GAMETOPHYTES AND SEED DEVELOPMENT IN PINEAPPLE

Y. C. WEE AND A. N. RAO
Department of Botany, University of Singapore, Singapore-10

THE pineapple, *Ananas comosus* (L.) Merr. of Bromeliaceae consists of herbaceous plants confined mainly to the tropics and subtropics of the new world. The taxonomic details of the genus and the cultivars of pineapple have been adequately reported[1,2]. The different cultivars used in Malaysia are also described[3]. The cultivated pineapple plant is self-incompatible, although it is generally cross-fertile and sporadic cross-pollination occurs in the field with the help of honey-bee and pineapple beetles[4,5]. The details of embryology and seed development in this genus is so far unknown though pineapple is widely grown commercially around the world for more than 50 years[6]. Some of the important points concerning the gametophyte and seed development in *A. comosus* are presented here. Seed structure and germination are described for *A. sativus*[7].

Artificial crosses were made by hand pollinating the flowers of Masmerah plants with pollen of Mauritius. The post-pollination changes recorded here were determined from the time the flowers were hand pollinated. The pollinated flowers were tagged with date, time and subsequently periodic collections were made. These were fixed immediately and processed for microtoming. In 70% of the crosses made the seeds developed with embryo and endosperm tissue. Customary methods were followed to obtain the paraffin sections and for staining them.

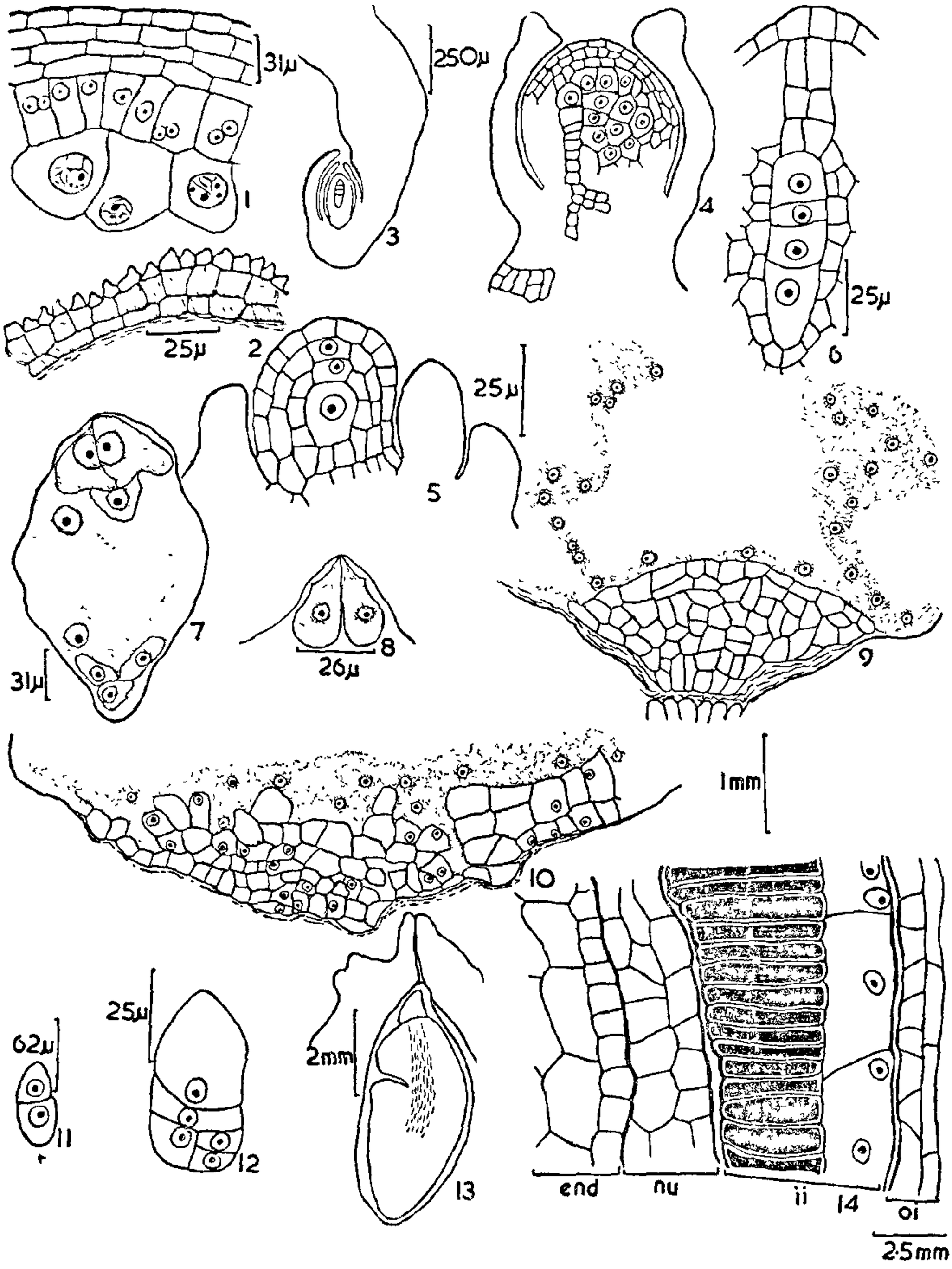
The flowers are zygomorphic and trimerous. The six stamens are arranged in two whorls, the outer episepalous and the inner epipetalous. The anthers are introse, dorsifixed with elongated pollen sacs. The wall of the young anther is made up of epidermis, endothecium, two middel layers and tapetum (Fig. 1). The tapetal cells are glandular, uninucleate becoming binucleate later on. At maturity the endothecium and a middle layer show fibrous thickenings (Fig. 2). The microspore mother cells undergo the usual reduction division showing dyad and tetrad stages. Separation of microspores takes place by cell plate formation and tetrads show isobilateral arrangement. The mature pollen grains are two celled at the shedding stage.

