THE OVULE AND GYNOECIUM IN LORANTHACEAE

BY ALFREDO E. COCUCCI[1] and MARGARIDA VENTURELL[2]

SUMMARY

Based in the comparative morphology of the loranthacean gynoeceum 2 evolutionary tendences are recognized: one, has the nucellar axis with their chalazal end pointing to the superior part of the ovary, the other, has an opposite arangement of the nucellar axis.

The gynoeceum peculiarities are correlated with some other features of the embryos and the chromosome complements in order to ameliorate the classification of the family; the result being 5 tribes, 2 of which (Tapinostemeae and Lysianeae) are new.

INTRODUCTION

In the family Loranthaceae, the ovary and the ovule have undergone profound changes during the course of evolution; they consist mainly of fusions and simplifications that confer, to such structures of the flower, very special characteristics in angiosperms that have largely contributed to hindering their interpretation.

The peculiarities noted earlier aroused the interest of embryologists, mainly in the Maheshwari and Johri school in India, who conducted many studies that have provided much valuable data. All information collected along with the experience, has been combined in this work where we present an interpretacion of the interactions between the ovules and the gynoecium that, in our judgment, is consistent from a phylogenetic point of view.

[1] Miembro de la Carrera del Investigador CONICET, Universidad Nacional de Córdoba. Laboratorio de Embriología Vegetal. Casilla de Correo 495. 5000 Córdoba. Argentina.

[2] Dep. de Botánica. Inst, de Biociéncias. Universidad de São Paulo, C. P. 11461-05421 São Paulo, Brasil.

GENERAL CONCEPTS AND NOMENCLATURE

To facilitate understanding of the arguments that will be discussed later, it is convenient to clarify some concepts and precise definitions for certain terms. For this one takes as an example the gynoecium of a species of *Tripodanthus* that, comparatively, is considered little modified since its ovules can be recognized as independent structures.

In Fig. 1 images C, D and E represent longitudinal sections corresponding to planes with different orientations as indicated under numbers 2, 1 and 3 in cross section B of the same figure. In these drawings, the shaded areas correspond to an amyliferous tissue through which the embryo sac can grow.

The ovary of *Tripodanthus* is trilocular (Fig. 1 B) and bears one ategmic ovule per locule which takes up the entire cavity without leaving free space. The three locules are connected together by an open compitum. This compitum consists practically of virtual space that extends over the surface of a conical projection called a mamelon. The mamelon consitutes the lower limit of the compitum while the base of the style forms its upper limit.

In the literature (Johri et al., 1965, 1969), the mamelon has been interpreted as a placenta. However, a trilocular ovary with axile placentation must have at least 3 placental regions, so that the mamelon cannot be interpreted in its entirety as a single placenta. In effect the mamelon has connections with 3 small placental areas at its base; however, they are excluded from the tissue that forms the conical projection that contribute 3 carpels that form the gynoecium.

