Chapter 2: Literature review

2.1 GROWTH HABIT AND PLANT MORPHOLOGY

A. sessilis 'Green' is a common weed found in paddy fields (Backer, 1949; Baki, 2006); waste grounds (Henderson, 1959; Ridley, 1924); damp areas (Backer, 1949; Henderson, 1959); shallow ditches, inundated areas, swamps (Backer, 1949) and occasionally aquatic areas (Trimen, 1980). *A. sessilis* 'Red' has not been reported as growing wild in Malaysia.

The habit of *A. sessilis* is highly variable depending on the habitats. In terrestrial areas, the solid stem is either erect, ascending or creeping (Trimen, 1980) and the leaves are smaller (Backer, 1949). In wetter areas, the plant is ascending or prostrate, rooting at the node (Trimen, 1980) and the leaves are bigger as compared with those from terrestrial areas (Backer, 1949). In aquatic areas, the stem is floating, fistular with a group of whitish rootlets at the node (Backer, 1949; Trimen, 1980).

Alternanthera philoxeroides is a popular invasive weed in the genus (Julien, 1995). Similar to A. sessilis, the stems of A. philoxeroides grown in aquatic areas are larger and hollow whereas those from terrestrial areas are narrower and solid (Buckingham, 1996). In fact, the anatomical structures of the stem and leaf also change significantly when switching from aquatic to terrestrial areas. The epidermal hair density, thickness of collenchyma cell wall and number of phloem fibre cell increase when the plant switches from the aquatic to terrestrial habitat (Tao *et al.*, 2009; Tao & Jiang, 2004). Many studies have revealed that the invasiveness of A. philoxeroides is due to phenotypic plasticity instead of genetic diversity. It has been shown that A. philoxeroides possesses lower genetic diversity and higher phenotypic plasticity when

compared with A. sessilis (Geng et al., 2006; Li & Ye, 2006; Wang et al., 2005; Xu et al., 2003).

Previous study shows that *Alternanthera brasiliana* is herb and is introduced and naturalized in moist and shaded areas, steep slopes or river banks (Backer, 1949). All the five stamens in *A. brasiliana* are fertile in Hawaii (Wagner *et al.*, 1990) but they are not described in Malesia (Backer, 1949). Nevertheless, fruit is produced in both areas. *Alternanthera bettzickiana* is introduced into Malesia as an ornamental plant or bedding plant in tea plantation (Backer, 1949). Two to three of *A. bettzickiana* stamens are sterile (Backer, 1949) and fruits have never been produced (Backer, 1949; Veldkamp, 1971). In Papua New Guinea, *A. bettzickiana* is a weed in damp areas (Womersley, 1978). The ornamental form, on the other hand, does not produce seed when it is introduced into Papua New Guinea (Womersley, 1978). *Alternanthera paronychioides* is a weed that can be found in dry, sandy or damp areas (Chen, 2008; Mishra, 1994; Trimen, 1980; Veldkamp, 1971). *A. ficoidea* (L.) Sm. has not been reported in Malesia (Backer, 1949; Henderson, 1959; Ridley, 1924).

According to Backer (1949), "Alternanthera species is either an erect, ascending, trailing, creeping, floating or clambering herb. The leaf is simple with a short petiole and the leaf arrangement is opposite. The shape and size of the leaf are variable; varying from linear-lanceolate to oval or obovate, acute at the base, obtuse, rounded or acute at the apex. The bisexual, small flower is sessile or with peduncle and is subtended by two scarious bracteoles. Five free tepals are equal or unequal in size, glabrous or hairy. They are often dorsally compressed. The androecium is made up of two to five stamens. The filaments fuse into a tube or a short cup at the base and occasionally alternate with the pseudo-staminodes. The anthers are small and two locules. The gynoecium is made up of a unicarpellate pistil which consists of a capitate stigma supported by a short style

and a superior ovary. The ovary is orbicular or ovoid with a single basal ovule supported by a long funiculus. The inflorescence is axillary and rarely terminal. It is sessile or supported by a short peduncle. The indehiscent and obcordate utricle will fall off with the perianth together with or without the bracteoles". In addition, the type of trichome present in the plant has been suggested as an important key for species identification especially for Malaysian *Alternanthera* species (Backer, 1949).

