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EMBRYOLOGICAL STUDIES IN CAPPARIDACEAE-LIFE HISTORY OF *NIEBUHRIA APETALA* DC.[1]

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ABSTRACT

The anther is tetrasporangiate and its wall development conforms to the Dicotyledonous type. Simultaneous cytokinesis in the pollen mother cells results in tetrahedral and isobilateral tetrads. Mature pollen grains are 2-celled and triaperturate.

The gynoecium is bicarpellary, syncarpous and unilocular with campylotropous, bitegmic and crassinucellate ovules on parietal placentation. Micropyle is zigzag. The nucellar cells extending between the embryo sac and chalaza appear as strands. A hypostase differentiates after fertilization. Archesporium is one or two celled. Megaspore tetrad is linear. Embryo sac development follows the Polygonum type. Endosperm is *ab initio* nuclear. Embryogeny conforms to the lythrum variation of Onagrad type. Seed coat is formed by both the integuments. The inner integument is multiplicative and the outer non-multiplicative. The seeds are exotegmic.

INTRODUCTION

The family Capparidaceae with 46 genera and 700 species (Lawrence, 1951) is chiefly tropical in distribution. Morphologically, at any rate, the family consists of two distinct groups, represented by two type genera, the *Capparis* and the *Cleome*. While the *Capparis* group is characterised by woody plants with indehiscent fruits the *Cleomes* are herbaceous with dehiscent fruits. In view of this morphological disparity, Bentham and Hooker (1862-1883) considered the two groups as two distinct tribes, the Cappareae and Cleomeae. However, Hutchinson (1969, 1973) has raised the status of these two tribes into independent families. This puts us in a situation where investigations become imperative to support whatever is true.

Keeping in view the gaining importance of the Embryology in solving such taxonomic problems, an effort has been made to investigate the embryological details in the woody members of the family for which information is wanting. The current paper presents the life history of *Niebuharia apetala* DC. a woody member of the family. An attempt has been made to discuss the controversial systematics of the family using the embryological evidences obtained from the present study and also from the earlier works.

The significant contributions to the Embryology of the family include those of Guignard (1893), Orr (1921a, 1921b), Mauritzon (1934), Rao (1936a, 1936b, 1938), Tiwary (1936), Billings (1937), Raghavan (1937, 1938), Raghavan and Venkata Subban, 1941), Maheshwari and

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Khan (1953), Maheshwari and Sachar (1954), Sachar (1956), Narayana (1962, 1965), Rao (1967), Fathima and Kumari (1970), Hanumantharao and Prakasarao (1975a, 1975b, 1977) and Prakasarao and Hanumantharao (1976).

MATERIAL AND METHODS

The material collected by the author from the Indian Botanical Gardens, Howrah, was fixed in Formalin-acetic-alcohol. Customary methods of dehydration, infilteration and embedding in paraffin wax were followed adopting the procedure given by Johansen (1940). The sections were cut between 6-15 μm and stained in Delafield's haematoxylin.

OBSERVATIONS

The flowers are produced in Corymbs and are apetalous. The calyx lobes are leathery and open in aestivation. An interesting feature is the development of hairs from the open ends of calyx lobes which interlock (Fig. 1). Probably, these hairs aid in protecting the developing essential organs in the absence of petals. The hairs shrivel and fall off by the time the gynoecium is raised over the other organs of the flower. Anthers are numerous and the gynoceium is borne on a gynophore, unique to the family. The ovary is bicarpellary, syncarpous and unilocular with numerous ovules arranged on parietal placentation (Fig. 1).

Microsporangium , microsporogenesis and male gametophyte :

The archesporium consists of a plate of four or five cells in a transverse section (Fig. 2). The development of anther wall conforms to the Dicotyledonous type (Figs. 3-5). It comprises an epidermis, endothecium, a middle layer and a tapetum (Fig. 5). Tapetum is secretory and monomorphic with binucleate cells (Fig. 6). The middle layer is ephemeral (Fig. 6). Fibrous thicknenings develop in the endothecium at a later stage (Fig. 7).

