

RANK OF THE SUBFAMILIES LORANTHOIDEAE AND VISCOIDEAE

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ABSTRACT

The family Loranthaceae has been divided into the subfamilies Loranthoideae and Viscoideae (Engler, 1888-89; Danser, 1929, 1933a, b). These two subfamilies show great dissimilarity in their morphological as well as their embryological characters.

In the Loranthoideae flowers may be unisexual or bisexual, but a calyculus is invariably present. The ovary may contain a lobed or unlobed mamelon, or the mamelon may be extremely reduced or absent. A collenchymatous pad or tube is invariably present in the ovary. The embryo sac is of the Polygonum type. Many embryo sacs may develop simultaneously in the same ovary and their tips grow up into the style and in some cases reach the stigma. The lower end of the sac sometimes produces a caecum. The endosperm is a composite structure formed by the fusion of all the endosperms developing in the same ovary. The first division of the zygote is always vertical and is followed by transverse divisions resulting in a long biseriolate proembryo. The fruit shows 4 distinct layers and the viscid layer is situated outside the vascular bundles of the corolla.

In the Viscoideae, flowers are unisexual and the calyculus is absent except in *Viscum orientale* and *V. articulatum*. The central ovarian papilla has 2 or more archesporial cells, each of which divides to form two dyad cells. Of these the upper dyad cell is the larger and functions, while the lower soon degenerates. Thus the development conforms to Allium type. A peculiar feature is that after the 4-nucleate stage there is a slow but steady curvature of the embryo sac, which causes its lower end to bend out of the papilla and proceed upwards into the carpellary tissue. The egg apparatus differentiates from the quartet in the originally lower pole, which is later situated at a higher level than the upper. Generally only one embryo sac develops which is said to show inverted polarity. The endosperm is derived from the primary endosperm nucleus of a single embryo sac. The first division of the zygote is transverse except in *Korthalsella*. The embryo lacks a suspensor. The viscid part of the fruit is situated within the vascular bundles of the perigone.

Thus, the Loranthoideae and the Viscoideae show important differences in floral structure, mode of development of the embryo sac, endosperm and embryo, and in the location of the viscid zone of the fruit. These differences adequately warrant the raising of the two subfamilies to the rank of families. As proposed by Miers (see Danser, 1929), the name Loranthaceae may be retained for the Loranthoideae, and the Viscoideae may be designated Viscaceae.

Most of the taxonomists (Engler, 1888-1889; Danser, 1929, 1933 a, b) classified the family Loranthaceae into the subfamilies Loranthoideae and Viscoideae. Miers (1851), however, treated the subfamilies as separate families-Loranthaceae and Viscaceae. Maheshwari (1954, 1958), Maheshwari, Johri and Dixit (1957) and Johri and Bhatnagar (1960) are also of opinion of giving the rank of families to these subfamilies.

During recent years several numbers of the Loranthaceae have been thoroughly investigated at the University of Delhi by Agrawal, S., Agrawal, J. S., Bhatnagar, S. P., Correa, J. P., Dixit, S. N., Johri, B. M., Maheshwari, P., Narayana, R. and Prakash, S. In light of huge available embryological and morphological data, the author strongly feels that these subfamilies deserve the rank of two different families.