2.2 REPRODUCTIVE BIOLOGY

Alternanthera sessilis is usually a perennial species and sometimes, an annual or short-lived plant under unfavourable situation (Backer, 1949). It can reproduce sexually or asexually. In sexual reproduction, seeds are produced and dispersed by wind or water (Brunel, 2009; Scher as cited in Singh *et al.*, 2011). In asexual reproduction by vegetative cuttings, the rooting nodes at the stem could develop into mature plants (Gnanaraj *et al.*, 2011).

Seed germination is greatly stimulated by continuous or diffuse light without chilling treatment in *A. sessilis*. In addition, germination stimulators such as potassium nitrate and thiourea interacting with optimum light or temperature could increase the germination rate (Datta & Biswas, 1968). Naked seeds of *A. sessilis* show a higher germination rate than those enclosed in pericarp or perianths (Kaul, 1967). Previous study on *A. tenella* Colla showed that sowing depth affected germination. The highest germination rate is achieved on the soil surface whereas germination is completely absent when seeds are sown at 10 cm below the soil surface (Canossa *et al.*, 2007). Viviparous germination has been reported in *Alternanthera littoralis* var. *maritima* (Mart.) Pedersen and this is the first record for *Alternanthera* (Antonucci *et al.*, 2011).

Alternanthera sessilis is distributed sympatrically along with *A. philoxeroides* in South China (Li, 1998). *A. philoxeroides* is a perennial amphibious weed that is able to

grow in both aquatic and terrestrial areas. In aquatic habitats, *A. philoxeroides* root along the shore or in shallow water before growing towards deeper water to form a dense floating mat. Reproduction is solely vegetative through the stem nodes whereas sexual reproduction does not play a role in the propagation process (Julien, 1995). This is because fruits and viable seeds are rarely produced due to pollen abnormality (Liu *et al.*, 2008). However, seeds is reported in Argentina (Pan *et al.*, 2007). The species is dispersed by fragmentation when the stems break and float to a new area.

Alternanthera brasiliana is a perennial shrub which is propagated sexually or asexually by vegetative cutting (Lemmens & Horsten, 1999) and apomixis has not been reported. In Amaranthaceae, three species have been reported as apomicts. *A. littoralis* var. maritima reproduced apomictically when pollination was absent (Antonucci *et al.*, 2011). *Aerva javanica* (Burm.f.) Juss. *ex* Schult. is a dioecious plant and the female inflorescence produces fruits and seeds in the absence of pollen grains (Khan *et al.*, 1970). Another species, *Aerva tomentosa* Forssk., produces fruits by diplosporous parthenogenesis (Sachar & Murgai, 1958; 1959).

The reproductive biology of the genus *Amaranthus* is more extensively studied as compared with the genus *Alternanthera*. Most of the *Amaranthus* species are annual, monoecious or dioecious herbs distributed in tropical and temperate regions (Mabberley, 2008). Generally, the emergence of new plants begins in April to June and the initiation of flower buds is dependent on photoperiod (Costea *et al.*, 2005). The breeding system of *Amaranthus* is autogamy with self pollinated flowers. The flowers are small, unattractive to pollinators, odourless and lack nectar. Examples are *A. retroflexus* L. (Costea *et al.*, 2004; Iamonico, 2010); *A. powellii* S.Watson, *A. hybridus* L. (Costea *et al.*, 2004); *A. albus* L. (Costea & Tardif, 2003); *A. tuberculatus* (Moq.) Sauer (Costea *et al.*, 2005); *A. cannabinus* (L.) Sauer (Bram & Quinn, 2000).

