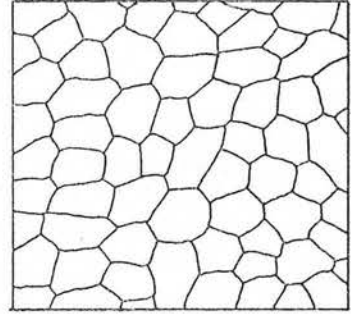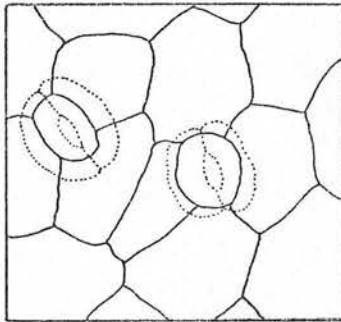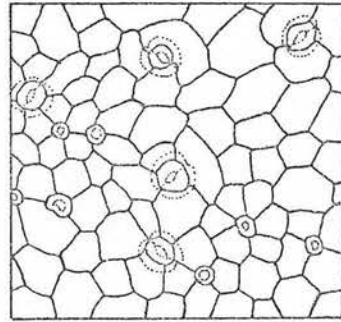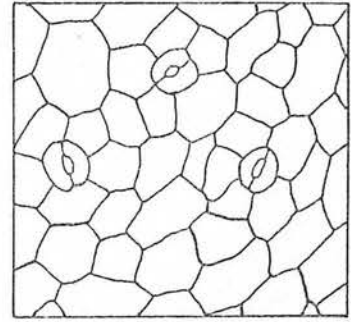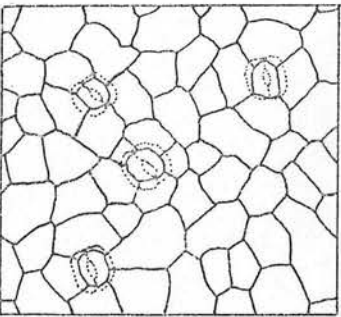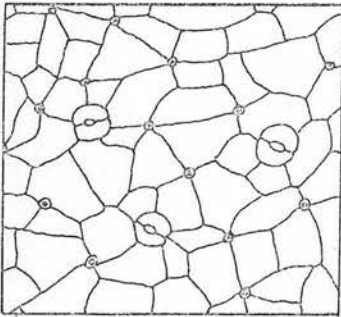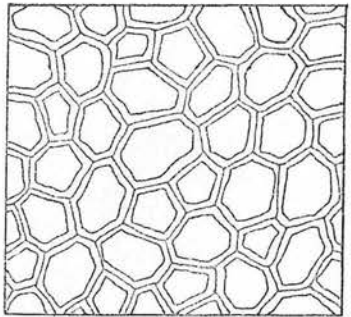
Fig. 10

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.

101
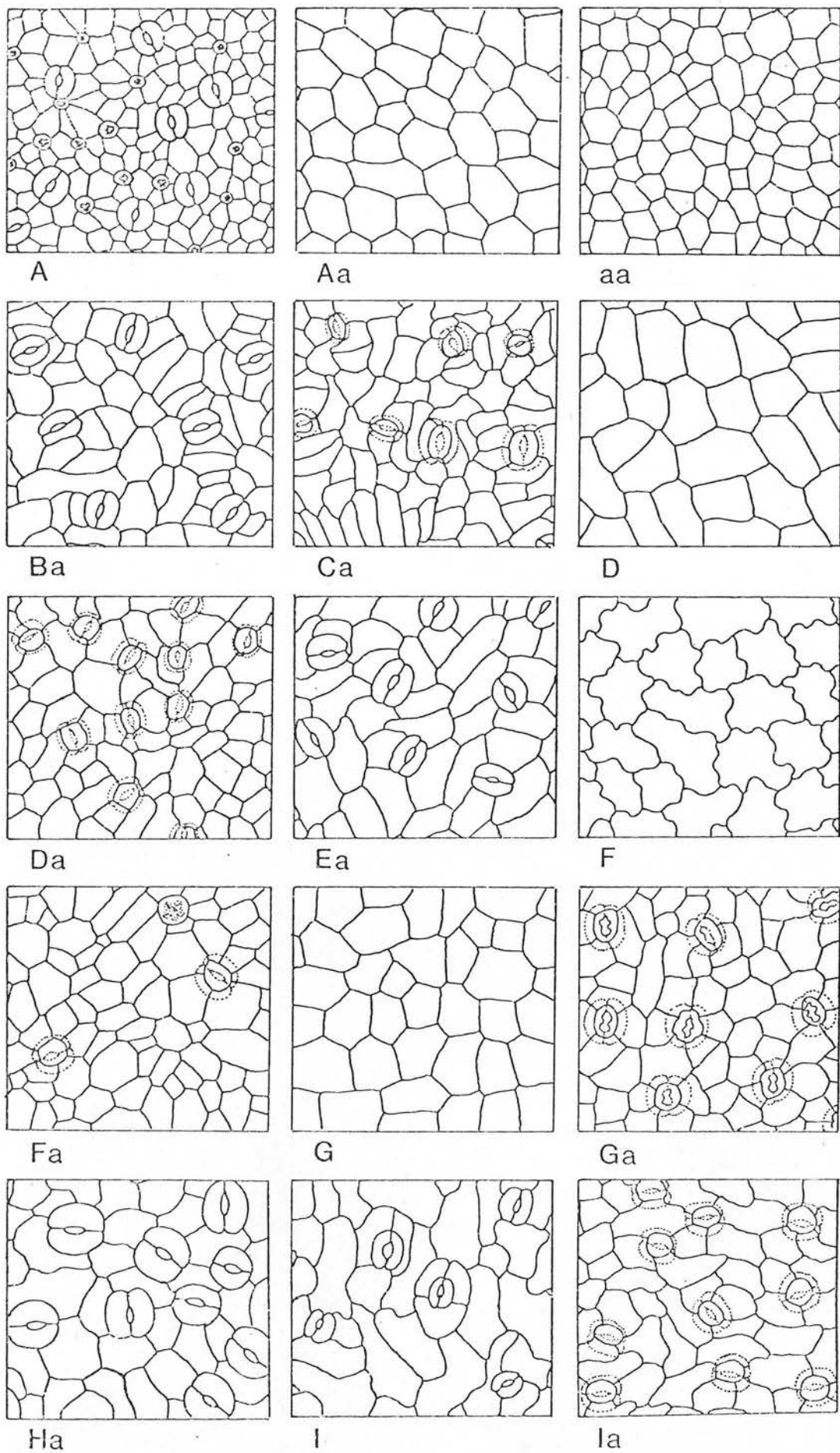
Fig. 11

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
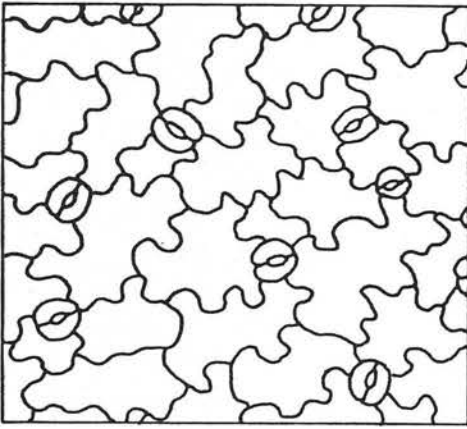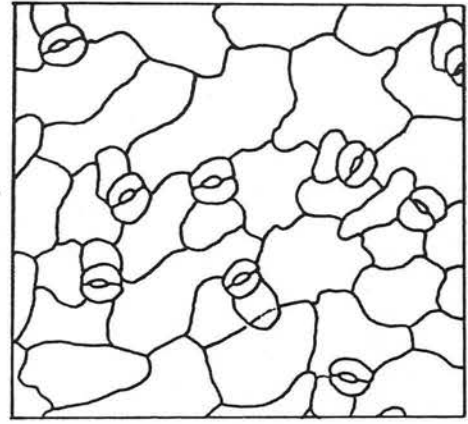
A   Aa
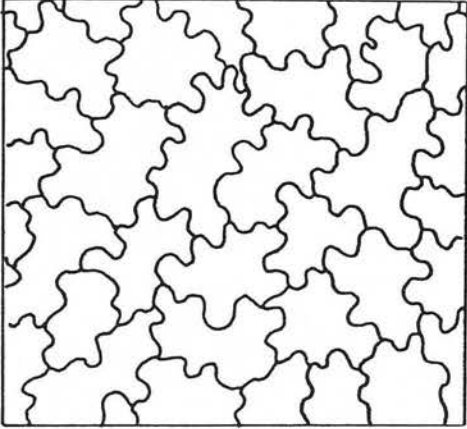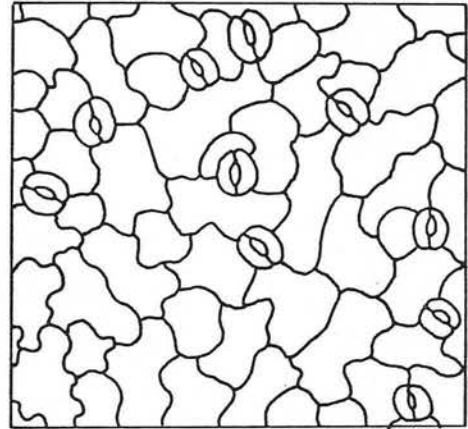
B   Ba
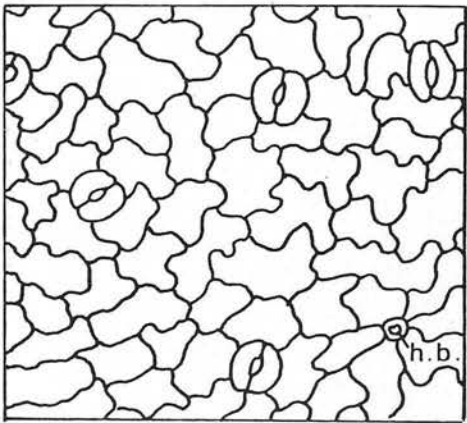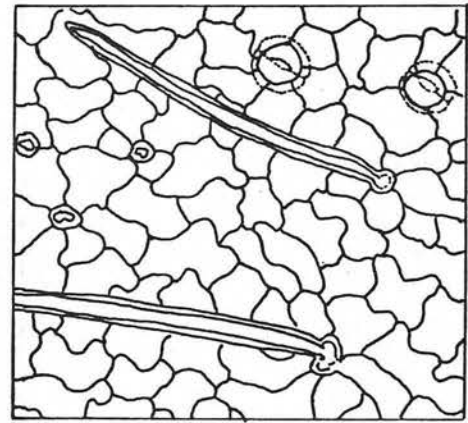
C   Ca
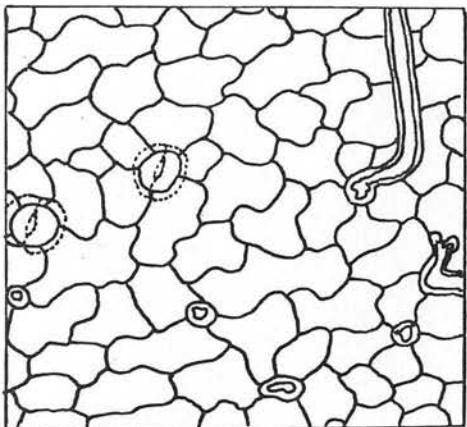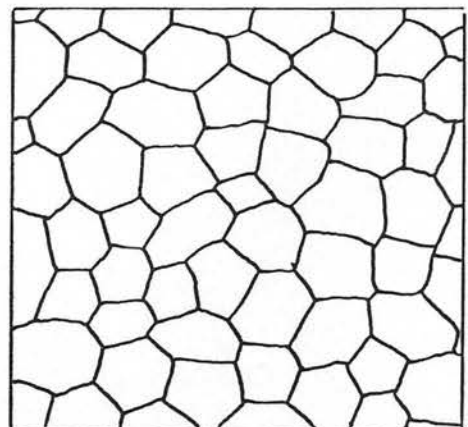
D   Dā

Fig. 12

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.

B/Ba.   D. lessertii (pilose form) upper/lower.   H.B. = hair base.

C/Ca.   D. stachyoides upper/lower.

D/Da.   D. arenaria upper/lower.

Ea.   Stelleropsis magakjanii lower.

F.   Stelleropsis altaica upper.

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

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

I/Ia.   Wikstroemia chamaedaphne upper/lower.
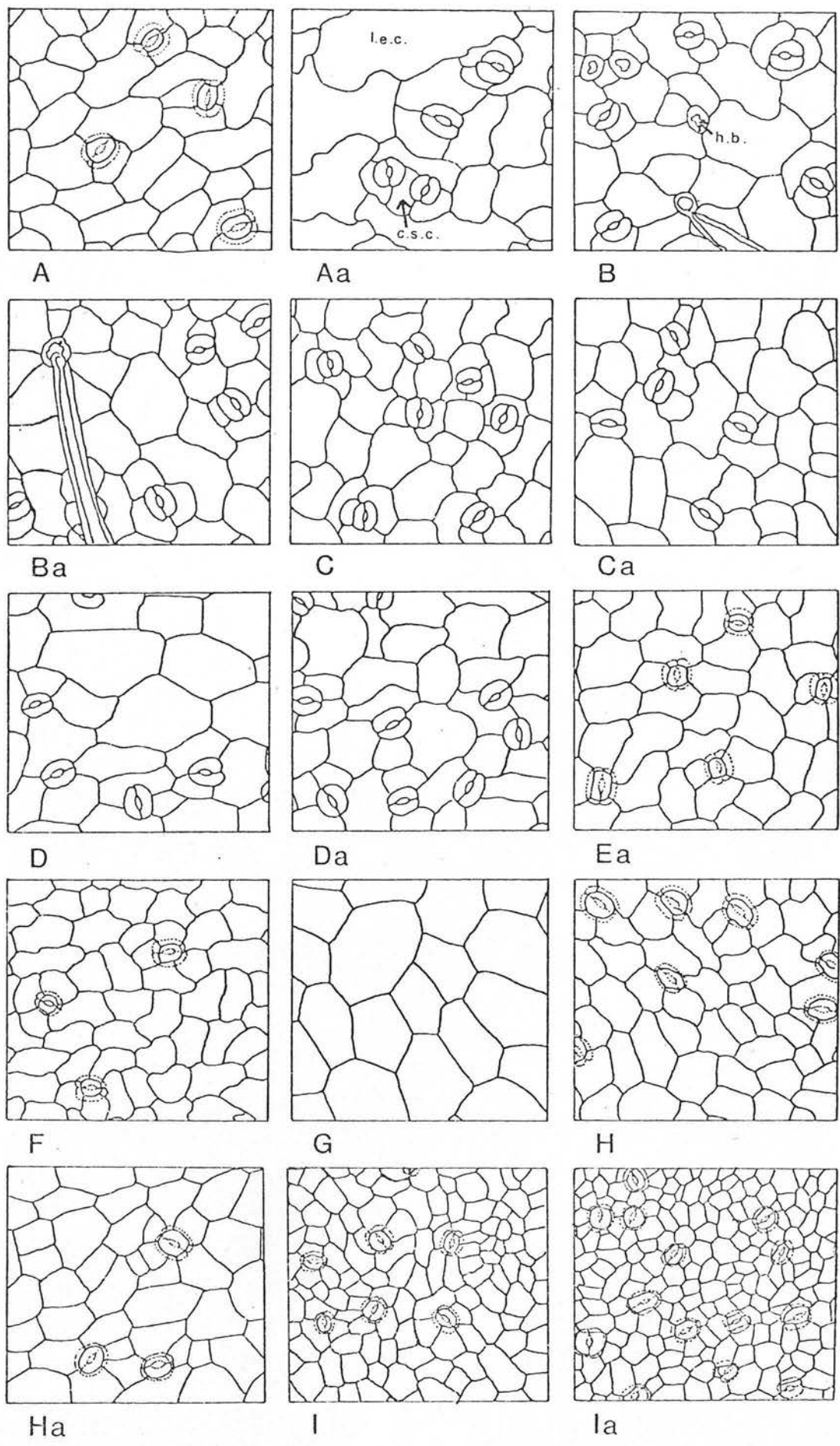
Fig. 13

Fig. 14. Cleared leaves of <u>Thymelaea</u> as seen in surface view.
All x 6.

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

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

C.   <u>T. villosa</u>. Narrowly elliptic, apex ca. right angled. Type 2.

Ca.   <u>T. villosa</u>. Young leaf narrowly elliptic, apex acute. Type 1.

Sect. <u>Thymelaea</u> D - G.

D.   <u>T. thesioides</u> subsp. <u>thesioides</u>. (narrow-leaved form). Linear, apex acute. Type 1.

E.   <u>T. sanamunda</u>. Narrowly elliptic, apex acute. Type 1.

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

G.   <u>T. thesioides</u> subsp. <u>thesioides</u>. Narrowly oblanceolate, apex acute. Type 3.

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

Sect. <u>Ligia</u> H - M.

H.   <u>T. cilicica</u>. Narrowly elliptic, apex acute. Type 1.

I.   <u>T. gussonei</u>. Very narrowly elliptic, apex acute. Type 2.

J.   <u>T. aucheri</u>. Very narrowly elliptic, apex acute. Type 1.

K.   <u>T. passerina</u>. Very narrowly elliptic, apex acute. Type 1.

Ka.   <u>T. passerina</u>. Cotyledons of 7-day old seedling. Wide obovate, apex rounded. Venation actinodromous, reticulate.

L.   <u>T. salsa</u>. Narrowly elliptic, apex acute. Type 1.

M.   <u>T. mesopotamica</u>. Elliptic, apex acute. Type 1.

A

B

C

Ca

D

E

I
1°
2°

J

K

L
angle of
divergence

M

Ka

Ga

G

H

Fig. 14

F
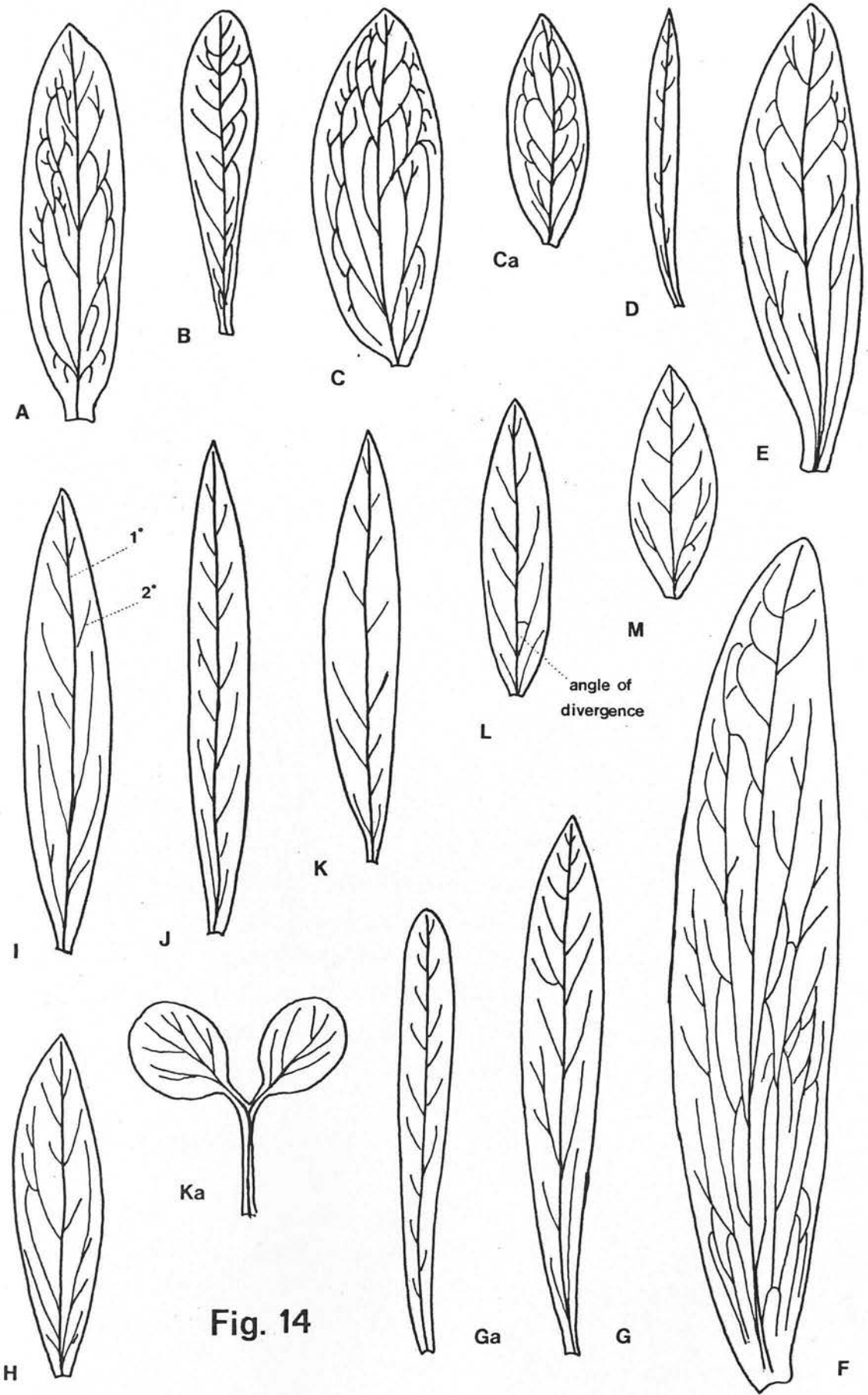
Fig. 15. Cleared leaves of Thymelaea as seen in surface view.
All x 6.

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.
Ha.   T. microphylla. Leaf from young sterile shoot elliptic,
       apex acute. Type 4.
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.
Na.   T. lythroides. Leaf from young sterile shoot lanceolate,
       apex acute. Type 4.
O.   T. hirsuta. Narrowly ovate, apex acute. Type 2.
Oa.   T. hirsuta. From smaller-leaved form. Type 2.
Ob.   T. hirsuta. Bract suborbiculate, apex acute. Type with 2°
       veins of upper half more acute than those of lower half.
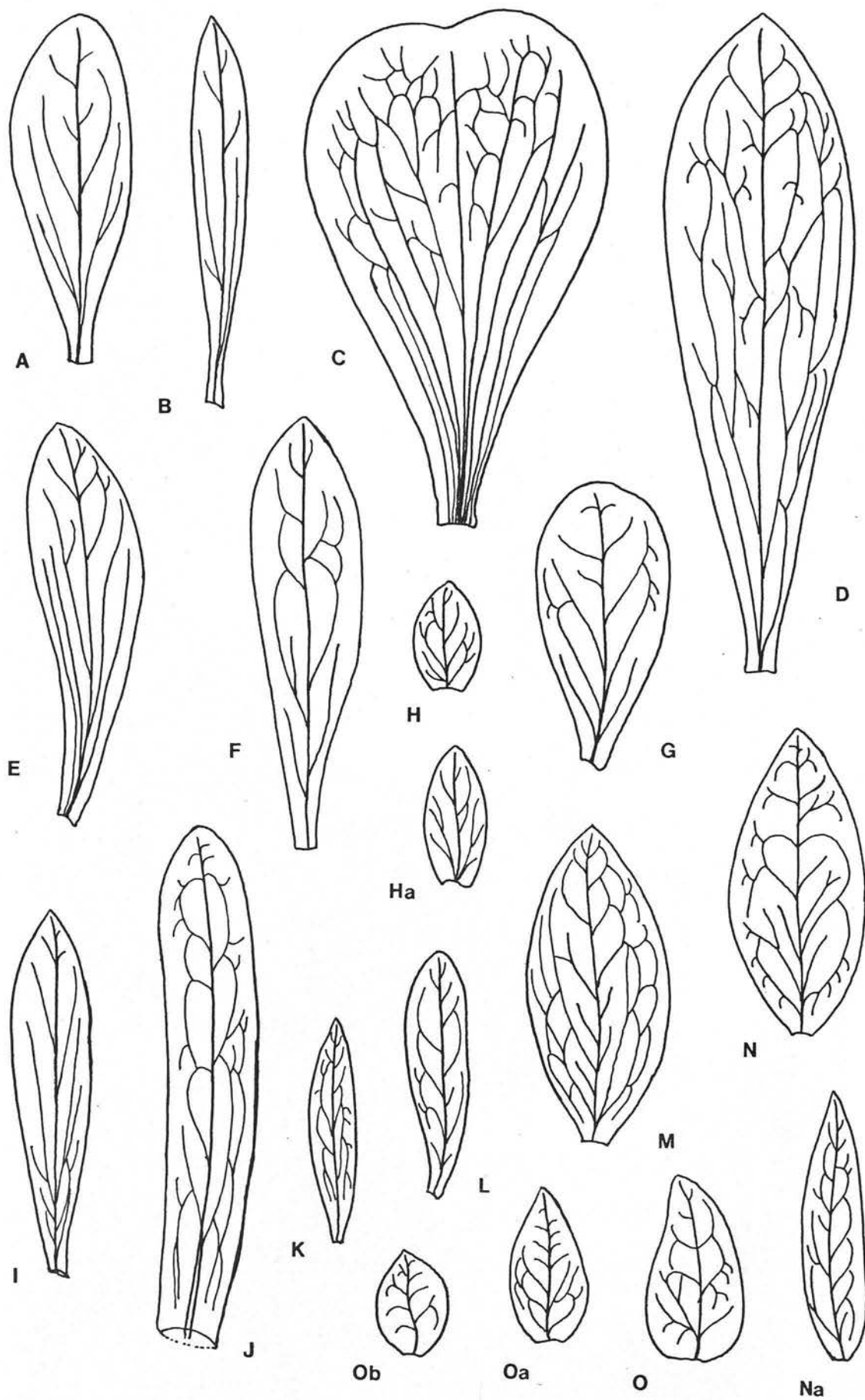
Fig. 15

Fig. 16.   <u>Thymelaea tartonraira</u> 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 - Ab. subsp. <u>valentina</u>

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. <u>argentea</u> var. <u>linearifolia</u>

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. <u>tartonraira</u> var. <u>transiens</u>

C.   Apex broadly triangular. Sclereids few (+).

Ca.   Upper epidermal hairs moderately long.
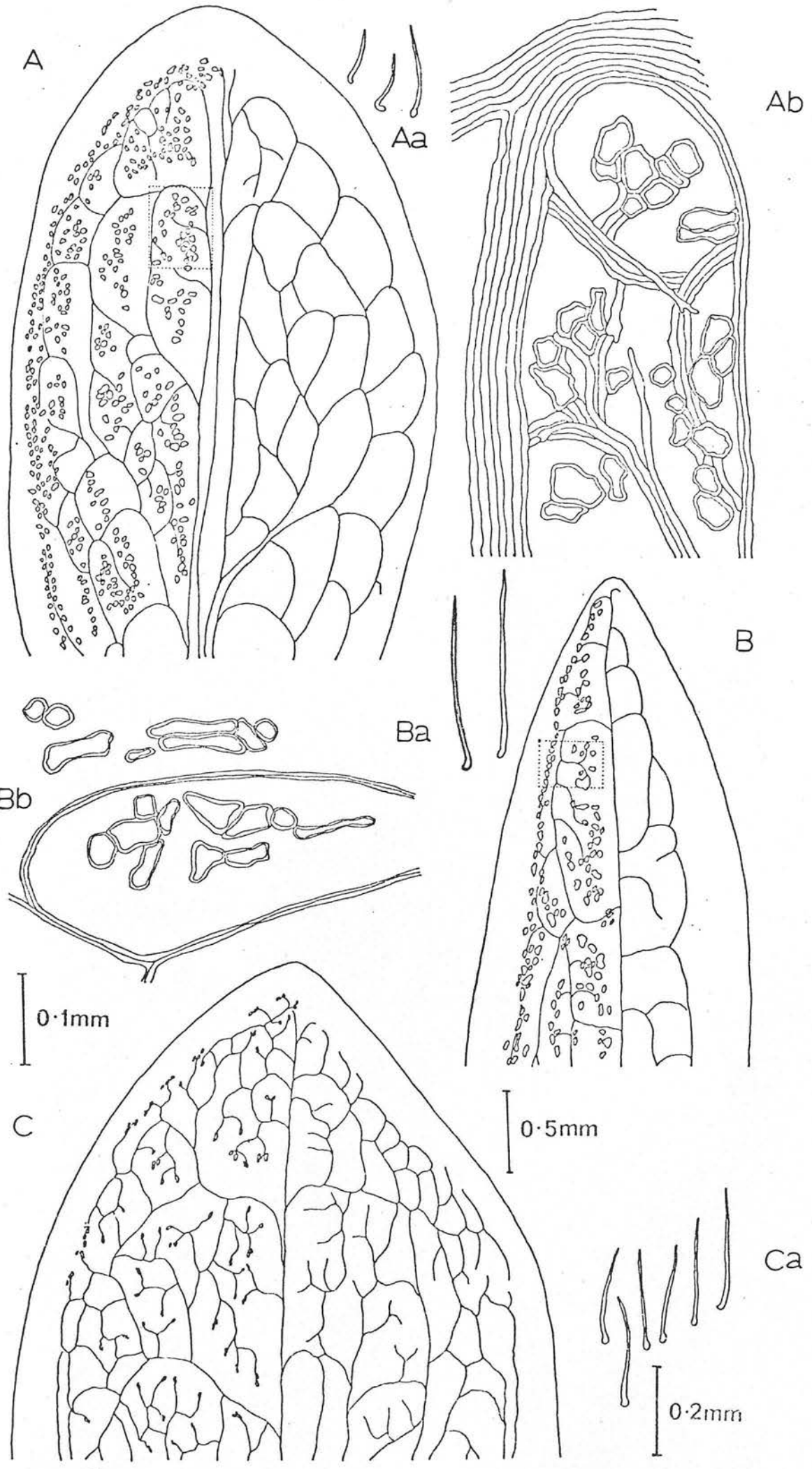
Fig. 16

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.
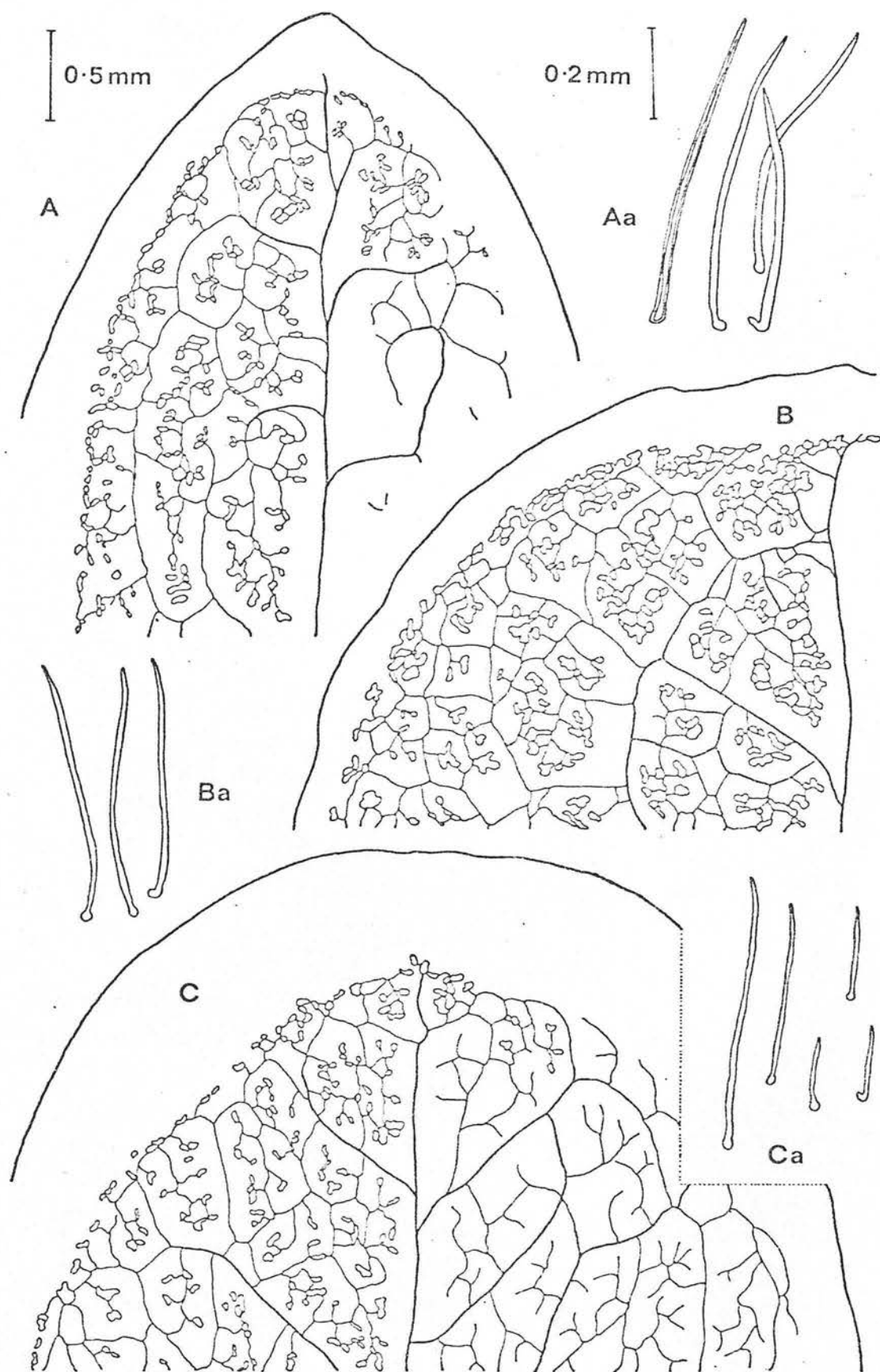
Fig. 17

Fig. 18. T.S. of <u>Thymelaea</u> leaves. All drawn to scale shown
(x 30).

Sect. <u>Ligia</u> A - E

A.   <u>T. aucheri</u>. Leaf with tendency to become revolute on
     drying.

B.   <u>T. cilicica</u>. Never revolute.

C.   <u>T. gussonei</u>. Indumentum present, often disappearing with
     age. Collenchyma well developed at midrib.

D.   <u>T. mesopotamica</u>. Indumentum persistent. Collenchyma
     absent.

E.   <u>T. salsa</u>. Glabrous. Two conspicuous lateral bundles at
     mid-laminar region.

Sect. <u>Thymelaea</u> F - K

F.   <u>T. thesioides</u> subsp. <u>thesioides</u>. Narrow-leaved form.

G.   <u>T. sanamunda</u>.

H.   <u>T. thesioides</u> subsp. <u>thesioides</u>.

I.   <u>T. antiatlantica</u>.

J.   <u>T. virgata</u> subsp. <u>virgata</u>. Collenchyma at midrib.

K.   <u>T. villosa</u>. Large sclereids in spongy mesophyll.

L.   <u>T. subrepens</u>.

M.   <u>T. dioica</u>.

N.   <u>T. virescens</u>.

O.   <u>T. coridifolia</u>. Stomata absent from abaxial surface.

P.   <u>T. ruizii</u>.

<u>Key to tissues</u>

xylem   chlorenchyma

phloem   collenchyma

sclerenchyma fibres and sclereids

0·5 mm
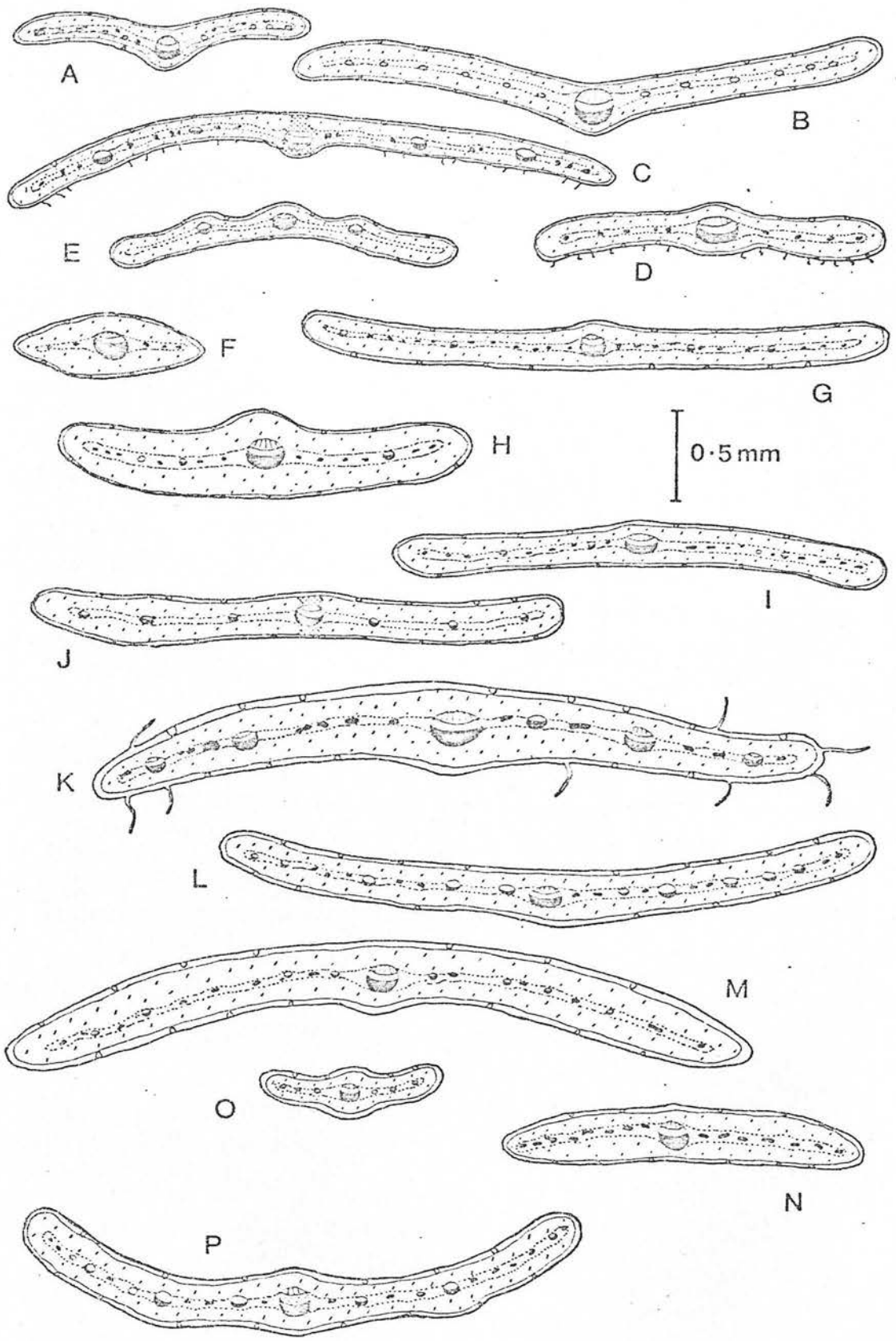
Fig. 18

Fig. 19. T.S. of <u>Thymelaea</u> leaves. All drawn to scale shown
(x 30) except Ia.

Sect. <u>Chlamydanthus</u> A - F, I - Ia.

A.   <u>T. calycina</u>. Stomata absent from abaxial surface.

B.   <u>T. tinctoria</u> subsp. <u>tinctoria</u>. Cuticle and epidermis
        contribute to leaf thickness.

C.   <u>T. velutina</u>.

D.   <u>T. tartonraira</u> subsp. <u>tartonraira</u> var. <u>transiens</u>. Indumentum
        more developed on the abaxial surface.

E.   <u>T. tartonraira</u> subsp. <u>argentea</u> var. <u>linearifolia</u>. Indumentum
        more developed on the adaxial surface.

F.   <u>T. tartonraira</u> subsp. <u>thomasii</u>. Indumentum completely
        absent from both surfaces.

I.   <u>T. broteriana</u>. Leaf folded to form groove. Stomata only
        on adaxial surface, none in section shown.

Ia.   <u>T. broteriana</u>. Drawn on separate scale, x 70.

Sect. <u>Piptochlamys</u> G - L.

G.   <u>T. argentata</u>.

H.   <u>T. lanuginosa</u>. Stomata absent from abaxial surface.

J.   <u>T. microphylla</u>.

K.   <u>T. lythroides</u>. Lanceolate-linear leaf from young sterile
        shoot. Margins slightly incurved. Collenchyma absent,
        stomata only on abaxial surface.

Ka.   <u>T. lythroides</u>. Lanceolate-ovate leaf from flowering branch.
        Margins not incurved. Collenchyma reaching adaxial epidermis
        at midrib.

L.   <u>T. hirsuta</u>. Indumentum woolly-tomentose on adaxial surface.
        Cuticle and epidermis thick. Stomata absent from abaxial
        surface.

Fig. 19

0·5mm

0·2mm
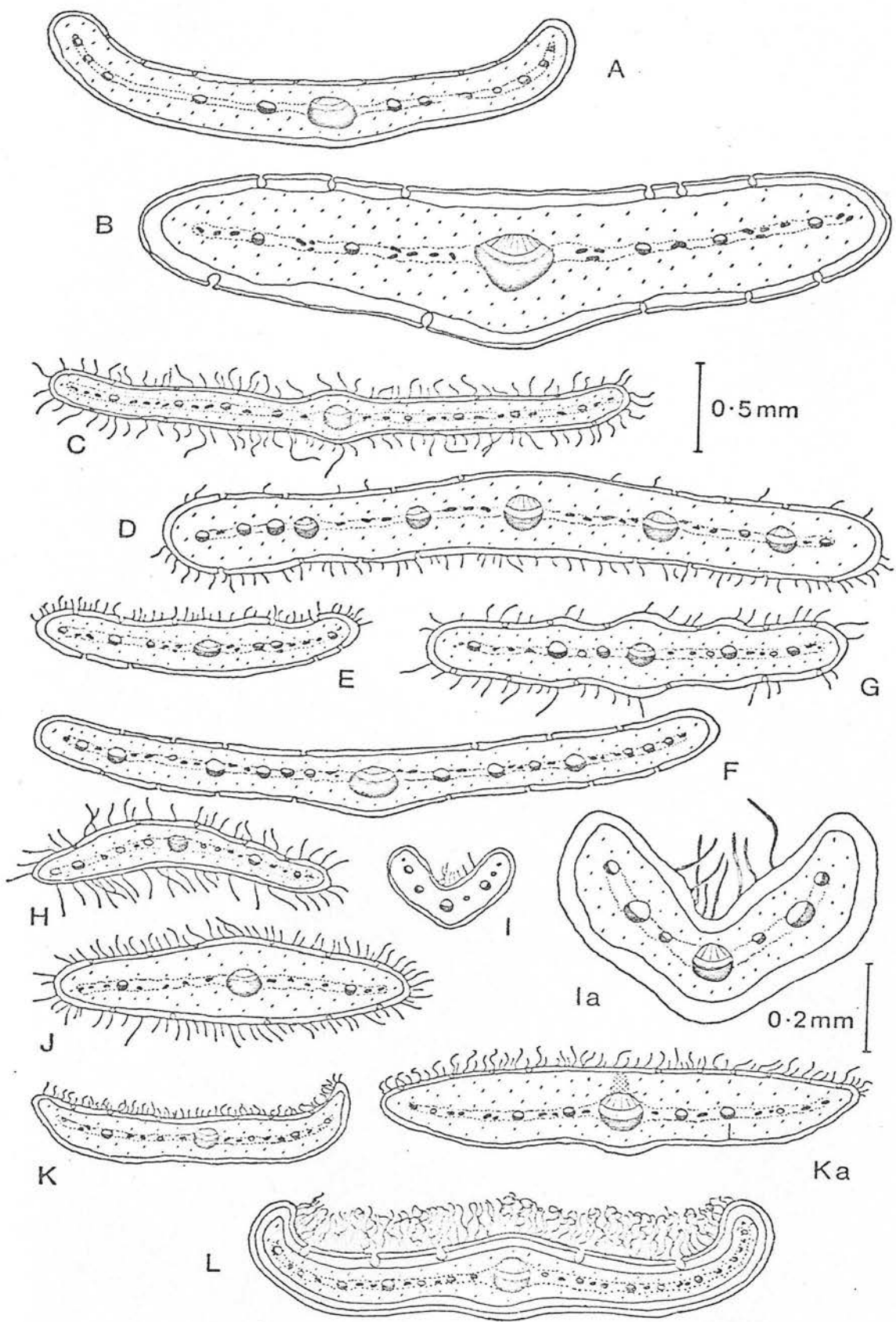
Fig. 20. T.S. of leaves. All drawn to scale shown (x 44).

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.

0·5mm
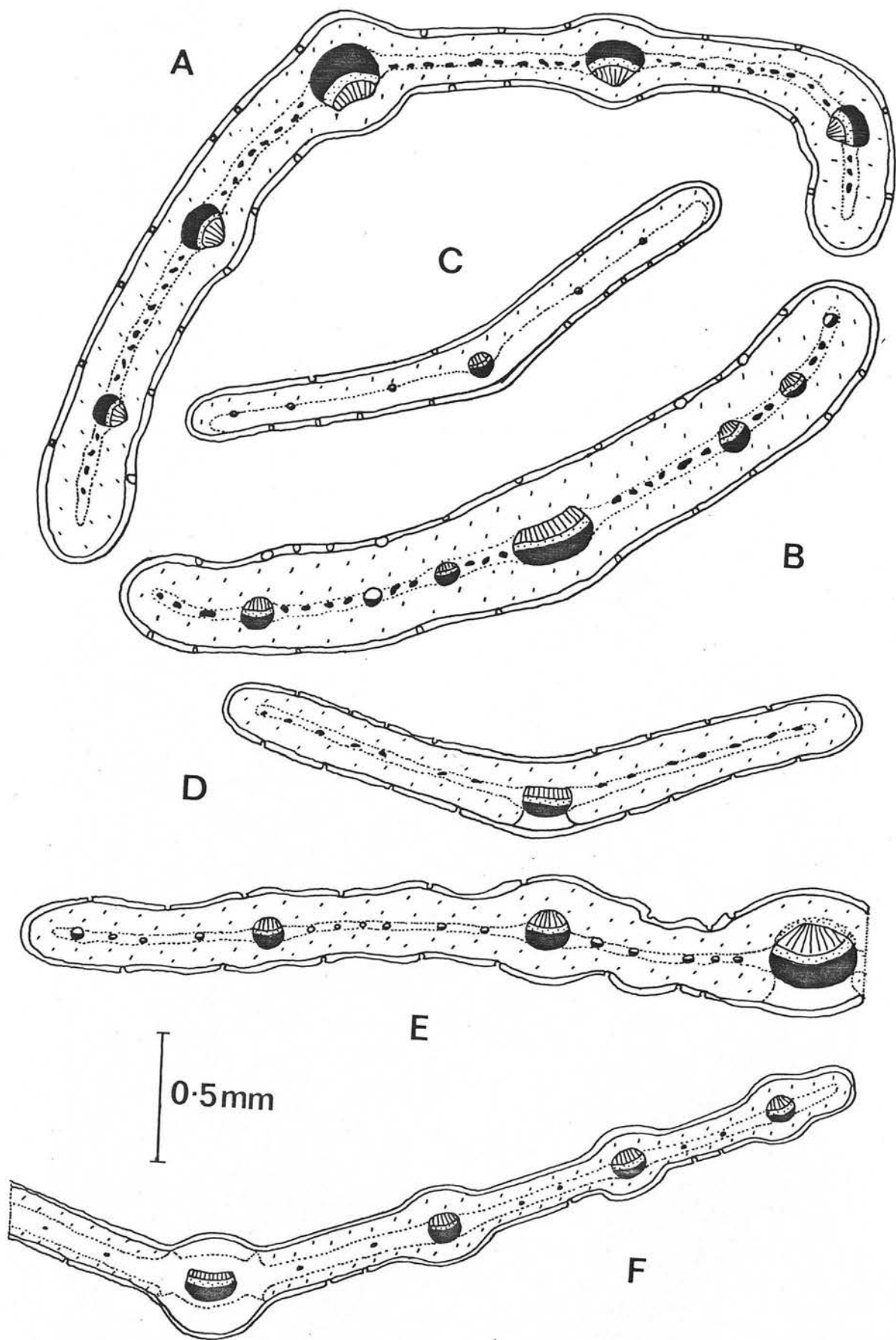
Fig. 20

Fig. 21. 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. 21
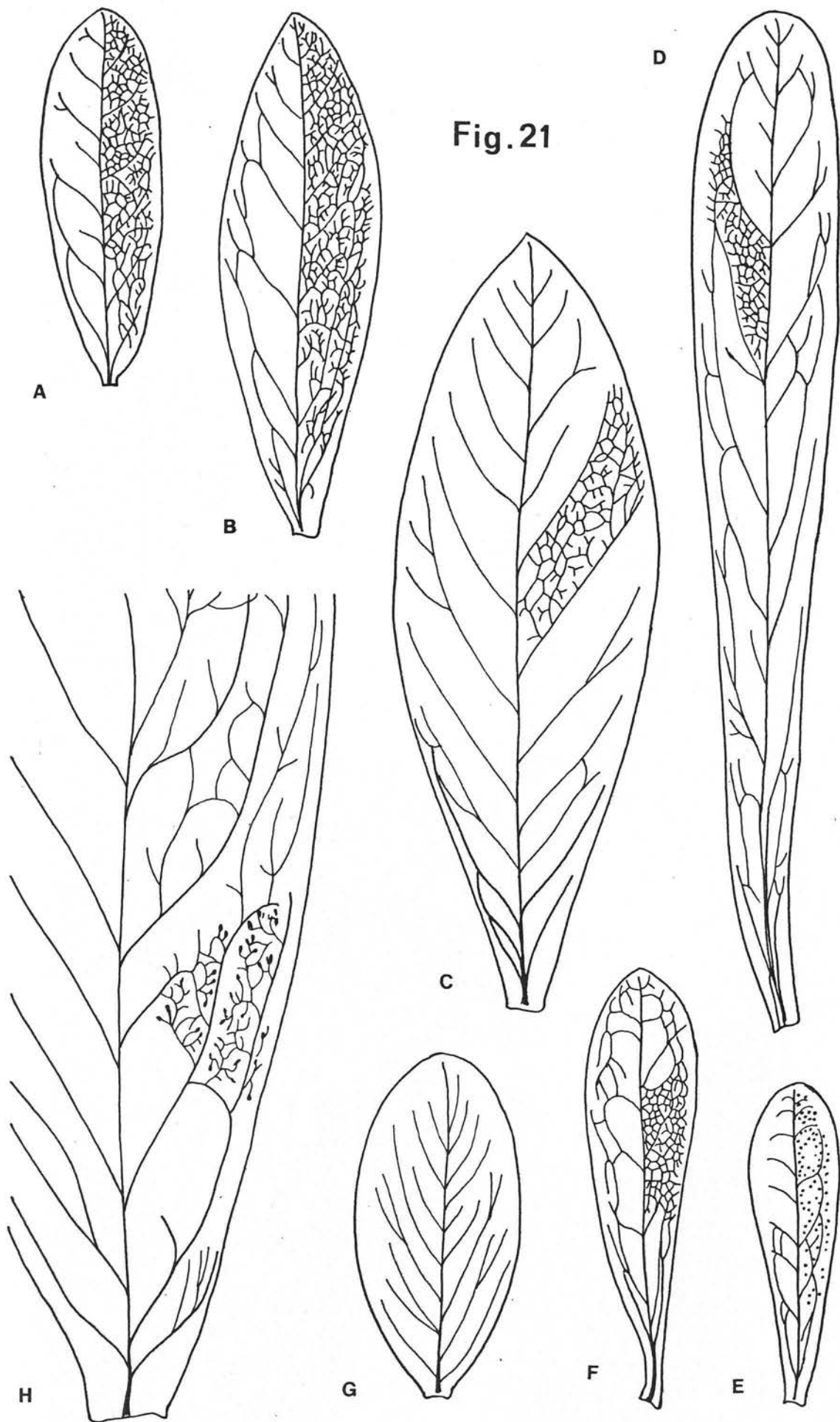
Fig. 22.   Cleared leaves of <u>Daphne</u> as seen in surface view.

x 6.

A. <u>D. oleoides</u>

B. <u>D. stapfii</u>

C. <u>D. retusa</u>

D. <u>D. giraldii</u>

Fig.22
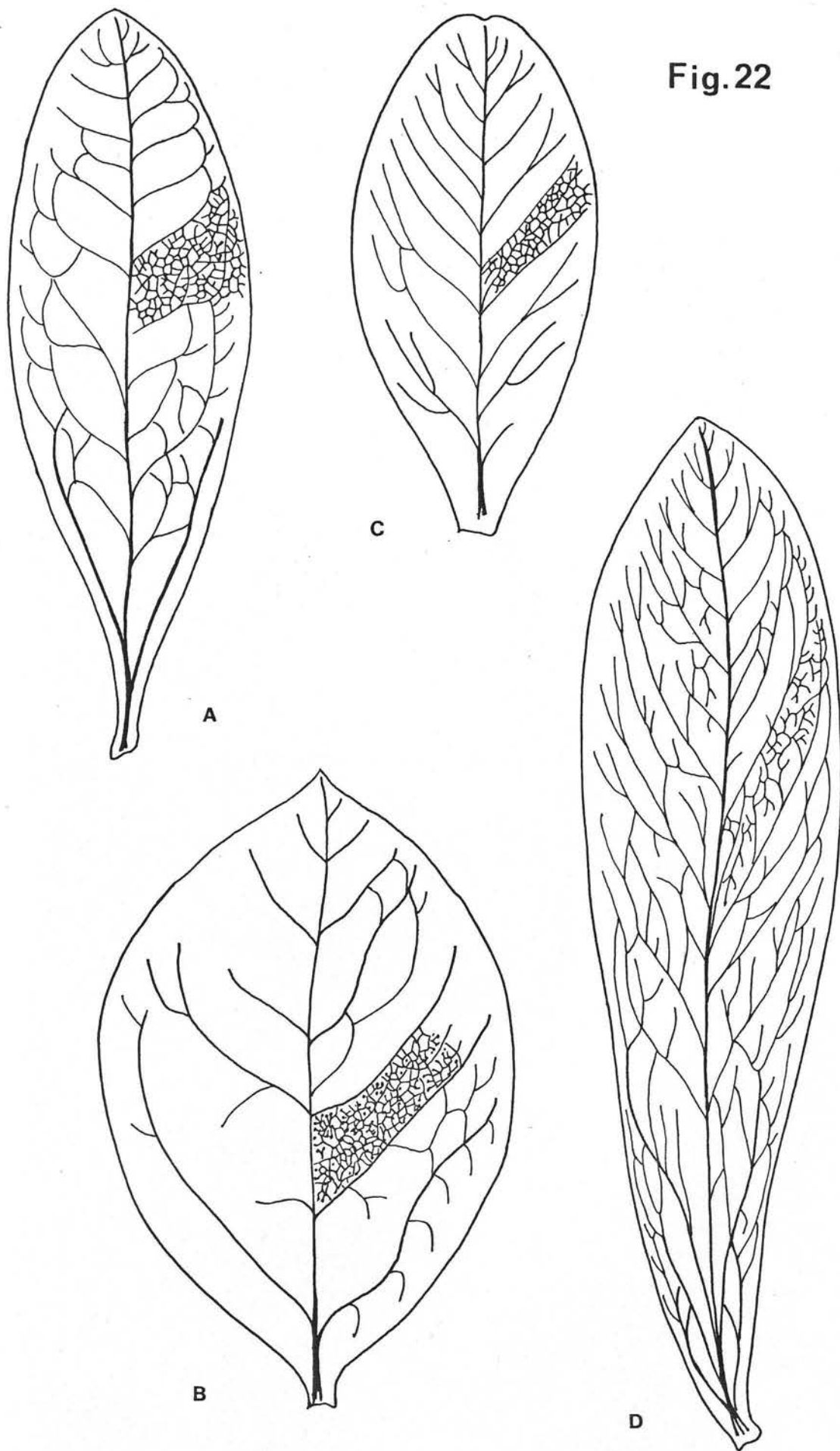
Fig. 23. Cleared leaves of <u>Daphne</u> as seen in surface view.

x 6.

A.   <u>D. blagayana</u>

B.   <u>D. alpina</u>

Fig. 23

A

B
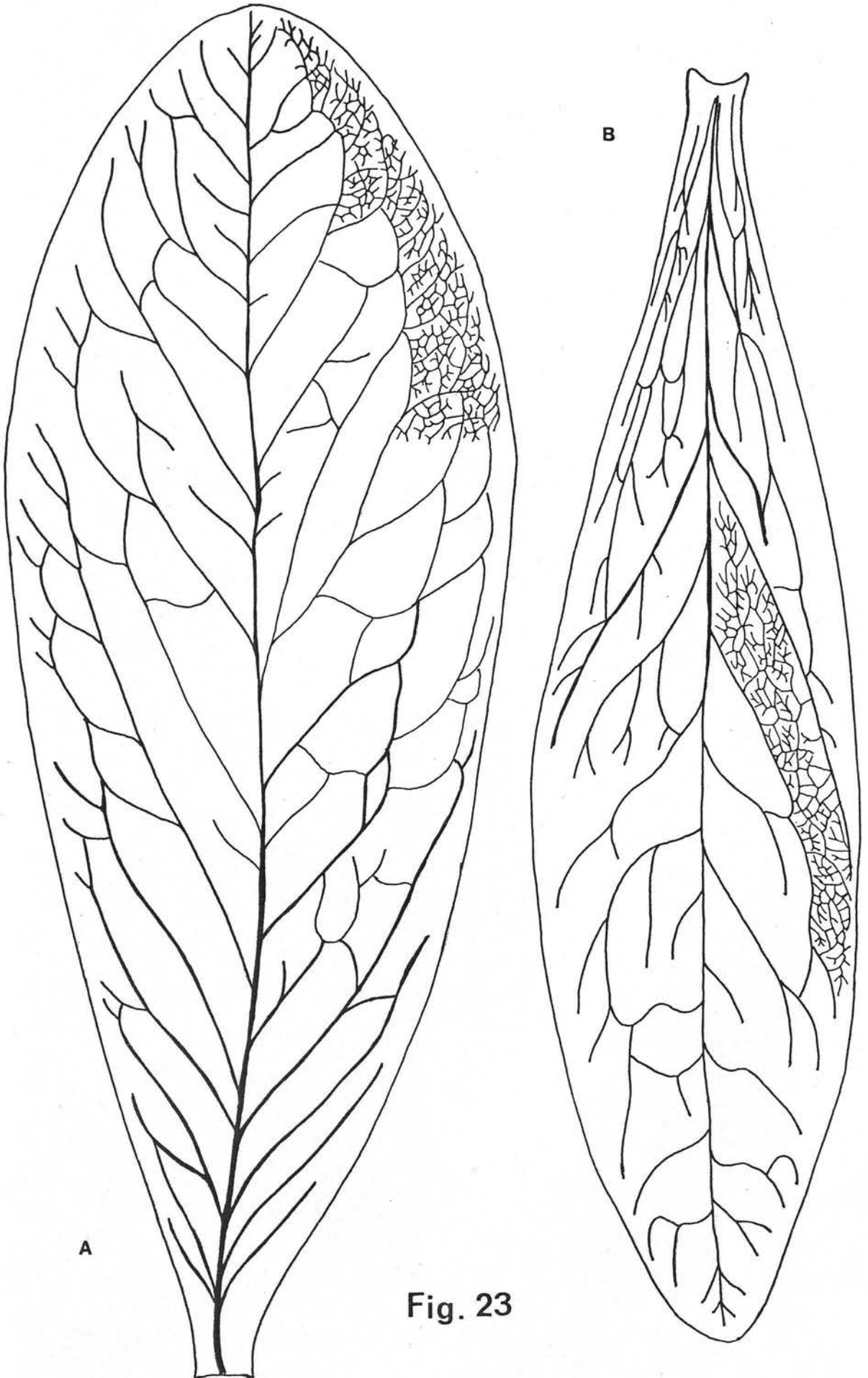
Fig. 24. Cleared leaves of <u>Dendrostellera</u> as seen in surface view.
All x 6.

A.   <u>D. stachyoides</u>. Type 4 - divergence angle of 2° veins
        nearly uniform.

B-F.   <u>D. lessertii</u> (a very polymorphic species). Type 4.

