Floral Development of Three *Maesa* Species, with Special Emphasis on the Position of the Genus within Primulales

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Floral development of three *Maesa* Forssk. species, *M. argentea* Wall., *M. japonica* (Thunb.) Moritzi ex Zoll. and *M. perlarius* (Lour.) Merr., was studied with a scanning electron microscope. The distinctive floral features of the genus, such as presence of two persistent bracteoles, perigynous flowers and many-seeded fruits, have been used to discuss the systematic position of the genus within Primulales. In addition, the development of common stamen-petal primordia, the number, arrangement and position of ovules and the shape of the anthers provide evidence in favour of placing *Maesa* in a separate family, Maesaceae, as suggested by Anderberg and Ståhl (Canadian Journal of Botany, 73: 1699–1730, 1995).

**Key words:** Primulales, *Maesa argentea* Wall., *Maesa japonica* (Thunb.) Moritzi ex Zoll., *Maesa perlarius* (Lour.) Merr., floral ontogeny, SEM.

**INTRODUCTION**

The Myrsinaceae R. Br. are a poorly known tropical family consisting mainly of woody species. Within the family 33 genera are recognized with about 1225 species (Mabberley, 1997). Myrsinaceae are present in tropical and subtropical regions with only a few representatives in more temperate areas. The family can be identified by the presence of a well-developed schizogenous secretory system, that consists of ducts filled with a red-brownish resinous substance. Scattered secretory cells are also common. The leaf has glandular dots or possesses secretory lines, and is often covered with glandular hairs which are multicellular and peltate or capitate. Stamens are situated opposite the petals and are lacking, but rudimentary remnants sometimes remain on the receptacle. Generally, the fruit is a berry or a drupe, one-seeded with small, dark seeds (Cronquist, 1981).

In their phylogenetic study of a great number of taxa, based on nucleotide sequence data from the chloroplast-DNA gene *rbc*L, Chase et al. (1993) included three genera of Primulales, viz. *Clavija* Ruiz & Pav. from Theophrastaceae Link, *Ardisia* Sw. from Myrsinaceae and *Anagallis* L. from Primulaceae Vent. Their results indicated that Primulales are monophyletic. Theophrastaceae are considered to be the sister group of a Myrsinaceae–Primulaceae-complex. Together with possibly related orders such as Theales, Violales, Ebenales, Ericales and Diapensiales, Primulales are included in a larger clade, called the asterid III clade, which is part of the extensive subclass Asteridae. These results are confirmed by the Angiosperm Phylogeny Group (1998). Morton et al. (1996) evaluated the monophyly of Ebenales and also examined several orders within Cronquist's Dilleniidae (1981). They concluded that the three families of Primulales can be considered a monophyletic unit, with Theophrastaceae sister to the other two. The results of their analysis show that Primulaceae are polyphyletic and Myrsinaceae *sensu stricto* (*Maesa* Forssk. excluded) are paraphyletic.

*Maesa* is a genus of some 100 species from the Old World, with representatives mainly centred in the Paleotropics, *viz.* Malesia, New Guinea and western Asia. It includes shrubs to 3 m, small trees to 10–12 m and scandent shrubs to woody vines from rainforest canopies. The inflorescences are placed laterally, usually axillary and they are racemose or paniculate. The small, greyish-white flowers are bisexual or unisexual, 2 to 4 mm long and usually described as pentameros. The plants with unisexual flowers are dioecious, and the stamens of the female flowers are reduced in size (Sleumer, 1987).

*Maesa* can be distinguished from the other genera of Myrsinaceae by its many-seeded fruit, perigynous flowers with a semi-inferior ovary (instead of a superior ovary as in the other genera) and inflorescences in which each flower is subtended by a bract and two bracteoles instead of a single bract only (Mabberley, 1997). In Africa there are some species whose ovules develop into one instead of several whorls. Therefore, they are placed in a different subgenus, *Monotaxis* Mez (Mez, 1902). However, the species studied here do not belong to this subgenus. This is not a problem because the two subgenera are obviously closely related and are sister groups in all phylogenetic analyses (see e.g. Anderberg and Ståhl, 1995).

