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STUDIES IN THE THYMELAEACEAE I:
Germination, seedlings, fruits & seeds

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ABSTRACT. Germination and seedling structure of *Daphne longilobata* (Lecomte) Turrill, *Diarthron vesiculosum* (Fisch. & C. A. Mey. ex Kar. & Kir.) C. A. Meyer and *Thymelaea passerina* (L.) Cosson & Germ. is described. Data on fruit and seed structure of various genera in Thymelaeaceae are given. The exotegmen consists of thick-walled, lignified cells and forms the main protective layer in the mature seed. The testa itself is non-indurated. Exotestal stomata are recorded for the first time in the family. On grounds of seed anatomy there are no similarities with the Elaeagnaceae or the Proteaceae, suggested by some workers as related families. The Thymelaeaceae appears to be a very natural grouping with no close relatives, although the exotegmic palisade perhaps allies it with the Malvales and some members of that large heterogeneous assemblage, the Euphorbiaceae. A chromosome count of 2n = 18 is recorded for *Daphne longilobata*.

CONTENTS

This paper is the first in a series reporting an investigation designed to elucidate the relationships of the Thymelaeaceae, often regarded as a natural family with no very close affinities. The study has centred on eight genera, *Daphne, Dendrostellera, Diarthron, Restella, Stellera, Stelleropsis, Thymelaea* and *Wikstroemia,* all of Thymelaeaceae subfamily Thymelaeoideae, and occurring in the Mediterranean, SW and C Asiatic regions.

The present communication is devoted to germination, seedlings, fruit and seed structure.

GERMINATION AND SEEDLING MORPHOLOGY

There has been little previous work on germination and the morphology of seedlings in the Thymelaeaceae, even though many species of *Daphne* are widely cultivated in gardens. In part this paucity of information is connected with the fact that seeds of *Daphne* are generally regarded as capricious and may take more than three years to germinate (Bissett, 1975, pers. comm.). During my investigations studies were made of germination in seven species, three of which are described separately below.

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 during April in sandy clay under greenhouse conditions. The seeds of the second batch (from an undated collection, probably two to three months old) were removed from the enclosing perianth by gentle hand-rubbing, sown in groups of five to ten on water-soaked blotting paper in covered Petri dishes and kept in a laboratory. Germination of both batches was observed over a six-week period, and stages recorded by drawings.

The radicle is the first organ to emerge during germination. Following its emergence, the tips of the seedcoat curl away from each other, exposing the cotyledons. Germination is epigeal and the cotyledons carry at their apices (Fig. 1A) the seedcoat which is ultimately dropped. The cotyledons are unequal in size, and tightly adpressed for the first few days but unfold by forcing open the seedcoat in the second week. Root-hairs form rapidly on the emerging radicle. Elongation of the root 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 (Fig. 1A–F): the two cotyledons are unequal initially but both reach the same size within a week. They are 2·5–3 × 1·5–2 mm, pale green on the lower surface and darker green above. They are slightly glaucous, oblong, obtusely rounded or shallowly retuse at the apex, sessile, fleshy with indistinct midrib and indiscernible venation and are 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 exstipulate, opposite or subopposite, 2–3 mm long, simple, entire, lanceolate-oblong, obtusely rounded at the apex, very shortly petiolate and glabrous throughout. They are produced by the fourth week and are long-persistent; venation is eucamptodromous and ptyxis conduplicate. The root is straight, penetrating 15–30 mm into the soil before branching; the system reaches 30 cm in depth within 10 weeks.

Diarthron vesiculosum: nine-year old seed (W Pakistan, *Lamond* 1880) was sown under the same conditions as the previous. 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 for the first three days. The hypocotyl is pale green and glabrous, growing to 12 mm in length. Seedlings failed to become established and became constricted 1 mm below the cotyledons, dying at the end of the second week.

