Floral Ontogeny in the Plumbaginaceae[1]

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A scanning electron microscopic study of the floral ontogeny of seven species of the Plumbaginaceae (representing five genera of the Armerioideae and two of the Plumbagoideae) is presented. The early ontogenetic stages in all species examined are sufficiently similar to propose the following familial description. The five sepal primordia are initiated simultaneously or spirally. These soon reach continuity and develop into the synsepalous calyx. Meanwhile, five common stamen-petal primordia that alternate with the sepal primordia are initiated simultaneously on the flattened apex. Soon, two distinct growth-centres can be observed on each of these primordia: a petal primordium at the abaxial side and a stamen primordium on the top. After inception of the common primordia, five gynoecial primordia alternating with the common primordia are initiated simultaneously on the corners of the apex that has become pentagonal. These primordia soon reach continuity and develop into the superior unilocular gynoecium. Continuity between the gynoecial primordia is reached earlier in the Plumbagoideae than in the Armerioideae. In the centre of the ovary a primordium arises that develops into the single basal circinotropous bitegmic ovule. The floral nectaries are associated with the androecium.

Key words : Character research — Common primordia — Continuity — Floral ontogeny — Plumbaginaceae

Plumbaginaceae (incl. Limoniaceae) are a nearly cosmopolitic family that consists of 27 genera and about 650 species (Kubitzki 1993). Kubitzki's estimates are rather high : Takhtajan (1986) gives about 20 genera and approximately 775 species, Stebbins (1974) 15 genera and 500 species, and Cronquist (1981) only about 12 genera and 400 species. The flowers are regular, hypogynous and pentamerous. Each flower consists of a synsepalous calyx, a corolla that is usually sympetalous, five antepetalous stamens and a superior pentacarpellary unilocular gynoecium with one basal ovule (Fig. 1). In general habit as well as in morphological and anatomical characters, the family is rather diverse, but a number of special features point to the monophyly of the group. Labbe (1962) lists as unique and constant features the

doubly inversed ovule (see discussion), the type of obturator (see discussion) and the type of epidermal glands. Multicellular epidermal salt glands that are superficially similar to those of the Plumbaginaceae are characteristic for the Tamaricaceae and the Frankeniaceae, but they differ in anatomical and histological details (Metcalfe and Chalk 1950, Schnepf 1969, Fahn 1979). Apart from these families, where they are characteristic, multicellular salt glands occur only sporadically in some other angiosperm families (Fahn 1979).

Within the Plumbaginaceae, there are two marked subfamilies, the Plumbagoideae and the Armerioideae (Cronquist 1981). The Plumbagoideae are sometimes also called Plumbaginoideae (e.g. Thorne 1981); the Armerioideae are sometimes also called Limonioideae (e.g. Dahlgren 1983) or Staticoideae (e.g. Kubitzki 1993). The most conspicuous differences are that the Plumbagoideae have racemes and a gynoecium with a single style that may be apically lobed, while the Armerioideae possess panicles or cymose heads and a gynoecium with more or less completely distinct styles. Moreover, vegetative and fertile shoots are rather similar in the Plumbagoideae, but higly different in the Armeroideae (Cronquist 1981, Dahlgren 1983, Labbe 1962).

According to Dahlgren (1983), the differences between the two subfamilies are big enough to treat them as
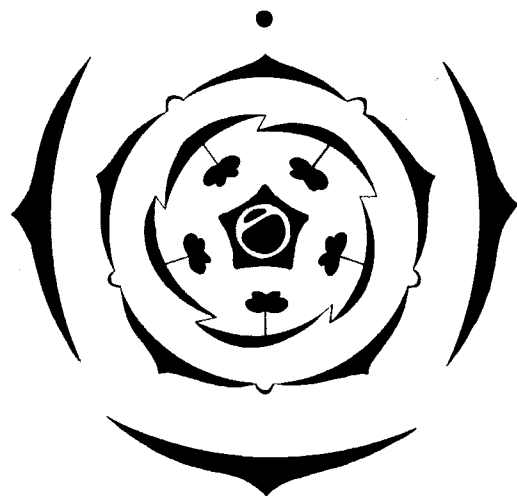
Fig. 1. Generalized floral diagram of the Plumbaginaceae.

separate families (Plumbaginaceae and Limoniaceae) that might not be closely related. Dahlgren's treatment suggests that both families are monophyletic, a hypothesis that can also be found in the phylogenetic considerations of Labbe (1962) and Baker (1966). This hypothesis could be tested in a cladistic analysis, but the isolated position of the family within the angiosperms and the associated rooting problems would certainly complicate such an analysis. Indeed, the relationships of the family within the angiosperms are one of the long-standing problems in angiosperm systematics. In recent treatments, the question centers around the relationship between the Plumbaginaceae (or Plumbaginales), the Primulales, the Polygonales and the Caryophyllales (see e.g. Cronquist 1988, Chase *et al.* 1993). While a close relationship between Primulales and Plumbaginaceae seems more and more improbable (Giannasi *et al.* 1992 : 12), the possibility has not completely been ruled out (e.g. Thorne 1981, Cronquist 1988). A relationship between Primulales and Plumbaginaceae is supported by chemical evidence (Thorne 1981), but it is clear that it was originally postulated on the basis of floral similarities between both taxa (Pax 1897, see also Clinckemaillie and Smets 1992).

Progress in the systematic problems that surround the Plumbaginaceae will depend in the first place on an increased knowledge of its characters. Because of the widespread occurrence of heteromorphic incompatibility systems in the family (Baker 1966), the characteristics of mature flowers have been studied intensely in the past. Apart from heterostyly, dimorphism in pollen size and pollen sculpturing and dimorphism in stigmatic surface occur troughout the family (see e.g. Baker 1948, 1966, Vuilleumier 1967, Dulberger 1975, Nowicke and Skvarla 1977). The first study of floral ontogeny in the Plumbaginaceae already dates from the middle of previous century (Payer 1857), but afterwards the floral development of the family has been neglected almost completely, certainly when compared to the high number of studies related to adult flower morphology (see Roth 1961a, 1961b, for an overview). As a contribution to the basic knowledge of the Plumbaginaceae and as part of a general research project on the characterisation of floral features, we present a scanning electron microscopic study of the floral ontogeny in seven species of seven different genera of the Plumbaginaceae.

Materials and Methods

Flower buds of *Acantholimon glumaceum* (Jaub. and Spach) Boiss., *Ceratostigma plumbaginoides* Bunge, *Goniolimon tataricum* (L.) Boiss. and *Limonium latifolium* (Sm.) O. Kuntze were collected in the National Botanical Garden of Belgium (BR) at Meise. Material of *Armeria maritima* (Mill.) Willd. and *Plumbago auriculata* Lam. was obtained from the Botanical Garden of the K.U. Leuven. Buds of *Limoniastrum monopetalum* (L.) Boiss. were collected in Jerba, El Kantara and Korbous (Tunisia) and kindly put to our disposal by Dr. L. Ronse Decraene.

Plumbago auriculata and *Ceratostigma plumbaginoides* belong to the *Plumbagoideae*, while the other species are representatives of the *Armerioideae*. Pickled voucher material of all species has been deposited at the Botanical Institute of the K.U. Leuven (LV).

The material was fixed in FAA (90 ml 70% ethanol, 5 ml 40% formaldehyde, 5 ml 99% acetic acid) and dissected under a Wild M 3 binocular microscope. The flowers were dehydrated and critical point dried with a CPD 030 (Balzers) using liquid CO_2, and coated with a 180 nm gold-layer (SCD 020, Balzers). The buds were observed under a Philips 501 B scanning electron microscope (SEM) at the National Botanical Garden of Belgium. Photographs were taken on Agfapan 25 using the Oscillophot M 20 of Steinheil.

For light microscopic observations, the material was embedded in paraffin and stained with safranine and fastgreen. We used a Leitz Dialux 20 microscope and photographs were taken with a Wild MPS 45/51 photoautomat.

Results

Terminology about "fusion"

Compound structures, such as a sympetalous corolla, a monadelphous androecium, a syncarpous gynoecium or a sympetalous corolla with the stamens attached to it, are commonly interpreted as fusion products. Usually a distinction is made between postgenital fusion, also called surface fusion or ontogenetic fusion, and congenital fusion, also called phylogenetic fusion or zonal growth (e.g. Cusick 1966 or more recently Verbeke 1992). Postgenital fusion "involves surface contact between organs that have already developed as individual entities", congenital fusion "refers to a compound structure that is formed as a unit but is thought in a phylogenetic sense to be composed of multiple parts" (Verbeke 1992 : 585).