4° and higher order venation very finely reticulate. Sclereids
moderately developed.

lateral 1° veins
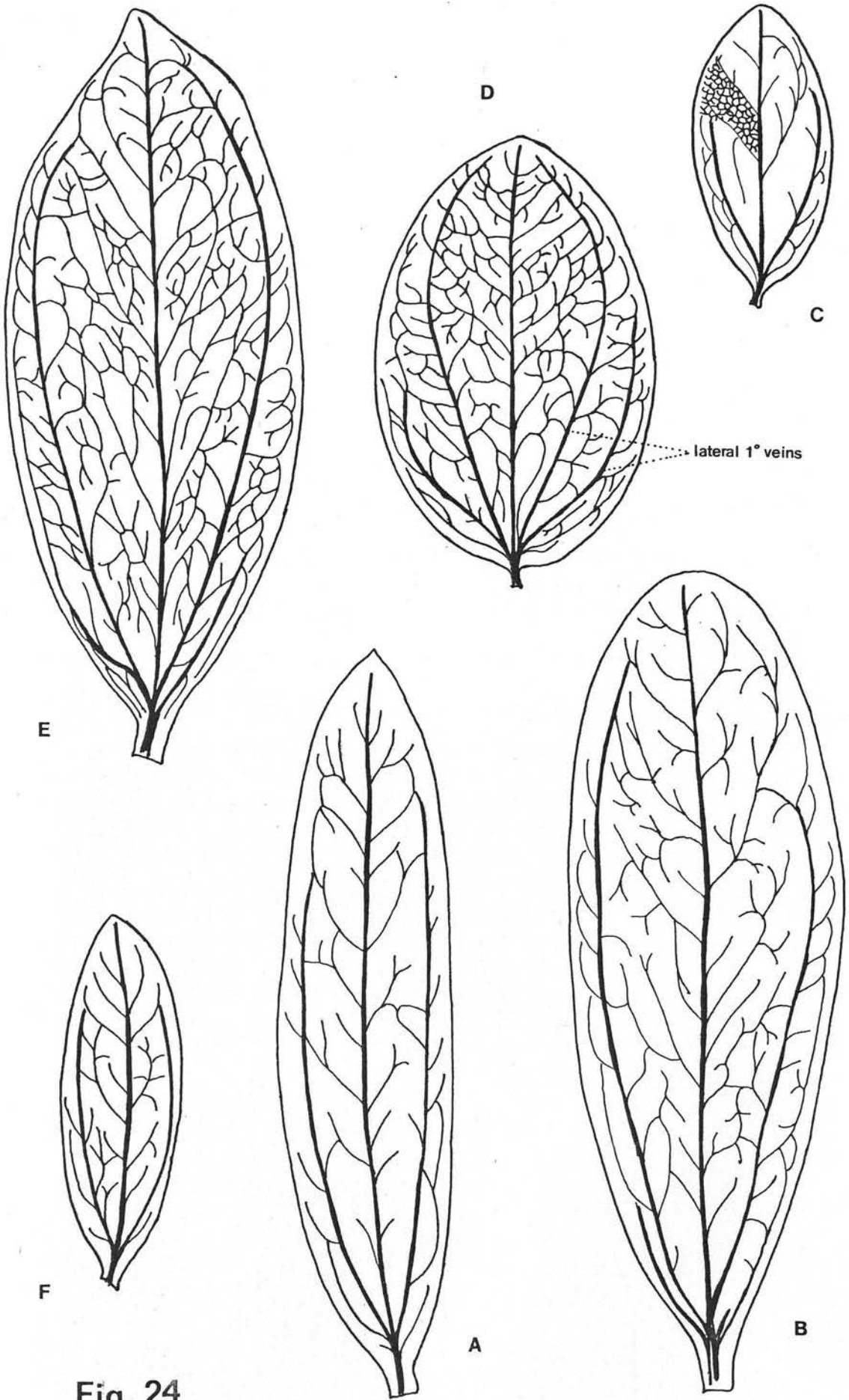
Fig. 24

Fig. 25. Leaf clearings and transverse sections.

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

A. D. oleoides. T.S. at midrib region. Adaxial cuticle smooth
    and thick, abaxial cuticle ridged. Epidermis with large
    mucilage cells. Palisade 2-3 layered, continuous. Sclereids
    present. Internal phloem absent. Stomata sunken. Collenchyma
    present. cu. = cuticle, epid. = epidermis, scl. = sclereids,
    st. = stoma.

B. D. mezereum. T.S. at midrib region. Cuticle smooth, thin
    on both surfaces. Epidermis with no differentiated secretory
    cells. Palisade 2-layered, interrupted at midrib. Sclereids
    absent. Phloem fibres not conspicuous. Internal phloem present.
    Stomata few or absent in this region. Collenchyma absent.
    par. = parenchyma, thin-walled, isodiametric or rounded-
    polygonal, not palisade-like.

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			
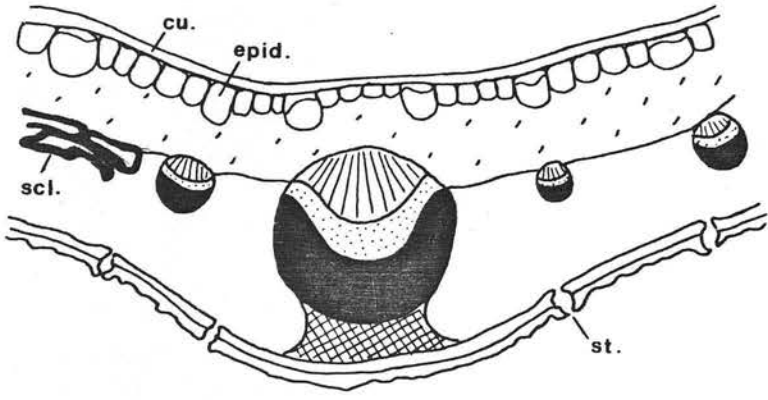
Fig. 25
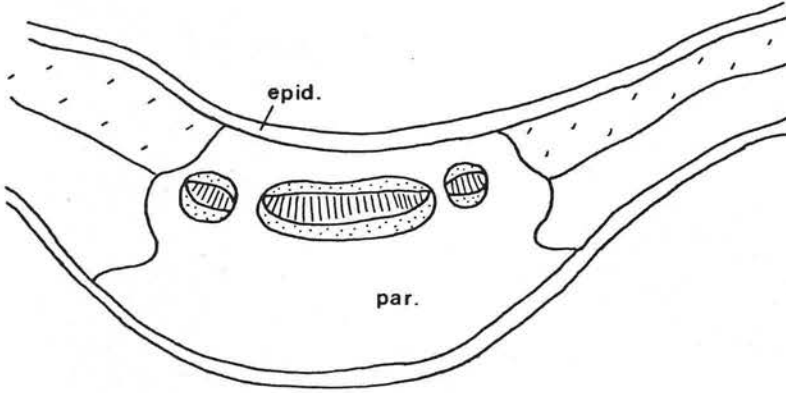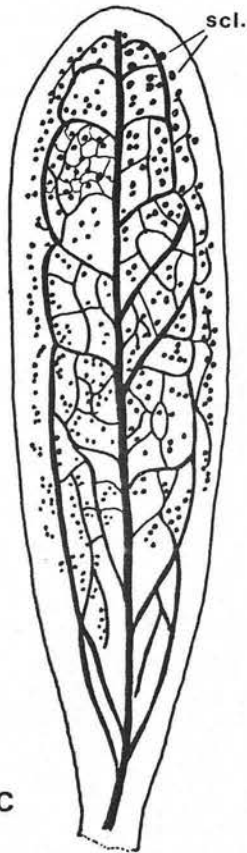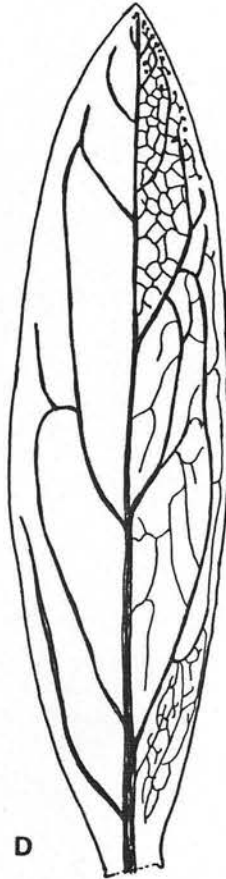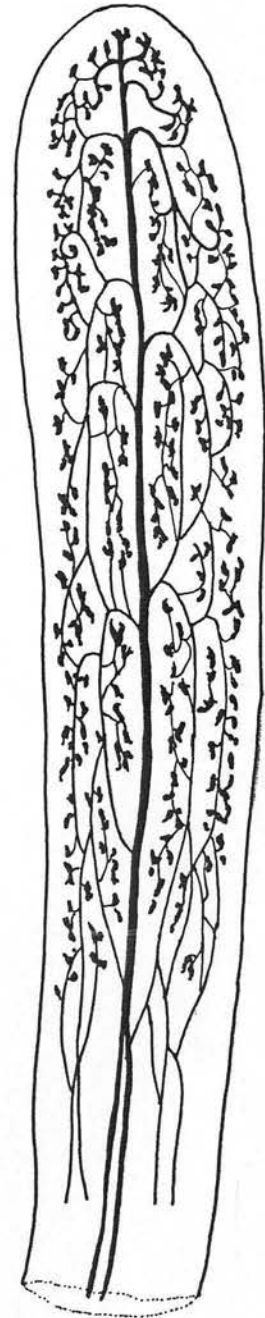
Fig. 26. T.S. of <u>Daphne</u> leaves. All drawn to scale shown (x 44).

A.   <u>D. altaica</u>. Palisade restricted to adaxial side.

B.   <u>D. gnidium</u> var. <u>sericea</u>. Palisade on both sides.

C.   <u>D. linearifolia</u>. s. cells = secretory/mucilage cells.

D.   <u>D. mucronata</u>. s. cells fewer on abaxial surface. Sclereids numerous.

E.   <u>D. jasminea</u>. Sclereids present.

F.   <u>D. rodriguezii</u>. Palisade restricted to adaxial side. Stomata on <u>both</u> surfaces.

B

s.cells

C

0·5mm

A

E

s.cells

D

F
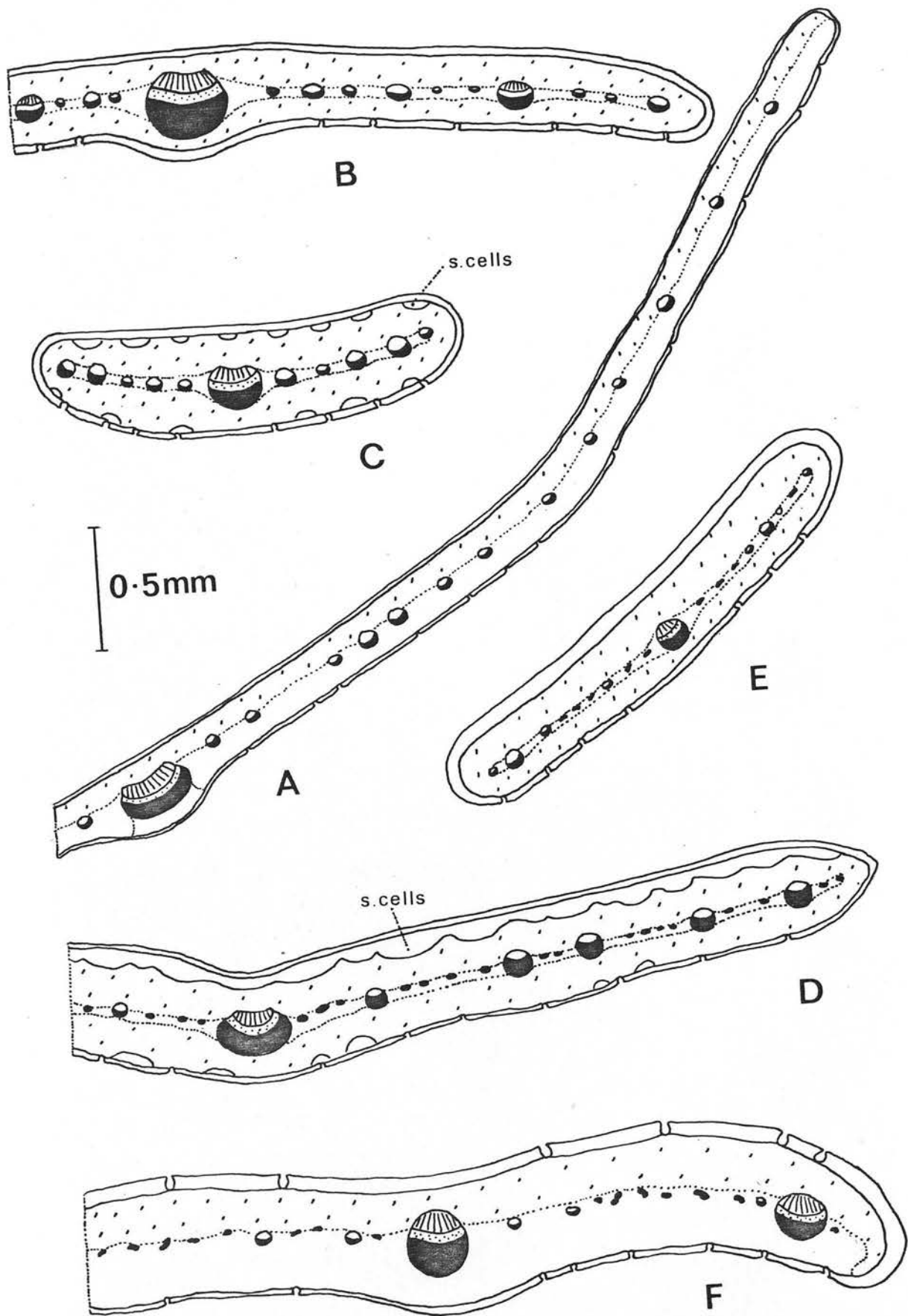
Fig. 26

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.

D. *Daphne cneorum.* Abaxial epidermis. Stomata sunken. Cuticular projections present.

E. *Daphne arbuscula.* Abaxial epidermis. Stomata level with inner wall of epidermal cells.

F. *Daphne glomerata.* Abaxial epidermis. Stomata not sunken. Cuticle smooth.

G. *Dendrostellera lessertii.* Adaxial epidermis. Cells often large and mucilaginous.

H. *Dendrostellera stachyoides.* Abaxial epidermis. Stomata sunken in shallow crypts.

A - C x 30, Ca x 350, D - H x 1400.
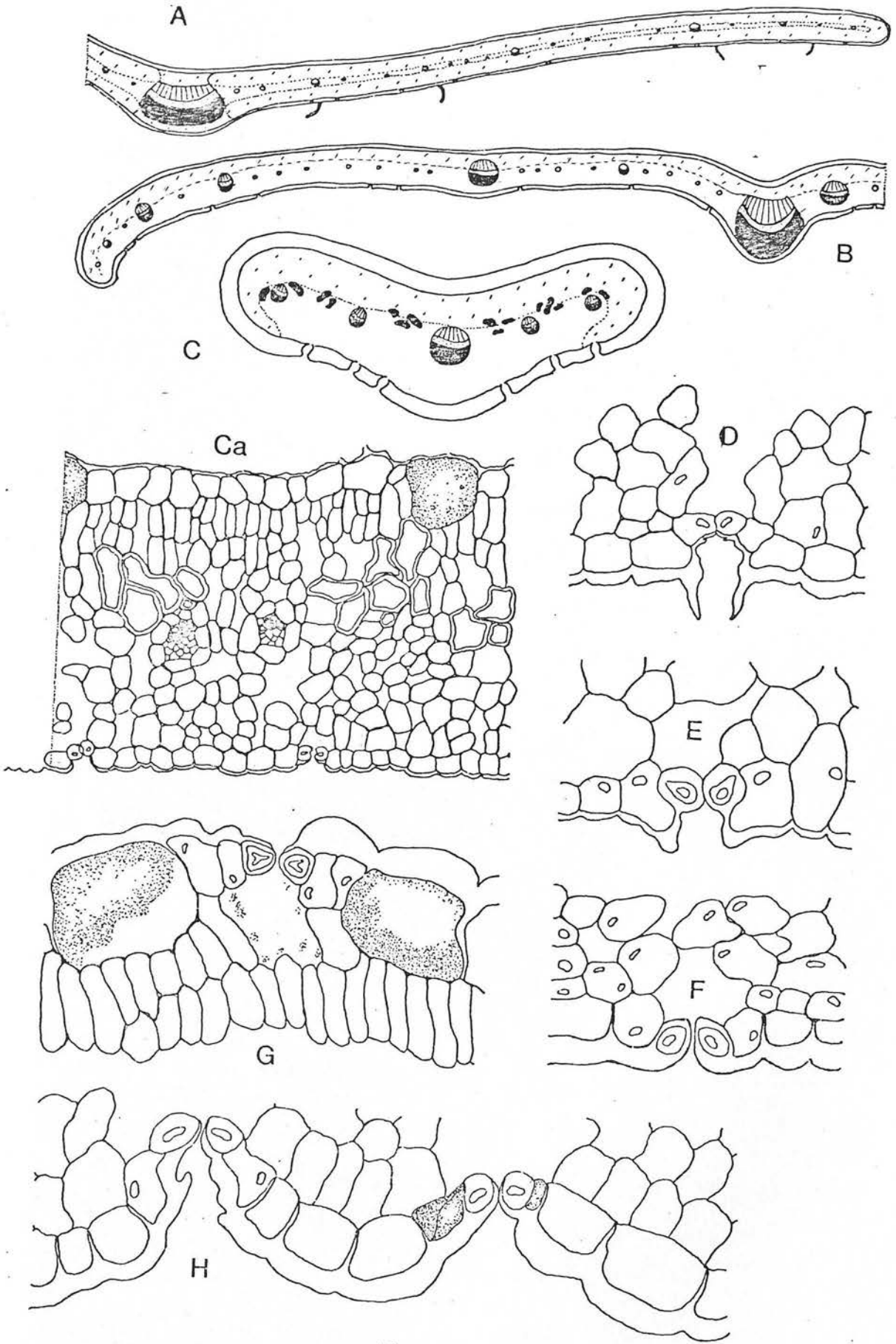
Fig. 27

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).

Aa. T. tartonraira subsp. argentea var. linearifolia. Abaxial
    epidermis. Stomata sunken because of raised cuticle.
    g.c. = guard cell.

B. T. lythroides. Adaxial epidermis. Hairs thin-walled, twisted.

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

Ca. T. tinctoria subsp. tinctoria. Phloem fibres (non-lignified)
    from midrib bundle. Walls thick, lumina small.

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

E. T. subrepens. Leaf section near margin. Epidermis with tannin
    inclusions. Palisade compact, isolateral.

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

G. D. rodriguezii. 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.

Ia. D. oleoides. Abaxial epidermis. Cuticle thick, ridged and
    furrowed. Mucilage cells also present but fewer in number.

A - D all drawn to scale shown, E on separate scale, F - Ia x 1400.
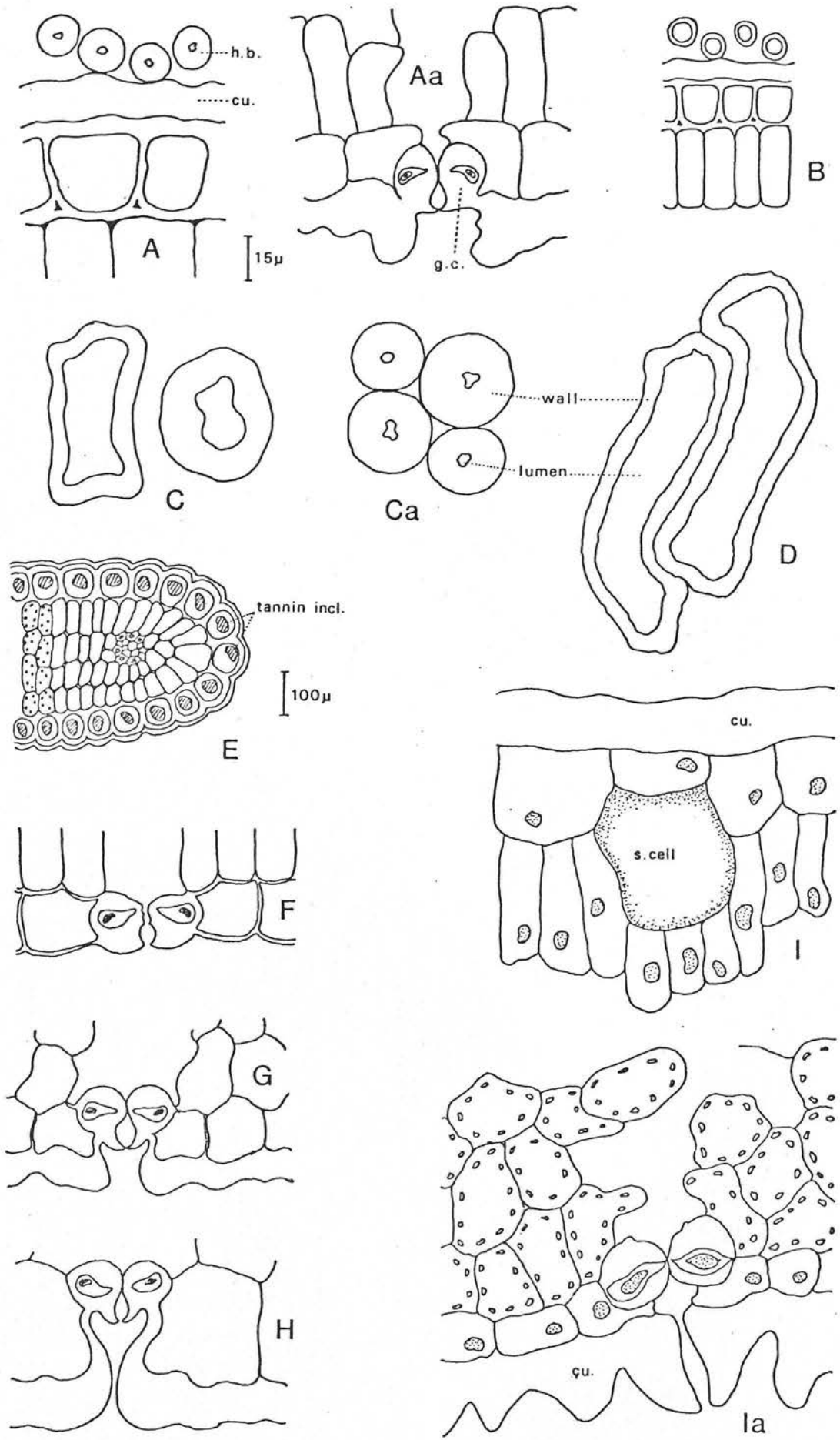
Fig. 28

Fig. 29.   Leaf clearings and transverse sections.

A.   <u>Stellera chamaejasme</u> subsp. <u>chamaejasme</u>. Whole leaf.

          Sclereids absent.   x 6.

Aa.   <u>S. chamaejasme</u> subsp. <u>chamaejasme</u>.   Leaf in section.

          Epidermal cells large.   Palisade 2-layered, restricted to

          the adaxial side.   x 2100.

B.   <u>Stelleropsis antoninae</u>.   Adaxial epidermis.   Stoma

          slightly sunken or level with inner wall.   x 2100.

C.   <u>Diarthron vesiculosum</u>.   Sclereids at leaf apex.   x 6.

D.   <u>Diarthron linifolium</u>.   Sclereids also present.   x 6.

Ca.   <u>Diarthron vesiculosum</u>.   Adaxial epidermis and 2-layered

          palisade.   Stoma level with inner wall.   x 2100.

Cb.   <u>D. vesiculosum</u>.   Abaxial epidermis and 2-layered

          palisade.   x 2100.
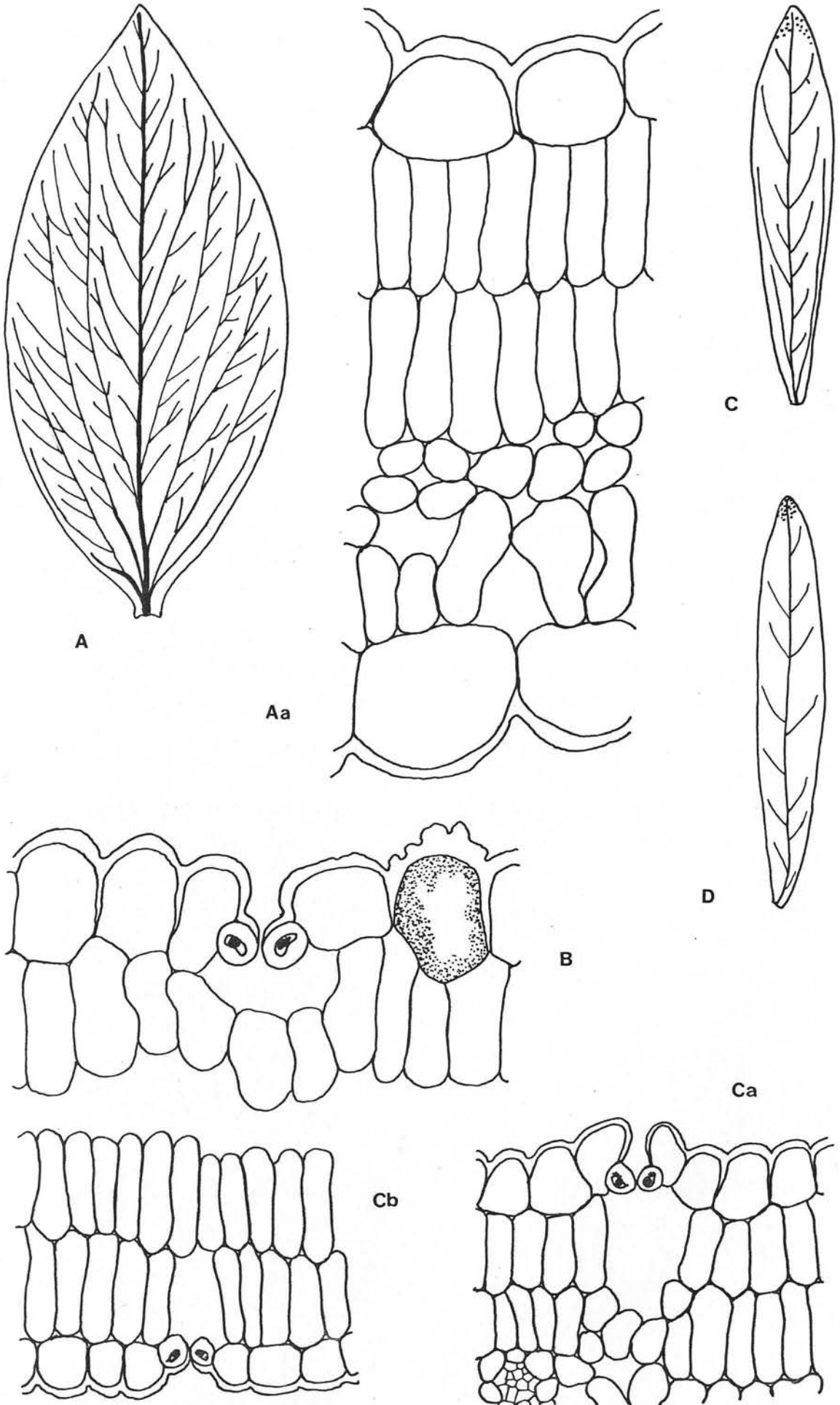
Fig. 29

Fig. 30. T.S. of leaves. Hairs drawn detached from surfaces.

A.   _Passerina filiformis._ Vascular bundle sclerenchyma
       (phloem fibres) not interrupting palisade. Stomata
       and indumentum present on adaxial surface only. Tannin
       not in all epidermal cells but present in parenchymatous
       bundle-sheath. Vascular bundles 7. x 250.

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

B.   _P. montana._ Sclerenchyma not interrupting palisade.
       Tannin in all abaxial epidermal cells but absent in
       bundle-sheath. Vascular bundles 9. x 250.

C.   _P. paleacea._ Sclerenchyma interrupting palisade. Tannin
       in all abaxial epidermal and bundle-sheath cells. Vascu-
       lar bundles 4. x 250.

D.   _P. vulgaris._ Mature leaf. Sclerenchyma interrupting
       palisade. Hypodermal fibres present, ramifying from
       all bundles. Stomata very slightly raised (see enlarge-
       ment). Tannin in abaxial epidermis and bundle-sheath.
       Vascular bundles 3. x 250.

Da.   _P. vulgaris._ Young leaf. Sclerenchyma _not_ interrupting
       palisade. Hypodermal fibres absent. Tannin absent from
       epidermal or bundle-sheath cells. Vascular bundles 3.
       Indumentum more conspicuous than in D. x 250.

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.
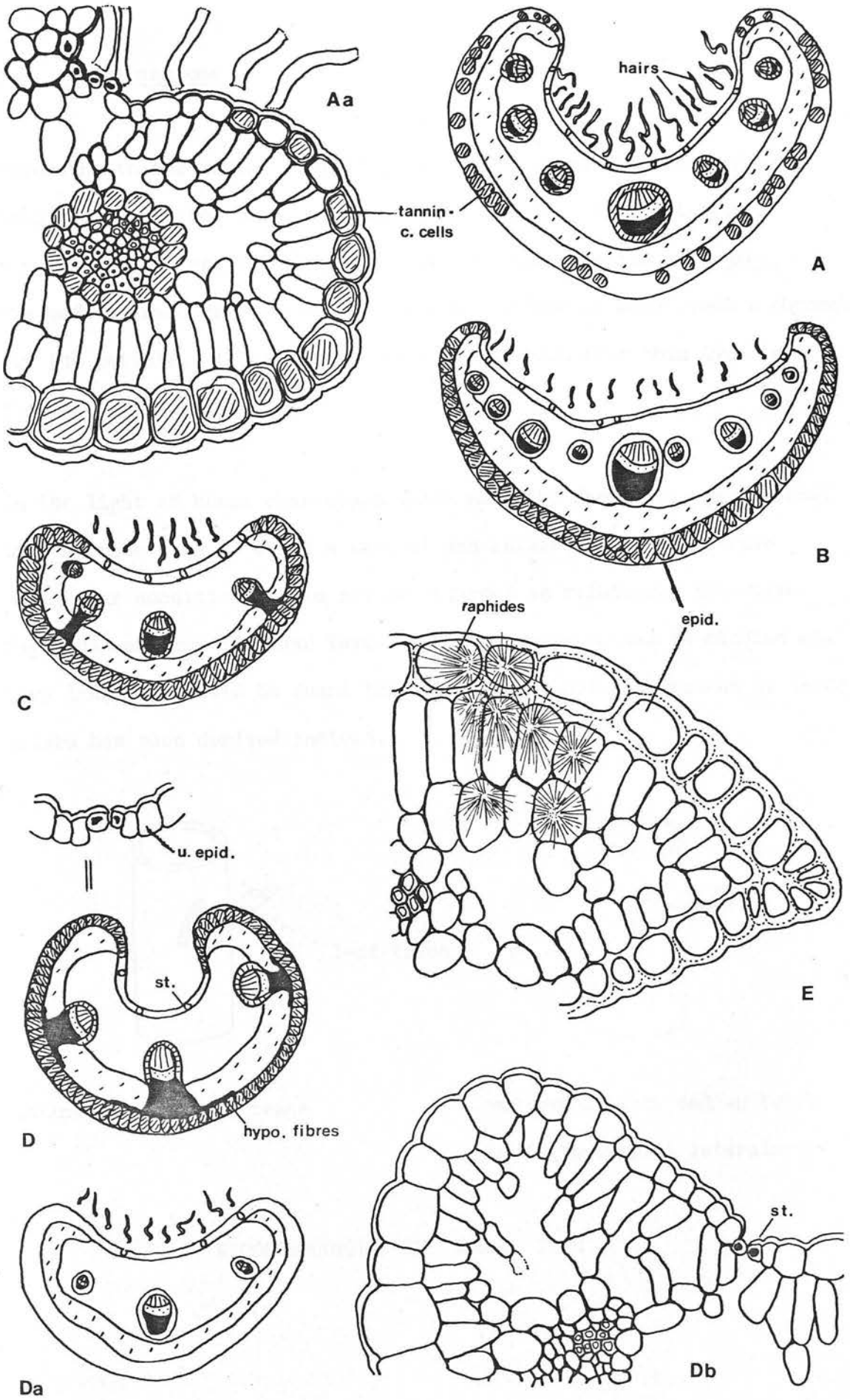
Fig. 30

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. 31 D,32C,33D,35Ca). In some species of Daphne,
the median trace has two laterals which continue as wing bundles through-
out 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.

leaf trace
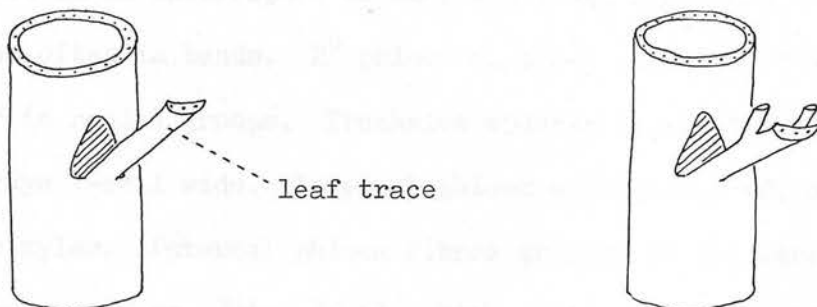
unilacunar with one trace   unilacunar with median trace
                                    having two split laterals

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, unlignified
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, 32 A). 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, dis-
appearing 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 unlignified, 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 $< 100 \, \mu m$), 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 some-
times 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 endo-
dermis?). Phloem fibres thick- or moderately thick-walled, unlignified,
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 collen-
chyma 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. 34 A-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 fibes 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. 34 Cb), 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
unlignified, 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. <u>Thymelaea</u> Sect. <u>Ligia</u>

A - Ac. <u>T. passerina.</u>

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.   <u>T. mesopotamica.</u> T.S. of stem. Internal phloem fibres
      absent. x 70.

C.   <u>T. salsa.</u> T.S. of stem. Internal phloem fibres absent.
      x 70.

Ca.   <u>T. salsa.</u> Stem epidermis in surface view. Stomata
      anisocytic. x 145.

D.   <u>T. aucheri.</u> T.S. of stem. Node unilacunar. Internal
      phloem fibres present. x 30.

147
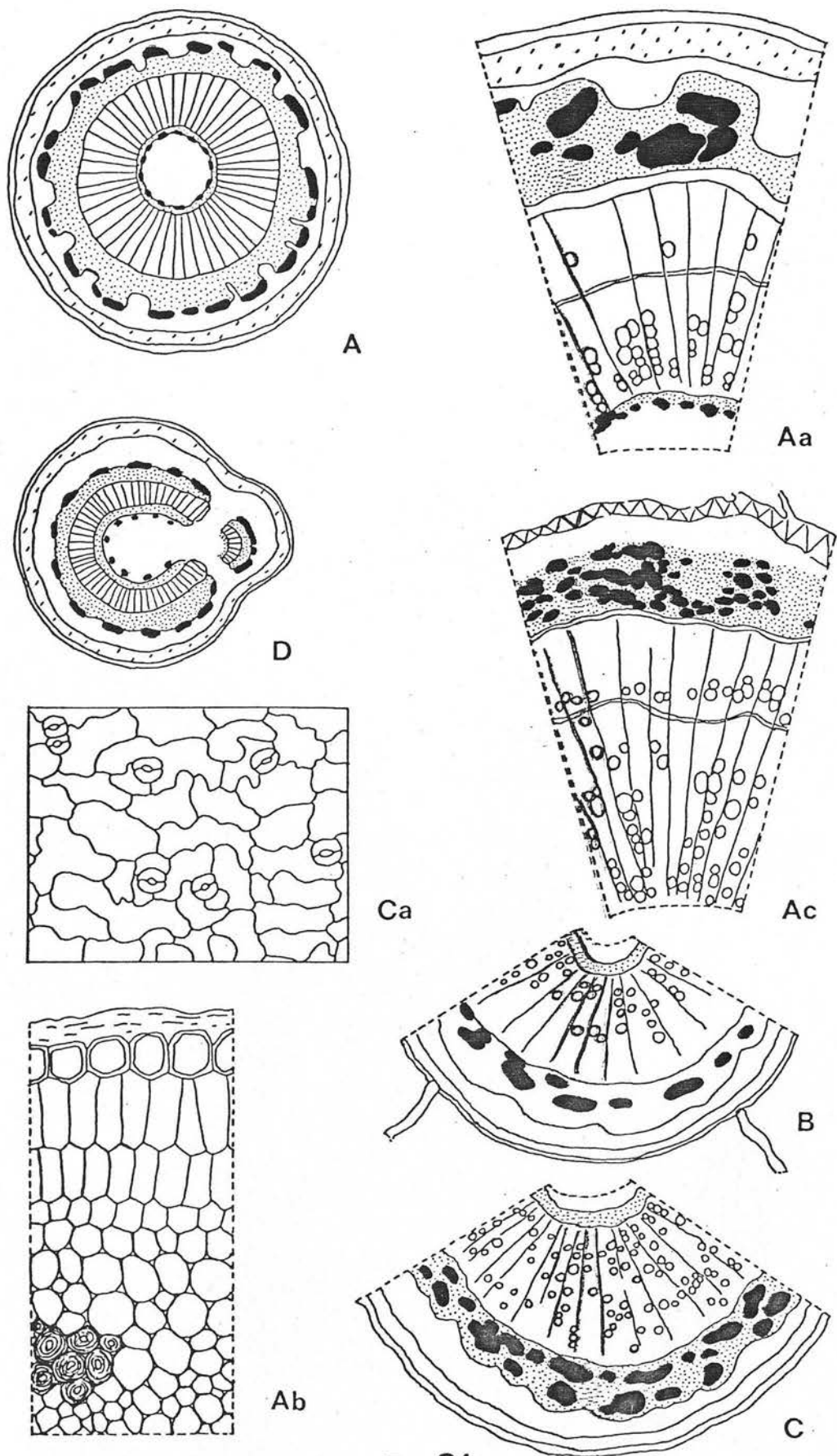
Fig. 31

Fig. 32. _Thymelaea_. Stems in transverse section.

A.   _T. virgata_ subsp. _virgata_. Epidermis tannified. Cortex
       of crushed primary phloem. Vessels oblique-radial. Internal
       phloem fibres present. x 70.

B.   _T. hirsuta_. Internal phloem fibres moderately developed
       or scanty. x 30.

C.   _T. velutina_. Node unilacunar. Internal phloem fibres
       absent. 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.

E.   _T. tinctoria_. Cork present. Tannin idioblasts in cortex.
       Growth rings present with vessels tangentially arranged.
       Pith cells moderately thick-walled. Internal phloem fibres
       absent. x 70.
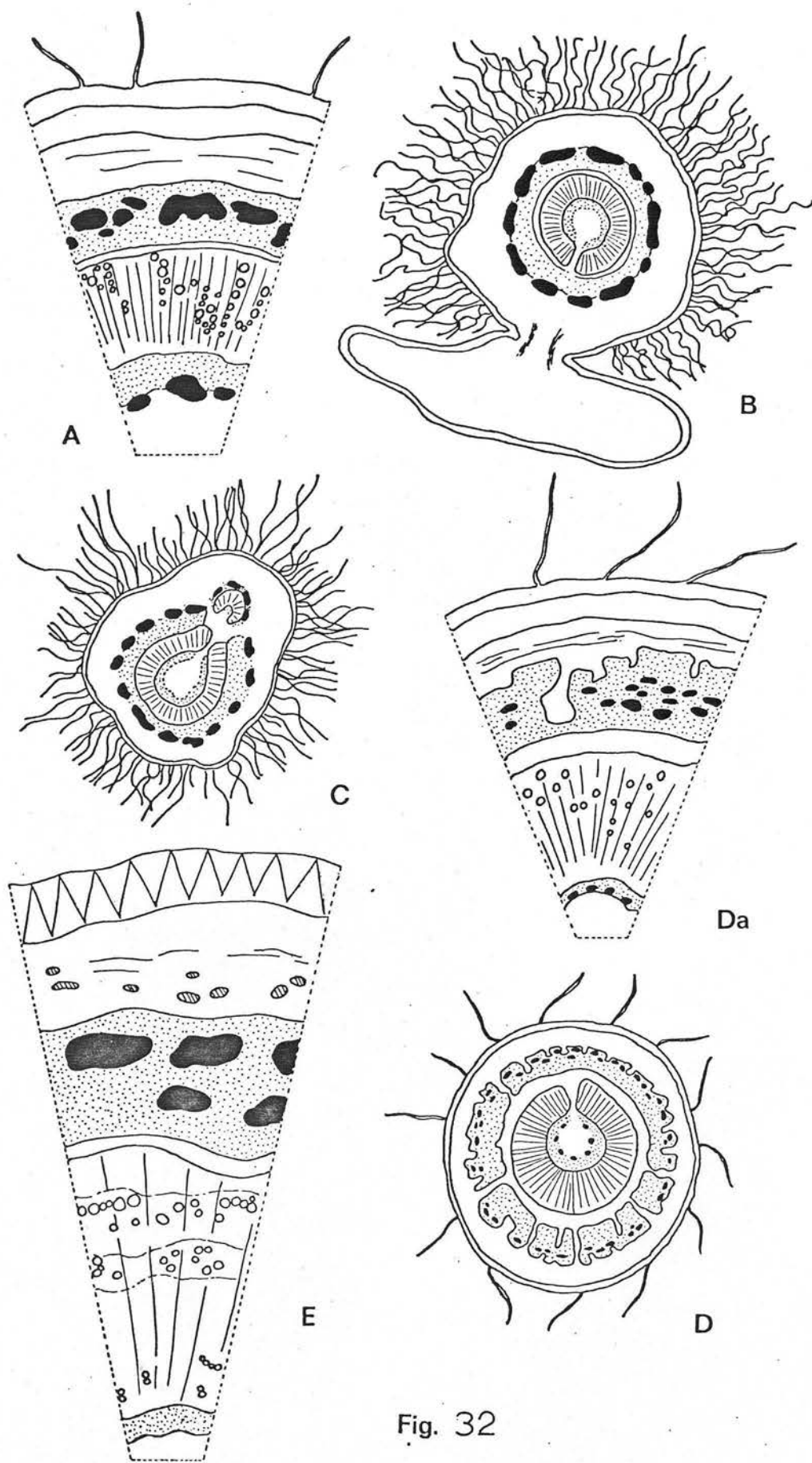
Fig. 32

Fig. 33. <u>Daphne</u>. Stems in transverse section. All x 70 except D.

A. <u>D. longilobata</u>. Internal phloem fibres present.
    Collenchyma well developed.

B. <u>D. mezereum</u>. Internal phloem fibres absent. Collen-
    chyma absent, cork well developed.

C. <u>D. gnidium</u>. Internal phloem fibres present. Cork
    not yet developed.

D. <u>D. arbuscula</u>. Internal phloem fibres present. Scleren-
    chyma also occurring in outer cortex. x 30.

151

0·2 mm

ray

late wood

A

B

C

D

Cork
Collenchyma
Chlorenchyma
Sclerenchyma
Phloem
Xylem

0·5mm
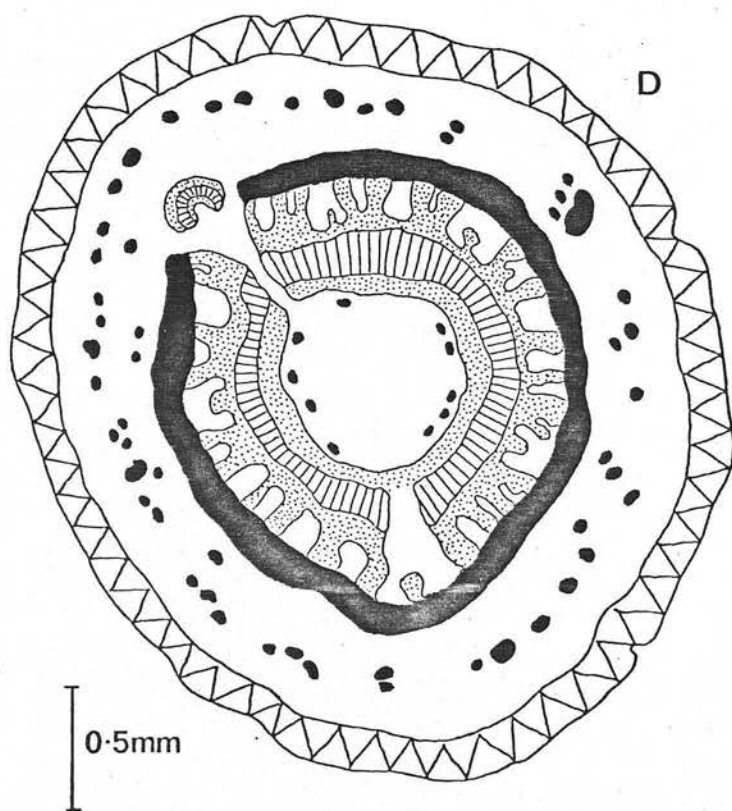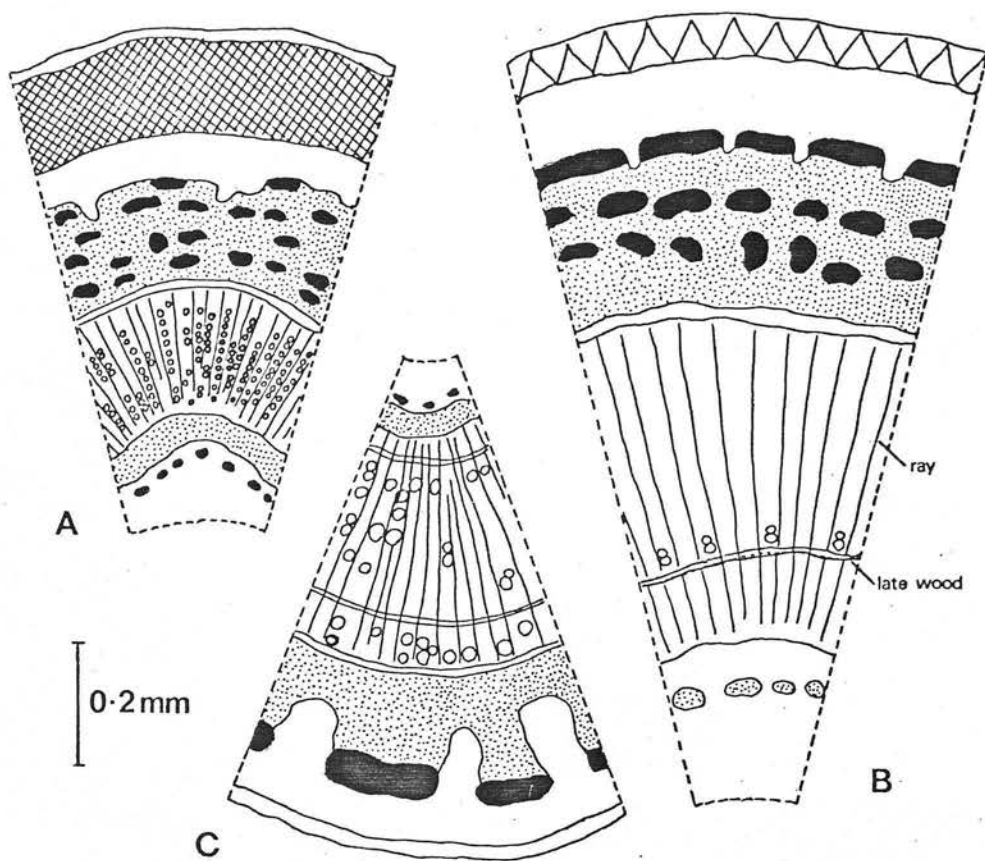
Fig. 33

Fig. 34.   T.S. of stems.

A.   Stellera chamaejasme subsp. chamaejasme. Pith wide,

cells thin-walled. Internal phloem in complete ring.

Chlorenchyma present. Collenchyma absent. x 30.

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.

C.   Dendrostellera lessertii. Old stem. Pith small. Internal

phloem not in complete ring. Growth rings and cork present.

Collenchyma and chlorenchyma absent. x 30.

Ca.   Dendrostellera lessertii. Section enlarged. Wood tending

to be ring-porous. x 70.

Cb.   Dendrostellera lessertii. Young stem. Cortex wide,

parenchymatous. Epidermal hairs present. x 30.

Stellera, Stelleropsis and Dendrostellera - internal phloem

fibres absent.

0·5mm

cambium

growth
ring

vessels

internal phloem

pith
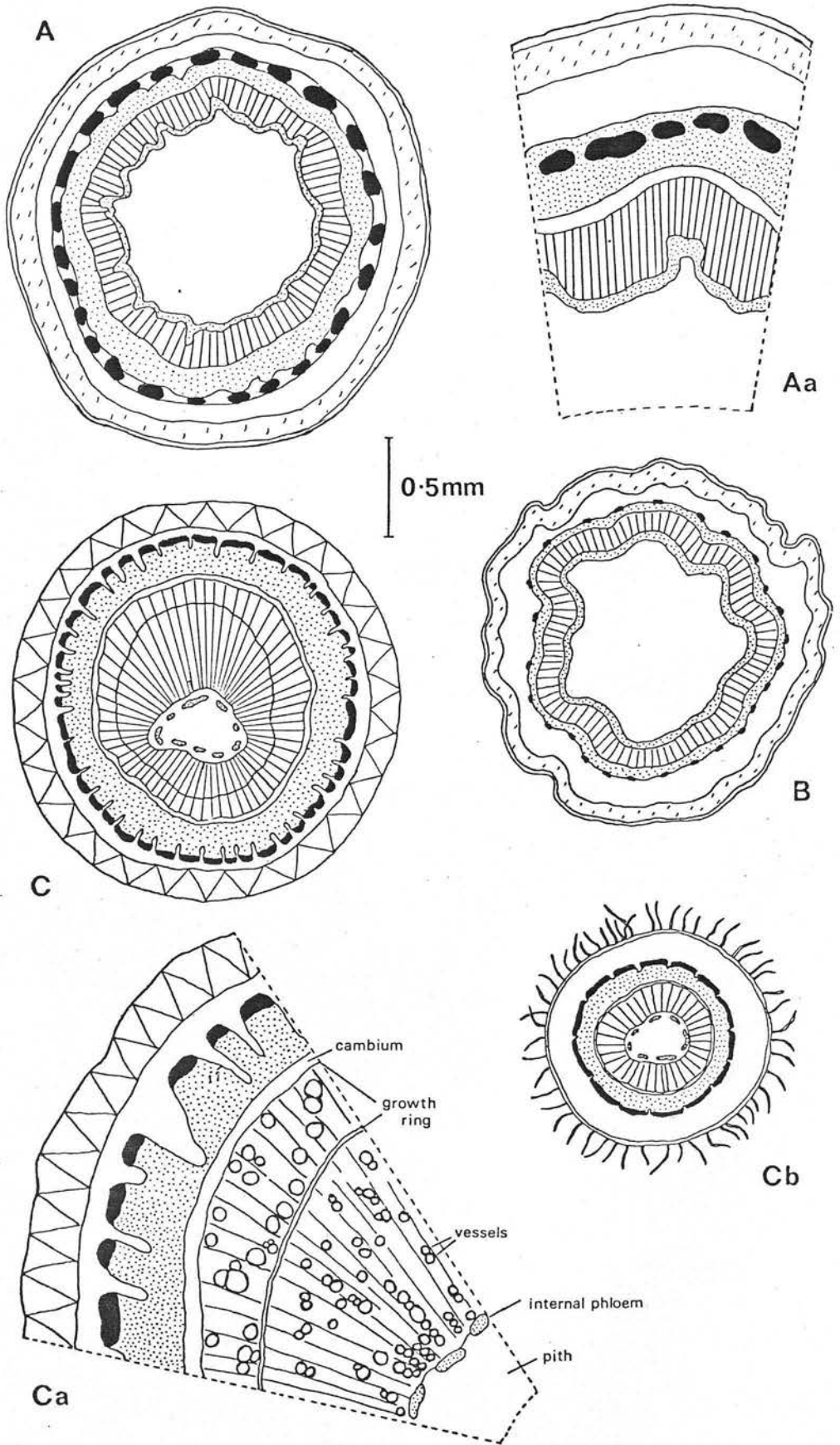
Fig. 34

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.

Ca.   Restella albertii. Node unilacunar.

D.   Wikstroemia chamaedaphne. Rays narrow. Vessels in radial
      rows.

Da.   Wikstroemia chamaedaphne. Section enlarged.

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.
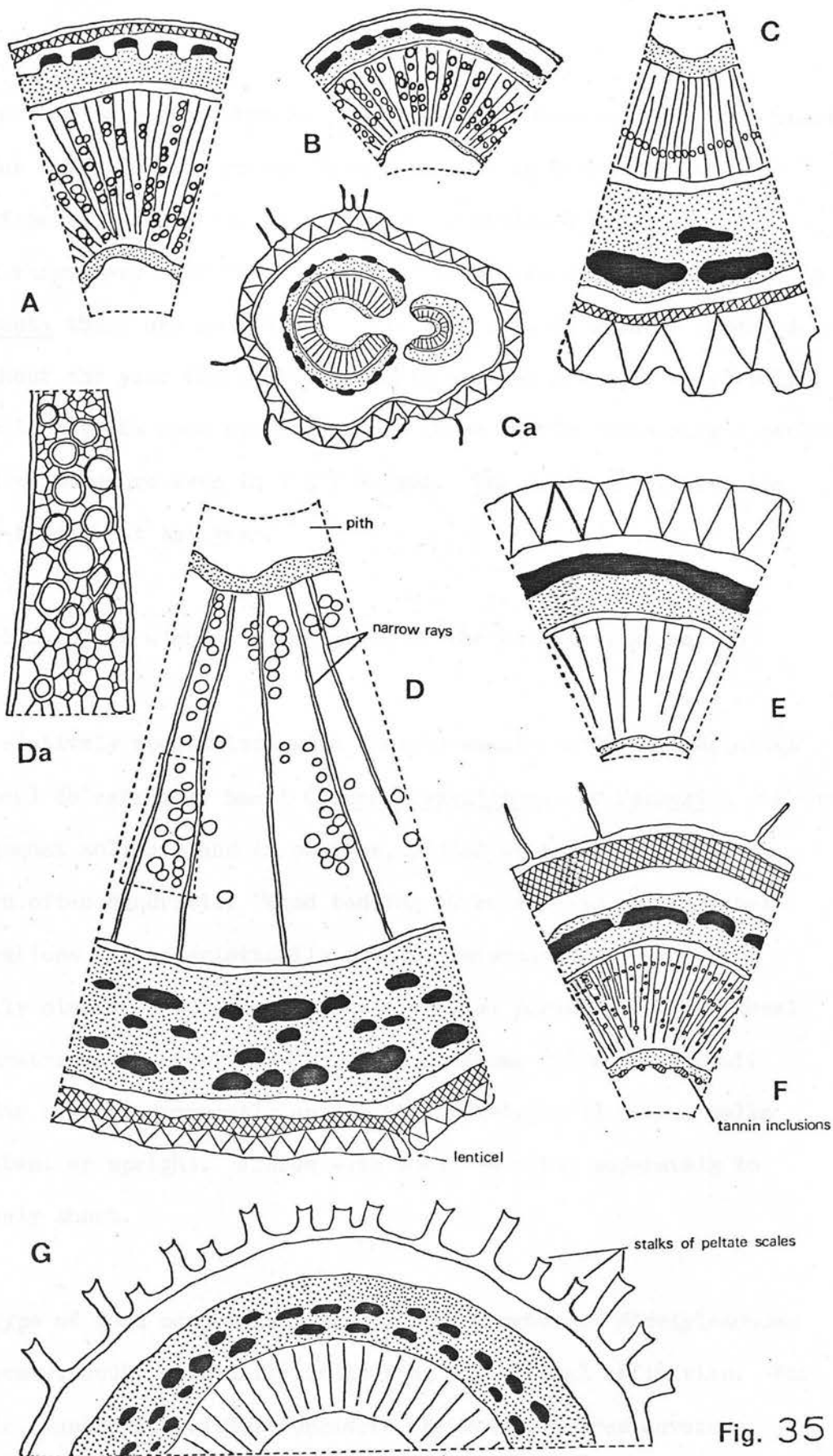
Fig. 35

Wood

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, intervascular pitting in
radially clustered vessels alternate. Axial perenchyma 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 paren-
chymatous. 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 environ-
ment.

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. 36C).

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.

160

collenchyma

B

epidermal hair

periderm

starch bodies

p.p.
s.p.

cortical parenchyma

s.x.

C
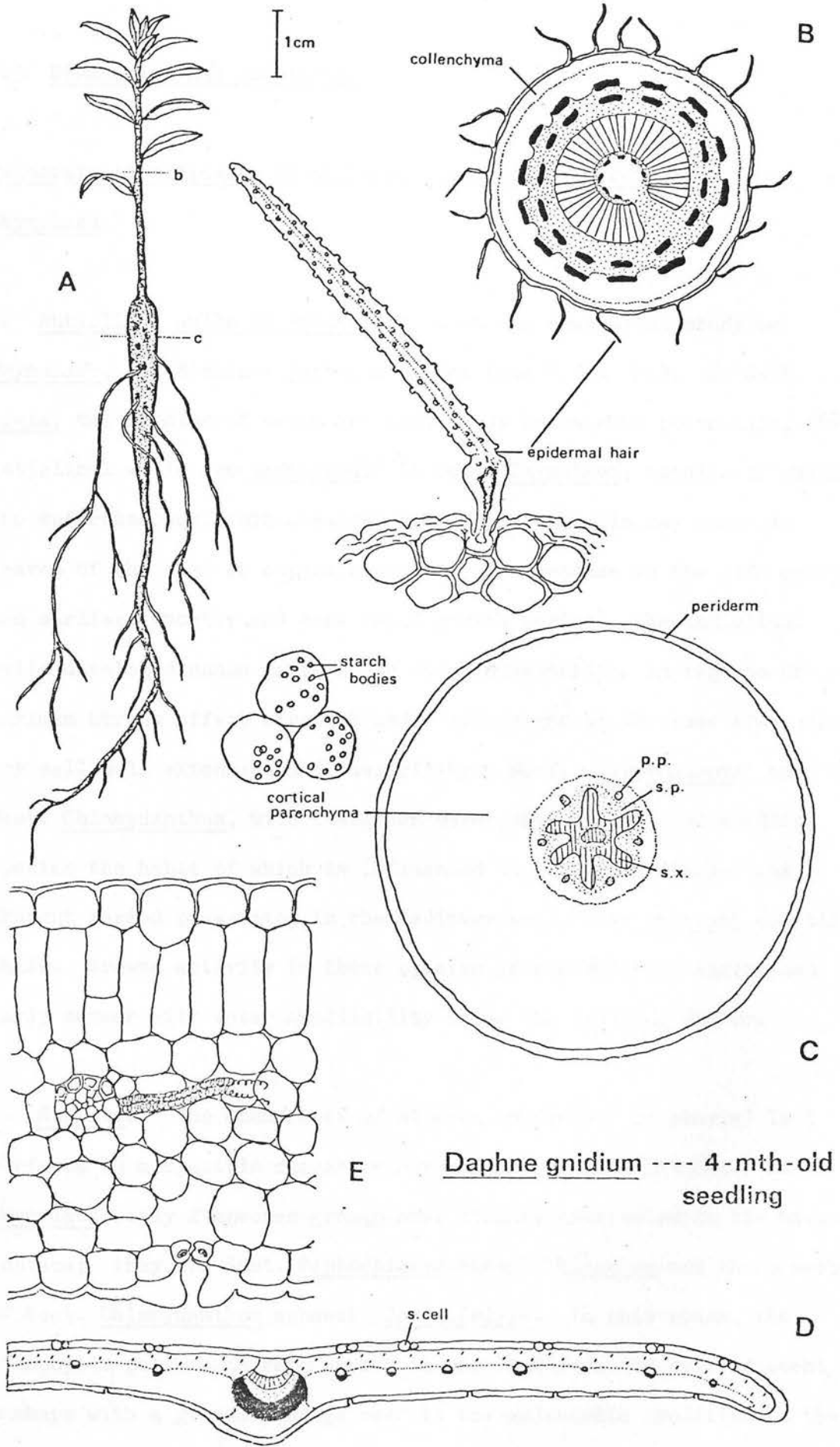
E   Daphne gnidium ---- 4-mth-old
seedling

s. cell

D

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 availibility 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. <u>Secondary (2°) phloem fibres in stem</u>: 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 <u>Thymelaea</u> although Vogl (1910) considers their arrangement diagnostic for species of <u>Daphne</u>. I did not investigate a wide enough range of material of <u>Daphne</u> to confirm this.

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

7. <u>Vessel distribution</u>: 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 <u>Thymelaea</u> and <u>Daphne</u> with vessels being solitary, and in radial, oblique and tangential groups.

8. <u>Vascular rays</u>: 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. <u>Internal phloem</u>: this is present in the stem of <u>all</u> 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. Ptochlamys. They have so far not been observed in Sect. Chlamydanthus. They are absent or present in Daphne and completely absent in Restella Wikstroemia, Stelleropsis, 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 unlignified phloem fibres is always well developed, forming a vascular

cap. 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. <u>Dorsiventrality of leaves</u>: 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: <u>Thymelaea</u>, <u>Daphne</u>

Leaves isobilateral: <u>Restella</u>, <u>Stelleropsis</u>, <u>Diarthron</u> <u>vesiculosum</u>

Leaves dorsiventral: <u>Wikstroemia</u>, <u>Passerina</u>, <u>Diarthron</u> <u>linifolium</u> (!)

<u>Dendrostellera</u> and <u>Stellera</u> have isobilateral or weakly dorsiventral leaves.

16. <u>Crystals</u>: sand-like, in the form of raphides or prismatic crystals, not in idioblasts. However, in <u>Daphne laureola</u> subsp. <u>philippi</u> 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. <u>Tannin</u>: 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 <u>Thymelaea</u>, e.g. <u>T. tinctoria</u>. The occurrence of tannin in the abaxial epidermis and bundle sheath of <u>Passerina</u> has already been commented on (see Table 3).

18. <u>Sclereids</u>: foliar sclereids were found to be present in mature leaves of all 30 species of <u>Thymelaea</u>. 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. 30 A - 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 ab-
sorption 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° 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

TABLE 4. _Thymelaea_. Some anatomical characters of the leaf.

Column groups: "Stomatal type" = anomocytic, modified tetracytic, anisocytic. "Anticlinal walls of epidermis" = Adaxial (straight, undulated) and Abaxial (straight, undulated). "Sclereids at apex" = weakly developed, well developed.