The pollen grains are also adapted to wind pollination by having a lot of sunken apertures to provide aerodynamic function. For instance, 90–110 apertures are found on the pollen grains of *A. tuberculatus* (Costea *et al.*, 2005).

Some of the *Amaranthus* species are occasionally pollinated by insects during seed dispersal. The monophagous micromoth, *Coleophora lineapulvella*, accidentally collected pollen grains of *A. retroflexus* and *A. powellii* during seed foraging (Costea *et al.*, 2004). In Malaysia, honeybees visit *A. lividus* L. and *A. spinosus* L. and the insects are believed to be pollen thieves (Kiew & Conner, 1993).

The fruits with a single seed of *A. albus* L. and *A. blitoides* S.Watson are dehiscent or indehiscent (*A. blitum* L.) (Costea & Tardif, 2003). As the fruits float easily, the seeds can be dispersed by water, wind, birds or farm machinery. Seed viability is high and takes about 3–8 days to reach 50% germination as shown in the seeds of *A. rudis* J.D.Sauer, *A. powellii, A. blitoides, A. hybridus, A. palmeri* S.Watson, *A. spinosus, A. retroflexus, A. tuberculatus, A. albus* (Lawrence *et al.*, 2004).

Optimal temperature for the seeds of *Amaranthus* to reach maximum germination was above 20°C (Lawrence *et al.*, 2004). For instance, optimal temperature was 25/20°C for *A. rudis* and 35/30°C for *A. palmeri* and *A. retroflexus* (Peiguo & Kassim, 2003). Apart from temperature, seed germination is also affected by the depth of sowing in soil. *Amaranthus spinosus* and *A. viridis* L. showed the highest germination rate when the seeds were sown on the surface of the soil. The germination rate decreases with the increase of soil depth. At depths of 4 cm and 6 cm, no germination was recorded for *A. spinosus* and *A. viridis* respectively (Chauhan & Johnson, 2009).

2.3 EMBRYOLOGY

The embryology of eleven genera in Amaranthaceae has been reported (Table 1.2). Generally, the anther is tetrasporiangiate with the wall development conforming to the Monocotyledonous type (Davis, 1966). Only a few exceptions to this rule occur; for example, the anther of *Amaranthus spinosus* is quadrisporangiate (Pullaiah & Narahara, 1987). The endothecium developed fibrous thickening except in *Achyranthes aspera* L. (Kajale, 1937a) and *Amaranthus leucocarpus* S.Watson (Sebastian & Deshpande, 1974). Ephemeral middle layer and glandular multinucleate tapetum are the rule. Rarely, uni-nucleate tapetum occurs, as seen in *A. spinosus* (Pullaiah & Narahara, 1987). In most of the genera studied, [for example: *A. spinosus* (Pullaiah & Narahara, 1987); *Psilostachys sericea* Hook.f. (Bakshi, 1952) and *Celosia argentea* L. and *Cyathula tomentosa* (Roth) Moq. (Kajale, 1940)], ubisch granules are deposited on the inner wall of the tapetum and endothecium but not in *A. spinosus* due to the short-lived endothecium (Sebastian & Deshpande, 1974).

Simultaneous cytokinesis during microsporogenesis results in tetrahedral, isobilateral and decussate pollen tetrads. For example, tetrahedral and isobilateral pollen tetrads were reported in *Amaranthus mangostanus* L. (Narahara & Pullaiah, 1986); decussate and tetrahedral pollen tetrads in *A. leucocarpus* (Sebastian & Deshpande, 1974); tetrahedral, isobilateral and decussate pollen tetrads in *A. spinosus* (Pullaiah & Narahara, 1987) and *Psilostachys sericea* (Bakshi, 1952). Pollen grains are three-celled when shed except in *Digera arvensis* Forssk., in which the mature pollen grains are two-celled (Puri & Singh, 1935).