Sattler (1977, 1978, see also Daniel and Sattler 1978) analysed this concept of fusion and reached two main conclusions. Firstly, neither the equation of congenital with phylogenetic fusion nor the equation of postgenital with ontogenetic fusion is correct, as can be easily demonstrated : meristem fusion is a process that is traditionally subsumed under congenital or phylogenetic fusion, but if ontogenetic fusions are to designate fusions that are observable during ontogeny, then meristem fusion is also an ontogenetic fusion, as Cusick (1966) already suggested. Surface fusion or postgenital fusion, on the other hand, is clearly an ontogenetic fusion, but at the same time it can be a phylogenetic fusion. An example would be the case where the degree of surface fusion between the petals in a certain lineage increases during phylogeny. Secondly, congenital fusion is often used to describe processes (or the end products of these processes) that do not involve fusion, such as meristem shifting or *de novo* formation of common meristems. It is easy to verify that for example Verbeke's definition suffers from this kind of inflation of meaning. We agree with Sattler

(1978 : 403) that this is more than playing with words : in order to avoid a false impression of understanding structures, terms that denote processes or their end products should not be used in descriptions of structures whose development or semophylesis is not known, unless one explicitly wants to state a hypothesis.

Patterns can be described with or without reference to the processes that brought them about. The concept of continuity (Clos 1879 : fide Sattler 1977, 1978) does not have any process connotations, neither developmentally nor phylogenetically, so it is particularly appropriate for descriptions that are free from references to processes. Using this concept, a sympetalous corolla can be described as a corolla in which the petals are continuous above the receptacle. Note that a description that is free from references to particular processes, is not a description that is completely free from interpretation or theory : in the example we still have to agree on the delineation of receptacle and petal.

Processes that may lead to continuity are surface fusion, meristem fusion, meristem extension, de novo formation of meristems, and heterotopy (Sattler 1977 : 35, 1978 : 404). As the end products of all these processes are often almost indistinguishable, it is useful to have a descriptive tool (continuity) that can be used in the absence of the proper developmental data. In comparative studies of the external surfaces of developing flower buds, it is relatively easy to infer surface fusion (e.g. in the formation of the stigma in many Apocynaceae and Asclepiadaceae, Baum 1949). However, in order to distinguish between meristem fusion, meristem extension or de novo formation of meristems (collectively referred to as interprimordial growth, Sattler 1977 : 35, 1978 : 404), supplementary research is necessary; e.g. measurement of mitotic activity enabled Daniel and Sattler (1978) to conclude that the corolla tube in Solanum dulcamara L. resulted from meristem fusion.

In the following, we will describe the compound structures that arise during floral development mainly in terms of continuity. In clear cases we will characterise the observed continuities as surface fusion or as interprimordial growth. Since this is mainly a SEM study, no attempt is made to distinguish between the different processes that lead to interprimordial growth.

Acantholimon glumaceum (Jaub. and Spach) Boiss.

Just before calyx inception, the floral bud is encircled by two bracteoles or prophylls (Fig. 2). A single bract is present below these bracteoles. The five sepal primordia are initiated simultaneously (Fig. 3), and subsequent interprimordial growth leads to a continuous rim (Fig. 4) that develops into a calyx tube (Figs. 6, 15, 16).

After calyx initiation, the apex flattens and five common primordia, alternating with the sepal primordia, are initiated simultaneously (Fig. 4). Soon two distinct growth-centres can be observed on each of these primordia : an abaxial oblate petal primordium and a spherical stamen primordium at the top (Figs. 5-7). During further develop-

ment, the anthers arise on very short filaments (Figs. 10-12) and a continuous structure develops at the base of corolla and androecium (Figs. 10, 14). The lowest part of this continuous structure appears as a tube in which filaments and petals cannot be distinguished (Figs. 14, 15). Five vascular bundles are present at that level (Fig. 15). At a higher level, each of these vascular bundles is divided into a petal bundle and a filament bundle (Fig. 16). Nectar-secreting tissue is found on the adaxial side of the filament bases (Figs. 15, 16). The nectarial tissue (Figs. 15, 16) consists of densely packed darkly staining cells with large nuclei. Nectarostomata were not observed.

After inception of the common primordia, five gynoecial primordia (sensu Sattler 1974) alternating with the stamen primordia are initiated simultaneously on the corners of the apex that has become pentagonal (Figs. 6, 8). Inter-primordial growth gives rise to a tubular structure below these primordia (Fig. 10). This tube develops into the unilocular superior ovary and the five gynoecial primordia develop into the five distinct styles and stigmata (Fig. 12).

After initiation of the five gynoecial primordia, the remaining apex is transformed into the single ovule primordium (Figs. 8, 9). A long and slender funicle develops and the ovule undergoes a curvature of 360°. In the mature ovule (Fig. 13), the micropyle points away from the basal placenta towards the top of the ovary. The micropylar end of the ovule is close to the obturator, a bulge of transmitting tissue that protrudes from the roof of the ovary into the locule (Fig. 13).

Armeria maritima (Mill.) Willd.

Armeria maritima possesses head-like inflorescences (Fig. 17) composed of small monochasia, with the lateral branches arising in the axil of a subtending bract (Fig. 18). Bracteoles are absent. The five sepal primordia are initiated simultaneously and subsequent interprimordial growth leads to a continuous rim (Fig. 20) that develops into a calyx tube (Figs. 23, 24).

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 19). Soon the petal primordium and the stamen primordium can be observed on each of these primordia (Figs. 20, 21). Initially, the stamen primordia grow much faster than the petal primordia (Figs. 22, 24). At the base of corolla and androecium, a continuous structure develops (Fig. 29). Nectar-secreting tissue (Fig. 31) and nectarostomata (Fig. 30) are present on the adaxial side of the filaments in this continuous petal-filament tube.

After inception of the common primordia, the apex becomes pentagonal and five gynoecial primordia alternating with the stamen primordia are initiated simultaneously on its corners (Figs. 21, 22). Subsequent interprimordial growth gives rise to a tubular structure (Fig. 23) that develops into the unilocular superior ovary (Fig. 25). The gynoecial primordia develop into the five distinct styles and stigmata.

After initiation of the gynoecial primordia, the remaining
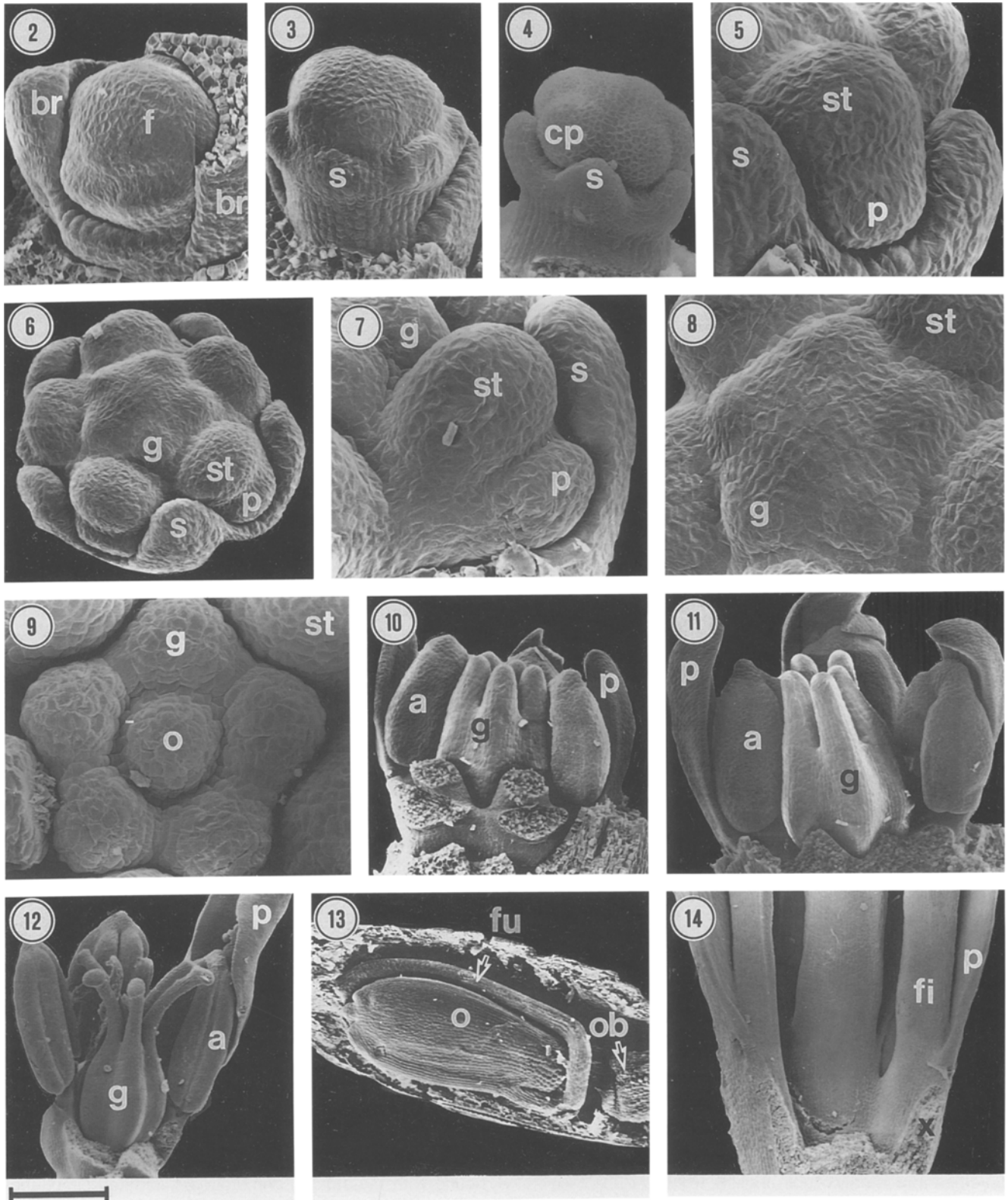
apex transforms into the single ovule primordium (Figs. 22, 23). During the development of the ovule (Figs. 26, 27), a long and slender funicle develops and the ovule undergoes a curvature of 360°. In the mature ovule (Fig. 28), the micropyle points towards the top of the ovary and is close to the obturator.