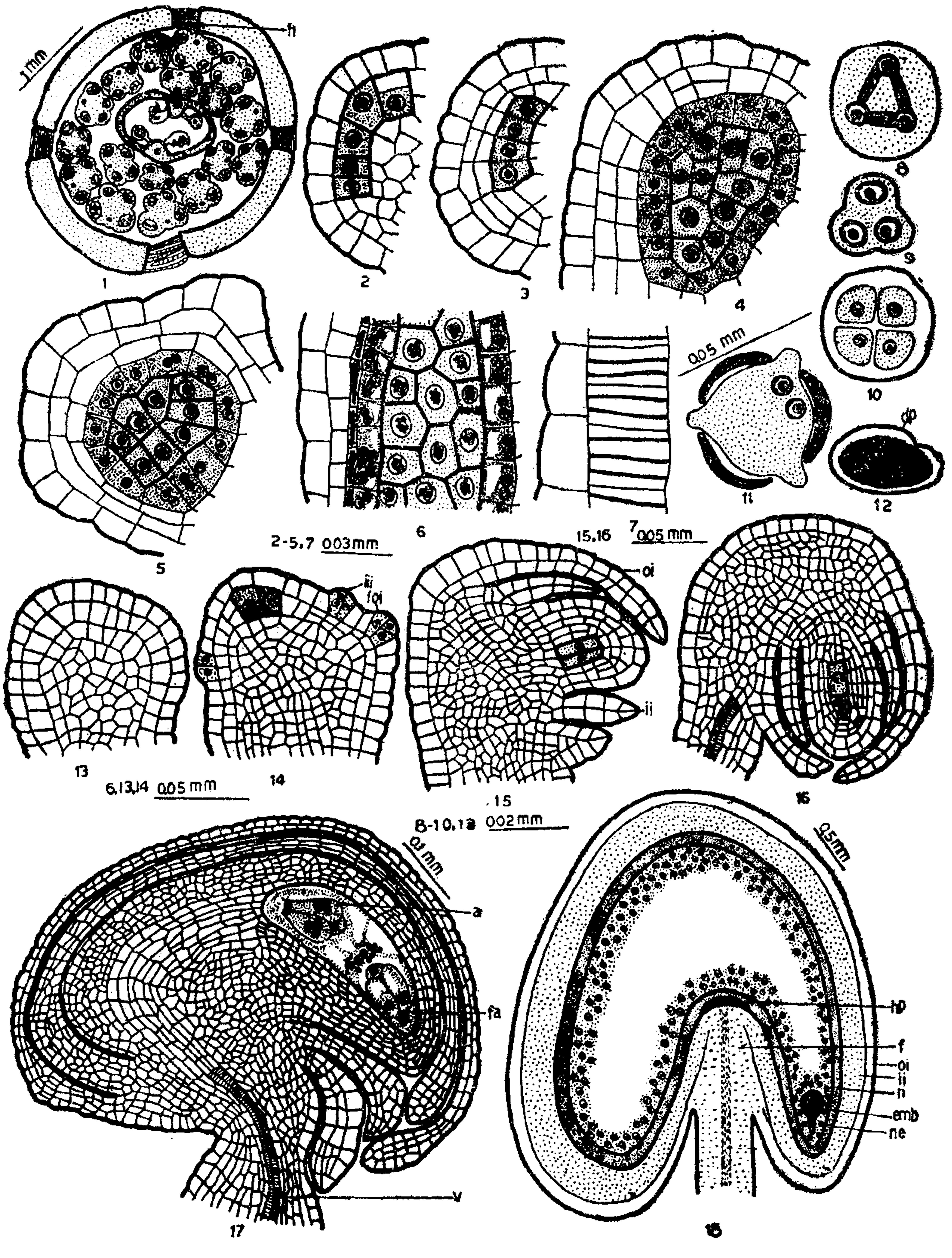
The primary sporogenous cells divide in all planes to form a sporogenous tissue (Fig. 6). Simultaneous cytokinesis in the pollen mother cells results in tetrahedral and isobilateral tetrads (Figs. 8-10). The mature pollen grain is spheroidal, triaperturate and 2-celled at the shedding stage (Fig. 11). Degenerating pollen have been observed occasionally (Fig. 12).

Ovule, megasporogenesis and female gametophyte :

The ovule is campylotropous, bitegmic and crassinucellate (Fig. 17). The ovular primordium is typically 3-zonate (Fig. 13). Both the integuments are dermal in origin and the integument initials appear simultaneously with the differentiation of the archesporium (Fig. 14). The outer integument overgrows the inner (Fig. 16). The exostome and the endostome do not lie in a straight line and the micropyle is zigzag (Fig. 17).