In our concept, the term mamelon should apply only in relation to the compitum, completely excluding placentas. In this regard the mamelon can achieve great tissue development and differentiation of the amyliferous tissue (Fig. 3 Elytrantheae).
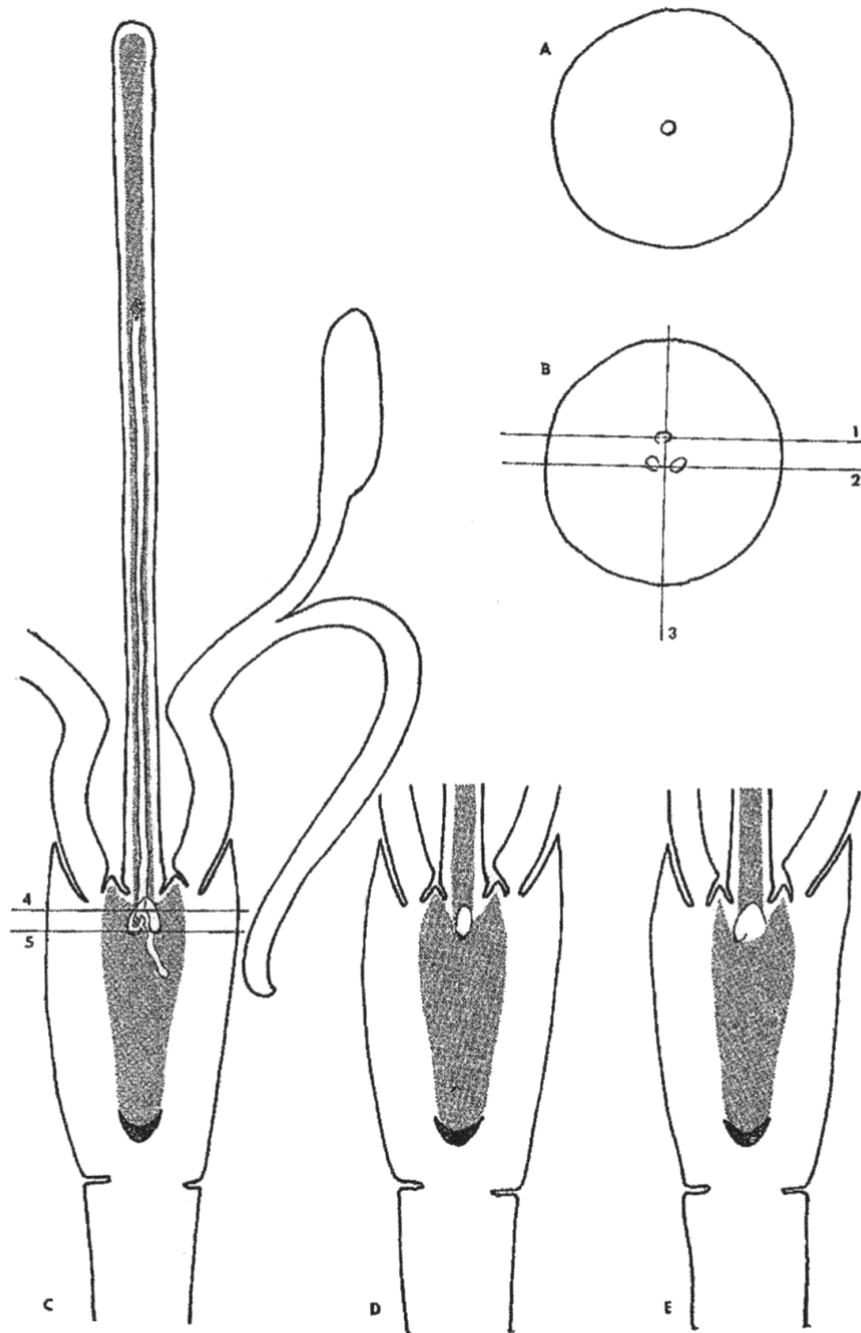
Fig. 1. - Perfect flower of *Tripodanthus*. A and B: cross sections through planes 4 and 5, respectively; C, D and E: longitudinal sections through planes 2,1 and 3 of B respectively. Shaded area: amyliferous tissue.

The placenta is defined as the carpellary tissue from which arise the ovules. This tissue is always present whenever differentiated ovules, or at least an archesporium, have occurred and when the reduction or fusion process have lost the limits of the nucellus. The placenta is placed at the base of the funiculus, in case there are different ovules, or immediately below the archesporium in instances where it is not possible to discern.

The nucellar axis is determined by uniting the two points corresponding to the zone of contact of the archesporium with the nucellar epidermis, on the one hand, and on the other it corresponds to a chalazal zone, so that the orientation of said axis coincides with the longitudinal axis of the archesporial mother cells (Fig. 2).

The prolongation of the nucellar axis towards the center axis of the ovary determine a point of concurrency that results in the vertices of the angles α and β (Fig. 2).