Goniolimon tataricum (L.) Boiss.

By the time of calyx inception, the floral bud is encircled by two bracteoles (Fig. 32). The five sepal primordia are initiated simultaneously (Fig. 33) and subsequent interprimordial growth leads to a continuous rim (Fig. 34) that develops into a calyx tube.

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 34). Soon the petal and stamen primordia can be observed on these primordia (Fig. 36). At the base of corolla and androecium, a continuous structure develops (Fig. 40). Nectariferous tissue (not shown) is present at the adaxial side of the broadened filament bases. Nectarostomata were not observed.

After inception of the common primordia, five gynoecial primordia alternating with the stamen primordia are initiated simultaneously on the corners of the apex that has become pentagonal (Fig. 35). Subsequent interprimordial growth gives rise to a tubular base (Fig. 37) that develops into the unilocular superior ovary (Fig. 38). The gynoecial primordia develop into the five distinct styles and stigmata (Fig. 38). After initiation of the gynoecial primordia, the remaining apex transforms into the single ovule primordium (Figs. 35, 36). A detail of the young ovary is shown in figure 39. The obturator is already present and the curvature of the funicle with the young ovule is half way.

Limonium latifolium (Sm.) O. Kuntze

The five sepal primordia are initiated simultaneously and subsequent interprimordial growth leads to a continuous rim (Fig. 41) that develops into a calyx tube.

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 41). Soon the petal and stamen

primordia can be observed on these common primordia (Fig. 43). At the base of corolla and androecium, a continuous structure develops (Fig. 46). Nectar-secreting tissue (Fig. 46) and nectarostomata (Fig. 45) are present on the adaxial side of the filaments in this continuous petal-filament tube.

After inception of the common primordia, five gynoecial primordia alternating with the stamen primordia are initiated simultaneously on the corners of the pentagonal apex (Fig. 42). Subsequent interprimordial growth gives rise to a tubular base that develops into the unilocular superior ovary (Figs. 43, 44). The gynoecial primordia develop into the five distinct styles and stigmata. After initiation of the gynoecial primordia, the remaining apex transforms into the ovule primordium (Fig. 43).

Ceratostigma plumbaginoides Bunge

After the initiation of a subtending bract, two bracteoles are initiated successively laterally on the floral bud (Fig. 47). The sepal primordia are initiated simultaneously in some flowers, but in a 2/5 spiral or more or less irregular in other. In all cases interprimordial growth leads to a calyx tube (Figs. 48-50).

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 49). Soon the stamen and petal primordia can be observed on the common primordia (Fig. 50). The petal primordia reach continuity very early, what results in a continuous rim (Fig. 50). At maturity, the filament bases are broadened and continuous among themselves and with the corolla (Figs. 55, 56). Nectar secretion occurs at the adaxial side of the filament bases in the petal-filament-tube. Nectarostomata were not observed.

After inception of the common primordia, the gynoecium is initiated directly as a continuous pentagonal ring (Fig. 51). The ovule primordium is derived from the remaining apex (Figs. 51, 52). The gynoecial ring elongates and forms a tubular structure on top of which five lobes are formed (Fig. 53). The tubular structure will develop into the superior unilocular ovary and the single style, while

Figs. 2-14. SEM observations of floral development in *Acantholimon glumaceum*. 2. Young floral bud with two bracteoles (bract removed, one bracteole partly removed; bar=100 μm). 3. Simultaneous inception of five sepal primordia (one bracteole removed; bar=100 μm). 4. Inception of five common stamen-petal primordia alternating with the sepal primordia (bar=100 μm). 5. Very soon after the initiation of a common stamen-petal primordium, the petal and the stamen primordium become visible on it (bar=50 μm). 6. Inception of five gynoecial primordia alternating with the stamen primordia (bar=100 μm). 7. The stamen primordium and the petal primordium have become clearly separate (bar=50 μm). 8. At inception, the gynoecial primordia are five distinct bulges on the corners of the pentagonal apex (bar=50 μm). 9. Soon the gynoecial primordia reach continuity; the remaining apex transforms into the ovule primordium (bar=50 μm). 10. The continuous zone beneath the gynoecial primordia has grown into a tube; beneath androecium and corolla a continuous structure has developed (bar=200 μm). 11. The gynoecial tube develops into the ovary; the gynoecial primordia grow out to form the five separate styles and stigmata; note the presence of well-developed anthers on short filaments (bar=200 μm). 12. Flower just before anthesis (bar=400 μm). 13. Mature ovule with slender funicle; the obturator protrudes from the roof of the ovary into the locule at right (bar=400 μm). 14. Adaxial side of the filament bases; the filaments are continuous among themselves and with the corolla (gynoecium removed; bar=400 μm). Abbreviations: a, anther; br, bracteole; cp, common stamen-petal primordium; f, floral apex; fi, filament; fu, funicle; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; o, ovule; ob, obturator; p, petal; s, sepal; st, stamen.
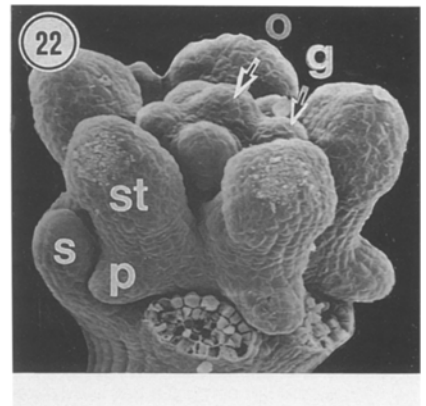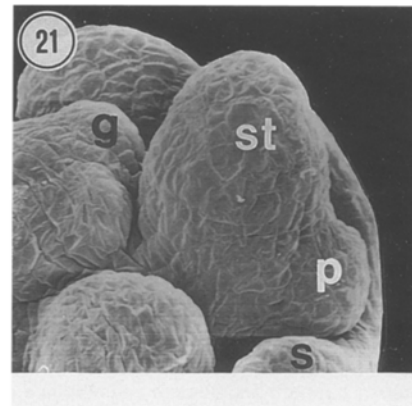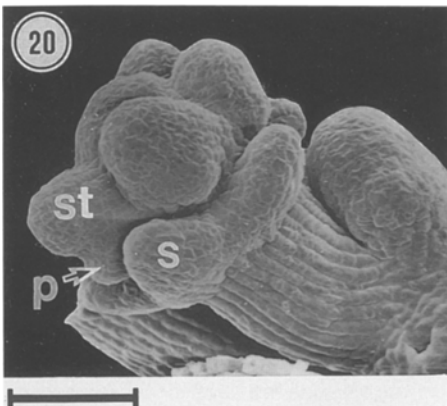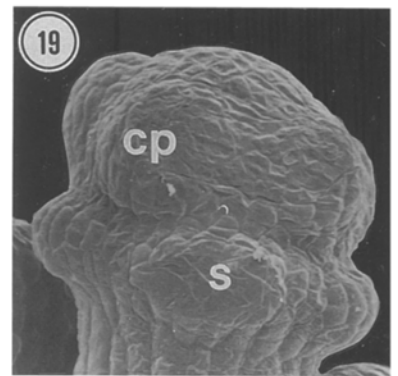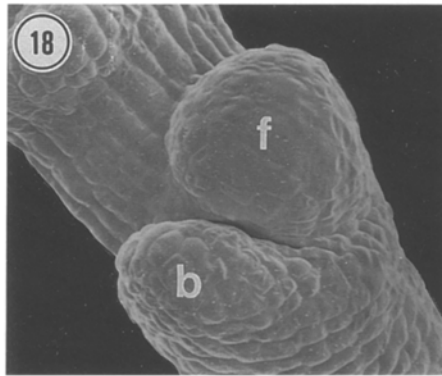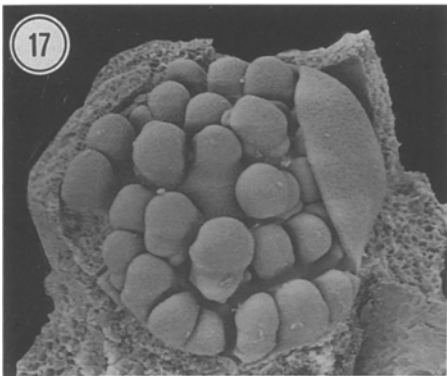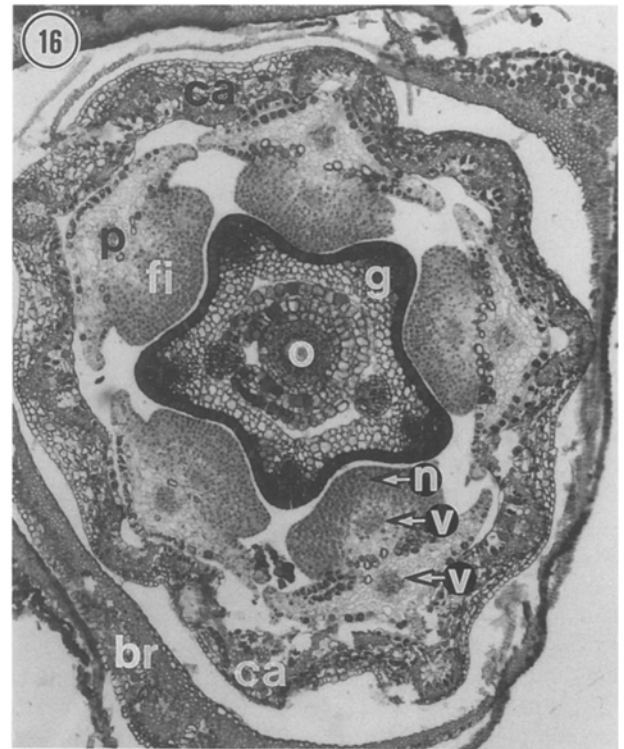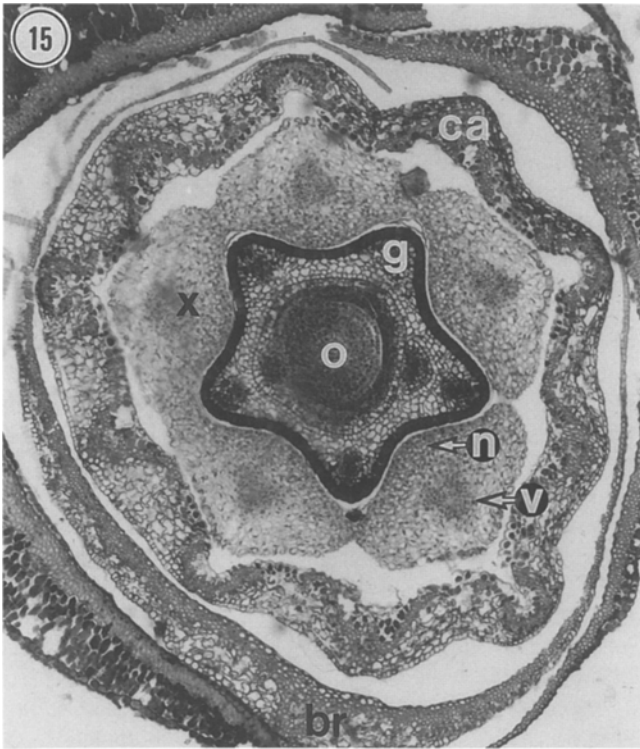
the five lobes on top of it will develop into the five-lobed stigma (Fig. 54).