The ovule is amphitropous in *Amaranthus leucocarpus* (Sebastian & Deshpande, 1974); *A. mangostanus* (Narahara & Pullaiah, 1986); *A. spinosus* (Pullaiah & Narahara, 1987) and *P. sericea* (Bakshi, 1952). However, *Aerva lanata* (L.) Juss.,

Amaranthus viridis, C. argentea, C. tomentosa (Kajale, 1940); *D. arvensis* (Joshi & Rao, 1934) and *Pupalia lappacea* (L.) Juss. (Kajale, 1940) were reported to have anacamplytropous ovules. The ovules of *Aerva tomentosa* (Sachar & Murgai, 1958); *Allmania nodiflora* (L.) R.Br. *ex* Wight (Kajale, 1940); *Amaranthus caudatus* L. (Woodcock, 1931); *A. hybridus* (Pal *et al.*, 1990) and *Celosia cristata* L. (Pal, 1968) were reported as camplylotropous. Both *Gomphrena celosioides* (Padhye, 1962) and *P. sericea* (Bakshi, 1952) were reported to have circinotropous ovules.

The micropyle is formed by the inner integuments only except in *G. celosioides* where both the integuments are involved (Padhye, 1962). An air space is present in between the two integuments in the basal region and occasionally a second air space is observed in between both the integuments and nucellus, as seen in *A. leucocarpus* (Sebastian & Deshpande, 1974).

In most of the genera studied, the archesporium was reported as multicellular but occasionally one-celled archesporium has also been observed in *Amaranthus* (Narahara & Pullaiah, 1986; Pullaiah & Narahara, 1987; Sebastian & Deshpande, 1974). Mostly, a single cell (Bakshi, 1952; Kajale, 1940; Sachar & Murgai, 1958) or sometimes two to five cells (Puri & Singh, 1935) of the multicellular archesporia cut off a parietal cell producing the parietal tissue. The megaspore mother cell divides meiotically to produce a linear tetrad of megaspores and rarely, only three megaspores are produced as the upper cell of the dyad does not undergo homotypic division [e.g. in *C. cristata* (Pal, 1968) and *D. arvensis* (Puri & Singh, 1935)].

The chalazal megaspore develops into the *Polygonum* type (Maheshwari, 1950) of embryo sac with two synergids, an egg cell, a pair of polar nuclei and three antipodals. Hooked synergids are reported in most of the genera except in *A. spinosus* (Pullaiah & Narahara, 1987) and *A. mangostanus* (Narahara & Pullaiah, 1986). *P. lappacea* (Kajale, 1937b; 1940) has been reported to have 30–40 antipodals but these

antipodals could have been the nucellar cells (Bakshi, 1954). During the enlargement of the embryo sac caecum, the antipodals are pushed laterally and they persist up to the early stages of the embryo development (Joshi, 1936; Kajale, 1937b). Nevertheless, a few exceptions have been reported; for example, ephemeral antipodals in *A. spinosus* (Pullaiah & Narahara, 1987); *A. mangostanus* (Narahara & Pullaiah, 1986); *C. cristata* (Pal, 1968) and *P. sericea* (Bakshi, 1952). The polar nuclei fuse before fertilization (Davis, 1966; Johri *et al.*, 1992) and lie beneath the egg (Sebastian & Deshpande, 1974).

Fertilization is reported as porogamous and accessory pollen tubes could be seen in *A. viridis* and *A. lanata* (Kajale, 1940); *G. celosioides* (Padhye, 1962); *P. sericea* (Bakshi, 1952) and *P. lappacea* (Kajale, 1940). The endosperm development is of the *ab initio* Nuclear type. Wall formation begins from the micropylar and proceeds to the chalazal region with the endosperm becoming completely cellular at the globular embryo stage (Johri *et al.*, 1992).

The development of the embryo follows the Chenopodiad-type as in *A. spinosus* (Pullaiah & Narahara, 1987); *A. mangostanus* (Narahara & Pullaiah, 1986); *P. sericea* (Bakshi, 1952); *Aerva tomentosa* (Sachar & Murgai, 1958; 1959) and *C. cristata* (Pal, 1968). The mature embryo is nearly annular and encloses the perisperm, with the two cotyledons about twice as long as the hypocotyl and radicle. This conspicuous character has been used to circumscribe the order Centrospermae (Nowicke, 1975).