In the past, *Maesa* has always been placed in the Myrsinaceae, stressing, however, differences with other
members of the family (e.g. Cronquist, 1981; Thorne, 1992; Takhtajan, 1997). Myrsinaceae are therefore often divided into two subfamilies: Maesoideae (A. DC.) A. DC., consisting only of the genus *Maesa*, and Myrsinoideae Burnett, including all other members of the family (Cronquist, 1981). De Candolle (1844) placed the genus in a separate tribe Maesae A. DC., and Pax (1889) established the subfamily Maesoideae Pax. Mez (1902) agreed with Pax, but noticed a strong relationship with *Samolus* L.; for this reason *Samolus* could better be excluded from Primulaceae and positioned in a separate group together with *Maesa*. However, our unpublished analyses (Caris, 1998) do not support this.

In a recent paper, Anderberg and Ståhl (1995) suggested that the genus *Maesa* could be removed from Myrsinaceae and put in a newly defined family Maesaceae, more closely related to Primulaceae than to the remaining families of the order.

Sattler (1962) is the only author to have studied the floral ontogeny of some representatives of Myrsinaceae. The aim of the present work is to study the floral ontogeny of three *Maesa* species in order to gain a better understanding of the systematic and phylogenetic position of the genus within Primulales.

**MATERIALS AND METHODS**

We studied flower buds and young flowers of three *Maesa* species, namely *Maesa argentea* Wall. (collection no. 19612068--; voucher no. S2526), *Maesa japonica* (Thunb.) Moritzi ex Zoll. (collection no. *19941174-11; voucher no. PCV01) and *Maesa perlaria* (Lour.) Merr. (collection no. 19574525; voucher no. S3340) (Myrsinaceae). Flower buds were obtained from greenhouses of the National Botanic Garden of Belgium at Meise.

The material was dissected in ethanol (70 %) under a stereomicroscope equipped with a cold light source (Wild M3 + Schott KL 1500; Leica MZ6 + Leica CLS 150 D). The buds were washed twice with ethanol (70 %) for 5 min before placing them in a mixture (1:1) of ethanol 70 % and DMM (dimethoxymethane) for 5 min. Finally the material was placed in pure DMM for 20 min before it was critical point dried (CPD030 Balzers) using liquid CO₂. Infiltrates with flower buds were then put on stubs and sputter coated with gold before being observed with a scanning electron microscope (Jeol JSM-5800 LV).

**RESULTS**

Floral ontogeny of *Maesa argentea*

The flower buds originate in spiral order on the conical inflorescence axis (Fig. 1A). Each bud develops in the axil of a bract (Fig. 1A) and is enclosed by two persistent bracteoles (Fig. 1B), which are often larger than the bract at maturity. In the pentamereous flowers, the basally inserted sepals arise in a 2/5 spiral (Fig. 1C): the first sepal emerges on the abaxial side of the bud, in the axil of the bract, but generally somewhat left or right of it. The second sepal arises opposite the bract, on the adaxial side of the bud. The third sepal originates on the left or the right of the first, again abaxially and in the axil of the bract. The fourth and fifth sepals develop, respectively, between the first and the second, and the third and the second, in both cases against the bracteoles. In tetramerous flowers the four sepals are initiated two by two opposite each other; in the hexamereous flowers a sixth sepal arises between the first and the third (Fig. 1D). The following description refers to pentamereous flowers.

While the sepals grow and fuse basally to form the synsepalous calyx, which has a quincuncial aestivation, five protuberances become visible on the remaining part of the receptacle (Fig. 1D). They soon develop into five common primordia, from which the petals as well as the stamens will be formed (Fig. 1E–G). As a result the stamens are placed in antipetalous position, and at maturity they are connate with the corolla tube becoming epipetalous (Fig. 2J). The common primordia alternate with the sepals (Fig. 1E–G) and arise more or less simultaneously, or in an indistinct 2/5 spiral. Adaxially of each of the common primordia, a stamen primordium is detached, while the upper third of the common primordium continues growth as the petal primordium (Fig. 1E). The larger petal primordia grow somewhat faster (Fig. 1H), hiding the rest of the floral parts from view (Fig. 1H, I). Towards the base the petal lobes merge into the corolla tube, which is formed by the common growth of the zone below the petal insertions. Within the petals, which show a variable imbricate aestivation, the anthers take shape (Fig. 2A): the introrse, didthed anthers consist of two pairs of pollen sacs; each pair becomes confluent at dehiscence (Fig. 2B) as they open with longitudinal slits.