Plumbago auriculata *Lam.*

At the time of calyx inception, the floral bud is encircled by two bracteoles. A single bract is situated below these bracteoles. The sepals are initiated in a 2/5 phyllotaxis (Fig. 57). Sepals one and three arise abaxially, sepals four and five develop laterally and sepal two arises adaxially. The sepal primordia grow rapidly and interprimordial growth leads to continuity (Figs. 58, 59).

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 58). Soon the petal and stamen primordia can be observed on these common primordia (Fig. 59). At maturity, the filaments are not continuous with the petals. The petals are continuous among themselves over approximately 3/4 of their length, while the filaments are only continuous at their swollen bases. The filament bases are nectariferous and posses nectarostomata.

After inception of the common primordia, the gynoecium is initiated as a continuous pentagonal ring (Fig. 60). The ovule primordium is derived from the remaining apex (Figs. 60, 61). The gynoecial ring elongates and forms a tubular structure (Fig. 61) that will develop into the superior unilocular ovary and the single style. The lobes on top of this structure (Fig. 61) will develop into the five-lobed stigma.

Limoniastrum monopetalum *(L.) Boiss.*

The five sepal primordia are initiated simultaneously and subsequent interprimordial growth leads to a continuous rim (Fig. 62) that develops into a calyx tube.

After calyx initiation, five common primordia, alternating with the sepal primordia, are initiated simultaneously on the flattened apex (Fig. 62). Soon the petal and stamen primordia can be observed on these common primordia (Fig. 63). At the base of corolla and androecium, a continuous structure develops. Nectarostomata are present on the basal adaxial side of the filaments.

After inception of the common primordia, five gynoecial primordia alternating with the stamen primordia are initiated on the corners of the pentagonal apex (Figs. 63-65). Subsequent interprimordial growth gives rise to a tubular

base that develops into the unilocular superior ovary. The gynoecial primordia develop into the five distinct styles and stigmata. After initiation of the gynoecial primordia, the remaining apex transforms into the ovule primordium (Fig. 65).

Discussion

Calyx

In all investigated Armerioideae, the sepal primordia are initiated simultaneously. In the Plumbagoideae, the sepal primordia are initiated spirally in *Plumbago auriculata*, and in *Ceratostigma plumbaginoides* they are initiated spirally in some flowers but simultaneously or irregular in other. This distribution allows for many different interpretations. Therefore, the patterns of calyx initiation will probably not be very informative in elucidating the relation between both subfamilies or the relationships of the family within the angiosperms.

Corolla and androecium

In all observed species, the development of corolla and androecium starts with the simultaneous appearance of five distinct common primordia on each of which soon two distinct growth-centres can be observed (e.g. Figs. 4-7 and 19-21).

In *Armeria vulgaris* and *A. maritima*, the original growth-centre of the common primordium becomes the growth-centre of the externally visible stamen primordium, while the petal primordium originates as a new growth-centre on the abaxial side of the developing common primordium (Roth 1961b). Roth interpreted this as evidence that the petals of the Plumbaginaceae should not be viewed as independent floral organs (such as "real" petals developing from independent primordia), but as dorsal leaflike appendages of the stamens. Consequently, she views the Plumbaginaceae as essentially petalless. It should be noted however, that a similar pattern can be equally well explained by a phylogenetic process of spatial and/ or temporal shifting of inception of "real" petals.

Moreover, in the Primulales, where similar common primordia are present, all possible intermediates occur between the case where the petal primordium appears as a growth-centre on the abaxial side of the common primordium and the case where the stamen primordium