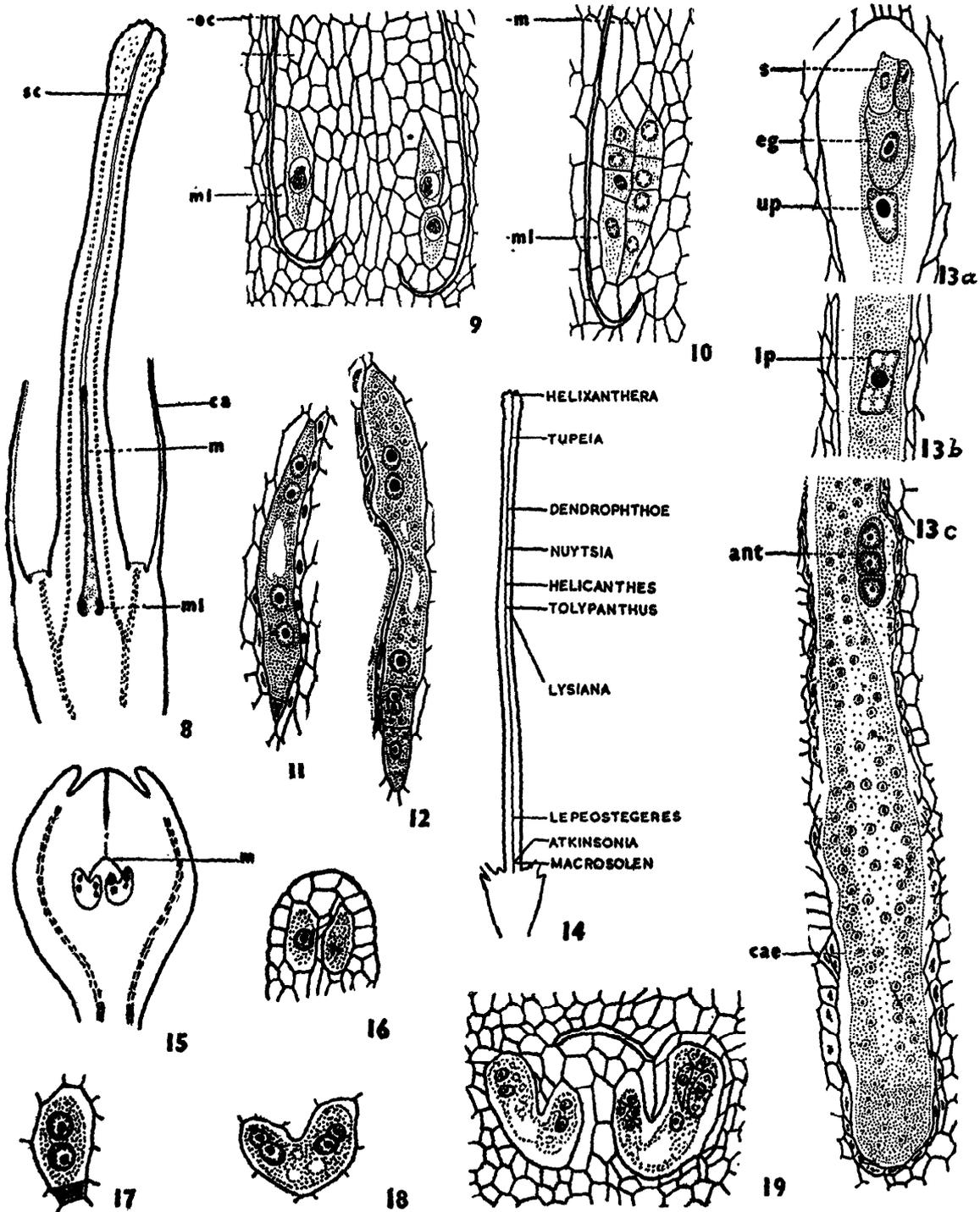
In the Loranthoideae the flowers are mostly bisexual but occasionally unisexual flowers occur in *Barathranthus*, *Tupeia*, *Struthanthus* and *Phthirusa*. *Nuytsia floribunda* shows polygamous condition.

The receptacle terminates into a fringed out growth called the calyculus. Taxonomists have used the presence or absence of the calyculus as a significant diagnostic character in subdividing the family Loranthaceae into Loranthoideae and Vis-

coideae. The calyculus is well developed in the dendroid *Atkinsonia* and *Gaiadendron*. In *Nuytsia* it is fleshy but reduced in size, and in *Lepeostegeres* it is equally well developed but remains membranous (Fig. 8). It is rather small in *Tolypanthus* and *Tapinanthus* and several other members, and inconspicuous in *Amyema*. The calyculus is devoid of vascular supply. However, in *Nuytsia floribunda* (Narayana, 1958 b) and *Atkinsonia* (Prakash, 1960) distinct vascular supply has been observed. The morphological nature of the calyculus has been a subject of much controversy and has been discussed by Maheshwari, Johri and Dixit (1957).

The pollen grains in the Loranthoideae are typically 3-rayed and have a smooth exine (Fig. 1). Rarely 4-rayed grains occur in *Helicanthes* (Johri, Agrawal and Garg, 1957), *Lysiana* (Narayana, 1958 a) and *Lepeostegeres* (Dixit, 1958 b). However, in *Tupeia* (Smart, 1952) and *Atkinsonia* (Prakash, 1960) the pollen grains are reported to be round and show irregular exine.