While the anthers are formed, the inception of the gynoecium starts centrally on the flat floral apex (Fig. 2A, C). The gynoecium develops from a ring primordium. Three or four primordial lobes are initiated on the ring primordium and become fused at a later stage to form the style (Fig. 2A, C). By intercalary growth of the ring primordium, the gynoecium becomes a saccate structure (Fig. 2D) topped with the style and stigma. Within the gynoecium, a free-central placenta (Fig. 2E) is formed out of the apical residue: it has a spherical shape to begin with, but quickly becomes conical-shaped with a large, sterile tip that disappears in a cut-away in the style. On the placenta ovule primordia develop basipetally (Fig. 2F). By the time the mushroom-shaped placenta has developed fully, the ovules are separated by outgrowths of placental tissue (Fig. 2I). Ovules are bitegmic; both integuments become visible simultaneously. The inner integument is positioned more to the top of the ovule and will cover the nucellus, followed by the outer integument which will fully enclose the ovule (Fig. 2G, H). The ovules have a more or less anatropous shape and many of them will develop into seeds in the mature fruit. While the semi-inferior ovary (Fig. 2J) develops, all the floral parts wither and drop off except for the persistent calyx which covers the mature fruit (Fig. 2K). The semi-inferiority is caused by the common zonal growth of the peripheral parts of the floral apex which enclose the developing placenta and lift the other floral parts.

We observed two types of trichomes, both of which are present on the pedicel, but not on the other floral parts:
multicellular peltate scales and simple, long trichomes (Fig. 2L).

On top of the gynoecium we observed a nectary with nectarostomata (SEM and light microscopic observations; Caris, 1998), as can also be found in some Ebenales (Vogel, 1997).

**Floral ontogeny of Maesa japonica**

The racemose or paniculate inflorescence is placed laterally and axillary. Flower buds originate in a spiral order. As in *M. argentea* the 3 to 5 mm long flowers are commonly described as pentamerous, but tetramerous and hexamerous flowers also occur. In our material most of the flowers were tetramerous.

Each flower is subtended by a single bract and two persistent bracteoles. The sepals of a pentamerous flower arise following a 2/5-spiral (Fig. 3A, B), comparable with the inception in *M. argentea*, and show a quincuncial aestivation. In some cases it is difficult to distinguish visually between the sepals and the bracteoles. In a tetramerous flower the sepals arise as two pairs: first the median sepals are initiated, in the axil of the bract and opposite to them, and then the lateral sepals develop on both sides, against the bracteoles. Alternating with the sepals, common primordia become visible (Fig. 3A, B) before the sepals fuse at their base to form the synsepalous calyx. The common primordia often arise more or less simultaneously (Fig. 3C), but sometimes the inception follows a 2/5-spiral, which may be very clear (Fig. 3D) or rather faint with a tendency to a unidirectional development. The common primordia split into a larger petal primordium and a smaller stamen primordium that arises on the adaxial side of the common primordium (Fig. 3D). The top of the primordium develops as the petal primordium (Fig. 3D). By upward growth of the sepal and petal primordia the floral centre becomes sunken (Fig. 3B–D). As in *M. argentea*, the petals grow somewhat faster and cover the young bud entirely while they fuse basally to form the corolla tube (Fig. 3E). The upper parts of the petals are free and have a quincuncial aestivation. The stamens are inserted on a common basal part with the corolla. Thus below the insertion zone of the stamens there is a zone of common growth, which originates from the basal parts of the common primordia.

In the centre of the flower the gynoecium starts its development as a ring-shaped primordium (Fig. 3F) between the developing anthers (Fig. 3G, H).

