



Floral Development and Anatomy of *Moringa oleifera* (Moringaceae): What is the Evidence for a Capparalean or Sapindalean Affinity?

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Floral development and anatomy of *Moringa* have been investigated in the context of the disputed view of a capparalean affinity. Flowers arise in terminal or axillary panicles. Sepals arise sequentially and petals simultaneously. Antepetalous stamens arise simultaneously and precede the antesealous staminodes, which emerge sequentially. Within their respective whorls, the petals and stamens become twisted along different orientations. The gynoecium develops as a ring primordium on which three carpellary lobes become demarcated simultaneously. A saccate ovary bears numerous ovules on a parietal placentation and is topped by a hollow style. The interpretation of laminal placentation is denied. Monothechal anthers are formed by the failure of one half to initiate. The flowers present a peculiar form of zygomorphy running transversally from the petal between sepals 3 and 5 to sepal 4. The shape and position of petals and stamens is related to a pollen presentation mechanism with bowl-shaped anthers on different levels. The floral anatomy also reflects the zygomorphy of the flower. Although *Moringa* shares important morphological features with certain members of the Sapindales and Capparales, differences in ontogeny make a close relationship with either Capparales or certain Sapindales appear uncertain. © 1998 Annals of Botany Company

Key words: *Moringa*, Moringaceae, Capparales, Sapindales, floral ontogeny, floral anatomy.

INTRODUCTION

Moringa is a small genus comprising ten–12 (14) species distributed in Africa and Asia (Willis, 1966; Verdcourt, 1985; Mabberley, 1990). *Moringa oleifera* L. is a large shrub or a small tree with bi-(tri-)pinnate leaves. The base of the stem is swollen in young stages and is edible, as are the leaves and young fruits (Ernst, 1963: horse-radish tree). The monogeneric family Moringaceae has been traditionally placed in or near the Capparales because of the shared presence of glucosinolates and mustard-oils, along with several other characters, such as zygomorphic flowers, the presence of a gynophore, parietal placentation, and lack of endosperm (e.g. Pax, 1891, 1936; Dahlgren, 1980, 1989; Cronquist, 1981; Takhtajan, 1997).

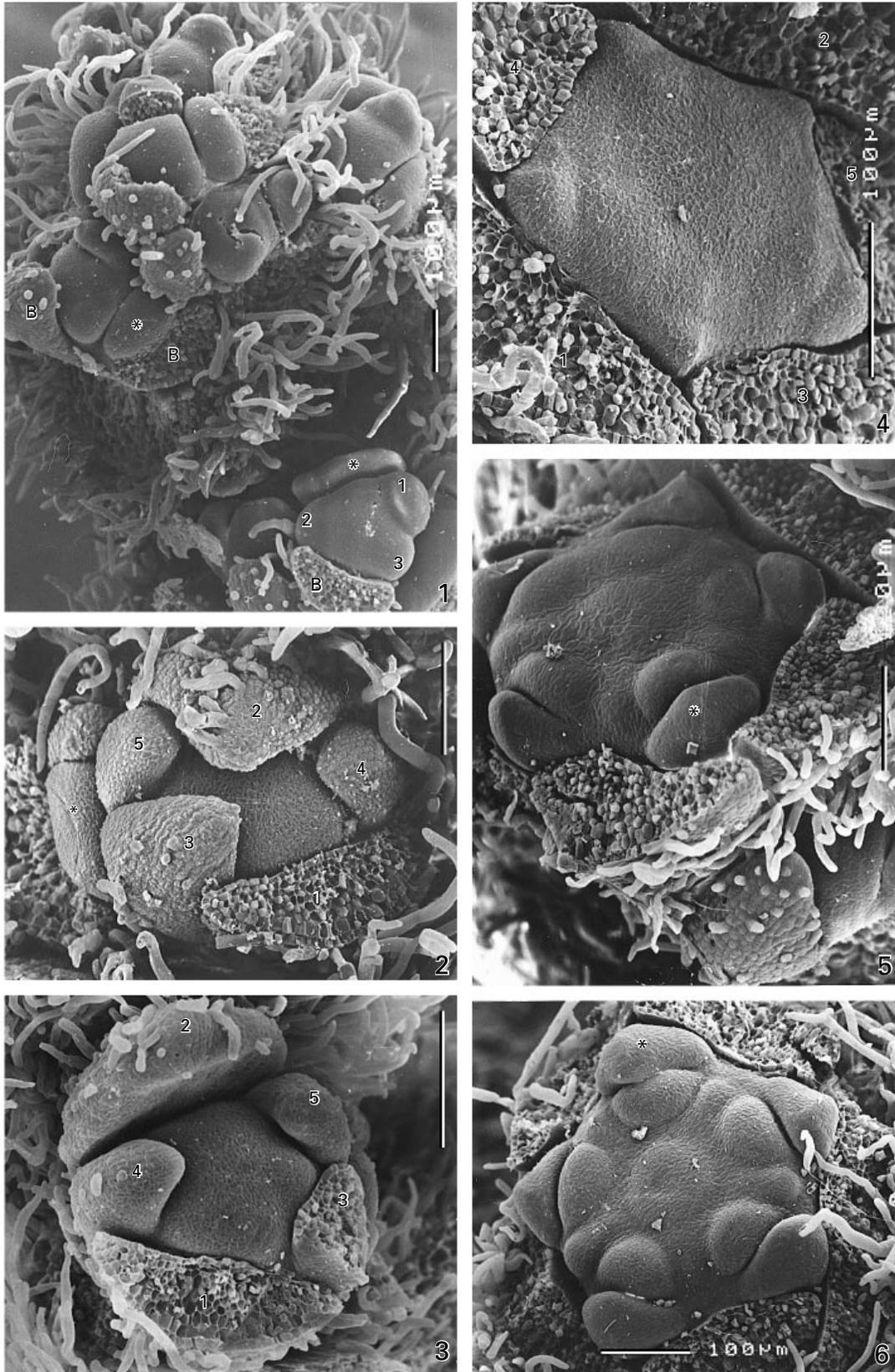
Especially in the light of recent cladistic analyses performed by Rodman and co-workers (1993, 1994, 1996) using macromolecular and morphological data, *Moringa* appears as part of an extended Capparales. Rodman *et al.* (1993) recognized a core group of Capparales (including Capparaceae, Tovariaceae, Brassicaceae and Resedaceae) and only two independent origins of mustard-oil producing plants were postulated, one leading to the Capparales (corresponding more or less with the 1975 and 1977 classifications of Dahlgren), and the other to *Drypetes* (Euphorbiaceae). A more recent study by Rodman *et al.* (1996) did not change this scheme but included the genus *Pentadiplandra* (Pentadiplandraceae). Rodman *et al.* (1996)

also accepted the order Capparales and extended it to all mustard-oil producing taxa, except for *Drypetes*. The hypothesis of a diphyletic convergence of glucosinate biosynthesis is thus well supported on a molecular and morphological basis (Rodman 1991*a, b*; Rodman *et al.*, 1996).