Daphne: seeds of *D. alpina, D. caucasica, D. giraldii, D. gnidium* and *D. longilobata* were received from botanic gardens. They germinated readily after being kept in cold moist sand (0°C) for a month, while seed of certain other species, e.g. *D. cneorum,* did not show any signs of germination after six months. The following description is of *D. longilobata* which serves as an example representative of all five species.

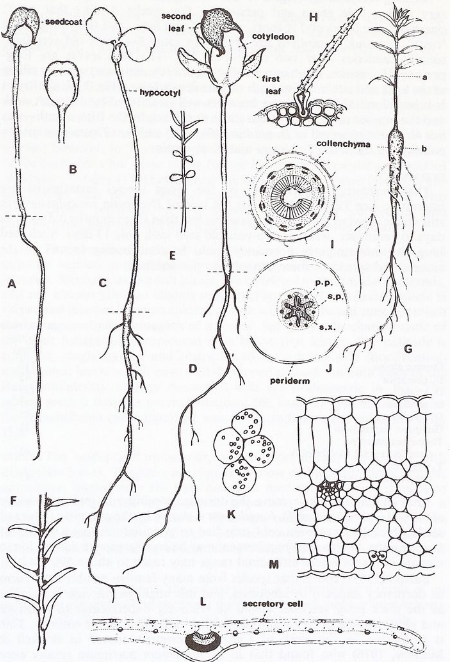

FIG. 1. A–F, *Thymelaea passerina*: A, at 2 days (× 5); B, cotyledons of 5-day old seedling (× 5); C, at 1 week (× 5); D, at 4 weeks (× 5); E, at 9 weeks, cotyledons still persistent (× ½); F, at 14 weeks, plant grown to flowering stage (× ½); G–M, *Daphne gnidium*: G, at 16 weeks with thickened primary root (× 4); H, stem epidermal hair; I, stem T.S. in region 'a'; J, root T.S. in region 'b', p.p. = primary phloem, s.p. = secondary phloem, s.x. = secondary xylem; K, parenchyma cells from root cortex; L, 4th leaf T.S.; M, leaf section enlarged. H–M, diagrammatic, not drawn to scale.

Seedling morphology (Fig. 2 H–L): the cotyledons are large, 8 × 5 mm, very fleshy, pale green and persist 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. 2K). The first leaves are long-persistent, opposite, often unequal in size, shortly petiolate, sparsely ciliate at the apex and either one or both may be deeply lobed (Fig. 2J & K). Ptyxis is supervolute. The root system becomes well established by the tenth week and the taproot of *D. longilobata* starts to thicken by the fifth month—this has also been observed in *D. gnidium* (Fig. 1G) and two *Thymelaea* species collected in the wild, *T. hirsuta* and *T. tinctoria*.

DORMANCY

The dormancy characteristics of the seven species investigated are interesting (see Table 1). Nine-year old seed of *Diarthron vesiculosum* was still viable. Seed of *Thymelaea passerina* less than three months old took 42 days to germinate, whereas two-year old seed took only 13 days. Such seed longevity and range in dormancy could be contributing factors to the success and spread of these annuals in open habitats.

TABLE 1

	% germination	germination period (days)
Daphne alpina	30	112
D. caucasica	30	43
D. giraldii	30	159
D. gnidium	60	12
D. longilobata	30	15
Diarthron vesiculosum	10	21
Thymelaea passerina (seed less than 3 months old)	60	42
T. passerina (seed nearly 2 years old)	50	13

That chilling tends to remove the dormant condition in seeds of *Daphne alpina, D. caucasica* and *D. longilobata* is shown by the complete failure of seeds which had not been cold-stratified to germinate during a period of four months. Such a cold-requirement may be correlated with adaptation to climate in plants whose altitudinal range may reach to above 3000 m.