SPECIES	amphistomatic	epistomatic	anomocytic	modified tetracytic	anisocytic	Adaxial straight	Adaxial undulated	Abaxial straight	Abaxial undulated	Sclereids throughout	weakly developed	well developed
Sect. Pintochlamys												
Subsect. Hirsutae												
1. T. lythroides		x	x			x		x			x	+
2. T. hirsuta		x	x			x		x			x	+
3. T. lanuginosa		x	x			x		x			x	x
4. T. gattefossei		x	x			x		x			x	x
Subsect. Argentatae												
5. T. argentata	x		x	x		x		x			x	+
6. T. virescens	x		x	x		x			x		x	+
7. T. putorioides	x		x	x	x	x		x			x	×
Subsect. Sempervirentes												
8. T. microphylla	x		x	x		x		x			x	x
9. T. sempervirens	x		x	x		x		x			x	+
Sect. Chlamydanthus												
Subsect. Tartonraira												
10. T. tartonraira	x		x	x		x		x			x	+
11. T. velutina	x		x	x		x		x			x	+
12. T. dioica	x		x			x	o	o	x		x	x
Subsect. Coridifoliae												
13. T. tinctoria	x		x	x		x		x			x	+
14. T. subrepens	x		x	x		x	o	x	o		x	x
15. T. procumbens	x		x			x		x			x	×
16. T. ruizii	x		x			x		x			x	x
17. T. calycina		x	x			x		x			x	x
18. T. coridifolia		x	x			x		x			x	x
19. T. broteriana		x	x			x		x			x	x
Sect. Thymelaea												
Subsect. Antiatlanticae												
20. T. antiatlantica	x		x	x		o	o	o	o		x	x
21. T. virgata	x			x		o	o	o	o		x	x
Subsect. Sanamunda												
22. T. villosa	x		x	x		x		x			x	x
23. T. thesioides	x		x	x			x		x		x	x
24. T. sanamunda	x		x	x		x		x			x	+
Sect. Ligia												
25. T. cilicica	x			x	x	x		x			x	x
26. T. aucheri	x			x	x	x		x			x	x
27. T. passerina	x			x	x	x		x			x	x
28. T. gussonei	x			x	x	x		x			x	x
29. T. salsa	x			x	x	x		x			x	+
30. T. mesopotamica	x			x	x	x		x			x	+

TABLE 5. THYMELAEA. Some anatomical characters of the stem.

SPECIES	Young stem		Old Stem				
	Indumentum	Internal phloem fibres	Stomata	Cork	Chlorenchyma	2° phloem rays dilated	Internal phloem fibres
1.	x	+		x		x	+
2.	x	+		x		x	+
3.	x			x		x	
4.	x	+		x	-	x	+
5.	x	x		x		x	x
6.	x	x		x		x	x
7.	x	x		x			x
8.	x	x	x	+	x		x
9.		x	x	+	x		x
10.	o			x			
11.	x			x			
12.				x			
13.	x			x		x	
14.	x			x			
15.	x			x		x	
16.	x			x		x	
17.	x			x		x	
18.	x			x			
19.	x			x		x	
20.	x	x	x	+			x
21.	x	x	x	+	x		x
22.	x			x			
23.	x	x	x	+	x		x
24.	o	x	x	+	x		x
25.			x		x		
26.		x	x		x		x
27.		x	x		x		x
28.	x	x	x		x		x
29.			x		x		
30.	x		x		x		

x = feature always present
blank = feature absent or
    not recorded
o = feature sometimes
    present
+ = feature moderately
    developed

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 chamaejasme 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 paren-chymatous 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 <u>Diarthron linifolium</u> and <u>Stellera</u> <u>chamaejasme</u> 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. 40.C). Stomata are absent from both filament and anther.

The outermost wall layer of the anther is the epidermis. In <u>Passerina</u> (Fig. 40 D), 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 <u>Thymelaea passerina</u> (see Sect. 4.3). Preparations of other species were of the older stages. According to Kausik (1940), all the wall
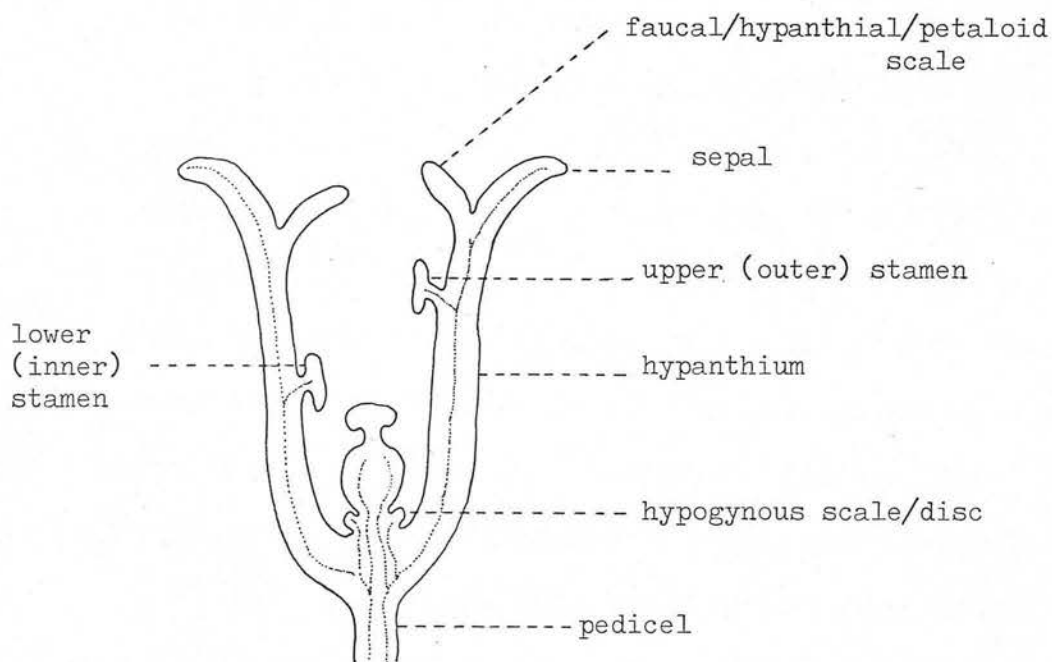
Fig. 38. Diagram of flower with hypogynous and faucal scales.
I have used the terms 'hypanthium' and 'sepal' to indicate the
perianth tube and lobes since anatomical evidence currently favours
this.
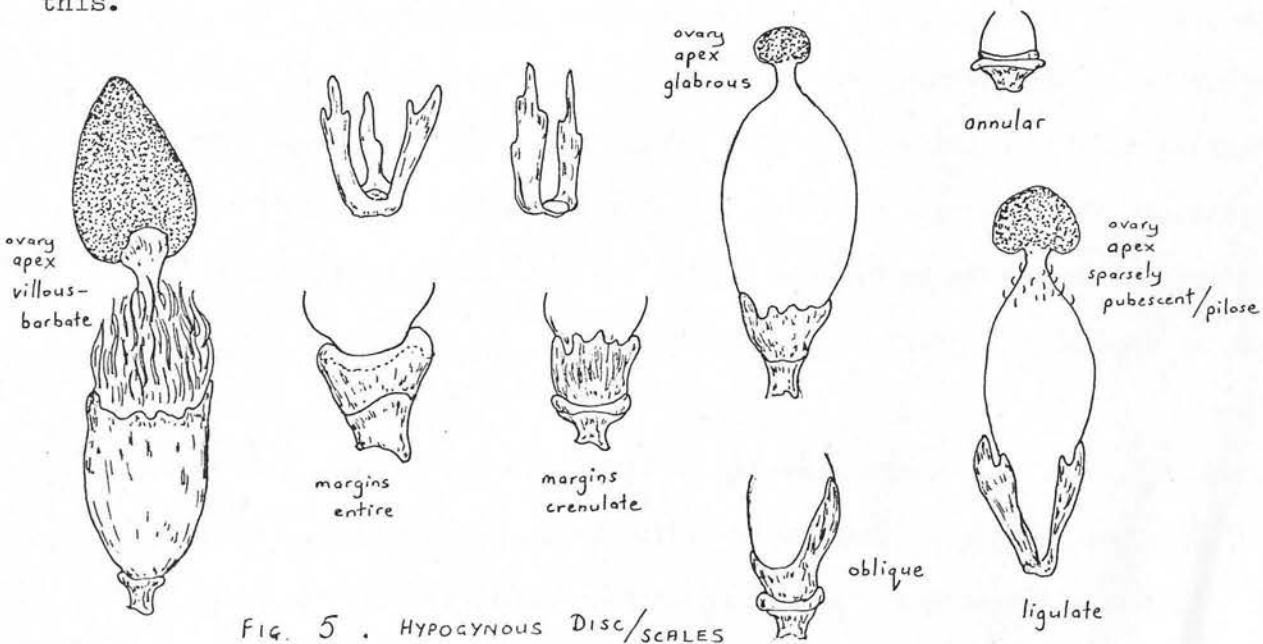
FIG. 5 . HYPOGYNOUS DISC/SCALES

layers in <u>Lasiosiphon eriocephalus</u>, 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. <u>Dicranolepis</u>, <u>Gnidia</u>, <u>Lachnaea</u>, <u>Struthiola</u>. 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 <u>Stellera chamaejasme</u> to represent a much reduced corolla because of its vascular supply from the receptacular stele (Fig. 200 B).

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 <u>intrastaminal</u>. <u>Gonystylus</u>, which is included in the Thymelaeaceae by some workers (Airy Shaw, 1947, 1973), does have 30 - 40 petaloid structures which are <u>extrastaminal</u> 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 <u>Thymelaea hirsuta</u> 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 <u>Stellera chamaejasme</u>. Present findings in this species conform in all respects to his investigations and additional studies on the gynoecium in <u>Thymelaea</u> appear to support his views too.

In <u>Thymelaea</u>, 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 Thymelaeaceae 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.

Aa

Ba

Ca

A

B

C

0·5mm

0·2mm
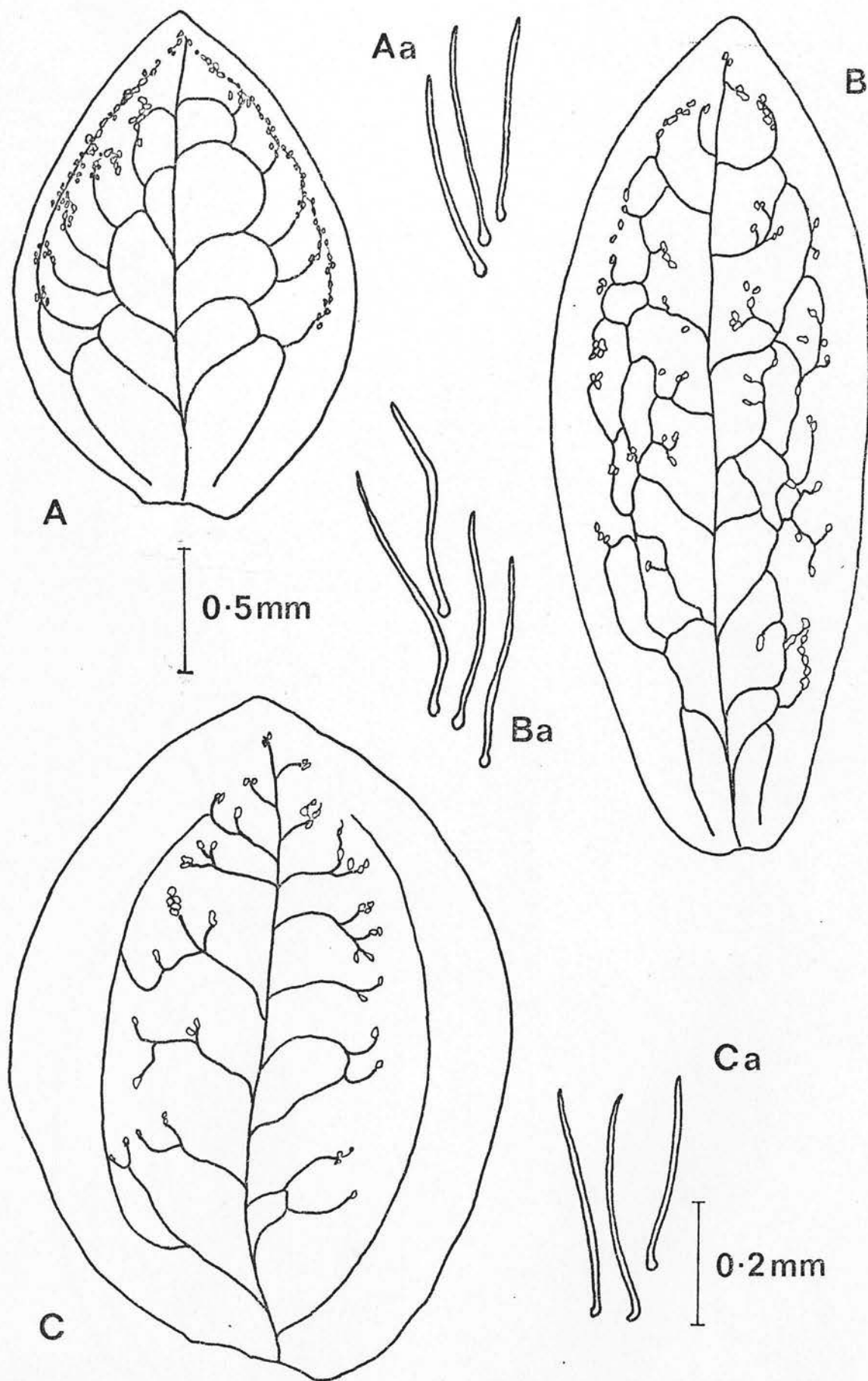
Fig. 37

Fig. 39.   <u>Thymelaea tartonraira</u> subsp. <u>tartonraira</u> var. <u>transiens</u>.

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).

sclereids

lateral
bundle

midrib
bundle

A

Aa

B

s.b.
l.b.
ovule

Ba

o.b.

s.b.

l.b.

Ab
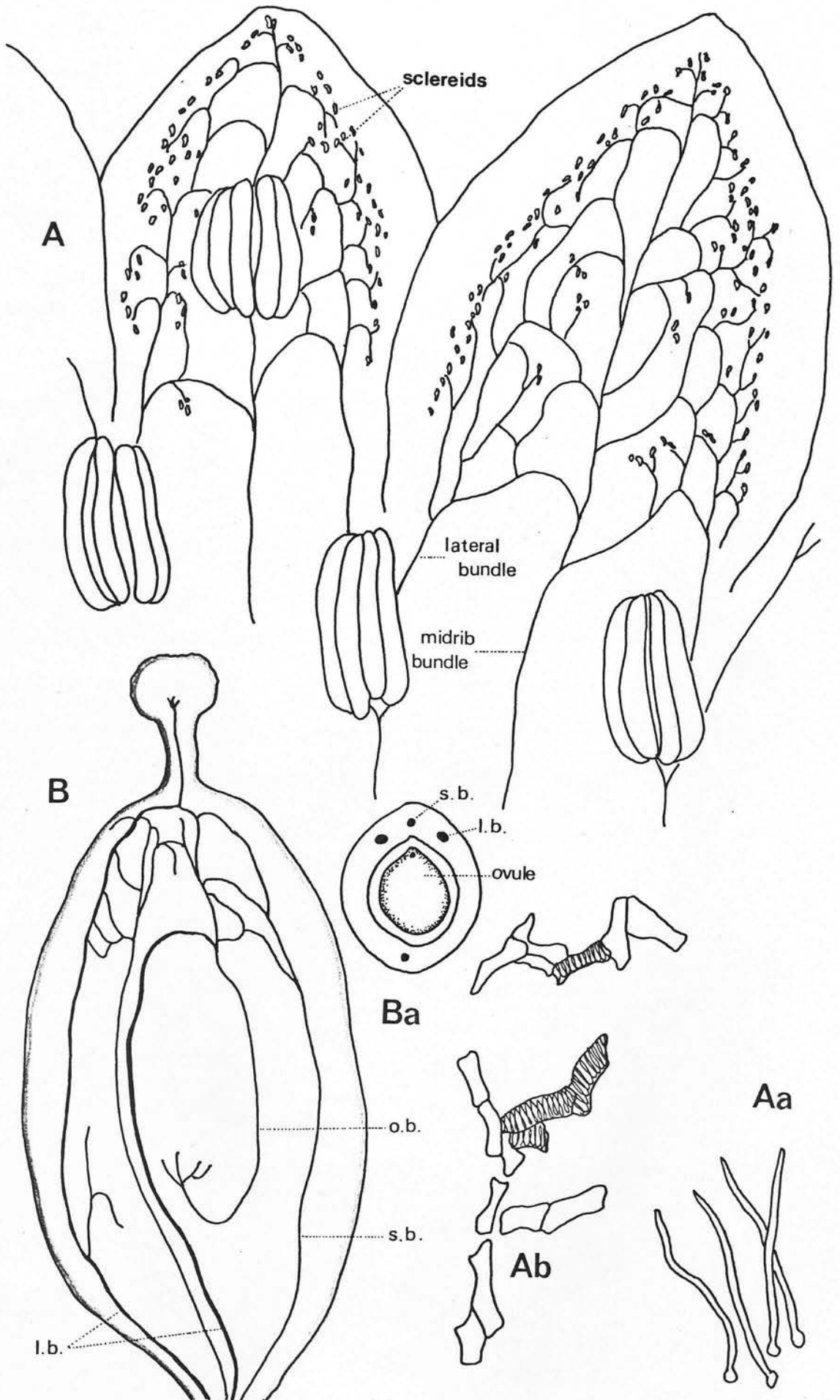
Fig. 39

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.

A

sepal

filament

stigma

B

sieve
element

xylem
element

C

D

0·4μ

E

F

Fig. 40
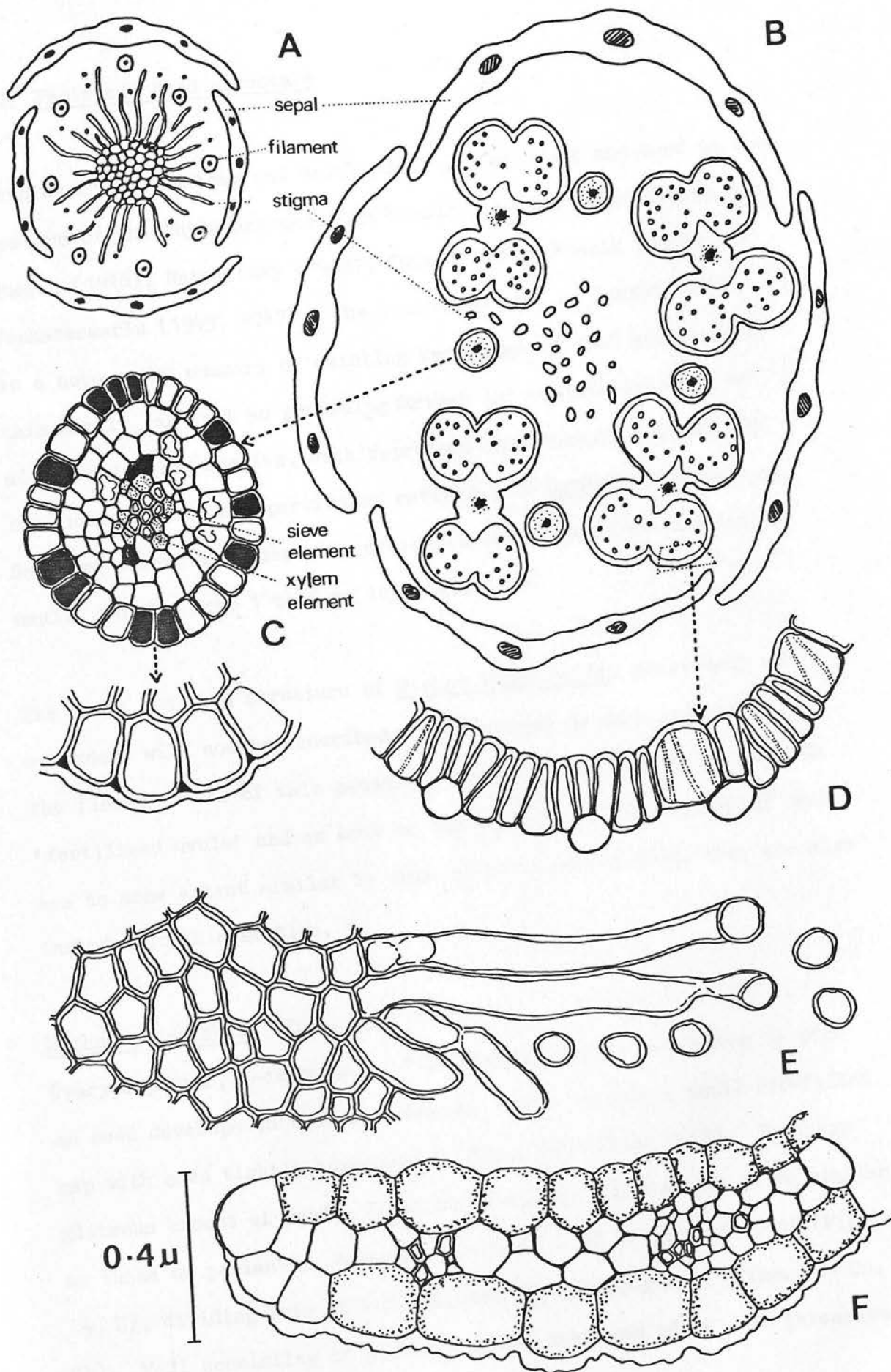
4.2 Fruit and seed structure

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 un-
recorded, 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 then 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. 42 D). 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. 42 D, 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 longifolia from China as having three layers - an external layer which is cellular and membraneous, 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 crustaceous, black or blackish-brown; tegmen membraneous, 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 endo-
carp 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 nuceller 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 eriocephalus 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. 41 B).
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. 41 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. 41 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. 44 Fa) are present
on the outer epidermis of the pericarp as well as on the testa (Fig.
44 Ea) 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. 43 Da, 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 seed-
ling stage. Anomocytic stomata were present on the upper epidermides
in most species of Thymelaea (Fig. 44 Ba).

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 familes 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 endo-
tegmen 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.
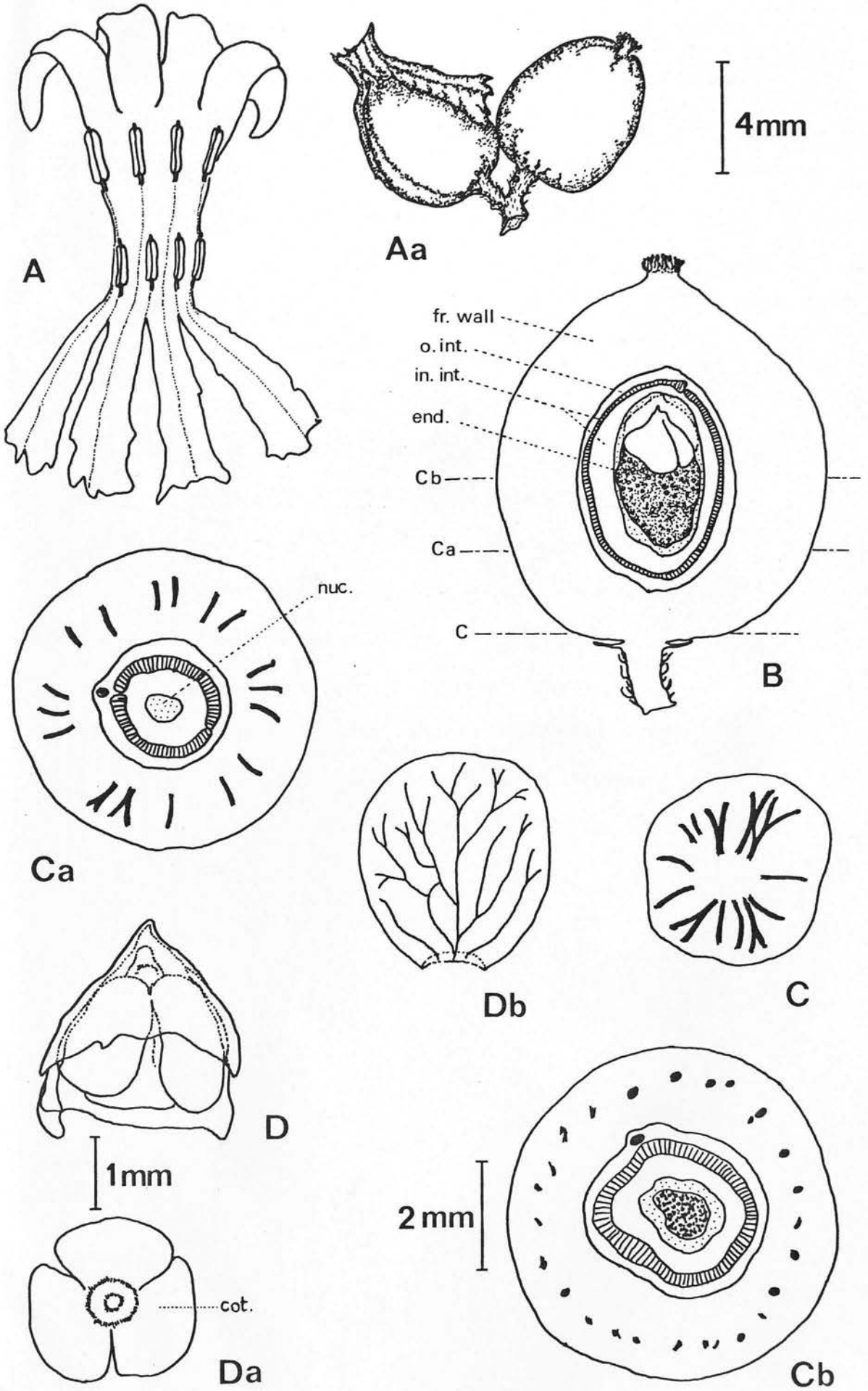
Fig. 41

Fig. 42. <u>Daphne longilobata</u>. 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.
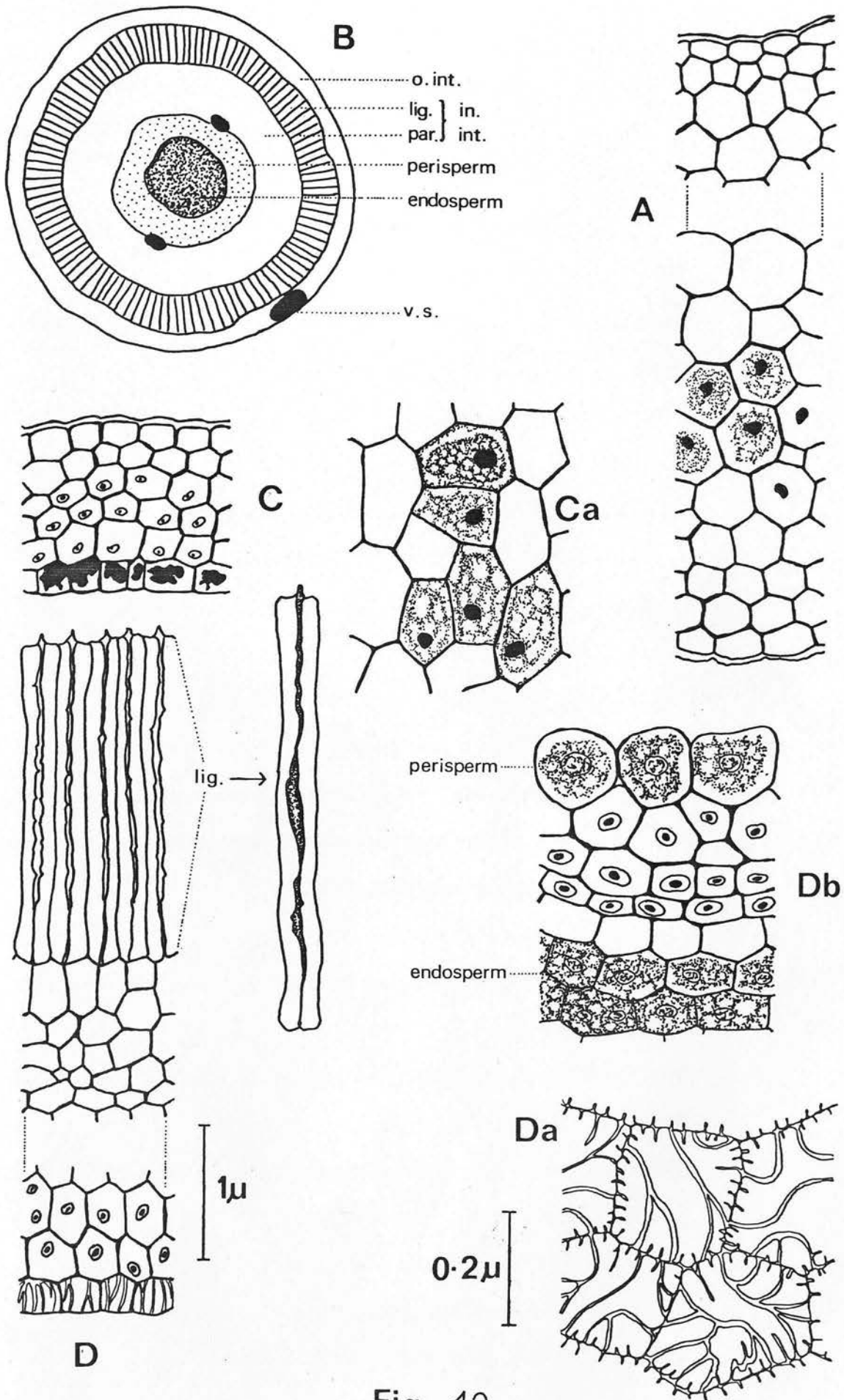
Fig. 42

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.

Aa.   Abaxial view of stamen. Dehiscence longitudinal, introrse.

B.   Ovary with hypogynous disc in section.

Ba.   View of stigma from above. Shape triangular, centre shallowly
depressed.

Bb.   Stigmatic papillae. Nuclei large, deep-staining.

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 membraneous
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.

Ga.   Endosperm cells from squash preparation.
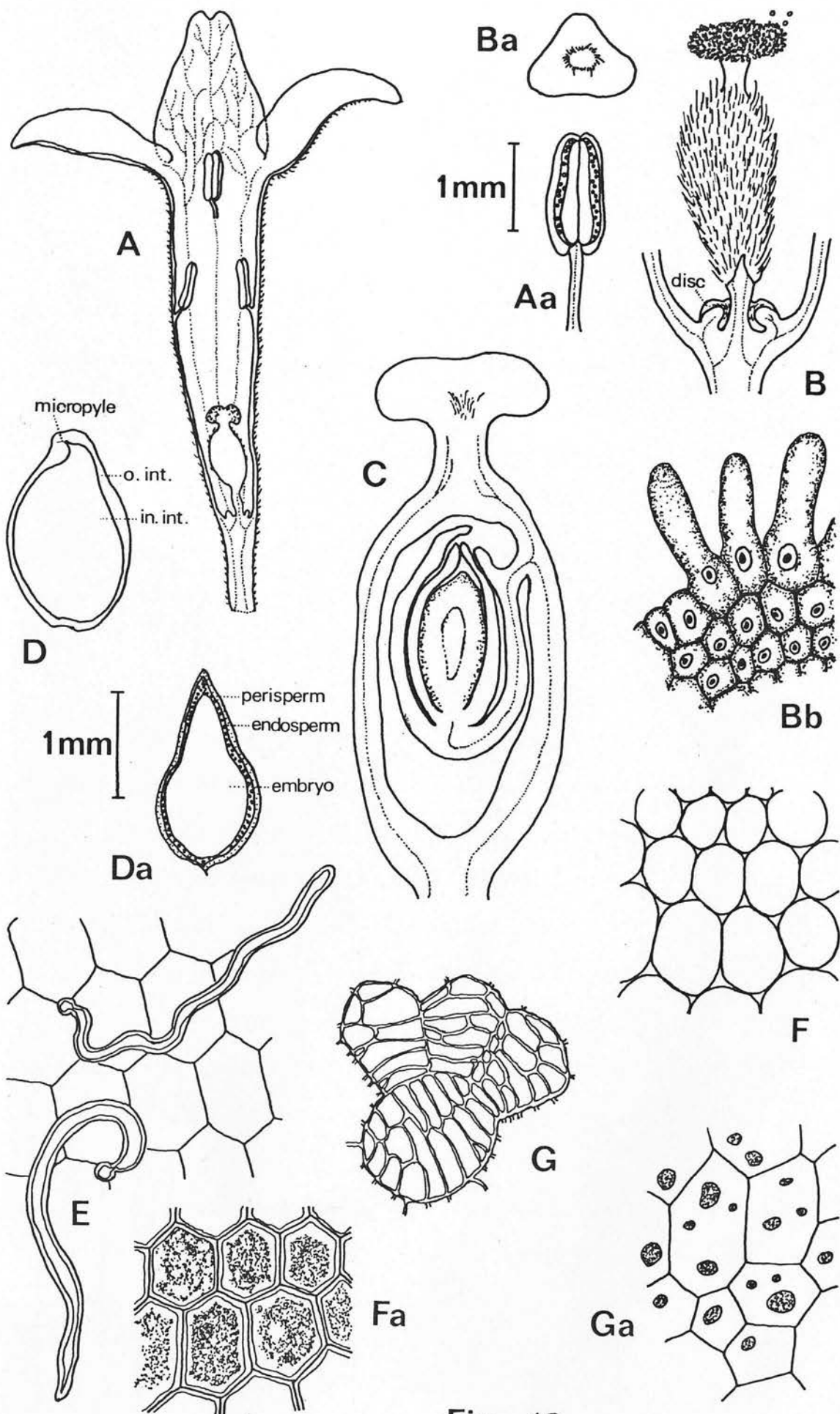
Fig. 43

Fig. 44.   <u>Thymelaea lythroides</u>. 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.

Fa.   Outer epidermis of pericarp in surface view. Stomata and
        hairs present. Cells with brown-coloured contents.

A, Ab & Ac on same scale; Ba - F on separate scale. Aa and B
not drawn to scale.
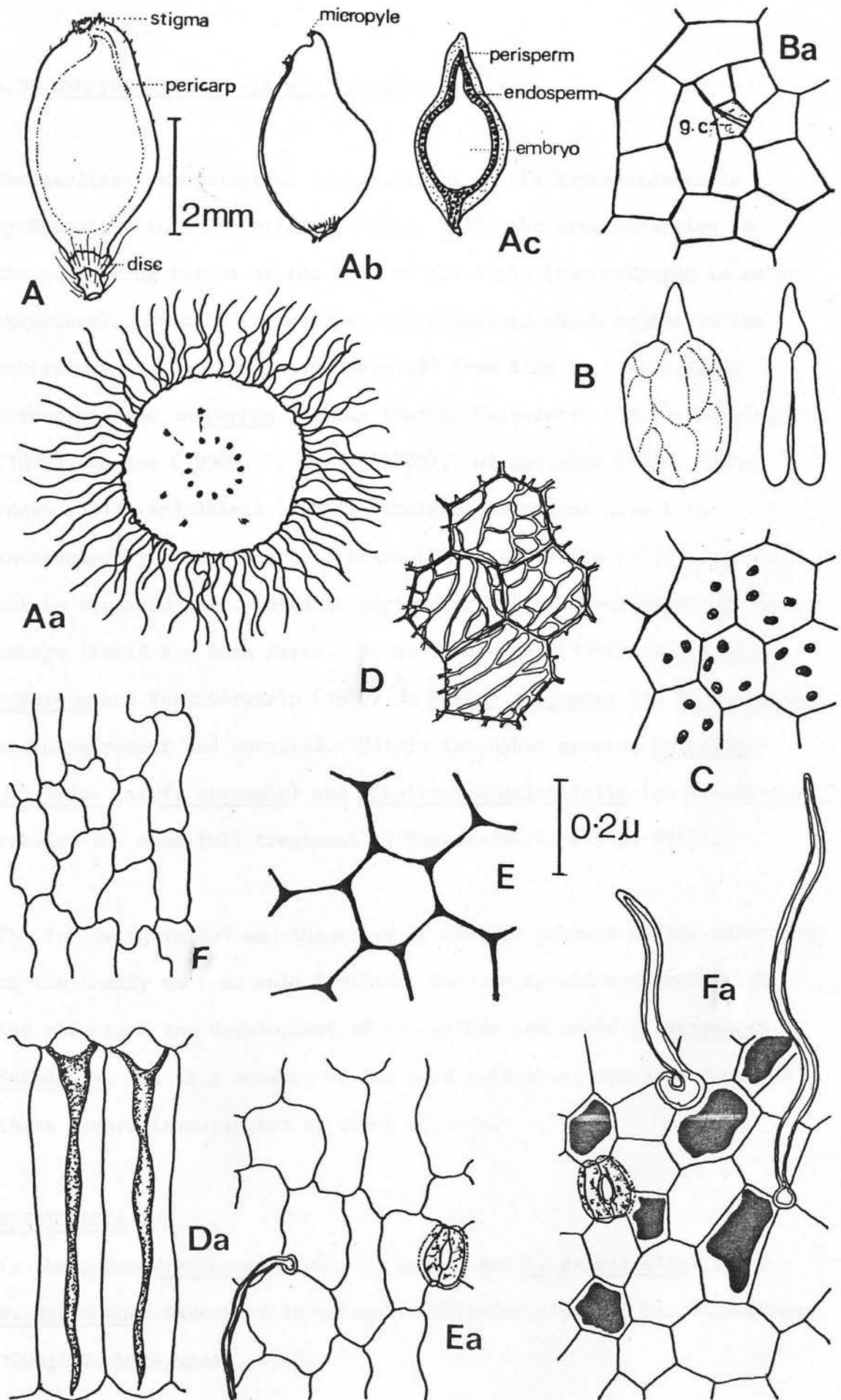
Fig. 44

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 periclinally 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 W. indica,
i.e. development of an embryo from a nucellar cell.

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

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 Daphne and
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 vestigal in mature seeds. Embryo development conforms
to the Erodium variation of the Asterad type, i.e. an epiphyseal
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. odora, 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. odora, 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. laureola, D. odora 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. laureola, 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 in-
tensely 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 membraneous 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 green-
house 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,
monoecious 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 fuchsin. The large grains,
on the other hand, do not stain as deeply.

In monoecious (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 <u>T. passerina</u> 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. hirsutâ
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. ruizii |
      | T. gattefossei | T. calycina |
      | T. velutina | T. coridifolia |
      | T. dioica | T. antiatlantica|
      | T. tinctoria | T. villosa |
      | T. subrepens | T. thesioides |
      | T. procumbens | 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 monoecious. 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. 52 Fc). 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, Nalepa 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 <u>D. mucronata</u>') 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. <u>Passerina</u> 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° 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. tartonraira 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. tartonraira from coastal France. No cytological studies of

the other subspecies in the T. tartonraira 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 geog-
raphical 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.

TAXA	2n	REFERENCE
DAPHNE alpina	18	Strasburger, 1909
blagayana	18	Nevling, 1962a
cneorum	18	Baksay, 1956
genkwa	18	Nevling, 1962b
giraldii	18	Nevling, 1962b
gnidium	18	Bjorkqvist et al., 1969; Delay, 1969
jezoensis	18	Kitamura,
kiusiana	18	Osawa, 1913
laureola	18	Loeve & Kjellqvist, 1974
* longilobata	18	Tan, H. K., unpubl.
mezereum	18	Maude, 1940; Sorsa, 1962; Majovsky et al., 1970
odora	28, 27	Hiraoka, 1958; Okura & Kono, 1959
oleoides	18	Bhat et al., 1974
papyracea	18	Venkateswarlu, 1946a; Sharma & Sarkar (ed.) 1967-68
pseudomezereum	18	Osawa, 1913
sericea	18	Nevling, 1964b
x burkwoodii	18	Nevling, 1964a, 1964b
x hybrida	18	Nevling, 1966
x mantensiana	18	Nevling, 1964a
DAPHNOPSIS americana	18	Nevling, 1962a, 1963; Nevling & Woodbury, 1966
helleriana	36	Nevling & Woodbury, 1966
philippiana	18	Nevling, 1963; Nevling & Woodbury, 1966
DICRANOLEPIS persei	18	Mangenot & Mangenot, 1957
polygaloides	18	Mangenot & Mangenot, 1957
DIPLOMORPHA trichotoma	28	Lee, Y. N., 1969
DIRCA occidentalis	38	Stebbins & Major, 1965
DRAPETES ericoides	18	Borgmann, 1964

* newly determined by author

TABLE 6 (contd.) Known chromosome numbers in the Thymelaeaceae.

TAXA	2n	REFERENCE
EDGEWORTHIA gardneri	18	Arora, 1961
papyrifera	36	Nishiyama & Watanabe, 1960
IASIOSIPHON eriocephalus	16	Subramanyam & Kamble, 1967
PIMELEA cinerea	36 diploid	Cruickshank, 1953
curvifolia	36	Cruickshank, 1953
drupacea	108 hexaploid	Cruickshank, 1953
flava	36	Cruickshank, 1953
glauca	36	Cruickshank, 1953
humilis	72 tetraploid	Cruickshank, 1953
ligustriana	36	Cruickshank, 1953
lindleyana	90 pentaploid	Cruickshank, 1953
longifolia	36	Rattenbury, 1957
nivea	36	Cruickshank, 1953
pauciflora	36	Cruickshank, 1953
pygmaea	36	Cruickshank, 1953
sericea	36	Cruickshank, 1953
serpillifolia	36	Cruickshank, 1953
spathulata	36	Cruickshank, 1953
urvilleana	36	Rattenbury, 1957
THYMELAEA passerina	18	Kuzmanov, 1973; Majovsky et al., 1974
micropylla	18	Reese, 1957
tartonraira subsp. thomasii	18	Contandriopoulos, 1964b
WIKSTROEMIA canescens	18	Venkateswarlu, 1946a
eugenioides	18	Gupta & Gillett, 1969
forbesii	18	Gupta & Gillett, 1969
furcata	18	Gupta & Gillett, 1969
indica	36	Chuang et al., 1962
isae	18	Gupta & Gillett, 1969
leptantha	18	Gupta & Gillett, 1969
oahuensis	18	Gupta & Gillett, 1969
phillyreifolia	18	Gupta & Gillett, 1969
pulcherrima	36	Skottsberg, 1955; Gupta & Gillett, 1969
recurva	18	Gupta & Gillett, 1969
sandwicensis	18	Gupta & Gillett, 1969
sellingii	18	Gupta & Gillett, 1969
uva-ursi	18,72	Skottsberg, 1955; Gupta & Gillett, 1969
vacciniifolia	18	Gupta & Gillett, 1969

TABLE 7. Known chromosome numbers in the Elaeagnaceae and Penaeaceae.

TAXA	2n	REFERENCE
HIPPOPHAË rhamnoides	24	Rousi, 1965a, 1971; Leveque & Gorenflot, 1969
salicifolia	24	Rousi, 1971
ELAEAGNUS thunbergii	28	Hsu, 1967
BRACHYSIPHON rupestris	20	Dahlgren, 1968a
PENAEA cneorum	20	Dahlgren, 1971
mucronata	20	Dahlgren, 1971
SALTERA sarcocolla	c.40	Dahlgren, 1968a

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

<u>Daphne longilobata</u> (Lecomte) Turrill

somatic metaphase, ovule. 2n = 18.
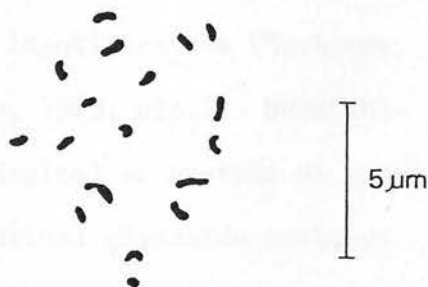
5.2 Phytochemistry

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.). Relation-
ships 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 familes
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.

and W. ovata C.A. Meyer ex Meissn.

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-8-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-β-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 $C_{20}H_{14}O_6$) 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 familes 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 <u>Daphne genkwa</u> Sieb. & Zucc.,
linarin from <u>D. laureola</u>, hesperidin from <u>D. mezereum</u>, luteolin-7-glucoside
from <u>D. oleoides</u> Schreb. and two unidentified glycosides from the root
of <u>D. papyracea</u>.

3. <u>Tannins</u>

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 <u>Daphne</u>, <u>Passerina</u> and <u>Thymelaea</u> 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. <u>Toxic constituents</u>

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 $(C_{27}H_{30}O_8)$: of which 0.02% is present in the dried bark of D. mezereum 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. mezereum.

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, Lachnaea, 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.

6. Sterines, terpenes, ethereal oils and waxes.

β-sitosterin is the most frequently occurring sterine. In addition,
0.33% 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. papyracea (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 γ-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 agarospirol, $C_{15}H_{26}O$),
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. <u>Pigments</u>: the leaf and bark of <u>Phaleria capitata</u> Jack contain a
bluish pigment which has been used to produce an indigo-dye. Carotenoids
are present in the bark and fruits of <u>Daphne</u>, 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 'pao d'aguila' which the French translated into 'bois d'aigle' and the

English, 'Eagle-wood' (fide Burkill, 1935).

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 Aloewood '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.

Gonystylus bancanus 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 over-
dose, 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 polycephala, 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 humours and cholers'

Other medicinal prescriptions include the use of seeds of D. gnidium
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 up-
wards 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 know-
ledge 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 morpho-
logical 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 treat-
ment 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 horti-
cultural interest. The five sections and six subsections provisionally
recognised here, follow Keissler's 1898 treatment of Section Daph-
nanthes, 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. Mezereum Spach
    1. D. jezoensis Maxim. ex Regel
    2. D. kamtschatica Maxim.
    3. D. koreana Nakai
    4. D. mezereum L. (incl. D. rechingeri Wendelbo)
    5. D. pseudomezereum A. Gray

II. Sect. Genkwa Benth. & Hook.
    1. D. championii Benth.
    2. D. genkwa Sieb. & Zucc.

III. Sect. Daphne
    1. D. albowiana Woron. ex Pobed.
    2. D. glomerata Lam.
    3. D. laureola L. (type of genus)
    4. D. pontica L. (incl. D. libanotica Mouterde)

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

V. Sect. Daphnanthes C. A. Meyer
    A. Subsect. Alpinae 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. jasminea Sm.
    3. D. kosaninii (Stoj.) Stoj.
    4. D. linearifolia Hart
    5. D. malyana Blecic
    6. D. mucronata Royle
    7. D. oleoides Schreb. (incl. D. baksanica Pobed.,
       D. euboica Rech. fil., D transcaucasica Pobed.)
    8. D. rodriguezii Texidor
    9. D. stapfii Bornm. & Keissl.

    C. Subsect Gnidium (Spach) Gilg
    1. D. gnidium L.

    D. Subsect. Cneorum Keissl.
    1. D. arbuscula Celak.
    2. D. cneorum L. (incl. D. juliae Kos.-Pol.)
    3. D. petraea Leybold
    4. D. striata Tratt.

    E. Subsect. Daphnanthoides (Gilg) Keissl.
    1. D. acutiloba Rehder
    2. D. bholua Buch.-Ham. ex D. Don
    3. D. grueningiana H. Winkler
    4. D. kiusiana Miq.
    5. D. longilobate (Lecomte) Turrill
    6. D. luzonica Robinson
    7. D. miyabeana Makino
    8. D. odora Thunb.
    9. D. papyracea Wall. ex Steud. emend Smith & Cave
   10. D. sureil Smith & Cave (incl. D. shillong Banerji)
   11. D. taiwaniana (Masamune) Masamune
   12. D. tangutica 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 (<u>fide</u> several authors) of which the Asiatic ones are the least understood. It is characterized by succulent fruits naked at maturity (some species, e.g. <u>D. cneorum</u>, 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. <u>D. papyracea</u>, have a cup-shaped disc), peri-.anth tube which does not separate into an upper or lower part after anthesis, and alternate leaves (some Chinese species, e.g. <u>D. aurantiaca</u> and <u>D. genkwa</u> 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. <u>WIKSTROEMIA</u> Endl., named in honour of J. E. Wikstroem a Swedish botanist of the 19th century.

<u>Wikstroemia</u>, which is closely related to <u>Daphne</u>, 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 <u>Daphne</u> — 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 <u>Wikstroemia</u> 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 <u>Daphne</u> and <u>Wikstroemia</u> from the subtropics and E. Asia, is necessary in order to circumscribe the genera. Domke (1934) proposed the subgenera <u>Euwikstroemia</u> (<u>Wikstroemia</u> s. str.) for the fleshy-fruited species and <u>Diplomorpha</u> for some of the dry-fruited ones.

3. <u>RESTELLA</u> Pobed., name obtained by anagrammatic rearrangement of the word 'Stellera'.

The sole species (<u>Restella albertii</u>) comprising this genus was first described under <u>Stellera</u> by Regel in 1886. Pobedimova (1941) transferred it to a new genus <u>Restella</u>, 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 <u>Stellera</u>, to be the main distinguishing characters.

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

I can find no consistent and clear-cut differences between <u>Restella</u> and <u>Wikstroemia</u> (see Table 9). <u>Restella albertii</u> appears to be a perfectly good <u>Wikstroemia</u> from a different region. It must be stated that <u>Wikstroemia</u> 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 9. Characters in Thymelaea and related genera

THYMELAEA	DAPHNE	WIKSTROEMIA	RESTELLA
1. Annuals, herbaceous or suffrutescent perennials, shrubs.	1. Shrubs, rarely small trees.	1. Shrubs or small trees.	1. Shrubs.
2. Leaves alternate.	2. Alternate, rarely opposite.	2. Alternate, subopposite or opposite.	2. Alternate or subopposite.
3. Inflorescence axis not elongating in fruit.	3. Not elongating.	3. Elongating or not elongating.	3. Not elongating.
4. Bracts present or absent.	4. Present or absent.	4. Absent.	4. Absent.
5. Flowers unisexual or hermaphrodite.	5. Hermaphrodite.	5. Hermaphrodite or unisexual.	5. Hermaphrodite.
6. Perianth persistent, rarely deciduous.	6. Deciduous, rarely persistent.	6. Deciduous or persistent.	6. Persistent.
7. Perianth lobes 4; stamens 8.	7. Lobes 4, stamens 8.	7. Lobes 4/5; stamens 8/10.	7. Lobes 4: stamens 8.
8. Hypogynous disc annular with entire or shallowly crenulate margins, or absent.	8. Disc annular or cup-shaped.	8. Disc cup-shaped or unequally divided into 2-5 segments.	8. Disc unequally divided into 2-5 segments.
9. Style becoming subterminal in fruit, rarely terminal.	9. Terminal.	9. Terminal.	9. Terminal.
10. Stigma globose or discoid.	10. Globose or centrally depressed.	10. Globose.	10. Globose.
11. Pericarp membraneous at maturity.	11. Fleshy, rarely semi-coriaceous.	11. Fleshy, semi-coriaceous or membranous.	11. Membranous.
12. Fruit enclosed in perianth, rarely naked.	12. Naked, rarely enclosed in perianth.	12. Naked or enclosed in perianth.	12. Enclosed in perianth.
13. Internal phloem fibres present or absent in stem.	13. Present or absent.	13. Absent in species investigated.	13. Absent.
14. Leaves amphi- or epistomatic.	14. Amphi- or hypostomatic.	14. Amphistomatic.	14. Amphistomatic.
15. Stomata modified tetracytic, aniso- or anomocytic.	15. Modified tetracytic, aniso- or anomocytic, rarely hexacytic.	15. Anomocytic or indistinct modified tetracytic.	15. Anomocytic.
16. Anticlinal walls of leaf epidermis straight or undulated.	16. Straight, rarely undulated.	16. Straight.	16. Undulated.
17. Sclereids present in leaf.	17. Present or absent.	17. Absent in species investigated.	17. Absent.
18. Venation eucamptodromous, very rarely actinodromous.	18. Eucamptodromous	18. Eucamptodromous.	18. Eucamptodromous.
19. Divergence angle of secondary veins Type 1,2,3 or 4.	19. Type 1, 2, 3 or 4.	19. Type 1 or 4.	19. Type 2.
20. Leaves isobilateral or dorsiventral.	20. Isobilateral or dorsiventral.	20. Isobilateral or dorsiventral.	20. Isobilateral.
21. Vascular system of one main bundle in leaf with sclerenchyma not extending to epidermis.	21. One main bundle with sclerenchyma not extending to epidermis or of one large and two small lateral bundles all without sclerenchyma.	21. One main bundle with sclerenchyma extending to epidermis in species investigated.	21. One main bundle with sclerenchyma not extending to epidermis.
22. Internal phloem absent in leaves.	22. Absent or present.	22. Absent in species investigated.	22. Absent.

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 afore-
mentioned 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 in-
advertent combination by Domke must be reinstated, although the reader
must bear in mind that Wikstroemia and Stellera are two quite dis-
tinct 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, an-
nular 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 10. Characters in Stellera and related genera

	STELLERA	STELLEROPSIS	DENDROSTELLERA	DIARTHRON
1.	Suffrutescent; stems unbranched, woody at base.	Suffrutescent, stems unbranched or sparingly branched, woody at base or up to middle.	Shrubs or suffrutescent; stems branched, woody up to middle.	Annual herbs.
2.	Leaves alternate.	Alternate.	Alternate.	Alternate
3.	Inflorescence axis not elongating in fruit.	Elongating.	Elongating.	Elongating.
4.	Bracts forming involucre.	Absent.	Absent.	Absent.
5.	Flowers hermaphrodite.	Hermaphrodite.	Hermaphrodite.	Hermaphrodite.
6.	Perianth persistent in lower part, deciduous above ovary.	Persistent in lower part, deciduous above.	Persistent in lower part, deciduous above.	Persistent in lower part, deciduous above.
7.	Perianth lobes 5/6; stamens 10/12.	Lobes 4; stamens 8.	Lobes 4; stamens 8.	Lobes 4; stamens 4 or 8.
8.	Hypogynous disc unilateral, ligulate, margin entire.	Disc oblique, margins entire or shallowly lobed.	Disc cup-shaped, margins entire or obliquely lobed.	Disc absent.
9.	Style terminal.	Terminal.	Terminal.	Style terminal or sub-terminal.
10.	Stigma globose, centrally depressed.	Rarely ovoid, usually globose and centrally depressed.	Conical, rarely ovoid.	Clavate.
11.	Pericarp membranous at maturity.	Membranous.	Membranous.	Membranous.
12.	Fruit enclosed in glabrous lower part of perianth.	Enclosed in glabrous or pubescent lower part of perianth.	Enclosed in densely sericeous-villous lower part of perianth.	Enclosed in slightly inflated lower part of perianth.
13.	Internal phloem fibres absent in stem.	Absent.	Absent.	Absent.
14.	Leaves amphi- or hypostomatic.	Amphistomatic.	Amphistomatic.	Amphistomatic.
15.	Stomata anomocytic to complex modified tetracytic.	Modified tetracytic or indistinct anomocytic.	Anisocytic or modified tetracytic.	Modified tetracytic.
16.	Anticlinal walls of leaf epidermis straight.	Weakly undulated, straight in costal region.	Straight or weakly undulated.	Undulated.
17.	Sclereids absent in leaf.	Absent.	Present.	Present.
18.	Venation acrodromous, suprabasal.	Eucamptodromous.	Acrodromous, basal.	Eucamptodromous.
19.	Leaves isobilateral or weakly dorsiventral.	Isobilateral.	Isobilateral or weakly dorsiventral.	Isobilateral or dorsiventral.
20.	Vascular system of one main bundle in leaf with sclerenchyma not extending to epidermis.	One main bundle with sclerenchyma not extending to epidermis.	One main bundle with sclerenchyma not extending to epidermis.	One main bundle with sclerenchyma not extending to epidermis.
21.	Internal phloem absent in leaves.	Internal phloem present in material examined.	Absent.	Absent.

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 Diarthon, 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 Dendro-
stellera (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 eucampto-
dromous 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 morpho-
logical 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 mag-
nitude.

8. STELLERA L., after G. W. Steller, traveller and naturalist who died
at thirty-seven.

Although undoubtedly allied to the 'Diarthron-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-merous 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 <u>Pimelea crassipes</u> Heer in the Middle
Sarmatian layer of E. Transcaucasia (Khatseba region), <u>Daphne personii-</u>
<u>formis</u> Weber in Tertiary deposits of Sakhalin (near Mgachi) and <u>Daphne</u>
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 <u>Pimelea</u> (Weyland, 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.
<u>Pimelea</u>, 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. <u>Thymelaea</u> is excluded, it being covered in greater detail
in Chapter VII.

1. <u>DAPHNE</u> (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 <u>D. mezereum</u> and in E. Asia, by <u>D. kamtschatica</u>, both of Sect. <u>Mezereum</u>. The former reaches to the Arctic Circle in Norway and Fennoscandia. In the south, <u>D. composita</u> (belonging to Sect. <u>Eriosolena</u>) extends to W. Java; on the western side, the limit is reached with <u>D. laureola</u> (Sect. <u>Daphne</u>) 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. <u>Daphne</u> (Map 1) and the subsections <u>Gnidium</u> (Map 2), <u>Oleoides</u>, <u>Collinae</u> and <u>Cneorum</u> (Map 3) of Sect. <u>Daphnanthes</u>, all occur in Europe with Subsect. <u>Oleoides</u> having one species extending further through Iraq and Iran to W. Pakistan. <u>Daphnanthes</u> subsect. <u>Alpinae</u> (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. <u>Daphnanthoides</u> (Map 2) is wholly Asiatic, ocurring mainly in the Himalayas, China, Japan, Formosa and also in high altitude moss-forest in N. Philippines.

Disjunctions are noted in Sect. <u>Mezereum</u> (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 <u>D. mezereum</u>. 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. <u>Eriosolena</u> (Map I) is a ditypic section restricted to montane
rain forests of Yunnan and S. E. Asia. Sect. Genkwa (Map I) again
is a very small section occurring in E. China, Formosa and S. Korea.
The type species, <u>D. genkwa</u> although widely cultivated in Japan is
not known to be native there.

2. <u>WIKSTROEMIA</u> (Map 5).

The distribution of only two species, <u>W. salicifolia</u> and <u>W. chamae-</u>
<u>daphne</u>, 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, <u>W. chamaedaphne</u>. This has a
more easterly distribution in the Northern Chinese provinces of Hupeh,
Shensi, Kansu, etc.

3. <u>RESTELLA</u> (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. <u>DIARTHRON</u> (Map 6).

One species, <u>D. vesiculosum</u>, is a widespread weed in C. and S.W. Asia.

The other, <u>D. linifolium</u> (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 <u>D. vesiculosum</u>.

5. <u>DENDROSTELLERA</u> (Map 7).

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

6. <u>STELLEROPSIS</u> (Map 8).

Pobedimova (1949) divides nine species into two series, <u>Altaicae</u> Pobed.
and <u>Turcomanicae</u> 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. <u>STELLERA</u> (Map 6).

The genus <u>Stellera</u>, represented by <u>S. chamaejasme</u>, 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. <u>PASSERINA</u> (Map 9).