The parietal tissue is well-developed and the nucellus is massive. Some of the nucellar cells extending between the embryo sac and chalaza elongate radially and appear like strands (Fig. 17). In a mature seed, one to three layers of nucellus persists as perisperm. A well-developed hypostase with tannin filled cells is differentiated after fertilization (Fig. 18). It persists even in a mature seed.

The hypodermal archesporium is 1 or 2-celled (Fig. 14). However, only one of them develops further and cuts off a parietal cell towards the outside and a megaspore mother cell towards the inner side. Rarely twin megaspore mother cells are formed (Fig. 15). Meiotic divisions in the megaspore mother cell result in the formation of a linear tetrad (Fig. 19). The chalazal megaspore after undergoing



Figs. 1-18. 1. T. S. of a flower; 2-5. T. S. of anther lobes showing development of wall layers; 6. T. S. of anther lobe showing prophase in pollen mother cells, note degenerating middle layer; 7. Fibrous endothecium; 8-10. Tetrahedral and isobilateral tetrads; 11. 2-nucleate pollen grain; 12. Degenerating pollen grain ; 13-18. Stages showing the development of ovule.

A-antipodals; d-degenerating pollen grain; emb-embryo; f-funicle; fa-filiform apparatus; h-hair; hp-hypostase; ii-inner integument; iii-initials of inner integument; ioi-initials of outer integument; n-nucellus; ne-nuclear endosperm; oi-outer integument; v-vasculature.

three mitotic divisions produces an 8-nucleate embryo sac of the Polygonum type (Figs. 19-21). The hooked synergids are provided with filiform apparatus. The three antipodals are large, trinucleate and simulate the egg apparatus. However, they degenerate after fertilization. The embryo sac contains abundant starch grains (Fig. 21).

Fertilization and endosperm:

The entry of pollen tube into the embryo sac is porogamous. Triple fusion precedes syngamy (Fig. 22). Endosperm is *ab initio* Nuclear. Divisions in the primary endosperm nucleus results in the formation of a large number of free nuclei which are arranged along the periphery of the embryo sac leaving a central vacuole (Figs. 23 and 24). Wall formation commences at the globular embryo stage and is completed atthe torpedo stage of the embryo (Figs. 25 and 26). In a mature seed only 3 or 4 layers of endosperm persist.

Embryogeny:

The zygote is rich in starch (Fig. 27). It undergoes a transverse division to form a terminal cell *ca* and a basal cell *cb* (Fig. 28). The former divides longitudinally and the latter transversely resulting in a 4-celled T-shaped proembryo (Fig. 29). The two superposed cells produced by the cell *cb* are designated as *ci* and *m*. The two juxtaposed cells of *ca* undergo one more vertical division at right angles to the first resulting in a quadrant *q*. By this time the cell *ci* divides transversely producing two cells *n* and *n*'. The quadrant divides transversely to form an octant with two tiers of four cells each. The two tiers are designated as *l* and *l'* (Fig. 30). Concomitantly, the middle cell *m* divides transversely producing the cells *d* and *f* and cell *n*' divides to form *o* and *p* (Fig. 30). In the two tiers *l* and *l'*, periclinal divisions occur resulting in dermatogen layer towards outside and periblem and plerome initials towards inside (Fig. 31). The cell *d* functions as the hypophysis. It divides transversely to produce superposed cells which by further divisions produce two groups of cells *iec* and *ico*. The tier *l* contributies to the cotyledons, and the stem apex. The tier *l'*, contributes to the hypocotyledonary region and the initials of the central cylinder of the stem. The derivatives of the cell *d* contribute to the central cylinder of the root and also to the initials of the root cap. The cells *f*, *n*, *o* and *p* constitute the four celled suspensor, which disorganise as the embryo matures (Fig. 32). The mature embryo is coiled (Figs. 33 and 34).