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**Fig. 1. Maesa argentea.** A, Inflorescence with primordial flower buds; B, C, flower bud, enclosed by two bracteoles, showing early sepal inception; D, E, sepal growth; inception of the common primordia; F, division of the common primordia in a petal and a stamen primordium; G, division of the common primordia in a petal and a stamen primordium in a hexamerous flower; H, I, the petal will overtake the stamen primordium in size; note the size differences between the primordia. *, Top of the floral axis; +, adaxial side of the flower; a, androecium; b, bract; br, bracteole; cp, common primordium; g, gynoecium; o, ovule; p, petal; pl, placenta; s, sepal; st, style; t, sterile tip on top of the conical placenta.
primordium grows centripetally and closes at the centre. The developing anthers are introrse, dithecal and tetrasporangiate and open with longitudinal slits. The pollen grains are tricolporate and are united into tetrads at a young stage.

While the anthers develop, four unequal lobes become visible on top of the ovary and meet to form the solitary style (Fig. 3I) that ends in a lobed stigma (Fig. 3I, J). The lobes of the style possibly refer to the original number of carpels which are fused congenitally. Beneath the gynoecium a spherical placental primordium arises on the floral apex (Fig. 3K, L). While the free-central placenta develops its conical shape with a sterile tip (Fig. 3M–P), the gynoecium chamber is formed very quickly by rapid growth of the gynoecium flanks (compare Fig. 3J and 3Q, R; see below). By the growth of the flanks of the ovary, the other floral parts (sepals, common basal part of petals and stamens) are pushed up so that the ovary becomes semi-inferior (Fig. 3Q, R). On the stalked, mushroom-shaped placenta, numerous ovule primordia originate in a downwards spiral (Fig. 3M, N), but the top of the placenta remains bare (Fig. 3M). They develop into bitegmic, anatropous ovules (Fig. 3P, Q) that are occasionally separated by small sections of placental tissue (Fig. 3O, P), as in *M. argentea*. However, in *M. japonica*, the placenta forms many more primordia, which develop within the many-seeded fruit.
Besides simple, short hairs and peltate scales, which can all be found on the pedicel, bract, bracteoles and sepals, we also observed multicellular peltate scales on the gynoecium.

**Floral ontogeny of Maesa perlarius**

Flowers of this species develop from rather flat buds, which are enclosed by two persistent bracteoles (Fig. 4A). The sepals arise in a distinct 2/5-spiral (Fig. 4B, C), the first always develops abaxially in the axil of the bract. The second sepal develops adaxially facing the first; the third and the fourth sepals follow next to the first, and the fifth develops between the third and the second.

While the last sepals are forming, five protuberances become visible on the floral apex (Fig. 4C–F). They arise more or less simultaneously or in an indistinct 2/5-spiral and develop as five common primordia (Fig. 4F–H). As a result of the growth of the common primordia the centre of the floral apex becomes sunken (Fig. 4G, H). In a somewhat later stage the common primordia develop unequally into inwardly-growing stamen primordia and upwardly-growing, larger petal primordia (Fig. 4I, J). At first the petal and the stamen primordia grow at equal rates, but soon the petals cover the stamens completely (Fig. 4K, L).

Basally there is zonal growth to form the corolla tube. It is in this stage that the gynoecium primordium arises, along with the development of the anthers (Fig. 5A–C), which release pollen by longitudinal dehiscence (Fig. 5D).

The gynoecium is initiated as a ring-like primordium on the rim of a depression (Fig. 5E), formed by upward growth of the surrounding tissue (Fig. 5C). It is by the growth of this tissue that the semi-inferior ovary develops: the ovary is partly surrounded by receptacular tissue and partly by the corolla tube because the receptacle and the corolla grow at equal rates at this stage (Fig. 5C). When the gynoecium primordium closes centripetally, three (Fig. 5F) or four (Fig. 5G) apical lobes become visible. While the style is formed, the lobes are pushed up to differentiate into the stigma (Fig. 5G, H). Within the gynoecium the placenta develops as a globular primordium (Fig. 5I) in the centre of the depression of the floral apex. The placenta is conical in shape while the ovule primordia are initiated (Fig. 5J). They develop centrifugally and become enclosed by two integuments, which develop in the same way as in *M. argentea* and *M. japonica*. While the space within the ovary enlarges, the placenta extends in size and the ovules become separated by small sections of placental tissue (Fig. 5K, L). On top of the placenta an irregularly lobed, sterile tip can be observed (Fig. 5L).