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Figs. 15-22. Light microscopic observations of floral development in *Acantholimon glumaceum* (15-16) and SEM observations of floral development in *Armeria maritima* (17-22). 15. Transverse section of an adult flower of *Acantholimon glumaceum* at the level of the continuous structure beneath filaments and corolla; at this level, five vascular bundles are present; its adaxial side is nectar-secreting (bar=285 μm). 16. A slightly higher transverse section; ten vascular bundles are present at this level; the nectar-secreting tissue is situated on the filaments only (bar=285 μm). 17. Early stage of the head-like inflorescence of *Armeria maritima* (bar=200 μm). 18. Young flower bud in the axil of a subtending bract (bar=50 μm). 19. Five common primordia are initiated alternating with the sepal primordia (bar=50 μm). 20. The sepals have become continuous (bar=100 μm). 21. Petal and stamen primordia from a common primordium (bar=50 μm). 22. Development of calyx, petals and stamens; inception of five carpel primordia and one ovule primordium (two sepals removed; bar=100 μm). Abbreviations: b, bract; br, bracteole; ca, calyx; cp, common stamen-petal primordium; f, floral apex; fi, filament; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; n, nectariferous tissue; o, ovule; p, petal; s, sepal; st, stamen; v, vascular bundle; x, continuous structure at the base of corolla and androecium.
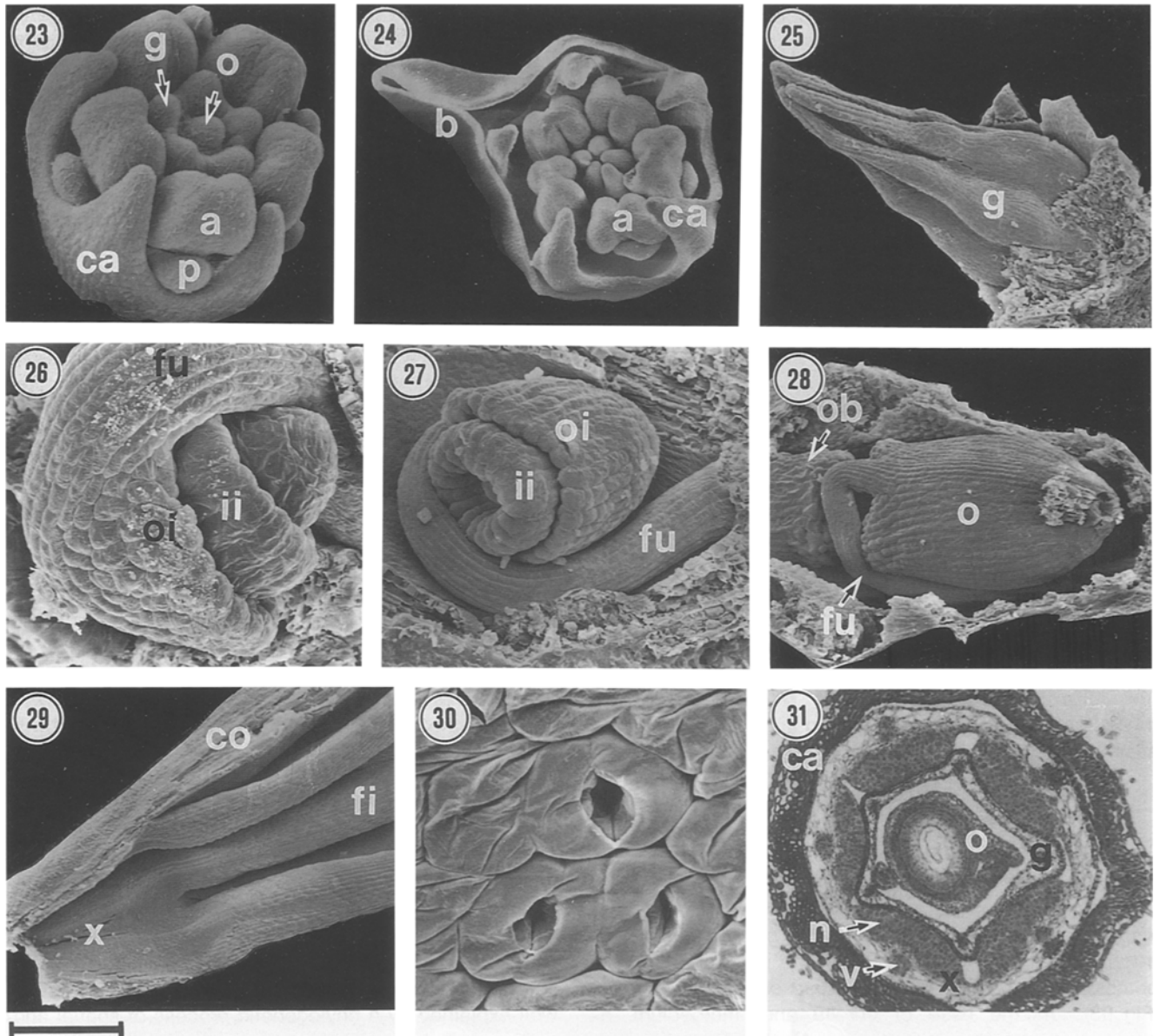
Figs. 23-31. SEM observations (23-30) and light microscopic observation (31) of floral development in *Armeria maritima*. 23. The calyx tube is well developed; the anthers arise on short filaments, petal development is retarded; the gynoecial primordia have reached continuity (bar=100 μm). 24. Nearly mature flower subtended by a bract (bar=200 μm). 25. Nearly mature gynoecium (sepals, petals and stamens removed; bar=200 μm). 26. Young ovule with a curvature of 180° (bottom of the locule at the right upper corner; bar=50 μm). 27. Slightly older ovule with a curvature of 360° (bottom of the locule at right; bar=100 μm). 28. Mature ovule; the obturator protrudes from the roof of the ovary (bottom of the locule at right; bar=400 μm). 29. Adaxial side of the filaments and the petal-filament tube (bar=400 μm). 30. Open nectarostomata situated on the adaxial side of the filament bases (bar=12.5 μm). 31. Transverse section, the adaxial side of the petal-filament tube is nectariferous (bar=285 μm). Abbreviations: a, anther; b, bract; ca, calyx; co, corolla; fi, filament; fu, funicle; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; ii, inner integument; n, nectariferous tissue; o, ovule; ob, obturator; oi, outer integument; p, petal; v, vascular bundle; x, continuous structure at the base of corolla and androecium.

appears as a growth-centre on its adaxial side (Sattler 1962, 1967). Both extremes are not fundamentally different and one should not rely to exclusively on the precise pattern for drawing phylogenetic conclusions about the "reality" of the petals.