Barton (1965) reports that species from many families exhibit some form of dormancy imposed by seedcoats, and this might be the case in *Daphne* as the thick inner seedcoat would be relatively impermeable to moisture and gases as well as physically preventing expansion of the embryo. This is supported by the work of Carter (experiment quoted in Brickell & Mathew, 1976) who found that in *D. mezereum* maximum results were obtained when the testa was removed; also that seeds from unripe fruits germinated better than those from ripened ones—the latter suggests that the presence of substances in the testa or sclerification of the tegmen during ripening play some inhibitory role. However, partial scarification of seedcoats carried out during this investigation did not appear to have any appreciable effect on germination.

SEEDLING ANATOMY

Only seven species representing three genera were available for study—insufficient for comparative purposes. One species, *Daphne gnidium* (Fig. 1 G–M), will serve as an example and be briefly described.

COTYLEDONS. The venation is actinodromous, with 3–5 conspicuous strands in the lamina diverging radially from two vascular bundles at the level of the node. Bailey (1956) in his survey of 99 dicotyledonous families found that many cotyledons were characterized by this type of pseudo-palmate or palmate-parallel venation. Stomata are absent in the cotyledons of this species; however, in *Thymelaea passerina* anomocytic stomata are present in the cotyledons but those in the foliage leaves are anisocytic or modified tetracytic. Thoday (1921) examined the cotyledons of *Passerina filiformis* and found that unlike foliage leaves which are ingrooved and with chlorenchyma restricted to the abaxial surface, the cotyledons had chlorenchyma and stomata restricted to the *convex adaxial* surface.

LEAF. The venation in the first foliage leaf is eucamptodromous. All ultimate veinlets are composed of tracheary cells not associated with sclereids. Stomata, as in adult leaves, are restricted to the abaxial epidermis, and are anomocytic and slightly sunken (Fig. 1M). The adaxial cuticle is ridged and inserted between epidermal cells while the abaxial cuticle is much thicker especially in the region of a stoma. Secretory cells characteristic of the adult foliage are conspicuous even in the first leaves. The palisade is compact, single-layered and restricted to the adaxial side (dorsiventral) unlike adult leaves which have well developed palisade on both sides of the leaf (isobilateral). Spongy mesophyll cells are isodiametric in T.S. The midrib ground tissue is parenchymatous; the vascular system simple with the sclerenchyma cap unlignified and not extending to the epidermis (Fig. 1L).

STEM. The nodes are unilacunar, a condition usually associated with exstipulate leaves. The hairs are similar to those of the adult plant: simple, unicellular, angled near the base and with moderately thick, verruculose outer walls (Fig. 1H). Collenchyma is present, often in the form of a complete ring (Fig. 1I). 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 due to prolonged meristematic activity (Fig. 1G, J). Starch is present in the large, thin-walled, cortical cells.

FRUIT AND SEED MORPHOLOGY

Fruit is here used to denote the product of post-fertilization development of the gynoecium. I have not broadened the term to include extracarpellary parts, e.g. the perianth, that may be associated at maturity, as is the case in *Dendrostellera, Diarthron, Restella, Stellera, Stelleropsis* and *Thymelaea.*