As in the other two species, there are two types of trichomes present, which occur on the pedicel, bract and bracteoles.

**DISCUSSION**

**Floral characters**

The three *Maesa* species seem to be closely related; at least floral development is highly similar in the three species. Minor differences were found in the division of the common primordia, ovule number and the presence of trichomes on the gynoecium of *M. japonica*.

In Primulales we can distinguish between a large number of different inflorescences. The flowers are clustered in panicles, racemes or umbels. According to Anderberg and Ståhl (1995) most of these inflorescences are derived from the racemose type. In some Primulaceae, e.g. *Anagallis*, the flowers seem to be solitary in the leaf axils. This may be the result of a reduction from lateral racemes or panicles. Such a reduction may also explain the presence of clustered flowers in some Myrsinaceae. The flowers of other Myrsinaceae are arranged in pseudo-umbels (e.g. *Aegiceras, Amblyanthus* and *Ardisia*) with the flowers more or less condensed towards the tips of the raceme or panicle, a state not directly comparable to the perfect umbel of Primulaceae (Anderberg and Ståhl, 1995).

A whole range of terms is used in the literature to describe inflorescences (see Weberling, 1989). Different authors may describe similar cases with different terms, and the situation can become rather complex. For instance, it is not always clear whether flowers are isolated or placed in inflorescences. On the one hand solitary flowers may form clusters so as to resemble inflorescences. On the other hand it is possible that the number of flowers within inflorescences becomes highly reduced. In the same way it is not always easy to determine whether a terminally placed cluster of flowers consists of one terminal and some lateral inflorescences or whether the whole structure must be seen as a single terminal inflorescence. In Myrsinaceae (incl. *Maesa*) inflorescences are terminal-sympodial and in *Maesa* racemes are united into paniculate inflorescences.

Most Primulales have persistent bracts, although some Myrsinaceae are characterized by caducous bracts (Anderberg and Ståhl, 1995). In *Maesa* we found a pair of persistent bracteoles around each flower bud besides the persistent bract, a unique character within Primulales, but more common in some Ebenales (Anderberg and Ståhl, 1995).

Myrsinaceae are hermaphrodite or frequently dioecious (Anderberg and Ståhl, 1995) thus the male or the female organs have been reduced (Mez, 1902). Within *Maesa*, unisexual flowers can be found (Mez, 1902), but the material we studied contained only bisexual specimens. We consider the bisexual state as the primitive state from which unisexual flowers have evolved by reduction. An argument for this is the fact that unisexual flowers of Myrsinaceae often have rudimentary or sterile male or female organs next to the respective functional female and male organs (Mez, 1902). Unisexual flowers may represent a more derived condition because they allow specific adaptation of the flowers which attract pollinating animals. In many cases male and female flowers differ in characteristics such as flowering time, corolla size, colour, presence of floral rewards, etc. (e.g. Bawa, 1980a; Lloyd and Barrett, 1996). In this way optimal pollination can be guaranteed. Furthermore the transition from bisexual towards unisexual flowers could antedate the evolution of dioecy, which may be an evolutionary step towards the development of anemophily (Bawa, 1980b) or specialized pollination types. Some authors (e.g. Bawa and Opler, 1975; Bawa 1980b) try to relate tropical dioecious
FIG. 3. For legend see facing page.
trees either with anemophily or with pollination by small generalist insects. Unfortunately, little is known about the pollination within Myrsinaceae (Anderberg and Sta˚hl, 1995; Otegui and Cocucci, 1999).

Flowers of Primulales are mostly hypogynous. Only the genera Samolus (Primulaceae) and the studied Maesa (Myrsinaceae) have perigynous flowers with a semi-inferior ovary.

Several Primulales have tetra- and/or hexamerous next to pentamerous flowers. Myrsine sometimes has trimerous flowers as well (Caris, 1998), which do not have to be primitive, because they may be the result of an advanced reduction. This reduction towards tetra- or trimerous flowers could, however, appear independently in different groups, being a homoplastic character state.