Common stamen-petal primordia in which the abaxial part develops into a petal and the adaxial part into a stamen, occur relatively frequently in taxa where petals
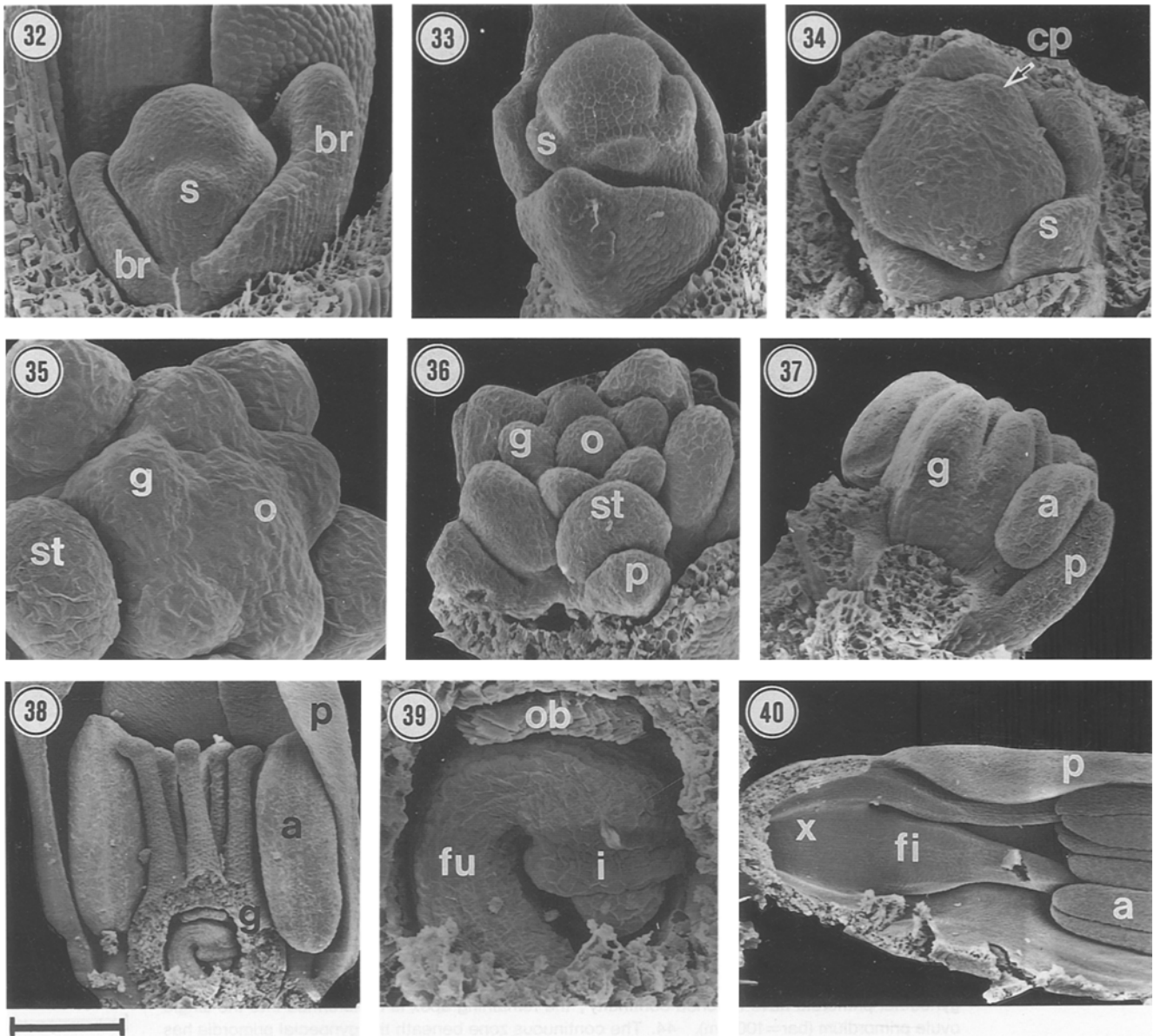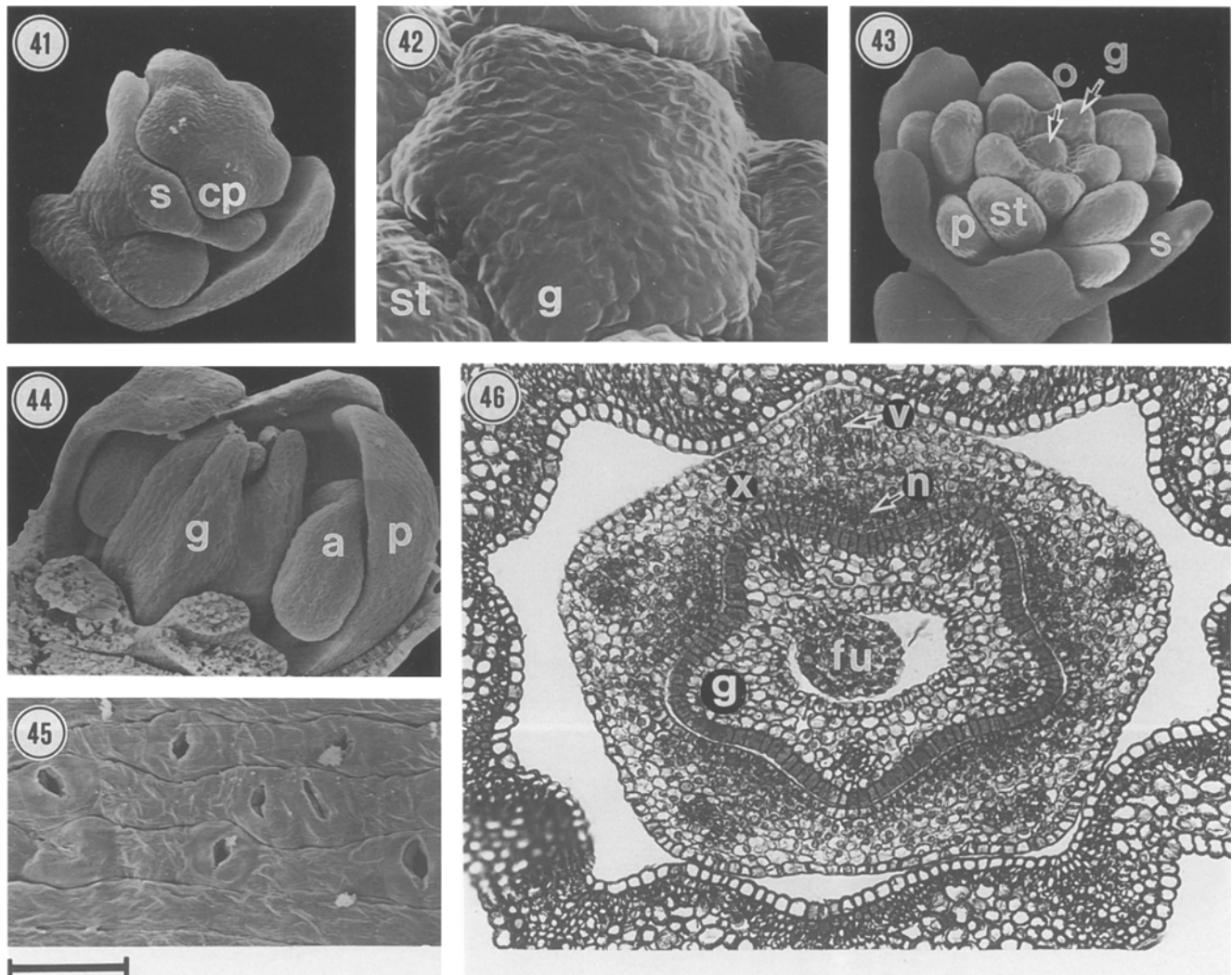
Figs. 32-40. SEM observations of floral development in *Goniolimon tataricum*. 32. Flower bud surrounded by two bracteoles; five sepal primordia are already initiated (bract removed; bar=100 μm). 33. Sepals slightly enlarged (bar=100 μm). 34. Inception of five common stamen-petal primordia alternating with the sepal primordia (bar=100 μm). 35. Inception of five gynoecial primordia and one ovule primordium (bar=50 μm). 36. The gynoecial primordia have become continuous (bar=100 μm). 37. The continuous zone beneath the gynoecial primordia has grown into a tube; the anthers arise on short filaments (bar=100 μm); stamens and petals develop at equal pace. 38. Lateral view of a young flower with superior ovary, five styles and the single developing ovule (ovary wall partly removed; bar=200 μm). 39. Developing ovule with a curvature of 180°; one integument initiated; the obturator is already present (bar=50 μm). 40. Adaxial side of the filaments and petal-filament tube (gynoecium removed; bar=400 μm). Abbreviations: a, anther; br, bracteole; cp, common stamen-petal primordium; fi, filament; fu, funicle; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; i, integument; o, ovule; ob, obturator; p, petal; s, sepal; st, stamen; x, continuous structure at the base of corolla and androecium.

and stamens are superposed. Ronse Decraene *et al.* (1993) list 21 Magnoliatae families in which they are known to occur. Beside these cases, other types of common stamen-petal primordia exist; e.g. in *Pisum sativum* L. (Tucker 1989) where the common primordia divide not radially but laterally and give rise to two petals and a stamen, to one petal and two stamens, or to a petal and a stamen. Moreover, common primordia are not

Figs. 41–46. SEM observations (41–45) and light microscopic observation (46) of floral development in *Limonium latifolium*. 41. Young flower with five sepals and inception of five common primordia (bar=100 μm). 42. Initiation of five gynoecial primordia (bar=25 μm). 43. The gynoecial primordia have reached continuity; the remaining apex is transformed into the single ovule primordium (bar=100 μm). 44. The continuous zone beneath the gynoecial primordia has grown into a tube (the young ovary); the anthers arise on short filaments (bar=100 μm). 45. Open nectarostomata on the adaxial side of the filament (bar=25 μm). 46. Tranverse section, the adaxial side of the petal-filament tube is nectariferous (bar=285 μm). Abbreviations: a, anther; cp, common stamen-petal primordium; fu, funicle; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; n, nectariferous tissue; o, ovule; p, petal; s, sepal; st, stamen; v, vascular bundle; x, continuous structure at the base of corolla and androecium.

restricted to stamens and petals: e.g. *Astrantia major* L. has common sepal-stamen primordia (Erbar and Leins 1985).

In our view, all these cases are best interpreted as a particular instance of the general trend of increasing synorganization between different floral whorls in angiosperms (Endress 1987). Within this context, common primordia can originate by every phylogenetic process that affects two or more organ primordia that are distinct during early ontogeny, in such a way that their earliest developmental stages become highly integrated. Possible processes include *in situ* inception of *de novo*