To illustrate the following discussion, longitudinal sections are chosen corresponding to plane 2, since it is in this view where the communication of the locules is best seen through the compitum while showing the position of 2 of the ovules.

DISCUSSION ON GYNOECIUM TYPES

The diagram in Fig. 3 illustrates the different ovarian structures found in various genera that have been chosen as representatives of each morphological type. They are sorted by the different tendencies operating in the course of evolution. They have a major role there changing position, and eventual fusion of the ovules together with the specialization of certain tissues.

Considered as the most primitive type, *Tripodanthus* exhibits ovules that can be recognized as separate entities, completely separated from the ovarian wall; although devoid of integuments, it possesses a well-developed nucellus.

A general analysis of Fig. 3 can recognize two divergent lines regarding the orientation of the ovules. In fact, considering the subepidermal nature of the archesporium and the particular orientation of its cells, it is possible to determine the longitudinal axis of the nucellus and the position of the placenta even in cases of fusion of the ovule with the ovarian wall and to each other. Charting these axes, in the diagrams in Fig. 3, one notices those 2 divergent lines that depart from the type corresponding to *Tripodanthus*. There the nucellar axes converge at a portion of the chalaza forming an angle β of approximately 90°.
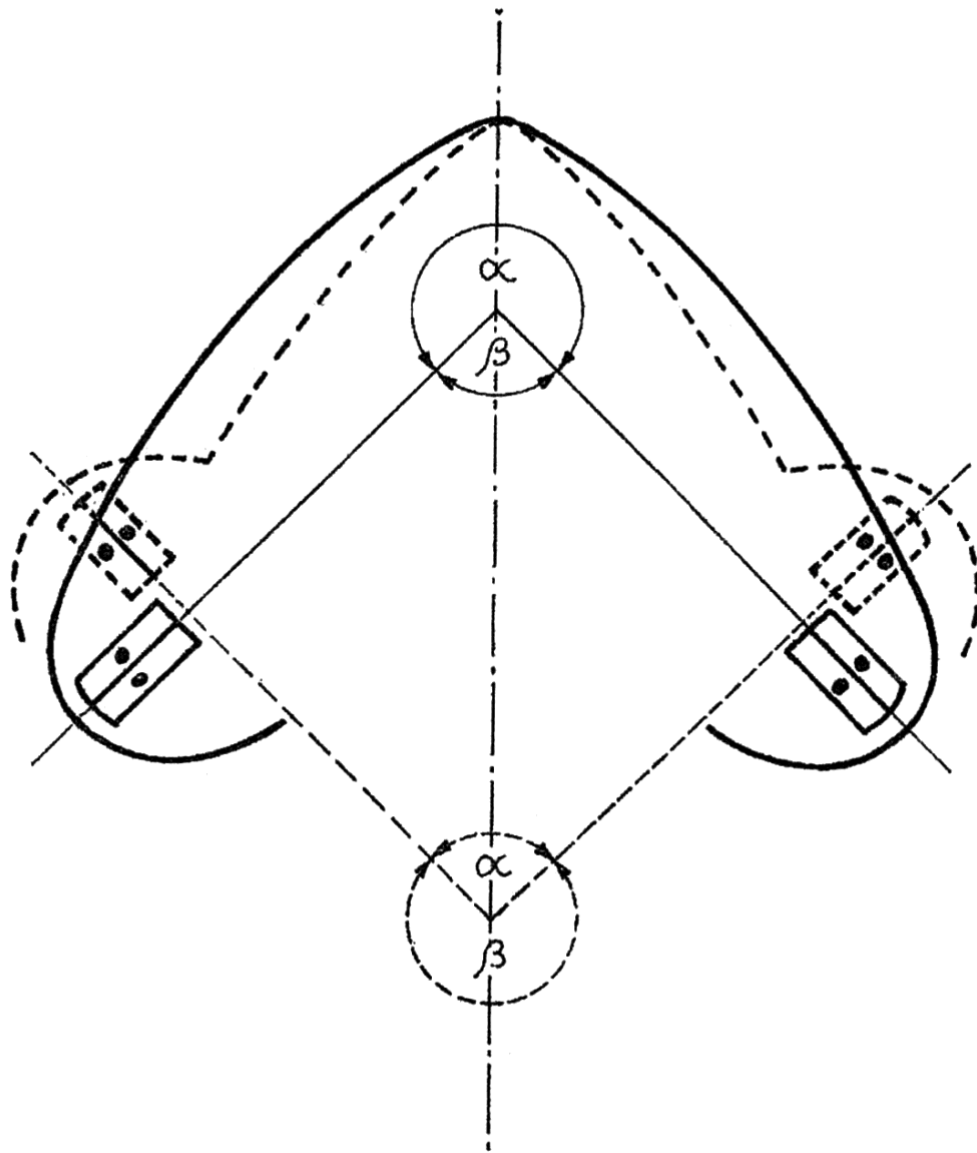
Fig 2 - Idealized diagram of a longitudinal section of the gynoecium of *Tripodanthus* (solid line) and *Tapinostema* (dashed line). The nucellar axes converge to form the α and β angles.