In discussing the different aestivation patterns of the perianth, we use the typology of Endress (1994), who considered three main types: apert, imbricate and valvate. The apert type is not present within Primulales. Most species have an imbricate aestivation pattern. Two subtypes

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**Fig. 3. Maesa japonica.** A, B, Sepal growth and inception of the common primordia; C–H, development of the common primordia in a petal and a stamen primordium; I, J, division of the common primordia in size; K, L, the petals overgrow the stamen primordia in size; L, common basal growth.

**Fig. 4. Maesa perlarius.** A, Developing flower bud, enclosed by two bracteoles; B, sepal inception; C–H, developing sepals; inception of the common primordia; I, J, division of the common primordia in a petal and a stamen primordium; K, L, the petals overtake the stamen primordia in size; L, common basal growth.
can be recognized: *viz.* the contorted subtype and the quincuncial subtype. According to Endress (1994) a contorted aestivation pattern—present in some Theophrastaceae, Myrsinaceae (including the *Maesa* species studied) and Primulaceae—evolves, starting from an apert pattern, and cannot be seen as evolutionarily derived from the quincuncial pattern. Therefore we consider it as further developed than the aestivation patterns, which can be derived directly from the quincuncial pattern (*the less developed subtype*). We consider a valvate aestivation (e.g. in *Parathesis serrulata* Mez, Myrsinaceae) as the most derived condition.

Within Primulales, sepals are free or fused to form a (short) calyx tube. However, it is impossible to determine objectively whether sepals are free or connate—this depends on the definition of the borderline between the calyx and receptacle.

Sometimes there is a whorl of petaloid or rudimentary staminodes, alternating with the stamens. If present, staminodes always arise in the same way, by their late initiation from the ’Ringwallsattels’ in between the common primordia (Sattler, 1962). Staminodes are most strongly developed within Theophrastaceae; Primulaceae sometimes show rudimentary structures and Myrsinaceae commonly lack staminodes. Thus this character acquires its most derived state within Myrsinaceae. Staminodes are completely absent from *Maesa*, which therefore has an advanced state compared to some other Myrsinaceae that possess...
stamnodes. However, loss of stamnodes may be a rather simple evolutionary step, as we can observe within the genus *Samolus*, where one species lacks stamnodes (Sattler, 1962).

Common primordia occur as complex structures from which petals as well as stamens arise. Space limitations may have resulted in a congenital fusion of originally free petal and stamen primordia, in this way forming a common primordium, a process described as ‘negative dédoublement’ by Ronse De Craene and Smets (1993).

How common primordia develop further into petals and stamens is described extensively by Sattler (1962). In *Maesa*, a lateral primordium is detached on the adaxial side of the common primordium and develops into a stamen; the top of the common primordium grows out abaxially to form a petal.

Sometimes the stamen primordia become connected laterally and a staminal tube develops. One may argue whether or not it is possible to speak of a distinct staminal tube. Yet, we think that in some cases a ring is present connecting the stamen primordia, which is not similar to the ring primordium responsible for the corolla tube. There are, however, also clear cases in which one cannot speak of a staminal tube and where, as a consequence, the filaments are positioned directly on the corolla. The latter situation can, amongst others, be found within the studied *Maesa* species.

In *Primulales* stamens are mostly introrse (extrorse in some *Theophrastaceae*). Anthers of most species open with longitudinal slits. In most *Myrsinaceae*, anthers are sagittate and broadest at the base, while other species of *Theophrastaceae* and *Primulaceae*, and the studied *Maesa* species, possess anthers which are broadest in the middle and rounded at the top.

Many species of *Primulales* possess a coenocarpous gynoecium. The gynoecium differs from an apocarpous gynoecium by a congenital fusion of the different carpels. Such fusion of individual carpels possibly results in an axillary placentation, from which the other placentation types can be derived. Supposing the septa of an axillary placenta become reduced so that a massive, fertile column remains in the centre bearing the ovules, then a primary aseptate gynoecium with a central placenta will result. Such a central placenta develops totally free from the gynoecium wall and is related to a so-called congenital loss of the septa. Hartl (1956a, *fide* Weberling, 1989) confirmed this hypothesis from a range of transitional forms which he found within *Scrophulariaceae* (Weberling, 1989). Such reduced septa can also be found in some *Primulaceae* (Ronse De Craene *et al.*, 1995).