Thoday's 1924 revision of the genus <u>Passerina</u> 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 spec-

ialised anatomy also provides an interesting contrast.
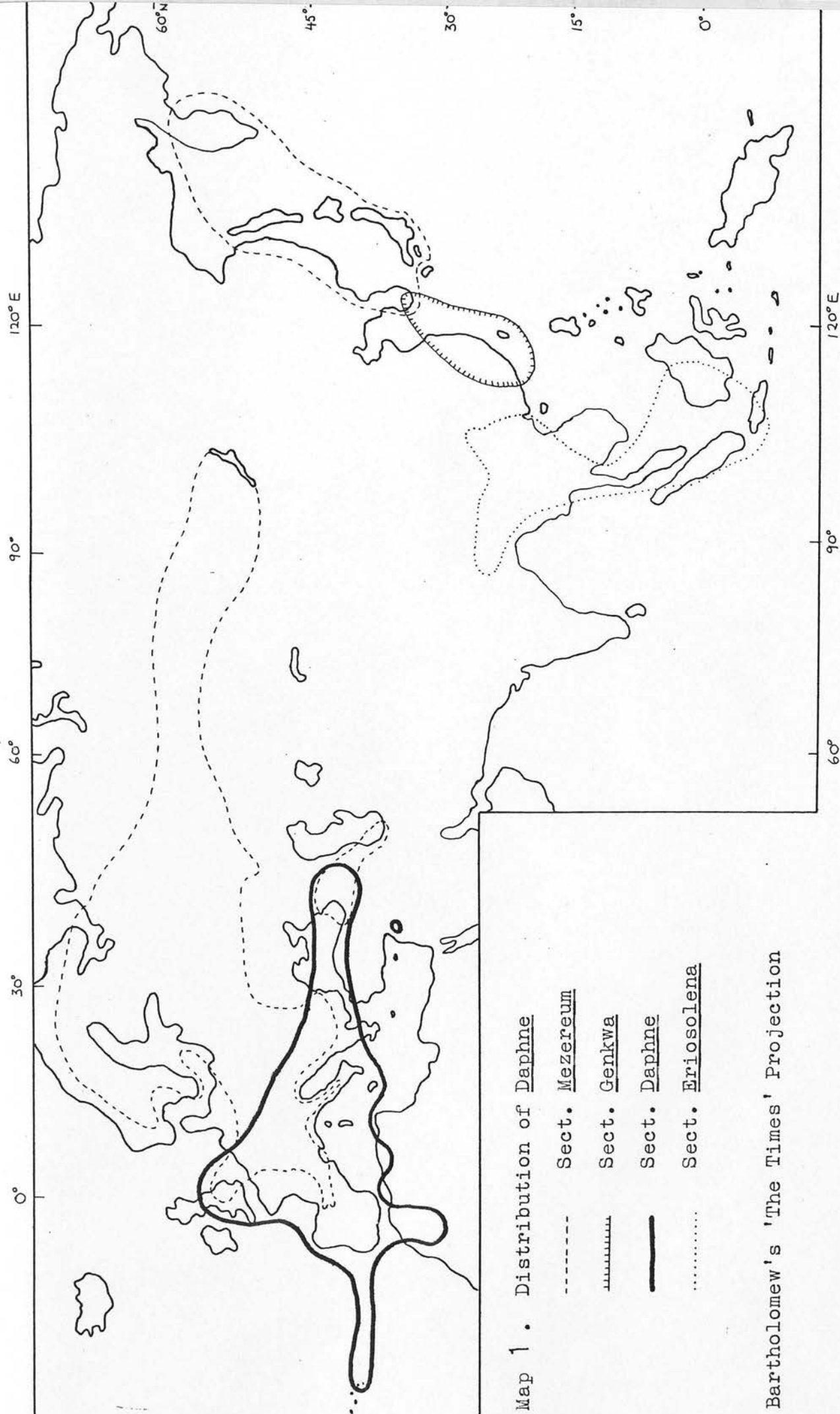
Map 1. Distribution of Daphne

Sect. Mezereum

Sect. Genkwa

Sect. Daphne

Sect. Eriosolena

Bartholomew's 'The Times' Projection
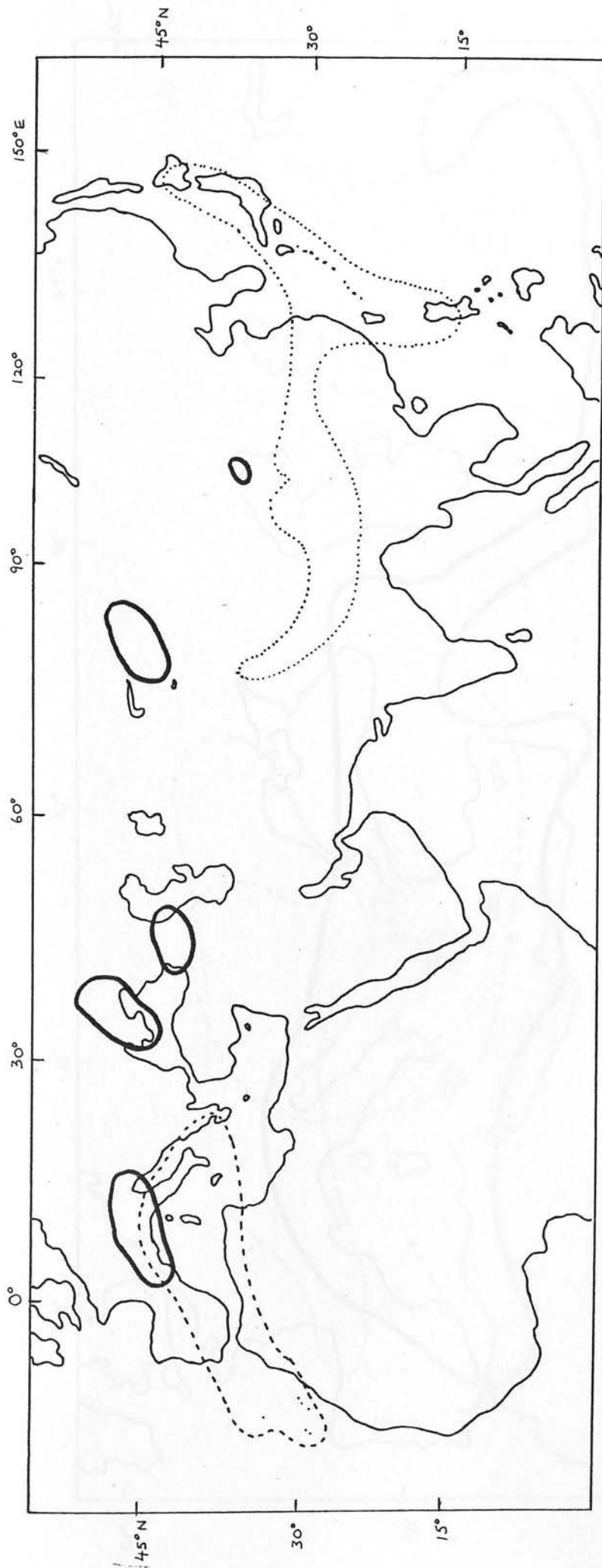
Map 2. Distribution of Daphne Sect. Daphnanthes

subsect. Alpinae

subsect. Gnidium

subsect. Daphnanthoides

Bartholomew's 'The Times' Projection
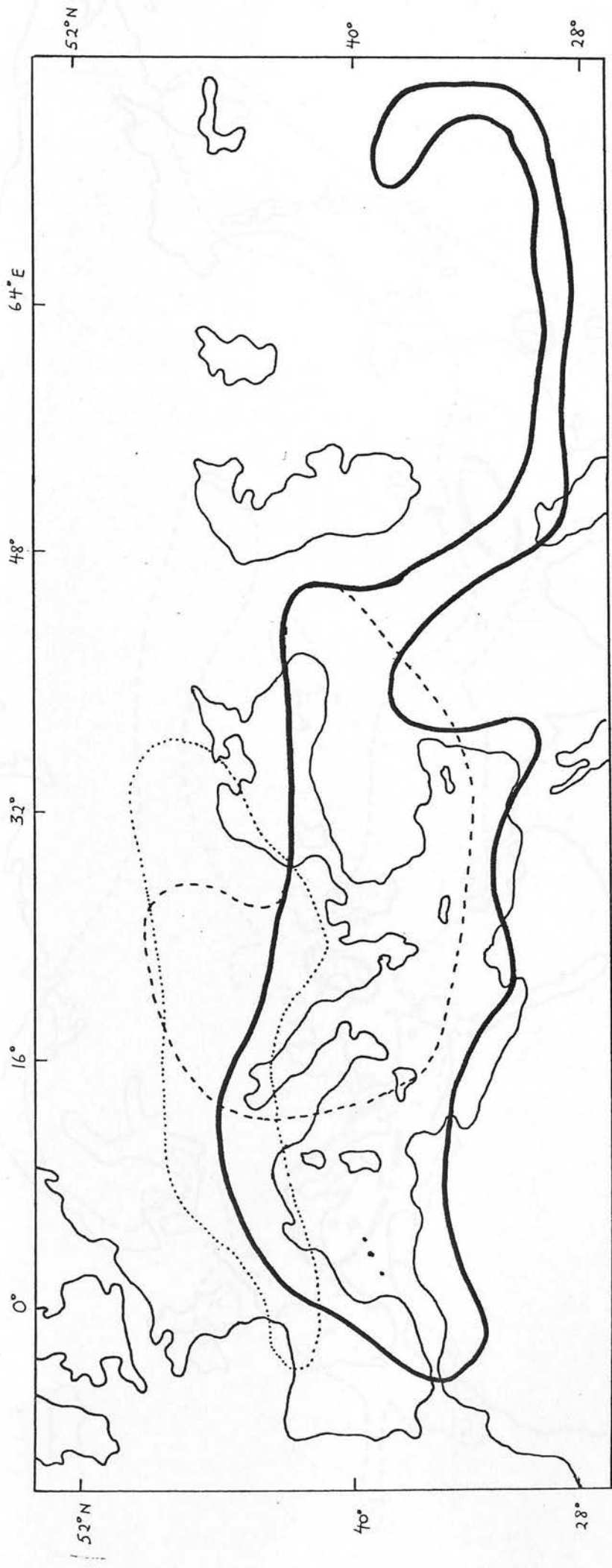
Map **3**. Distribution of _Daphne_ Sect. _Daphnanthes_

——— subsect. _Oleoides_

– – – subsect. _Collinae_

· · · · subsect. _Cneorum_

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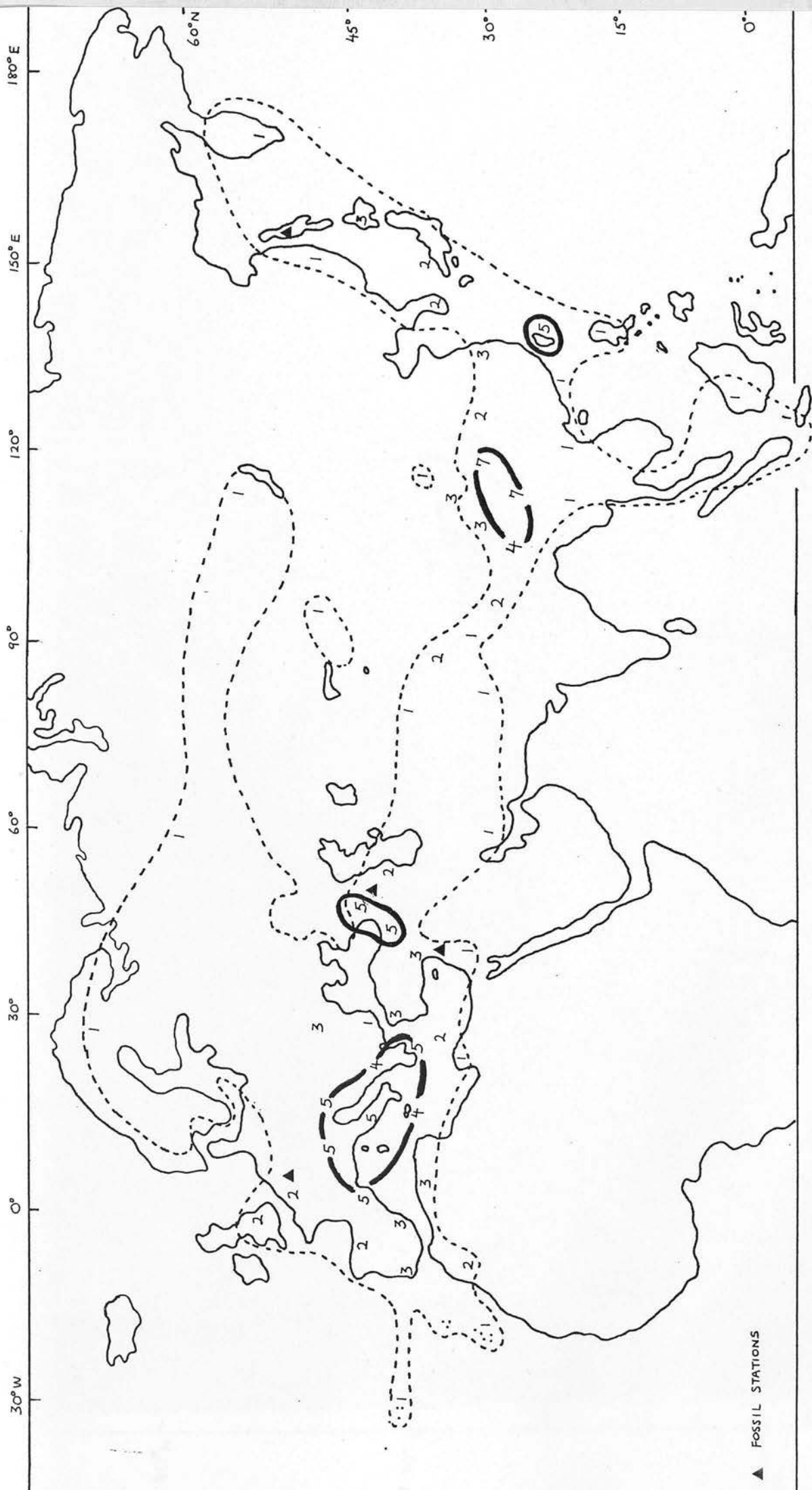
Map 4. Distribution of the genus Daphne showing numbers of species in the different countries. Solid black lines indicate several centres of development (4-7 spp.). It would appear that there was an ancient centre from which wide migration occurred though there are no fossil records for the intervening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

Bartholomew's 'The Times' Projection

▲ FOSSIL STATIONS
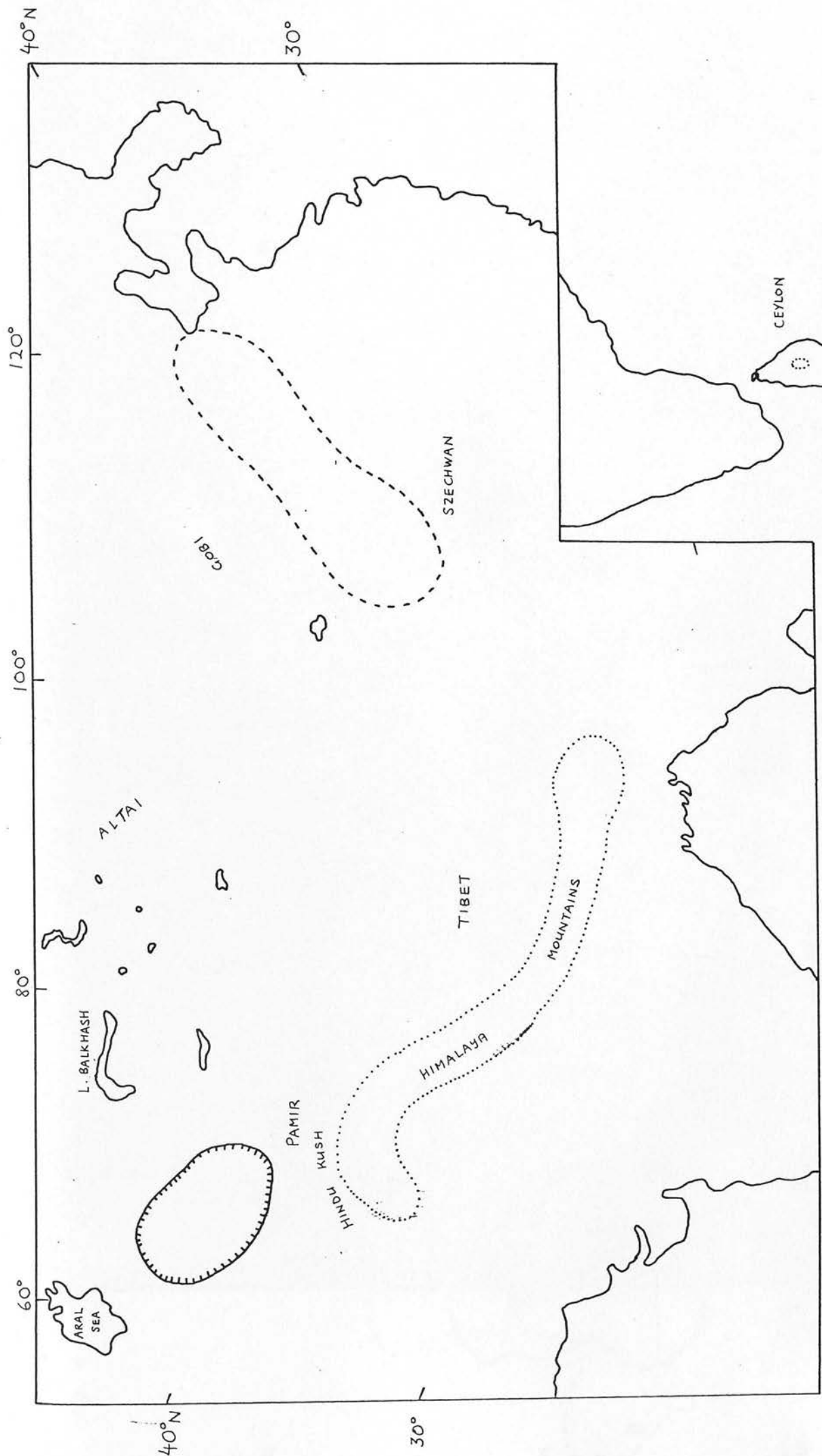
Map 5. Distribution of <u>Restella albertii</u>

<u>Wikstroemia chamaedaphne</u>

<u>Wikstroemia salicifolia</u>

Lambert Azimuthal Equal-Area
Projection

Map 6. Distribution of <u>Diarthron vesiculosum</u>
              <u>Diarthron linifolium</u>
              <u>Stellera chamaejasme</u>

Lambert Azimuthal Equal-Area Projection
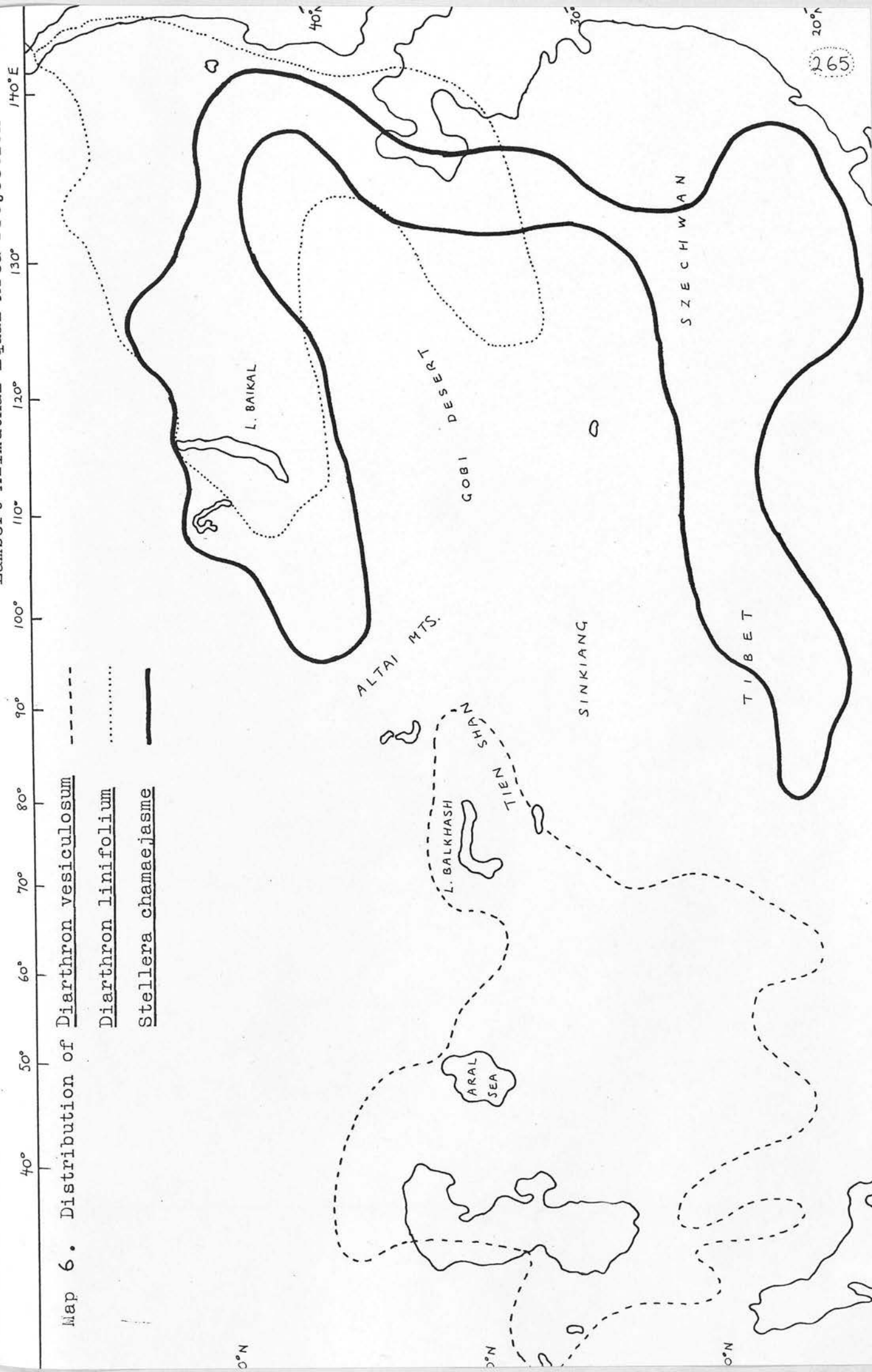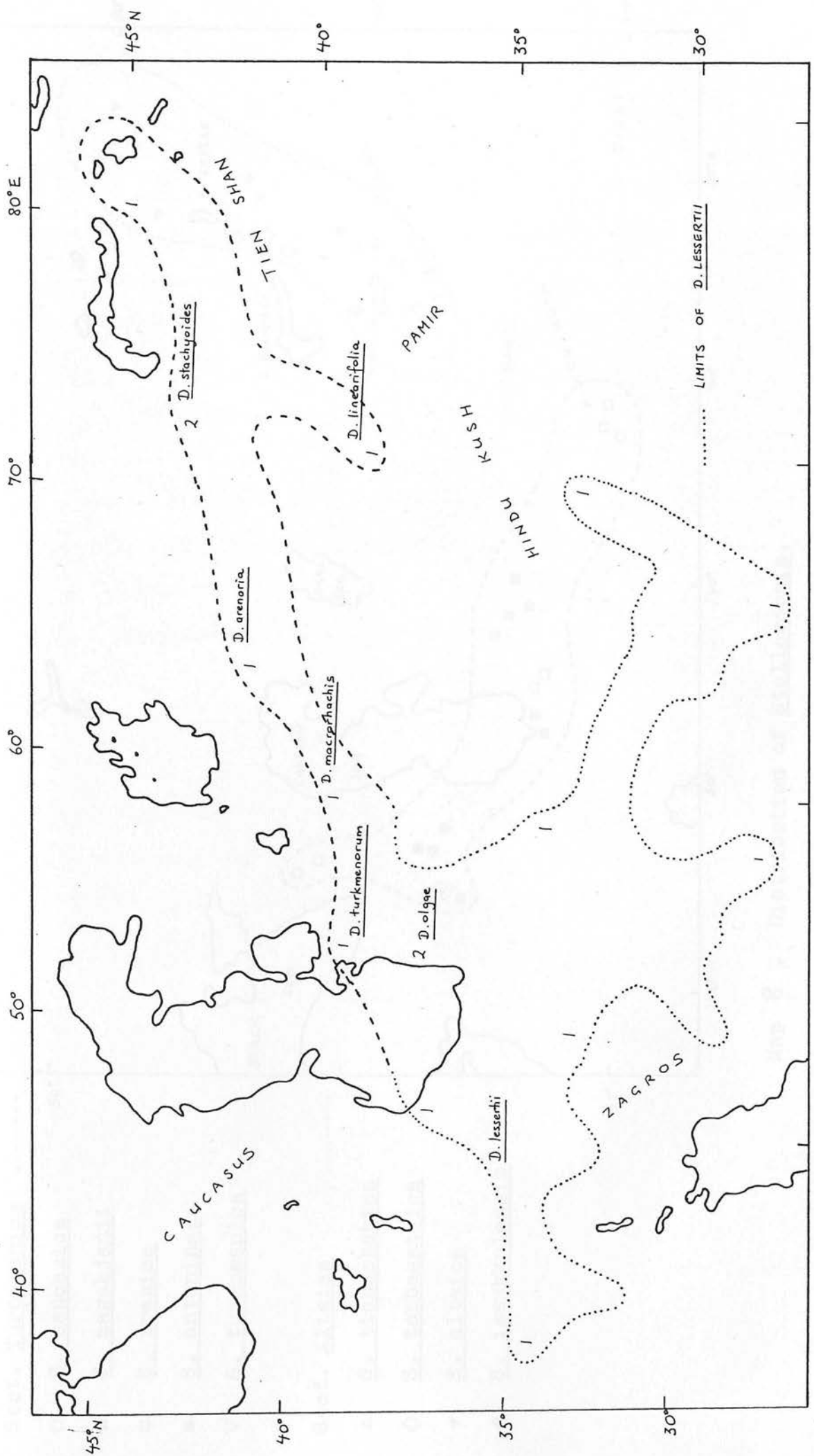
Map 7. Distribution of the genus *Dendrostellera* showing number of species in the different areas.

Bonne Projection
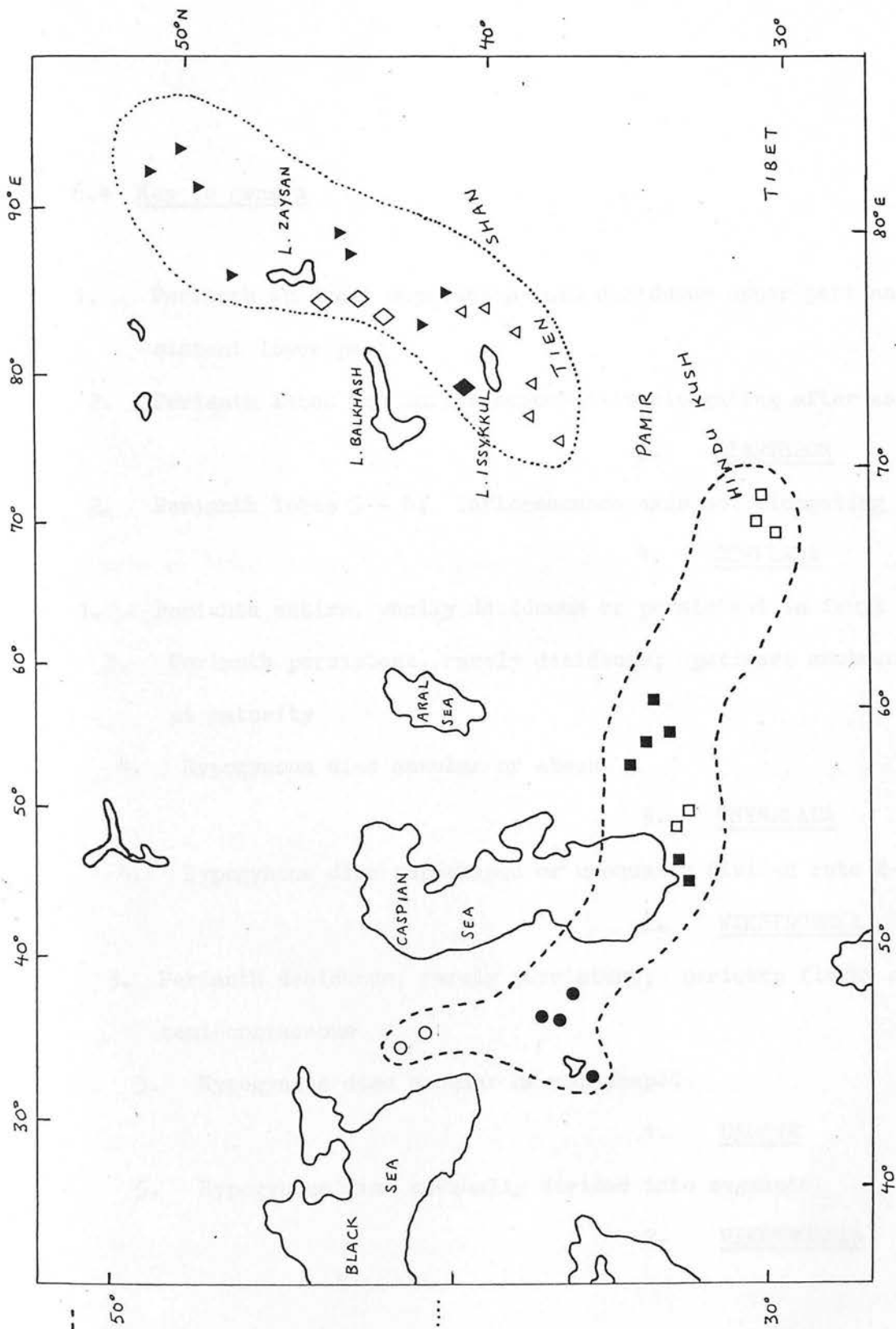
Sect. _Turcomanica_ `- - - - - -`
S. **caucasica**
S. **magakjanii**
S. **iranica**
S. **antoninae**
S. **turcomanica**

Sect. _Altaica_ `· · · · · ·`
S. **tianschanica**
S. **tarbagataica**
S. **altaica**
S. **issykkulensis**

○ ● □ ■ ▷

◁ ◇ ▶ ◆

T I B E T

TIEN SHAN

PAMIR

HINDU KUSH

L. ISSYKKUL

L. BALKHASH

L. ZAYSAN

ARAL SEA

CASPIAN SEA

BLACK SEA

90° E   80°   70°   60°   50°   40°   30°   40°   30°

50° N   40°   30°

80° E

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 per-
     sistent 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

Genus Diarthron Turcz. in Bull. Soc. Nat. Mosc. 5:204 (1832).

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   Sect. Diarthron

2.   Stamens 8   Sect. Arthrochlamys

1.   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

Syn.: Eu-diarthron C. A. Meyer in Bull. Phys. -Math. Acad. (Pétersb.) 1:359 (1843).

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

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

B. Sect. Arthrochlamys C. A. Meyer, loc. cit. (1843).

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

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

II. Subgen. Dendrostellera (C. A. Meyer) H. K. Tan, comb. et stat. nov.

Syn.: Stellera Sect. Dendrostellera C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:359 (1843).

Dendrostellera (C. A. Meyer) Van Tiegh. in Ann. Sci. Nat. Ser. 7(17): 199 (1893); Bull. Soc. Bot. France 40:74 (1893), pro gen.

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: <u>Diarthron lessertii</u> (Wikstr.) H. K. Tan, comb. nov.

Syn.: <u>Passerina lessertii</u> Wikstr. in Kungl. Svenska Vet.-Akad. Handl.,
341 (1818).

Other species: omnia comb. nov.

I. <u>Diarthron stachyoides</u> (Schrenk) H. K. Tan

Syn.: <u>Stellera stachyoides</u> Schrenk in Bull. Phys.-Math. Acad. (Pétersb.)
10:253 (1842).

2. <u>Diarthron arenaria</u> (Pobed.) H. K. Tan

Syn.: <u>Dendrostellera arenaria</u> Pobed. in Fl. URSS 15:689 (1949).

3. <u>Diarthron linearifolia</u> (Pobed.) H. K. Tan

Syn.: <u>Dendrostellera linearifolia</u> Pobed. in Fl.URSS 15:689 (1949).

4. <u>Diarthron macrorhachis</u> (Pobed.) H. K. Tan

Syn.: <u>Dendrostellera macrorhachis</u> Pobed. in Fl. URSS 15:690 (1949).

5. <u>Diarthron turkmenorum</u> (Pobed.) H. K. Tan

Syn.: <u>Dendrostellera turkmenorum</u> Pobed. in Fl. URSS 15:691 (1949).

III. Subgen. <u>Stelleropsis</u> (Pobed.) H. K. Tan, <u>comb. et stat nov.</u>

Syn.: <u>Stellera</u> Sect. <u>Chamaestellera</u> C. A. Meyer in Bull. Phys.-Math.

Acad. (Pétersb.) 1:359 (1843), pro parte excl. typ.

<u>Stelleropsis</u> Pobed. in Not. Syst. (Leningrad) 12:148 (1949), pro gen.

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: <u>Diarthron altaica</u> (Thieb.) H. K. Tan, <u>comb. nov.</u>

Syn.: <u>Stellera altaica</u> Thieb. in Pers. Syn. 1:436 (1805).

A. Sect. <u>Altaica</u> (Pobed.) H. K. Tan, <u>stat nov.</u>

Syn.: <u>Altaicae</u> Pobed. in Not. Syst. (Leningrad) 12:149 (1949) pro ser.

Distribution: C. Asia.

Type: <u>Diarthron altaica</u> (Thieb.) H. K. Tan

Other species: <u>omnia comb. nov.</u>

1. <u>Diarthron tarbagataica</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis tarbagataica</u> Pobed. in Not. Syst. (Leningrad)

12:151 (1949).

2. <u>Diarthron issykkulensis</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis issykkulensis</u> Pobed., op. cit. 152 (1949).

3. <u>Diarthron tianschanica</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis tianschanica</u> Pobed., op. cit. 153 (1949).

B. Sect. <u>Turcomanica</u> (Pobed.) H. K. Tan, stat. nov.

Syn.: <u>Turcomanicae</u> Pobed., op. cit. 155 (1949), pro ser.

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

Type: <u>Diarthron turcomanica</u> (Czern.) H. K. Tan, comb. nov.

Syn.: <u>Stellera turcomanica</u> Czern. in Feddes Rep. 27:273 (1930).

Other species: omnia comb. nov.

4. <u>Diarthron antoninae</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis antoninae</u> Pobed., op. cit. 157 (1949).

5. <u>Diarthron iranica</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis iranica</u> Pobed., op. cit. 158 (1949).

6. <u>Diarthron caucasica</u> (Pobed.) H. K. Tan

Syn.: <u>Stelleropsis caucasica</u> Pobed., op. cit. 161 (1949).

7. <u>Diarthron magakjanii</u> (Sosn.) H. K. Tan

Syn.: <u>Stellera magakjanii</u> Sosn. in Dokl. Akad. Arm. SSR 7(3): 138 (1947).

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 sub-genera 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 Daphneæ 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'.

Perianth entire		Perianth separating into upper and lower parts		
		Inflorescence axis not elongating in fruit	Inflorescence axis elongating in fruit	
deciduous	persistent		Perianth not sericeous in lower part	Perianth densely sericeous in lower part

Shrubs: DAPHNE, WIKSTROEMIA, THYMELAEA Sect. PIPTOCHLAMYS Sect. CHLAMYDANTHUS

Suffrutescent or herbaceous perennials: THYMELAEA Sect. THYMELAEA, THYMELAEA Sect. LIGIA, STELLERA, DIARTHRON Subgen. STELLEROPSIS, DIARTHRON Subgen. DENDROSTELLERA

Annuals: DIARTHRON Subgen. DIARTHRON

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 para-
cytic 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.

14. Development of aril.
The aril is generally interpreted as arising from the funicle. The fleshy or membraneous 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 geographical 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. <u>Some primitive genera in the Thymelaeaceae</u>

1. <u>GONYSTYLUS</u> Teysm. & Binn. (Fig. 46).

The genus <u>Gonystylus</u>, consisting of about twenty species, occurs in the Malesian region (except E. Java and the Lesser Sunda Islands), with one species, <u>G. macrophyllus</u> (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, exstipulate, 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 deciduous. 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. Membraneous 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 11. Characters in some primitive genera

	AQUILARIA Lam.	MICROSEMMA Labill.	OCTOLEPIS Oliver
1.	Medium-sized trees or shrubs.	Shrubs or small trees.	Shrubs or small trees.
2.	Leaves alternate, chartaceous or sub-coriaceous, not glandular-punctate.	Alternate, coriaceous, not glandular-punctate.	Alternate, chartaceous, not glandular-punctate.
3.	Inflorescence subumbellate or paniculate, sometimes cauliflorous.	Flowers solitary in leaf axils.	Solitary or in fascicles at nodes.
4.	Bracts absent or minute.	Absent.	Absent or very minute.
5.	Pedicels usually shorter than calyx-tube.	Longer than calyx tube.	As long as or longer than calyx.
6.	Sepals imbricate, (4-)5(-6), persistent in fruit, pubescent on inner surface.	Imbricate, 4 or 5, persistent in fruit, densely sericeous in central part of inner surface.	Imbricate, 4 or 5, persistent in fruit, densely sericeous on outer surface, pubescent or subglabrous on inner surface, free to base or nearly so.
7.	Corolla of (8-)10(-12) lanceolate, ovate or rim-like petals, free or united.	10-13 semi-woody, oblong or linear-oblong petals, united only at base.	8-10 oblong or linear-oblong petals, united only at base.
8.	Stamens twice number of sepals. Filaments absent or very short. Anthers dorsifixed, linear-oblong.	Numerous, in fascicles. As long as or longer than petals. Dorsifixed, linear-oblong.	8 or 10, free or only joined at base. As long as or longer than petals. Basifixed, ovate or ovate-cordate.
9.	Hypogynous disc annular or absent.	Absent.	Absent.
10.	Ovary sessile or stalked, densely pubescent, 2-loculate style short, terminal stigma capitate, terminal.	Stalked, densely pubescent, 4-5 loculate short, terminal capitate.	Sessile, densely sericeous 4-5 loculate short, terminal capitate or lobed.
11.	Ovule 1 per locule, pendulous, anatropous.	1 per locule, pendulous, anatropous.	1 per locule, pendulous, anatropous.
12.	Fruit a loculicidal, coriaceous or woody capsule.	Loculicidal, woody-coriaceous capsule.	Loculicidal, coriaceous capsule.
13.	Seed with caruncle-like appendage at the chalazal end, usually hanging out of fruit on a slender funicle.	With a caruncle-like thickening at the chalazal end.	With chalazal thickening.

to petals. Filaments free, anthers hippocrepiform. Hypogynous disc
absent. Ovary sessile, 3-4-loculate. Style filiform, 'kinked'; para-
styles 5-6, conspicuous. Fruit a thin-walled, beaked, dehiscent capsule.
Seeds large, funicle thickened but not expanded into an aril.

3. AËTOXYLON 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. <u>Gonystylus macrophyllus</u> (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.
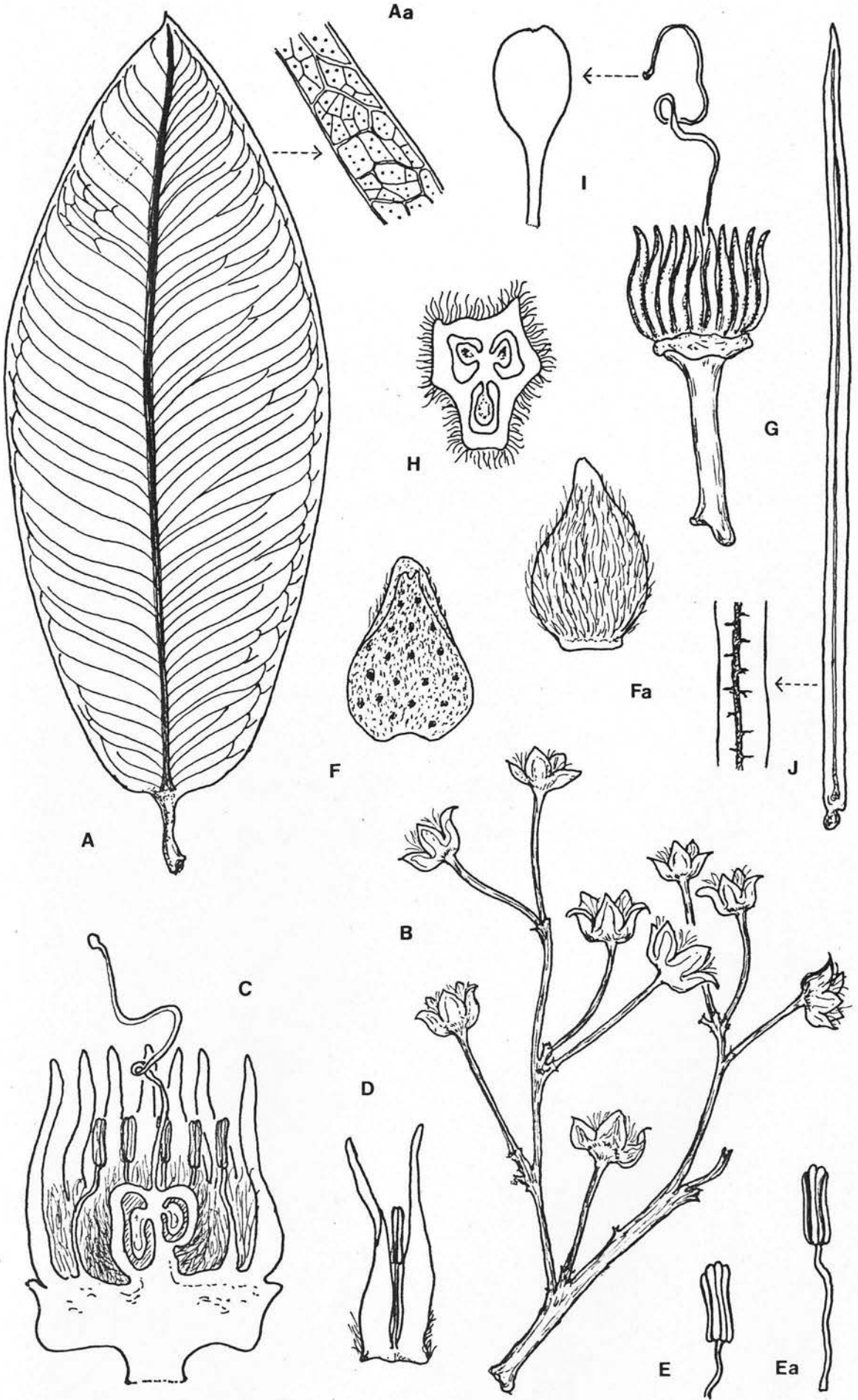
Fig. 46

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.

F, Fa. Mature stamens with hippocrepiform anthers. Lateral
    views. x 20.

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).
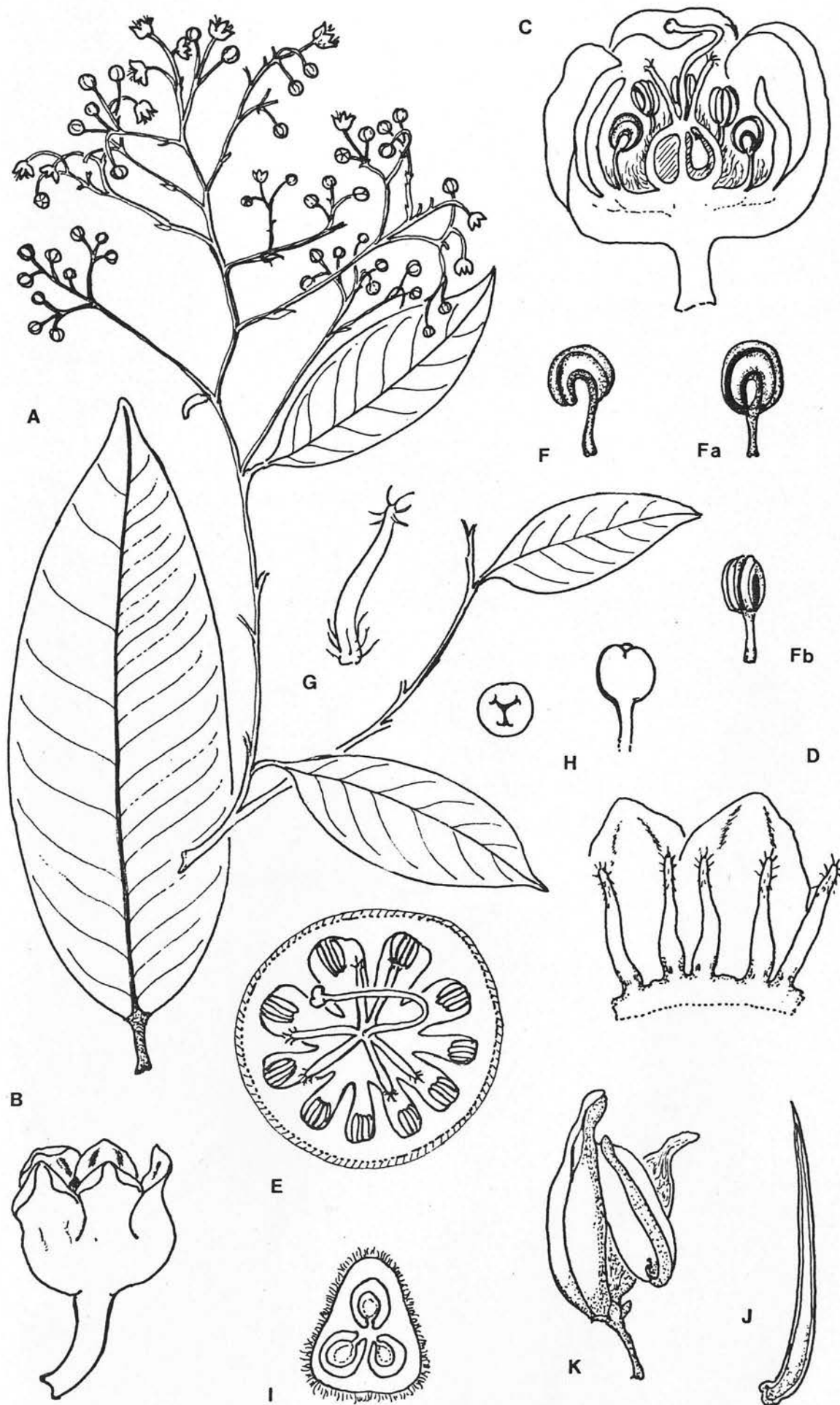
Fig. 47

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.
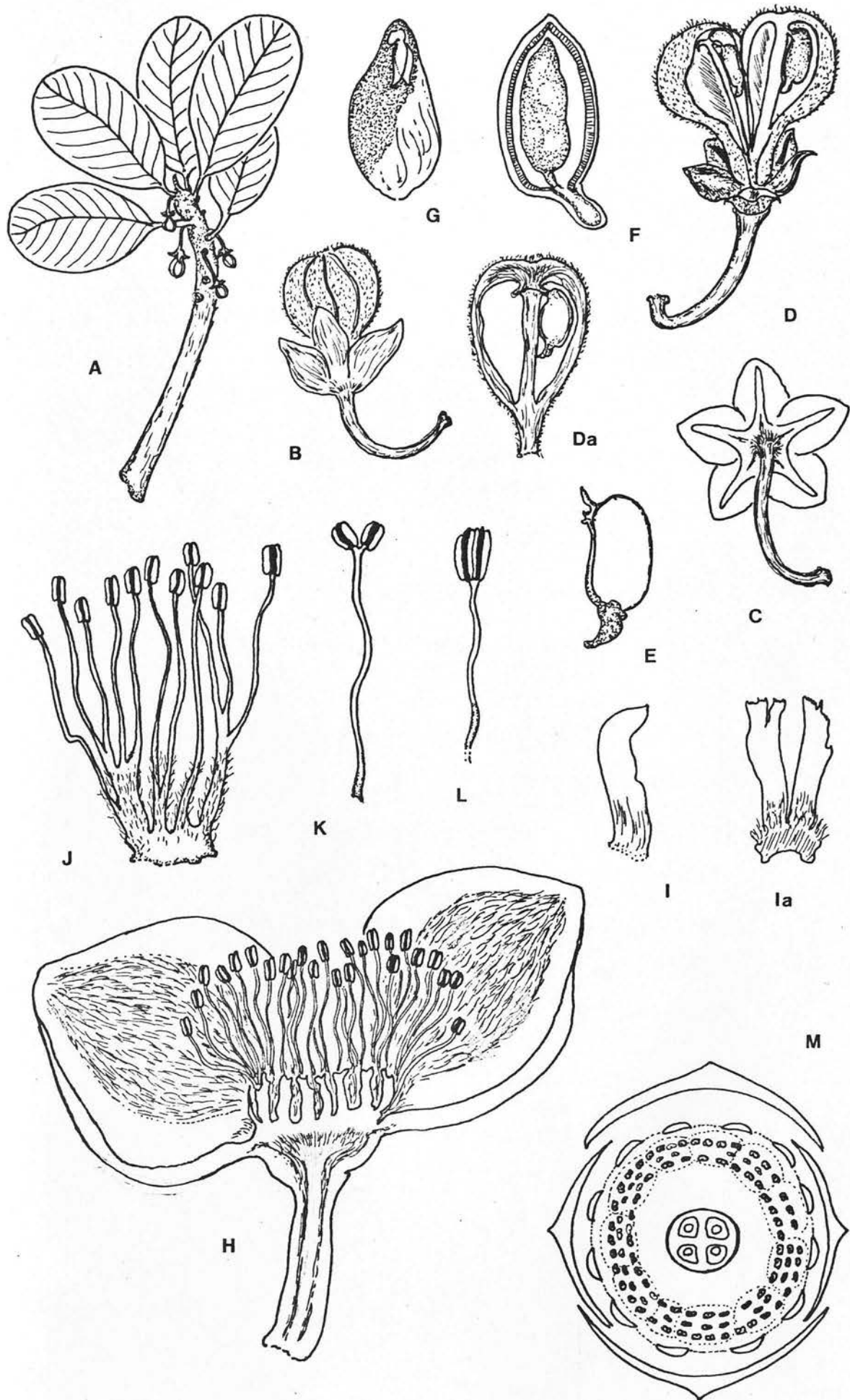
Fig. 48

Fig. 49 A - L excepting H.   Aquilaria grandiflora Benth.

H. Aquilaria malaccensis Lam.

A.   Flowering branch. x $\frac{2}{3}$.

B.   Flower. x 5.

C.   Half-flower. Stigma capitate, centrally depressed. x 6.

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.
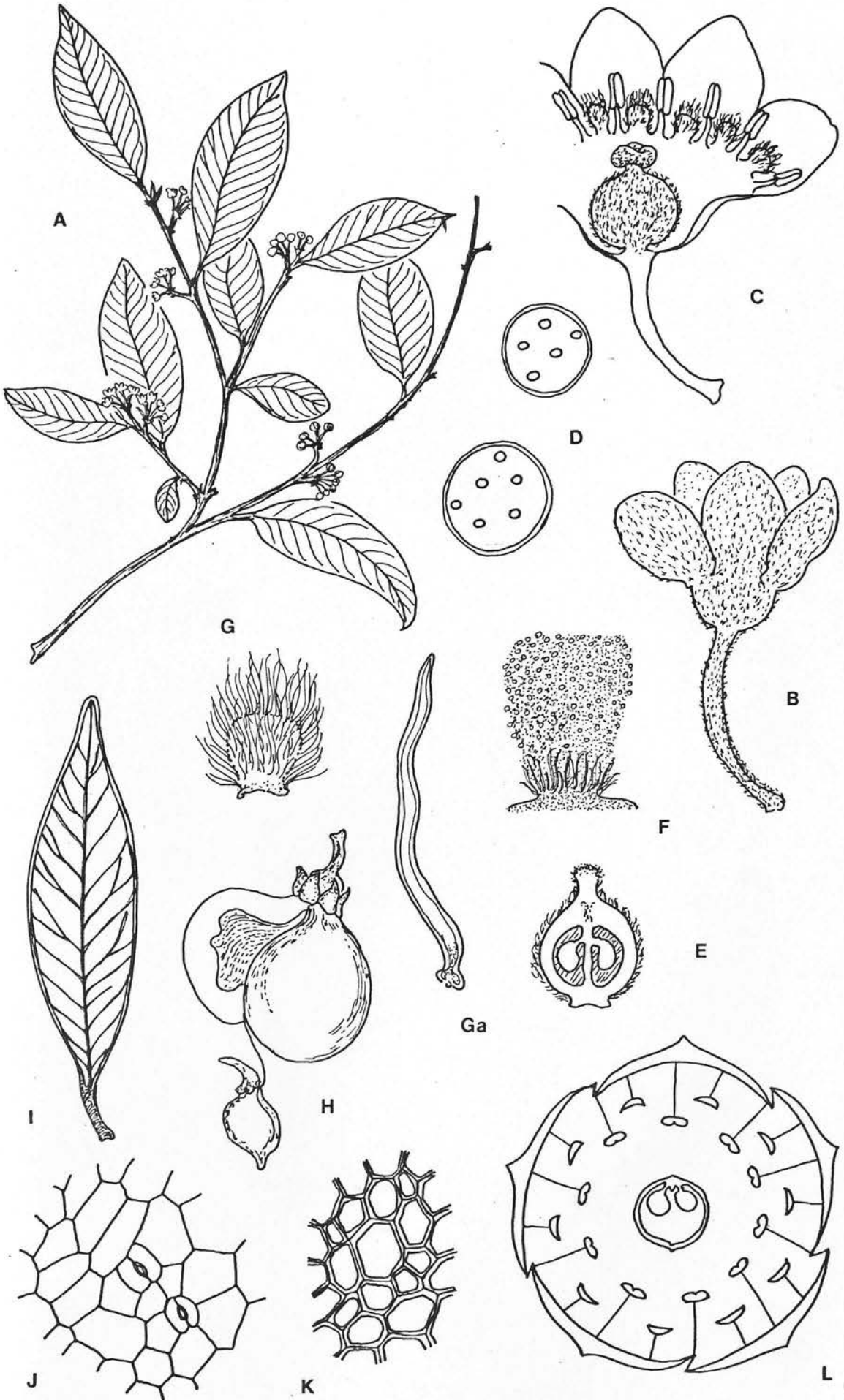
Fig. 49

Fig. 5O. *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.
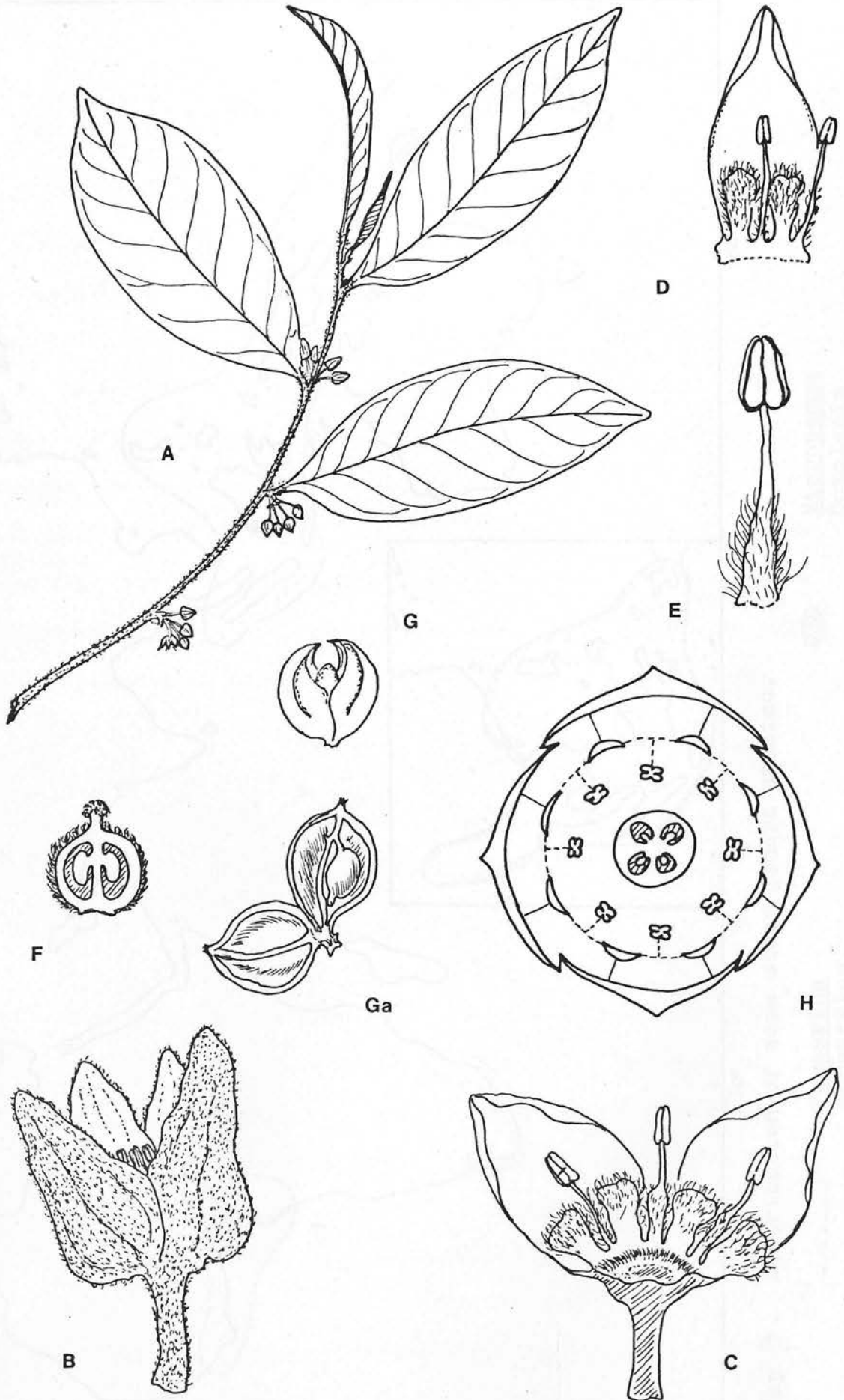
Fig. 50
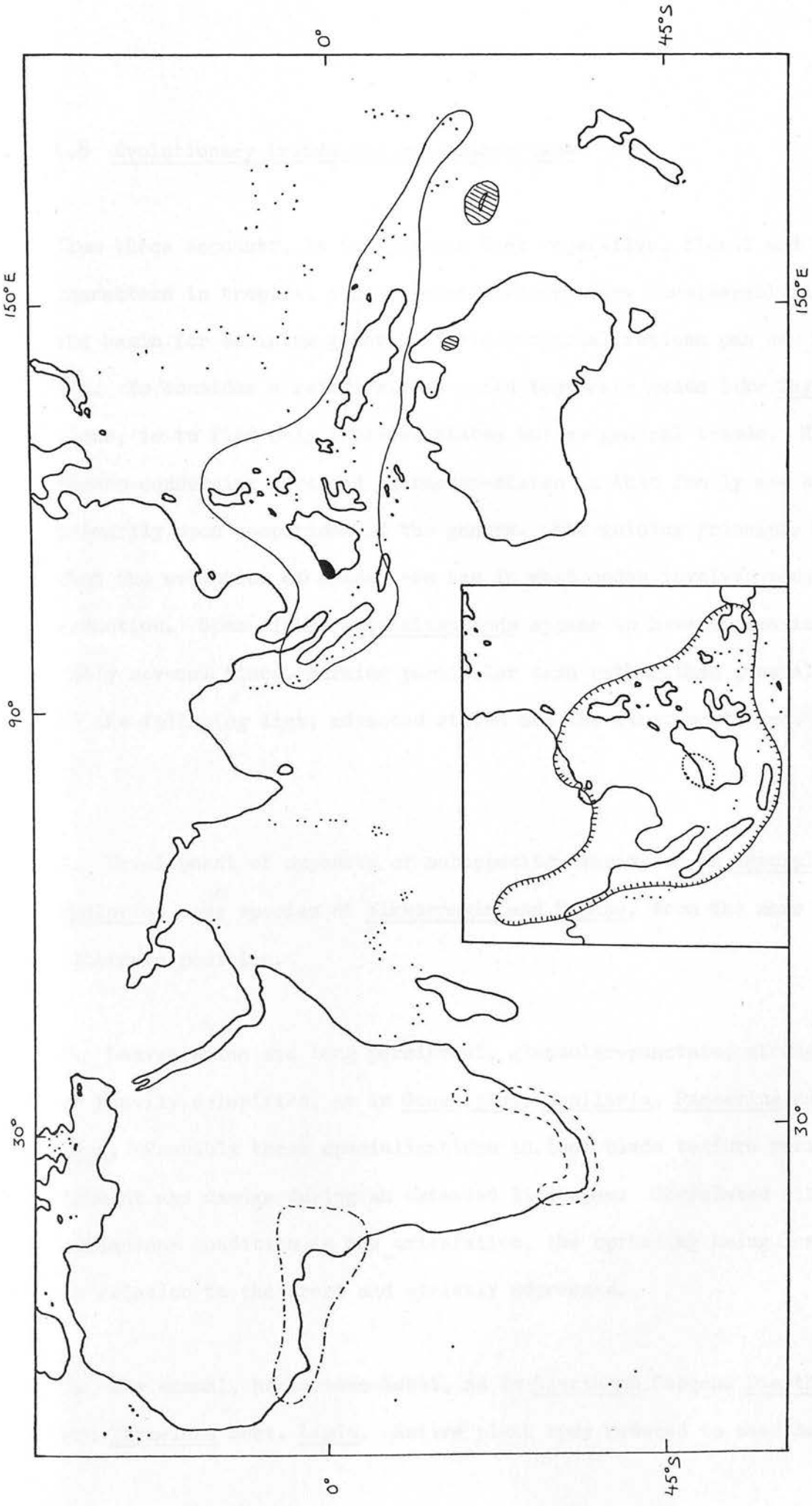
Map 9 . Distribution of some other genera studied.

Passerina ------
Gonystylus (monotypic) ——————
Amyxa (monotypic) ················
Aëtoxylon (monotypic)

Microsemma
Octolepis
Aquilaria

■

Bartholomew's 'The Times' Projection

0°

45°S

150°E

90°

30°

45°S

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. Hypo-
theses 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 independ-
ently 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 Thyme-
laea. 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 thyr-
soid type (cymose). However the post-anthesis elongation of the herb-
aceous inflorescence axis in Diarthron and related genera, is a second-
ary 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 vestigal 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 <u>Thymelaea</u>. 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 <u>Daphne</u> is regarded as derived. The circumscissile condition in <u>Diarthron</u>, <u>Stellera</u> and <u>Passerina</u>, 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-membraneous in <u>Diarthron vesiculosum</u> and <u>D. linifolium</u>, which may aid in dispersal. It is densely villous in <u>D. lessertii</u>. 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 <u>Microsemma</u> and some species of <u>Gonystylus</u> to four in <u>Diarthron linifolium</u> (equalling number of sepals) or in <u>Pimelea</u> <u>prostrata</u>, culminating in two (equalling half the number of sepals!).

15. Attachment of stamens to calyx tube, as in <u>Daphne</u>, 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 indiviudals, 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.