However, the comfortable position of *Moringa* in the Capparales has been repeatedly challenged by several authors. Unusual characters are the regular pentamerous calyx and corolla (though occasionally present in a few Capparales such as Pentadiplandraceae), obhaplostemony with five antesealous staminodes, hairy filaments with monothechal anthers, a trimerous gynoecium with deviating placentation, an aberrant pollen morphology, absence of a chlorophyllous embryo, and seed coat characteristics (e.g. Baillon, 1868; Hallier, 1908; Corner, 1976; Dutt, Narayana and Parvathi, 1978; Rao, Avita and Inamadar, 1983; Ferguson, 1985; Periasamy and Indira, 1986). Kolbe (1978) did not find any evident serological relationship between *Moringa* and the other Capparales. Although Dahlgren (1989) placed *Moringa* in the Capparales, she admitted that 'the resemblance [of *Moringa*] to some Sapindaceae may be of phylogenetic significance since *Moringa* is strongly reminiscent of some members of this family' (Dahlgren, 1990: 155).

Puri (1942) and Periasamy and Indira (1986) pointed to the unusual laminal position of the placentation (in the middle of the carpels) in the tricarpellate gynoecium of *Moringa*, not parietal (alternating with the carpels) as in most Capparales. Datta and Mitra (1949) proposed to shift Moringaceae to Violales near Violaceae, because of super-

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FIGS. 1-6. For legend see facing page.

ficial similarities in the pentamerous zygomorphic flowers and embryological characters. Dutt *et al.* (1978) also found sufficient morphological evidence to raise Moringaceae to an order Moringales and pointed to similarities with Malvales. On the basis of vegetative characteristics, Rao *et al.* (1983) could not find evidence for a relationship of *Moringa* with either Violaceae or Capparaceae. Hallier (1908) placed *Moringa* together with *Bretschneidera* within his Leguminosae (Caesalpiniaceae). Certain similarities of *Moringa* and *Bretschneidera* with Leguminosae are indeed impressive, such as the stipules reduced to glands ('Stipularnarben'), compound leaves, pentamery, hairy filaments with versatile anthers, a hypanthium ('Becherkelch'), and the curved 'Leguminosae'-style associated with zygomorphy. Thorne (1992*a, b*) also removed Moringaceae from his Brassicales and transferred them to his Sapindineae of Rurales.

Floral ontogeny has become a new potential source of characters for discussing phylogenetic affinities. As the aggregation of different glucosinolate-producing families from traditionally widely separated orders is intriguing in the light of important floral dissimilarities, we plan to perform floral ontogenetic studies of representatives of Caricaceae, Tropaeolaceae (forthcoming studies), as well as Moringaceae (this study) to investigate whether their floral ontogenies coincide with the hypothesis of Rodman *et al.* (1996). The relationships of the taxa investigated should, in the best case, correlate with certain similarities in ontogeny. In a following step we want to check the position of *Moringa* in the glucosinolate clade by a renewed cladistic investigation, comprising a large number of morphological characters, including ontogenetic data. Besides the study of Baillon (1868) on *Moringa oleifera* L. (as its synonym *M. pterygosperma* Gaertn.) and limited data on the gynoeceum from Puri (1942) and Periasamy and Indira (1986), no ontogenetic studies have been carried out and there are several gaps in the data set for *Moringa*. It also seemed worthwhile to reinvestigate floral anatomy in this study.

MATERIALS AND METHODS

Flower buds of *Moringa oleifera* Lam. were collected by Jan De Laet in Burundi in 1991 (Kajaga, along Route Nationale 4, near Bujumbura). Material was fixed in FAA (85 ml ethanol 70%, 10 ml acetic acid, 5 ml formaldehyde 40%). The buds were transferred to 70% ethanol and dissected under a Wild M3 dissecting microscope. The material was washed repeatedly in 70% ethanol and dehydrated in a 1:1 mixture ethanol-dimethoxyethane (DMM or formaldehyde-dimethylacetal) for 5 min and in pure DMM for 20 min (cf. Gerstberger and Leins, 1978). Buds were critical-point dried using liquid CO₂ in the CPD 030

(Balzers). The dried material was mounted on aluminium stubs using Leit-C (after Göcke) or double tape and coated with approx. 180 nm of gold (Spi Sputter Coater of Spi Supplies) before observation with the SEM.

For light microscopy, preanthetic buds were prepared following usual methods. The material was run through an ethanol as well as an ethanol-tertiary butanol series and was embedded in paraplast, using the histokinette 2000 (Reichert-Jung) automatic tissue processor and the paraffin dispenser PAG 12 (Medite). Serial sections, about 8–11 µm thick, were stained with safranin and fast green using the automatic staining machine Varistain 24-3 (Shandon). Photographs were taken under a Leitz Dialux 20 equipped with a Wild MPS 45/51 photoautomat.

Fixed voucher material and a herbarium specimen (De Laet 91-61) are kept at the botanical institute of the K. U. Leuven (LV) and the National Botanical Garden of Belgium (BR).