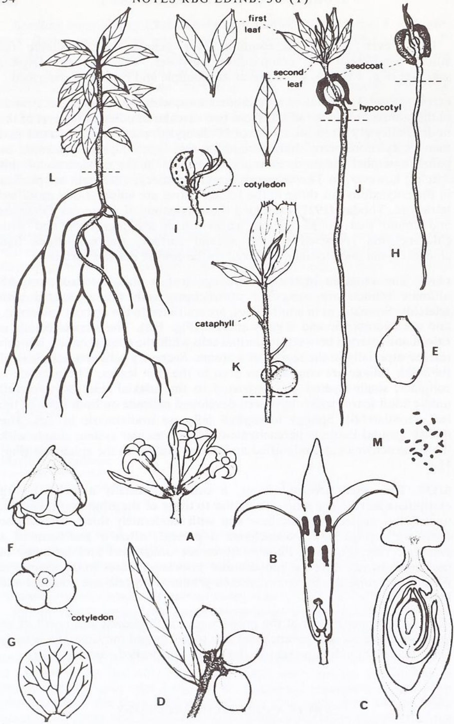

FIG. 2. *Daphne longilobata*: A, inflorescence (× 1); B, half-flower (× 3); C, gynoecium in L.S. (× 12); D, fruits (× 1); E, seed (× 3·5); F, lateral and apical views of tricotyledonous embryo (× 7); G, single cotyledon, cleared to show venation (× 20); H and I, 2-week old seedlings, I with seedcoat removed and first leaves unfolding (× 1); J, 3½-week old seedling with first leaves equal in size and deeply lobed, cataphylls absent (× 1); K, another 3½-week old seedling with first leaves unequal, entire or slightly lobed at apex, cataphylls present (× 1); L, well established 14-week old plant, first leaves still persistent (× 0·6); M, somatic metaphase, 2n = 18 (× 2450).

Daphne: The fruits are indehiscent, one-seeded berries (Fig. 2D), ovoid, globose or subglobose, green, ripening orange-red to scarlet (*D. mezereum*) or black (*D. laureola*). In some (*D. alpina, D. arbuscula*) 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, which it is commonly called 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.

The seed is ovoid, ellipsoid or pyriform (Fig. 2E), covered by a moderately thick, pale, semitransparent, soft and almost smooth testa (outer seedcoat). The outer epidermis of the inner seedcoat is thick, lignified and a shiny blackish-brown. Although hard and crustaceous, it is brittle when dry. The inner epidermis of the inner seedcoat is white or pale brown and membranous. Perisperm and endosperm are present, either copious or as a thin film round the embryo. Gilg (1894), Rendle (1925) and Domke (1934) all consider endosperm is generally absent or scanty, but the 'Nährgewebe' of Gilg refers to endosperm plus perisperm. The cotyledons are thick, fleshy and plano-convex, turning dark green in the light; the radicle and plumule are minute.

To avoid unduly long descriptions, the characters of the other genera are written in abbreviated form.

Dendrostellera. Fruit dry, indehiscent, one-seeded, enclosed by sericeous-villous, persistent lower half of perianth. Whole structure forms dispersal unit. Pericarp pubescent, villous-barbate at apex. Seed pyriform, greenish ripening to reddish-brown or black.

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

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

Stellera. Fruit dry, indehiscent, one-seeded, enclosed in persistent lower half of perianth. Seed pyriform, brown, 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 pyriform. Pericarp thin, membranous or chartaceous, glabrous or pubescent, green ripening dark brown. Seed ovoid or pyriform, pendulously and laterally attached near apex of locule. Testa pellicular (skin-like), thin, semitransparent as in *Daphne*. Outer epidermis of tegmen thick, hard, black, shallowly and regularly sculptured. 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 an ovoid to globose, indehiscent, one-seeded berry completely exposed at maturity (perianth deciduous) or, in the species investigated (*W. chamaedaphne, W. salicifolia*), dry, indehiscent, ± exposed at maturity. Pericarp membranous, brownish-black. Seed pyriform. Testa pellicular, thin and soft; outer epidermis of tegmen hard, crustaceous, shiny black. Perisperm and endosperm present.

FRUIT AND SEED ANATOMY

Studies on the anatomy and development of the ovule and seed in members of the Thymelaeaceae this century include contributions from Guérin (1916), Netolitzky (1926), Fuchs (1938), Kausik (1940) and Venkateswarlu (1945, 1947). The more recent account by Corner (1976) is a noteworthy summary of existing knowledge of seed structure of this family, and also provides further information based on an additional three species belonging to separate genera. My own investigations have particular reference to *Daphne* and *Thymelaea*.

The fruit and seed structure of *Daphne longilobata,* not previously examined anatomically, will now be described (Fig. 2 & 3). This serves as an example for the fleshy fruits of this genus.