The ovary does not contain any normal ovule but several species show a special mammiliform structure, called the mamelon, which arises from the base of the ovarian cavity. The mamelon may be lobed and may be fused with the ovary wall in between the lobes (Fig. 3a, b) e.g., *Lepeostegeres* (Dixit, 1958 b), *Lysiana* and *Nuytsia* (Narayana,



Figs. 8-19. (*ant*-antipodal cells, *ca*-calyculus, *cae*-caecum, *eg*-egg, *lp*-lower polar, *m*-mameelon, *ml*-lobe of mameelon, *oc*-ovarian cavity, *s*-synergid, *sc*-stylar canal, *up*-upper polar). Figs. 8-14. megasporogenesis and female gametophyte in the Loranthoideae. Figs. 8-13. *Lepeostegeres gemmiflorus* (After Dixit, 1958b). Fig. 8. L.s. carpel at megaspore cell stage. Fig. 9. Enlarged view of mameelon from Fig. 8. Fig. 10. L.s. single lobe of the mameelon showing two linear tetrads. Fig. 11. 4-nucleate embryo sac. Fig. 12. 6-nucleate embryo sac. Fig. 13 a, b, c. Upper, middle and lower part of embryo sac showing egg apparatus and upper polar nucleus, lower polar nucleus and the antipodal cells respectively. Fig. 14. L.s. carpel showing extension of embryo sacs in the style; the names indicate the level of the tips of embryo sacs in respective genera. Figs. 15-19. megasporogenesis and female gametophyte in the Viscoideae. Fig. 15. *Korthalsella opuntia*. L.s. pistillate flower showing mameelon and the position of embryo sacs (After Correa, 1958). Fig. 16. *K. opuntia* L.s. placenta showing two megaspore mother cells (After Rutishauser, 1937). Figs. 17, 18. *K. dacrydii*. 2- and 4-nucleate embryo sacs (After Rutishauser, 1935). Fig. 19. Embryo sacs enlarged from fig. 15.