RESULTS

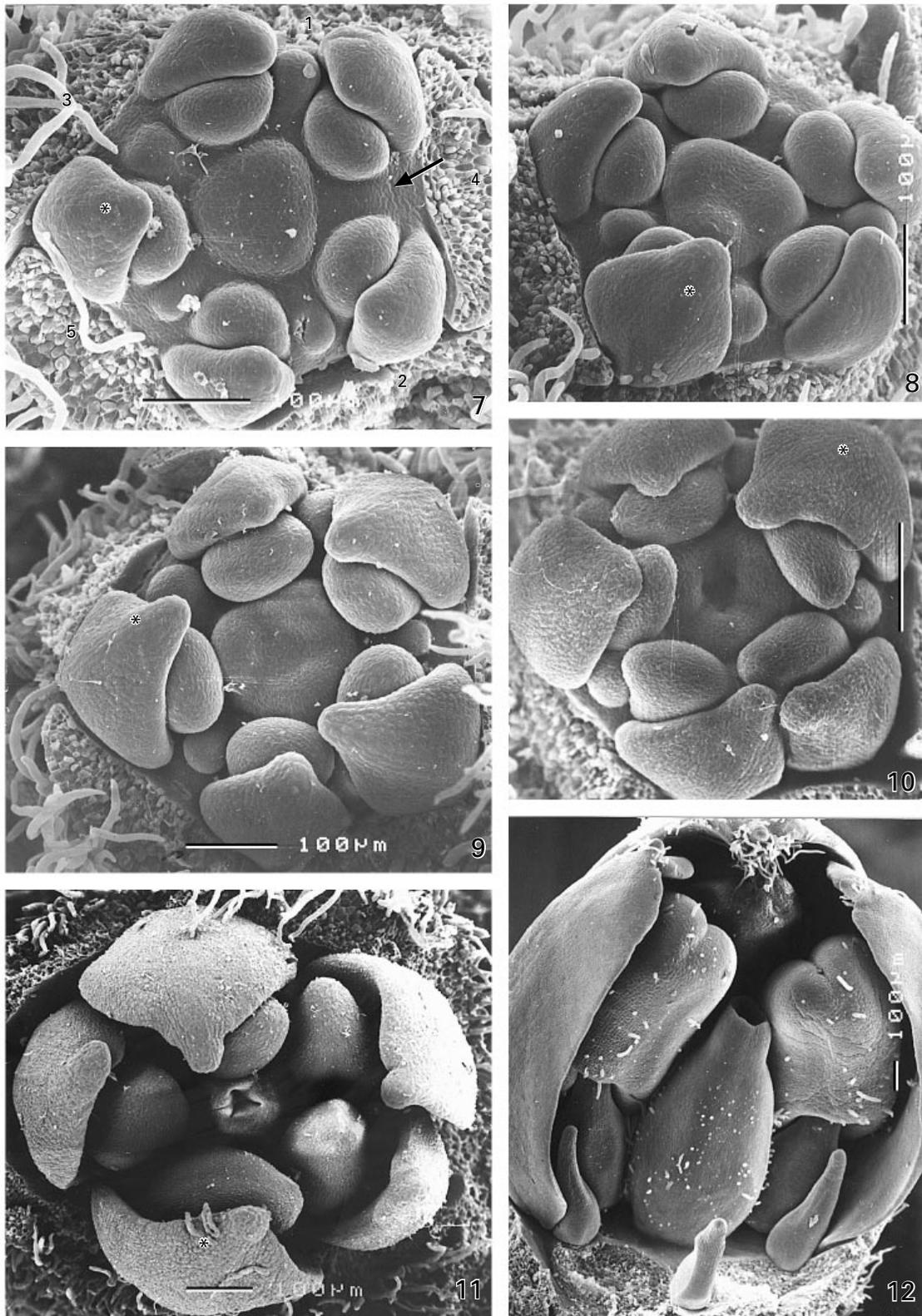
Floral ontogeny

Inflorescences arise as terminal or axillary panicles with short, widely separated branches (Figs 1 and 33). Top flowers develop before the lower branches; on each branch flowers develop basipetally. Each top flower is subtended by a bract with two bracteoles (Figs 1 and 2). Secondary flowers arise in the axils of the bracteoles and are eventually flanked by tertiary flowers (Fig. 2). Occasionally, secondary flowers are formed on one side only, leaving the other bracteole without a flower [Figs 1 (asterisks) and 2]. As this occurs on a whole partial inflorescence, the flowers appear to hang on one side of the inflorescence. At maturity the bracteoles become displaced on the stem.

Sepal initiation is sequential in a two/five phyllotaxis (Figs 1–3); the sepals grow rapidly and cover the bud in a quincuncial aestivation before initiation of petal primordia takes place. The two outer sepals precede the inner in size; the third is intermediate and arises either left or right of the first sepal in equal proportions; size differences are maintained during ontogeny of the flower (Figs 3 and 5). Following their initiation, the sepals become covered with a thick indumentum of long unicellular hairs (Fig. 2). At maturity they are long, petaloid and recurved.

A flattened five-angled platform is initiated in the next step. Alternisepalous protuberances arise more or less simultaneously in the corners of this platform (Figs 3 and 4). They grow rapidly into triangular petal primordia. The petal primordium situated between sepals three and five remains regular and rapidly becomes the largest petal. The four other petals become distorted by irregular growth of their apices (Figs 5–11). They have their apices bent two by

Figs. 1–6. Early stages in the floral development of *Moringa oleifera*. Fig. 1. Partial view of young paniculate inflorescence showing different stages of floral development; first order and second order bracts or bracteoles (B) have been partially removed. Note younger lateral flowers (asterisk) in the axil of the bracteoles. Fig. 2. Detail of flower with sepals before the initiation of the petals; the first sepal has been removed. Younger flower bud in the axil of a bracteole (asterisk). Fig. 3. Detail of flower at petal initiation; sepals one and three have been removed. Fig. 4. Initiation of the petals and antepetalous stamens. Antepetalous primordia appear on a low girdle; all sepals removed. Fig. 5. Lateral view at the initiation of antesealous staminodes. The staminode opposite sepal one arises first; asterisk indicates the petal between sepals three and five. Fig. 6. View of the flower with the sequential initiation of antesealous staminodes. Note the development of a gynoeceal girdling primordium; asterisk indicates the petal between sepals three and five. In Figs 1–4, numbers indicate sequence of sepal initiation. Bars = 100 µm.



FIGS. 7–12. Floral ontogeny of *Moringa oleifera* at androecial and gynoecial development. Fig. 7. Development of a triangular gynoeceum and sequential differentiation of the staminodes. The stamens and petals have a twisted growth in different directions. A staminode is missing opposite sepal four (arrow). Numbers indicate sepal initiation sequence. Fig. 8. Slightly older stage with appearance of three protuberances on the triangular gynoeceum primordium. Fig. 9. The petals start to overtop the stamens and the carpellary protuberances extend in size. Fig. 10. Formation of a central gynoeceal depression. Note the twisting of the petals and stamens. Fig. 11. Apical view of flower with upward growth of

two towards each other; those between sepals five, four and two are curved towards sepal two and those between sepals three, four and one are turned towards sepal one. Petal growth is not rapid; petals only start to cover the stamens at anther differentiation (Fig. 11). Later a few tufts of hairs develop near the apex of each petal (Fig. 12). The petals appear twisted in bud and have an imbricate-quincuncial aestivation (Figs 10, 11 and 34). Each petal of the overlapping pair lying farthest away from the larger petal covers one of the intermediate petals. The apical part of each petal appears elongated and becomes prominent in later stages of development (Figs 11 and 12). The arrangement of petals is characteristic of the species and the plane of symmetry of the flower is not median but nearly transversal. Floral zygomorphy is pronounced at maturity, as the larger, posterior petal remains erect, while the others are reflexed together with the sepals (Fig. 33). The intermediate and front petals are curved forward. The front petals bear short hairs on their ventral side and are smaller; they apparently function as a landing platform for visiting insects.

As soon as petals have been initiated, stamen primordia are formed almost simultaneously opposite the petal primordia (Fig. 4), followed by antesealous primordia lying slightly externally (Figs 5 and 6). At the time of their initiation all stamen primordia appear to be inserted on a low girdle (Figs 4 and 5). Contrary to the antepetalous primordia, the initiation and growth of the antesealous primordia is not simultaneous and appears to be unidirectional or in a spiral sequence, starting with the primordium opposite sepal one (Figs 5–8). The largest antesealous primordia are situated opposite the two outer sepals and between each lateral petal pair (Fig. 8). The smallest antesealous primordium, which sometimes fails to develop, lies opposite sepal four [Figs 7 (arrow) and 8]. Like the petals, stamens grow in an irregular way. The antepetalous stamen primordia tend to grow away from the petal pairs; in other words, they form converging pairs opposite sepals four and five, while the remaining stamen points towards sepal three (Figs 8 and 10). The antesealous primordia develop into filament-like staminodes without preferable growth direction (Figs 12 and 13); the staminode situated on the opposing side of the larger petal (opposite sepal four) lags behind the other and remains smaller at maturity (Figs 12 and 33). In this way the zygomorphic appearance of the flower is not only expressed by the corolla but also by the androecium.