By varying the position of the nucellar axes we obtain two basic lines: one in which the chalazal ends point to the upper part of the ovary (*Nuytsia, Peraxilla, Lepeostegeres* and *Lysiana*); while in the other, the position is inverted in a manner such that a portion of the chalaza of the nucellar axes points towards the base of the ovary (*Tapinostema, Helicanthes, Amyema* and *Moquiniella*).

Accompanying the shift of the nucellar axes, in both evolutionary lines occurs: 1) fusion of the ovule with carpellary tissues and 2) modification of the function of the mamelon or disappearance thereof; in the latter case, ovule fusion from different carpels occurs (Fig. 3 Lorantheae). In the first line or evolutionary trend the result of the interaction between the change in position and the accompanying phenomena leads to the fusion of the inner surface of the nucellus with carpel tissues in the central region of the ovary, while at the same time the mamelon enlarges and specializes developing amyliferous tissue capable of accommodating the embryo sac. Such is the case in *Peraxilla* and *Leptostegeres*, which also corresponds to the genera *Amylotheca, Atkinsonia, Elytranthe* and *Macrosolen* (Prakash 1961, Maheshwari et al, 1952). This line ends with the type represented by *Lysiana* where the degree of fusion is such that it is not possible to distinguish the ovules or the mamelon as independent units, the latter reaches high into the stylar canal and, at the same time, fuses with the wall, whereby the longer compitum opens. In all these cases a multilocular ovary condition is always maintained.

In the second evolutionary trend, the crux lies in the type represented by *Tapinostema*; where the end of the nucellar calazal axis changed to a lower position with respect of the ovary, forming an angle of almost 90˚ without experiencing major changes in the mamelon except in size reduction. But, that is if one missed the trilocular character of the ovary that is going to become unilocular. The next step in this evolutionary trend is the progressive reduction of the mamelon until its total disappearance; which entails the approaching and fusion of ovules in one conical body that originated in different carpels. Said body is reminiscent of the mamelon by external morphology, but in no way is it homologous thereto; the reason for which, in order to avoid confusion, it is best to call it a "collective ovule". This type is represented by *Helicanthes, Amyema, Dendrophtoe* (pro part), *Scurrula* (pro part), *Tolypanthus* and *Strutanthus* (Johri et al 1957; Dixit 1958 a and b, and 1961; Narayana 1956; Singh 1952; Agrawal 1954; Venturelli 1981). Another step in this course of events is the progressive collapse of the collective ovule until it is completely embedded in the ovarian tissue. Such a structure is characteristic of *Moquiniella, Baratranthus, Dendrophtoe* (p.p.), *Helixanthera, Scurrula* (p.p.), *Tapinanthus* and *Taxillus* (Maheshwari et al 1950; Johri et al, 1969; Prakash 1963; Singh 1952; Narayana 1956).