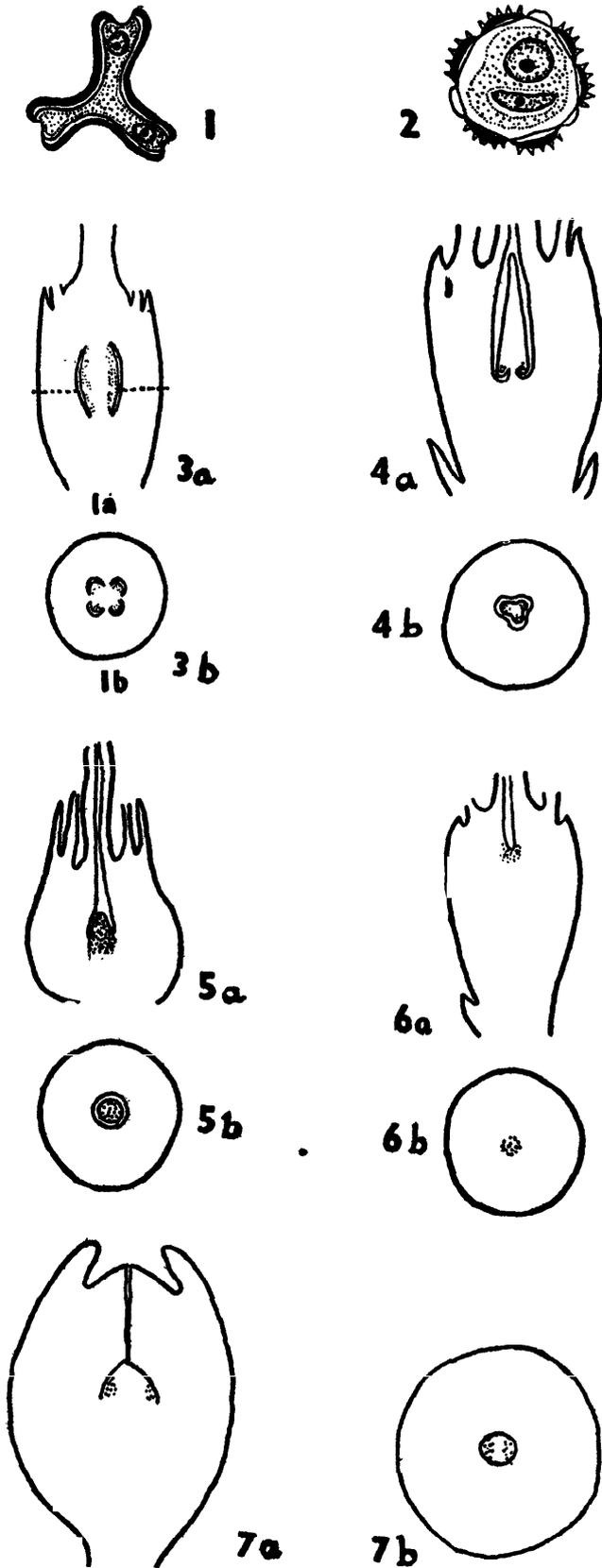


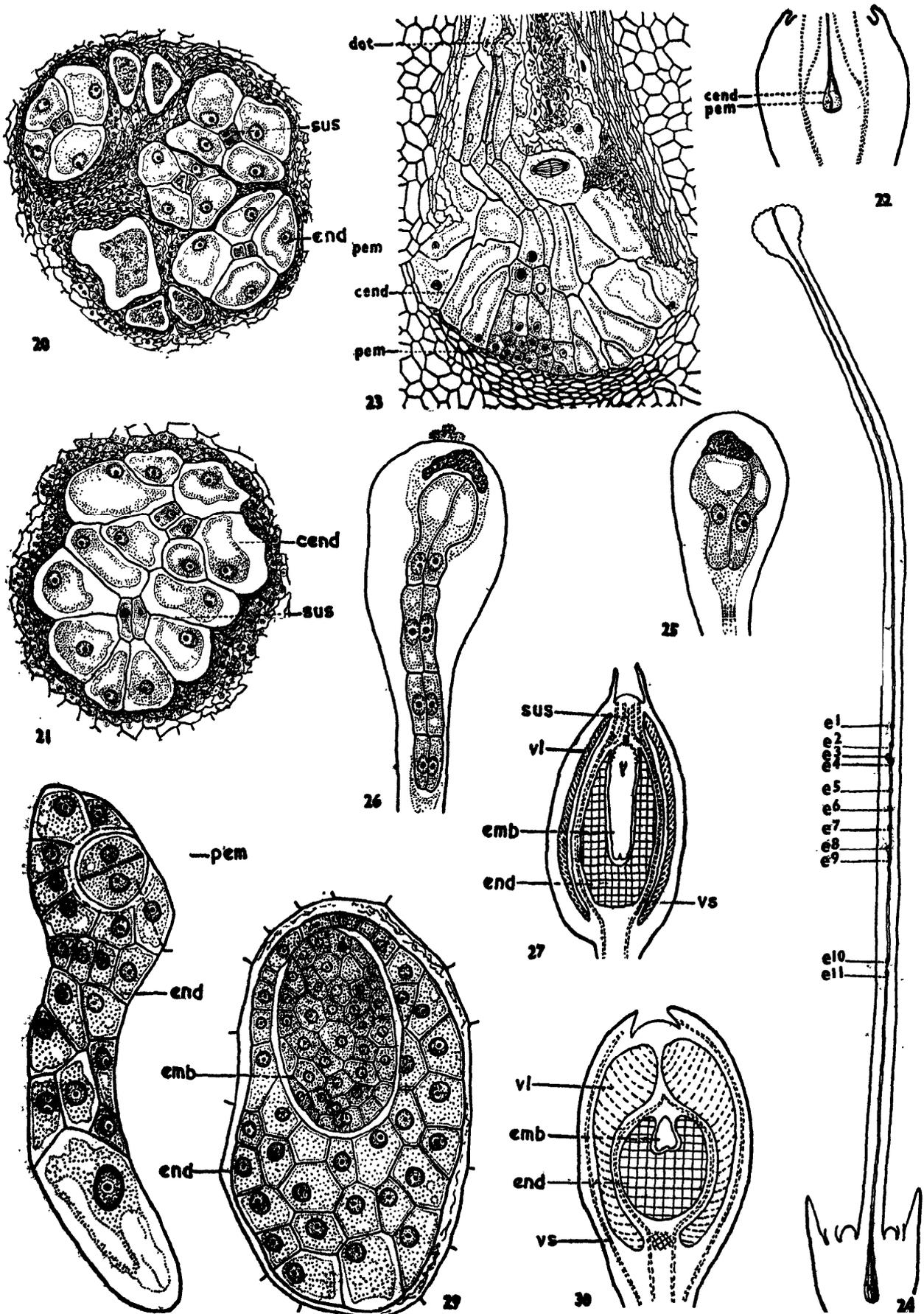
Fig. 1-7b. Pollen and placenta of Loranthoideae and Viscoideae. Fig. 1. *Scurrula pulverulenta*. Tri-radiate pollen grain (After Agrawal, 1953). Fig. 2. *Arceuthobium minutissimum*. Spherical pollen grain (After Correa, 1958). Figs. 3a-6b. L.s. and t.s. of ovaries showing types of placenta in the Loranthoideae; the dotted regions indicate the sporogenous tissue. Figs. 3a, b.