Gonystylus
filaments free,
anthers included

Microsemma
filaments free,
elongated

Aquilaria
filaments
attached

Daphne
filaments attached,
anthers included

Dicranolepis

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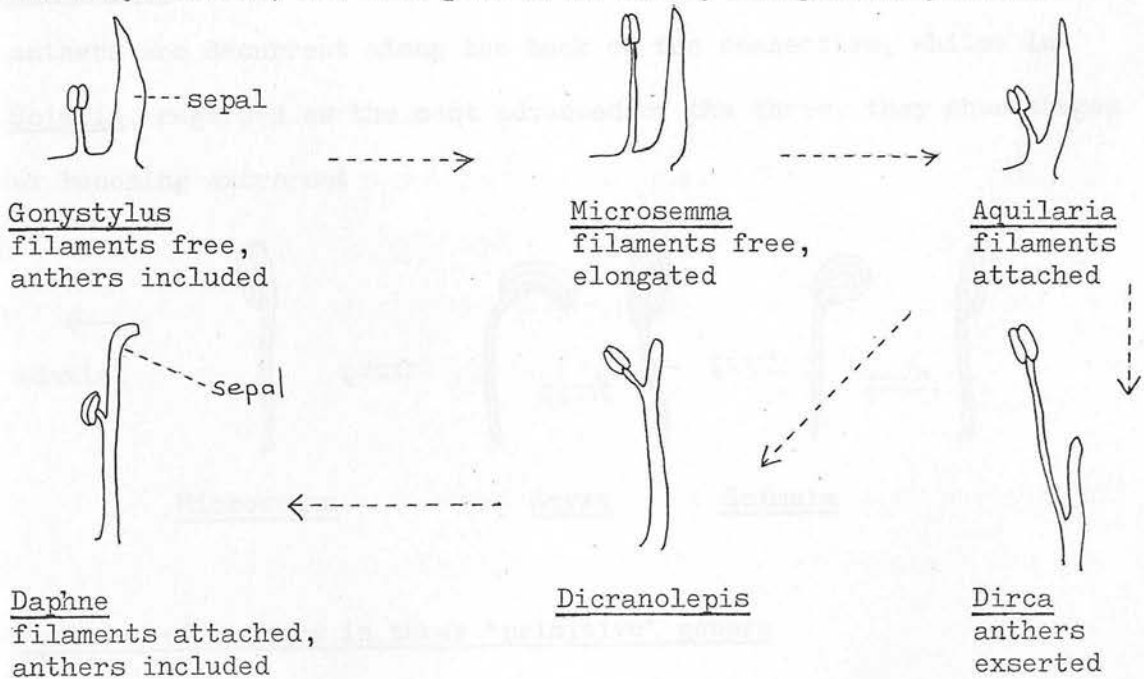
Diagram of some possible stages in the evolution of an episepalous
stamen, as seen from extant genera.

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 effect-

ive 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!

adaxial

Microsemma   Amyxa   Solmsia
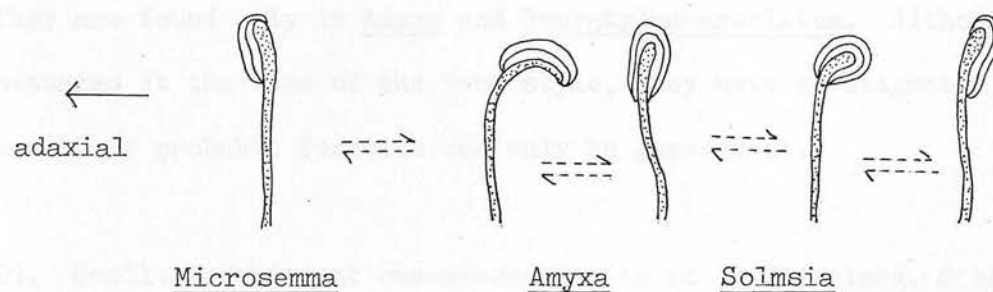
Position of anthers in three 'primitive' genera

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, Microsemma).

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 append-
ages, all or some of which are present in tropical genera and are
probably related to endozoochory.

PART D

TAXONOMIC TREATMENT OF THE GENUS THYMELAEA

CHAPTER VII

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.

Syn: Stellera L., diss. Dassow, Nov. Pl. Gen. (1747), p.p.; Amoen.
Acad. 1:126 (1749); Daphne L., Sp. Pl., 356 (1753), p.p; Passerina L.,
op. cit., 559 (1753), p.p.; Sanamunda Adanson, Fam. 2:285 (1763);
Ligia Fasano in Atti Accad. Napoli 1:245 (1788), as 'Lygia' apud C.A.
Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:356 (1843); Sanamunda
Necker, Elem. Bot. 2:179 (1791), sub Daphne; Gastrilia Rafin., Fl.
Tellur. 4:105 (1838), p.p.; Pausia Rafin., ibid., p.p.; Tartonia
Rafin., Autikon Botanikon, 146 (1840); Chlamydanthus C.A. Meyer, op.
cit., 358 (1843); Piptochlamys C.A. Meyer, ibid.; Stellera L. emend.
Kuntze, Rev. Gen. Pl. 2:585 (1891); Giardia Gerber in Bull. Soc.
Bot. Fr. 46 (sess. extr.) :112 (1899).

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
hermaphrodite 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 sub-terminal; 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.

Taxonomic revision: Brecher, Gy. (1941). A Thymelaea - génusz és fajai. Ind. Horti. Bot. Univ. Budapest. 5:57-116.

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'.

Endlicher, S. - 1848 - Gen. Pl. Suppl. 4(2): 65-66

Lygia Fasano
1. L. passerina
2. L. pubescens

Thymelaea Endl.
A. Sect. Piptochlamys (C.A. Meyer) Endl.
1. T. hirsuta
B. Sect. Chlamydanthus (C.A. Meyer) Endl.
a. Subsect. Tartonraira (C.A. Meyer) Endl.
2. T. tartonraira
3. T. argentea
4. T. canescens = T. lanuginosa
5. T. nitida = T. argentata
6. T. villosa
7. T. tomentosa (species obscura)
8. T. tinctoria
9. T. virgata
b. Subsect. Euthymelaea Endl.
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

Meissner, C. F. - 1857 - Thymelaeaceae in DC., Prodr. 14: 551-558.

Sect. I. Lygia (Fasano) Meissn.
1. T. arvensis = T. passerina
2. T. cilicica
3. T. aucheri
Sect. II. Chlamydanthus (C.A. Meyer) Endl.
§ 1. Suffrutescentes Meissn.
4. T. virgata
5. T. sanamunda
6. T. thesioides
7. T. coridifolia
§ 2. Fruticulosae Meissn.
8. T. villosa
9. T. nitida = T. argentata
10. T. dioica
11. T. virescens
12. T. calycina
13. T. nivalis = T. tinctoria subsp. nivalis
14. T. tinctoria
15. T. velutina
16. T. tartonraira
17. T. microphylla
18. T. canescens = T. lanuginosa
Sect. III. Piptochlamys (C.A. Meyer) Endl.
19. T. hirsuta
Species obscurae.
20. T. orientalis
21. T. tomentosa
22. T. pubescens

Bentham, G. & Hooker, J.D. - 1883 - Gen. Pl. 3: 191.

1. Sect. Lygia (3 spp.)
2. Sect. Chlamydanthus
3. Sect. Piptochlamys

The genus contains c. 20 spp.

Gilg, E. - 1894 - Thymelaeaceae in Engler & Prantl, Nat. Pflanzenfam. 3 (6a): 237.

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

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

Sect. III. Piptochlamys (C.A. Meyer) Meissn.
1 sp. namely T. hirsuta

Brecher, Gy. - 1941 - A Thymelaea - génusz es fajai -
Ind. Horti. Bot. Univ. Budapest. 5: 70.

I. Sect. Lygia (Fasano) Meissn.
1. T. passerina
2. T. aucheri
3. T. cilicica
II. Sect. Chlamydanthus (C.A. Meyer) Endl.
1. Subsect. Sanamunda (Lange) Brecher
4. T. antiatlantica
5. T. virgata
6. T. sanamunda
7. T. thesioides
2. Subsect. Euthymelaea (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. nitida = T. argentata
20. T. microphylla
21. T. lanuginosa
22. T. broteriana
23. T. sempervirens
24. T. lythroides
III. Sect. Piptochlamys (C.A. Meyer) Endl.
25. T. hirsuta

Proposed Classification

I. Sect. Piptochlamys (C.A. Meyer) Endl.
Subsect. Hirsutae H.K. Tan
1. T. lythroides
2. T. hirsuta (type of sect.)
3. T. lanuginosa
4. T. gattefossei
Subsect. Argentatae H.K. Tan
5. T. argentata
6. T. virescens
7. T. putorioides
Subsect. Sempervirentes H.K. Tan
8. T. microphylla
9. T. sempervirens

II. Sect. Chlamydanthus (C.A. Meyer) Endl.
Subsect. Tartonraira (C.A. Meyer) Endl.
10. T. tartonraira (type of sect.)
11. T. velutina
12. T. dioica
Subsect. Coridifoliae H.K. Tan
13. T. tinctoria
14. T. subrepens
15. T. procumbens
16. T. ruizii
17. T. calycina
18. T. coridifolia
19. T. broteriana

III. Sect. Thymelaea
Subsect. Antiatlanticae H.K. Tan
20. T. antiatlantica
21. T. virgata
Subsect. Sanamunda (Lange) Brecher
22. T. villosa
23. T. thesioides
24. T. sanamunda (type of sect.)

IV. Sect. Lygia (Fasano) Meissn.
25. T. cilicica
26. T. aucheri
27. T. passerina (type of sect.)
28. T. gussonei
29. T. salsa
30. T. mesopotamica

TABLE 12. PROPOSED INFRA-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

Sect. Chlamydanthus subsect. Coridifoliae.

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 13. THYMELAEA: comparison of morphological characters.

SPECIES	\<FLOWER — Sex distribution\> hermaphrodite	monoecious	dioecious	polygamodioecious	\<Position\> terminal	axillary	\<Arrangement\> aggregated	single	\<Bracts\> more than 2	2	absent	Indumentum on perianth	\<LEAF\> Planar	Involute/revolute
Sect. Piptochlamys														
Subsect. Hirsutae														
1. T. lythroides		o	x		x		x				x	x		x
2. T. hirsuta		x	o		x		x				x	x		x
3. T. lanuginosa			x		x		x		x			x	x	
4. T. gattefossei			x		x		x		x			x	x	
Subsect. Argentatae														
5. T. argentata			x	o	x		x				x	x	x	
6. T. virescens	x		o		x		x				x	x	x	
7. T. putorioides		x			x		x			↯	x	x	x	
Subsect. Sempervirentes														
8. T. microphylla			x		x		x		x			x	x	
9. T. sempervirens			x		x		x		x			x	x	
Sect. Chlamydanthus														
Subsect. Tartonraira														
10. T. tartonraira			x	o	x	x		x				x	x	
11. T. velutina			x		x	x		x				x	x	
12. T. dioica			x		x			1-2	x		o	o	x	
Subsect. Coridifoliae														
13. T. tinctoria			x		x			x	x				x	
14. T. subrepens			x		x			x	x				x	
15. T. procumbens			x		x			x	x			x	x	
16. T. ruizii			x		x			x	x					x
17. T. calycina			x		x			x	x			x		x
18. T. coridifolia			x		x			1-2	x			x		x
19. T. broteriana			x		x			1-2	x					x
Sect. Thymelaea														
Subsect. Antiatlanticae														
20. T. antiatlantica			x		x	x			x			x	x	
21. T. virgata			x		x	x		o	x			x	x	
Subsect. Sanamunda														
22. T. villosa			x		x			x			x	x	x	
23. T. thesioides			x		x		o	o			x	x	x	
24. T. sanamunda			x		x		o	o			x	o	x	
Sect. Ligia														
25. T. cilicica		x			x	x			x			x	x	
26. T. aucheri		x			x	x			x			x		x
27. T. passerina	x				x	x		o	x			x	x	
28. T. gussonei	o	x			x	x		o	x			x	x	
29. T. salsa	o	x			x	x			x			x	x	
30. T. mesopotamica	o	x			x	x			x			x	x	

7.2 TABLE 14. THYMELAEA: comparison of sectional characters.

PIPTOCHLAMYS	CHLAMYDANTHUS	THYMELAEA	LIGIA
1. Shrubs.	1. Shrubs.	1. Semi-shrubby or suffrutescent.	1. Suffrutescent perennials; annuals.
2. Monoecious; dioecious; more rarely polygamodioecious or flowers hermaphrodite.	2. Dioecious; rarely polygamodioecious.	2. Dioecious.	2. Monoecious; flowers hermaphrodite.
3. Terminal; aggregated.	3. Flowers axillary; aggregated or single.	3. Axillary; aggregated or single.	3. Axillary; aggregated, rarely single.
4. Absent, more than 2.	4. Bracts 2; more than 2.	4. Absent; more than 2.	4. 2.
5. Sessile; shortly pedicellate.	5. Flowers sessile, shortly pedicellate.	5. Sessile.	5. Sessile.
6. Persistent, semi-persistent or deciduous.	6. Perianth persistent.	6. Persistent.	6. Persistent.
7. Amphistomatic; epistomatic.	7. Leaves amphistomatic; epistomatic.	7. Amphistomatic.	7. Amphistomatic.
8. Anomocytic; modified tetra-cytic; very rarely anisocytic.	8. Stomata anomocytic; modified tetracytic.	8. Anomocytic; modified tetracytic.	8. Modified tetracytic; anisocytic.
9. Straight, very rarely undulated.	9. Anticlinal walls of leaf adaxial and abaxial epidermides straight, very rarely undulated.	9. Straight or undulated.	9. Undulated.
10. Absent except in 2 spp.	10. Stomata and chlorenchyma absent from old stems.	10. Present or absent.	10. Present.
11. Well developed except in some 2 spp.	11. Cork well developed.	11. Moderately well developed.	11. Absent.
12. Dilated or not so.	12. Secondary phloem rays of stem dilated or not so.	12. Not dilated.	12. Not dilated.
13. Present except in 1 sp.	13. Internal phloem fibres absent from young or old stems.	13. Present except in 1 sp.	13. Present or absent.

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. tarton-raira 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. Chlamyd-
anthus, within subsect. Tartonraira, 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. Coridifoliae.

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 abbrevia-
tions and usuage 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.

SECT. CHLAMYDANTHUS

SECT. PIPTOCHLAMYS

SECT. LIGIA

SECT. THYMELAEA
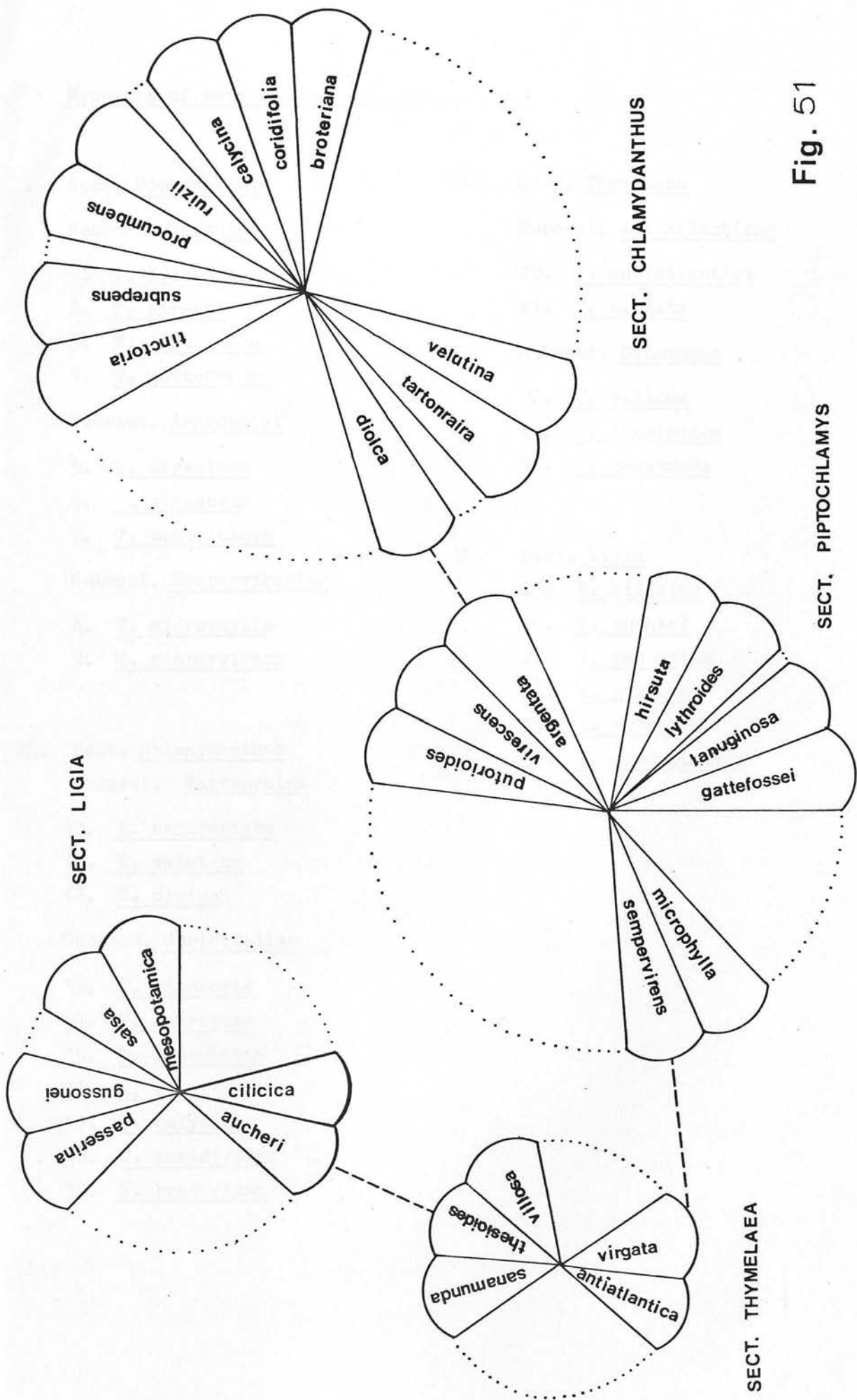
Fig. 51

7.4 Synopsis of sections and species.

I. Sect. Piptochlamys

Subsect. Hirsutae

1. T. lythroides
2. T. hirsuta
3. T. lanuginosa
4. T. gattefossei

Subsect. Argentatae

5. T. argentata
6. T. virescens
7. T. putorioides

Subsect. Sempervirentes

8. T. microphylla
9. T. sempervirens

II. Sect. Chlamydanthus
Subsect. Tartonraira

10. T. tartonraira
11. T. velutina
12. T. dioica

Subsect. Coridifoliae

13. T. tinctoria
14. T. subrepens
15. T. procumbens
16. T. ruizii
17. T. calycina
18. T. coridifolia
19. T. broteriana

III. Sect. Thymelaea

Subsect. Antiatlanticae

20. T. antiatlantica
21. T. virgata

Subsect. Sanamunda

22. T. villosa
23. T. thesioides
24. T. sanamunda

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

7.4.1 Synoptic descriptions of sections and subsections

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

    Syn: _Piptochlamys_ C.A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.)
    1:358 (1843), pro gen.

    Sect. _Chlamydanthus_ (C.A. Meyer) Endl., loc. cit. (1848), p.p.

    Piptochlamys C.A. Meyer in Rouy, Fl. Fr. 12:126 (1910), pro subgen.

Monoecious, dioecious, or more rarely, 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).

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

    Syn: _Chlamydanthus_ C.A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.)
    1:358 (1843), p. pro. gen.

    Subsect. _Fruticulosae_ Meissn. in DC., Prodr. 14: 554 (1857), p.p.

    Subsect. _Euthymelaea_ (Lange) Brecher in Ind. Horti. Bot. Univ.
    Budapest. 5:70 (1941) p.p.

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).

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

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

Flowers clustered except in _T. dioica_ where they may be solitary or paired. Bracts (5-) 10 - 15 except in 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_

Syn: Subsect. _Euthymelaea_ Endl., Gen. Pl. Suppl. 4(2): 65 (1848), excl. _T. dioica_.

Subsect. _Suffrutescentes_ Meissn. in DC., Prodr. 14: 552 (1857), excl. _T. coridifolia_.

Subsect. _Sanamunda_ (Lange) Brecher in Ind. Horti Bot. Univ. Budapest. 5:70 (1941).

Dioecious, semi-shrubby or suffrutescent perennials; stems virgate, simple or branched. Flowers sessile, clustered or solitary in leaf axils. Bracts present or absent. Perianth persistent.

Leaves: amphistomatic; stomata anomocytic and/or modified tetracytic. Anticlinal walls of adaxial and abaxial epidermides straight or 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).

Syn: _Daphne thymelaea_ L., Sp. Pl., 356 (1753).

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.

Type: _T. antiatlantica_ Maire in Bull. Soc. Sci. Nat. Maroc 13: 273 (1933).

Subsect. _Sanamunda_ (Lange) Brecher, loc. cit. (1941), p.p.

Syn.: Sect. _Sanamunda_ Lange in Willk.& Lange, Prodr. Fl. Hisp. 1: 298 (1862), incl. _T. villosa_.

Plants rarely more than 20 cm tall. Flowers solitary or in fascicles of 2-3(-5). Bracts absent.

Type: <u>T. sanamunda</u> All., loc. cit. (1785).

IV.   Sect. <u>Ligia</u> (Fasano) Meissn. in DC., Prodr. 14:551 (1857), as

'Sect. <u>Lygia</u>'.

Syn: <u>Ligia</u> Fasano in Atti Accad. Napoli 1: 245 (1788), pro gen.

Annuals or suffrutescent perennials; stems simple or branched.

Monoecious or flowers hermaphrodite. Flowers sessile, solitary or

2 - 4(-7) in leaf axils.

Bracts 2, green. Perianth persistent.

Leaves: amphistomatic; stomata anisocytic and modified tetracytic.

Anticlinal walls of adaxial and abaxial epidermides undulated.

Stem: stomata and chlorenchyma present. Cork absent. Secondary

phloem rays not dilated. Internal phloem fibres present or absent.

Type: <u>T. passerina</u> (L.) Cosson & Germ., Syn. Fl. Env. Paris, ed.

2, 360 (1859).

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. <u>argentata</u>

  7. Branches divergent, not fastigiate; leaves with at least one surface glabrous

    8. Branches thick, often tortuous, dusty-white; leaves completely glabrous   6. <u>virescens</u>

    8. Branches slender, not tortuous nor dusty-white; adaxial or abaxial leaf surface glabrous   7. <u>putorioides</u>

II. Sect. <u>CHLAMYDANTHUS</u>

1. Bracts absent or more than 2 (subsect. <u>Tartonraira</u>)

  2. Flowers single or rarely, paired; perianth glabrous or sparsely pilose   12. <u>dioica</u>

  2. Flowers in fascicles of 2-5; perianth sericeous or densely pubescent

    3. Young shoots and leaves glabrous, pubescent or sericeous   10. <u>tartonraira</u>

    3. Young shoots and leaves yellow-velutinous or lanate   11. <u>velutina</u>

1. Bracts 2 (subsect. <u>Coridifoliae</u>)

  4. Leaves planar

    5. Perianth pubescent   15. <u>procumbens</u>

    5. Perianth glabrous

      6. Leaves elliptic-ovate, acute   14. <u>subrepens</u>

      6. Leaves lorate, obtuse   13. <u>tinctoria</u>

  4. Leaf margins involute or slightly involute

7. Perianth pubescent

   8. Leaves 2-4 mm broad   17. <u>calycina</u>

   8. Leaves 0.5 - 1 mm broad   18. <u>coridifolia</u>

7. Perianth glabrous

    9. Mature leaves glabrous on both surfaces   16. <u>ruizii</u>

    9. Mature leaves tomentose on adaxial surfaces

                                  19. <u>broteriana</u>

III. Sect. <u>THYMELAEA</u>

1. Bracts absent (subsect. <u>Sanamunda</u>)

 2. Young shoots hirtellous or white-pilose   22. <u>villosa</u>

 2. Young shoots not hirtellous

  3. Stems pubescent in leafy parts; perianth tube densely pubescent

                                      23. <u>thesioides</u>

  3. Stems glabrous or very sparsely pilose at tips; perianth tube

    glabrous or sparsely pilose   24. <u>sanamunda</u>

1. Bracts present (subsect. <u>Antiatlanticae</u>)

   4. Stems white-villous or pilose in flowering parts; bracts

    2-3   20. <u>antiatlantica</u>

   4. Stems grey-villous in part; bracts 5-7   21. <u>virgata</u>

IV. Sect. <u>LIGIA</u>

1. Suffrutescent perennials; stems many

 2. Leaves narrowly elliptic, less than 1 cm long, margins never

   revolute   25. <u>cilicica</u>

2. Leaves linear-filiform, more than 1 cm long, margins usually
    revolute on drying   26. aucheri

1. Annuals; stem single

  3. Stems glabrous or very sparsely pilose at tips

    4. Flowers hermaphrodite; ovary hirsute-villous at apex
                                   27. passerina

    4. Flowers unisexual, very rarely hermaphrodite; ovary
        puberulous at apex   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

7.6   Taxonomic account of species

1. __T. lythroides__ Barr. & Murb. in Acta Univ. Lund. n.s. 2(1); 69 (1906).

    Ic: 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-
Bahraoui to Kenitra, 150 m, D. 54391! near Moulay-Bou-Selham, 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.

Chlamydanthus (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).

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

Syn: **Passerina hirsuta** L., Sp. Pl., 559 (1753), photo! non Asso (1779), nec Brot. (1804).

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!

Thymelaea hirsuta (L.)Endl. var. **microphylla** Reynier in Bull. Assoc. Pyrén. Échange Pl., (1904), n.v. et in Bull. Soc. Bot. France 53 (sess. extr.): 64 (1906).

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

Distribution: circum-Mediterranean. Europe, S.W. Asia and N. Africa.

Selected specimens

PORTUGAL. Algarve: Faro, Bourgeau 1853: 2024! SPAIN. Barcelona: Montjuich, 16 iv 1870, Thompson! Valencia: Willkomm 298! Alicante: Salinas at Santa Pola, Gibbs 27.63! Murcia: Sierra de Carrascoy, 15 x 1851, Bourgeau! Cadiz: Cadiz, sea level, Davis 50984! Malaga: San Anton, Ball 914 a! Granada: 2 km from Alhama de Granada to Veléz Malaga, 1219 m, K.& L. Tan 373! Almeria: near Nijar, sea-level, Allen 9868! BALEARICS. Majorca: Soller, 15 ix 1910, Bianor! Ibiza: 4.8 km W. of S. Antonio, Hedge 17.54! S. FRANCE. Bouches-du-Rhone: Mont-Redon near Marseilles, iv 1874, Perret! Herault: Montpellier, ann. 1837, Chapel! Pyr. or.: Port Vendres, 2 xi 1878 & 29 v 1884,

Thompson! Var: Toulon, anon.! Aude: Ile St. Lucia, near Narbonne,

19 v 1825, Walker-Arnott & Bentham 77! Vaucluse: Avignon, 29 iii

1825, anon.! CORSICA. Calvi, iv 1962, Archibald! Bastia, 9 xi 1854,

Ball! ITALY. Orbetello, Mt. Argentario, 15 iv 1905, Baccarini et al.!

Anzio to Nettuno, Pirotta 896.1! Capri, v 1842, Ball! near Brindisi,

iv 1874, Ball! SARDINIA. Santa Teresa Gallura, Tempio, 1 & 6 iv

1881, Reverchon! Cagliari, Thomas s.n.! SICILY. Syracuse, Somerville

63! Tranpani, near San Julians beach, Davis 40199! YUGOSLAVIA. Istria,

anon! BULGARIA. Plovdiv, Curle 38! GREECE. Athens, Orphanides

1850: 270! Hymettus, Davis 58! Mt. Lycabetto, x 1867, Ball!

AEGEAN ISLANDS. Crete: Sfakia, near Aj. Andonios E. of Vuvás,

250 m, Greuter 7692! Euboea: near Chalkis, Adamovic; Scyros: Tuntas;

Delos: Watzl; Nisiros: Papatsou 657; Rodhos: iii 1944, Finkl!

TURKEY (Turkey-in-Europe, W. and S. Anatolia) A$_2$ (E) Istanbul:

Büyükdere, v 1944, Noë! C$_2$ Muğla: Kaunos (Dalyan) Fitz & Spitzenberger

93! Antalya: Kalamaki near Patara, Spratt & Forbes; C$_3$ Antalya:

Antalya, Kayacik 10! C$_5$ İçel: Mersin, sea-level, Sintenis 1888: 17!

Adana: Karataş area, S. of Adana, Findlay 266! CYPRUS. Cape Gata,

Davis 3545! 8 iv 1859, Kotschy! SYRIA. unloc., Aucher 2521!

Hama, anon.! LEBANON. Beirut, Bornmüller 12326! ISRAEL. Kyriat

Haim, Davis 3854! W. Sheriba near Beersheba, 1 - 20 m, Whiting 1335!

Jaffa, 5 iv 1870, Ramley! Carmel, 800 m, Meyers & Dinsmore 7335!

JORDAN. Petra, 1000 m, Dinsmore 15335! Hunting Aero Survey 1955:

87b! MOROCCO. Casablanca, Rein & Fritsch s.n.! 69 km from Tiznit to

Tafraoute, 1100 m, Davis 48761! Tafraoute to Col du Kerdous, 1100 m,

Davis 53794! ALGERIA. Oran, Macta, v 1909, Faure! Layoune to

Khemisti, 950 m, Davis 58536! Mustapha, Romain 1649! El Outaïa, ii

1880, Ball! TUNISIA. 16 km from Sbiba, 730 m, Davis, 57178! Maktar

to Sbeitla, 1075 m, <u>Davis</u> 57264! E. of Gafsa, El Guettar to Bou Saad,

350 m, <u>Davis</u>! 61204! Monastir, sea-level, <u>Davis</u> 48051! LIBYA. Cyrenaica,

70 km W. of Tubruq, sea-level, <u>Archibald</u> 976! El Abiar, E. of Benghazi,

300 m, <u>Davis</u> 49893! Gebel Nefoussa, Iefren-Giado, 700 - 800 m, <u>Davis</u>

49560! EGYPT. Ramleh near Alexandria, <u>Scott-Elliot</u> 3549! <u>Ball</u>

1877: 58! Mariout, Burg-el-Arab, <u>Davis</u> 6397!

As in <u>T. lythroides</u> 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. <u>angustifolia</u> as having leaves

narrowly ovate-oblong or lanceolate, <u>acute</u>, 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 (<u>Richard</u> 2) and Egypt (<u>Aucher</u> 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.

<u>T. hirsuta</u> var. <u>polygalaefolia</u> (Lapeyr.) Endl. has been described as 'foliis ovatis utrinque tomentosis, dorso demum glabratis' by Meissner, loc. cit. It is remarkable that there can be a variety with leaves white-tomentose on <u>both</u> surfaces and certainly extremely rare to have 'hirsuta' leaves glabrous on the <u>adaxial surface</u>, 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 <u>Passerina hirsuta</u> for <u>T. tinctoria</u> (Pourret) Endl. The abaxial surface of leaves in this species is grey-puberulous and perhaps may account for any taxonomic confusion.

Economic note: <u>T. hirsuta</u> is poisonous to livestock. In Cyrenaica it was formerly used as a substitute for <u>Imperata cylindrica</u> 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, cited by Keith, 1965), a 'valuable potential cellulose and fibre plant'.

3. **T. lanuginosa** (Lam.) Ceballos & Vicioso, Estud. Veg. Fl. Forest.
Málaga, 235 (1935), n.v.; **T. lanuginosa** (Lam.) Brecher in Index Horti.
Bot. Univ. Budapest. 5: 102 (1941).

Syn: **Daphne lanuginosa** Lam., Encycl. 3: 436 (1792), photo!

Passerina canescens Schousboe in Willd., Sp. Pl. 2: 432 (1799)!

Chlamydanthus canescens (Schousboe) C.A. Meyer in Bull. Phys.-Math.
Acad. (Pétersb.) 1: 358 (1843)!

T. canescens (Schousboe) Endl., Gen. Pl. Suppl. 4 (2); 65 (1848)!

P. kalifolia Pourret apud Willk. & Lange, Prodr. Fl. Hisp. 1: 301
(1862), pro syn.

Stellera lanuginosa (Lam.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

P. lanuginosa (Lam.) Pau in Mém. Mus. Ci. Nat. Barcelona 1(1): 67
(1922), photo!

Ic: Boiss., Voy. Bot. Espagne, t. 157a, f. 1-4 (1839-1845); H.K. Tan
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. <u>Fl. Jan. - Jun.; fr. till</u>

<u>Aug.</u> <u>Abandoned race course, scrub forest, sandy and dry rocky soils</u>
<u>near sea, rare in hills, sea-level - 15 m.</u>

Type: /Spain/ communiquée par M. de Jussieu (holo. P, photo!).

Distribution: S. Spain, Gibraltar and Morocco.

<u>Selected specimens</u>

SPAIN. unloc., <u>Schousboe</u> s.n.! B-Hb. Willd. 7591, photo! (type of
<u>P. canescens</u>). Hb. Pourret 2390, 6319 (type of <u>P. kalifolia</u>). Cadiz:
Algeciras, 15 m, <u>Stocken</u> 271.64! Malaga: Estepona to Marbella, vi
1837, <u>Boissier</u>! GIBRALTAR. beach of St. Roch, 18 iv 1889, <u>Dautez &</u>
<u>Reverchon</u>! old Spanish race course, 7 i 1858, <u>anon.</u>! MOROCCO. Tanger,
<u>Schousboe</u> s.n.!

A species closely related to <u>T. gattefossei</u> H.K. Tan.

4. <u>T. gattefossei</u> H.K. Tan in Notes R.B.G. Edinb. 35(3): 345 (1977).
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. <u>Fl. Feb. – Mar. Sandy plains, littoral region with Chamaerops
humilis L.</u>

Type: /M̄orocco͞/ Chaouïa, chamaeropaie sur sable á Bouskoura, ii 1937,
<u>Gattefossé</u> (holo. MPU!).

Distribution: endemic to W. Morocco (refer Appendix B).

5. <u>T. argentata</u> (Lam.) Pau in Cavanillesia 5: 44 (1932).

Syn: <u>Daphne argentata</u> Lam., Encycl. 3:436 (1792), photo!

<u>D. nitida</u> Vahl, Symb. 3:53 (1794), photo!

<u>Passerina nitida</u> (Vahl) Desf., Fl. Atl. 1: 331 (1798), photo!

<u>Chlamydanthus nitidus</u> (Vahl) C.A. Meyer in Bull. Phys.-Math. Acad.
(Pétersb.) 1: 358 (1843), photo!

<u>T. nitida</u> (Vahl) Endl., Gen. Pl. Suppl. 4(2): 65 (1848), photo!

<u>P. segobricensis</u> Pau in Not. Bot. Fl. Espan. 1: 25 (1887)!

<u>Stellera nitida</u> (Vahl) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

<u>T. nitida</u> (Vahl) Endl. var. <u>segobricensis</u> Pau in Willk., Suppl.
Prodr. Fl. Hisp., 69 (1893)!

<u>T. virgata</u> (Desf.) Endl. var. <u>microphylla</u> Willk., loc. cit. (1893),
pro syn.

<u>P. argentata</u> (Lam.) Pau in Mém. Mus. Ci. Nat. Barcelona, 1(1): 67
(1922), photo!

Ic: Desf., Fl. Atl. 1: t. 94 (1798); Fig. 54 D - F, map 10.

Erect shrub, 10 - 50 cm. Branches ± fastigiate, rarely divergent,
pilose; flowering shoots short, sericeous, densely leafy. Leaves
imbricate, sessile, subcoriaceous, oblanceolate or spathulate, 3-8
x 0.5-2 mm, obtuse or apiculate, adpressed-sericeous. Flowers
hermaphrodite 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. <u>Fl. Apr. - Jun. Calcareous rock, sandstone steppe,</u>
<u>limestone pavement (with Quercus ilex and Stipa tenacissima), Pinus</u>
<u>halepensis - Tetraclinis articulata scrub, 10 - 1500 m.</u>

* sessile, in terminal fascicles of 4-6 (-9). Bracts absent. Hermaphrodite ......

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 over-
looked 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. Reverchon 1898: 254 . Pistillate flowers are ....

6. <u>T. virescens</u> Meissn. in DC., Prodr. 14: 554 (1857).

Syn: <u>Passerina virescens</u> Cosson & Dur. in Munby, Cat. Pl. Alg., 30
(1866) et apud Bal., Pl. Alg. exsicc. no. 1007 (1853)! nom. nud.
<u>Stellera virescens</u> (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, spathulate-oblanceolate, 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.
<u>Fl. and fr. Apr. - Jul. Dry rocky ground, 1650 - 2200 m.</u>

Type: /Ālgeria7 ad fontes fl. Oued-Abdi et in sylvâ Lambèse, <u>Balansa</u>
1853: 1007 (holo. G - DC, photo! iso. E!).

Distribution: N.W. Africa.

<u>Selected specimens</u>
MOROCCO. Haute Moulouya, Itzer, 1650 m, <u>Jahandiez</u> 210! Grand Atlas,
plateau des Lacs, <u>Emberger</u> s.n.!

<u>T. virescens</u> var. <u>glaberrima</u> 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

(ex Jah. & Maire, 1932), Djebel Aissa and Dj. Bechar in Algeria (ex

Batt. & Trabut, 1890). I have not seen any material.

Affinities of this species are closest to T. putorioides Emb. & Maire.

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

Syn: <u>T. virescens</u> Lit. & Maire in Mém. Soc. Sci. Nat. Maroc 26: 35
(1931)! non Meissn. (1857)!

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 <u>putorioides</u>

Syn: <u>T. putorioides</u> Emb. & Maire var. <u>chlorantha</u> Emb. & Maire, op. cit.,
23: 215 (1932)!

Ic: Fig. 53 A - G; map 10.

Leaves spathulate-obovate, 5-9 x 1.5-3 mm; adaxial surface pubescent,
abaxial becoming glabrous. Flowers yellow. <u>Fl.Jul. Mountains, calcareous
rock, 1800 m.</u>

Type: /Morocco_7in rupibus calcareis secus amnem Tessaout, prope Aït-Alla,
1800 m, 28 vii 1926, <u>Maire</u> (holo. MPU!).

Distribution: endemic to Grand Atlas, above Demnat.

b) var. <u>rhodantha</u> Emb. & Maire, op. cit. 23: 215 (1932). Ic: Fig. 53
H - J.

Differs from var. <u>putorioides</u> in having leaves spathulate-oblanceolate,
3-5 x 1-1.75 mm; adaxial surface glabrous, abaxial sparsely pilose,
sparsely ciliate. Flowers purplish. <u>Fl. Aug. Calcareous rock</u>,
<u>3400 m.</u>

Type /Morocco7 in rupibus montis Maaghal, 3400 m, 7 vii 1931, <u>Emberger</u>
(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.

<u>T. putorioides</u> is related to <u>T. virescens</u> Meissn. and <u>T. microphylla</u>
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.

8. **T. microphylla** Cosson & Dur. in Bull. Soc. Bot. France 3: 744 (1856).

Syn: *Passerina microphylla* Cosson & Dur. apud Bal., Pl. Alg. exsicc. no. 256 (1852)! no. 826 (1853)! et apud Kralik, Pl. Tun. exsicc. no. 333 (1854)! omnia nom. nud.

T. microphylla Meissn. in DC., Prodr. 14: 556 (1857)!

Stellera microphylla (Cosson & Dur.) Kuntze, Rev. Gen. Pl. 2: 585 (1891)!

Ic: Barr. in Cosson Illustr. Atl. 2: 106, t. 166 (1897); Fig. 54 G - J, map 10.

Monoecious erect shrub 20 - 150 cm. Branches virgate, soon naked; young shoots white-puberulous or sericeous. Leaves few, $\pm$ 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 Saharae totius, nempe a deserto Tunetano, Kralik pl. Tun. 333 (G - DC, photo! iso. E!).

Distribution: N. Africa.

Selected specimens:

ALGERIA. ex Sahara Algeriensi juxta Biskra, ii 1880, <u>Ball</u>! Aghalesta
to Djelfa, 28 iii 1873, <u>Maw</u>! 3 km S. of Hassi Bahbah, 800m, <u>Davis</u>
53286! Ain Sefra, 1100 m, 30 v 1934, <u>Faure</u>! TUNISIA. Oudref, iii
1907, <u>Pitard</u>! 10-20 km E. of Moulares, 400 m, <u>Davis</u> 61216! Djebel
Ben Younes near Gafsa, 500 - 600 m, <u>Murbeck</u> s.n.! LIBYA. near Univ.
of Libya (Tripoli), 100 m, <u>Davis</u> 49481! Tripoli to Sabrătah, 20 m,
<u>Davis</u> 49795! <u>Taubert</u> 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 <u>not</u> poisonous to livestock whereas <u>T. hirsuta</u>
(L.) Endl. growing nearby <u>is</u> 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
<u>T. sempervirens</u> Murb. from Tunisia and <u>T. putorioides</u> Emb. & Maire
from the Grand Atlas.

9. <u>T. sempervirens</u> Murb. in Acta Univ. Lund. 35(3): 14 (1899).

Ic: Murb., op. cit. 15: f. 1; t. 12: f. 1-2 (1899);

map |O .

Monoedious 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. <u>Fl. Apr. Calcareous rock, 350 m.</u>

Type: /Tunisia/ Rochers calcaires du ravin qui descend du Ksar Sakket
vers le caravansérail de Bir Saad, 19 (in errore 29) iv 1896, <u>Murbeck</u>
(holo. LD!).

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. <u>microphylla</u> 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.

<u>Thymelaea tartonraira</u> (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 <u>argentea</u> while the rest are treated as <u>tartonraira</u>,
with the exception of <u>thomasii</u> 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 <u>T. argentea</u> (Sm.) Endl. and <u>T. tartonraira</u> (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. <u>thomasii</u> (2n = 18, Contandriopoulos, 1964).

10. <u>T. tartonraira</u> (L.) All., Fl. Pedem. 1: 133 (1785), as
'<u>T. tarton-raira</u>'.

Dioecious, rarely polygamodioecious, 20-60 cm shrub. Lower branches
with tuberculate scars, young shoots densely leafy, ± glabrous or
pubescent- sericeous. Leaves sessile, subcoriaceous, spathulate-
obovate to narrowly linear/ _-oblanceolate, obtuse or acute, ± glabrous and glaucous, adpressed-_ pubescent or sericeous on both surfaces,
glabrescent. Flowers sessile, axillary, 2-5. Bracts imbricate, (5-)
10-15; sericeous. Perianth 3-6 mm, pale yellow, pubescent or sericeous;
lobes 1-2.5 mm, ovate, obtuse or acute. Ovary pubescent; style
becoming subterminal.

Entirely Mediterranean, distribution extending from S. Spain and
Morocco to Cyprus.

<u>Key to subspecies and varieties</u>:

1. Leaves ± glabrous   6. subsp. <u>thomasii</u>

1. Leaves pubescent or sericeous

  2. Leaves adpressed-pubescent; hairs only 0.1-0.2 mm long

                                       5. subsp. <u>valentina</u>

  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. <u>tartonraira</u> var. <u>tartonraira</u>

4. Leaves spathulate-oblanceolate, 3-4(-5) mm broad

                  2. subsp. <u>tartonraira</u> var. <u>transiens</u>

3. Leaves 4-12 times longer than broad (predominantly E. Medit.)

  5. Leaves spathulate-oblanceolate, (2-)3-4 mm broad

                  3. subsp. <u>argentea</u> var. <u>argentea</u>

  5. Leaves narrowly linear-oblanceolate, c. 1.5 mm broad

                  4. subsp. <u>argentea</u> var. <u>linearifolia</u>

1. subsp. <u>tartonraira</u> var. <u>tartonraira</u>.

Syn: <u>Daphne tarton raira</u> L., Sp. Pl., 356 (1753), photo!

<u>D. candicans</u> Lam., Fl. Fr. 3: 221 (1778).

<u>Passerina tartonraira</u> (L.) Schrader /ās 'P. tartonreira'7 in Neues J.
Bot. 4: 89 (1810), photo!

<u>D. osyroides</u> Vahl ex Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 333
(1818).

<u>Tartonia obovata</u> Rafin., Autikon Botanikon, 146 (1840).

<u>Chlamydanthus tartonraira</u> (L.) C.A. Meyer in Bull. Phys.-Math. Acad.
(Pétersb.) 1: 358 (1843), photo!

<u>Thymelaea tartonraira</u> (L.) Meissn. in DC., Prodr. 14: 556 (1857), s.
str.

<u>Thymelaea tartonraira</u> (L.) All. var. <u>genuina</u> Lange in Willk. & Lange,
Prodr. Fl. Hisp. 1: 300 (1862), p.p.

<u>Stellera tartonraira</u> (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

<u>Thymelaea tartonraira</u> (L.) All. var. <u>typica</u> Fiori in Fiori & Paol.,
Fl. Anal. Ital. 1: 284 (1898), photo!

<u>Giordia tartonraira</u> (L.) Gerber in Bull. Soc. Bot. France 46 (sess. extr.):

112 (1899), photo!

Thymelaea tartonraira (L.) All subsp. linnaei Briq. in R. Lit.,
Prodr. Fl. Corse 3(1): 3 (1938).

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 spathulate-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
1129!

2. subsp. tartonraira var. transiens (Briq.) H. K. Tan, comb. nov.
Syn: Tartonia cuneifolia Rafin., Autikon Botanikon, 146 (1840),
p.p.
Thymelaea tartonraira (L.) All var. genuina Lange in Willk. & Lange,
Prodr. Fl. Hisp. 1: 300 (1862), p.p.
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
Iter Maroc. no. 287 (1928).
Thymelaea tartonraira (L.) All. var. angustifolia R. Lit. & Maire in
Mém. Soc. Sci. Nat. Maroc 26: 35 (1931), non Meissn. (1857), photo!
nec Lange (1862).
Thymelaea tartonraira (L.) All. subsp. linnaei Briq. var. genuina
Lange emend. R. Lit. subvar. transiens Briq. in R. Lit., Prodr.
Fl. Corse 3(1): 4 (1938)!
Ic: Fig. 55 D - Fa, map 11.

Leaves spathulate-oblanceolate, 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,
steppe (Lygeum and Artemisia herba-alba predominant), calcareous
crusts (previous Pinus halepensis forest) rare along coast, 900 -
1800 m.

Type: /C̄orsica̱7sommet 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!

Chlamydanthus argenteus (Sm.) C. A. Meyer in Bull. Phys.-Math. Acad.
(Pétersb.) 1: 358 (1843)! p. p.

Thymelaea argentea (Sm.) Endl., Gen. Pl. Suppl. 4(2): 65 (1848)! p.p.

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)!

T. tartonraira (L.) All. var. candiliana Beauv. & Top. in Bull. Soc.
Bot. Gen. 28: 134 (1938).

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

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 59! Mt. Kerata above Eleusin, ann, 1885, Haussknecht! Attika, x 1867, Ball! Peloponnesi, ii 1836, Kotschy! AEGEAN ISLANDS. Crete: Palaiokhora, 915 m, Davis 115! 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! Nisiros: 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). A_1 (A) Çanakkale:

18 km S. of Çanakkale, <u>Huber-Morath</u> 17469! A₁ (E) Çanakkale:

Ariburnu, <u>A.& T. Baytop</u> 12.611! B₁ Çanakkale: plains of Troy, tomb

of Ajax, <u>Clarke</u> s.n.! Izmir: Ilica, 3 km E. of Çeşme, <u>Alava & Regel</u>

4824! C. Aydin: 3 km from Didyma, 10m, <u>Bocquet</u> 2653!

4. subsp. <u>argentea</u> (Sm.) Holmboe var. <u>linearifolia</u> H. K. Tan, <u>var.</u>
<u>nov.</u>

Syn: <u>Thymelaea tartonraira</u> (L.) All. subsp. <u>argentea</u> (Sm.) Holmboe,

Veg. Cyprus 133 (1914), as '<u>T. tartonraira</u> subsp. <u>T. argentea</u>', quoad

typ. haud comb.

Ic: Holmboe, op. cit. 282: f. 122: Fig. 55 A - Cb, map ||.

Leaves narrowly linear-oblanceolate, (10-)20-25 x c. 1.5 mm, greyish

or silvery-sericeous. Bracts 10-15, triangular-acute in Cretan plants,

more ovate-obtuse in Cyprian ones. <u>Fl. Feb. - Jun. Dry igneous</u>

<u>rock, limestone slopes, maquis on serpentine, sea-level to 830 m.</u>

Type: /C̄yprus͞7 Mazoto, <u>Holmboe</u> 163 (C?).

Distribution: confined to S.W. Anatolia, Rodhos, Crete and Cyprus,

the last two being the most southern and eastern part of subsp.

<u>argentea</u>'s range.

Selected specimens:

AEGEAN ISLANDS. Crete: above Palaiokhora at Kephala, c. 130 m,

<u>Davis</u> 1221! Selinos, Omalos, 24 v 1884, <u>Reverchon</u>! Mt. Sfakia,

<u>Sieber</u> s.n.! Rodhos: iii 1944, <u>Finkl</u>! W. slope of mt. Paradisou,

100 - 250 m, Kjellqvist & Snogerup 22042! TURKEY (S.W. Anatolia).
C$_2$ Muğla: Marmaris to Emecik, 200 m, Davis 25326! C$_3$ Antalya: Kayran
(N.W. Antalya) Bozakman & Fitz 181! 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, Deflers 1135! 1136! 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.

A$_1$(E) Çanakkale: S.S.W. Çanakkale, c. 2 km S. of Güzelyali, Lewejohann
Tu - 74 - 066! C$_1$ Izmir: Samsun Dağ above Güzelçamli, 800 m, Davis
41727! C$_3$ Antalya: Antalya to Serik, Huber-Morath 14248! 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.

Thymelaea tartonraira (L.) All. subsp. angustifolia (Boiss.) Goday &
Chueca in Anal. Real. Acad. Farm. 38(3): 462 (1972).
Syn: Passerina tartonraira (L.) DC. var. angustifolia Boiss., Voy.
Bot. Espagne 2: 555 (1839 - 1845), non d'Urv. (1822) sub Daphne.

T. tartonraira (L.) All var. angustifolia (d'Urv.) Lange in Willk. &
Lange, Prodr. Fl. Hisp. 1: 300 (1862), excl. typ.

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

can be ascertained.

<u>Daphne tomentosa</u> Lam., Encycl. 3: 436 (1792).

Syn: <u>Passerina tomentosa</u> (Lam.) Wikstr. in Kungl. Svenska Vet.-Akad.
Handl., 332 (1818).

Of some interest is the real identity of <u>D. tomentosa</u>. Lamarck describes
it as 'Daphne floribus sessilibus axillaribus, foliis oblongis obtusis
utrinque sericeo-tomentosis, N.' Endlicher (1848) following Lamarck,
summarizes it as <u>T. tomentosa</u> from the Orient. Lamarck lists <u>D. tomentosa</u>
immediately after <u>D. tartonraira</u> L. and in fact regards it as a variety
of the latter with a similar habit but/longer and white-tomentose
leaves. <u>D. tartonraira</u> 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 <u>D. tomentosa</u>
Lam. with <u>T. tartonraira</u> subsp. <u>argentea</u>. Unfortunately the voucher
specimen designated 'il croit dans le Levant' could not be traced.

5. subsp. <u>valentina</u> (Pau) O. Bolós & Vigo in But. Inst. Catal.
Hist. Nat. 38(1): 73 (1974).

Syn: <u>Daphne myrtifolia</u> Poiret in Lam., Encycl. Bot. Suppl. 3: 315
(1813), photo!

<u>Passerina tartonraira</u> (L.) Schrader var. <u>valentina</u> Pau in Bol. Soc.
Ibér. Ci. Nat. 25: 72 (1926)!

<u>P. tartonraira</u> var. <u>genuina</u> Lange f. <u>virescens</u> Pau, ibid.!

<u>P. tartonraira</u> var. <u>angustifolia</u> d'Urv. f. <u>valentina</u> Pau, ibid.!

<u>Thymelaea tartonraira</u> (L.) All. subsp. <u>linnaei</u> Briq. var. <u>genuina</u>

Lange emend. R. Lit. subvar. <u>valentina</u> (Pau) R. Lit., Prodr. Fl. Corse
3(1): 7(1938)!
Ic: Fig. 55 G - Gb; map II .

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. <u>Fl. Mar. Dry uncultivated
hills, schistose rock, 150-200 m.</u>

Type: /S̄pain/ Valencia, near Alcira, ann. 1890, <u>Porta & Rigo</u> Iter
hisp. II: 101 (iso. E!).

Distribution: confined to E. Spain.

<u>Selected specimens:</u>
Valencia: Mts. Puig-Campaña, <u>Porta & Rigo</u> Iter hisp. III: 63! Murcia:
Ajanque near Fortuna, 5 iii 1855, Guirao! P - Hb. Jussieu 3975; FI
- <u>Pourret</u> 124; MA - <u>Pourret</u> 6319.

Aymonin (1969) discovered that the obscure taxon, <u>Daphne myrtifolia</u>
Poiret, is in fact a member of the <u>T. tartonraira</u> complex. Specimens
in Hb. Poiret are marked 'Daphne, myrtifolia (n) encycl. suppl. Espagne'
and with the polynomial 'Thymelaea hispanica foliis <u>myrthi</u> incanis'.
The latter is an exact duplicate of the text description by Tournefort
(1700), 'Thymelaea hispanica, foliis myrti incanis. Tourn. Inst. R.
Herb., 395' except for the orthographical error underlined. The type

of this polynomial is from Valencia (P - Hb. Tournefort 5828, photo!)
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.
thomasii) as sufficiently distinct to be described at varietal level
(sub Passerina). He defined two forms which in my opinion do not deserve
taxonomic recognition.

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

D. A. Webb (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.

6. subsp. thomasii (Duby) Briq. in R. Lit., Prodr. Fl. Corse 3(1):
5 (1938).

Syn: Passerina thomasii Duby, Bot. Gall. 1: 406 (1828)!

T. thomasii (Duby) Endl., Gen. Pl. Suppl. 4(2): 66 (1848)!

T. tartonraira (L.) All (as 'tartonrarina') var. thomasii (Duby)
Reichb.,

Ic. Fl. Germ. 11: 13 (1849)!

P. tartonraira var. calvescens Gren. in Gren & Godr., Fl. Fr. 3: 63
(1855), photo!

T. tartonraira (L.) All.var. calvescens (Gren.) Meissn. in DC., Prodr.
14: 556 (1857), photo!

Daphne thomasii (Duby) Boullu in Ann. Soc. Linn. Lyon 24: 73 (1899)!

P. corsica J. Gay ex R. Lit., Prodr. Fl. Corse 3(1): 6 (1938), in
adnot., pro syn.

Ic: Reichb., op. cit. t. 552, f. 1172 (1849): map II.

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: /Corsica7 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, <u>Ph. Thomas.</u>

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. <u>thomasii</u> but subsp. <u>valentina</u> (Pau) O. Bolós & Vigo.

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

Syn: <u>Passerina velutina</u> Pourret ex Camb., Enum. Pl. Balear., 183 (1827), reprint in Mém. Mus. Hist. Nat. (Paris) 14: 304 (1827), non Boiss., Elenchus, 81 (1838)!

<u>T. velutina</u> (Pourret ex Camb.) Meissn. in DC., Prodr. 14: 555 (1857)!

<u>P. incana</u> Pourret in Willk. & Lange, Prodr. Fl. Hisp. 1: 300 (1862), pro syn.

<u>Stellera velutina</u> (Pourret ex Camb.) Kuntze, Rev. Gen. Pl. 2: 585 (1891)!

<u>P. velutina</u> Pourret ex Camb. f. <u>parvifolia</u> Knoche, Fl. Balear. 2: 214 (1922). f. <u>folia acuminata</u> Knoche, ibid.

<u>T. velutina</u> (Pourret ex Camb.) Endl. var. <u>angustifolia</u> Willk. in Knoche, ibid.

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

<u>T. velutina</u> (Pourret ex Camb.) Endl. subsp. <u>montana</u> (Malag.) Malag. in Lab. Bot. Sennen. Barc., 149 (1975), n.v.

Ic: Fig. 54 A - C, map 10.

Dioecious dwarf shrub, young branches yellow-velutinous. Leaves sessile, subcoriaceous, spathulate 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. <u>Fl. Feb. -</u> <u>Jul.</u> Rocky shores, calcareous hills, with Helichrysum angustifolium,

Teucrium subspinosum, Astragalus balearicus, Rosmarinus officinalis,
s.l. - 1500 m.

Provisional lectotype : /Balearics7 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.

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

Dioecious shrub. Leaves subsessile or with petioles 0.5 mm, sub-
coriaceous, spathulate or oblanceolate. Flowers sessile, solitary
(rarely paired), fragrant, yellow. Bracts 0-8, lanceolate. Mature
ovary pubescent. Seed c. 3 mm.

subsp. **dioica**

Syn: **Daphne dioica** Gouan, Ill. Obs. Bot., 27 (1773)!

Passerina dioica (Gouan) Ramond in Bull. Soc. Philom. (Paris) 41:
131 (1800)!

Daphne calicina Berger, Fl. Bas. Pyr. 2: 211 (1803), non '**D. calycina**'
Lam. (1792) nec Lapeyr. (1782).

P. empetrifolia Lapeyr., Hist. Abr. Pyr., 212 (1813)!

Stellera dioica (Gouan) Kuntze, Rev. Gen. Pl. 2: 585 (1891), 'dioeca'
orth. mut.!

'**P. geminiflora** Ramond' 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 spathulate 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: /France7 in apricis pyrenaicis eundo á pago S. Pauli de
Fenouilhedes ad pagum St. Martin, ann. 1768, Gouan (holo. K!).

Distribution: W. Pyrenees to S. W. Alps.

Selected specimens:

SPAIN. Huesca: Saumeres near Benasque, v 1831, Endress! Lerida: Pic
de Peguera (Mt. Peguere), 30 viii 1903, Neyraut! FRANCE. Gard: Ardoises,
Reverchon 1886: 138! Hautes-Pyr.: Cauterets, 2100-2150 m, 6 vi 1902,
Neyraut! Pyr.-Or.: St. Anton, near St. Paul, 1524 m, vi 1839, Rugel!
Al Roc del Mas de la Guardia, near Arles, vii 1830, Endress! Walker-Arnott
555! Trancade d'Embouillaz, vi 1829, Endress! Font de Comps, Walker-Arnott
& Bentham s.n.! Walker-Arnott 871! vi 1831, Macreight! Prato de Mollo,
Walker-Arnott 652! Alpes-Maritimes: 850 m, Charpin & Greuter 8405!
Val de Caros, 20 vii 1860, Ball! Col de Tende, Bordère s.n.! Hort
s.n.!

subsp. granatensis (Pau) Fernández Casas in Candollea 30: 288 (1975); also
subsp. granatensis (Pau) Malag. in Lab. Bot. Sennen. Barc., 149 (1975),
n.v.

Syn: Passerina granatensis Pau, Carta Bot. 1: 7 (1904)!

T. granatensis Lacaita in Bull. Soc. Bot. Genève, Sér. 2(21): 133 (1929),
nom. nud.!

T. granatensis Pau ex Lacaita in Cavanillesia 3: 40 (1930)!

'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: G 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, Bordére! 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. Intermediates between the two are met with e.g., above Ufsat towards Andorra, Ariege, 1 & 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. Coridifoliae. The latter is
characterized by the presence of only two floral bracts.

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

Dioecious shrub. Branches glabrous, with tuberculate leaf scars; young shoots reddish-brown, crispate - pubescent at tips. Leaves sessile, coriaceous, lorate, obtuse, becoming entirely glabrous. Flowers sessile, solitary. Bracts ovate, concave. Staminate flowers 4-6(-10) mm; pistillate 4-5 mm. Perianth yellow, glabrous; lobes connivent in pistillate flowers, unequal, broadly ovate, 1-1.5 mm, obtuse. Upper stamens semi-exserted. Ovary crispate-pubescent at apex; style becoming subterminal. Seed 3-3.5 mm.

subsp. <u>tinctoria</u>

Syn: <u>Passerina hirsuta</u> Asso, Syn. Stirp. Arag., 49 (1779), photo! non L. (1753), photo! nec Brot. (1804).

<u>P. tinctoria</u> Pourret, Chlor. Narb., 27 et in Mém.Acad. Sci. Toulouse 3: 323 (1788).

<u>Daphne vermiculata</u> Vahl, Symb. 1: 28 (1790).

<u>P. orientalis</u> Willd., Sp. Pl. 2(1): 431 (1799), p.p.

<u>Chlamydanthus tinctorius</u> (Pourret) C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1: 358 (1843).

<u>T. tinctoria</u> (Pourret) Endl. var. <u>vermiculata</u> (Vahl) Lange, Pug. Hisp., 103 (1861), n.v.

<u>Stellera tinctoria</u> (Pourret) Kuntze, Rev. Gen. Pl. 2: 585 (1891).

<u>P. imbricata</u> Sennen in Ann. Soc. Linn. Lyon 70: 69 (1923)!