The ovary is inferior, syncarpous, tricarpellary, trilocular and bears 15–20 ovules per locule arranged in axile placentation. The ovules are crassinucellate and mainly anatropous, however, about 3% are of the orthotropous type (Figs. 3, 4). The anatropous ovules are bitegmic and functional while the orthotropous ovules are unitegmic. In the orthotropous ovules a few of the nucellar cells enlarge to no consequence and the ovules ultimately abort. The subsequent description is based on the development seen in anatropous ovules only.

The archesporial cell is hypodermal and divides periclinally to form primary parietal cell and megaspore mother cell (Fig. 5). The former divides further, either periclinally or anticlinally, before the megaspore mother cell enlarges. The subsequent division of megaspore mother cell results in the formation of dyad and later into a linear tetrad (Fig. 6). Only the chalazal megaspore functions further. The functional megaspore enlarges and the nucleus divides thrice to form the eight nucleate embryo sac of the polygonum type (Fig. 7)[8]. The mature synergids are hooked, pyriform, and show filiform apparatus (Fig. 8). The antipodals are organized as cells and lie in the narrow chalazal end of the embryo sac. They degenerate early, about 12–24 hours after anthesis.

The two polar nuclei meet near the chalazal end or towards the centre of embryo sac. The entry of the pollen tube is porogamous and fertilization takes place within two hours after pollination. About six hours after fertilization the primary endosperm nucleus divides in the chalazal end resulting in a larger micropylar and a smaller chalazal chamber. The nucleus in the micropylar chamber divides repeatedly to form numerous endosperm nucleii which are arranged peripherally. Nucleus in the chalazal chamber divides and soon after cytokinesis sets in organizing a triangular tissue (Fig. 9). Ultimately, the endosperm cells of both micropylar and chalazal regions merge together (Fig. 10). Endosperm formation is thus of the helobial type[8]. The cells of the micropylar region are much bigger than those organized in the chalazal end (Fig. 10). The mature endosperm cells are rich with contents.