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. 3A). Pericarp glabrous except at apex; fruit stalk short, covered with hairs similar to those on perianth. Vascular bundles 9–12 at base of fruit (Fig. 3B), dividing into 25–30 strands which supply wall (Fig. 3Ba, Bb). Wall consisting of pericarp alone (perianth deciduous), composed of 14–20 parenchymatous layers measuring 1–1·5 mm in thickness at maturity (Fig. 3C). Sclereids completely absent. Outer and inner epidermides cuticularized. Fruit and stalk abscissing together with enclosed seed; 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 most of their length during development and remain distinct even at maturity. In most seeds where there are two integuments, the outer is often more strongly developed than the inner, but this is not the case in the Thymelaeaceae. Here 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. 2C).

The *testa* (= outer integument), which forms a thin, easily removed covering at maturity, is composed of 5–6 parenchymatous cell layers with the innermost (= *endotesta,* Corner, 1976) containing tannin-coloured matter (Fig. 3E). Corner (1976) refers to such a testa as pellicular. 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 (Fig. 3Ea). 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 cell layers, 10–15 being the most common. The outer epidermis (= *exotegmen,* Corner, 1976)

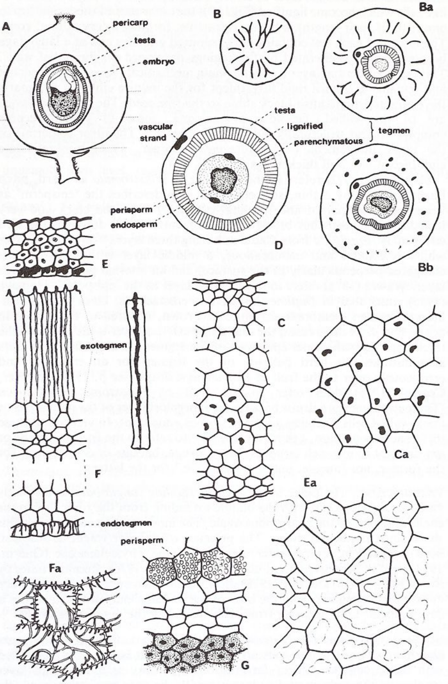

FIG. 3. *Daphne longilobata*: A, young fruit L.S. (× 5·5); B–Bb, T.S. at regions indicated in A, vascular tissue black (× 5·5); C, pericarp T.S. (× 160); Ca, outer epidermis of pericarp (× 325); D, seed T.S. (diagrammatic); E, testa T.S. (× 120); Ea, exotesta (× 350); F, tegmen T.S. (× 120); Fa, endotegmen (× 330); G, perisperm and endosperm T.S. (× 330). Ca, Ea and Fa in surface view.

differentiates as a single layer of closely packed, radially elongate, palisade-like cells which become lignified (Fig. 3F); the outer part of these cells (up to one-fifth of their length) is highly refractive, forming a 'crystalline' zone. The lumen of each cell contains dark coloured granules and at a later stage becomes nearly obliterated by thickenings developed on the radial walls. This outer epidermal layer forms the main mechanical tissue of the seedcoat and remains as a hard rigid investment for the mature embryo. It imparts the characteristic reddish-black shine to the ripe seed. The inner cell layers are of thin-walled, lacunose parenchyma, some of which become compressed and structurally indistinct at maturity. The inner epidermis of the inner integument (= *endotegmen,* Corner, 1976) has reticulate endothecial-like wall thickenings (Fig. 3F, Fa).

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 [peeling] off easily from the black and very lustrous crustaceous but brittle cover'. Lecomte (1914) describes the seed cover of *W. longifolia* from China as having three layers—an external layer which is cellular and membranous, a middle layer with lignified cells elongated perpendicularly to the surface, and an internal parenchymatous layer. Wawra (1875) refers to this external layer as the 'episperm'. Hamaya (1955) states that in *Daphne* the 'testa is crustaceous, black or blackish-brown, tegmen membranous, white or brown, adhered to the testa'. In actual fact in all these cases, the thin pulpy external layer is the testa and the thick hard layer the outer epidermis of the tegmen. A majority of workers also mistake this hard palisade of the tegmen for an endocarp and erroneously refer to the fruit of *Daphne* as a drupe (see p. 155). However, Corner (1976) does refer to the fruit of *Linostoma pauciflorum* (Thymelaeaceae) 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 preferable to refer to the fruits as *fleshy* or *dry* and not to use such terms as 'berry, drupe, baccate or drupaceous' for the former, nor 'nucule, nutlet, achene, etc.' for the latter.