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, <u>tomentose</u> on both surfaces when young. <u>Fl. Apr.</u>

- Sep. Screes, degraded calcareous rock, garigue (Quercus valentina,
Q. coccifera, Carex humilis, Erica multiflora, Rosmarinus officinalis,
Bupleurum fruticescens, 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 65! Barcelona: Centellas to S. Feliu de Codinas,
792 m, K.& L. Tan 129! Montserrat, 800 - 1000 m, K. & L. Tan 134!
La Panadella, 800 m, Heywood .3! 2 km from Igualada to Santa Coloma
de Queralt, 366 m, K.& L. Tan 158! Valencia: Sierra de Segorbe,
500 m, Reverchon 1891: 596! Benicarlo, Sennen 793! Castellon de la
Plana, ii & iv 1909, iii & iv 1909 - 1917, Sennen! Chulilla to Requena,
366 m, K. & L. Tan 272! Murcia: ann. 1837, Boissier!

subsp. nivalis (Ramond) H. K. Tan, stat. nov.
Syn: Daphne calycina Lam., Encycl. 3: 435 (1792), photo! non Lapeyr.
(1782), photo! nec 'calicina' Berger (1803).
Passerina nivalis Ramond in Bull. Soc. Philom. (Paris) 41: 131, t. 9,
f. 3 (1800)!
Thymelaea nivalis (Ramond) Meissn. in DC., Prodr. 14: 555 (1857)!
T. tinctoria (Pourret) Endl. var. nivalis (Ramond) Lange, Pug. Hisp.,
104 (1861), 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;

map 12.

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-scree, limestone ridge, cropped turf in mountains, 914 - 2500 m.

Syntypes: /Spain, France/ In summis alpibus Pyrenaeorum ad Port de Gavarnie et circa Mont Perdu, Ramond (P!).

Distribution: endemic to C. and W. Pyrenees, rather rare.

Selected specimens:

SPAIN. unloc. P - Hb. Tournefort 5819, photo! Huesca: Benasque, 4 vii 1925, Walker-Arnott & Bentham 1529! Saumères, v 1831, Endress! near Cabone, 914 - 1219 m, 14 viii 1861, Ball! vi 1860, Bordère! Ordessa National Park, 1200 - 1600 m, 20 v 1961, Money-Coutts! Pic du Pourtalet, 2100 m, Harrold & McBeath 308! FRANCE. Hautes-Pyr.: Gourette area, ann. 1971, Holford, photo! c. Gavarnie, vi 1885, Timbal-Lagrave & Marcais! Gedre, vi 1867, Becker! In cultivation, Dean House, Kilmeston Hants, Money-Coutts BM 61009! cult. Rock Garden, Kew, 16 iii 1912, Bean!

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.

14. <u>T. subrepens</u> Lange in Dansk. Vidensk. Selsk. Forh., 193 (1893).
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. <u>Fl. and fr. Mar. - Jun. Pinus forest, calcareous soil,
1500 m.</u>

Type: /Spain/ Sierra Valdemaca, near Cuenca, 30 v 1892, <u>Dieck</u> (holo.
C, photo!).

Distribution: endemic to E. Spain, rare.

<u>Selected specimens:</u>
Teruel: Sierra del Pinar d'Albarracin, 1500 m, iv 1895; iii & iv
1896, <u>Reverchon</u>! Orihuela del Tremedal, 1500 m, v 1895, <u>Reverchon</u>!

Affinities with <u>T. tinctoria</u> (Pourret) Endl. Staminate flowers not
examined.

15. <u>T. procumbens</u> A.& R. Fernandes in Bol. Soc. Brot. ser. 2, 26:
266 (1952).

Syn: <u>T. coridifolia</u> (Lam.) Endl. subsp. <u>procumbens</u> (A. & R. Fernandes)
Malag. in Lab. Bot. Sennen. Barc., 148 (1975), n.v.

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. <u>Fl. Apr. - May;</u>
<u>fr. Jun. Schistaceous rock (pH 5.8), ground layer of Quercus pyrenaica</u>
<u>forest.</u>

Type: /Portugal7 Ribeira d'Arnes, pr. Sabugal, <u>Fernandes, Sousa &</u>
<u>Matos</u> 4038 (holo. COI!).

Distribution: endemic to E. Portugal and W. Spain.

<u>Selected specimens:</u>

PORTUGAL. Arredores do Sabugal, ribeira d'Arnes, <u>Fernandes</u> et al.
3970! 3971! 3972! SPAIN. Sierra de Gata, vi 1904, <u>Gandoger</u>.

Three separate sheets of <u>Fernandes, Sousa & Matos</u> 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. <u>Fernandes</u> et al. 3970 and 3971 are of sterile

material. No. 3972 had some 6-merous/flowers and pistillate flowers
(staminate)

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 <u>T. coridifolia</u> (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 <u>T. coridifolia</u>,

being 5-7 mm instead of 3-5 mm.

16. **T. ruizii** Loscos in Restaur. farm. 27(11): 169 (1872), n.v.

Syn: T. calycina (Lapeyr.) Meissn. var. pilosa Lange, Pug. Hisp.,
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.!

Stellera ruizii (Loscos) Kuntze, Rev. Gen. Pl. 2:585 (1891).

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

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.
Bot. Sennen. Barc., 149 (1975), n.v.

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

Type: /Spain/ Picos de Europa, near Refugio Aliva, <u>Loscos</u>.

Distribution: N. Spain, N. E. Portugal.

<u>Selected specimens:</u>

PORTUGAL. Trás-os-Montes e Alto Douro: above Paçó, near Vinhais,
1070 m, <u>Silva & Teles</u> 8733. SPAIN. Santander: near La Colladuna
and Cuetos de Juan Toribis, 1800-1900 m, <u>Harrold & McBeath</u> 56! Picos
de Europa, vii 1879, <u>Boissier</u>! near Puerto de Aliva, 1800 m, 12 vii
1879, <u>Levier</u>! Navarra: near Caparroso, iii 1882, <u>Casaviella</u>. Logrono:
near Haro, 17 iv 1907, <u>Elias</u>! Fonzaleche (Rioja), <u>Elias</u> LISE 33891.
Logrono/Soria: between Viniegra de Arriba and Montenegro de Cameros
(Sierra de Urbion), 1700 m, <u>Dresser</u> 605! 699!

The distribution of <u>T. ruizii</u> 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 Logrono down to
the mountains of Old Castille (Sierra de Guadarrama).

Its closest affinities seem to be with <u>T. calycina</u> (Lapeyr.) Meissn.
from which it can be distinguished by the amphistomatic leaves, villous
bracts and glabrous perianth.

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

Syn: <u>Daphne calycina</u> Lapeyr. in Mém Acad. Sci. Toulouse 1: 209, t. 15 (1782), photo! non Lam. (1792) nec '<u>calicina</u>' Berger (1803).

<u>Passerina calycina</u> (Lapeyr.) DC. in Lam & DC., Fl. Fr. 3: 360 (1805), photo!

<u>P. tinctoria</u> Pourret var. <u>angustifolia</u> Boiss., Voy. Bot. Espagne 2: 556 (1839 - 1845).

<u>T. tinctoria</u> (Pourret) Endl. var. <u>calycina</u> (Lapeyr.) Endl., Gen. Pl. Suppl. 4 (2): 66 (1848), photo!

<u>T. calycina</u> (Lapeyr.) Meissn. var. <u>glabra</u> Lange, Pug. Hisp., 104 (1861), n.v.

<u>Stellera calycina</u> (Lapeyr.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

Ic: Lapeyr., Fig. Fl. Pyr., t. 88 (1812); Fig. 57 A - 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. <u>Fl. May - Sept</u>. Mountains, calcareous rock, 500 - 1500 m.

Syntypes: /France7 Ariege, montagne de Bernadouze; Vallée de Vicdesso, <u>La Peyrouse</u> (G, photo!).

Distribution: C. Pyrenees, rare.

Selected specimens:

SPAIN. Huesca: Saumères near Benasque, 1000 - 1500 m, v 1831, <u>Endress</u>!
(not to be confused with material of <u>T. tinctoria</u> subsp. <u>nivalis</u> or
or <u>T. dioica</u> subsp. <u>dioica</u> from the same locality).

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

non sensu Henriques (1885)!

Syn: Daphne coridifolia Lam., Encycl. 3: 437 (1792), photo!

Passerina coridifolia (Lam.) Wikstr. in Kungl. Svenska Vet.-Akad.

Handl., 354 (1818), photo!

D. ericaefolia Vahl in Lange, Pug. Hisp., 103 (1861), pro syn.,

n.v.

P. cantabrica Pourret in Willk. & Lange, Prodr. Fl. Hisp. 1: 299

(1862) pro syn.

Stellera coridifolia (Lam.) Kuntze, Rev. Gen. Pl. 2: 585 (1891),

photo!

T. dendrobryum Rothm. in Cavanillesia 7: 116 (1935).

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: /Spain7 ex Galica (holo. P - Hb. Juss., photo!)

Distribution: endemic to N. Spain (Galicia, Asturias to Navarra),

not further east than 2° W.

Selected specimens:

Leon: Puerto del Ponton, Cordillera Cantabrica near Picos de Europa,
1750 - 1800 m, <u>Dresser</u> 1066! Picón de la Bana, Sierra Cabrera, 8 viii
1933, <u>Rothmaler</u>; la Garganta near Santa Eulalia de Oscos, 9 v 1960,
<u>Lainz</u>! Burgos: Castro Valnera, 1200 m, vii 1928, <u>Loso</u>!

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 <u>T. coridifolia</u> 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 <u>T. ruizii</u> loscos is also
near Refugio Aliva in Picos de Europa, Dresser's specimens certainly
cannot be <u>T. ruizii</u> as the latter has a different habit and a glabrous
perianth.

<u>T. coridifolia</u> 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 <u>T. broteriana</u> Coutinho.

19. <u>T. broteriana</u> Coutinho in Bol. Soc. Brot. 24(1): 145 (1909).

Syn: <u>Passerina hirsuta</u> Brot., Fl. Lusit. 2: 28 (1804), non L. (1753),

photo! nec Asso (1779), photo!

<u>T. coridifolia</u> sensu Henriques in Bol. Soc. Brot. 3: 191 (1885)!

non Endl. (1848), photo!

<u>P. broteriana</u> (Coutinho) Sampaio, Herb. Port., 104 (1913).

<u>T. coridifolia</u> (Lam.) Endl. subsp. <u>broteriana</u> (Coutinho) Malag. in

Lab. Bot. Sennen. Barc., 148 (1975), n.v. as '<u>broterana</u>'.

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. <u>Fl.</u>

<u>Jun. - Jul.</u> Mountain heaths, c. 800 m.

Type: /¯Portugal_7 Serra do Gerez, <u>Brotero</u> (holo. COI!).

Distribution: endemic to N. and C. Portugal.

<u>Selected specimens:</u>

N. Portugal: Serra do Gerez, near Curral and Vidueiro, vi 1885,

<u>Aarão F. de Lacerda</u>! Vidoal e Borrageiro, <u>Henriques</u>! <u>Moller</u> 880!

C. Portugal: Sierra de Alpedrinha and S. de Arrabida, <u>R. da Cunha</u>!

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.

20. <u>T. antiatlantica</u> Maire in Bull. Soc. Sci. Nat. Maroc 13: 273
(1933).

Syn: <u>T. linifolia</u> Andr. in Index Horti. Bot. Univ. Budapest. 3:
78 (1938).

Ic: Fig. 59 A - Cb; map 13.

Dioecious suffrutescent perennial, 50-60 cm. Stems branched at base,
flowering parts white villous or pilose. Leaves narrowly lanceolate,
(8-)10-15 x 2-3 mm, subobtuse, sericeous, later glabrescent. Flowers
axillary, sessile, 6-8. Bracts paired or one outer and two inner,
white villous.   Perianth yellow, sericeous; lobes slightly unequal,
ovate, obtuse. Ovary villous-pubescent at apex. <u>Fl. Mar. - Jun. In</u>
<u>stony desert, dry mountain pastures, 800 - 1500 m.</u>

Type: /Morocco/ In pascuis lapidosis aridis Anti-Atlantis: prope
Taliouine, 950 m, solo arenaceo, 16 v 1932, <u>Maire</u> (holo. MPU! iso.
K!).

Distribution: N. W. Africa.

<u>Selected specimens:</u>
MOROCCO. Anti-Atlas: Sidi Mezal, Ida-ou-Guidif, 25 iii 1937, <u>Maire</u>!
ALGERIA. Sud-Oran: Colomb Béchar at foot of Djebel Béchar, 1500 m,
ann. 1928, <u>Andreánszky.</u>

This is the only apparently Saharo-Sindian species of Sect. <u>Thymelaea</u>,
having affinities with <u>T. virgata</u> (Desf.) Endl. from which it can be
easily distinguished by its woody habit, narrower leaves and fewer bracts.

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

Predominantly androdioecious, perennial, 20-60 cm. Leaves elliptic-
lanceolate, (10-)20-25(-40) 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!
Chlamydanthus virgatus (Desf.) C.A. Meyer in Bull. Phys.-Math. Acad.
(Pétersb.) 1: 359 (1843).
Stellera virgata (Desf.) Kuntze, Rev. Gen. Pl. 2: 585 (1891).
T. virgata (Desf.) Endl. var. typica Maire in Bull. Soc. Nat. Afr.
Nord. 20: 201 (1929).
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: /Algeria7 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

Hassiane-Ed-Dih, Davis 58574! Layoune to Kemisti (S. of Teniet-el-Had),

Davis 58539! Chott-ech-Chergui between Bouktoub and le Kreider,

Davis 58778! 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.

Desfontaines and have thus been named var. densiflora Lange (Pug. Pl.

Hisp., 101). They may be similar to Salzmann's Tanger specimens

which have an unusally 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.

Syn: Passerina virgata Desf. var., Fl. Atl. 1: 331 (1798).

T. virgata (Desf.) Endl. var. broussonetii Ball. in J. Linn. Soc.

(Bot.) 16: 654 (1878).

Similar to subsp. virgata but stems glabrous in lower half or at least near base; middle stem leaves green, glabrous, not grey-villous. Smell reported as foetid. Fl. May - Jul; fr. Aug. Abundant and common in uncultivated mountain pastures and valleys, in meadows between Cedrus atlantica zone, sandstone gullies with Dyris, etc, on limestone slopes, basalt and schistose rock, miocene marne, 600 - 2650 m.

Type: /̄Morocco7 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.

22. <u>T. villosa</u> (L.) Endl., Gen. Pl. Suppl. 4(2): 66 (1848).

Syn: <u>Daphne villosa</u> L., Sp. Pl. ed. 2, 510 (1762), photo!

<u>Passerina villosa</u> (L.) Wikstr. in Kungl. Svenska Vet.-Akad. Handl.,
332 (1818), photo!

<u>Chlamydanthus villosus</u> (L.) C. A. Meyer in Bull. Phys.-Math. Acad.
(Pétersb.) 1: 358 (1843), photo!

<u>P. tingitana</u> Salzm. apud Meissn. in DC., Prodr. 14: 554 (1857), pro
syn.!

<u>Stellera villosa</u> (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

Ic: Boiss., Voy. Bot. Espagne, t. 157b, f. 1-4 (1839 - 1845);
Fig. 60K - N; map 12.

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. <u>Fl. Mar.-Jun. A calcifuge. Open rocky slopes, forestry
roads, near sea-level - 700 m.</u>

Type: /S̲pain̲/ Alstroëmer 235 (Hb. Linn. 500/5, photo!).

Distribution: S. Portugal and Spain, Gibraltar, Morocco.

Selected specimens:

PORTUGAL. Algarve, <u>anon</u>.! <u>Welwitsch</u> 403! Sierra de Monchique,
<u>Bourgeau</u> 1853: 2025! SPAIN. unloc., P - Hb. Tournefort 5811, photo!
B - Hb. Willd. 7539, photo! Cadiz: San Roque, <u>Willkomm</u> 1844: 670!
<u>Schott</u> s.n.! Carbonera, <u>Porta & Rigo</u> s.n.! Algeciras, Sierra above
Rio de la Miel, <u>Gibbs</u> 81.5! S. de Palma, <u>Reverchon</u> 1887: 108! Las
Navas, 305 m, <u>Allen</u> 7677! GIBRALTAR. unloc., P - Hb. Juss., photo!
ann. 1837, <u>Boissier</u>! MOROCCO. Tanger, <u>Schousboe</u> s.n.! iii 1912,
<u>Pitard</u>! ann. 1849, <u>Boissier & Reuter</u>! ann. 1835, <u>Salzmann</u>! Djebel
Kebir, ann. 1887, <u>Ball</u>!

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

23. **T. thesioides** (Lam.) Endl., Gen. Pl. Suppl. 4(2): 66 (1848).

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: <u>Daphne thesioides</u> Lam., Encycl. 3: 437 (1792), photo!

<u>Passerina thesioides</u> (Lam.) Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 333 (1818), photo!

<u>P. linariaefolia</u> Pourret apud Wikstr., ibid., pro syn.

<u>Chlamydanthus thesioides</u> (Lam.) C.A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1: 359 (1843), photo!

<u>Daphne humilis</u> Vahl apud Willk. & Lange, Prodr. Fl. Hisp. 1: 299 (1862), pro syn.

<u>Stellera thesioides</u> (Lam.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

<u>P. pubescens</u> (L.) Loscos in Mem. Mus. Ci. Nat. Barc. (Bot.) 1(1): 67 (1922), non sensu Wikstr. (1818) nec Guss. (1843).

<u>P. pubescens</u> (L.) Loscos var. <u>virgata</u> Pau, op. cit. 1(3): 33 (1925).

<u>P. pubescens</u> (L.) Loscos f. <u>latiorifolia</u> Pau, ibid. (1925).

<u>T. sanamunda</u> All. subsp. <u>thesioides</u> (Lam.) Sagr. & Malag. in Lab. Bot. Sennen. Barc., 9 (1974)!

Ic: Lam., Tabl. Encycl. 2(1): t. 290 f. 4 (1792); Fig. 61 A - F; map 13 .

Leaves conferted 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/ communiquée par M. de Jussieu (iso. G - DC, photo!).
Orthography here and as originally published is 'theosioides' 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:
SPAIN. unloc. B - Hb. Willd. 7542, photo! Dufour Arag. no. 1693,
photo! Huesca: Jaca, vi 1874, Bordère! Zaragoza: Calatayud, 21
v 1911, Viciosa! Segovia: near Prádena, Gibbs & Dominguez 85.1!
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.

pubescens Meissn., op. cit., 553.

Syn: Daphne pubescens L., Mant. 1: 66 (1767), non Röhling (1812).

Passerina pubescens (L.) Wikstr. in Kungl. Svenska Vet.-Akad. Handl.,
332 (1818).

T. sanamunda All. subsp. pubescens (L.) Sagr. & Malag. in Lab. Bot.
Sennen. Barc., 9 (1974), n.v.

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'/ description however, is clearly not that of T. coridifolia. Although his 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.

subsp. elliptica (Boiss.) Brecher in Index Horti. Bot. Univ. Budapest.
5: 84 (1941).

Syn: Passerina velutina Boiss., Elenchus, 81 (1838)! non Pourret ex
Camb. (1827) !

P. elliptica Boiss., Voy. Bot. Espagne 2: 556 (1839 - 45)!

Chlamydanthus ellipticus (Boiss.) C. A. Meyer in Bull. Phys.-Math.
Acad. (Pétersb.) 1: 359 (1843)!

T. elliptica (Boiss.) Endl., Gen. Pl. Suppl. 4(2): 66 (1848)!

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'.

P. pubescens (L.) Loscos f. elliptica Pau in Mem. Mus. Ci. Nat. Barc.
(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.
Jun. - Jul. Hills and mountains, calcareous rock, 1100 - 2740 m.

Type: /Spain7 in aridis calcareis in Sierra Nevada, 1829 - 2134 m,
vi 1837, Boissier (holo. G - DC, photo! iso. K! E!).

Distribution: Pyrennes, 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.

24. <u>T. sanamunda</u> All., Fl. Pedem. 1: 132 (1785).

Syn: <u>Daphne thymelaea</u> L., Sp. Pl., 356 (1753), photo!

<u>Passerina thymelaea</u> (L.) DC. in Lam. & DC., Fl. Fr. 6: 366 (1815),

photo!

<u>Chlamydanthus thymelaea</u> (L.) C. A. Meyer in Bull. Phys.-Math. Acad.

(Pêtersb.) 1: 359 (1843), photo!

<u>T. bauhinii</u> Endl., Gen. Pl. Suppl. 4(2): 66 (1848).

<u>T. cneorum</u> Reichb., Ic. Fl. Germ. 11, t. 551 (1849).

<u>Stellera thymelaea</u> (L.) Kuntze, Rev. Gen. Pl. 2: 585 (1891), photo!

<u>P. sanamunda</u> (All.) Bub., Fl. Pyr. 1: 135 (1897).

<u>Giardia sanamunda</u> (All.) Gerber in Bull. Soc. Bot. Fr. 46 (sess. extr.):

112 (1899).

Ic: Fig. 60 F - 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. <u>Fl. May
- Jul. Hills, stony mountains, 600 - 1800 m.</u>

Type: described from Spain and Montpellier (Hb. Linn. 500/3, photo!).

Distribution: Spain, S. France and Italian Riveria. Record from N.
Africa (Meissner 1857: 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 Guaderrama, 4 vii 1854, Bourgeau!
FRANCE. Basses-Alpes: Sausses, 13 v 1885, Reverchon 33! Herault:
Pas-du-Loup near Beziers, 5 vi 1862, Cosson! Aude: near Narbonne,
v 1846, Irat! Pyr.-or.: Villefranche, vii 1839, Rugel! Walker-Arnott
& Bentham 872! Font di Comps, 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.

25. T. cilicica Meissn. in DC., Prodr. 14: 552 (1857).

Syn: Ligia (as Lygia) multicaulis Schott & Kotschy in Kotschy, Reise

in den cilicischen Taurus, 381 (1858)!

Ligia (as Lygia) cilicica (Meissn.) Boiss., Fl. Or. 4: 1053 (1879)!

Stellera cilicica (Meissn.) Kuntze, Rev. Gen. Pl. 2: 585 (1891)!

Ic: Fig. 62 ; map 14b.

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.

Fl. Jul.- Aug. Calcareous scree, rocky slopes, 1150 - 2440 m.

Type: ⟨Turkey C₅ Içel⟩ in montibus Ciliciae, c. Güllek Boghas

(Cilicischer Engpass), 1158 m, Kotschy 234b (holo. G - DC, photo! iso.

W! K!).

Distribution: endemic to S. Turkey (Cilician Taurus).

Selected specimens:

C₅ Içel: Taurus, Kotschy 53! Arpalik gorge, Kotschy 154! near Karli

Boghas and Gizyl Deppe, Bulgar Dağ, 1830 - 2440 m, Kotschy 1853: 48!

178a!

Niğde: Ala Dağ, Narpiz Gorge, 2338 m, Wood & Gibson 183! Demirkasik,

Findlay 129!

E. Mediterranean (mt.) element. Related to T. aucheri Meissn.

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

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.

Ligia (as Lygia) amani Kotschy apud Boiss., loc. cit. (1879) pro syn.!

Stellera aucheri (Meissn.) Kuntze, Rev. Gen. Pl. 2: 585 (1891)!

Ic: Fig. 63 ; map 14b.

Monoecious suffrutescent perennial. Stems as in **T. cilicica** but 10-18, 30-75 cm, glabrous or with tips minutely pubescent. Leaves subsessile, closely adpressed to stem on drying, linear-filiform, 8-20 x 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 C_5 Içel/ in monte Tauro, prope portus Ciliciences, Balansa 1855: 715 (G - DC, photo! W! E!), Kotschy 1836: 426 (W! K!).

Distribution: Syria, Lebanon, W. Iran; disjunct in N. and S. Anatolia.

Selected specimens:

TURKEY. A_4 Zonguldak: Karabük to Kel Tepe, 850 m, Davis 38848!

Kastamonu: W. of Kastamonu, 800 m, <u>Davis</u> 38754! C$_5$ Adana: S. end

of Ülükişla Pass, 914 m, <u>Findlay</u> 238! C$_6$ Hatay: Tolos Dağ, Kara Gaja,

305 m, <u>Kotschy</u> 1862: 107 (type of <u>L. amani</u>)! W. Amanus, 8-10 km

N. of Iskenderum, 15 m, <u>Aberdeen Univ. Amanus Exped.</u> L$_1$ 766! above

Yeşilkent, 305 m, <u>Darrah</u> 614 (leaves atypically broad)! Gaziantep:

near Tullugo, Aintab (Gaziantep), 305 & 610 m, 23 vi 1865, <u>Haussknecht</u>!

SYRIA. Aleppo, <u>Peyron</u> s.n.! LEBANON. Barghoutié near Saida, <u>Gaillardot</u>

s.n.! above Sidone, <u>Blanche</u> s.n.! Becherre, above Mar Tserkis, 1460 m,

<u>Kotschy</u> 1855: 257! mt Torbol above Tripoli, <u>Boissier</u> s.n.! IRAN.

Shiraz, <u>Hohenacker</u> s.n.! v 1842, <u>Kotschy</u> 443, photo!

Three separate sheets of <u>Kotschy</u> 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:-
T. passerina (L.) Cosson & Germ., T. gussonei Boreau, T. salsa Murb.
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 geo-
graphical 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 crispate-pilose. The flowers are unisexual, only
one or two imperfectly hermaphrodite flowers (without the full
complement of stamens) have been observed.

It is rather difficult to decide how to treat this species-complex
but since 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.

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

Syn: Stellera passerina L., Sp. Pl., 559 (1753), 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).

Passerina stellera Ramond ex Lam. & DC., Fl. Fr. 3: 361 (1805).

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).

P. diarthronoides Griffith, Ic. Pl. Asiat. 4: 365 (1854)!

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, photo!).

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 7452!). No records from S. America or S. Africa.

Selected specimens:

SPAIN. Huesca: Broto, Bordere 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, Schoenefeld 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.! CZECHOSLAVAKIA. Moravia, distr. Břeclav, 320 m, Unar 1543! HUNGARY. near N. Hörcsöl and Vám, Schilberszky s.n.! Homokmegy,

Wiesbaur s.n.! Pannoniâ, near Budam, Ball S.N.! Dorugh near

Strigonium, Grundl s.n.! RUMANIA. near Istria and Şariurt, 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. Parnethe near Dekeleiam, Heldreich 659!

Aznavour 1909! 17 vi 1891, Charrel! TURKEY. Widespread in Anatolia

but absent in Mesopotamia. A_2 (A) Istanbul: Bostandjik to Erenköy,

6 vii 1897, Aznavour! A_2 (E) Istanbul: Makriköy, 8 x 1893, Aznavour!

A_3 Sakarya: Adapazari, near Geyve, 100 m, Davis 36309! A_5 Sinop:

Boyabat, 350 m, Davis 38041! Samsun: Lâdik Istasyon, Karadağ Grid,

1000 m, Tobey 1152! A_8 Çoruh (Artvin): above Artvin, 850 m, Davis

30020! A_9 Kars: river Aras, 30-38 km W. of Tuzlu towards Kagizman,

1100 m, Rechinger 57417! B_2 Manisa: Salihli to Turgutlu, 120 m,

Buttler & Erben 17232! B_4 Ankara: Atatürk Orman Çiftligi, near Dolap

Dere, Alinoğlu 23! 39! Niğde: Tuz Golü N. W. of Ülükişla, 900 -

950 m, Davis 32818! B_5 Kayseri: Plain of Césarée (Kayseri), 1107 m,

Balansa 978! Everek (Develi), 1800 m, Siehe 249! B_6 Malatya:

Derendeh (Darende) to Kavak Aghatch (Akçadag), G. & B. Post 24! Sivas:

Sivas to Suşehri, 1310 m, Buttler 15659! B_7 Erzincan: between

Selepur and Erzincan, 1250 m, 6 vii 1955, Simon! Tunceli: Pertek to

Hozat, 1100 m, Davis 31014! B_8 Siirt: Silvan to Kurtalan, Davis

22115! B_9 Agri: c. 10 km E. of Agri, 1650 m, Uotila 19581! Bitlis:

Hisan, E. of Bitlis, 1372 m, Kotschy 480! Van: 5 km N. of Şatak,

1500-2000 m, Davis, 23197! C_2 Muğla: 1 km W. of Muğla, 660 m,

Lambert & Thorp 532! Denizli: Pamukkale, Alava & Bocquet 5283!
Antalya: Sivri Dağ, 610 m, Tricker s.n.! C_4 Konya: Kaşinhan, Davis
14767! C_5 Adana: 5 km N. of Toros Dağ, 225 m, Aberdeen Univ. Amanus
Exped. D1 307! C_6 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. Baghlan, 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, 2338-2591 m, Webster & Nasir 6287! Phandu,
305 m, Deane 111! Abogni, Deane s.n.! Hazara, Duthie s.n.! U.S.S.R.:
Prov. Saratov, near Chvalynsk, mt. Taschi, Gross s.n.! Georgia,
Elisabethpol (distr. Arés), Woronow s.n.! Lugansjkiensis, near Zakotne,
Oxijuk s.n.! Turkestan, Socalski 287! Taschkent, Regel s.n.! Kashgar,
Creswell 12! Transcaspia, Aschabad near Bagir, Sintenis 795! Songaria
near Ajagus, Karelin & Kiriloff 1845: 1935! Crimea, Callier 267!
Lewpatorÿa, Léveillé s.n.!

A weed of arable and wasteland, particularly widespread in early summer. It is the only species in Sect. <u>Ligia</u> in which unisexual flowers have rarely been noted (an exception being <u>Wängsjö</u> 2733! collected at 1050 m in June from Antalya in Turkey. This has staminate as well as hermaphrodite flowers, rather resembling the state of <u>T. salsa</u> Murb.).

28. <u>T. gussonei</u> Boreau in Mém. Soc. Acad. (Angers) 4: 121 (1958) as
'T. gussoni'.

Syn: <u>Stellera pubescens</u> Guss., Fl. Sic. Prodr. 1: 466 (1827), non
<u>Thymelaea pubescens</u> (L.) Meissn. (1857).

<u>Passerina annua</u> (Salisb.) Wikstr. var. <u>pubescens</u> (Guss.) Ten., Syll.
Fl. Nap., 565 (1831).

<u>P. pubescens</u> (Guss.) Guss., Fl. Sic. Syn. 1: 451 (1843), non Wikstr.
(1818).

<u>Ligia</u> (as <u>Lygia</u>) <u>pubescens</u> (Guss.) C. A. Meyer in Bull. Phys.-Math.
Acad. (Pétersb.) 1: 356 (1843).

<u>T. arvensis</u> Lam. var. <u>pubescens</u> (Guss.) Meissn. in DC., Prodr. 14:
552 (1857).

<u>T. passerina</u> var. <u>pubescens</u> (Guss.) Ces., Pass.& Gib., Comp. Fl. Ital.,
257 (1874).

<u>P. gussonei</u> (Boreau) Boullu in Bull. Soc. Bot. Fr. 24 (sess. extra) 66:
100 (1877), as 'P. gussoni'.

<u>P. annua</u> (Salisb.) Wikstr. var. <u>algeriensis</u> Chab. in Bull. Soc. Bot.
Fr. 36: 319 (1889).

<u>T. arvensis</u> Lam. f. <u>pilifera</u> Rohlena in Sitz.-Ber. Böhm. Ges. Wiss.
17: 54 (1903).

<u>T. passerina</u> (L.) Lange var. <u>sericea</u> Coutinho, Fl. Port., ed. 1, 177
(1913); ed. 2, 213 (1939).
* <u>T. puberula</u> Hand.-Mazz. in Ann. Naturh. Mus. (Wien) 27: 86 (1913)!
<u>T. algeriensis</u> (Chab.) Murb. in Contr. Fl. Maroc 2: 13 (1923).

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

<u>Ligia</u> (as <u>Lygia</u>) <u>passerina</u> (L.) Fasano f. <u>pilifera</u> (Rohlena) Hayek,
Prodr. Fl. Balc. 1: 933 (1926).

Ic: Fig. 64D - J; map 14b.

Annual, resembling <u>T. passerina</u> 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. <u>Fl. late Apr. -

Sep. Dry fallow fields, sand dunes, calcareous and rocky slopes, near

sea-level to 920 m.</u>

Type: /S̄icily7 in argillosis, inter segetes et p st messem in ar is,

Palermo, <u>Gussone</u>.

Distribution: S. Europe, Turkey, Cyprus, W. Syria, Algeria, Tunisia;

recorded from Crimea.

<u>Selected specimens:</u>

FRANCE. Montpellier, <u>Bentham</u> s.n.! CORSICA. Biguglia, <u>Mabille</u> 269!

near Bastia, <u>Mouterde</u> s.n.! ITALY. Mandorli, near Florence, <u>anon.</u>!

near Barga, <u>Ball</u> s.n.! SICILY. Castelbuona, Pl. Sic. rar. 194,

<u>Lojacono</u>! near Panormum, <u>Huet du Pavillon</u> s.n.! <u>Parlatore</u> s.n.!

Palermo, <u>Todaro</u> 255! TURKEY (Mainly N. W. Turkey, E. (southern) Anatolia).

A_2 (A) Istanbul: Yakadjik Dağ, 25 ix 1893, <u>Aznavour</u>! A_2(E) Istanbul:

Zékériékeuy, Tatli Sou near Kilia, 15 viii 1897, <u>Aznavour</u>! C_7

Adiyaman/Urfa: Kjachta, Karamubara, 650 m, <u>Handel-Mazzati</u> 403! C_8

Mardin: Botan Su, 5 km W. of Tilo, 750 m, <u>Frödin</u> 207! CYPRUS. Kyrenia,

<u>Casey</u> 960! Mia Milea, 160 m, <u>Chapman</u> 676! SYRIA. near Doumar,

<u>Gaillardot</u> s.n.! Haleb (Aleppo), 400 m, <u>Hakim</u> 14 (type of <u>T. puberula</u>)!

ALGERIA: Oran, Le Figuier, <u>Munby</u> s.n.! <u>Faure</u> s.n.! Fragm. Fl. Alg.

183, <u>Choulette</u>! Mitidja, <u>Munby</u> s.n.! Tunisia: Zaghouan, <u>Kralik</u> 332!

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T. passerina	T. gussonei	Spain: Reverchon 179!	Iraq: Wheeler-Haines 1216!
flowers hermaphrodite	hermaphrodite and uni-sexual	unisexual	unisexual
☿ 2.5-3 mm long	☿ 4-5 mm	—	—
	♀ 3-4 mm	♀ 2.5 mm	♀ 2.5 mm
	♂ 2.5-5 mm	♂ 1.75-2 mm	♂ 1.75 mm — 1♀, 4-5 ♂ per cluster, subtended by 4 or more bracts.
ovary apex hirsute	hirsute	hirsute	hirsute
bracts 3 mm long	1.5 - 2 mm	1.5 mm	1 mm
sparsely ciliate at base	ciliate in lower half	ciliate in lower half	ciliate in lower half
stem glabrous	with straight-adpressed hairs	glabrous	glabrous

TABLE 15. T. passerina and T. gussonei. Comparison of some morphological features.

LEBANON. <u>Aucher</u> 2932! PALESTINE. Jerusalem, 800 m, <u>Meyers</u> 156!
El Reina (Nazareth), <u>Davis</u> 4719! Kefr Yasif, 85 m, <u>Meyers & Dinsmore</u>
B. 5054!

This species is more southern and restricted in distribution than
<u>T. passerina</u>, the peak flowering period a little later, August to
September, rather than from April to June. The frequently reddish-
purple stems of <u>T. gussonei</u> 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. <u>T. salsa</u> Murb. in Lunds Univ. Årsskr. n.s. 19(1): 11 (1923).

Syn: <u>Passerina annua</u> (Salisb.) Wikstr. var. <u>salsa</u> Munby, Cat. Pl.

Alg., 30 (1866), nom. nud.

<u>T. passerina</u> (L.) Lange var. <u>salsa</u> Munby in Lit. & Maire, Contr. Gr.

Atlas, Mém. Soc. Sci. Nat. Maroc, 35 (1930), nom. nud.

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. <u>Fl. and fr.</u>

<u>Apr. - Oct.</u> Dry places, salt flats, 800 - 1300 m.

Type: /Algeria/ Rel. <u>Maillefer</u> no. 1650 (LD).

Distribution: S. Spain, Morocco and Algeria.

<u>Selected specimens:</u>

SPAIN. Jaen: near Jaen, 20 viii 1845, <u>Willkomm</u>! Granada: Sierra

Nevada, El Pulche, vii 1883, <u>Nilsson</u>; Serrania de Ronda, <u>Boissier</u>

& <u>Reuter</u> s.n.! MOROCCO. Oued Mehedouma, <u>Grant</u> s.n.! Guicer, <u>Pitard</u>

1452! Dar Chafai, <u>Pitard</u> 1453! Nechra ben Abbou, <u>Pitard</u> 1454!

Reraja, Urical, vi 1872, <u>Rein & Fritsch</u> ! Grand Atlas, Mzuda, v

1871, <u>Hooker</u> fil.! Moyen Atlas, El Ramman, 1100 m, <u>Jahandiez</u> 946!

halfway between Fez and Imouzzer, 800 m, <u>Davis</u> 55019b! ALGERIA. Oran,

Plain Eghris near Mascara, viii 1849, <u>Romain</u>! 'Le Sénia to le Figuier',

x 1851, Munby! along road to Sebka and Senia, vi - vii 1883, <u>Debeaux</u>!

Bossuet vicinity, 1300 m, ix 1929, <u>Faure</u>! Sidi-bel-Abbès, <u>Warion</u> 950!

Individuals with hermaphrodite flowers have been recorded by <u>Murbeck</u>

(1923) but this state appears to be extremely rare and has not been

observed in the material examined.

Its affinities are with <u>T.mesopotamica</u> (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 <u>T. passerina</u> (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 sub-

tending bracts.

30. <u>T. mesopotamica</u> (Jeffrey) Peterson in Rech. fil., Fl. Iranica
95: 8 (1972).

Syn: <u>T. arvensis</u> Lam. var. <u>pubescens</u> (Guss.) Meissn. in DC., Prodr.
14: 552 (1857), p.p. excl. typ.

<u>Ligia mesopotamica</u> Jeffrey in Kew Bull. 22: 469 (1968).

Ic: Jeffrey, op. cit., 470: f. 1; Fig. 65 F - L; map 14 a.

Annual, similar to <u>T. passerina</u> 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-
spreading. 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. <u>Fl. and fr. late</u>
<u>Apr. - Aug.</u> Fields, steppe, dry river beds, s.l. - 1400 m.

Type:/Turkey C$_7$ Urfa_7 Akçakale, 400 m, <u>Davis</u> 28108 <u>& Hedge</u> (holo.
K! iso. E!).

Distribution: Turkey, Iraq, W. Iran, Kuwait.

<u>Selected specimens:</u>

TURKEY (S. E. Anatolia). C$_6$ Gaziantep: Aintab (Gaziantep), 914 m,
13 vi 1882, <u>B. Post</u>! C$_7$ Urfa: between Sizan and Khan-Hauseher, 17
viii 1888, <u>Sintenis</u> 1401! C$_9$ Hakkari: Zap Gorge 2-3 km from Hakkari,
1400 m, <u>Davis</u> 45476! IRAQ. Diyala, Jabal Hamrin, <u>Wheeler-Haines</u> 718!
3rd range near Khanaquin, <u>W-Haines</u> 910! Jazira, + 50 km from Baghdad,
K$_2$ pipeline, <u>W-Haines</u> s.n.! Ba'aj to Talail al-Nil, 350 m, <u>Guest</u>

T. passerina	T. mesopotamica	Rawi & Chapman specimens
flowers hermaphrodite	polygamous	polygamous
☿ (8 stamens) 2.5-3 mm	☿ (4 stamens <2 upper, <2 lower)	☿ (4 stamens, upper) 3.5 mm
—	☿ and ♀ 2.5-3 mm	♀ 4 mm
—	♂ 2-3.5 mm	♂ 3 mm
ovary apex hirsute	puberulous or glabrescent	puberulous or glabrescent
bracts 3mm,	3.25-3.5 mm,	3 mm,
sparsely ciliate at base,	ciliate in lower half,	ciliate in lower half,
lanceolate	ovate-lanceolate	ovate-lanceolate
stem glabrous	greyish-pilose	greyish-pilose
leaves glabrous	greyish-pilose	glabrous
height 15-60 cm	6-35 cm	45 cm
pollen nearly homomorphic ○	nearly homomorphic ○	dimorphic <95% ○, <5% ○

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
26350!) 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 413!), powdered and
applied to sores on animals (Gillett 11088!). It was not ment-
ioned which part of the plant was used.

Abbreviations excluding those of authorities, books, journals or herbaria

anon.	collector unknown
c. or ca.	circa (about)
cm	centimetre(s)
comb. illegit.	combinatio illegitima
comb. nov.	combinatio nova
E.	East
e.g.	exempli gratia (for instance)
et al.	et alii (and other people)
excl.	excluding
f./fig.	figure
Fl. & fr.	flowering and fruiting period (in months)
holo.	holotypus
Ic.	Icon (illustration)
ibid.	in the same place
incl.	including
iso.	isotypus
km	kilometre(s)
loc. cit.	on the page previously cited
m	metre(s)
mm	millimetre(s)
mt.	mountain
N.	North
nom. nud.	nomen nudum
n.v.	non vidi (refers to publication not seen)
obs.	observed

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. Tartonraira (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 uni-
sexual 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. lanuginosa

◆   T. gattefossei

●   T. argentata

□   T. virescens var. virescens

■   T. virescens var. glaberrima

◇   T. putorioides

◀   T. microphylla (inset map)

◁   T. sempervirens

Distribution of Sect. Chlamydanthus

▶   T. velutina

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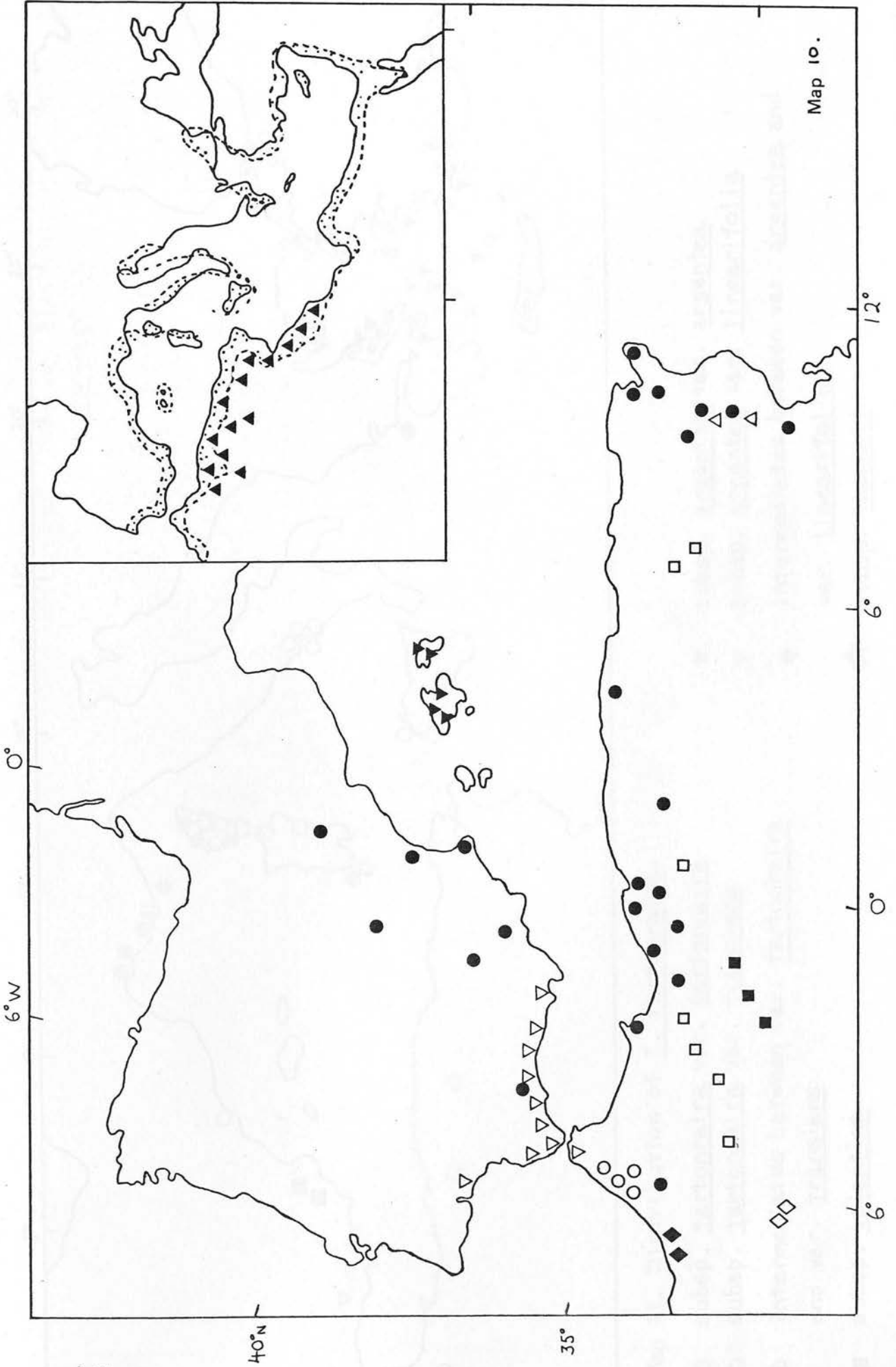
Map 10.
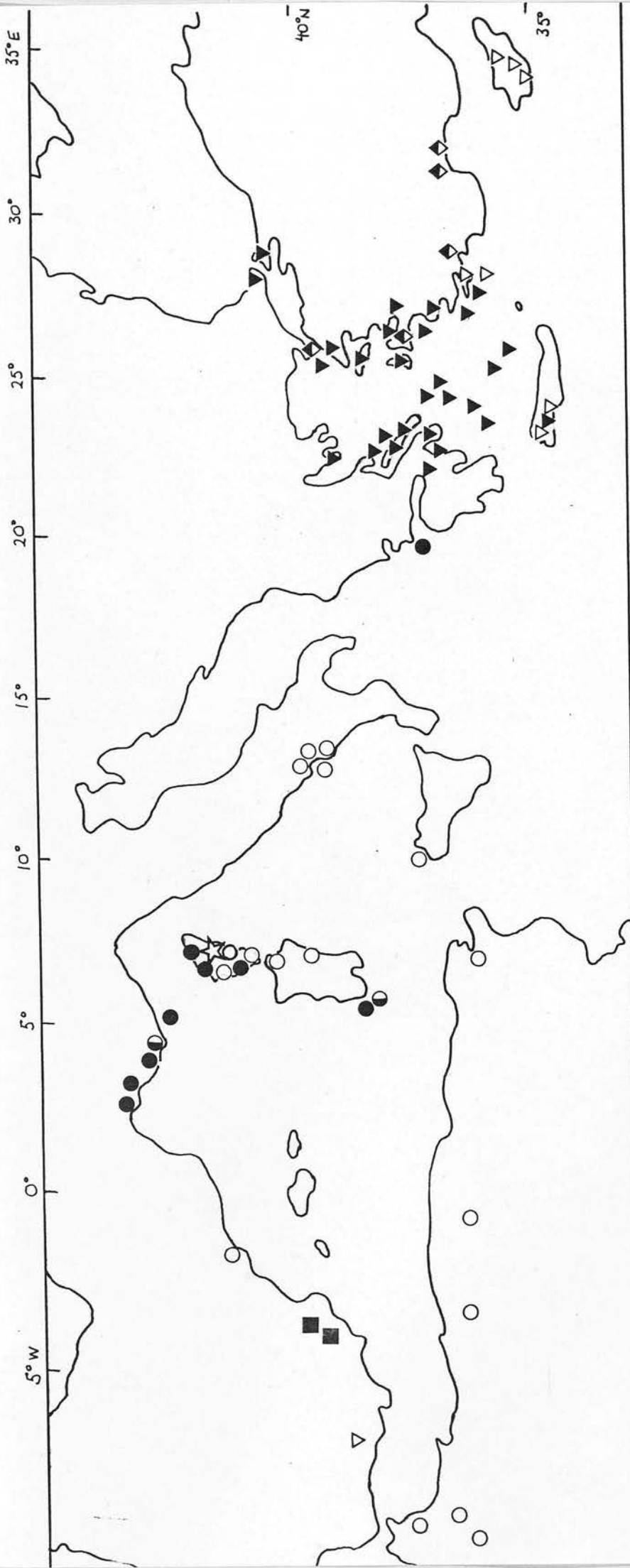
Map 11. Distribution of T. tartonraira.

○ subsp. tartonraira var. tartonraira
○ subsp. tartonraira var. transiens
◐ 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. thomasii

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Bonne Projection

Map 12. Distribution of Sect. Chlamydanthus

T. dioica subsp. dioica   △
T. dioica subsp. granatensis   ▲
T. tinctoria subsp. tinctoria   ●
T. tinctoria subsp. nivalis   ○
T. subrepens   ◇
T. procumbens   □
T. ruizii   ▶
T. calycina   ◆
T. coridifolia   ▷
T. broteriana   ■
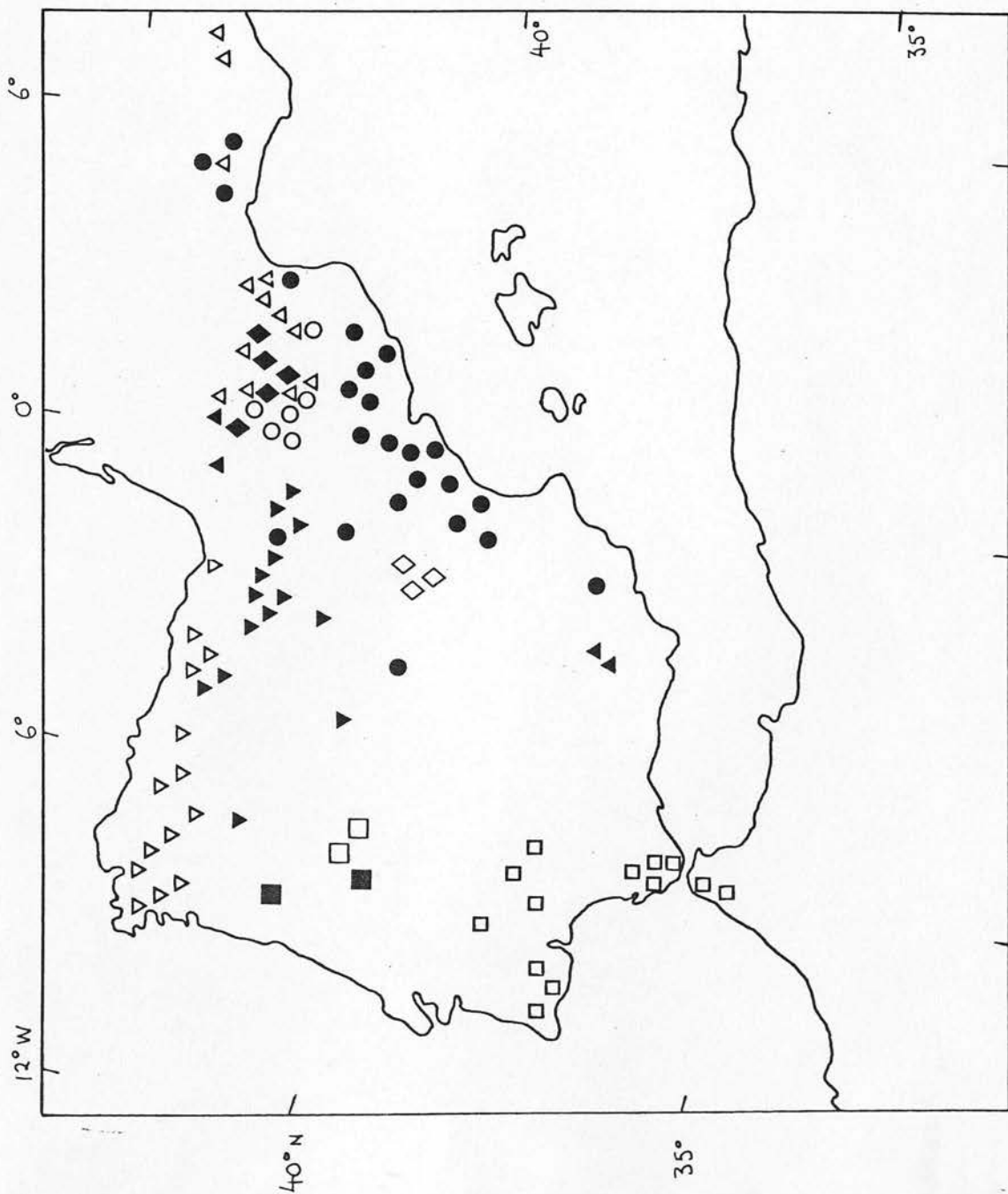
Distribution of Sect. Thymelaea

T. villosa   □

Map 13. Distribution of Sect. Thymelaea.

◆ 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

Map 13.

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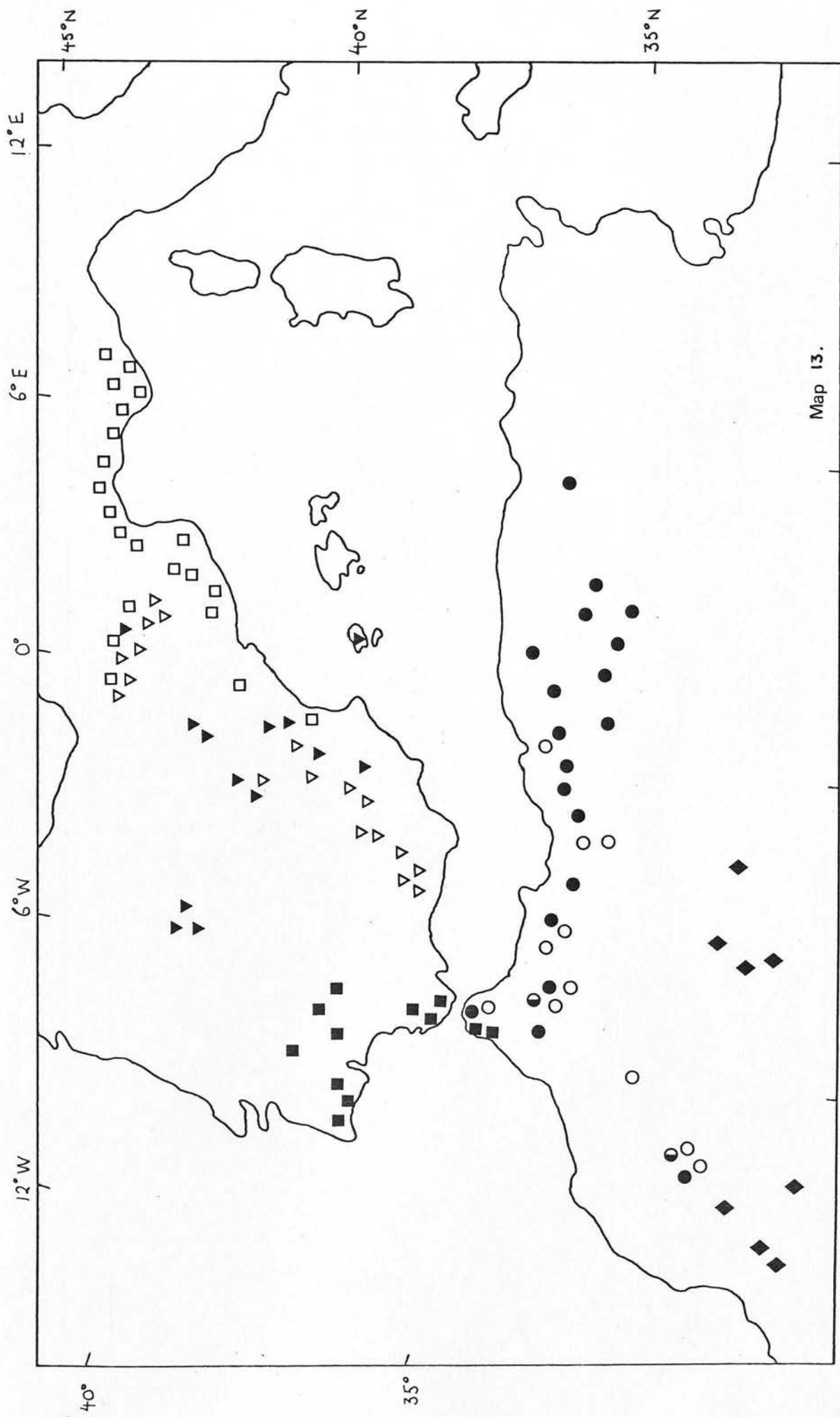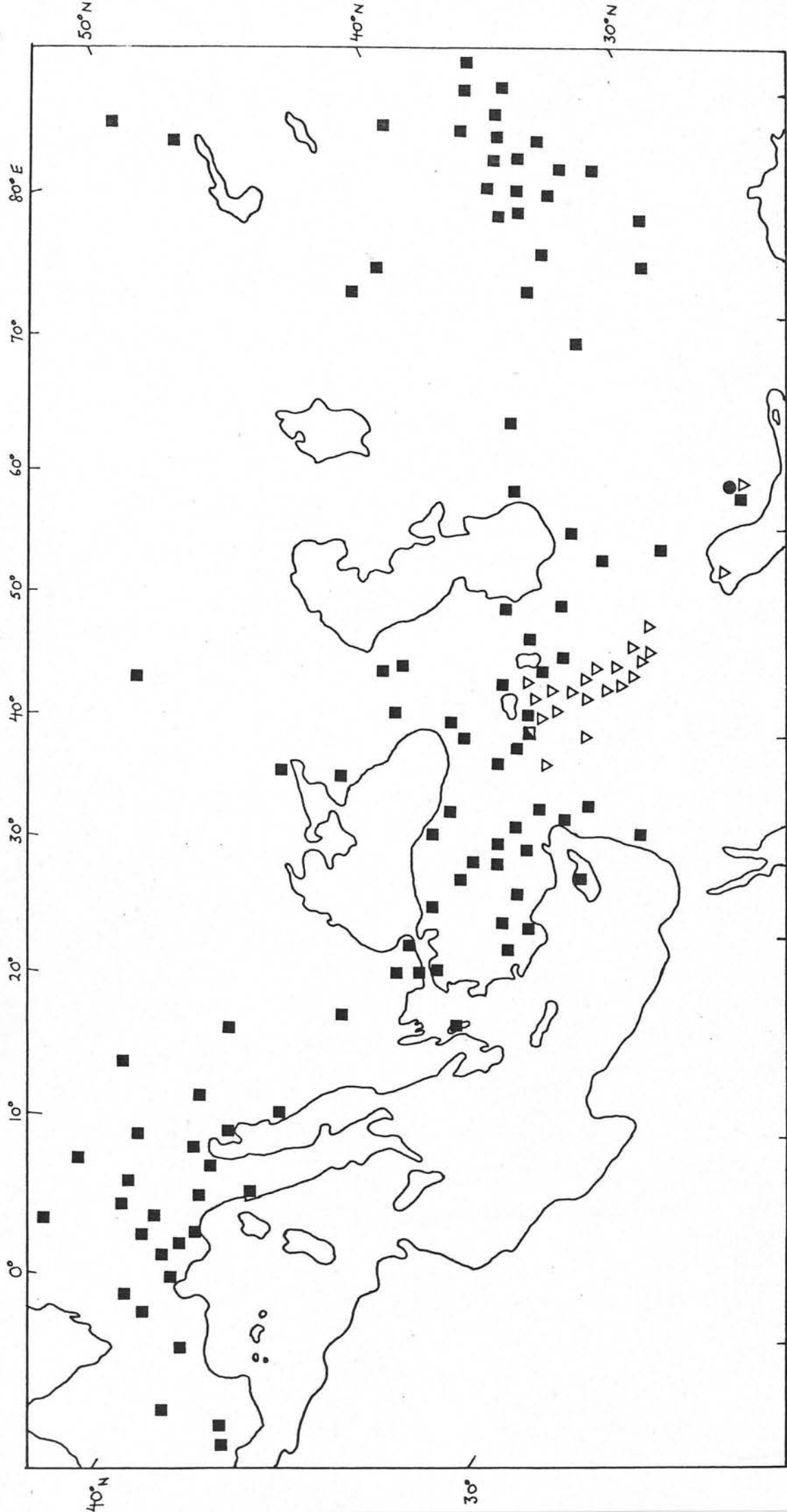
Map 14a. Distribution of Sect. Ligia (in part).

See Map 14b for legend.