1958 a, b) or the memelon may be free (Fig. 4 a, b) as in *Elytranthe* (Schaeppi and Steindl, 1942) and *Macrosolen* (Maheshwari and Singh, 1952). A free memelon but without any lobes occur in *Helicanthes* (Fig. 5 a, b) (Johri, Agrawal and Garg, 1957); it is extremely short in *Amyema* (Dixit, 1958 a), *Dendrophthoe neelgherrensis* (Narayana, 1954) and *Tolypanthus* (Dixit, 1961), and is absent (Fig. 6a, b) in *Barathranthus* (Schaeppi and Steindl, 1942), *Dendrophthoe falcata* (Singh, 1952), *Helixanthera* (Maheshwari and Johri, 1950), *Scurrula* (Agrawal, 1954), *Tapinanthus* (Dixit, 1956), *Taxillus* (Narayana, 1955) and *Tupeia* (Smart, 1952). The morphological nature of the memelon has also been much debated and has been recently discussed by Maheshwari, Johri and Dixit, (1957).

At the time when reduction divisions are taking place in the megaspore mother cells some of the cells lying below them start developing thickenings and later on form a saucer-shaped or tubular hypostage. Saucer-shaped hypostage which is also referred to as collenchymatous pad has been reported in *Nuytsia* (Narayana, 1958 b), *Amyema* (Dixit, 1958 a), *Tolypanthus* (Dixit, 1961) etc., while tubular hypostage which is known as collenchymatous tube has been reported in *Macrosolen* (Maheshwari and Singh, 1952), *Lysiana* (Narayana, 1958 a), *Lepeostegeres* (Dixit, 1958 b) etc. The presence of collenchymatous thickenings or hypostage has been reported in all the members of the Loranthoideae worked out so far.

The archesporial cells are one-to-four-celled in *Elytranthe* (Schaeppi and Steindl, 1942), *Macrosolen* (Maheshwari and Singh, 1952), *Lepeostegeres* and *Tolypanthus* (Dixit, 1958 b, 1961), while there is a much larger number in *Dendrophthoe* (Singh, 1952), *Scurrula* (Agrawal, 1954), *Helicanthes* (Johri, Agrawal and Garg, 1957), *Lysiana* and *Nuytsia* (Narayana, 1958 a, b). The sporogenous cells elongate and function as megaspore mother cells (Fig. 8, 9). The reduction divisions are normal and linear tetrads are formed (Fig. 10). Occasionally, wall formation may be delayed in the dyad cell towards the epidermis and a triad may be formed. Such a behaviour has also been reported in *Dendrophthoe* (Singh, 1952; Narayana, 1954) and *Scurrula* (Agrawal, 1954). Sometime \perp -shaped tetrads occurs in *Amyema* (Dixit, 1958). Usually the basal megaspore of the tetrad produces the gametophyte but Singh (1952) mentions that in *D. falcata* all the megaspores of a tetrad excepting the one lying towards the upper part of the ovary have the power of further growth. In *Amyema* and *Tolypanthus* (Dixit, 1958 a, 1961) sometimes all the megaspores develop concurrently up to the two-nucleate stage.