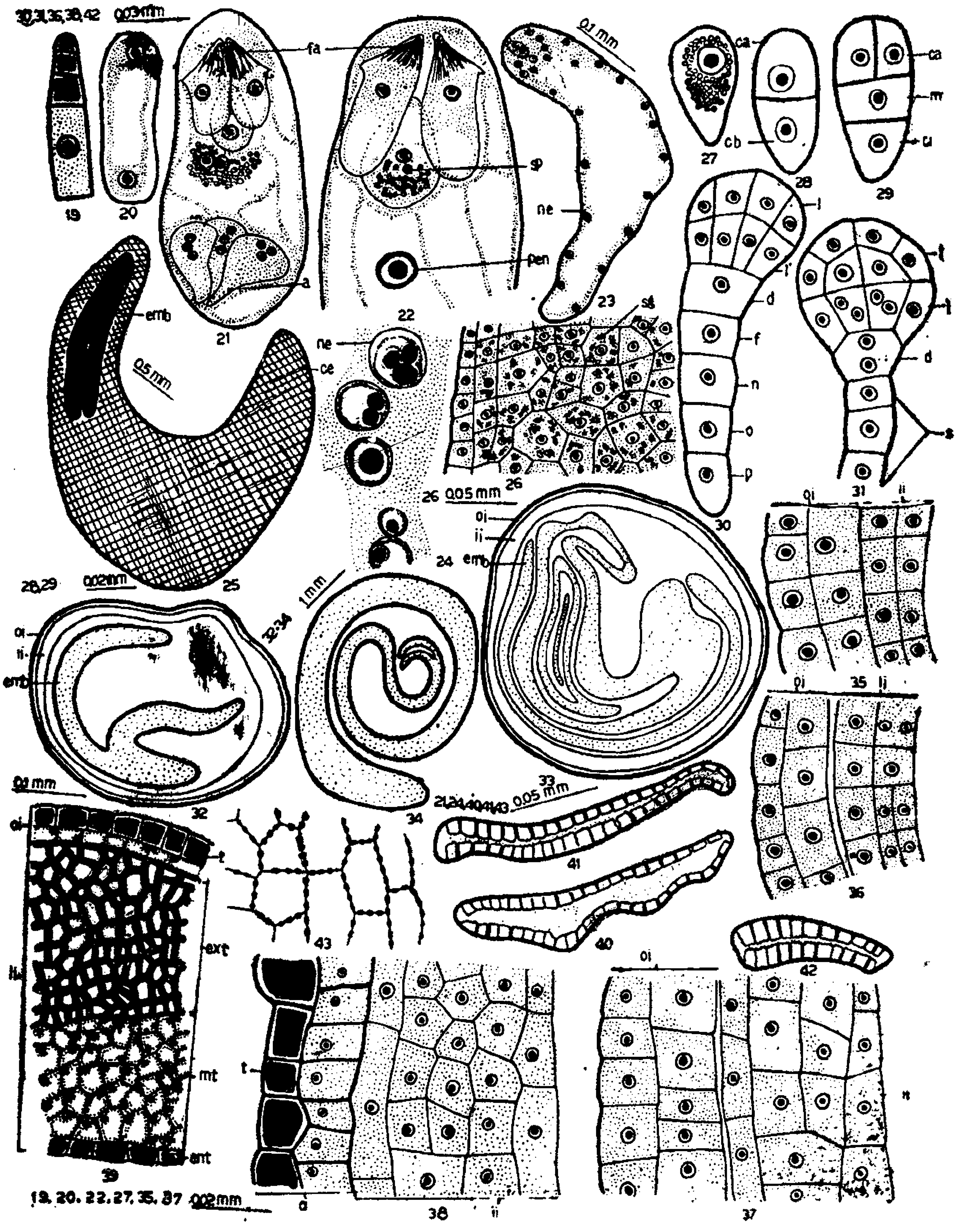
From the above, it is evident that the 4-celled proembryo is T-shaped and the major part of the embryo is contributed by the derivatives of the cell *ca*. Thus the embryogeny conforms to the Onagrad type. Further, the hypophysis cell *d*, is the upper daughter cell of the cell *m* and thus keys out to the lythrum variation.

Seed coat:

In the initial stages both the integuments are two-layered (Fig. 35) and both of them take part in the formation of seed coat.

The outer integument is non-multiplicative and remains two layered throughout. After fertilization the cells of the outer integument become radially elongated. At the globular embryo stage the cells of the outer layer develop tannin (Fig. 38). At about maturity, the cells of both the layers become thick-walled (Fig. 39).