Anther differentiation starts simultaneously with the growth of a short, stout filament (Figs 12 and 24). Only one theca is formed, concomitant with the asymmetric growth of the stamen. The single theca of each stamen points towards the largest petal. At later stages the lower part of the filament becomes abundantly covered with hairs (Figs 14 and 17). At anthesis the intermediate filaments (those opposite the petal between sepals one and three and the

petal between sepals two and five, see Fig. 34) are higher than those situated near sepal four, and all are curved forward. The stamen opposite the larger petal overtops the others. Even though the thecae are inserted laterally and are directed towards the larger posterior petal, they become placed in a frontal position through the curvature of the filament, as if presenting pollen in a hanging bowl (Figs 33 and 34). Because of the different length of the filaments, pollen is presented at three different levels. The two anthers situated between sepals two–four and sepals one–four may occasionally be sterile.

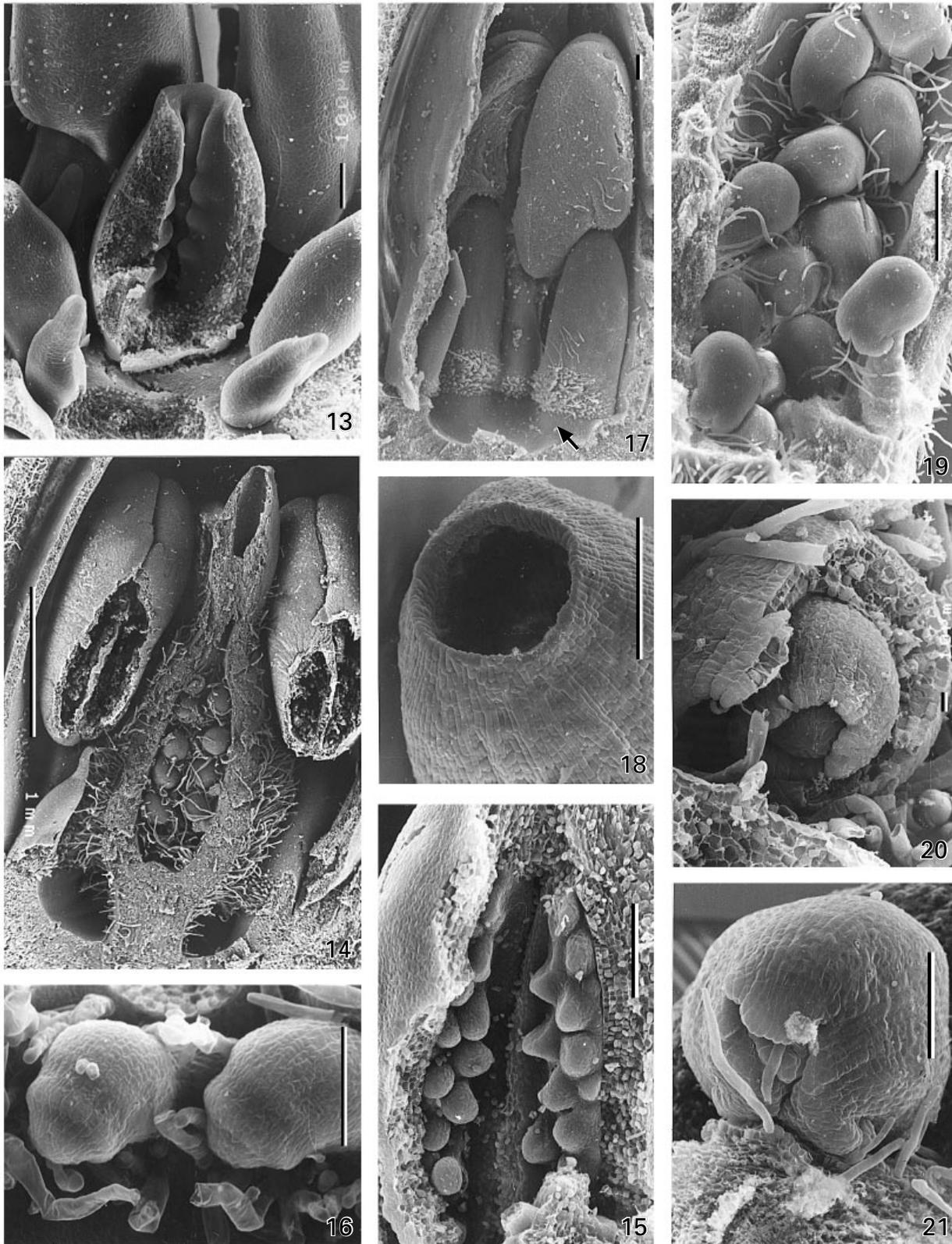
Following stamen initiation, the gynoecium is delimited as a flat disc (Figs 4 and 5), rapidly changing into a depression surrounded by a circular rim (Fig. 6). The outline becomes triangular and three large carpellary primordia are demarcated around the central depression (Figs 7–9). One carpel is always situated opposite the largest petal (between sepals three and five), while the others are placed opposite sepals one and two (Figs 9–11). Carpel primordia grow asymmetrically in a way similar to the petals and stamens, as they tend to overlap each other by their sides. The gynoecium grows into a tubular structure around a triangular depression. The result is a bottle-like ovary with a terminal part that grows later into a long neck with terminal aperture (Figs 12 and 22). There are no stigmatic lobes (Fig. 18), as erroneously stated by Willis (1966). The lower part of the gynoecium, containing the ovules, becomes covered with long unicellular hairs. The style reaches about one and a half times the size of the ovary and turns to one side of the flower, away from the largest petal (Fig. 14). A gynophore lifts the gynoecium to the same level as the stamens, concomitant with the invagination of the gynoecium into a depression due to zonal growth of the receptacle bearing stamens, sepals and petals (Figs 14, 17 and 23).

The flanks of the depression surrounding the gynophore appear to be nectariferous with a few scattered nectarostomata. Placentation is parietal, and is formed on the connection of two carpels. The ovules arise in two rows separated by a groove (Figs 13 and 15). They are interspersed with numerous hairs (intraovarian trichomes) resembling the external trichomes (Figs 14 and 19). The first ovules arise in the lower half of the placental ridge and are followed by other ovules in acropetal direction in a zigzag pattern (Figs 13, 15 and 22). Two integuments are differentiated as circular lobes around the nucellus while the ovule becomes anatropous with the micropyle turned inwards and upwards (Fig. 16). The inner integument grows as a circular rim while the outer integument grows irregularly as a crenelated flap of tissue and appears basally interrupted (Figs 19–21). Mature ovules appear to be campylotropous.