Lysiana exocarpi (After Narayana, 1958a). Figs. 4a, b. *Macrosolen cochinchinensis* (After Maheshwari & Singh, 1952). Figs. 5a, b. *Helicanthes elastica* (After Johri, Agrawal and Garg, 1957). Figs. 6a, b. *Helixanthera ligustrina* (After Maheshwari and Johri, 1950). Figs. 7a, b. Diagrammatic representation of L.s. and t.s. of ovaries showing placenta in the Viscoideae. *Korthalsella opuntia*.



Figs. 20-30. (Cend-composite endosperm, dot-degenerated ovarian tissue, emb-embryo, end-endosperm, pem-procambryo, susp-suspensor, vl-viscid layer, vs-vascular supply). Figs. 20-27. Endosperm, embryo and fruit of the Loranthoideae. Figs. 20, 21. *Tolypanthus involucreatus*. T.s. portion of ovaries showing formation of composite endosperm (After Dixit, 1961). Fig. 22. *Anzema niquelii*. L.s. ovary showing a proembryo embedded in composite endosperm (After Dixit, 1958). Fig. 23. Magnified view of endosperm and proembryo from Fig. 22. Fig. 24. *Tolypanthus involucreatus*. Diagrammatic representation of a carpel showing tips of 11 embryo sacs in the style (After Dixit, 1961). Fig. 25. Two-celled proembryo enlarged from Fig. 24; note the longitudinal division of zygote. Fig. 26. Young biserial proembryo enlarged from Fig. 24. Figs. 28-30. Endosperm, embryo and fruit of the Viscoideae. Fig. 28. *Arceuthobium minutissimum*. Two celled proembryo and endosperm (After Correa, 1958). Fig. 29. *A. minutissimum*. Globular proembryo with advanced stage of endosperm (After Correa, 1958). Fig. 30. *Korthalsella opuntia* L.s. fruit (After, Correa, 1958.)

Traub (1881) reported a three-nucleate stage in *Macrosolen cochinchinensis* but this has been contradicted by Maheshwari and Singh (1952). They have shown that a four-nucleate embryo sac is formed as usual. This has been observed in all the plants worked out by the author (Fig. 11.). However, the two lower nuclei divide earlier resulting in a six-nucleate condition (Fig. 12.). Subsequently, the upper two nuclei also divide and the two quarters organize in the usual manner (Fig. 13 a, b, c.). Several embryo sacs develop simultaneously in the same ovary (Fig. 24). During their growth they digest the contents of the adjacent cells which are rich in starch.

The embryo sacs extend down up to the collenchymatous pad or tube. Upward they go up to the base of the style or still higher (Fig. 14). In *Atkinsonia* (Prakash, 1961), *Macrosolen cochinchinensis* (Maheshwari and Singh, 1952) the tips of the embryo sacs extend only to the base of the style; up to one-fifth the length of the style in *Lepeostegeres gemmiflorus* (Dixit, 1958 b); half the style in *Helicanthes elastica* (Johri and Agrawal and Garg, 1957), *Lysiana exocarpi* (Narayana, 1958 a), *Taxillus cuneatus*, *T. tomentosus* (Narayana, 1955), *Tolypanthus lagenifer* (Dixit, 1961), and *Tapinanthus uhehensis* (Dixit, 1956); and to two-thirds the height of the style in *Taxillus sclerophyllus* (Schaeppi and Steindl, 1942), *Dendrophthoe falcata* (Singh, 1952), *D. neelgherrensis* (Narayana, 1954), *Amyema* (Dixit, 1958 a), *Nuytsia floribunda* (Narayana, 1958 b) and *Tolypanthus involucratum* (Dixit, 1961). In *Helixanthera hookeriana* (Schaeppi and Steindl, 1942) and *Tupeia antarctica* (Smart, 1952) the apex of the embryo sac reaches up to the stigma and in *Helixanthera ligustrina* (Maheshwari and Johri, 1950) it grows as far as the stigmatic epidermis.