Abnormal development of the embryo has been reported in several genera. In *D. arvensis*, two embryo sacs were observed and most likely they developed from two megaspore mother cells (Puri & Singh, 1935). Fusion of three polar nuclei instead of two polar nuclei to form a secondary nucleus in *P. sericea* was reported (Bakshi, 1952).

Aerva tomentosa is regarded as an apomict which produces embryos by diplosporous parthenogenesis (Sachar & Murgai, 1958; 1959). The sporogenous cell

directly develops into an eight-nucleate embryo sac without undergoing any meiotic division. In many embryo sacs, the synergids and egg degenerate while the polar nuclei and antipodals remain healthy. A case of two embryo sacs is observed and this could be due to the simultaneous functioning of two sporogenous cells. A few abnormal embryo sacs with supernumerary polar nuclei have also been reported. Eventually, the unreduced egg cell would undergo parthenogenesis and the embryo development follows that of the Chenopodiad-type. The polar nuclei fuse to form a secondary nucleus which directly functions as the primary endosperm nucleus. This nuclear endosperm divides autonomously before the development of the embryo.

2.3.1 Embryology of Alternanthera

The anther of *A. sessilis* is bisporangiate with four archesporial cells. These cells divide periclinally to form the outer primary layer and sporogenous cell. The outer primary layer undergoes two successive divisions which produces four layers of anther wall including the epidermis. The sporogenous cell divide mitotically and subsequently differentiates into the microspore mother cells. Each of the microspore mother cell divides meiotically producing four pollen grains after simultaneous cytokinesis. The middle layer is ephemeral and the endothecium starts to develop fibrous thickening when the pollen grains reach the bi-nucleate stage. The uni-nucleate tapetum becomes bi-nucleate when the microspore mother cells undergo meiosis I. It persists up to the cytokinesis stage during microsporogenesis and degenerates completely when the pollen grains are mature. The mature pollen grains are three-celled when shed (Kajale, 1940).

In the female gametophyte of *A. sessilis*, one cell from the primary archesporium develops to produce the sporogenous cell (Kajale, 1935). Subsequently, three megaspores were produced and this resembles the development in *C. cristata* (Pal, 968). Similar to the other genera, the functional chalazal megaspore develops further to form

a normal eight-nucleate embryo sac. Thus, the embryo sac development conforms to the monosporic *Polygonum* type (Kajale, 1935).

The mature embryo sac consists of one pair of hooked synergids, a flask-shaped egg cell, two polar nuclei and three antipodals. Abnormalities are observed when one of the synergids is found to be devoid of any large vacuole and its nucleus is situated in the chalazal end (Kajale, 1935). The antipodals differentiate before the egg apparatus and are pushed laterally during the development of the embryo sac caecum. These antipodals persist until the early stage of the embryo development as reported in *A. sessilis* (Kajale, 1935) as well as in other genera such as *D. arvensis* (Joshi, 1936) and *P. lappacea* (Kajale, 1937b).

The embryo development in *A. sessilis* was described as the Chenopodiad-type (Joshi & Kajale, 1937). However, the embryogeny of *A. sessilis* was reviewed and it was suggested that it should represent a transitional form between the Chenopodiad-type and Solanad-type (Johansen, 1950; Padhye, 1962). The endosperm development follows the *ab initio* Nuclear type. The wall formation begins in the micropylar region and proceeds to the other part of the embryo sac except the chalazal region and this is different from the endosperm development in the other genera such as *C. argentea*, *A. nodiflora*, *A. viridis*, *C. tomentosa* and *P. lappacea* (Kajale, 1940).