Figure 34 represents the floral diagram of *Moringa oleifera*. At anthesis the larger transversal petal is bent upwards, while the others are reflexed downwards together with the sepals. Stamens are erect and surround the style.

the gynoecium and formation of anthers. The larger petal is at the base of the figure. Fig. 12. Lateral view of partially dissected flower; two stamens removed. Note the staminodes, saccate gynoecium and unitecal stamens. Asterisks indicate the larger regular petal between sepals three and five.

Bars = 100 μ m.



FIGS. 13–21. Late floral ontogeny and ovule development of *Moringa oleifera*. Fig. 13. View of dissected ovary with rows of ovules arising on the parietal placenta; two carpels with attached ovules have been partially removed. Fig. 14. Nearly mature flower showing the gynophore and hairy filaments. Fig. 15. Detail of dissected ovary showing two placentas with two rows of ovules each. Fig. 16. Detail of two ovules. Note the presence of intraovarian trichomes and the development of the two integuments. Fig. 17. Section of flower prior to anthesis. Note the unithecal stamens with basal trichomes and the peripheral growth area below the stamens (arrow). Fig. 18. Detail of stigmatic crater. Fig. 19. Nearly mature

For illustrations of mature flowers we refer to Fig. 33, Baillon (1872) and Pax (1936).

Floral anatomy

Sections of the upper part of the flower show the arrangement of the anthers with two orientations pointing in the same direction (Figs 24 and 25). Each anther is laterally inserted and encloses the filament. Filaments show a broad arc of vascular tissue (Figs 25 and 28). At lower levels stamens become confluent with each other and with the petal bases, first at the side away from the larger petal, and extending to the other side (Figs 27–29). Traces for the petals and sepals converge at the same level and fuse with the vascular ring formed by the stamens (Figs 29 and 30), before connecting with the traces of the gynoecium (Fig. 31). Petal traces spread fan-like within the petals (Fig. 27). We found that the supply of the lateral traces of sepals four, two and one arise by the splitting of a common bundle to the petals. For sepals three and five, next to the larger abaxial petal, only one lateral trace arises by the splitting of a petal bundle (petals between sepals two–five and between sepals one–three); the other sepal lateral trace emerges by the early splitting of the sepal median bundle.

The ovules are inserted in two rows against large marginal carpel bundles, which form broad arcs of tissue (Fig. 25). In alternation with these marginal bundles and in a more peripheral position there are two laterally spreading dorsal bundles (Figs 25 and 26). Between the ovules and marginal carpel bundle is the vascular tissue supplying the ovules. Abaxially a groove is visible on each carpel. At the base of the ovary the ovular traces disappear and marginal carpel bundles become laterally concrescent with the lateral extensions of the dorsal traces. The fused bundles appear as a triangular structure (Fig. 27). At the base of the depression formed by fused petals and stamen bases the ovary becomes connected with receptacular tissue, at the side opposite to the free staminode (Fig. 28). At a lower level gynoecium vascular tissue becomes connected with the vasculature of the androecium and petals. At the level of the pedicel one finds a siphonostele (Fig. 32).

DISCUSSION

General considerations

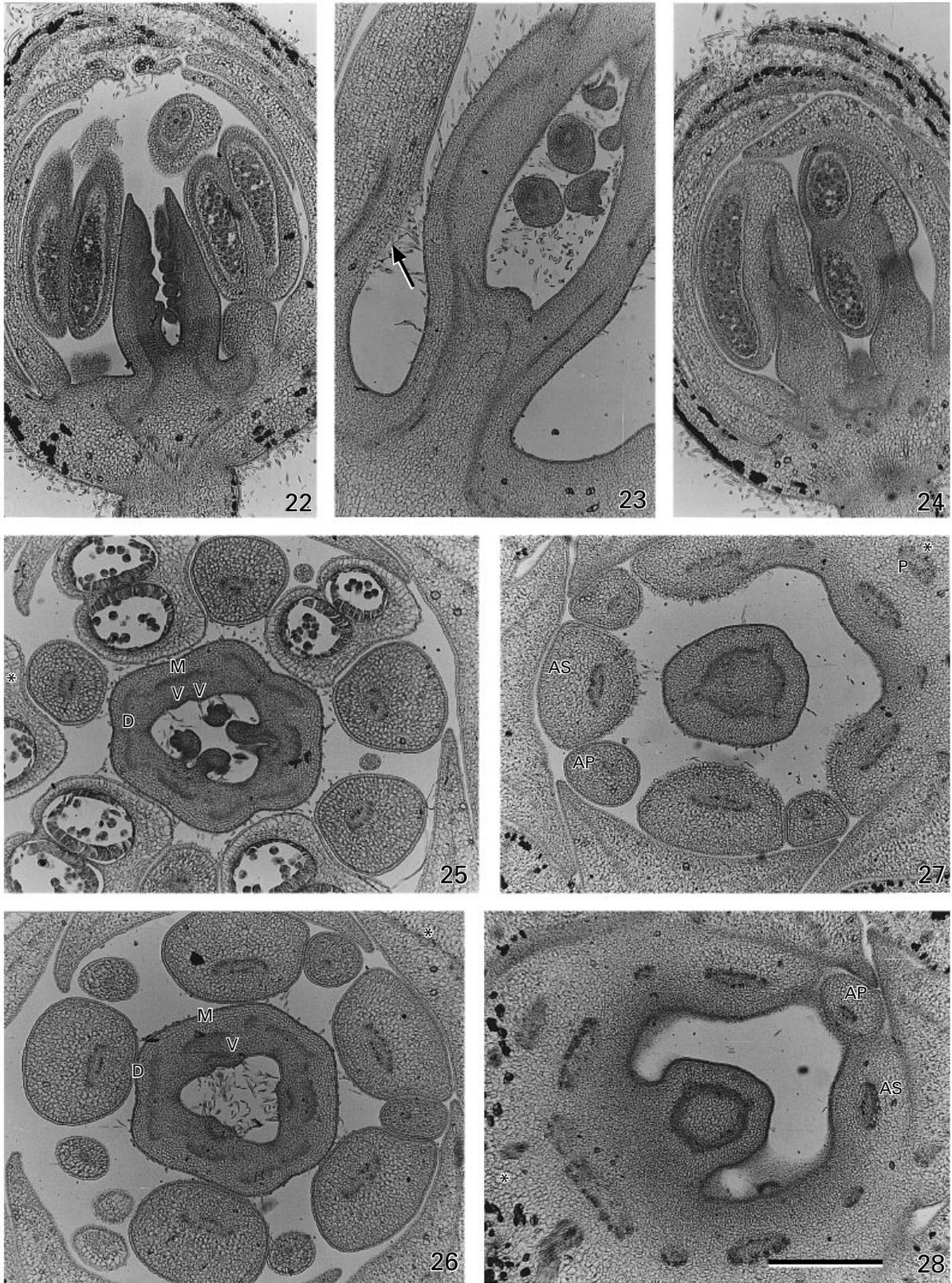
Floral development of *Moringa* has also been described by Baillon (1868), but without illustrations. His description lacks details but bears similarities to ours. Extensive floral anatomical investigations were carried out by Dutt *et al.* (1978) on *Moringa concanensis*. Their observations are congruent with the floral anatomy of *Moringa oleifera* presented here. Dutt *et al.* (1978) reported that all sepal laterals arose by the splitting of the sepal bundles in *Moringa concanensis*; we did not find this to be true for *M. oleifera*. The floral zygomorphy is strongly apparent in the

floral anatomy as the side of the flower towards the largest petal fuses at a higher level than the other side (Figs 28–30). We found that development and vasculature of *Moringa* followed a constant pattern.