The antipodal cells appear to be ephemeral and have been missed in a number of species. Occasionally, only two cells are organized, one being binucleate, e.g., *Lepeostegeres gemmiflorus* (Fig. 12, 13c) (Dixit, 1958b). Persistent antipodal cells have been reported in *Macrosolen cochinchinensis* (Maheshwari and Singh, 1952), *Helicanthes elastica* (Johri, Agrawal and Garg, 1957) and *Lepeostegeres gemmiflorus* (Dixit, 1958 b).

Polar fusion has so far been observed only in *Macrosolen cochinchinensis* (Maheshwari and Singh, 1952) and *Lysiana exocarpi* (Narayana, 1958a) but may be presumed to occur in other species also. It is the lower polar nucleus which migrates to the upper part of the embryo sac and fuses with the upper polar.

Maheshwari and Singh (1952) showed that in *Macrosolen cochinchinensis* a lateral pouch arises slightly above the level of the antipodals and progresses downwards as far as the collenchymatous tube forming a caecum. This has since been con-

firmed also in *Lysiana* (Narayana, 1958a) and *Lepeostegeres* (Fig. 13c) (Dixit, 1958 b) and others.

The earliest observations on the development of the endosperm are by Griffith (1844) on *Dendrophthoe falcata* and *Macrosolen cochinchinensis*, and Hofmeister (1959) on *Hyphëar europaeum*. A more detailed account has been given by Maheshwari and Singh (1952) in *Macrosolen* and Singh (1952) in *Dendrophthoe*, Agrawal (1953) in *Elytranthe*, *Helicanthes*, *Scurrula*, Narayana (1955) in *Lysiana*, *Nuytsia* and *Taxillus*, Dixit (1956) in *Amyema*, *Lepeostegeres*, *Tapinanthus* and *Tolypanthus*. The primary endosperm nucleus travels to the lower end of the embryo sac and the first division is followed by a transverse wall. Further divisions produce a four-seriate arrangement followed by additional divisions. Endosperm formation occurs in several embryo sacs in the same ovary and finally all of them fuse to form a composite structure (Fig. 20-23). The mature endosperm is vase-shaped and its appearance largely depends on the vascular skeleton of the ovary. During these changes the collenchymatous pad may often be shifted to a lateral position.

Griffith (1844) recorded that in *Dendrophthoe falcata*, *Macrosolen cochinchinensis* and *Scurrula parasitica* the first division of the zygote is vertical. Traub (1881) confirmed it in *M. cochinchinensis* and since then it has been found to be normal condition in the Loranthoideae (Fig. 25). The vertical division of the zygote is rather rare in angiosperms. The second and subsequent divisions are transverse resulting in a long biseriata proembryo (Fig. 26). In *Helicanthes elastica* (Johri, Agrawal and Garg, 1957), sometimes two proembryos, derived from different zygotes, may develop in a common cavity formed by the fusion of adjacent embryo sacs. Several proembryos develop simultaneously in the style (Fig. 24) but only a few grow down to the ovary. They pass through the endosperm and reach as far as the collenchymatous pad or tube. The terminal tier of the proembryo undergoes repeated divisions forming a mass of cells (Figs. 22, 23). Due to the growth of the endosperm below the embryonal mass, the latter is eventually seen to occupy a more central position. Normally only a single embryo reaches maturity but two well developed embryos have been seen sometimes in *Dendrophthoe* (Singh, 1952; Narayana, 1954) and *Lepeostegeres* (Dixit, 1958 b). The embryo is dicotyledonous but the cotyledons may fuse for part of the distance resulting in a pseudomonocotyledonous condition (Fig. 27). A true radicle is absent and the radicular end has endarch collateral bundles (Singh, 1954).

The structure of the fruit is more or less uniform. The pericarp is distinguishable into three distinct zones (Fig. 27). The outermost is the leathery or sometimes fleshy zone. The next is the viscid, followed by a parenchymatous zone through which

traverse the vascular traces to the perianth, androecium and style. The viscid layer is situated outside the vascular supply to corolla. The seed is 'naked' in the sense that it lacks a testa and the pericarp directly surrounds the endosperm (Fig. 27).