The inner integument is multiplicative. The two-layered inner integument becomes three-layered at the mature embryo sac stage due to divisions in the



Figs. 19-43. Figs. 19-21. Stages showing the development of embryo sac; 22. Embryo sac showing syngamy and primary endosperm nucleus; 23. Embryo sac showing free nuclear endosperm; 24. A portion of nuclear endosperm enlarged; 25. Embryo sac showing cellular endosperm; 26. A portion of cellular endosperm enlarged; 27-34. Stages in the development of embryo; 35-39. Stages in the development of seed coat; 40-42. Macerated exotegmic sclereids; 43. Endotegmic facets.

ce-cellular endosperm; emb-embryo; ent-endotegmen; ext-exotegmen, fa-filiform apparatus; ii inner integument; mt-mesotegmen, ne-nuclear endosperm; oi-outer integument; pen-primary endosperm nucleus; sg-starch grains; sp-sperm nucleus; t-tannin.

inner layer of the integument (Figs. 35 and 36). Of these, the cells of the outermost layer distend tangentially and undergo periclinal divisions to form eight to ten layers of cells (Figs. 37-39). The cells of the middle and inner layers divide both anticlinally and periclinally resulting in the formation of five or six layers of parenchymatous cells (Figs. 37-39). In a mature seed the tangentially elongated cells become sclerotic and develop pit connections (Figs. 39-42). This region constitutes the exotegmen and it gives mechanical support to the seed. The parenchymatous cells constitute the mesotegmen (Fig. 39). The components of the inner delimiting layer become lignified, pitted and develop tannin and this constitutes the endotegmen (Figs. 39 and 43). The seeds are exotegmic.

DISCUSSION

The anther wall development in *Cleome monophylla* (Rao, 1967), *Cleome aspera, Capparis zeylanica* (author, unpublished) and in the present investigation follows Dicotyledonous pattern. However, Basic type of wall development has been reported in *Cleome tenella, Capparis decidua* (Hanumantha Rao and Prakasa Rao, 1975a, 1977), *Capparis grandis, Capparis sepiaria* and *Cadaba indica* (author, unpublsihed). It is thus evident that both Basic and Dicotyledonous type of anther wall developments are common in members of both the groups of the family.

The members of the family are characterised by a secretory, monomorphic, uniseriate tapetum, tetrahedral, decussate and/or isobilateral tetrads and simultaneous cytokinesis.

Although pollen grains are 2-celled at the time of shedding, in *C. indica* (Narayana, 1965), *C. tenella, C. decidua* (Hanumantha Rao and Prakasa Rao, 1975a, 1977), *C. zeylanica,* and *C. aspera* (author, unpublished), 3-celled pollen grains are also reported in *Crataeva nurvala* (Narayana, 1965), *Cleome viscosa* (Fathima and Kumari, 1970) and *C. grandis* (Padhye and Vaidya, 1970). Thus both 2-and 3-celled pollen occur in members of both the groups of the family.

The ovule in the family in Campylotropous, bitegmic and crassinucellate. The dermal initiation of integuments appears to be typical of all the members of the family.

The presence of massive nucellus is another common feature shared by all the members of the family. The nucellar cells extending between the embryo sac and chalaza appear as strands in *C. chelidonii* (Raghavan, 1937), *Gynanadropsis pentaphylla, C. grandis* (author, unpublished) and in the present investigation. As these strands connect the vasculature and the embryo sac, it is probable that they serve as a means for translocation of food materials from placental bundle to the embryo sac. Raghavan (1937) regards these strands as the vestiges of a conducting tract. This belief is strengthened by the fact that tracheids occur in the nucellus of another Capparidaceous member, *Steriphoma cleomoides* (Orr, 1921a).

Interestingly, the differentiation of hypostase in *C. decidua C. nurvala, C. indica* (Narayana, 1962, 1965), *C. viscosa, C. aspera, G. pentaphylla, C. divaricata* (author, unpublished) and in the present investigation is a post fertilization event.

The embryo sac development uniformly follows the Polygonum pattern. The members of the two groups differ in the size and shape of the synergids. The synergids in the members of group Cappareae, *Maerua arenaria, Capparis galeata, C. sepiaria, Capparis horrida* (Rao, 1936a, 1938), *C. decidua, C. nurvala, C. indica* (Narayana, 1962, 1965) and in the present investigation are flask shaped and are usually provided with a filiform apparatus. However, in the Cleomes, *C. viscosa* (Fathima and Kumari, 1970), *C. monophylla* (Rao, 1967,) *C. aspera* and *G. pentaphylla* (author, unpublished) the synergids are pear shaped and usually lack a filiform apparatus.