These ovarian structures are correlated, in a certain way, with peculiarities of the embryos (fusion of the cotyledons) and others such as their chromosome complements (Barlow and Wiens 1971). Indeed, the line leading from *Peraxilla* to *Lysiana* exhibits embryos with free cotyledons and a chromosome complement of X = 12 whereas the line from *Tapinostema* to *Moquiniella* has embryos with fused cotyledons (some species of *Strutanthus* have free cotyledons) and chromosome complements that correspond to X = 8, 9 or 10. At the point of divergence of these two evolutionary trends are *Tripodanthus* and *Nuytsia* which have the two types of embryos, in terms of fusion of the cotyledons and chromosome complements X = 8, 9, 10 or 12 (Narayana 1958b).
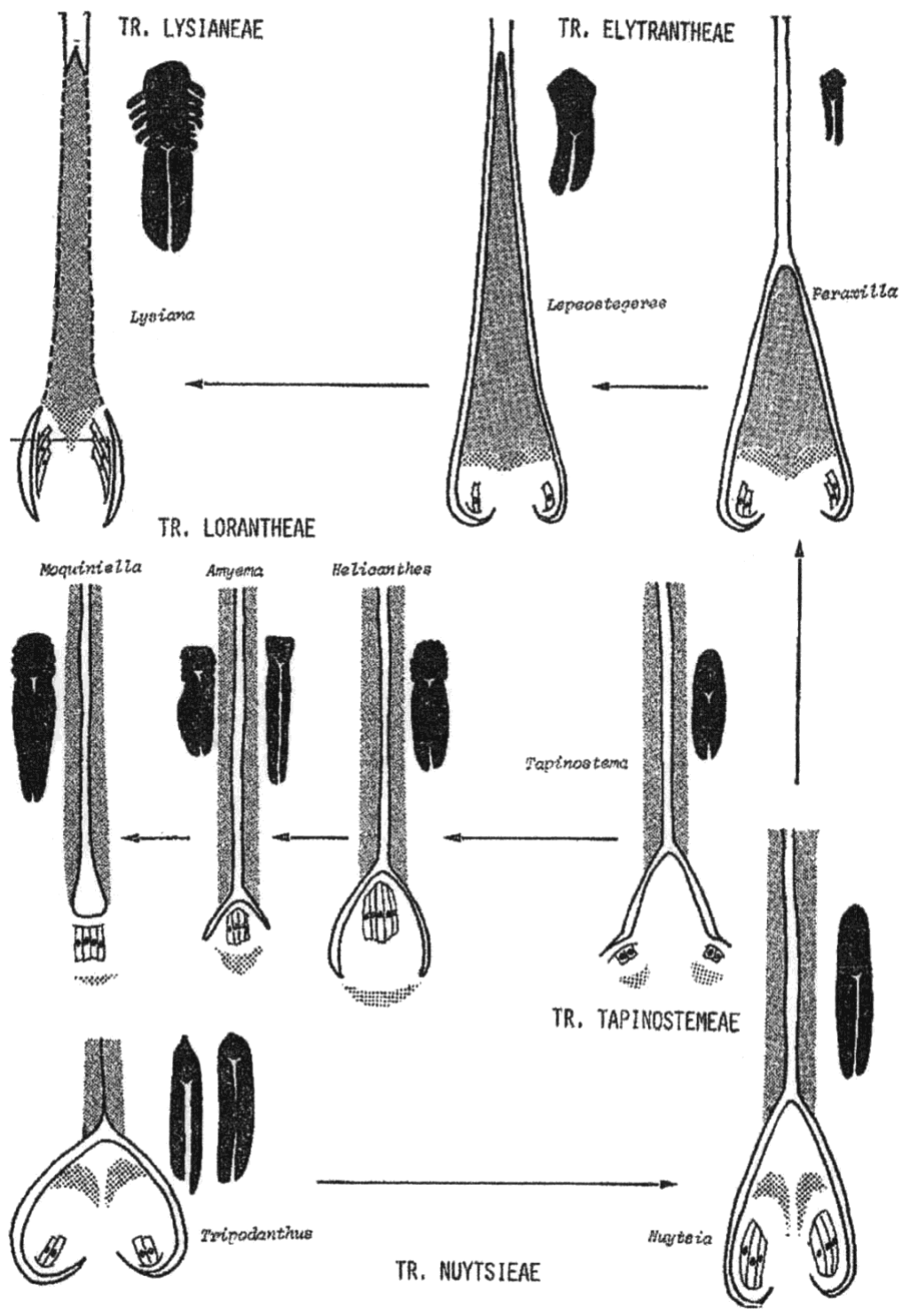
Fig 3 - Diagram illustrating evolutionary trends in the family Loranthaceae (Loranthoideae) based on the organization of the gynoecium and specialization of the embryo. Dark black: longitudinal sections of embryos; shaded areas: amyliferous tissue; thick stippling: indicates the area of the placenta.