meristems (sensu Sattler 1978) or spatial and temporal shifting of primordial inception. Ronse Decraene and Smets (1993 : 119) and Ronse Decraene *et al.* (1993 : 108) proposed to group all these diverse phylogenetic processes that give rise to common primordia of this type under the name "negative dédoublement", thereby reviving and slightly modifying a concept of Celakovsky (1894). Consequently, to invoke negative dédoublement for explaining the occurrence of common stamen-petal primordia in the Plumbaginaceae comes down to the hypothesis that the family is phylogenetically linked with ancestors in which petal and stamen primordia were distinct. The precise
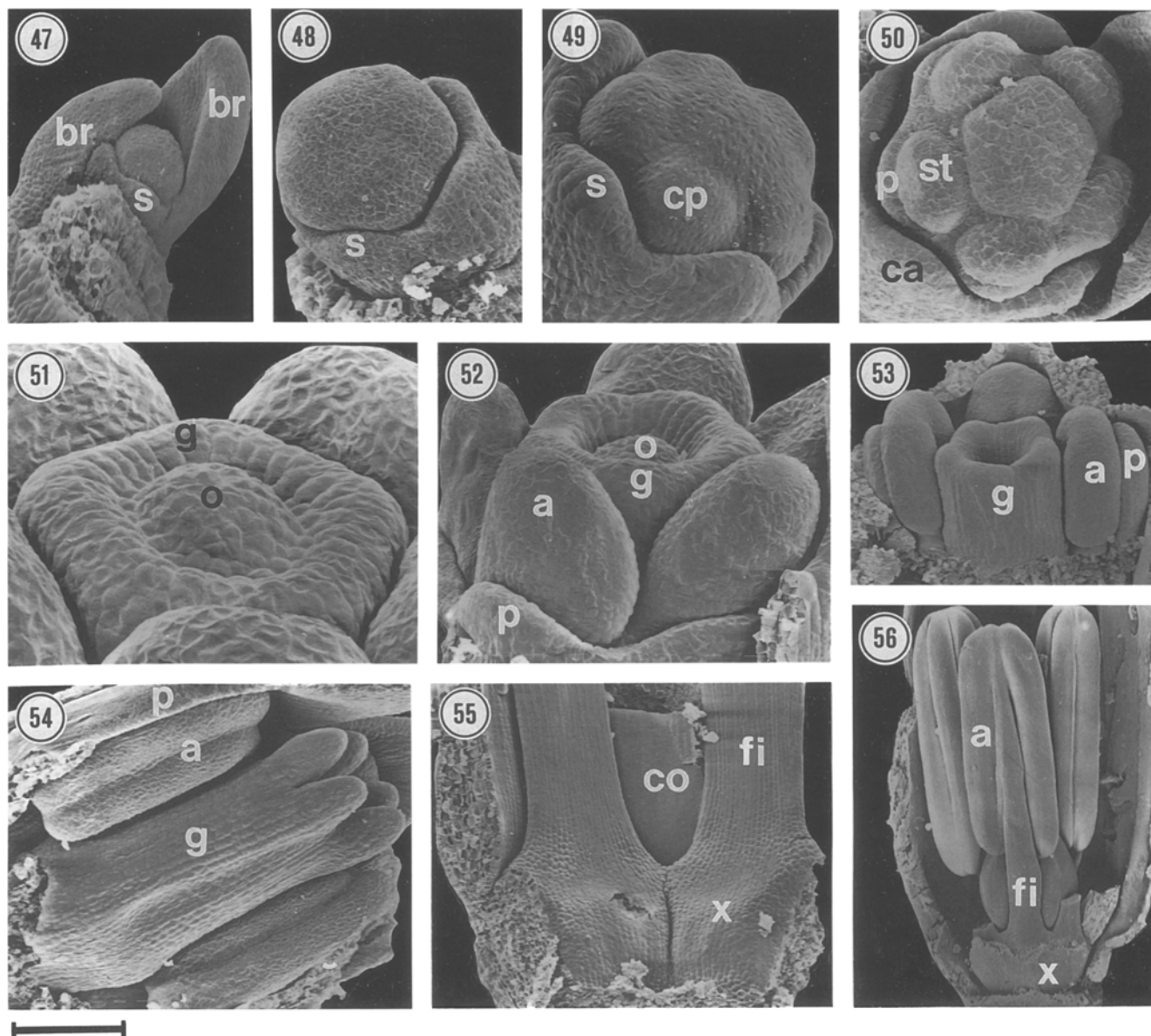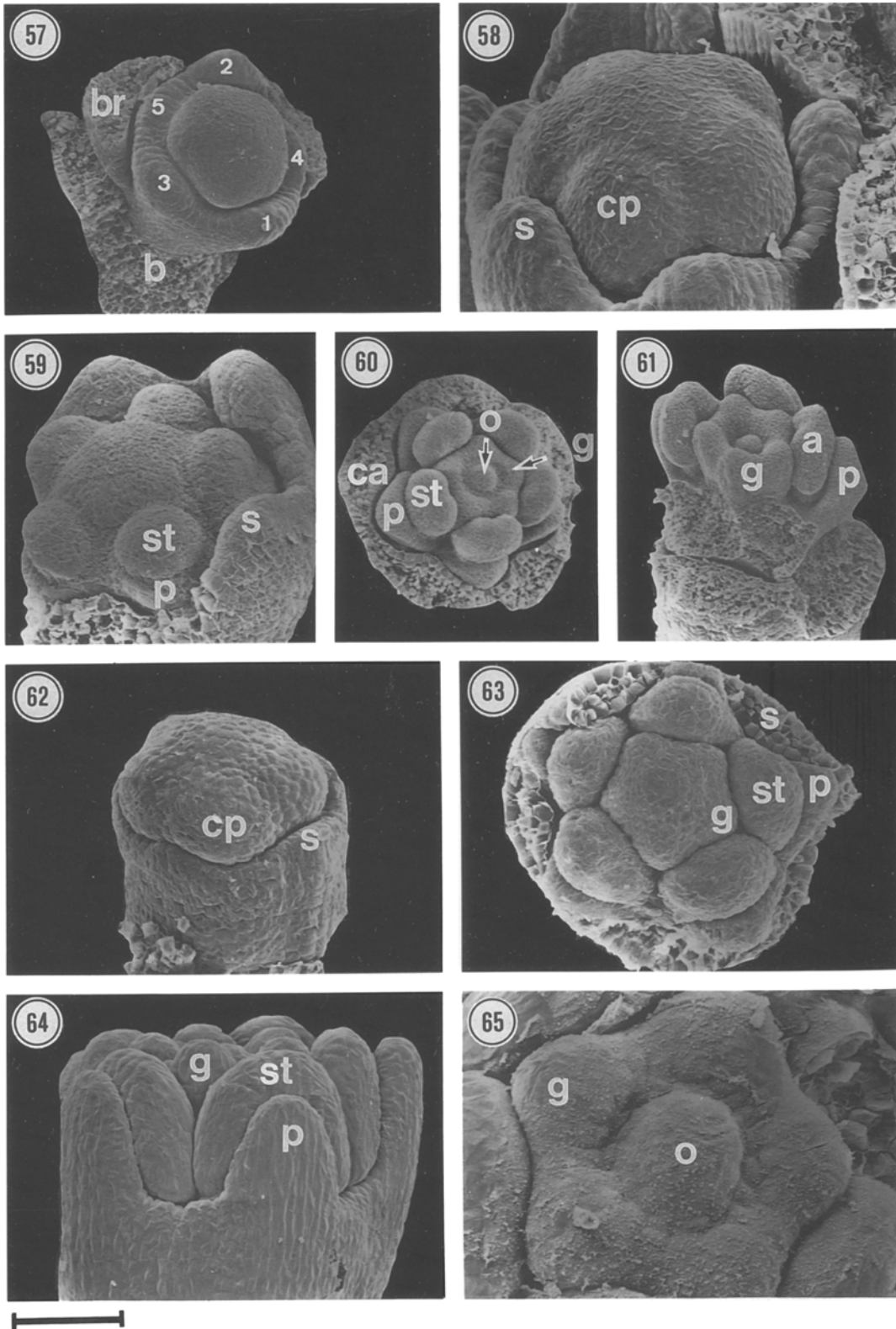
Figs. 47-56. SEM observations of floral development in *Ceratostigma plumbaginoides*. 47. Young floral bud surrounded by two bracteoles, showing sepal inception (bract removed; bar=100 μm). 48. Initiation of sepal primordia (bar=50 μm). 49. Development of the sepals and inception of the common primordia (bar=50 μm). 50. Separation of petal and stamen primordia; the petal primordia have already reached continuity; inception of the gynoecium as a pentagonal ring (bar=50 μm). 51. Ringlike gynoecium and ovule inception (bar=25 μm). 52. The gynoecial ring is slightly elongated; petal development lags behind stamen development (bar=50 μm). 53. Five lobes appear on top of the gynoecial tube (bar=100 μm). 54. Ovary, style and stigmata become visible on the gynoecium (bar=200 μm). 55. Adaxial side of the swollen, nectar-secreting filament bases (bar=200 μm). 56. Flower before anthesis showing petal-filament tube at base (bar=400 μm). Abbreviations: a, anther; br, bracteole; ca, calyx; co, corolla; cp, common stamen-petal primordium; fi, filament; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; o, ovule; p, petal; s, sepal; st, stamen; x, continuous structure at the base of corolla and androecium.

nature of the phylogenetic processes involved is left open.