The antipodals in all the members of the family are small and degenerate after fertilization. In *M. arenaria* (Rao, 1936a) and present observation, the antipodals are however large and simulate an egg apparatus.

The endosperm in all the members of the family is *ab initio* Nuclear.

There is a great variation in the embryogeny of the family. In *G. pentaphylla* the disposition of various tiers resembles that of *Myosurus minima* (Phouphas, 1952). Solanad type of embryogeny is reported in *Isomeris arborea* (Sachar, 1956) and *C. nurvala* (Narayana, 1965). Interestingly in *C. decidua* (Narayana, 1962) the embryo development shows points of resemblance to the Solanad, Onagrad and Caryophyllad types. In *C. indica* (Narayana, 1965) Caryophyllad type of embryogeny is reported. In *C. chelidonii* (Raghavan, 1937), *C. tenella* and *C. aspera* (Hanumantha Rao and Prakasa Rao, 1975b; Prakasa Rao & Hanumantha Rao 1976) and present investigation, the embryo development follows Onagrad type.

Regarding seed structure the members of both the groups share a number of characters such as-contribution of both the integuments to the seed coat, the non-multiplicative outer integument, the presence of tannin in the cells of testa, differentiation of tegmen into a fibrous exotegmen, parenchymatous mesotegmen and a lignified endotegmen and exotegmic seed. The members of the two groups, however differ in the number of exotegmic layers. In the Cappareac, *C. zeylanica*, *C. divaricata*, *C. sepiaria*, *C. grandis* (Corner, 1976) and in the present investigation the exotegmen is four to ten-layered. However, in the Cleomes, *Polanisia graveolens* (Guignard, 1893), *C. chelidonii* (Raghaven, 1937), *C. monophylla* (Rao, 1967), *C. Viscosa* and *G. pentaphylla* (Corner, 1976) the exotegmen is single-layered.

It is obvious from the foregone, that barring for few minor differences, the two groups are similar for a large number of characters indicating that the embryological evidence does not support the contention of Hutchinson (1969, 1973) for providing an independent family status to the two groups. Evidences from Anatomy (Aleykutty and Inamdar, 1978b). Palynology (Mitra Krishna, 1970, 1975) and Foliar epidermal studies (Aleykutty and Inamdar, 1978a,) also render support to this veiw. The classification of Bentham and Hooker (1862-1883), in assigning tribal position to the two groups seems to be justified.

REFERENCES

ALEYKUTTY, K. M. AND J. A. INAMDAR 1978a. Structure, Ontogeny and taxonomic significance of trichomes and stomata in some Capparidaceae. *Feddes Repert.* **89** : 19-30.

ALEYKUTTY, K. M. AND INAMDAR 1978b. Studies in the vessels of some Capparaceae. *Flora* **167** : 5. 103-109.

BENTHAM, G. AND J. D. HOOKER 1862-1883. *Genera Plantarum*. Reeve & Co., Williams & Norgate, London.

BILLINGS, F. H. 1937. Some new features in the reproductive cytology of angiosperms, illustrated by *Isomeris arborea*. *New Phytol.* **36** : 301-326.

CORNER, E. J. H. 1976. *Seeds of Dicotyledons*. Cambridge Univ. Press, Cambridge, U.K.

FATHIMA, T. AND P. KUSUMA KUMARI 1970. Embryological studies in Capparidaceae. Sporogeneses and the development of gametophytes in *Cleome viscosa* L. *Proc. Indian Acad. Sci.* **72B**: 207-215.

GUIGNARD, L. 1893. Recherches surle developpment de la graine et an particulier du tegument Seminal *J. de Bot.* **7** : 57-66.

HANUMANTHA RAO, B. AND P. S. PRAKASA RAO

1975a. Anther development in *Cleome tenella* L. *Curr. Sci.* **44** : 438-440.

Hanumantha Rao, B. and P. S. Prakasa Rao 1975b. Embryo development in *Cleome tenella* L. *Curr. Sci.* **44** : 559-560.