Lambert Azimuthal Equal-Area Projection

431
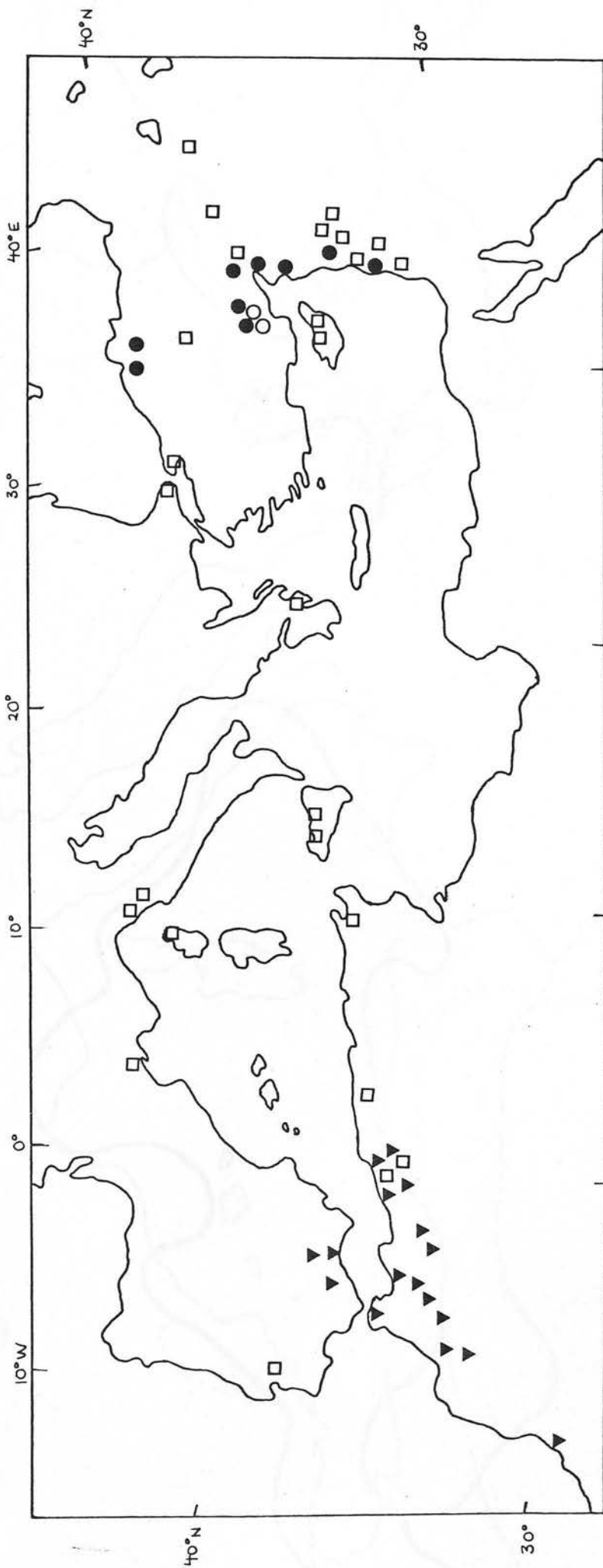
Map 14b. Distribution of Sect. Ligia (in part).

○	T. cilicica	▼	T. salsa
●	T. aucheri	▽	T. mesopotamica
■	T. passerina	◨	intermediate between T. mesopotamica
□	T. gussonei		and T. passerina

Miller's Prolated Stereographic Projection
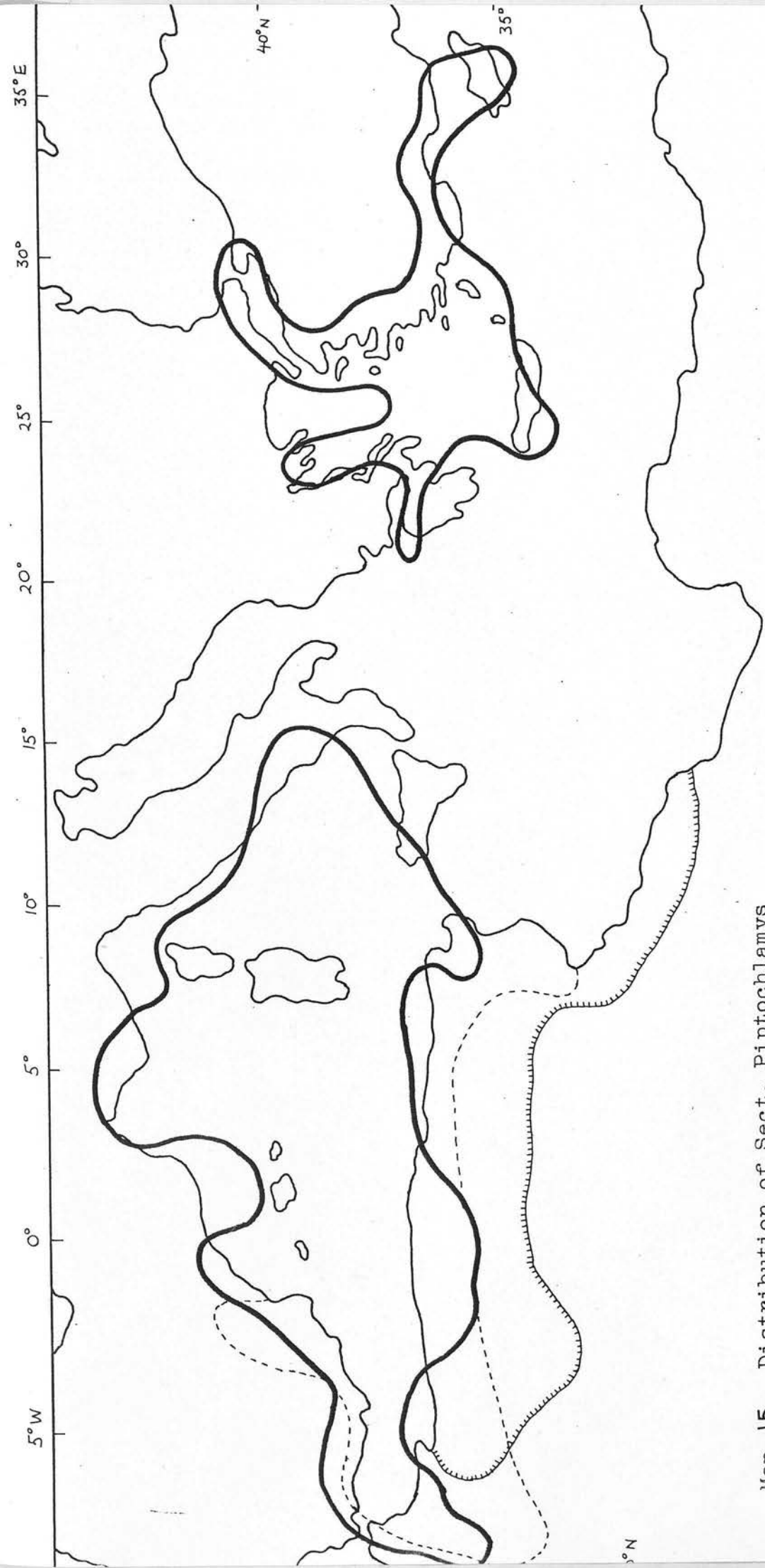
Map 15. Distribution of Sect. Piptochlamys

------   subsect. _Argentatae_ (3 spp.)

········   subsect. _Sempervirentes_ (2 spp.)

▬▬▬▬   Sect. _Chlamydanthus_ subsect. _Tartonraira_ (2 spp. excluding _T. dioica_)

Bonne   Projection

432
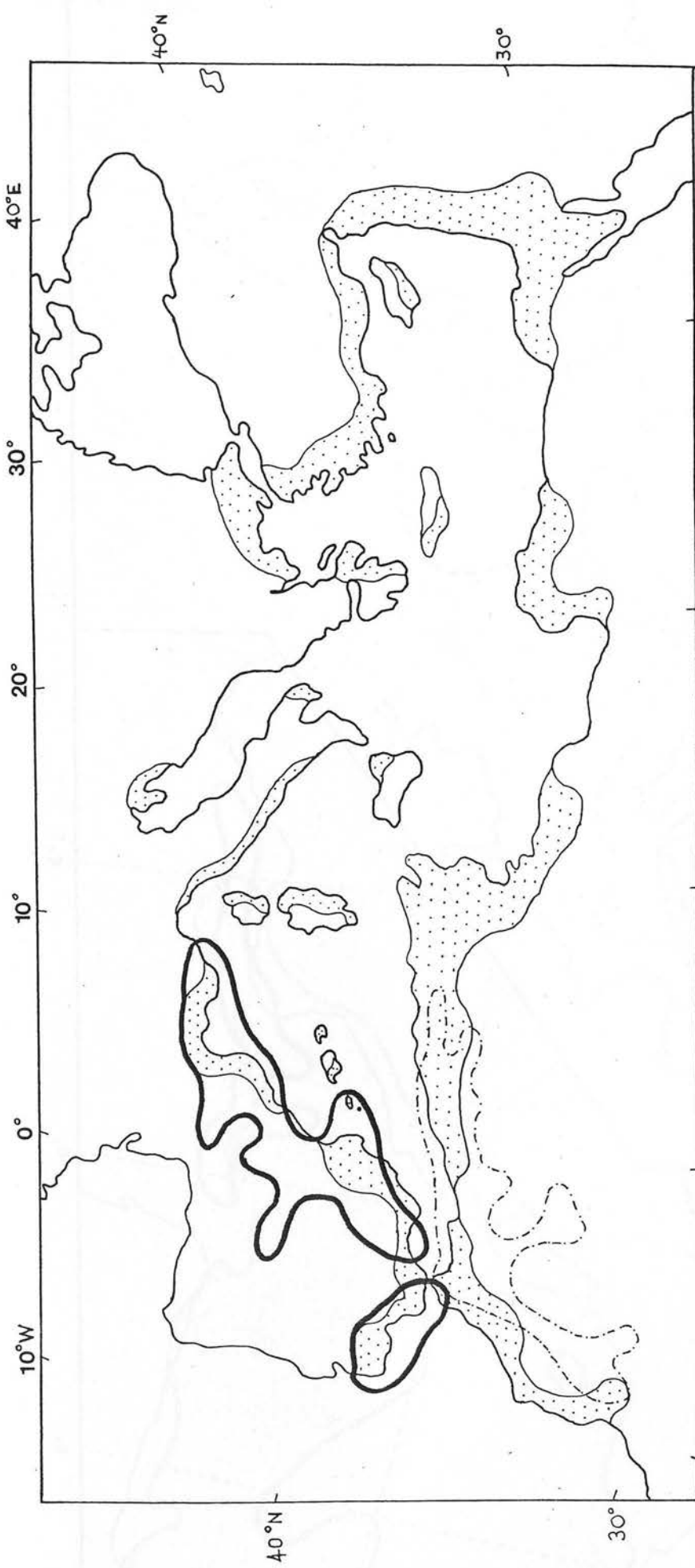
Map 16. Distribution of Sect. Piptochlamys subsect. Hirsutae (4 spp.)

Sect. Thymelaea subsect. Antiatlanticae (2 spp.)

subsect. Sanamunda (3 spp.)

Miller's Prolated Stereographic Projection

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Map 17. Distribution of:

Sect. Chlamydanthus subsect.
Coridifoliae (7 spp.)
Littttt

T. dioica which is placed in

Sect. Chlamydanthus subsect.
Tartonraira

Map 18. - - - -Distribution of Sect. Ligia (6 spp.). The range is greatly extended by T. passerina. Also showing number of species of the genus Thymelaea in different areas.
Centre of development indicated by thick solid line.

Zenithal Equidistant Projection

6°E

0°

6°

°W

10°N

5°

Fig. 52A - Ca <u>Thymelaea lythroides</u>

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 <u>Thymelaea hirsuta</u>

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.
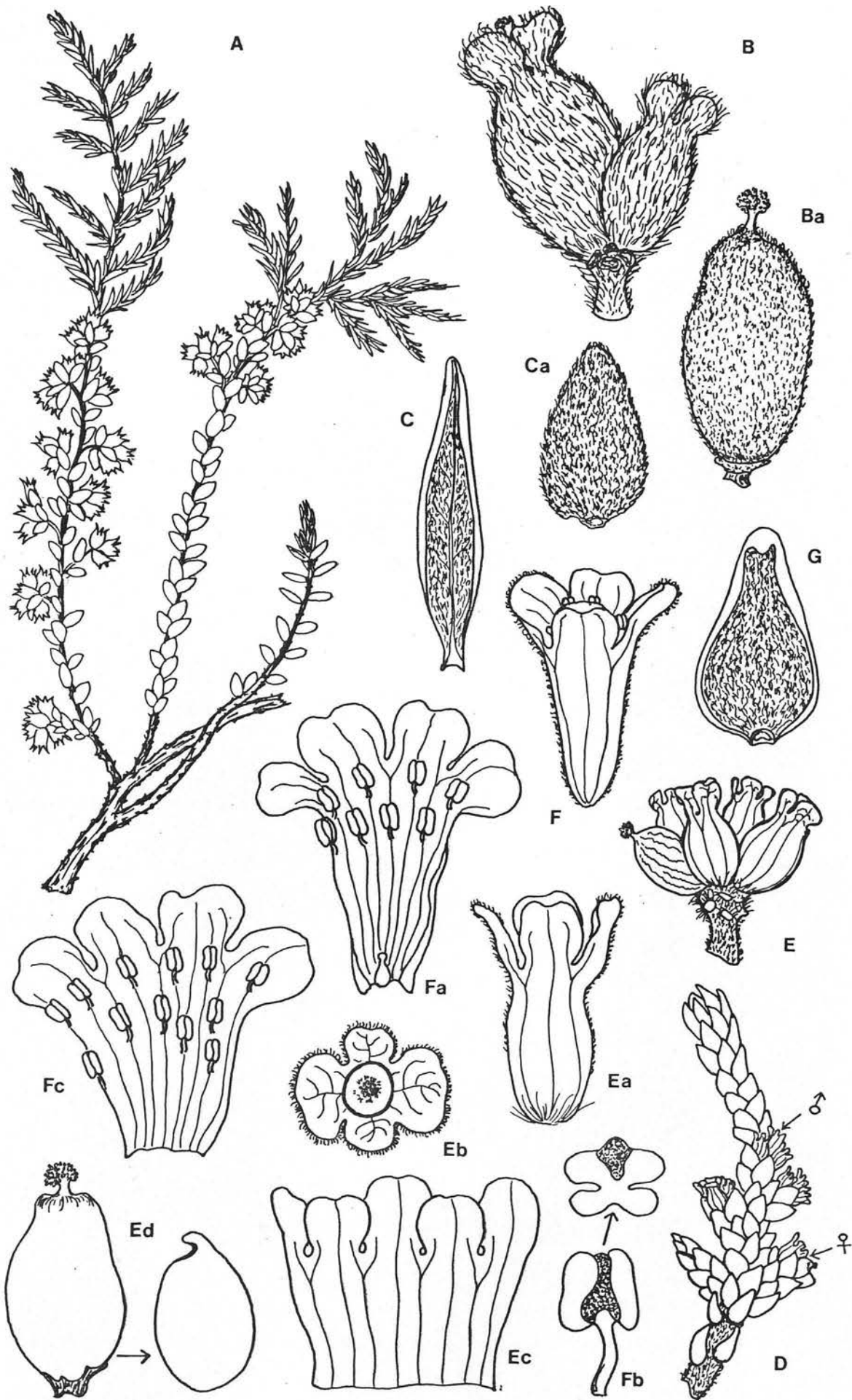
Fig. 52

Fig. 53. Thymelaea putorioides

A - G var. putorioides   (28 vii 1926, Maire)

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.

B-G   x 10.

H - J var. rhodantha   (7 vii 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.
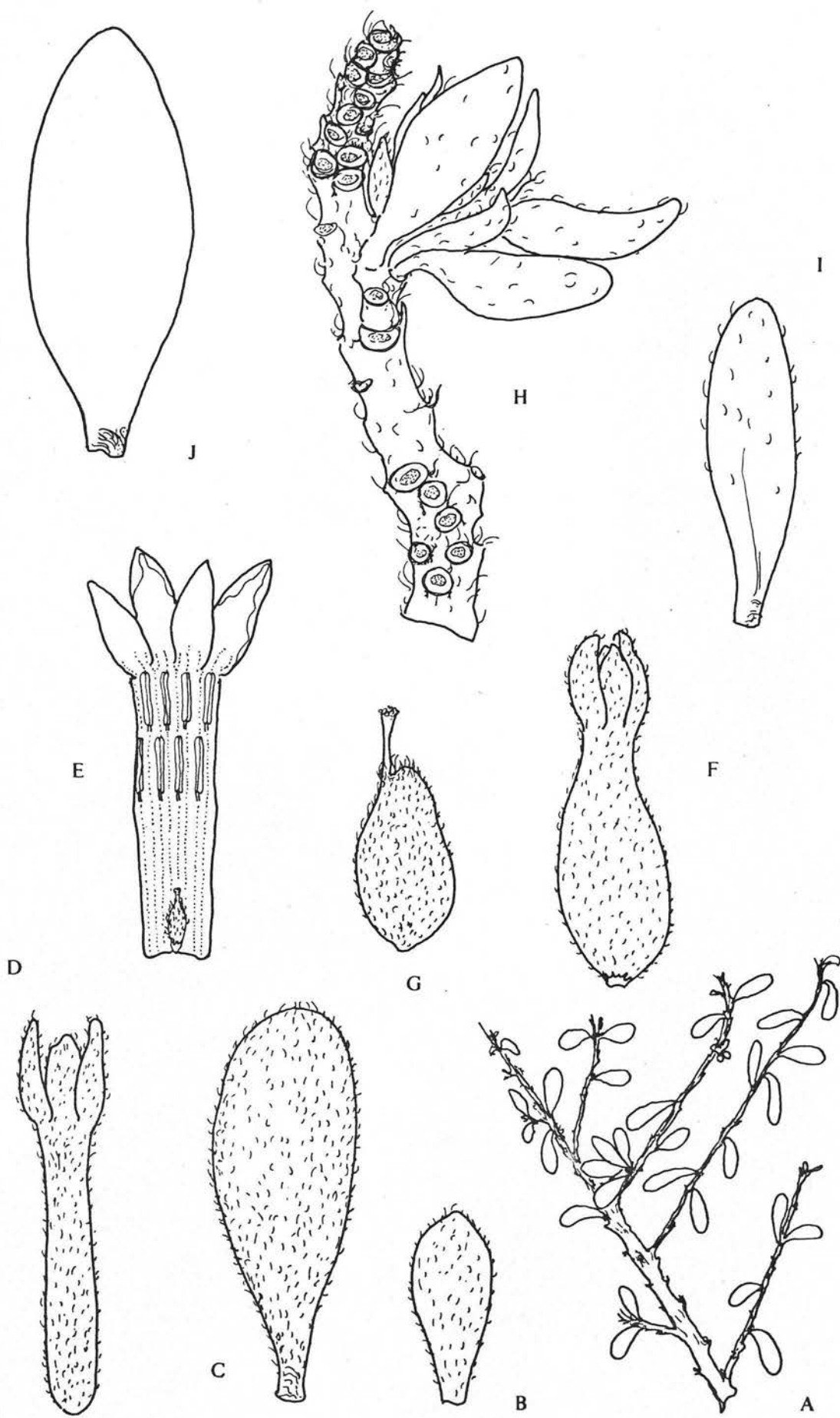
Fig. 53

Fig. 54 A - C.   <u>Thymelaea velutina</u>

A.   Staminate flower.

Aa.   Staminate flower dissected.

B.   Pistillate flower.

Ba.   Ovary.

Bb.   Seed.

C.   Leaf, abaxial view.   x 5.

D - F. <u>Thymelaea argentata</u>

D.   Flowering branch.   x 1.

E.   Hermaphrodite flower.

Ea.   Hermaphrodite flower dissected;   ovary immature.

Eb.   Fruit.

F.   Leaf, abaxial view.

G - J.   <u>Thymelaea microphylla</u>

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.
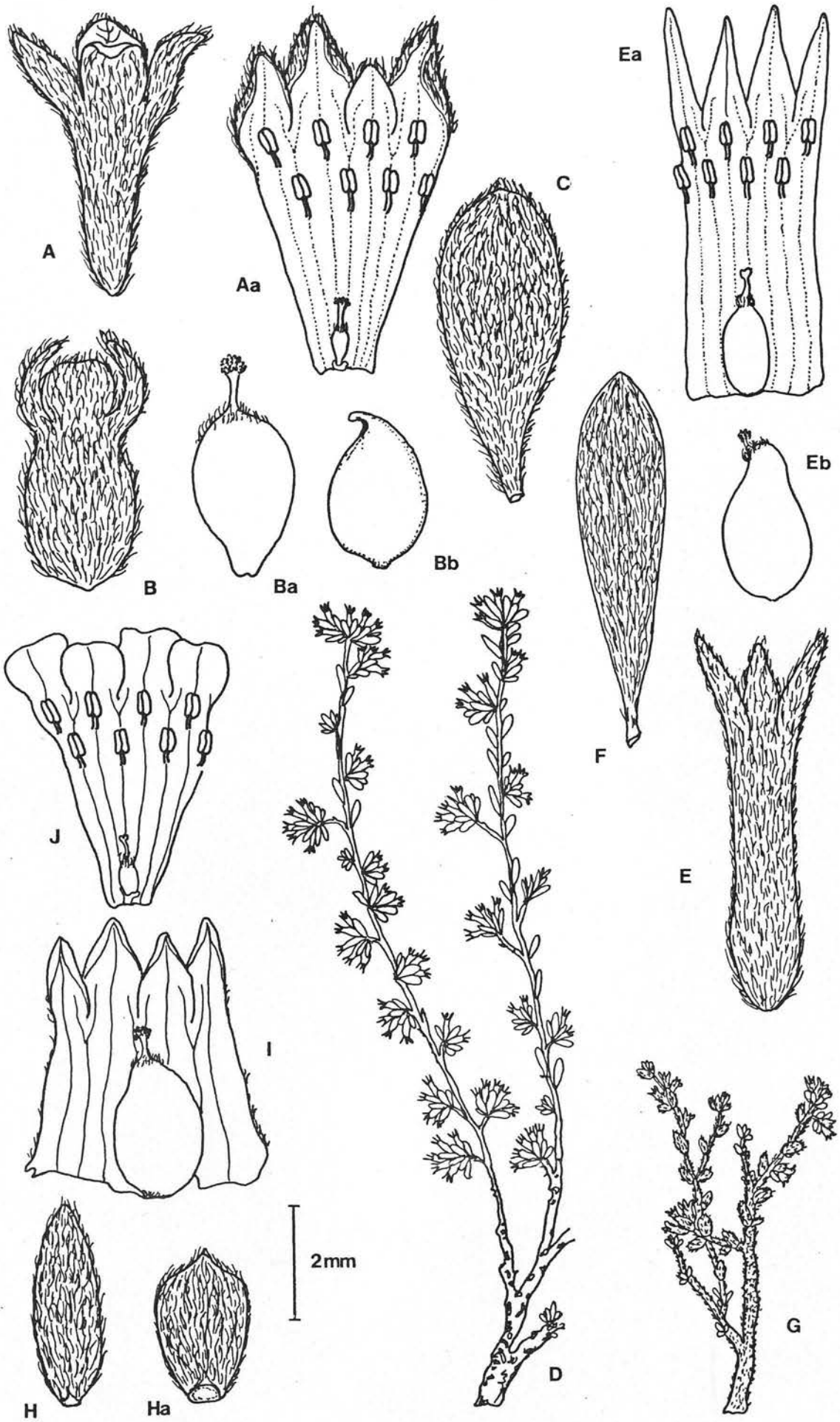
Fig. 54

Fig. 55. <u>Thymelaea tartonraira</u>   All x 10 or x 20.

A - Cb. subsp. <u>argentea</u> var. <u>linearifolia</u>

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. <u>tartonraira</u> var. <u>transiens</u>

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. <u>valentina</u>

G.   Pistillate flower.

Ga.   Immature ovary.

Gb.   Fruit.

H - I subsp. <u>tartonraira</u> var. <u>tartonraira</u>

H.   Staminate flower.

Ha.   Rudimentary ovary of staminate flower. x 20.

Hb.   Upper bract, abaxial view.

I.   Floral diagram of staminate flower.
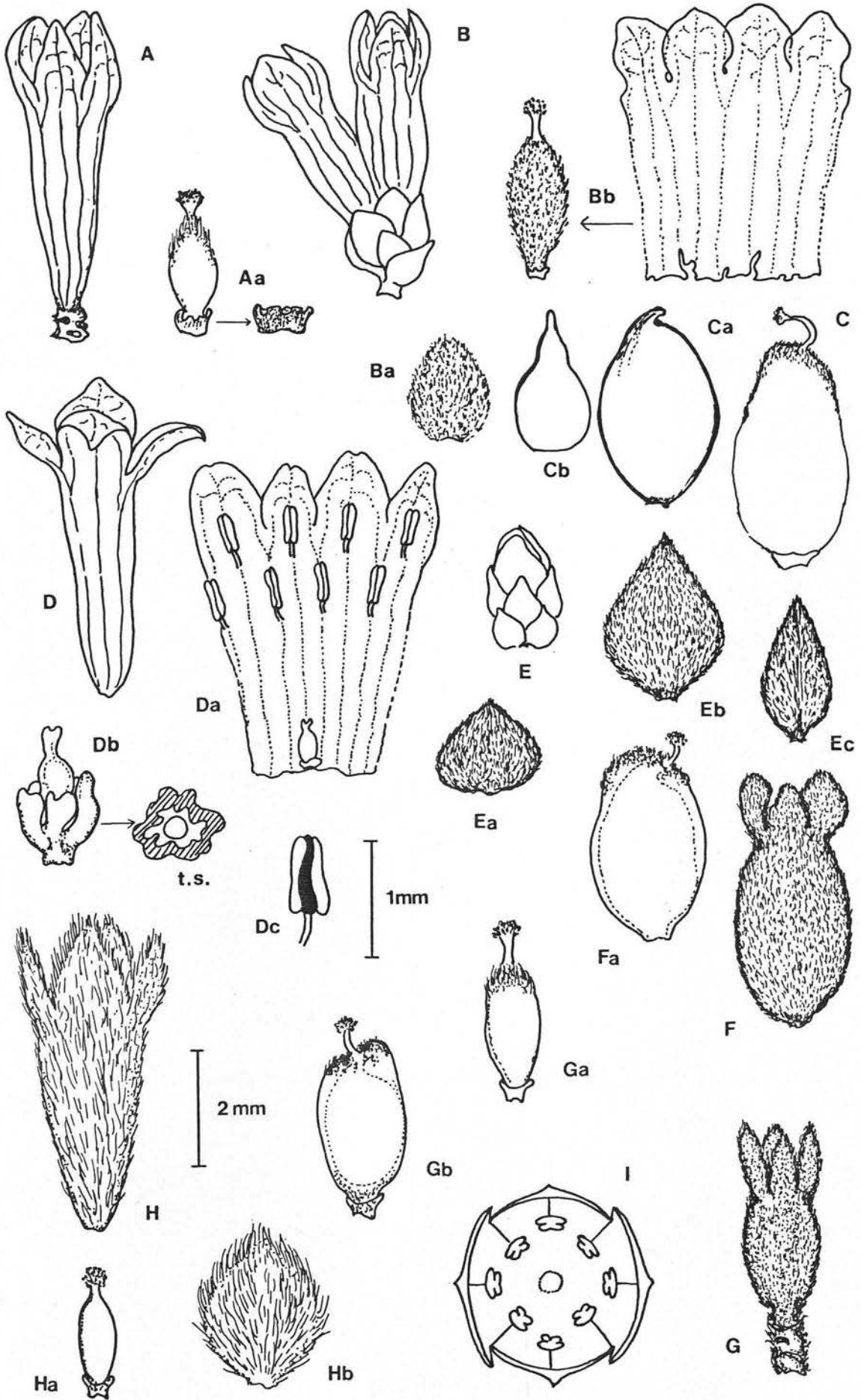
Fig. 55

Fig. 56. <u>Thymelaea dioica</u>

A - F   subsp. <u>dioica</u>

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. <u>granatensis</u>

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.

flower

innermost 1 6

B

Ba

A

C

Ca

D

Da

Eb

E

Ea

G

I

H

2·5mm

F

Fig. 56

445
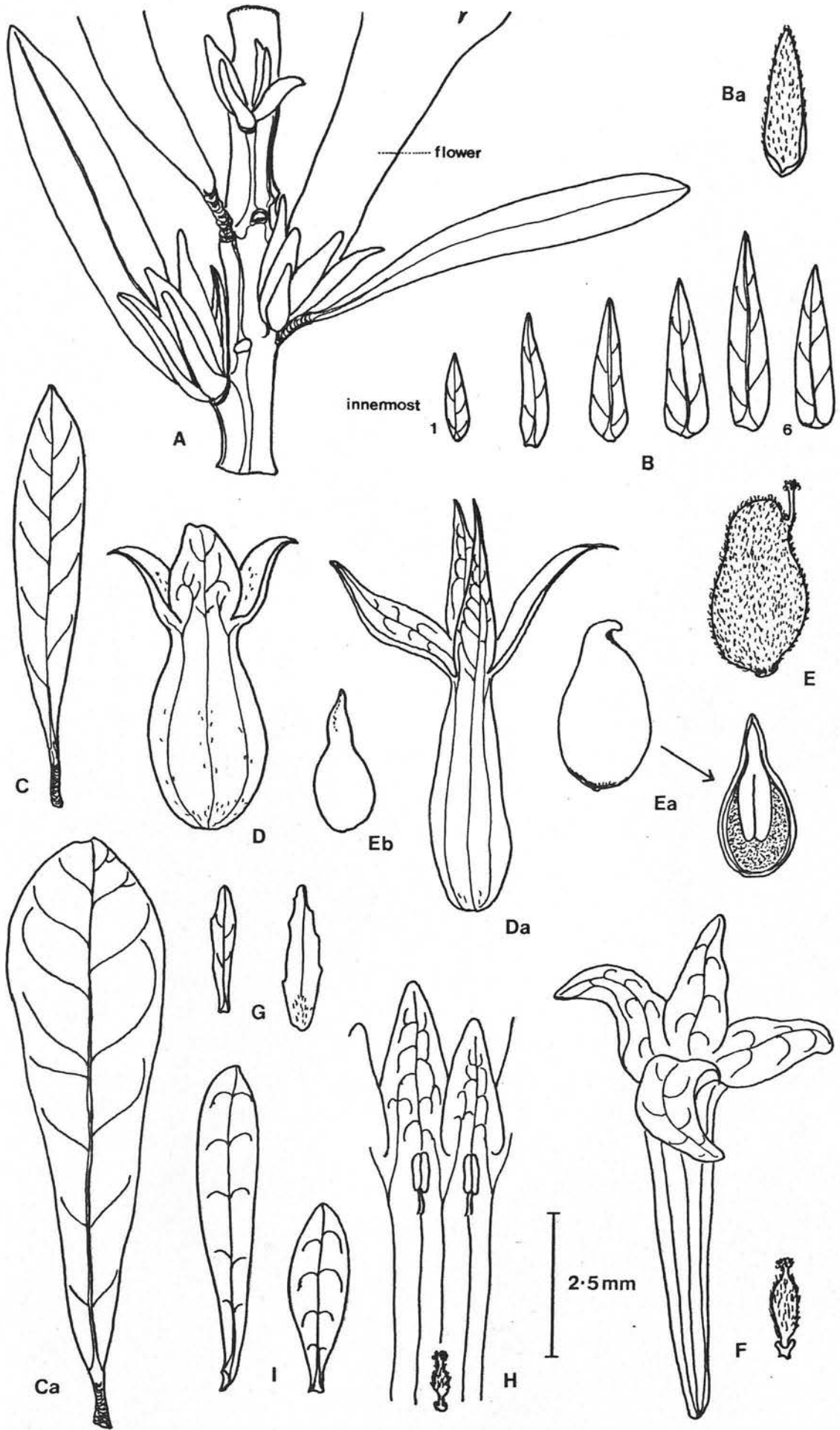
Fig. 57 A - B. Thymelaea calycina

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.
Da.   Mature leaf, abaxial view. Glabrous. x 5.
E.   Staminate flower; upper stamens semi-exserted.
Ea.   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.
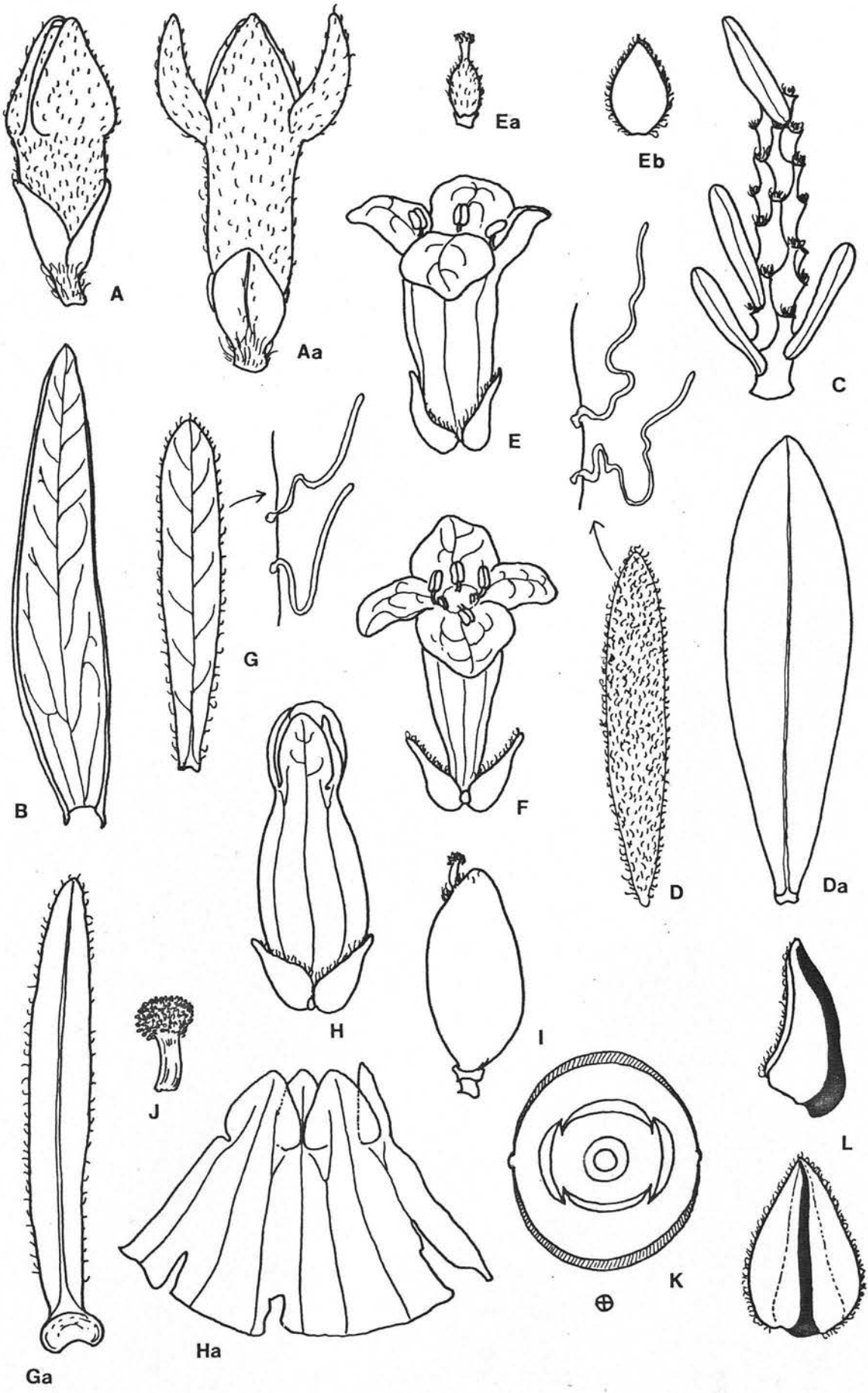
Fig. 57

Fig 58 A – 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.
Ga. Perianth lobe of staminate flower, outer surface
     pubescent.

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.
Hc. View of staminate flower from above. Upper stamens semi-
     exserted.
I.   Young leaf, abaxial surface villous.
Ia. Mature leaf, adaxial view. ± glabrous, margins involute.

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.
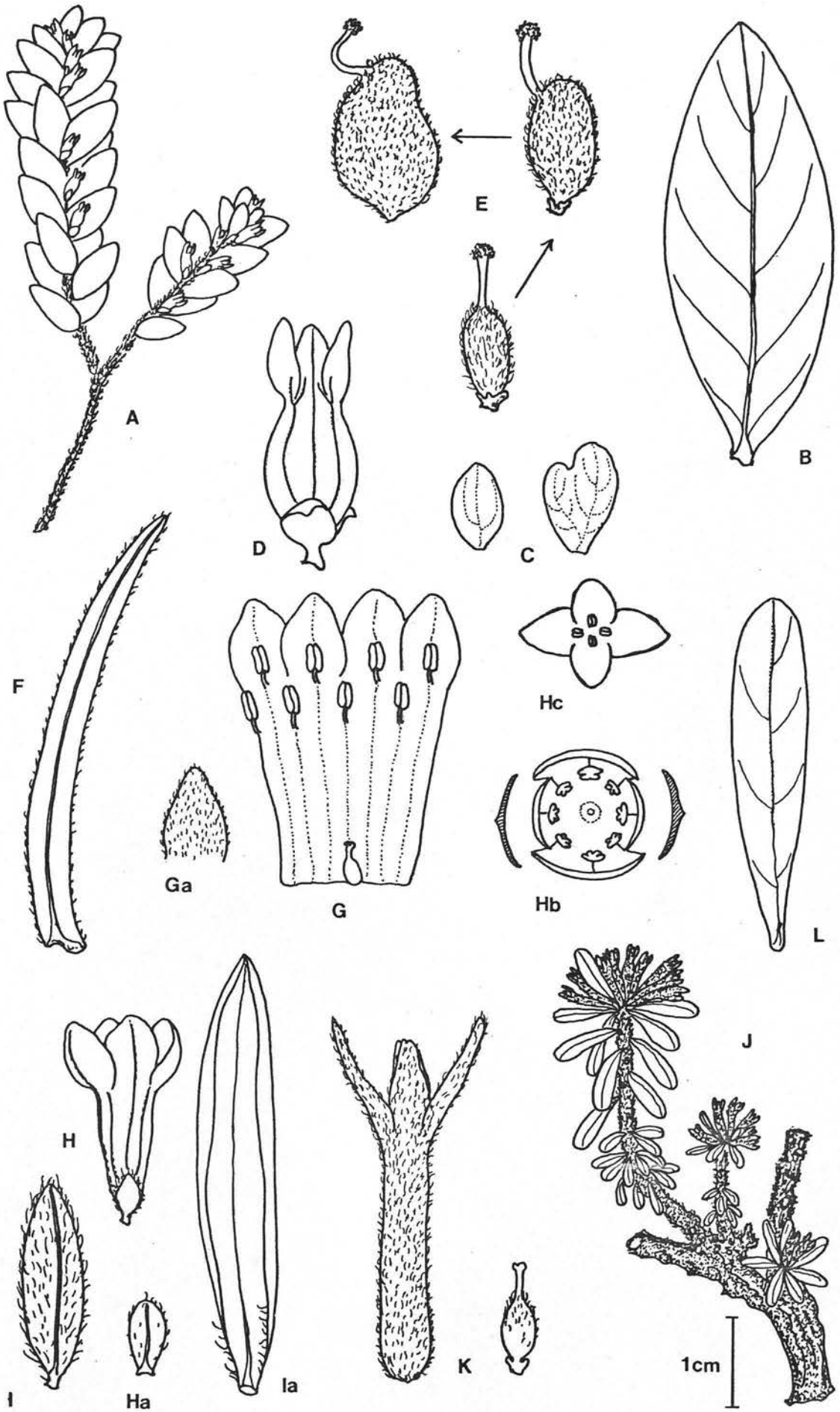
Fig. 58

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.   Infloresence 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.
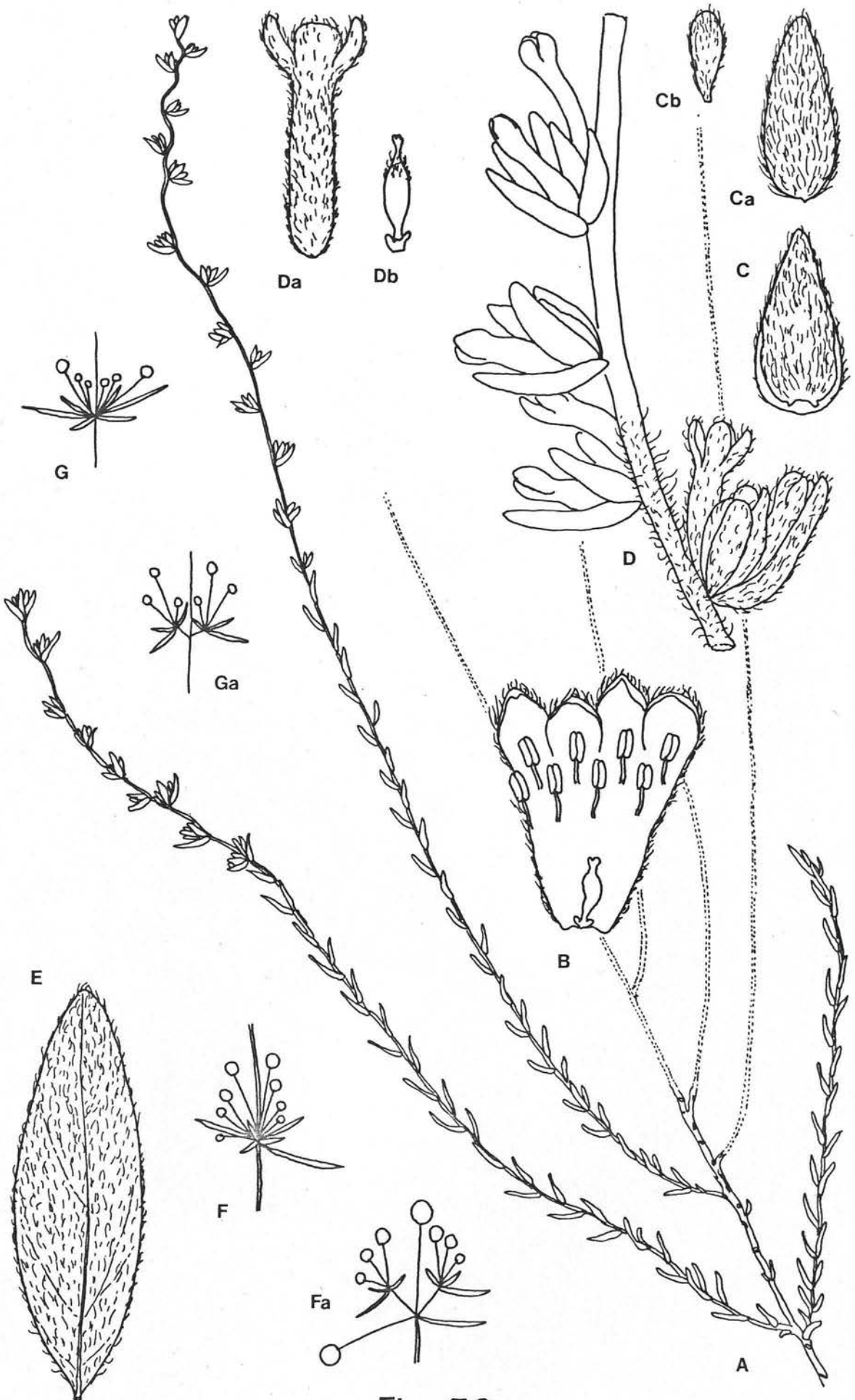
Fig. 59

Fig. 60A - 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.
La.   Mature ovary, style subterminal.
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.
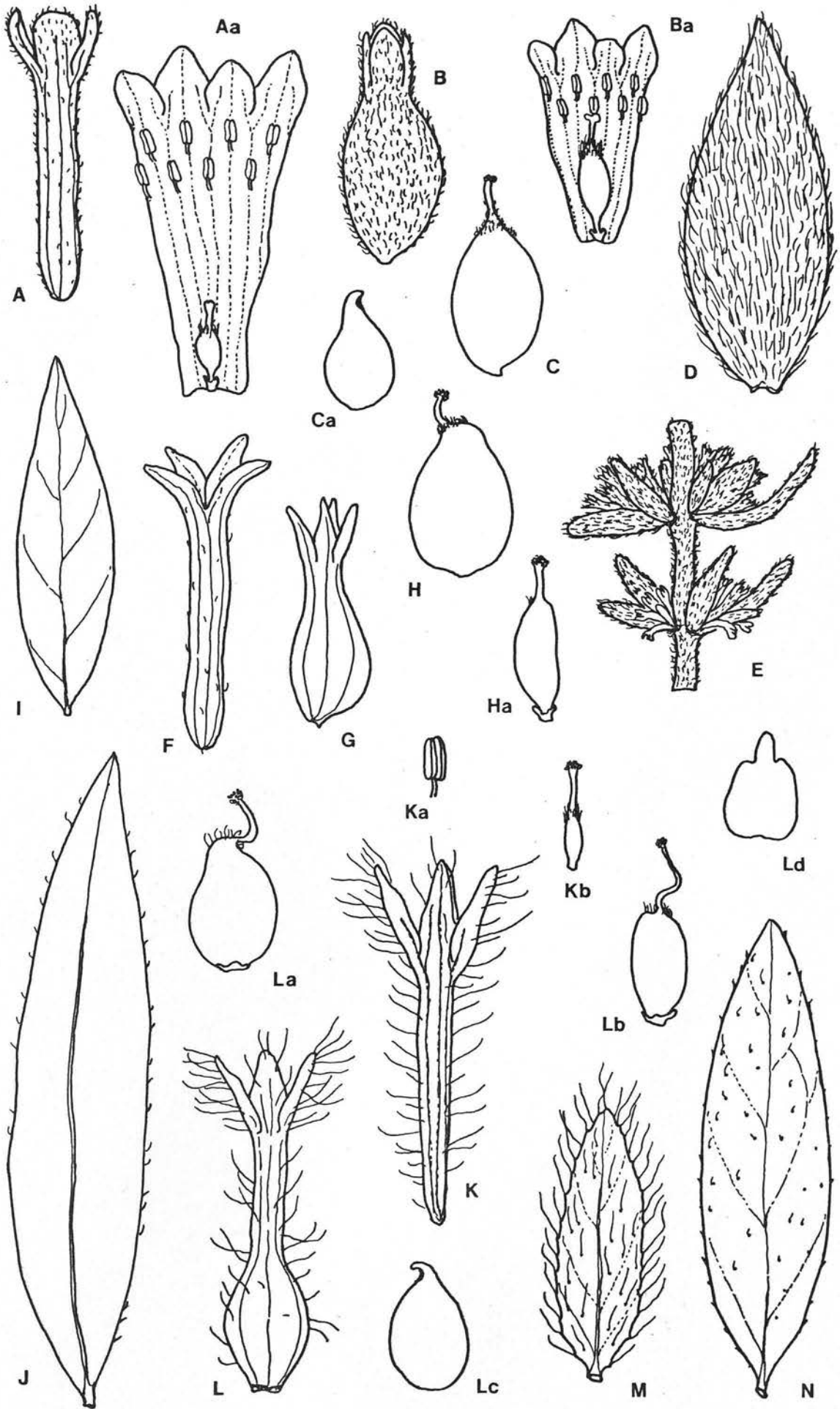
Fig. 60

Fig. 61. <u>Thymelaea thesioides</u>

A - F. subsp. <u>thesioides</u>

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. <u>elliptica</u>

G.   Leaf, abaxial view.

A and C x 1. The rest drawn to scale shown.
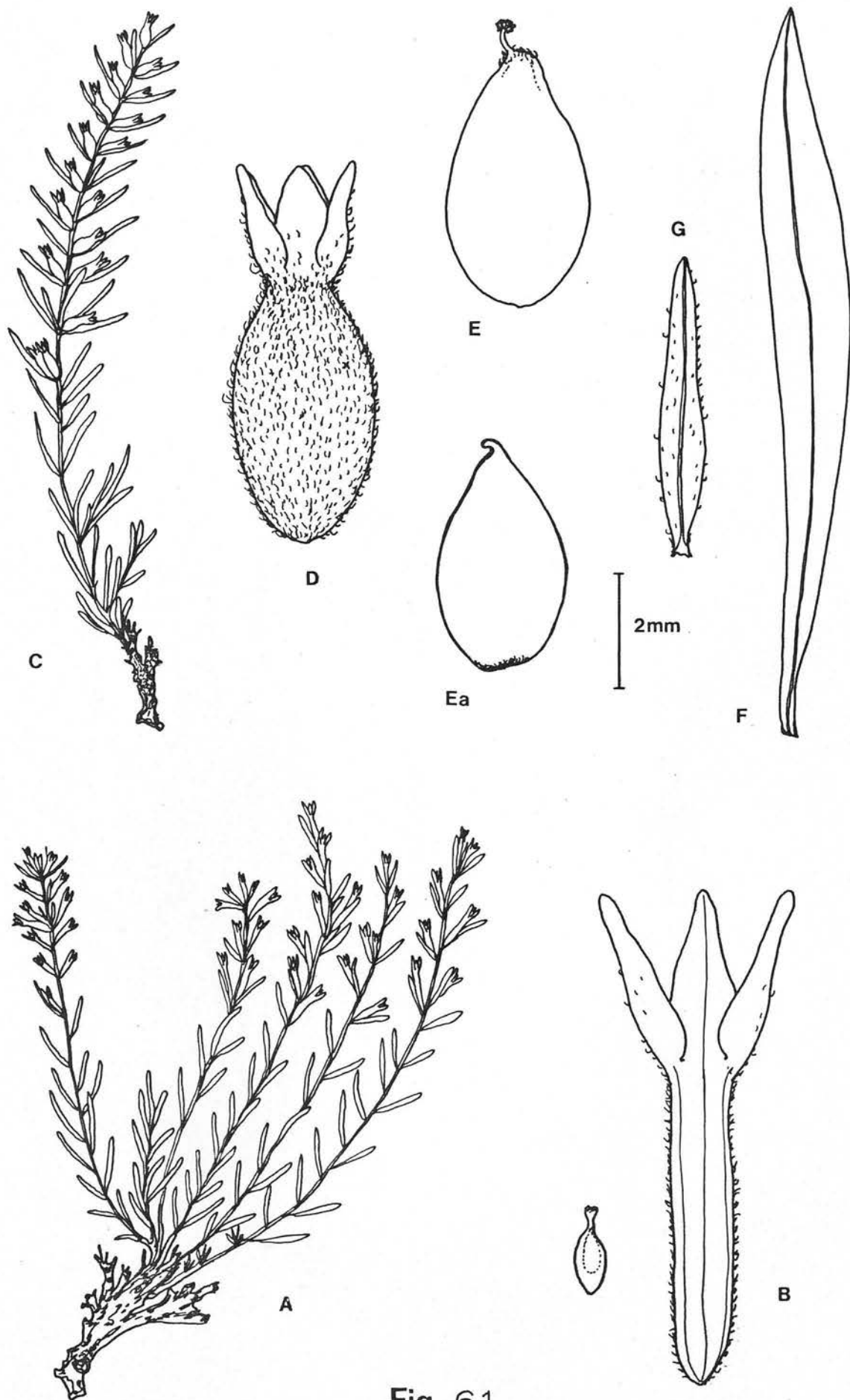
Fig. 61

Fig. 62. <u>Thymelaea cilicica</u>   (<u>Wood & Gibson</u> 183)

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.

F

G

E

C

D

B

bract

1cm

A

Fig. 62

457
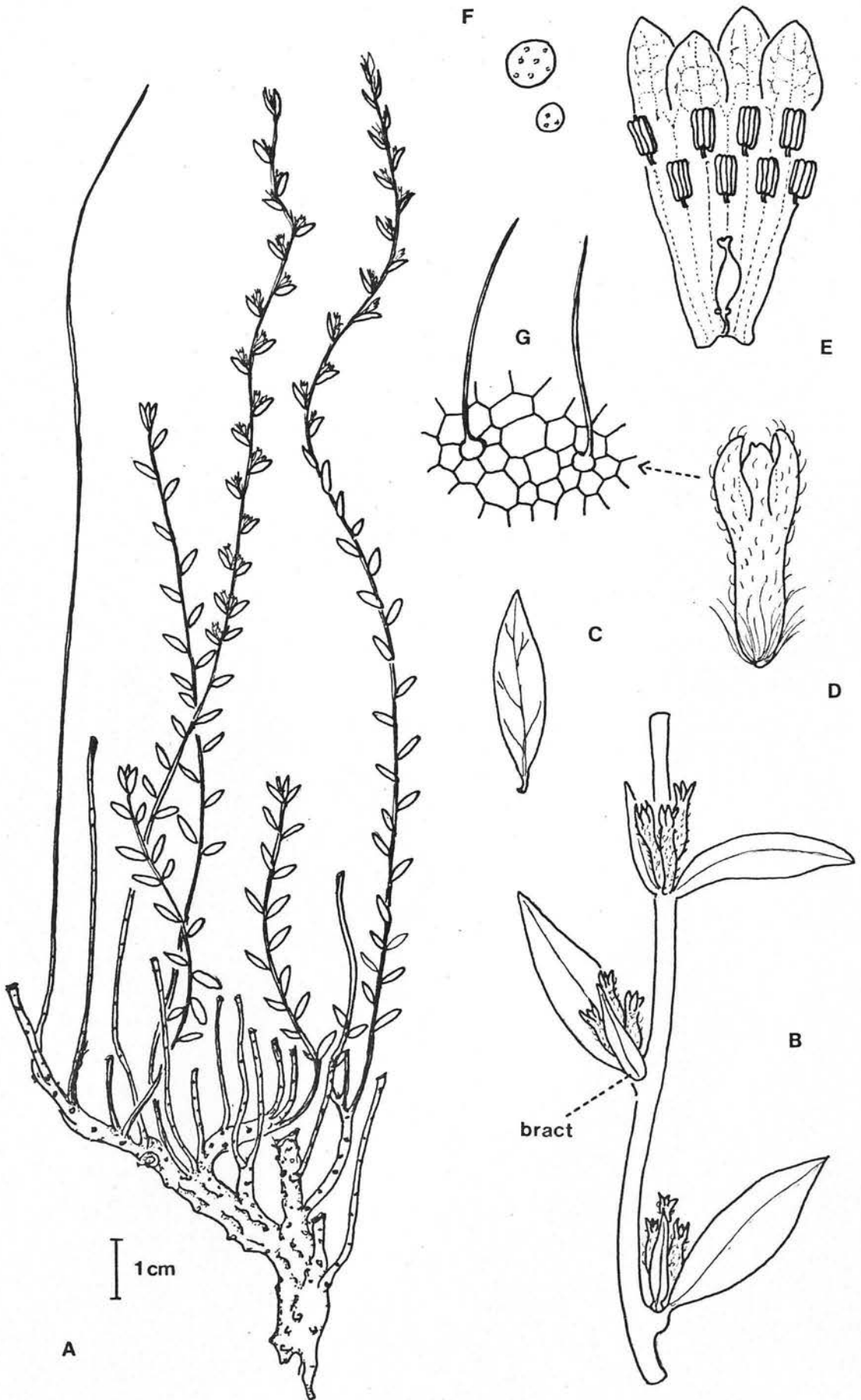
Fig. 63. Thymelaea aucheri

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.

458
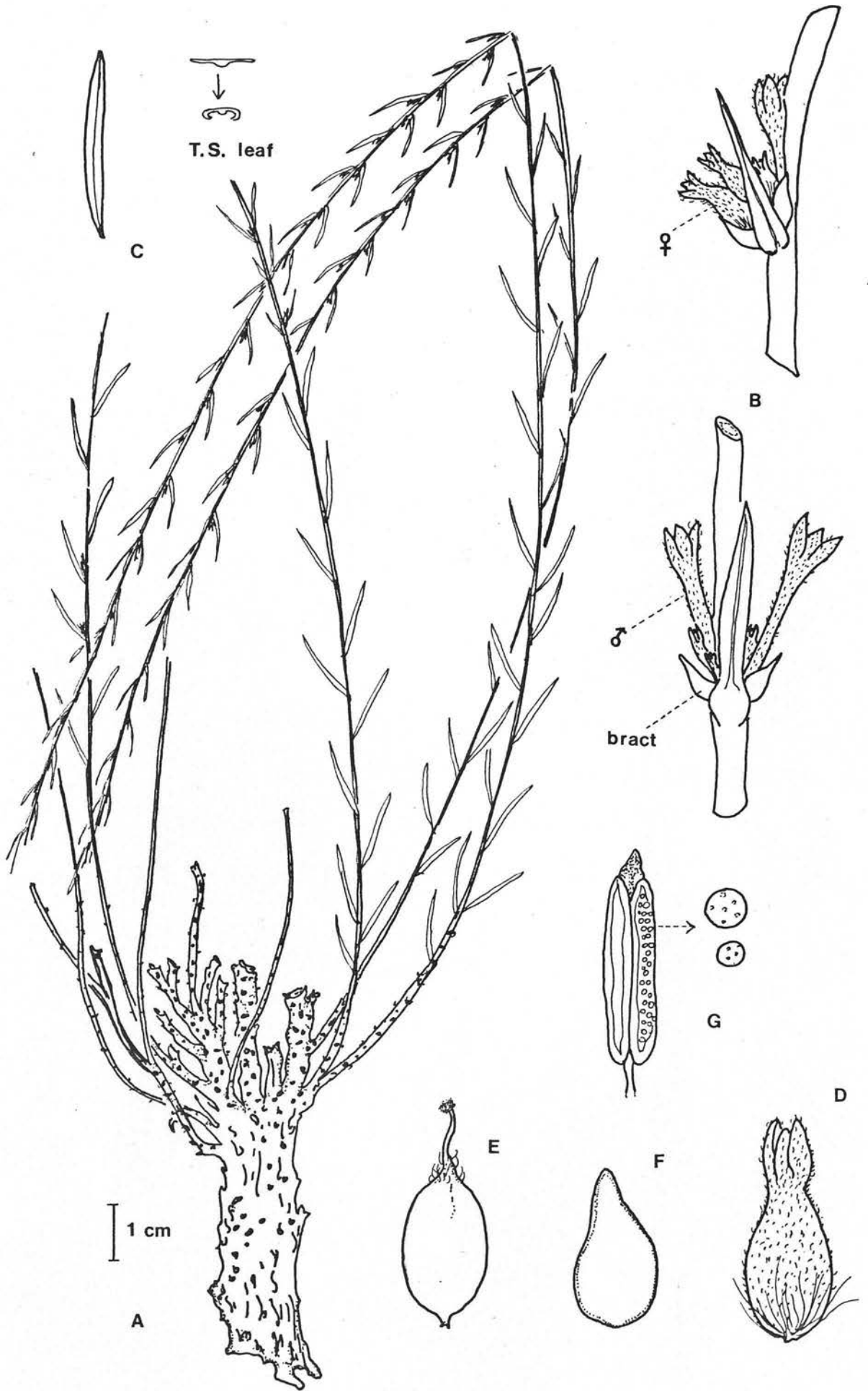
Fig. 63

Fig. 64A - 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.
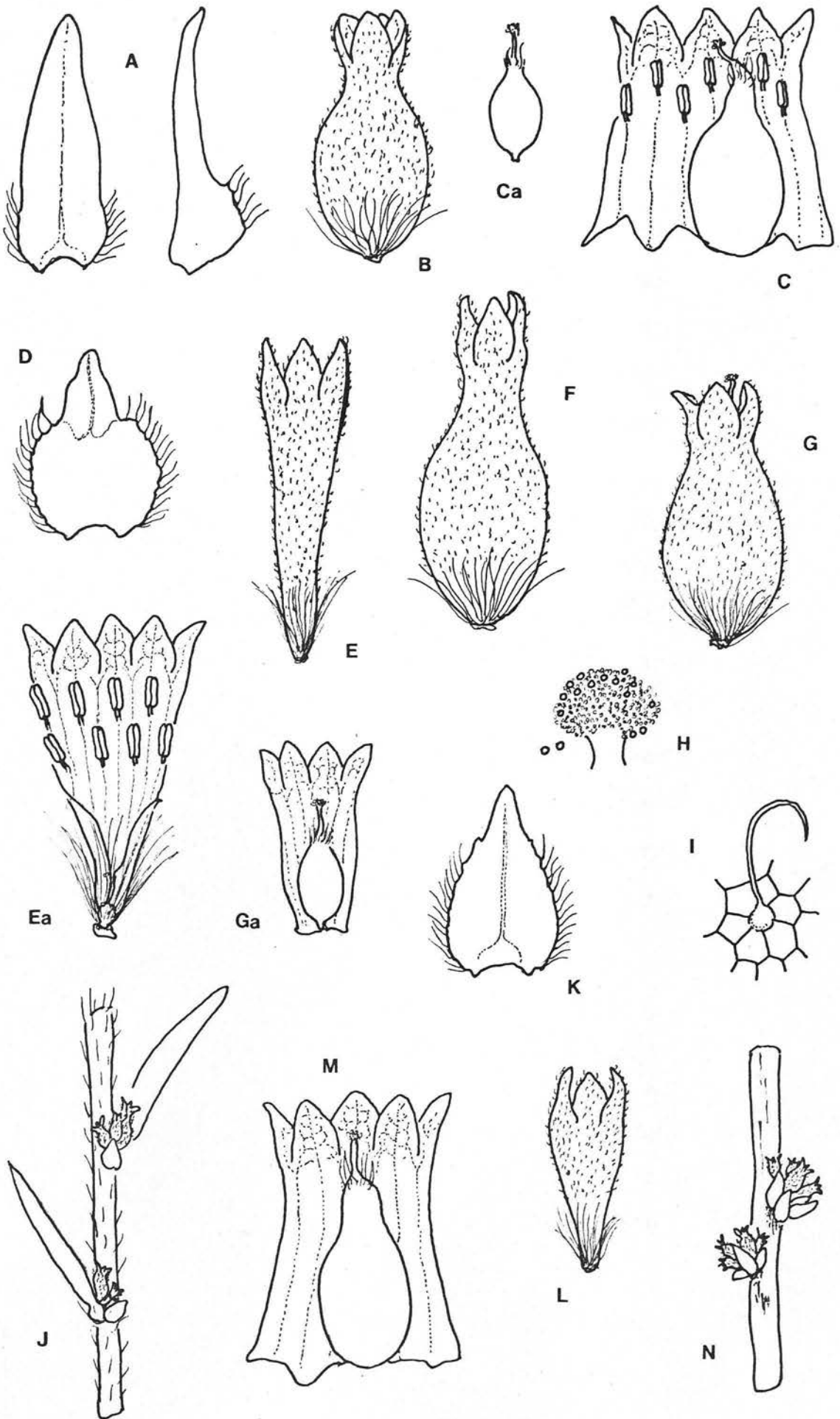
Fig. 64

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.