In the Viscoideae, the flowers are unisexual (Danser, 1931), and the calyculus is absent except in staminate flowers of *Viscum orientale* and *V. articulatum* (Schaepfi and Steindl, 1945). The pollen grains are invariably spherical (Fig. 2). The ovary has a distinct central papilla or mamelon which may contain two or more hypodermal archesporial cells (Figs. 7 a, b, 16). Each archesporial cell divides to form two dyad cells. Of these, the upper dyad cell is the larger and functions, while the lower soon degenerates (Fig. 17). Thus the development conforms to the *Allium* type and has been described in *Ginalloa* (Rutishauser, 1937), *Korthalsella* (Rutishauser, 1935, 1937; Schaepfi and Steindl, 1945) and *Viscum* (Schaepfi and Steindl, 1945). A peculiar feature is that after the four-nucleate stage there is a slow but steady curvature of the embryo sac, which causes its lower end to bend out of the papilla and proceed upwards into the carpellary tissue (Figs. 15, 18, 19). The egg apparatus differentiates from the quarter in the originally lower pole, which is, however, now situat-

ed at a higher level than the upper (Fig. 19) e.g. *Dendrophthora* (York, 1913), *Phoradendron* (Billings, 1933) and *Korthalsella* (Rutishauser, 1935, 1937; Correa, 1958). The embryo sac is straight in *Viscum* (Schaepfi and Steindl, 1945), *Arceuthobium* (Thoday and Johnson, 1930; Correa, 1958) and *Ginalloa* (Rutishauser, 1937). Generally only one embryo sac develops which is said to show inverted polarity. Maheshwari (1948) draws attention to the fact that the embryo sacs "although apparently inverted, are not really so." The endosperm is derived from the primary endosperm nucleus of a single embryo sac. The first division of the zygote is transverse (Fig. 28) except in *Korthalsella* (Rutishauser, 1935; Correa, 1958) and *Arceuthobium* (Correa, 1958). The embryo lacks a suspensor (Figs. 28-30) (Thoday and Johnson, 1930; Schaepfi and Steindl, 1945; Correa, 1958). The fruit shows three zones; the outer fleshy coat is followed by the viscid and parenchymatous zones. The viscid layer is situated internal to the vascular supply to perianth. In *Korthalsella* viscid layer is surrounded by the vascular tissue on either side.

Thus the two subfamilies show marked embryological as well as morphological characters. This becomes quite clear from the following comparative chart:

CHARACTER	LORANTHOIDEAE	VISCOIDEAE
Habit	Stem parasites; some root parasites	Stem parasites.
Leaf	Leathery	Leathery, sometimes absent
Flowers	(i) Mostly bisexual, sometimes unisexual (ii) Calyculus invariably present	(i) Always unisexual. (ii) Calyculus absent except in <i>Viscum</i> Spp.
Pollen grains	Triradiate except in <i>Tupeia</i> and <i>Atkinsonia</i>	Spherical
Embryo sac	(i) Polygonum type (ii) Several embryo sacs develop concurrently in the same ovary; their tips reach upto the base of the style or upto different heights in the style and stigma; the lower end produces a caecum leaving the antipodal cells <i>in situ</i> (iii) Collenchymatous pad or tube (hypostage) always present.	(i) <i>Allium</i> type. (ii) A peculiar feature is that at the 4-nucleate stage the 'lower' end bends out of the papilla and proceeds upwards towards the carpellary tissue. The embryo sac is straight in <i>Viscum</i> , <i>Arceuthobium</i> and <i>Ginalloa</i> . (iii) Collenchymatous pad or tube absent.
Endosperm	Composite structure formed by the fusion of different endosperms developing in the same ovary	Develops individually in each embryo sac and do not fuse.
Embryo	(i) Division of zygote always vertical (ii) Suspensor highly elongated	(i) Division of zygote mostly transverse (except in <i>Korthalsella</i> and <i>Arceuthobium</i>). (ii) Suspensor absent.
Pericarp	The viscid layer situated outside the vascular supply to perianth.	The viscid layer is situated internal to the vascular supply to perianth; in <i>Korthalsella</i> viscid layer is surrounded by the vascular tissue on either side.

Thus, the Loranthoideae and the Viscoideae show important differences in their floral structure, mode of development of the embryo sac, endosperm, embryo and pericarp, and therefore, they can adequately be raised to the rank of families. As suggested by Miers (1851) name Loranthaceae may be

retained for the Loranthoideae and the Viscoideae may be designated as Viscaceae.

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