VASCULATURE. The outer integument in *Daphne longilobata* is distinctly vascularized (Fig. 3D) with the bundle extending from the funiculus to the chalazal region of the anatropous ovule. The inner integument and nucellus share some tracheidal tissue. The presence of nucellar tracheids has also been reported in several other members of the Thymelaeaceae (Guérin, 1913, cited in Schnarf, 1931; Fuchs, 1938; Corner, 1976). Recent studies by Bor & Kapil (1976) and Bor (1978) show that in anatropous ovules the inner integument originates from the base of the nucellus and with it embodies a development 'unit' separate from that producing the outer integument.

NUCELLUS. The nucellus is massive in pre-fertilization stages and appears glandular as most of the cells are thin-walled with large nuclei and filled with dense contents. After fertilization it persists as a very thin layer enveloping the embryo and endosperm with the apex projecting conically into the micropyle. The nucellar cuticle adpressed closely to the inner integument has reticulate markings similar to those found on the endotegmen. Cronquist (1968) states that perisperm is clearly an advanced feature with nutritive matter absorbed from it by the endosperm and passed on to the embryo during germination. It is often associated with embryos classified as 'peripheral' by Martin (1946).

ENDOSPERM. The embryo does not occupy the entire volume of the seed and endosperm is found at the apices of the cotyledons (Fig. 3A). As understood from the work of Hamaya (1955, 1963), endosperm is very poor or lacking in the genus *Daphne*. The majority of workers refer to it as 'wanting or scanty'. The tissue in *D. longilobata* is composed of large thin-walled cells with oil globules (Fig. 3G) and is utilized during germination. There is little or no starch. Earle & Jones (1962) included seeds of *D. mezereum* among their samples analysed for biochemical data. The protein content of the seed was found to be 24·4% and that of the pericarp 7·5%. Seed lipid was of an unusually high level, reaching 65·4% but that of the pericarp was only 6·0%.

EMBRYO. Following the twelve categories of Martin (1946), the seeds of *D. longilobata* (and of the other seven genera studied) can be described as having the embryo large, axile, erect, and spathulate with expanded cotyledons. Venation of the cotyledons is nearly actinodromous with 3–5 vascular strands in the lamina (Fig. 2G) and stomata are absent. Although a normal embryo of *Daphne* has two cotyledons, tricotyly is occasionally met with in cultivated plants, e.g. in *D. giraldii* and *D. longilobata*—in these cases all three cotyledons are well developed and equal in size (Fig. 2F). Species of *Wikstroemia* with dry fruits have embryos with rather thin cotyledons as compared with the fleshy cotyledons of *Daphne*.

GENERA WITH DRY INDEHISCENT FRUITS

With the exception of *Daphne*, the genera in the Mediterranean, SW and C Asiatic regions have dry fruits. Their structure is similar to that described for *Daphne*, but the pericarp is thin, composed of fewer cell layers, and becomes membranous on ripening. In *Dendrostellera, Stellera* and *Thymelaea* it is supplied with only 4–6 main vascular bundles. Within the genus *Thymelaea,* four species, viz. *T. hirsuta, T. lythroides, T. lanuginosa* and *T. microphylla,* have photosynthetic pericarps, with stomata being present on the outer epidermides (Fig. 4B). The anticlinal walls of the inner epidermis in *T. lythroides* are sinuous in surface view (Fig. 4Ba); they are straight in the other species.