The occurrence of common stamen-petal primordia (i.e. an integration of the earliest stages of stamen and petal development) does not necessarily imply that the later developmental stages of petals and stamens are also integrated, as is clear from *Plumbago auriculata*. Common stamen-petal primordia are present in this species (Figs. 58, 59), but the common base beneath petal primor-

dium and stamen primordium in the earliest stages does not develop any further (as it does in e.g. *Acantholimon glumaceum*). Since also any other kind of process that leads to continuity is absent during these later stages, corolla and androecium are not continuous at maturity. Conversely, in many angiosperm taxa the later stages of corolla and androecium development are highly integrated while no common primordia are present in the earliest stages (e.g. in *Eucnide*, Hufford 1988),

The fact that common primordia are not necessarily linked with synorganization during later developmental stages (and vica versa), probably reflects a difference in the main constraints that act in the earliest stages on the one hand and in the later stages on the other. Integration of the earliest stages is part of the evolution of the phyllotactic pattern of the flower and as such it is heavily constrained by the underlying mechanisms of phyllotaxis. Synorganization during the later stages is probably more constrained by functional concerns relating to pollination, fertilisation and fruit development. Consequently both can evolve more or less independently and it may be useful to have a term that refers only to synorganization of the earliest stages (negative dédoublement). It is interesting to note that similar conclusions can be drawn from recent advances in the genetics of flower development, where it has been shown that the genetic mechanisms of establishment of organ number (related to phyllotaxis) and specification of organ identity (related to the further development of primordia) are to some degree separate (Coen 1991, Coen and Meyerowitz 1991).

These considerations do not imply that the evolution of the early stages on the one hand, and the later stages on the other, are completely independent or are ruled by nonintersecting sets of constraints. The primordia that are initiated during the earliest stages are the raw material for the later stages, so that these later developmental stages are indirectly influenced by floral phyllotaxis. On the other hand, there is no *a priori* reason why evolutionary changes of the earliest stages (restricted by the constraints of the phyllotactic mechanism) cannot be compatible with functional concerns later on.

The tube beneath the filament bases has been variously interpreted in the past. In a purely descriptive sense it is often simply seen as part of the corolla (e.g. Heywood 1978 : 79 : "stamens... inserted at the base of the corolla"). In a second interpretation, it is seen as a structure that is essentially androecial (e.g. Friedrich 1956, Roth 1961b). Lastly, it has been interpreted as an axial structure, i.e. as a receptacular outgrowth (e.g. Pfeffer 1872 : fide Roth 1961b). In our view, the question whether the tube beneath the filament bases is essentially corollous, androecial or receptacular is the wrong kind of question. It possesses properties of all three and as a whole it cannot be reduced to any of them (see Sattler's 1988 concept of dynamic morphology).

Gynoecium

The gynoecium of the Plumbaginaceae is acarpellate *sensu* Sattler (1974), meaning that the ovules do not arise on the structures that develop from the gynoecial primordia (which they do in carpellate gynoecia). Sattler's approach to gynoecial morphology is in the first place an attempt to make a clear distinction between empirical observation and theoretical interpretation in those cases where the classical carpel concept is difficult to apply. It is intentionally meant to be purely descriptive and neutral with respect to evolutionary interpretations. So, carpellate and acarpellate gynoecia may or may not be fundamentally different within the angiosperms; the one may be derived from the other or vice versa; transitions between both may be frequent or not: all possibilities are left open, and all kinds of evolutionary and morphological models and interpretations can be superimposed on Sattler's approach. While it is intentionally meant to be purely descriptive, it does of course not exclude phylogenetic interpretation. Because of the heterogenous distribution of acarpellate gynoecia in the Magnoliatae, Cresens and Smets (1989a, 1990) rejected the idea that carpellate gynoecia on the one hand and acarpellate on the other are homologous in all angiosperms. Based on the various ways in which pistils become visible during early ontogeny, they defined the character carpel-form with the states leptate, pseudoleptate and coenoleptate (Cresens and Smets 1989a, 1989b, 1990, 1992). This characterisation, not to be confused with peltate carpel theory (e.g. Troll 1932), is relatively straightforward to apply in a majority of angiosperms and seems to define three major complexes of angiosperm families (Cresens and Smets 1989a, 1990). However, it is difficult to interpret the early gynoecial development in the Plumbaginaceae as one of the three basic states defined

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Figs. 57-65. SEM observations of floral development in *Plumbago auriculata* (56-59) and *Limoniastrum monopetalum* (62-65). 57. Young floral bud of *Plumbago auriculata* with the 2/5 spiral inception of the sepals (bract removed; bracteoles partly removed; bar=100 μm). 58. Initiation of five common stamen-petal primordia alternating with the sepal primordia (bar=50 μm). 59. Petal and stamen primordia are clearly separated on the common primordia (two sepals removed; bar=50 μm). 60. Inception of the gynoecium as a pentagonal ring; inception of the ovule primordium (sepals removed; bar=100 μm). 61. The gynoecial ring is slightly elongated; five lobes appear on top of it (sepals, two petals and two stamens removed; bar= 100 μm). 62. Young flower of *Limoniastrum monopetalum* with five sepals and inception of five commmon primordia (bar= 100 μm). 63. Inception of the gynoecial primordia (sepals removed; bar=100 μm). 64. Lateral view of a developing flower (bar=100 μm). 65. Ovule initiation (bar=50 μm). Abbreviations: b, bract; br, bracteole; ca, calyx; cp, common stamen-petal primordium; g, gynoecial primordium (sensu Sattler 1974) or gynoecium; o, ovule; p, petal; s, sepal; st, stamen.

by Cresens and Smets. If one agrees that the Plumbaginaceae are related to the Caryophyllales (belonging to the leptate group of families), then their gynoecium can be interpreted as composed of leptate carpels in which the adaxial portions of the circumplastic carpel primordia are extremely reduced (i.e. a latently leptate carpel form according to Cresens and Smets 1992).

Mainly on the basis of the ovule implantation relative to the ontogenetic closure of the carpels, Taylor (1991) defined the character 'carpel morphology'. In terms of this character, the Plumbaginaceae possess an ascidate gynoecium. However, the correctness of this homologisation in all angiosperms can be doubted on the grounds that ascidate gynoecia can arise developmentally in very dissimilar ways, while different states of this character may be produced by rather similar ontogenies (cf. Cresens and Smets 1990).

The single basal ovule of the Plumbaginaceae is often characterised as anatropous (e.g. Kubitzki 1993, Cronquist 1981, Heywood 1978), but because of the presence of a long funicle that is curved around the ovule (e.g. Figs. 13, 28), it has also been called circinotropous (e.g. McLean and Ivimey-Cook 1956, Melchior 1964, Bouman 1984). Long and curved funicles are also present in Cactaceae, but the circinotropous ovule of the Plumbaginaceae is characteristic due to the very slender funicle and the doubly inverted position of the mature ovule, with the micropyle pointing away from the basal placenta to the top of the ovary. In a mature ovary, the micropyle is in close contact with transmitting tissue that protrudes from the roof of the ovary into the locule. Protrusions of transmitting tissue into the locule develop in several angiosperm families and are called obturators irrespective of their morphological origin (Schnarf 1929). The obturator of the Plumbaginaceae consists of endotrophic transmitting tissue (Schnarf 1929 : 288) projecting from the base of the style(s) inwards ; this type of obturator seems to be unique within angiosperms.

The floral nectaries

All the observed species possess nectarial tissue on the adaxial side of the broadened filament bases, often extending downwards on the tube. As discussed earlier, this tube is neither essentially corollous, androecial or receptacular, but has properties of all three. Within this family, the presence of nectarial tissue on it is clearly an androecial property. First of all, the nectarial tissue is situated at its adaxial side and extends into the region where the filaments can be clearly recognized. Secondly, in the case of Plumbago auriculata, where corolla and androecium are not continuous with each other, nectarial tissue is only present on the filament bases, and not on the corolla.

Smets (1986, 1988, 1989 ; see also Smets and Cresens 1988) delineated floral nectary types that have a maximal predictive value for the higher magnoliophytinean taxa. His hierarchical ordering of nectaries is based on their association or homology with the major floral morphomes,

namely the androecium, the gynoecium, the receptacle and the different perianth morphomes. Within this framework, the nectaries of all observed species of the Plumbaginaceae are associated with the androecium and belong to the androphyllominous caducous nectaries of the staminal type. It is obvious that an interpretation of the cylindrical tube as essentially corollous or receptacular will lead to a wrong characterization of the nectarial type in the Plumbaginaceae ; e.g. according to Swales (1979), the nectaries of Armeria are situated on the corolla.

In general, nectar secretion occurs through rigid stomata ("nectarostomata" sensu Ronse Decraene and Smets 1991 ; cf. Smets 1988), through submicroscopical pores in the cuticle, or by diffusion through the epidermis. Nectarostomata were observed in Armeria maritima, Limonium latifolium and Limoniastrum monopetalum of the Armerioideae and Plumbago auriculata of the Plumbagoideae, but not in the other investigated species. This distribution reinforces Smets' conclusion (1988) that the mode of nectar secretion is generally only relevant at a low taxonomical level.

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