The zygote divides transversely resulting in apical (Ca) and basal cells (Cb) (Fig. 11). Ca divides longitudinally and Cb transversely resulting in four celled stage of the embryo. The two cells of the tier Ca divide longitudinally at right angles to the first division giving rise to the quadrant cells (Fig. 12). The derivatives of the quadrant cells and the lower derivatives of Cb give rise to embryo



Figs. 1–14. (*end*, endosperm, *i.i.*, inner integument, *nu*, nucellus, *o.i.*, outer integument). Fig. 1. T.S. young anther wall. Fig. 2. T.S. mature anther wall. Note the persistent middle layer with thickenings, and papillose epidermis. Figs. 3, 4. L.S. anatropous and orthotropous ovules respectively. Fig. 5. L.S. Ovule showing MMC and parietal cells (4, 5, common scale). Fig. 6. Linear tetrad. Fig. 7. A young embryo sac. Fig. 8. Synergids showing hooked condition and filiform apparatus. Figs. 9, 10. Two stages in helobial endosperm development. Figs. 11–12. Young embryos. Fig. 13. L.S. part of the seed showing mature embryo. Fig. 14. L.S. seed coat.

proper. The upper derivatives of Cb organize the suspensor. The mature embryo is elongated with a distinct cotyledon, and a lateral stem tip (Fig. 13). The embryo development is of the Asterad type[8].

The mature seed is elongated, broad at one end and pointed at the other. The embryo is situated at the pointed end surrounded by endosperm. The seed coat is dark brown with numerous longitudinal ridges and furrows. The varying thickness of the middle layers results in the formation of ridges and furrows of the seed. Both the integuments contribute towards the formation of seed coat (Fig. 14). Seed germination and seedling development have been studied.

The literature on the embryology of Bromeliaceae has been recently reviewed and only *Tillandsia*, of the 65 genera, has been so far investigated[6]. The major observations made currently compare well with the embryological data presented for the other members of this family. Apart from the data recorded above, other variations are noticed in pollen germination, in the development of the ovule, embryo sac, the behaviour of polar nuclei as well as endosperm formation. Such variations are mostly confined to sterile hybrids as well as their abortive seeds and these will be discussed in detail in a subsequent paper. Occurrence of two types of ovules in the same species has been reported in members of Rananculaceae and Valerianaceae[9,10].

It is to be noted that cytokinensis sets in the chalazal chamber earlier than in the micropylar chamber (Fig. 9). Thus the sequence of endosperm formation observed in this species is different from the developmental changes recorded for other monocots[11].

1. Collins, J. L., *The Pineapple,* Leondard Hill, London, 1961.
2. Purseglove, J. W., *Tropical Crops. Monocotyledons,* Longman, London, 1972.
3. Wee, Y. C., *Malaysian Pineapple,* 1972, 2, 7.
4. Okimoto, M. C., *Bot. Gaz.*, 1948, 110, 217.
5. Brewbaker, J. L. and Gorrez, D. D., *Amer. Jour. Bot.*, 1967, 54, 611.
6. Davis, G. L., *Systematic Embryology of the Angiosperms,* John Wiley and Sons, New York, 1966.
7. Miles Thomas, E. N. and Homes, L. E., *New Phytol.*, 1930, 29, 199.
8. Maheshwari, P., *An Introduction to the Embryology of Angiosperms,* McGraw-Hill Book Co., New York, 1950.
9. Bhandari, N. N., *Phytomorphology,* 1962, 12, 70.
10. Johri, B. M., *Female Gametophyte in Rec. Adv. in Embryology of Angiosperms,* Univ. of Delhi, 1963, and personal communication.
11. Swamy, B. G. L. and Parameswaran, N., *Biol. Rev.*, 1963, 38, 1.