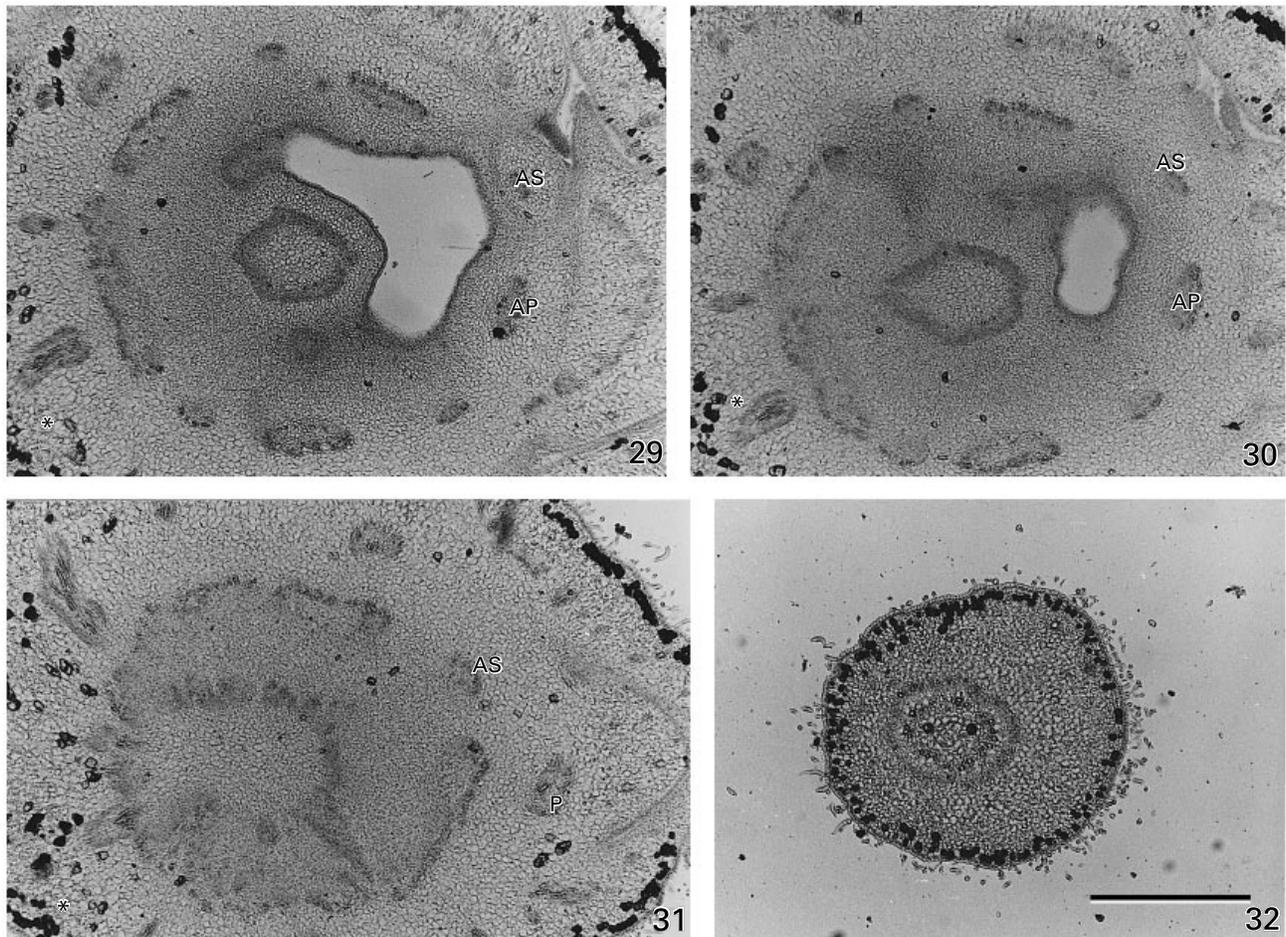
The vasculature of the gynoecium has been accurately described by Dutt *et al.* (1978) and Periasamy and Indira (1986), although their interpretations of the bundles differ. Puri (1942) and Periasamy and Indira (1986) illustrated the ontogeny and anatomy of the gynoecium of *Moringa*. They stated that the ovules are not situated marginally, but laminally (in the middle of the carpels). For this they relied on the inversion of ventral bundles and on the presence of the three grooves on the abaxial side of the carpels that they interpreted as carpellary margins. Periasamy and Indira (1986) explained this anomalous arrangement by postulating a progressive shift from a marginal position of ancestrally free conduplicate carpels to a laminar position. This leads to a totally different interpretation of vasculature and the nature of placentation. However, in their illustrations Periasamy and Indira (1986) give no indication of the position of carpels in relation to the rest of the flower. Our observations clearly demonstrate that one carpel always stands opposite the larger posterior petal (not opposite the posterior sepal as stated by Baillon, 1868), and the others opposite sepals one and two (Figs 8, 9, 25 and 34). Referring to these positions the floral anatomy indicates that the placentation develops marginally and not laminally, supporting the classical interpretation of most authors (e.g. Baillon, 1872; 334: ‘dans l’intervalle des feuilles carpellaires’: Pax, 1936; Dutt *et al.* 1978; Cronquist, 1981).