Note that we do not want to exclude the possibility that a primitive gynoecium was characterized by a parietal placentation, and that the growth of septa resulted in a more derived axillary placentation. In that case the congenital fusion of carpel margins is implied instead of a fusion of carpel flanks as in the hypothesis described above.

The central placenta of *Primulales* shows a sterile, conical outgrowth at the top, which is nested in the stylar canal and possibly serves as a kind of pollen transmitting tissue. This tip was interpreted as the sterile end of the floral axis and also as a secondarily developed structure.

Within many Primulales the gynoecium originates as a ring-shaped primordium without a partition into separate carpels. The ring closes centripetally and the top continues into the solitary style with the stigma. Within the ovary the placenta develops from a spherical primordium, which rapidly develops a conical shape. The top of this cone forms the sterile tip as discussed above.

On the conically-shaped placenta the ovules become visible next. The shape of ovules is often described using a whole range of terms, which are difficult to determine unambiguously. We opted for the use of three types: orthotropous ovules, anatropous ovules and, intermediate, curved ovules. This terminology only refers to the external shape of the ovule and not to the position of the nucellus or the embryo because we did not study these features. Anatropous ovules are considered to be primitive (Endress, 1994).

The ovules may be inserted on the placental tissue in different ways. This is an interesting feature because it is more or less specific to families: we observed that embedded ovules can be found within *Myrsinaceae* while protruding ovules are more common within *Primulaceae*. *Lysimachia minoricensis* has ovules which are not embedded in the youngest stages (Caris, 1998; unpubl. res.), as is normal for *Primulaceae*, but gradually the seeds become embedded in the placenta. This is one of the arguments used to consider the genus *Lysimachia* as a transitional genus between *Primulaceae* and *Myrsinaceae*. *Maesa* has ovules which are not really embedded, but separated from each other by sections of placental tissue, which can be considered as an intermediate state. It is notable that ovules are free at inception and that the placenta covers them in later stages. This ontogenetic criterion is used to consider embedded ovules as derived. Moreover we considered a reduction in the number of ovules appearing within *Myrsinaceae* to be a transition to a state in which the ovules are arranged in one instead of several series. In the genus *Maesa*, ovules are always arranged in more whorls, but the number of whorls and the number of ovules within a whorl differs between species. *M. japonica* has many more ovules than the other two species that we investigated, and they are arranged in more series.

Whether the bitegmic ovules of *Primulales* should be considered primitive or derived cannot be answered at present. Bitegmic, crassinucellar ovules are often thought to be primitive (e.g. Philipson, 1977). Because *Primulales* are characterized by bitegmic, tenuinucellar ovules, it cannot be excluded that we are dealing with a derived condition.

Trichomes are abundant in many *Primulales* and different types can be distinguished. For our general description, we refer to the types recognized by Theobald *et al.* (1979). In the species studied we found trichomes of two different types. Multicellular peltate scales, which may be nectariferous, and simple trichomes which can be either short (as in *M. japonica*) or longer. Anatomically the latter type seems to be non-glandular and unicellular.

According to Smets (1988), caducous nectaries as well as persistent nectaries are found in *Primulales*; the nectar is often secreted by trichomes. Within *Myrsinaceae*, trichomes which may be nectariferous can be found on the calyx,
corolla and gynoecium and in some cases the filaments also produce nectar. Smets (1988) observed no trichomes in *M. argentea*, but he remarked that there could be secretion in the slits between adjacent epidermal cells on the upper side of the sepal. We found trichomes on the pedicel, but do not know if they are nectariferous. Theophrastaceae possess nectar-secreting staminodes which belong to the nectaria caduca as defined by Smets (1986, 1988; Smets and Cresens, 1988). Primulaceae have trichomes arranged in a ring at the base of the corolla. In contrast to Theophrastaceae, staminodes, which are less developed in this family, are not nectariferous. Primulaceae are, however, also characterized by a different type of nectary, nectaria persistentia, associated with the gynoecium, at the base (e.g. *Primula, Hottonia*), at the top (e.g. *Androsace, Samolus*) or on the flanks (e.g. *Soldanella*). The nectar is commonly secreted through pores, called nectarostomata by Ronse Decraene and Smets (1991).