The testa in *Thymelaea* is 4–5 cells thick. It is not lignified and the parenchymatous layers become disorganized as they dry up on the hard tegmen at maturity. Stomata occur on the outer epidermis of the testa in the four species previously mentioned (Fig. 4C, 4I)—such exotestal stomata have never been previously recorded for the genus, nor indeed for the family. Corner (1976) lists 19 families (and the genera) in which such stomata occur. All of them are in the 'lower orders' of dicotyledons with endotestal or exotegmic seeds. They include the Bixaceae, Flacourtiaceae, Violaceae, Euphorbiaceae, Bombacaceae, Malvaceae and Sterculiaceae—all families which have, at one time or another, been allied to the Thymelaeaceae; so far, the Elaeagnaceae and the Proteaceae have not been surveyed for stomatal distribution in seedcoats. According to Corner (1976), the presence of stomata might indicate a primitive or unspecialized state of the outer epidermis of the testa. Stomata do not occur on the

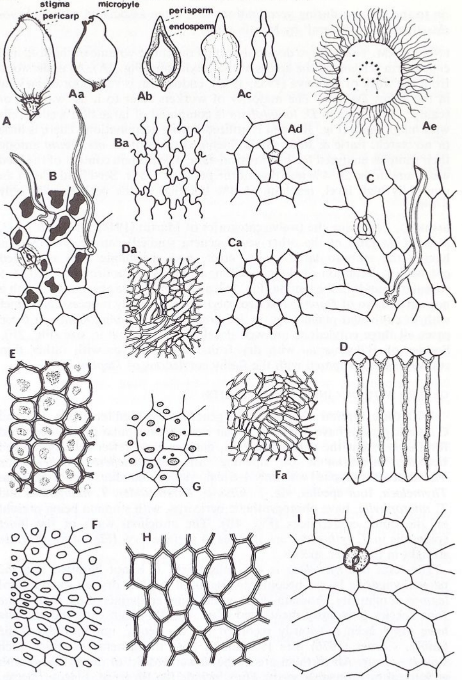

FIG. 4. A–Da, *Thymelaea lythroides*: A, fruit (× 6); Aa, seed (× 6); Ab, seed with both coats removed (× 6); Ac, embryo in two different views (× 9); Ad, adaxial epidermis of cotyledon (× 230); Ae, fruit stalk T.S. (× 22); B, outer epidermis of pericarp (× 230); Ba, inner epidermis of pericarp (× 230); C, exotesta (× 300); Ca, endotesta (× 230); D, exotegmen T.S. (× 300); Da, endotegmen (× 330); E–G, *T. hirsuta*: E, outer epidermis of pericarp (× 165); F, exotegmen (× 300); Fa, endotegmen (× 330); G, endosperm, squash preparation (× 330); H, *T. thesioides* subsp. *thesioides*: outer epidermis of pericarp (× 230); I, *T. microphylla*: exotesta (× 330). Ad–I, as seen in surface view unless otherwise indicated.

endotesta, the tegmen or the nucellus. The endotegmen has reticulate thickenings (Fig. 4Da, Fa), which together with the palisade-like exotegmen seem to be characteristic of the family.

Nucellar tracheids have not been observed in *Thymelaea*. The perisperm of all the dry-fruited genera consists of only a few cell layers in the mature seed. Endosperm is only obvious in young ovules. It becomes nearly absorbed when the seed matures and exists only as a very thin film round the embryo (Fig. 4Ab) 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 are often photosynthetic and persistent for a long time during the seedling stage. Anomocytic stomata are present on the upper epidermides in most species of *Thymelaea* (Fig. 4Ad).

CONCLUSIONS

The relative similarity in seed structure in *Daphne* and *Thymelaea,* the genera most intensively studied, gives some indication of close relationships. The exotegmen, which is the most characteristic feature of the family, and therefore, of some taxonomic value, is always palisade-like, thick-walled and lignified. It provides the protective function of the endotesta of seeds of most other families, and may also be assumed to have a high degree of impermeability and thus produce the late germination of seeds in several species. The occurrence of reticulate thickenings on the walls of the endotegmen and cuticularization of the exotesta probably contribute to the impermeability of the seedcoat as well.