CLASSIFICATION OF LORANTHACEAE

All features described above have been employed to improve the classification of Loranthaceae intending to effect the following five tribes distinguished by the key inserted below:

l. Gynoecium multilocular, placentation region in a superior position.

  2. Ovules differentiated, mamelon free.

    3. Mamelon without amyliferous tissue. Style with amyliferous tissue suitable for development of the megagametophyte. ....1. Tribe **NUYTSIEAE**

    3'. Mamelon with amyliferous tissue suitable for the development of the megagametophyte. Style without amyliferous tissue....... 2. Tribe **ELYTRANTHEAE**

  2'. Ovules not differentiated. Mamelon with amyliferous tissue suitable for the developing megagametophyte, solidified with tissues of the stylar canal....... 3. Tribe **LYSIANEAE**

1'. Gynoecium unilocular, placentation region inferior. Style with amyliferous tissue suitable for the development of the megagametophyte.

  4. Mamelon present. Ovules embedded but not fused to each other. ....4. Tribe **TAPINOSTEMEAE**

  4'. Mamelon absent. Ovules fused together forming a collective ovule, sometimes forming a conical prominence or fully embedded................................... 5. Tribe **LORANTHEAE**

This classification system includes 3 of the known tribes, although their boundaries have changed slightly, and two new ones are proposed with accompanying diagnoses.

<p align="center">Tribe. Lysianeae nov. trib.</p>

Gynoecium multilocular, placenta superior, stylar mamelon conical. Typical genus: *Lysiana*

<p align="center">Trib. Tapinostemeae nov. trib.</p>

Gynoecium unilocularis, placenta inferior, stylar mamelon free. Typical genus: *Tapinostema*

<p align="center">CONCLUSIONS</p>

Based on the comparative analysis of the gynoecium of Loranthaceae one can distinguish two evolutionary lines that are characterized: one, maintaining a nucellar axis with a chalazal pole pointing toward the top of the ovary; another, for varying said pole to a reverse position. These processes are accompanied by reductions, fusions and specializations that are themselves related to other characters of the respective embryos and karyotypes; all of them have been used to improve the taxonomic system of the family, recognizing five tribes, 2 of which are new (Lysianeae and Tapinostemeae).

BIBLIOGRAPHY

AGRAWAL, J. S. 1954. Female gametophyte, endosperm, and embryo of *Scurrula* Linn. *Indian Science Congress, 41st. Proceedings* 3: 137.

BARLOW, B. A., AND D. WIENS. 1971. The cytogeography of the loranthaceous mistletoes. *Taxon* 20: 291-312.