Vogel (1986) distinguished between two kinds of floral nectaries within Primulae; trichomatous nectaries in some Theophrastaceae, in Aegicarpaetaeae and in Lysimachiaeae, and carpellar mesenchymatous glands in Primulae and Samoleae. Because the first type occurs in the ‘primitive’ Theophrastaceae and Aegicarpaetaeae, it is seen as less derived within the order. Therefore the ancestors of the order probably possessed no floral nectaries, a situation that still can be found within some Theophrastaceae, most Myrsinaceae and some groups of Primulaceae. Because, however, in the related Ebenales a gynoecial nectary often occurs, one cannot exclude the possibility that such a disc-like nectary was also present in the ancestors of Primulales and that it disappeared in the course of evolution (Smets, 1988; Vogel, 1997). Thus, Vogel (1997) remarked that either type of primulaean nectary may be substitutive, i.e. they occur in a family characterized by a different nectary type or by complete absence of nectaries.

A carpellar mesenchymatous nectary with nectarostomata, similar to the type recognized by Vogel (1997), could be found on top of the semi-inferior ovary of *M. argentea* (light microscopic observations; Caris, 1998). *M. argentea* possesses two types of trichomes on the pedicel, but further examination is needed to see if these are nectariferous; the same goes for the trichomes that can be found on different floral parts in the other two species. On the gynoecium of *M. japonica* we observed peltate scales which probably are nectariferous.

The systematic position of the genus Maesa

Maesa differs in a wide range of floral characteristics from most other Myrsinaceae: flowers are perigynous and are enclosed by two extra bracteoles; petal primordia develop first and stamens start their growth later on; there is no staminal tube so the filaments attach directly on the corolla tube; the introrse anthers are not sagittate; the gynoecium has stomatic nectaries and in the case of *M. argentea* a disc-like gynoecial nectary is present; the fruit is many-seeded and is formed by the semi-inferior ovary as well as by the surrounding tissue; numerous, anatropous ovules are positioned close to each other on the placenta; they are not fully immersed and they are separated by small portions of placental tissue. Maesa also differs in many other characteristics from Myrsinoideae, which form a rather homogeneous entity (Andeberg and Stähl, 1995).

So where should we place the genus Maesa? According to Andeberg and Stålhl (1995) it would be best to assign a family rank to Maesa. In that case there is a differentiation between four monophyletic groups within Primulales, viz. Theophrastaceae, Maesaeeae, Myrsinaceae (excluding the genus Maesa) and Primulaceae.

Previous analyses of morphological data (e.g. Andeberg and Stålhl, 1995) and the conclusions of Andeberg et al. (1998), based on nucleotide sequence data from the chloroplast DNA gene *rbcL*, indicate that Theophrastaceae and Myrsinaceae *sensu stricto* (viz. the genus Maesa excluded) are monophyletic. However, if *Maesa* is put into Myrsinaceae the latter appear to be paraphyletic. According to the results of Morton et al. (1996) Maesa is sister to a group combining Myrsinaceae *sensu stricto* and Primulaceae. The basal position of *Maesa* is supported by a cladistic analysis of Myrsinaceae *sensu lato* carried out by Otegui and Cocucci (1999) in which *Maesa* is sister to the remaining Myrsinaceae. The results of the macromolecular analysis of Andeberg et al. (1998) show that Primulaceae are paraphyletic. *Maesa* is part of an unresolved clade, which includes Theophrastaceae, Primulaceae and Myrsinaceae *sensu stricto*.

On the basis of ontogenetic observations we have tried to contribute to the elucidation of the phylogenetic relationships of *Maesa* within Primulales. In the poorly known tropical Myrsinaceae we can find a complex of genera and species that is difficult to order and which still demands much study. We may conclude that floral ontogenetic studies can certainly clarify some of the relationships. In particular the development of the common primordia, the shape of the anthers, the number, arrangement and position of ovules and the degree of embedding of the ovules in the placential tissue are potentially interesting features, which certainly deserve attention within Myrsinaceae and related taxa.

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