N & Na. Mature and immature ovaries.

All   x 15 except A and F.
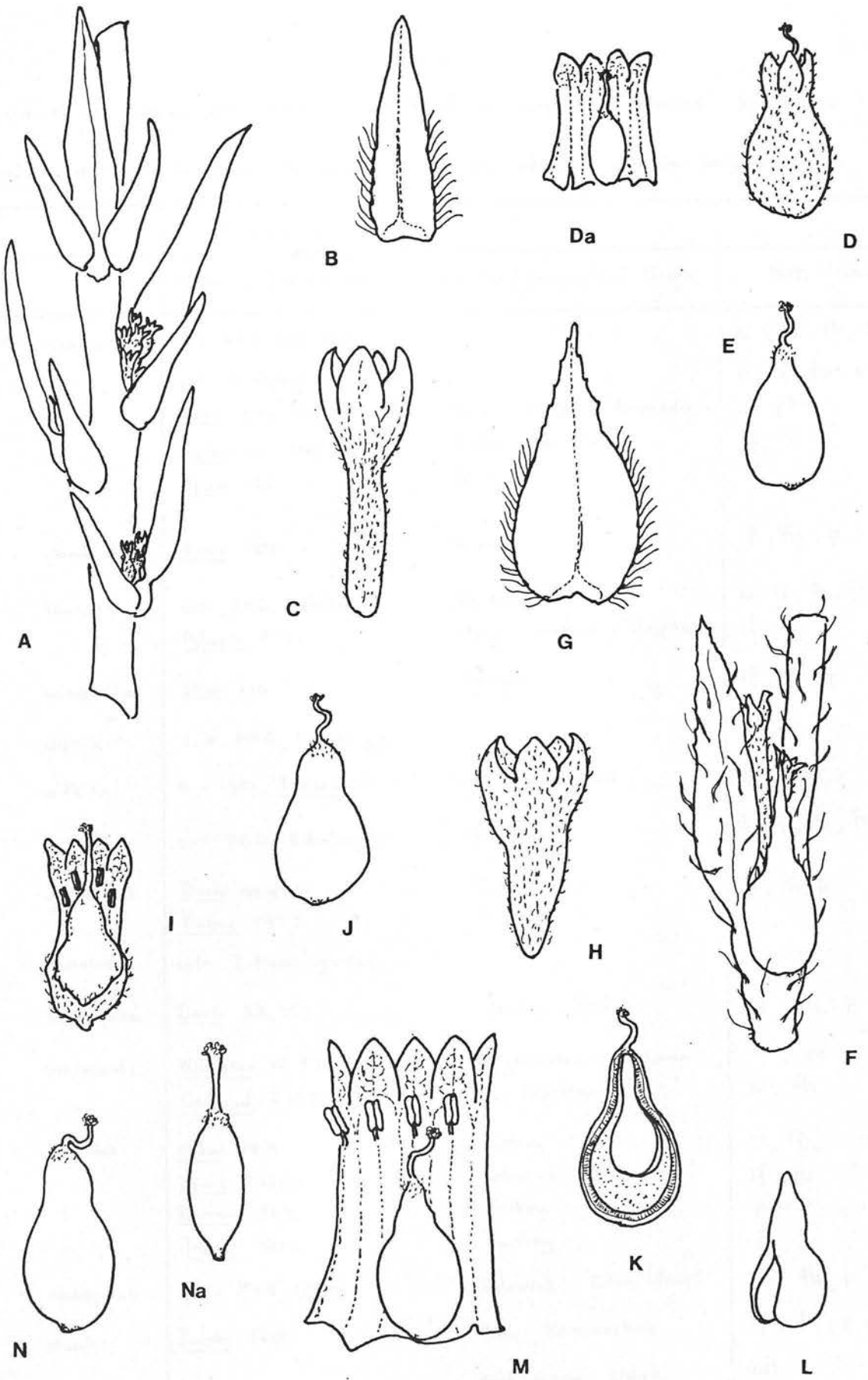
Fig. 65

APPENDIX A

Provenance of species and materials examined for anatomical studies. Species in
Thymelaea arranged in same taxonomic order as adopted in main body of thesis.

| Taxa | Provenance | | Parts Studied |
	Voucher / Specimen No.	Locality / Geographical Origin	
DAPHNE mezereum	cult. RBG, Edinburgh		st, lf, fls, fr, sd
	cult. G. Taylor's garden		st, lf, fls, p
	Parris s.n. (det. K.Tan)	Italy : Cortina d'Ampezzo	p, pS
	Fischer s.n. (det. K.Tan)	Austria : mt. Rax	lf
	Apold 132	Turkey	lf
glomerata	Apold 124	Turkey	lf, fls, p
laureola	cult. RBG, Edinburgh	Pyrenees	st, lf, fls, fr, sd
	Polunin 8121	Italy : Cortina d'Ampezzo	lf, p
composita	Shah 616	Malaya	lf, fls, p
alpina	cult. RBG, Edinburgh		lf
altaica	9 v 1901, Sukaczen	USSR : Bielgorod	lf, fls
giraldii	cult. RBG, Edinburgh	W. China	st, lf, fls, fr, sd, p
gnidioides	Davis 40474	Turkey	lf, fls, p
	Kühne 1457	Turkey	
jasminea	cult. J.Mains' garden		lf
linearifolia	Davis 38,758	Jordan : Petra	lf, fls, p
mucronata	Wendelbo W. 9721	Afghanistan : Laghman	lf, sd
	Lamond 2452	W. Pakistan	lf, fls
oleoides	Kühne 1419	Turkey	st, lf,
	Davis 6386A	Lebanon : Sîr	lf, fls
	Darrah 369	Turkey	p
	Tobey 1212	Turkey	p
rodriguezii	24 iv 1903, White	Balearics : Colom (isle)	lf, fls, p
stapfii	Jacobs 6604	Iran : Kermanshah	lf, fls, p, fr
gnidium	cult. RBG	seed source Lisboa	sdl
	Margalef s.n.	Spain : Barcelona	sdl
	Reverchon 220	Spain	lf, p
	Davis 40156	Sicily	lf, p
	Davis 54921	Morocco	st, lf, fls, p,

TAXA	PROVENANCE		Parts Studied
	Voucher / Specimen No.	Locality / Geographical Origin	
DAPHNE arbuscula	cult. RBG, Edinburgh	Hungary	st, lf, fls, p, pS
	Filarszky & Kümmerle 4 vi 1906	Hungary	lf, fls, p
cneorum	cult. RBG, Edinburgh	Bavarian Alps	st, lf, fls, p, pS
	Parris s.n. (det. K. Tan)	Italy: Auronzo	fls, p
petraea	cult. J. Mains' garden		lf
	vi 1905, Porta	Italy: Cima Tombea	lf, fls, p
striata	Parris s.n. (det. K. Tan)	Switzerland: Bernina Pass	fls, p
	Davis 17582	Italy: Cortina d'Ampezzo	lf, fls, p
bholua	cult. G. Taylor's garden	W. Himalayas	lf
* longilobata	cult. RBG, Edinburgh		st, lf, fls, p, pS, fr, sd, sdl
odora	cult. RBG, Edinburgh	Garden Origin	
	cult. Yokohama Nursery	Japan (not native)	lf, fls, p
papyracea	Burtt 1550	W. Himalayas	lf, p
sureil	18 xi 1913, Cave	W. Himalayas	lf
tangutica	cult. RBG, Edinburgh	W. China	st, lf, fls, p
blagayana	cult. RBG, Edinburgh	Carpathians	st, lf, fls, p, pS
	Paulin 282	Austria	p
sericea	Davis 116	Crete	p
	Kühne 1351	Turkey	lf, p
	Deaver T10	Turkey	lf
x burkwoodii	cult. RBG, Edinburgh		lf, fls, p
x rosetti	cult. RBG, Edinburgh	Garden Origin	lf, fls
WIKSTROEMIA			
chamaedaphne	Purdom 772	N. China: Kansu	st, lf, fls
	Fang 4403	Szechwan	lf, fls, p, pS
	Ling 9384	Shansi	pS
tenuiramis	Paiae 28028	Malaysia	lf, fls
salicifolia	Wallich 1046a	Nepal	lf, fls
RESTELLA albertii	18 viii 1960, Vassikzenko	USSR: Tashkent	st, lf, fls, p, fr
THYMELAEA lythroides	Davis 54391	Morocco: Mamora	st, lf, fls, p, pS, fr, sd
	Paunero et al. 1973/69	''	

* chromosome count	st = stem lf = leaf fls = flowers	p = pollen pS = pollen for SEM fr = fruit	sd = seed sdl = seedling

Taxa	Provenance		Parts Studied
THYMELAEA hirsuta	K. & L. Tan 373	Spain: Granada	st, lf, fls, p, sd, sdl
	Stamatiadou 8957	Greece: Lakonia	sd
	Davis 52021	Morocco: Tafraoute	st, lf, fls, p, fr
	Archibald 976	Libya: Cyrenaica	st, lf, fls, p
	and other material from similar localities		
lanuginosa	7 i 1858, anon.	Gibraltar	st, lf
	Stocken 271/64	Spain: Cadiz	st, lf, fls, p, pS
	vi 1837, Boissier	Spain: Malaga	lf, fls, p
gattefossei	ii 1937, Gattefossé	Morocco: Chaouïa	st, lf, fls, p
argentata	Sennen 715	Spain: Valencia	lf
	Reverchon 1898:254	Algeria	lf, fls
	Davis 58620	Algeria	lf
	Davis 56982, 56815, 57145	Tunisia	st, lf, fls, p, pS
virescens	Jahandiez 210	Morocco: Haute Moulouya	lf, fls, p, pS
	Domergue s.n.	Algeria: Oran	fls, p
putorioides var. putorioides	28 vii 1926, Maire	Morocco: Grand Atlas	st, lf, fls
var. rhodantha	7 vii 1931, Emberger	Morocco: Grand Atlas	st, lf, fls
microphylla	Davis 49481, 49795	Libya: Tripoli	st, lf, fls, p, pS
	Davis 53289, 53286	Algeria	st, lf, fls, p
sempervirens	19 iv 1896, Murbeck	Tunisia	st, lf, fls
tartonraira subsp. tart. var. tartonraira	Müller s.n.	Sardinia	lf, fls, p, pS
	Davis 1129	Cephalonia	lf, fls, p
var. transiens	Davis 53304, 51461	Algeria	lf, fls
	Alexander & Kupicha 320	Morocco	lf, fls, p, pS
	iv 1874, Ball	Italy: Capri	lf
subsp. argentea var. argentea	Gathorne-Hardy 86	Aegean Islands: Siphnos	st, lf
	Zerlentis 639	Greece	lf, fls, p, pS
	Alava & Regel 4824	Turkey	st, lf
var. linearifolia	Davis 1221	Crete	st, lf
	Davis 2029, 2452, 1899	Cyprus	st, lf, fls, p
	18 iii 1884, Deflers	Cyprus	lf

TAXA	PROVENANCE		PARTS STUDIED
subsp. valentina	5 iii 1855, Guirao	Spain : Murcia	st, lf, fls, p
	Porta & Rigo Iter hisp. 2 : 101 3 : 63	} Valencia	lf, fls, p
subsp. thomasii	Ph. Thomas s.n.	Corsica	lf, fls, p
velutina	8 iv 1919, Bianor	Balearics : Mallorca	st, fls, p
	v 1881, Boissier	Mallorca	st, lf
	27 iv 1885, Porta & Rigo	Menorca	st, lf
dioica subsp. dioica	Reverchon 1886 : 138	France	st, lf
	Charpin & Greuter 8405	Alpes - Maritimes	lf
	Endress s.n.	Spain : Huesca	st, lf, fls, p, pS
	30 viii 1903, Neyraut	Spain : Lerida	st, lf, fls
subsp. granatensis	vi 1903, Reverchon	Spain : Jaen	lf, p
	vi 1865, Bordère Woods s.n.	} Pyrenees	st, lf, fls, p
tinctoria subsp. tinctoria	Sennen 793	Spain : Valencia	lf, fls, p
	K. & L. Tan 129, 158	: Barcelona	st, lf, fls, p, fr, sd, sdl
	Heywood 3	: Barcelona	lf, fls, pS
	K. & L. Tan 272	: Valencia	st, lf, fls, p
subsp. nivalis	Arnott & Bentham 1529	: Huesca	lf
	20 v 1961, Money - Coutts	Pyrenees	lf, fls
	H. & McBeath 308	Pyrenees	st, lf, fls
	vi 1867, Becker	Pyrenees	st, lf, fls, fr, sd
	cult. Dean House, Money - Coutts 61009		st, lf
subrepens	iv 1895 & v 1895 } Reverchon	Spain : Teruel	st, lf, fls, fr, sd
procumbens	Fernandes et al. 4038, 3970, 3971, 3972	Portugal : Sabugal	st, lf, fls, fr (immature)
ruizii	12 vii 1879, Levier vii 1879, Boissier }	Spain : Picos de Europa	st, lf, fls
	Dresser 605, 699	''	st, lf
	H. & McBeath 56	Spain : Santander	st, lf, fls
	17 iv 1907, Elias	: Logrono	lf, fls
calycina	v 1831, Endress	Pyrenees	st, lf, fls, fr (immature)
coridifolia	Dresser 1066 vii 1928, Loso 9 v 1960, Lainz }	Spain : Cordillera Cantabrica	st, lf, fls, p, pS

TAXA	PROVENANCE		PARTS STUDIED
broteriana	Moller 880 Lacerda vi 1885	} Portugal	st, lf, fls, p, fr (immature)
antiatlantica	16 v 1932, Maire 23 iii 1937, Maire	} Morocco: Anti-Atlas	st, fls, lf, p, pS
virgata subsp. virgata	Davis 58692, 58521, 58574, 58539, 58778, 53279	} Algeria	st, lf, fls, p, pS, fr, sd
subsp. broussonetii	Paunero et al. 1940/69 Davis 54928, 55233, 55105, 55053	} Morocco: Middle Atlas	st, lf, fls, p, fr, sd
villosa	Reverchon 1887:108	Spain: Cadiz	st, lf
	Willkomm 1844:670	··	lf, fls, p
	Allen 7677	··	st, lf
	Gibbs 81.5	··	st, lf
thesioides subsp. thesioides	Gibbs 85.1	Spain: Segovia	lf
	Huxley 17	: Cuenca	st, lf, fls, p, pS
	28 v 1957, Lainz	: Salamanca	st, lf, fls, p
	21 v 1911, Vicioso	: Zaragoza	lf
subsp. elliptica	Bourgeau 1851:1472	Spain: Granada	st, lf, fls, p
	Huter et al. 870	: Granada	lf, fls
	27 vi 1851, Ball	: Granada	st, lf
sanamunda	13 v 1885, Reverchon 33	France: Basses Alps	st, lf, fls, p, pS
	v 1846, Irat	: Aude	st, lf, fls
	4 vii 1854, Bourgeau	Spain: Valencia	lf
cilicica	Wood & Gibson 183	Turkey	st, lf, fls, p, pS
	Kotschy 1853:48	Turkey	st, lf, fls
aucheri	Davis 38848	Turkey	st, lf, p, pS
	Davis 38754	Turkey	lf
	Kotschy 1855:267	Lebanon	st, lf, p
passerina	Alava 5283	Turkey	st, lf, p, pS
	Davis 31014	Turkey	st, lf, p
	Davis 23197	Turkey	st, lf, p
	Podlech 11967	Afghanistan	st, lf, p, fr
	Awrchai 15 v 1969	Israel	sd source → sdl
	Topel 15 vi 1972	Israel	sd source → sdl
gussonei	Kralik 332	Tunisia	st, lf, fls, p
	Lojacono Pl. Sic. rar. 194	Sicily	lf, lf
	anon.	Italy: Firenze	st, lf
salsa	Jahandiez 946	Morocco: Middle Atlas	st, lf, fls, p, pS
	Davis 55019b	Morocco: Middle Atlas	fls, sd
	viii 1849, Romain	Algeria: Oran	fls, sd

TAXA	PROVENANCE		PARTS STUDIED
THYMELAEA mesopotamica	Rechinger 9653	Iraq	lf
	W. Haines 368	Iraq	st, lf, fls
	Gillett 8200, 11088	Iraq	st, lf, fls, p
	Rawi 20628, 20785	Iraq	lf, fls, p
DENDROSTELLERA lessertii	Assadi et al. 1844	Iran : Kerman	st, lf
		Iran : Tehran	fls, p, ps
	Alava 10447	: Yezd	p, sd
	Archibald 1158		
	Hedge & Ekberg W 7121	Afghanistan : Kandahar	lf, p, ps
	Agnew & Haines 5075	Iraq : Najef	lf, fr, sd
stachyoides	Michelson 16 viii 1909	USSR : Kopal	st, lf, p
	Roldugin 28 vi 1960		lf
STELLEROPSIS antoninae	Amin-Bazargan 11555	Iran : Firuzkuh	st, lf, p, sd
	Furse & Synge 470	Iran	lf, fls
magakjanii	Davis 22522	Turkey	p, fr, sd
altaica	Preston s.n.	Tien-Shan	st, lf, fl
DIARTHRON vesiculosum	Lamond 1880	W. Pakistan : Kurram	fr, sd, sdl
	Burtt 553	W. Pakistan : Peshawar	lf, fr
	Ekberg W 9024	Afghanistan : Kunduz	lf, sd
	Davis 23266	Turkey : Van	st, lf, fls, p
	Koelz 16693	Iran : Khorassan	st, lf, p
linifolium	Balfour s.n.	E. China	st, lf, p
	Potanin s.n.	Mongolia	lf, ps
	vii 1910, Chaneti	E. China : Chili Prov.	lf
STELLERA chamaejasme subsp. chamaejasme	cult. RBG, Edinburgh	C. Asia (seed from Lowndes 913)	st, lf, fls, p, ps, sd
	Lowndes 1150	Nepal	lf
	Stainton et al. 764	Nepal	lf, fls, p
	Forrest 30066	W. China : Yunnan	
	Forrest 4788	: Yunnan	lf
	Farrer 93	: Yunnan	lf, fls
		: Yunnan	st, fls, p
subsp. angustifolia	Forrest 12413	: Yunnan	st, fls, p
	Kingdon Ward 3899	: Yunnan	lf
PIMELEA spectabilis	Ashby 2695	Australia	p
PASSERINA vulgaris	cult. RBG, Edinburgh	S. Africa	st, lf, fls, p, ps
rigida	Hilliard & Burtt 7163	S. Africa	lf, fls, p, ps
montana	Hilliard & Burtt 7139, 6897, 7220	S. Africa	st, lf, fls, p, ps
paleacea	Boucher 469	S. Africa	fls, p
ericoides	Dümmer 18/9	S. Africa	fls, p
filiformis	Bayer 6059	S. Africa,	lf, p, ps

A NEW THYMELAEA FROM MOROCCO

H. K. TAN

A NEW THYMELAEA 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, ramulis floriferis brevioribus 1–2-foliatis, bracteis ovato-lanceolatis (haud linearibus) differt.

Frutex dioecius, 50–100 cm altus (?), ramis gracilibus flexuosis, junioribus incano-lanuginosis, inferne denudatis et glabrescentibus. *Folia* sessilia, herbacea, late ovato-lanceolata, 4–5×2–3 mm, obtusa, utrinque dense incano-lanata, subtus minus tomentosa, imbricata, deinde patula. *Inflorescentia*: flores (staminati) 9–14 in fasciculos congestos ad apicem ramulorum valde abbreviatorum 1–2-foliatorum aggregati, brevissime pedicellati, argenteo vel flavido incano-lanati. *Bracteae* 3–5, ovato-lanceolatae, obtusae, 4 × 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 hermaphroditi ignoti. *Fl.* Febr.–Mar.

Sandy plains with *Chamaerops humilis* L., littoral region.

MOROCCO. Chaouïa, chamaeropaie sur sable á Bouskoura, Février 1937, *Gattefossé* [holo. MPU; as *T canescens* (Schousb.) Endl.]. Chaouïa 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 Âïn Saïerni 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:

	T. gattefossei	*T. lanuginosa*
Inflorescence	At end of very short branch-lets with 1–2 leaves so that the fascicles appear±axillary.	At end of short, densely leafy branchlets so that the fascicles are obviously terminal.
	Flowers 9–14 (staminate); bracts 3–5, ovate-lanceolate, 3·5–4×1·5–2 mm.	Flowers usually 7–10; bracts 7–10, linear-lanceolate, 6–7×1·5 mm.

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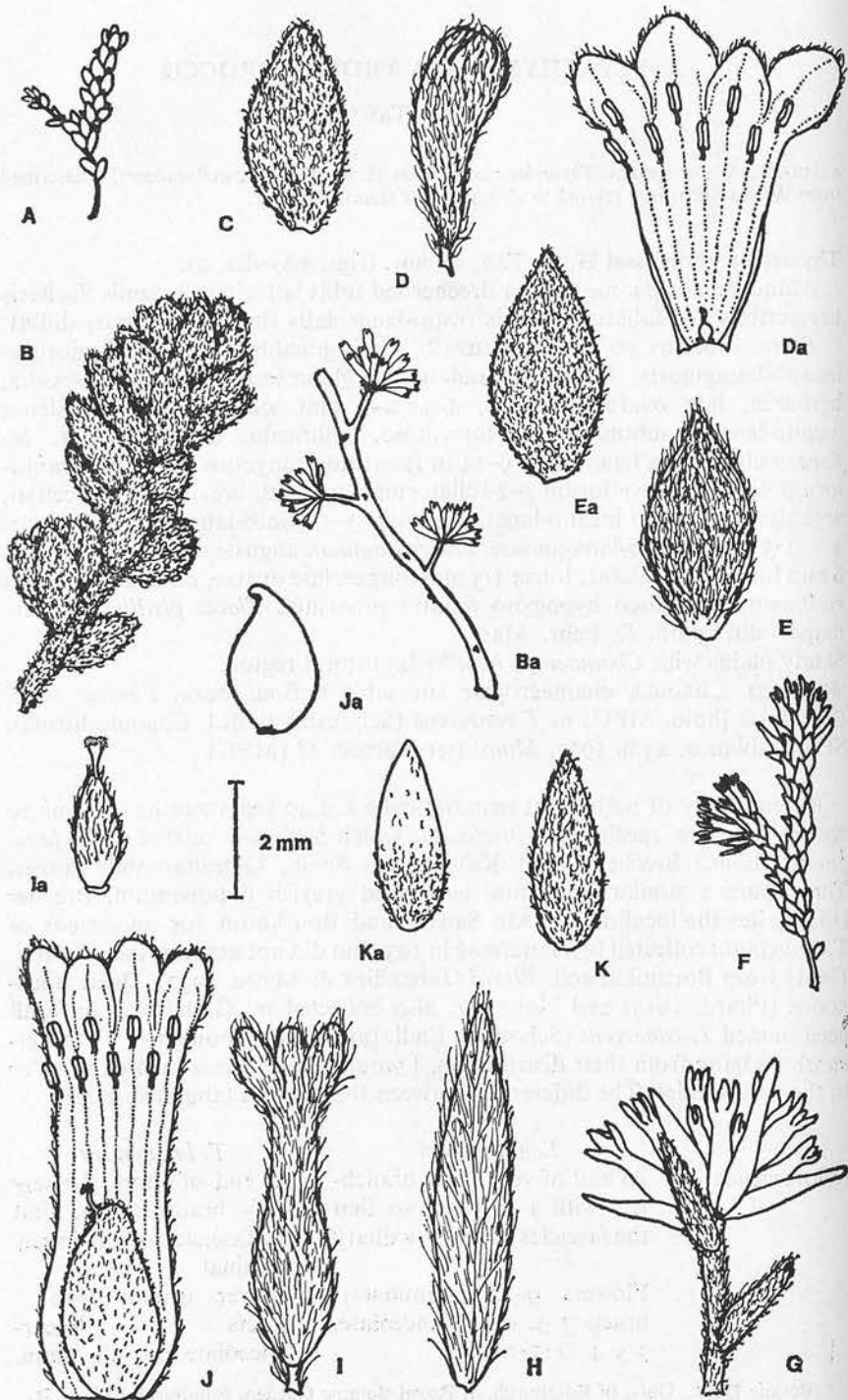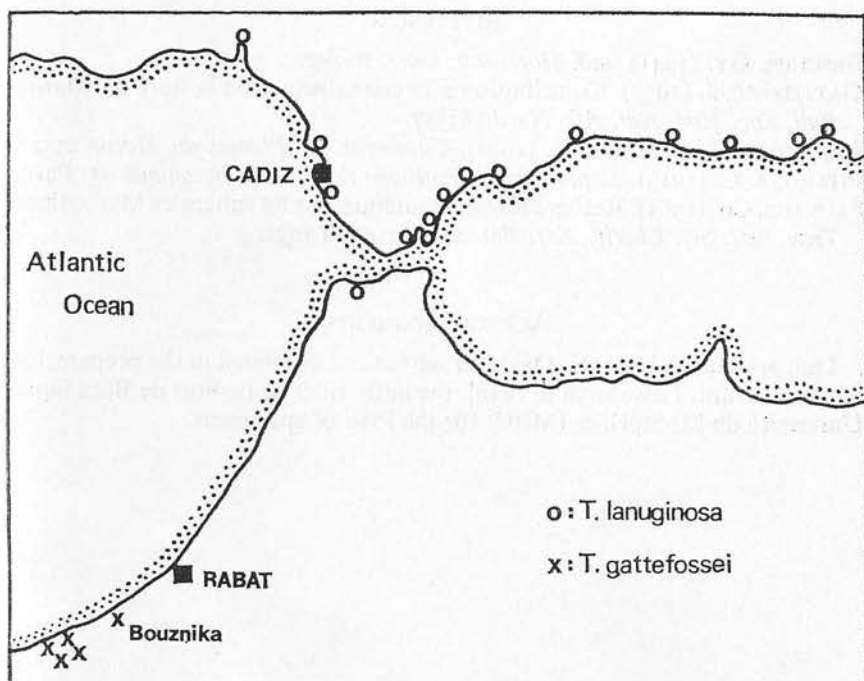
FIG. 2. The total distribution of *Thymelaea lanuginosa* (based on checked herbarium specimens) and *T. gattefossei*.

	T. gattefossei	*T. lanuginosa*
Sex distribution (on separate plants)	Staminate or pistillate.	Hermaphrodite or pistillate, rarely staminate.
Perianth	Narrowly infundibuliform, 6 mm (staminate)	Tubular, 7–8·5 mm (hermaphrodite), 5·5–6 mm (pistillate)
Leaf	4–5 × 2–3 mm	2–4 × 1·5–2 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 (×⅔); B, part of flowering shoot, enlarged (×3·5); Ba, leaves and bracts removed to show inflorescences (×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 (×1·5); G, terminal inflorescence with subtending bracts (×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 (×7) except when indicated.

REFERENCES

BRECHER, GY. (1941). *Ind. Hort. Bot. Univ. Budapest* 5:104.

GATTEFOSSÉ, J. (1937). Contribution á la connaissance de la flore du Maroc. *Bull. Soc. Hist. Nat. Afr. Nord* 28:537.

JAHANDIEZ, E. & MAIRE, R. (1932). *Catalogue des Plantes du Maroc* 2:511.

PITARD, J. C. (1913). *Exploration scientifique du Maroc, Botanique* 95. Paris.

SAUVAGE, CH. (1961). Recherches géobotaniques sur les subéraies Marocaines. *Trav. Inst. Sci. Chérif., Sér. Bot.* 21, 462 pp. Tanger.

ACKNOWLEDGMENTS

ADD TO WORKS CITED

AYMONIN, G.-G. (1971). Chorologie régionale et chorologie générale. Intérêt pour l'étude du polymorphisme: un exemple chez les Thyméléacées méditerranéenes. Bull. Soc. Bot. France 118: 827-834.

ELLENBERG, M. & MUELLER-DOMBOIS, D. (1967). A tentative physiognomic-ecological classification of the foundations of the earth. Rübel 37: 21-55.

ENDLICHER, S.L. (1833). Prodr. Fl. Norfolk. Vindobonae.

HEER, O. (1856). Flora tertioria Helvetiae II. Wurster & Co., 110 pp.

JOHNSON, A.M. (1931). Taxonomy of the flowering plants. New York.

KEITH, H.G. (1965). A Preliminary Check List of the Libyan Flora.

RECHINGER, K.H. (1943). Flora Aegaea. Flora der Inseln und Halbinseln des Ägäischen Meers. Springer, Wien.

WAWRA, H. (1875). Beiträge zur Flora der Hawai'schen Inseln. Flora 58: 171-176; 184-192.

<u>WORKS CITED</u>

1. Airy-Shaw, H.K. (1947). Notes on the genus <u>Gonystylus</u> Teijsm. et
   Binnend. (Thymelaeaceae). <u>Kew Bull.</u> 1:9-16.

2. _____ (1950). New or Noteworthy species of <u>Gonystylus</u>
   and related genera. <u>Kew Bull.</u> 138-147.

3. _____ (1953). Thymelaeaceae -- Gonystyloideae. <u>Fl.</u>
   <u>Malesiana</u> I (4): 349-365.

4. _____ (1973). Willis, J.C., <u>A Dictionary of the Flowering</u>
   <u>Plants and Ferns</u>, ed. 8. Cambridge Univ. Press.

5. Arora, C.M. (1961). New chromosome report. II. <u>Bull. Bot. Surv.</u>
   <u>India</u> 3:37.

6. Asai, T. (1930). Über das Vorkommen und die physiologische
   Bedeutung des Daphnins bei <u>Daphne odora</u>. <u>Acta Phytochem. (Tokyo)</u>
   5: 9-21.

7. Aymonin, G.-G. (1969). Etude sur le "<u>Daphne myrtifolia</u>" Poiret
   (Thyméléacées). <u>Bull. Soc. Bot. France</u> 116: 531-537.

8. _____ (1974). Polymorphisme chez le "<u>Thymelaea tarton-</u>
   <u>raira</u> (L.)All. et position du "<u>Passerina</u>" thomasii Duby de la
   Corse. <u>Bull. Soc. Bot. France</u> 121 (sess. extr.): 41-43.

9. Bailey, I.W. (1956). Nodal anatomy in retrospect. <u>J. Arnold</u>
   <u>Arb.</u> 37:269-287.

10. Baillon, H. (1877). Thymelaeacées. <u>Histoire des Plantes</u>, Vol. 6.

11. Baksay, L .(1956). Cytotaxonomical studies on the flora of
    Hungary. <u>Ann. Hist.-Nat. Mus. Natl. Hung.</u> 7:321-334.

12. Baranova, M.A. (1962). The structure of stomata and epidermal
    cells in magnolias as related to the taxonomy of the genus
    <u>Magnolia</u>. Bot. Žurn. 47: 1108-1115 (in Russian).

13. _____ (1972). Systematic anatomy of the epidermis in
    the Magnoliaceae and some related families. <u>Taxon</u> 21: 447-469.

14. Barton, L.V. (1965). Dormancy in seeds imposed by the seed coat. Encycl. Pl. Physiol. 15: 727-745.

15. Bate-Smith, E.C. (1956). The commoner phenolic constituents of plants and their systematic distribution. Sci. Proc. Roy. Dublin Soc. 27: 165-176.

16. _____ (1962). The phenolic constituents of plants and their taxonomic significance. J. Linn. Soc. (Bot.) 58:95-173.

17. _____ (1973). Chemotaxonomy of Geranium. Bot. J. Linn. Soc. 67:347-359.

18. Bate-Smith, E.C. & Lerner, N.H. (1954). Leuco-anthocyanins. 2. Systematic distribution of leuco-anthocyanins in leaves. Biochem. J. 58:126-132.

19. _____ & Metcalfe, C.R. (1957). Leuco-anthocyanins. 3. The nature and systematic distribution of tannins in dicotyledonous plants. J. Linn. Soc. (Bot.) 55: 669-705.

20. Beauregard, M. (1877). Structure et développement du fruit des Daphne. Bull. Soc. Bot. France 24:385-387.

21. Belling, J. (1928). A method for the study of chromosomes in pollen mother cells. Univ. Calif. Publ. Bot. 14: 293-299.

22. Bentham, G. & Hooker, J.D. (1883). Thymelaeaceae. In: Genera Plantarum, Vol. 3. Lovell Reeve, London.

23. Bessey, C.E. (1915). the phylogenetic taxonomy of flowering plants. Ann. Missouri Bot. Gard. 2(1 & 2): 109-164.

24. Bhat, B.K. et al. (1974). In: IOPB chromosome number reports XLIII. Taxon 23: 193-196.

25. Bjorkvist, I. et al. (1969). Chromosome numbers in Iberian Angiosperms. Bot. Not. 122: 271-283.

26. Blatter, E.(1929). Beautiful Flowers of Kashmir. Vol. 2. London.

27. Bokhari, M.H. (1970). Morphology and taxonomic significance of foliar sclereids in Limonium. Notes Roy. Bot. Gard. Edinb. 30: 43-54.

28. Porgmann, E. (1964). Anteil der Polyploiden in der Flora des bismarcksgebirges von Ostneuguinea. Z. Bot.52: 118-172.

29. Brecher, Gy. (1941). A Thymelaea-génusz és fajai. Index Horti Bot. Univ. Budapest. 5: 57-112.

30. Breckle, S.-W.(1971). Ist Diarthron vesiculosum (Thymelaeaceae) ein Ökologisches Rätsel? Bot. Jahrb. Syst. 90(4): 550-561.

31. Brewbaker, J. (1967). The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in angiosperms. Amer. J. Bot. 54: 1069-1 83.

32. Brickell, C.D. & Mathew, B. (1976). Daphne, the genus in the Wild and in Cultivation. Alp. Gard. Soc., Surrey.

33. Briquet, J. & Litardière, R. de (1938). Thymelaeaceae. In: Prodrome de la Flore Corse 3(1): 3-7. Paris.

34. British Pharmaceutical Codex (1973). London.

35. Burkill, I.H. (1935). A Dictionary of the Economic Products of the Malay Peninsula, Vol. 1. Crown Agents for the Colonies, London.

36. Chuang, T.-I. et al. (1962). Chromosome numbers of the vascular plants of Taiwan I. Taiwania 8: 51-66.

37. Contandriopoulos, J. (1964). Recherches sur la flore endémique de la Corse et sur ses origines. Rev. Gén. Bot. 71: 361-384.

38. Cook, M. T. & Taubenhaus, J.J. (1911). The relation of parasitic fungi to the contents of the cells of the host plants. I. The toxicity of tannin. Del. Agr. Exp. Sta. Bull. 91: 3-77 (n. v.).

39. Corner, E.J.H. (1976). The seeds of dicotyledons, Vols. 1 & 2. Cambridge Univ. Press.

40. Cronquist, A. (1968). The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston.

41. Crowzet, A. (1967). Sur les adaptations morphologiques et anatomiques d'Helianthemum lavandulaefolium et Thymelaea tartonraira. Ann. Fac. Sci. Marseille 39:93-117.

42. Cruickshank, R.H. (1953). Chromosome numbers in the genus Pimelea. Pap. & Proc. Roy. Soc. Tasmania 87: 13-16.

43. Dahlgren, R. (1968). Studies on Penaeaceae II, the genera Brachysiphon, Sonderothamnus and Saltera. Opera Bot. 18: 1-72.

44. _____ (1971). Studies on Penaeaceae. VI. The genus Penaea L. Opera Bot. 29: 1-58.

45. Darlington, C.D. & La Cour, L.F. (1962). The Handling of the Chromosomes, ed. 4. Allen & Unwin, London.

46. Davis, G.L. (1966). Systematic Embryology of the Angiosperms. John Wiley, New York.

47. Davis, P.H. (1978). The Moving Staircase: a discussion on taxonomic rank and affinity. Notes Roy. Bot. Gard. Edinb. 36: 325-240.

48. Dean, F.M. (1952). Naturally occurring coumarins. Prog. Chem. Organic Nat. Prod. 9: 225-291. Springer-Verlag.

49. Delay, J. (1969). Determinations nouvelles. Inf. Ann. Caryosyst. et Cytogenet. 3: 13-16.

50. De Roon, A.C. (1967). Foliar sclereids in the Marcgraviaceae. Acta Bot. Neerl. 15: 585-623.

51. Ding Hou (1960). Thymelaeaceae. In: Fl. Malesiana I. 6(1): 1-15.

52. Domke, W. (1934). Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen. Biblioth. Bot. 111: 1-151.

53. Du Rietz, G.E. (1930). The fundamental units of biological
    taxonomy. Bot. Tidsskr. 24: 333- 428.

54. Earle, E.R. & Jones, Q. (1962). Analyses of seed samples from
    113 plant families. Econ. Bot. 16: 221-250.

55. Eichler, A.W. (1877). Blütendiagramme, Vol. 2. Leipzig.

56. El-Ghonemy, A.A. et al. (1977). Thymelaea hirsuta (L.)Endl.,
    a possible cellulosic raw material for paper pulp industry in
    Egypt. II. An introduction. J. Egypt Acad. Sci. (in press).

57. Endlicher, S.L. (1848). Generum Plantarum Suppl. 4(2):65-66.
    Vindobonae.

58. Erdtman, G. (1960). The acetolysis method. A revised descrip-
    tion. Svensk Bot. Tidskr. 54: 561-564.

59. _____ (1969). Handbook of Palynology. Munksgaard,
    Copenhagen.

60. _____ (1972). Pollen morphology and Plant taxonomy.
    Angiosperms. Hafner, New York. (Corrected reprint of 1952
    edition with a new addendum).

61. Ettingshausen, C. von (1861). Die Blattskelete des Dicotyledon.
    Staatsdruckeri, Vienna.

62. Fagerlind, F. (1940). Zytologie und Gametophyten bildung in
    der Gattung Wikstroemia. Hereditas 26: 23-50.

63. Fahn, A. (1974). Plant Anatomy, ed. 2 (revised). Pergamon
    Press, Oxford.

64. Fahn, A. & Sarnat, C. (1963). Xylem structure and annual rhythm
    of development in trees and shrubs of the desert. IV. Shrubs.
    Bull. Res. Counc. Israel, Sect. D (Bot.) 11: 198-209.

65. Ferguson, D.K. (1971). The Miocene flora of Kreuzau, Western
    Germany, I. The leaf remains. North Holland Publ. Co.,
    Amsterdam, London.

66. Fryns-Claessens, E. & van Cotthem, W.R.J. (1973). A new classification of the ontogenic types of stomata. Bot. Rev. 39: 71-138.

67. Fuchs, A. (1938). Beiträge zur Embryologie der Thymelaeaceae. Oesterr. Bot. Z. 87(1): 1-41.

68. Fuchs, C. (1963). Fuchsin staining with NaOH Clearing for Lignified Elements of whole plants or plant organs. Stain Technology 38: 141-144.

69. Fukuda, Y. (1967). Anatomical study of the internal phloem in the stems of dicotyledons with special refernce to its histogenesis. . J. Fac. Sci. Tokyo Univ. (Bot.) 9: 313-375.

70. Gerber, C. (1899). Les passerina provenceaux; essai de classification et recherches sur la nature du disque hypogyne et des écailles périanthiques. Bull. Soc. Bot. France 46:108.

71. _____ (1900). Recherches morphologiques, anatomiques, systématiques et tératologiques sur les Thymelaea des environs de Marseille. Bull. Sci. France et Pelg. 33: 430-454.

72. Gibbs, R.D. (1974). Chemotaxonomy of Flowering Plants, Vols. I-IV. McGill-Queen's Univ. Press, Montreal & London.

73. Gilg, E. (1894). Thymelaeaceae. In: Engler & Prantl, Nat. Pflanzenfam. 3(6a):237.

74. Gray, A. (1865). New or little known Polynesian Thymeleae. J. Bot. 3:302-307.

75. Greguss, P. (1959). Holzanatomie der europäischen Laubhölzer und Sträucher, ed. 2. Akadémiai Kiadó, Budapest.

76. Guérin, P. (1916). Reliquiae Treubianae I. Recherches sur la structure anatomique de l'ovule et de la graine des Thyméléacées. Ann. Jard. Bot. Buitenzorg 2(14): 3-35.

77. Gupta, S. & Gillett, G.W. (1969a). Chemotaxonomic studies of Hawaiian _Wikstroemia._ _Econ. Bot._ 23: 24-31.

78. _____ (1969b). Observations on Hawaiian species of _Wikstroemia_ (Angiospermae: Thymelaeaceae). _Pacific Sci._ 23: 83-88.

79. Hallier, H. (1912). L'Origine et la système phylétique des angiospermes exposés a l'aide de leur arbre généologique. _Archiv. Néerl. Ser._ 3B(1): 146-234.

80. Hamaya, T. (1955). A dendrological monograph on the Thymelaeaceae plants of Japan. _Bull. Tokyo Univ. For._ 50: 45-96.

81. _____ (1959). Dendrological studies of the Japanese and some foreign genera of the Thymelaeaceae. Anatomical and phylogenetic studies. _Bull. Tokyo Univ. For._ 55: 1-80.

82. _____ (1963). Taxonomical notes on _Daphne_ (Thymelaeaceae). _Acta Horti Gothob._ 26: 63-99.

83. Hara, N. (1957). On the types of the marginal growth in dicotyledonous foliage leaves. _Bot. Mag. Tokyo_ 70: 108-114.

84. _____ (1961). Apical views of the veg. shoot apex. _Bot. Mag. Tokyo_ 74: 267-268.

85. _____ (1962a). Structure and seasonal activity of the vegetative shoot apex of _Daphne pseudomezereum._ _Bot. Gaz._ 124: 30-42.

86. _____ (1962b). Histogenesis of foliar venation of _Daphne pseudo-mezereum_ A. Gray. _Bot. Mag. Tokyo_ : 107-113.

87. Harborne, J.B. (1966). The evolution of flavonoid pigments in plants. In: Swain, T. (ed.) _Comparative Phytochemistry_, pp. 271-295. Academic Press, London & New York.

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,_

pp. 257-293. Academic Press, London & New York.

89. Hare, H.A. et al.(1905). The National Standard Dispensatory. London.

90. Hecker, E. (1971). Cocarcinogens from Euphorbiaceae and Thymelaeaceae. In: Wagner, H. & Hörhammer, L. (eds.) Pharmacognosy and Phytochemistry. Springer-Verlag, Berlin.

91. Hedge, I.C. (1976). A systematic and geographical survey of the Old World Cruciferae. In: Vaughan Macleod & Jones, The biology and chemistry of the Cruciferae, pp. 1-45. Academic Press, London & New York.

92. Hegnauer, R. (1973). Chemotaxonomie der Pflanzen. Vol. 6, 882 pp. Birkhauser, Basel.

93. Heinig, K.H. (1951). Studies in the floral morphology of the Thymelaeaceae. Amer. J. Bot. 38: 113-132.

94. Hemsley, W.B. (1895). On two small collections of dried plants from Tibet. J. Linn. Soc. (Bot.) 30: 101-140.

95. _____ (1902). The Flora of Tibet or Higher Asia. J. Linn. Soc. (Bot.) 35: 124-265.

96. Hickey, L.J. (1973). Classification of the Architecture of dicotyledonous leaves. Amer. J. Bot. 60(1): 17-33.

97. Hideux, M.J. & Ferguson, I.K. (1976). The stereostructure of the exine and its evolutionary significance in Saxifragaceae s.l. In: Ferguson, I.K. & Muller, J. (eds.) The evolutionary significance of the exine, pp. 327-377. Academic Press, London.

98. Hillebrand, W. (1888). Flora of the Hawaiian Islands. Heidelberg.

99. Hiraoka, T. (1958). Somatic syndesis in Daphne odora. I & II. Proc. Jap. Acad. 34: 300-705; 706-711.

100. Hofmeister, W. (1849). Die Enstehung des embryo der Phanerogam. Leipzig.

101. Hsu, C.-C. (1967). Preliminary chromosome studies on the vascular plants of Taiwan (I). _Taiwania_ 13: 117-130.

102. Hutchinson, J. (1926). _The Families of Flowering Plants (ed. 1)_, Vol. 1. Dicotyledons. Macmillan, London.

103. _____ (1967). _The Genera of Flowering Plants, Vol. 2_. Clarendon Press, Oxford.

104. Janssonius, H.H. (1950). Wood anatomy and relationship. _Blumea_ 6: 407-461.

105. Johansen, D.A. (1940). _Plant Microtechnique_. McGraw-Hill, New York.

106. _____ (1950). _Plant Embryology_. Waltham, Mass.

107. Joshi, A.C. (1936). Anatomy of the flowers of _Stellera chamaejasme_ Linn. _J. Ind. Bot. Soc._ 15: 77-86.

108. _____ (1937). A study of pollen in the Thymelaeaceae. _Proc. 24th Ind. Sci. Congr., Sect. 4, Bot._ (Abstr.).

109. Kashyap, S.R. (1930). _Stellera chamaejasme_ Linn. _J. Ind. Bot. Soc._ 9: 208-210.

110. Kausik, S.B. (1940). Structure and development of the ovule and embryo-sac of _Lasiosiphon eriocephalus_ Decne. _Proc. Natl. Inst. Sci. Ind._ 6:117-132.

111. Keissler, K. von (1898). Die Arten der Gattung _Daphne_ aus der Sekt. Daphnanthes. _Bot. Jahrb. Syst._ 25: 29-125.

112. Kershaw, E.M. (1909). The Structure and Development of the ovule of _Myrica gale_. _Ann. Bot._ 23: 353-362.

113. Kupchan, S.M. & Baxter, R.L. (1975). Mezerein: antileukaemic principle isolated from _Daphne mezereum_ L. _Science, N.Y._ 187: 652-653.

114. Kuprianova, L.A. (1969). On the evolutionary levels in the morphology of pollen grains and spores. _Pollen & Spores_ 11(2):

333-351.

115. Kuzmanov, B. (1973). In: IOPB chromosome number reports XLII.
     Taxon 22: 647-654.

116. Lapeyrouse, P. (1813). Histoire abrégée des plantes des Pyrénées.
     Toulouse.

117. Lawrence, G.H.M. (1951). Taxonomy of Vascular Plants. New York.

118. Leandri, J. (1930). Recherches anatomiques sur les Thyméléacées.
     Ann. Sci. Nat. Ser. Bot. 10(12): 125-237.

119. Lecomte, H.M. (1914). Sur les graines des Thyméléacées. Bull.
     Soc. Bot. France 61: 410-418.

120. Lee, Y.N. (1969). Chromosome number of flowering plants in
     Korea (2). J. Korean Res. Inst. Better Living. 2: 141-145.

121. Leveque, M. & Gorenflot, R. (1969). Prospections caryologiques
     dans la flore littorale du Boulonnais. Bull. Soc. Bot. Nord.
     France 22: 27-58.

122. Linnaeus, C. von (1753). Species Plantarum (ed. 1), Vol. 1.
     Stockholm.

123. Loeve, A. & Kjellqvist, (1974). Cytotaxonomy of Spanish plants.
     IV. Dicotyledons. Lagascalia 4: 153-211.

124. Maheswari, P. (1950). An Introduction to the Embryology of
     Angiosperms . McGraw-Hill, New York.

125. Maiti, P.C. et al. (1963). Daphne cannabina Wall. Sci. & Cult.
     (India) 29: 160. (n.v.).

126. _____ (1967). Curr. Sci. (India) 36: 99 (n.v.).

127. Majovsky, J. et al. (1970). Index of chromosome numbers of
     Slovakian flora (Part 1). Acta Fac. Rerum Nat. Univ. Comenianae
     Bot. 16: 1-26.

128. _____ (1974). Op. cit., 23: 1-23.

129. Mangenot, S. & Mangenot, G. (1957). Nombres chromosomiques nouveaux chez diverses dicotylédones et monocotylédons d' Afrique occidentale. Bull. Jard. Bot. (Bruxelles) 27: 639-654.

130. Martin, A.C. (1946). The comparative internal morphology of seeds. Amer. Midl. Nat. 36: 513-660.

131. Mears, J.A. & Mabry, T.J. (1971). Alkaloids in the Leguminosae. In: Harborne, J.B. et al. (eds.) Chemotaxonomy of the Leguminosae. Academic Press, London & New York.

132. Meissner, C.F. (1857). Thymelaeaceae. In: de Candolle, Prodr. Syst. Regni Veget. Vol. 14: 551-558. Paris.

133. Metcalfe, C.R. (1961). Anatomy of the Monocotyledons. Vol. I. Clarendon Press, Oxford.

134. Metcalfe, C.R. & Chalk, L. (1950). Anatomy of the Dicotyledons. Vols. 1 & 2. Clarendon Press, Oxford.

135. Miller, P. (1754). The gardeners dictionary abridged. London.

136. _____ (1768). The gardeners dictionary, ed. 8. London.

137. Nalepa, A. (1900). Diagnose d'Eriophyses passerinae, nov. sp. Bull. Sci. France et Belg. 33: 455-457.

138. Nechayeva, N.T. et al. (1969). Ecological classification of the annual plants of the Karakumy desert. Bot. Zhurn. SSSR 54: 1689-1704 (Russian; English summary).

139. Nelson, A.(1935). The Elaeagnaceae. Amer. J. Bot. 22: 681-683.

140. Netolitzky, F. (1926). Anatomie der Angiospermensamen. In: Linsbauer, K. (ed.) Handbuch der Pflanzenanatomie, Vol. 2 (Bd.10). Borntraeger, Berlin.

141. Nevling, L.I. (1962). Chromosome counts of two Thymelaeaceae. Rhodora 64: 277-281.

142. _____ (1963). In: Documented chromosome numbers of plants. Madroño 17: 116-117.

143. Nevling, L.I. (1964a). Cytological evidence for the hybrid status of Daphne x mantensiana. Baileya 12: 134-136.

144. _____ (1964b). In: IOPB chromosome number reports II. Taxon 13: 201-209.

145. _____ (1966). In: IOPB chromosome number reports VI. Taxon 15: 117-128.

146. Nevling, L.I. & Woodbury, R. (1966). Rediscovery of Daphnopsis helleriana. J. Arn. Arb. 47: 262-265.

147. Niklewski, J. & van Zeist, W. (1970). A late Quaternary Pollen Diagram from Northwest Sysia. Acta Bot. Neerl. 19(5): 737-754.

148. Nishiyama, I. & Watanabe, T. (1960). Studies on artificial polyploid plants. XXI. Morphological and cytological studies on F1 hybrids of Edgeworthia. Jap. J. Breed. 10: 228-232.

149. Okura, E. & Kono, M. (1959). Cytogenetical consideration of Daphne odora Thunb. based on its karyotype. Biol. J. Okayama Univ. 5:51-56.

150. Orshan, G. (1953). Note on the application of Raunkiaer's System of Life forms in Arid regions. Pal. J. Bot. (Jer. ser.) 6(2): 120-122.

151. Osawa, I. (1913). On the development of the Pollen-grain and Embryo-sac of Daphne, with special reference to the sterility of Daphne odora. J. Coll. Agri. Tokyo 5(4): 237-264.

152. Ozenda, P. (1949). Recherches sur les dicotylédones apocarpiques; contribution a l'étude des angiospermes dites primitives. Ecole Normale Supér. Publ. Lab. Biol. Paris. 2: 1-183. (n.v.)

153. Pant, D.D. (1965). On the ontogeny of the stomata and other homologous structures. Pl. Sci. (Allahabad) 1: 1-24.

154. Pant, D.D. & Kidwai,P. (1971). The Origin and Evolution of Flowering Plants. J. Ind. Bot. Soc. (Golden Jubilee Vol.) 50A: 242-274.

155. Parsa, A. (1934). Contribution à l'étude structurale de quelques Dicotylédones xérophiles de l'Iran. Thèse: Poitiers, 92 pp. (n.v.).

156. Peterson, B. (1972). Thymelaeaceae. In: Rechinger, fil. Fl. Iranica 95: 1-17.

157. Pettersson, M. (1956). Diffusion of a New Habit among Green-finches. Nature 177: 709-710.

158. Pobedimova, E.G. (1949). Thymelaeaceae. In: Fl. URSS 15: 481-515. (English transl., 1974, Keter Press, Jerusalem).

159. Prohaska, K. (1883). Der embryosack und die endospermbildung in der gattung Daphne. Bot. Zeitung 41: 865-868.

160. Puri, V. (1951). The role of floral anatomy in the solution of morphological problems. Bot. Rev. 17: 471-553.

161. Rao, A.N. (1977). Sclereid variation in Scaevola frutescens from two different habitats. Flora 166(2): 111-116.

162. Rao, S. & Ramayya, N. (1977). Stomatogenesis in the genus Hibiscus L. (Malvaceae). Bot. J. Linn. Soc. 74: 47-56.

163. Rattenbury, J.A. (1957). Chromosome numbers in New Zealand Angiosperms. Trans. Roy. Soc. N.Z. 84: 936-938.

164. Raunkiaer, C. (1934). The Life forms of Plants and Statistical Plant Geography (transl.) Clarendon Press, Oxford.

165. Reese, G. (1957). Über die Polyploidiespektren in der nord-saharischen Wüstenflora. Flora 144: 598-634.

166. Rendle, A.B. (1925). Classification of Flowering Plants, Vol.2.

167. Rice, E.L. (1974). Allelopathy. Academic Press, New York.

168. Rindl, M. (1933). The crystalline glucoside of Gnidia polycephala (Januarie Bossie), II. S. African J. Sci. 30: 455-457.

169. _____ (1934). Isolation of a glucoside from Gnidia polycephala (Januarie Bossie). Trans. Roy. Soc. S. Africa 21: 239.

170. Rousi, A. (1965). Observations on the cytology and variation of

European and Asiatic populations of Hippophae rhamnoides.
Ann. Bot. Fenn. 2: 1-18.

171. Rousi, A. (1971). The genus Hippophae L. A taxonomic study.
Ann. Bot. Fenn. 8: 177-227.

172. Sisido, K. et al. (1967). Perfumery and Essent. Oil Record
58: 528. (n.v.).

173. Solis, P.P. et al. (1938). A pharmaceutical study of Wikstroemia
ovata Meyer (Fam. Thymeliaceae). Rev. Filipina Med. Farm. 29:
317-326.

174. Sporne, K.R. (1954). Statistics and the evolution of dicotyledons.
Evolution 8: 55-64.

175. Saleh, M.R.I. & Sarg, T.M. (1966). Macro- and micromorphology
of the stems and the leaves of Thymelaea hirsuta L. J. Pharm.
Sci. U.A.R. 6: 147-162. (n.v.).

176. Sass, E.J. (1958). Botanical Microtechnique, ed. 3. Iowa State
Univ. Press, Iowa.

177. Saunders, E.R. (1933). The cause of petaloid colouring in
"apetalous" flowers. J. Linn. Soc. (Bot.) 49:199-218.

178. Schnarf, K. (1931). Vergleichende Embryologie der Angiospermen.
Berlin.

179. Sharma, A. & Sarkar, A.K.eds. (1967-68). Chromosome number
reports of plants. Res. Bull. (Calcutta). 2:38-48.

180. Skottsberg, C. (1955). Chromosome numbers in Hawaiian flowering
plants. Ark. Bot. 3: 63-70.

181. _____ (1972). The genus Wikstroemia Endl. in the
Hawaiian Islands. Acta Reg. Soc. Sci. Gothob. (Ser. Bot.), Vol.
1, 154 pp.

182. Smith, A.C. (1971). An appraisal of the orders and families of
primitive extant angiosperms. J. Ind. Bot. Soc. (Golden

Jubilee Vol.) 50A: 215-226.

183. Smith, P.M. (1978). Chemical evidence in Plant Taxonomy. In: Street, H.E.(ed.) Essays in Plant Taxonomy, pp.19-38. Academic Press, London & New York.

184. Solereder, H. (1908). Systematic Anatomy of the Dicotyledons. Vols. 1 & 2 (Engl. transl. by L.A. Boodle & F.E. Fritsch). Oxford Univ. Press.

185. Sorsa, V.(1962). Chromosomenzahlen Finnischer Kormophyten I. Ann. Acad. Sci. Fenn. Ser. A. 58: 1-14.

186. Souéges, R. (1942). Embryogenie des Thymélaéacées. Développement de l'embryon chez le Daphne mezereum L. Acad. Sci.: 569-571.

187. Stace, C.A. (1965). Cuticular studies as an aid to plant taxonomy. Bull. Brit. Mus. Bot. 4: 1-78.

188. Stebbins, G.L. Jr. (1965). The probable growth habit of the earliest flowering plants. Ann. Missouri Bot. Gard. 52: 457-468.

189. _____ (1974). Flowering Plants. Evolution above the species level. Harvard Univ. Press, Cambridge.

190. Stebbins, G.L. Jr. & Major, J. (1965). Endemism and speciation in the California flora. Ecol. Monogr. 35: 1-35.

191. Strasburger, E. (1884). Die endospermbildung bei Daphne. Ber. Deutsch. Bot. Ges. 2: 112-114.

192. _____ (1885). Zu Santalum und Daphne. Op. cit., 3: 105-113.

193. _____ (1909). Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und reductionsteilung. Hist. Beitr., 7. Jena.

194. Subramanyam, K. & Kamble, N.P. (1967). In: IOPB chromosome number reports XII. Taxon 16: 341-350.

195. Supprian, K. (1894). Beiträge zur Kenntnis der Thymelaeaceae.

Bot. Jahrb. Syst. 18: 306-353.

196. Takhtajan, A.L. (1966). Sistema i Filogeniia Tsvetovikh Rastenii. Izdatelstvo Nauk, Moscow. Leningrad. (In Russian).

197. _____ (1969). Flowering Plants — Origin and Dispersal. Oliver & Boyd, Edinburgh.

198. Thoday, D. (1921). On the behaviour during drought of leaves of two Cape species of Passerina , with some notes on their anatomy. Ann. Bot. 35:585-601.

199. _____ (1924). A Revision of Passerina. Kew Bull. 146-168.

200. Tomlinson, P.B. (1969). Anatomy of the Monocotyledons. III. Commelinales & Zingiberales. Clarendon Press, Oxford.

201. Troll, W. (1964). Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskorpers, Pt. 1. Fischer Verlag, Stuttgart.

202. Tseng, K.F. & Chao, C.-Y. (1963). Flavonoids in Chinese drugs. IX. A new flavone glycoside isolated from Wikstroemia viridiflora. Yao Hsueh Hsueh Pao 10(5): 286-292. (n.v.).

203. Tucker, S.C. (1977). Foliar sclereids in the Magnoliaceae. Bot. J. Linn. Soc. 75: 325-356.

204. Van Cotthem, W.R.J. (1970). A classification of stomatal types. Bot. J. Linn. Soc. 63: 235-246.

205. Van Tieghem, Ph. (1893). Recherches sur la structure et les affinities des Thymeleacées et des Péneacées. Ann. Sci. Nat. Bot.Ser. 7: 198-227.

206. Venkateswarlu, J. (1945). Embryological studies in the Thymelaeaceae. 1. Thymelaea arvensis Lamk. J. Ind. Bot. Soc. 24: 45-46.

207. _____ (1947). Embryological studies in the Thymelaeaceae. 2. Daphne cannabina Wall. and Wikstroemia canescens Meissn. J. Ind. Bot. Soc. 26: 13-39.

208. Vermeulen, N.M.J. & Pieterse, M.J. (1968). J. S. African Chem. Inst. 21: 190. (n.v.).

209. Vesque, J. (1879). Nouvelles recherches sur le développement des Phanerogames Angiospermes. Ann. Sci. Nat. Bot. 6(8): 261-390.

210. Vickery, J.R. (1971). The fatty acid composition of the seed oils of Proteaceae: a chemotaxonomic study. Phytochemistry 10: 123-130.

211. Vogl, K. (1910). Anatomische Studien über Blatt und Asche der einheimischen Daphne-Arten mit. bes. Ber. Bastfasern. Staats-Gymnas, Oberhollabrunn.

212. Webb, D.A. & Ferguson, I.K. (1968). Thymelaeaceae. In: Flora Europaea Vol. 2: 258-260.

213. Weberling, F. (1965). Typology of inflorescences. J. Linn. Soc. Bot. 59: 215-221.

214. Weyland, H. (1934). Beiträge zur Kenntnis der rheinischen Tertiärflora. I. Floren aus den Kieseloolith- und Braunkohlen - schichten der wiederrheinischen. Bucht. Abhandl. Preuss. Geol. Landesanstatt, N.F. 161: 1-122. (n.v.).

215. Willkomm, H.M. & Lange, J.M. (1862). Prodromus Florae Hispanicae, Vol. 1. Stuttgart.

216. Winkler, H. (1904). Die parthenogenesis bei Wikstroemia indica (L.) C.A. Meyer. Ber. Deutsch. Bot. Ges. 22: 573-580.

217. _____ (1906). Botanische untersuchungen aus Buitenzorg. II. Über parthenogenesis bei Wikstroemia indica. Ann. Jard. Bot. Buitenzorg 2(5): 208-276.

218. Wunderlich, R. (1967). Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 301-311.