The zygomorphic appearance of the flower of *Moringa* differs from most other taxa with zygomorphic flowers, because zygomorphy is not median, but transversal, running from sepals three–five towards sepal four (Fig. 34). In this case the inflorescence axis cannot be used as a point of reference and one has to rely on the left hand side and right hand side in relation to the subtending bract, depending on the clockwise or counterclockwise initiation of the sepals. A similar transversal zygomorphy (‘schräg-zygomorph’, cf. Kopka and Weberling, 1983) with the axis of symmetry running through sepal four is rare, and known only for a few families of the Polygalales and Sapindales, viz. Vochysiaceae (e.g. *Salvertia*: Kopka and Weberling, 1983), Sapindaceae (e.g. *Serjania* and *Koelreuteria*: Eichler, 1878, pers. obs.), and Hippocastanaceae (e.g. *Aesculus*) (Eichler, 1878; pers. obs.). In most pentamerous flowers the zygomorphic symmetry line crosses the first or third sepal more or less in a median line (e.g. Payer, 1857; Eichler, 1878; Tucker, 1984; Endress, 1994; e.g. Caesalpiniaceae, Fabaceae, Lythraceae, Saxifragaceae, Trigoniaceae, Krameriaceae, Malpighiaceae, Anacardiaceae, Rutaceae, Tropaeolaceae, Akaniaceae, Violaceae, Scrophulariales). This is also the case in dimerous–octomerous flowers, such as Capparaceae, Brassicaceae, Tovariaceae and Resedaceae; one exception is *Corydalis* (Fumariaceae) with a transversal

campylotropous ovules and intraovarian trichomes. Fig. 20. Detail of partially dissected ovule showing the inner integument and nucellus. Fig. 21. The same, not dissected. Note the irregularly fringed outer integument. Bars = 100 μ m, except Figs 16, 20 and 21 (10 μ m) and Figs 14 and 17 (1 mm).



FIGS. 22–28. For legend see facing page.



FIGS. 29–32. Transverse sections of the base of the flower of *Moringa oleifera*. Fig. 29. Section at the level of departure of the adaxial petal and sepal traces. Note the abaxial staminode and zygomorphic appearance. Fig. 30. Section slightly lower showing the formation of a stamen and staminodial ring of traces. Fig. 31. Departure of sepal and petal traces and convergence of stamen and gynoecial rings of traces. Fig. 32. Section through the pedicel showing the siphonostele. Asterisks indicate the posterior side of the flower; AS, fertile antesepalous stamen; AP, antepetalous staminode; P, petal. Bars = 150 μm .

zygomorphy brought about by the presence of a spur (Eichler, 1878). Unfortunately, no such data are available for the zygomorphy of *Bretschneidera*, which has sometimes been related to *Moringa*. An irregular development is visible in the early ontogeny of *Moringa*, as the petal situated between sepals three and five remains regular and larger (the anterior petal as mentioned by Baillon, 1872), while the others grow pairwise in an oblique manner. The staminode opposite sepal four (named posterior by Dutt *et al.*, 1978, but actually in the lowest position in the mature flower) lags behind in development and is reported to be suppressed in *Moringa concanensis* (Dutt *et al.*, 1978). It also fuses with the receptacle at a lower level (Fig. 28). In *Aesculus carnea*

zygomorphy is also transversal but runs in the opposite way: the petal between sepals three–five is reduced or lost; there is also a displacement of stamens caused by the loss of some antepetalous stamens (Eichler, 1878; Ronse Decraene, 1992).

Contorted growth of the flower is common in many Malvaceae, Bombacaceae and Sterculiaceae (van Heel, 1966), but also in Caricaceae (pers. obs.). In *Moringa*, twisting tends to follow more than one direction, as can be visualized on a floral diagram (Fig. 34). The strongly zygomorphic appearance of the flower is stressed by the downward growth of the four latero-anterior petals and all sepals, the erect position of the larger petal (functioning

FIGS. 22–28. Longitudinal and transverse sections of the flower of *Moringa oleifera*. Fig. 22. Longitudinal section of young flower bud at ovule initiation. Fig. 23. Detail of the base of the ovary, showing the gynophore and nectariferous pits covered by the tufts of hair on the filaments (arrow). Fig. 24. Lateral view of the two monotheical stamens lying opposite the petals between sepals one, three and five. Fig. 25. Transverse section in the middle of the flower. Note orientation of the anthers and gynoecial vasculature. Fig. 26. Section at the level of the staminodes. Note the broad bands of vascular tissue in the filaments. Fig. 27. Detail at the fusion of a very short stamen ring, coalescing with the petals. The carpellary traces have converged to three points. Fig. 28. Section at the base of the gynophore. The antepetalous bundles extend laterally and fuse with the staminodial traces into a ring. Asterisks indicate the posterior side of the flower; D, dorsal; V, ventral; M, marginal traces; AS, fertile antesepalous stamen; AP, antepetalous staminode; P, petal. Bars = 150 μm , except Figs 22 and 24 (70 μm).

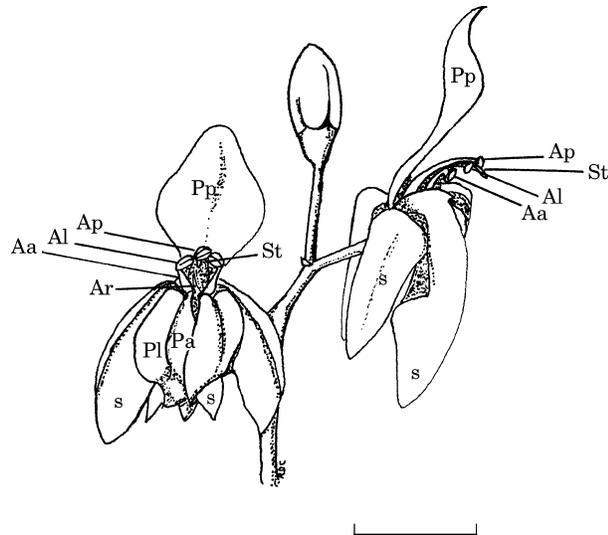


FIG. 33. Scale drawing of a mature inflorescence of *Moringa oleifera*. Note the zygomorphic flowers with landing platform. In the frontally placed flower one can see the erect posterior petal (Pp) with dehiscent anther (Ap), two non-dehiscent anthers standing lower (Al), and two antherless filaments (Aa). Also note the lowermost staminode (Ar) and the style (St) just below the upper anther; in the lateral flower one can discern the three horizontal levels of pollen presentation, and the style. Ap, Posterior stamen; Al, lateral stamen; Aa, anterior (sterile) stamen; Pp, posterior petal; Pl, lateral petal; Pa, anterior petal; S, sepal; St, style. Bar = 1 cm.

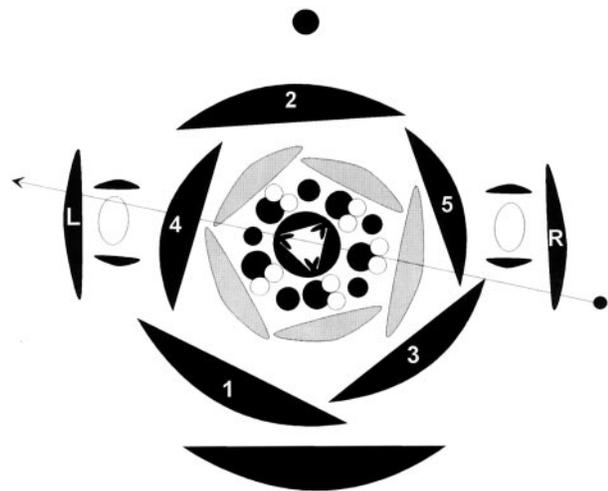


FIG. 34. Floral diagram of *Moringa oleifera*. Bracts, bracteoles (left, L and right, R) and sepals (numbers give sequence of initiation), black arcs; petals, grey arcs; black dots, staminodes; black dots with white twin-dots, stamens. Ovary shown with ovules in three pairs. Arrow represents the plane of symmetry.

mainly as a visual attractant), the reduction or loss of the staminode opposite sepal four, and the different orientations of the anthers (Fig. 33). To our knowledge this type of twisting is unique in the angiosperms.