Other families with a similar palisade-like exotegmen are the Euphorbiaceae (subfamily Crotonoideae), Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae, Bixaceae, Passifloraceae, and Piperaceae. 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. Wunderlich (1967) and Corner (1976) rightly point out that resemblance of the Elaeagnaceae to the Thymelaeaceae is superficial, as its seed structure and development is typically Rhamnaceous, and that similarities of the Thymelaeaceae, Euphorbiaceae and Malvales are much greater. The Proteaceae has also been stated to have affinities with the Thymelaeaceae (Hutchinson, 1969), the Elaeagnaceae (Taktajan, 1966, 1969) or both (Cronquist, 1968), but the outer layers of the tegmen in Proteaceae are *fibriform* and thereby differ from the exotegmen in the other two families. Seed characters (based mainly on data from Corner, 1976, together with some original observations) in five putatively allied families, three of which have seeds with exotegmic construction, are given in Table 2. The morphological similarities with the Thymelaeaceae may indicate true affinities or be considered as parallel developments.

The type of embryo in the Thymelaeaceae is characteristic of so many unrelated families that, although seed structure is very conservative, it is likely it has arisen several times independently. However, such embryos do not occur in families considered to be primitive. Families listed by Martin (1946) as having a similar embryo type to the Thymelaeaceae include the Euphorbiaceae: the Elaeagnaceae on the other hand have the embryo partly

TABLE 2

COMPARISON OF SEED CHARACTERS

		Thymelaeaceae	Elaeagnaceae	Proteaceae	Euphorbiaceae (Crotonoideae)	Malvaceae	Myrtaceae
Ovule							
1.	l/locule	+	+	+	+	+	+
	>l/locule			+		+	+
2.	anatropous	+	+	+	+	+	+
	hemianatropous			+		+	+
	orthotropous			+			
3.	bitegmic	+	+	+	+	+	+
	unitegmic						+
4.	crassinucellate	+	+	+	+	+	+
Seedcoat							
5.	micropyle formed by inner integument	+	?	+			
	by outer integument				+	+	+
	by both integuments				+	+	
6.	tegmen much thicker than testa	+		+	+	+	
	much thinner than testa		+				+
7.	exotesta the main mechanical layer		+				+
	unspecialized	+	+	+	+		
8.	exotegmen the main mechanical layer	+		+	+	+	
	unspecialized			+			+
9.	endotegmen with reticulate thickenings	+					
10.	vascular strand in raphe		+				+
	in raphe and tegmen			+	+	+	
	in raphe, tegmen and nucellus	+					
11.	aril present	+			+	+	
	absent	+	+	+	+	+	+
Nucellus							
12.	persistent or crushed in mature seed	+		+	+	+	+
	not persistent		+		+	+	
13.	hypostase present	+	+		+	+	+
	absent			+	+		
Endosperm							
14.	present or reduced	+			+	+	+
	± absent at maturity	+	+	+			+
	oily	+			+	+	
Obturator							
15.	present	+	?		+		?
Embryo							
16.	straight	+	+	+	+		+
	curved				+	+	+
Germination							
17.	epigeal	+	+	+	+	+	+
	hypogeal			+	+		+

investing, while the Malvaceae have curved embryos with folded cotyledons.

It is concluded that the Thymelaeaceae has no close relatives and that it possibly diverged early from the Rosalean line. There is every justification for placing the family in a separate order, Thymelaeales, as proposed by Taktajan (1969, 1973) and Dahlgren (1977), instead of including it in an order containing other families to which its affinities are very doubtful.

Although Thorne's classifications and his re-evaluations (1968, 1976, 1977) have been considered rather aggressively phylogenetic, it is worth noting that in an early outline synopsis (1973), he had already removed the Thymelaeaceae from the widely accepted Myrtales to the Euphorbiales. It remains for further characters to be investigated to see if this treatment can be supported or if a more natural grouping will eventually emerge.

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