Hanumantha Rao, B. and P. S. Prakasa Rao 1977. Anther in *Capparis decidua* (Forsk.) Pax. *Curr. Sci.* **46** : 683-684.

Hutchinson, J. 1969. *Evolution and Phyolgeny of Flowering Plants*. Academic Press, London.

Hutchinson, J. 1973. *The families of Flowering Plants* (3rd. ed) Oxford Univ. Press, Oxford.

Johansen, D. A. 1940. *Plant Microtechnique*, Mc-Graw Hill, New York.

Lawrence, G. H. M. 1951. *Taxonomy of Flowering Plants*. The MacMillan Company, New York.

Maheshwari, P. and R. Khan 1953. Development of the embryo sac, endosperm and embryo in *Isomeris arborea*--A reinvestigation. *Phytomorphology* **3** : 446-459.

Maheshwari, P. and R. C. Sachar 1954. A reinvestigation of the embryology of *Isomeris arborea*. *Curr. Sci.* **23** : 61-63.

Mitra, Krishna 1970. Pollen morphology of some Indian Capparidaceae. *J. Indian bot. Soc.* **49** : 136-141.

Mitra, Krishna 1975. Contribution to the pollen morphology of the family Capparaceae. *Bull. Bot. Surv. India.* **17** : 7-31.

Mauritzon, J. 1934. Die Embryologie einiger Capparidaceen Sowie von *Tovaria pendula Arkiv. f. Bot.* **26A** : 1-14.

Narayana, H. S. 1962. Studies in Capparidaceae I. Floral morphology and embryology of *Capparis decidua* (Forsk.) Pax. *phytomorphology* **12** : 167-177.

Narayana, H. S. 1965. Studies in Capparidaceae II. Floral morphology and embryology of *Cadaba indica* Lamk. and *Crataeva nurvala* Buch-Ham. *Phytomorphology* **15** : 158-175.

Orr, M. Y. 1921a. The occurrence of tracheids in the nucellus of *Steriphoma cleomoides* . *Notes Roy. Bot. Gard. Edinb.* **60** : 241.

Orr, M. Y. 1921b. The occurrence of a trachael tissue enveloping the embryo in certain Capparidaceae. *Notes Roy. Bot. Gard. Fdinb.* **60** : 249.

Padhye, M. D. and P. B. Vaidya 1970. Tapetal degeneration in *Capparis grandis* Linn. F. Suppl. *Curr. Sci.* **39** : 397-378.

Phouphas, C. 1952. Development du proembryon chez le *Gynandropsi pentaphylla* DC. (Capparidacees). *Bull. Soc. Bot. Fr.* **99** : 18-20.

Prakasa Rao, P. S. and B. Hanumantha Rao 1976. Embryo development in *Cleome aspera.* L. *Journ Jap Bot.* **51**(4) : 110-116.

Raghavan, T. S. 1937. Studies in the Capparidaceae L. The life history of *Cleome chelidonii* Linn. *J. Linn. Soc. Bot.* **51** : 43-72.

Raghavan, T. S. 1938. Morphological and cytological studies in the Capparidaceae II. Flora morphology and cytology of *Gynandropsis pentaphylla* DC. *Ann. Bot.* **2** : 75-96.

Raghavan, T. S. and K. R. Venkata Subban 1941. Studies in the Capparidaceae. The floral morphology of *Crataeva religiosa* Forst. *Proc. Indian Acad. Sci.* **13B** : 235-243.

Rao, A. V. N. 1967. Embryological studies in *cleome monophylla* Linn. *Proc. Indian Acad. Sci.* **65B** : 249-256.

Rao, V. S. 1936a. Studies on Capparaceae I. The embryo sac of *Maerua arenaria* Forsk. *J. Indian bot. Soc.* **15** : 71-85.

Rao, V. S. 1936b. Studies on Capparidaceae II. The embryology of *Gynandropsis pentaphylla* DC. *J. Indian bot. Soc.* **15** : 335-344.

Rao, V. S. 1938. Studies on Capparidaceae III. Genus *Capparis* Linn. *J. Indian bot Soc.* **17** : 69-80.

Sachar, R. C. 1956. The embryology of *Isomeris*—A reinvestigation. *Phytomorphology* **6** : 346-363

Tiwary, N. K. 1936. Megasporogenesis and embryo development in *Cleome viscosa* L. *Sci. & Cult.* **1** : 476-477.