The androecial configuration of the flower could be described as diplostemonous, as the insertion base of the antesealous staminodes is situated slightly more towards the periphery. However, initiation patterns of the an-

droecium differ between the two whorls. The antepetalous stamens are initiated before the antesealous whorl and arise simultaneously, while the antesealous staminodes lag behind and emerge sequentially. The androecium could be described as functionally obhapplostemonous (Ronse Decraene and Smets, 1995), which is an uncommon feature in the angiosperms. A similar androecium exists in Primulaceae, such as *Samolus valerandi* L. An analogous situation also occurs in the Malvales (e.g. *Theobroma cacao* L.) with antesealous staminodes. However, *Theobroma* differs in the position of the staminodes (inner whorl). We described this developmental pattern as primary obdiplostemony (Ronse Decraene and Smets, 1995), but it leads to a similar configuration as in *Moringa*.

Hairs on the base and upper part of the filament are fairly common in the angiosperms, (see, for example, Endress and Stumpf, 1991). Apart from Moringaceae, pubescent filaments occur on a frequent basis in the Sapindales (e.g. Bretschneideraceae, Sapindaceae, Hippocastanaceae, Anacardiaceae), but are absent in the Capparales. Monotheal anthers on the contrary, are rare in the dicotyledons. Endress and Stumpf (1990) gave a list for the dicotyledons (their Table 2); they also described the anthers of *Moringa oleifera*. As observed on sections, the monotheal anthers in *Moringa* are probably the result of the complete reduction of one theca without trace, linked with the strongly twisted anthers. The development of dish-like pollen-presenters may also be an explanation for this partial reduction.

The semi-inferior position of the ovary of *Moringa* 'Achsenskupula' of Pax, 1936) is caused by zonal growth below the perianth and stamens (cf. Figs 14, 17 and 23). The ovary remains free from receptacular tissue because a gynophore is initiated at the same time. In this way a chamber is created with smooth walls producing nectar by diffusion or through nectarostomata (a few are present). As the hairs on the filament bases are in contact with those of the gynoeceum and are situated just above the nectarial depression, they probably play some role in pollination, maybe as a nectar cover (cf. Endress and Stumpf, 1991). However, in the few sections we made, no clearly definable nectar-producing tissue could be detected, probably because the material was too young (Fig. 23). The flowers are reported to be sweet-smelling (Verdcourt, 1985).

The presence of a hole-like stigmatic aperture tends to be rare in eudicotyledons. A similar structure was observed in some Mimosaceae by Endress (1994) and Caesalpiniaceae by Kantz and Tucker (1994), besides Bretschneideraceae.

The occurrence of intraovarian trichomes (trichomes that occur inside the mature gynoeceum) is not widespread in the angiosperms (see Dickison, 1993 for an overview). It has been suggested that the trichomes facilitate the growth of the pollen tubes, functionally resembling obturators. This is probably also the case in *Moringa* with a relatively spacious ovular cavity.

Comparison of the morphology of Moringa with the Capparales and Sapindales

We have already mentioned certain similarities of *Moringa* with the Sapindales, such as hairy filaments, a trimerous

ovary and transversal zygomorphy. However, in other characters similarities are not so obvious and the ontogeny of the androecium and gynoecium is different (Payer, 1857; pers. obs.). Sapindaceae, Bretschneideraceae, Akaniaceae, Aceraceae and Hippocastanaceae show a reduced androecium with the loss of a few to all antepetalous stamens. Antesepalous stamens are always fertile. Apart from the characters presented in the introduction, *Moringa* differs in certain important morphological, ontogenetical and structural characters from the core Capparales. Floral development of Capparaceae (see, for example, Karrer, 1991; Erbar and Leins, 1997; Ronse Decraene and Smets, 1997a) and Brassicaceae (e.g. Payer, 1857; Polowick and Sawhney, 1986; Smyth, Bowman and Meyerowitz, 1990) differs strongly from that of *Moringa* being dimerous with unilateral or paired sepal initiation, having a two-whorled androecium (or multistaminate androecium with alternatively dimerous and tetramerous whorls arising centrifugally), and a dimerous gynoecium arising as a bag-like structure with strongly developed parietal placentae.

Gynoecial vasculature of Capparaceae shows weak dorsals (and carpel primordia) and strongly developed ventral bundles (with their placentae) (see, for example, Eggers, 1935; Leins and Metzenauer, 1979; Ronse Decraene and Smets, 1997b). These correspond with the position of the marginal bundles in *Moringa*. The presence of placental ridges with ovules in two irregular rows, apparently set in a zigzag pattern in *Moringa* closely resembles the placentation of certain species of *Capparis*. The interrupted fringed outer integument is also similar (pers. obs.; Ronse Decraene and Smets, 1997a).

The initiation of a low girdle delimiting the androecium and gynoecium is common in the Capparales, where numerous stamens arise centrifugally on a girdling primordium as in *Capparis* (Leins and Metzenauer, 1979; Karrer, 1991; Endress, 1992; Ronse Decraene and Smets, 1997a) and Resedaceae (Sobick, 1983). However, such initiation is not restricted to that order, but is widespread in the dilleniids, rosids and caryophyllids (e.g. Ronse Decraene and Smets, 1992).

The distinction between the merosities of Capparales and *Moringa* has more importance. The Capparales are basically dimerous (Ronse Decraene and Smets, 1993, 1994, 1997a) and disymmetric (Endress, 1992), or by derivation hexamerous-octomerous in Tovariaceae and Resedaceae. Therefore, tetramery is not derived from pentamery, but has a dimerous origin, contrary to the acceptance of other authors (e.g. Dahlgren, 1983; Rodman *et al.*, 1993) who described the Capparales as tetramerous without making this distinction of homology. The occurrence of pentamerous flowers in Capparales is incidental (e.g. *Pentadiplandra* which needs to be investigated, both on a morphological, ontogenetic, and anatomical basis). On the other hand, pentamery is widespread in most taxa of Malvales, Violales or Sapindales.

The floral morphology and ontogeny of *Moringa* demonstrates its isolated position. Floral ontogeny alone cannot be decisive about relationships with either Sapindales or Capparales. In a following cladistic analysis we will discuss the relationships of *Moringa* on a morphological basis.

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