DIXIT, S. N. 1958. Morphological and embryological studies in the family Loranthaceae. IV. *Amyema* Van-Tiegh. *Phytomorphology* 8: 346-364.

DIXIT, S. N. 1958. Morphological and embryological studies in the family Loranthaceae.V *Lepeostegeres gemmiflorus* (Bl.) Bl. *Phytomorphology* 8: 365-376.

DIXIT, S. N. 1961. Morphological and embryological studies in the family Loranthaceae VIII. *Tolypanthus* Bl. *Phytomorphology* 11 (4): 335-345.

JOHRI, B. M., J. S. AGRAWAL, AND S. GARG. 1957. Morphological and embryological studies in the family Loranthaceae. I. *Helicanthes elastica* (Desr.) Dans. *Phytomorphology* 7(3-4): 336-354.

JOHRI, B. M., AND S. PRAKASH. 1965. Morphological and embryological studies in the family Loranthaceae. XI. *Tapinostemma acaciae* (Zucc.) Van Tiegh. *Phytomorphology* 15(2): 150-158

JOHRI, B. M., AND B. RAJ. 1969. Morphological and embryological studies in the family Loranthaceae. XII. *Moquiniella rubra* (Spreng. f.) Balle. *Oesterr. Bot. Z.* 116 (5): 475-485.

JOHRI, B. M., AND S. P. BHATNAGAR. 1972. Council of Scientific and Industrial Research. Botanical Monograph no. 8. Loranthaceae. 1-155. New Dehli.

MAHESHWARI, B., AND B. M. JOHRI. 1950. Development of embryo sac, embryo and endosperm in *Helixanthera ligustrina* (Wall.) Dans. *Nature* 165(4196): 978-979.

MAHESHWARI, P., AND B. SINGH. 1952. Embryology of *Macrosolen cochinchinensis*. *Botanical Gazette* 14(1): 20-32.

NARAYANA, R. 1956. Morphological and embryological studies in the Loranthaceae. Loranthoideae II. *Dendrophthoe neelgherrensis*. *J. Mysore Univ.* 16(1): 185-204.

NARAYANA, R. 1958a. Morphological and embryological studies int he family Loranthaceae. II. *Lysiana exocarpi* (Behr.) Van Tiegh. *Phytomorphology* 8(1-2): 146-169.

NARAYANA, R. 1958b. Morphological and embryological studies int he family Loranthaceae. III. *Nuytsia floribunda* (Labill.) R. Br. *Phytomorphology* 8(3-4): 306-323.

PRAKASH, S. 1960. Morphological and embryological studies in the family Loranthaceae.

 VI. *Peraxilla tetrapetala* (L. f.) Van Tiegh. *Phytomorphology* 10: 224-234.

PRAKASH, S. 1961. Morphological and embryological studies in the family Loranthaceae VII. *Atkinsonia ligustrina*. *Phytomorphology* 11(4): 325-335.

PRAKASH, S. 1963. Morphological and embryological studies in the family Loranthaceae. X. *Barathranthus axanthus* (Korth.) Miq. *Phytomorphology* 13: 97-103.

RAJ, B. 1970. Morphological and embryological studies in the family Loranthaceae XIII. *Amylotheca dictyophleba* van Tiegh. *Oest. Bot. Z.* 118: 417-430.

SCHAEPPI, H., AND F. STEINDL. 1942. Blütenmorphologische und embryologische Untersuchungen an Loranthoideen. *Vierteljahrssch. Naturf. Ges. Zürich* 87: 301-382.

SINGH, B. 1952. A contribution to the floral morphology and embryology of *Dendrophthoe falcata* (L. f.) Ettingsh. *J. Linn. Soc. Botany* 53: 449-474.

VENTURELLI, M. 1981. Embriolgia de *Struthanthus vulgaris* (Loranthaceae - Loranthoideae). *Kurtziana* 14: 73-100.