2.4. PALYNOLOGY

Undoubtedly, the role of pollen morphology in plant systematics is as important as other studies such as morphology, embryology or molecular. For instance, a detailed study on the pollen morphology revealed the misinterpretation of three *Pfaffia* spp. as *Iresine* spp. (Borsch, 1995). This is especially meaningful as in recent years pollen morphology has not only helped to resolve the relationship among genera of the family Amaranthaceae, (Borsch, 1998) but has also supported findings in phylogenetic studies of the subfamily Gomphrenoideae (Müller & Borsch, 2005a; Sánchez del-Pino *et al.*, 2009). Apart from this, pollen morphology has also been used as a tool to distinguish superficially similar medicinal plants from different family (Bashir & Khan, 2003).

Prior to the introduction of the acetolysis method (Erdtman, 1960), the pollen morphology of quite a number of genera has already been reported. Examples are, *Celosia argentea, Allmania nodiflora, Amaranthus viridis, Cyathula tomentosa, Pupalia lappacea, Aerva lanata, Achyranthes aspera, Alternanthera sessilis, Gomphrena globosa* L. (Kajale, 1940); *Amaranthus palmeri* S.Watson, *A. retroflexus, A. spinosus, A. hybridus, A. graecizans* L. and *Acnida tamariscina* (Nutt.) Alph.Wood (Wodehouse, 1965). The pollen data of these species were mainly on the size of pollen and pore morphology with very little information on the sexine ornamentation.

The palynology of Amaranthaceae became more advanced after the introduction of the acetolysis method. This method removed all non-sporopollenin substances from the pollen grains and exposed the sexine ornamentation clearly. Since then, the pollen grains of Amaranthaceae were classified into two types based on the pore structure and sexine ornamentation. The *Amaranthus*-type pollen grains are without recessed pores whereas the *Gomphrena*-type pollen grains are reticulate or undulatitegillateinfrareticulate with deeply recessed pores (Erdtman, 1966). This classification was further refined by a more detailed study on the sexine ornamentation (Mittre, 1963) (Table 2.1).

Nevertheless, Erdtman (1966) and Mittre's (1963) classifications are still too broadly defined. Fortunately, with the utilization of Transmission Electron Microscopy (TEM) and Scanning Electron Microscopy (SEM), fine structures on the sexine ornamentation were examined and studied; thus contributing to a better understanding of the pollen morphology of Amaranthaceae. From the literature reviewed, very few studies on the ultrastructure have been reported (Nowicke & Skvarla, 1979; Skvarla & Nowicke, 1976; Livingstone *et al.*, 1973) and this was probably due to the timeconsuming and laborious TEM procedures.

On the other hand, extensive research was carried out using SEM. One of the most significant findings was the subdivision of the pollen grains from as many as 17 genera and 20 species in Amaranthaceae into two categories (Table 2.2). In fact, emphasis was generally placed on the order level (Centrospermae) rather than the family level (Amaranthaceae) (Nowicke, 1975). (Nowicke, 1975) (Nowicke, 1975)

Meanwhile, confusion occurred when the term, reticulate, was used to describe the sexine ornamentation of the pollen in this family, especially those from the *Gomphrena*-type (Borsch & Barthlott, 1998). In order to resolve this problem, a new term 'metareticulate' was proposed to distinguish the truly reticulate from the metareticulate pollen. As such, metareticulate is used to describe a reticulum of higher order such as the *Gomphrena*-type of pollen grains and at the same time, distinguished *Gomphrena*-type from the *Amaranthus*-type of pollen grains (Erdtman, 1966).

Soon after the proposal of the new term, the pollen morphology of Amaranthaceae was extensively studied. Thus, Erdtman's (1966) classification was further classified into thirteen groups of pollen types in the *Amaranthus*-type and six in the *Gomphrena*-type based on the shape and size of pollen, structure of the pores,

sexine ornamentation, frequency of perforations and the number of microspines per tectum area (Borsch, 1998) (Table 2.3).

2.4.1 Palynology of Alternanthera

Palynological data of 66 genera and 222 species in Amaranthaceae have been reported so far. For *Alternanthera*, palynological data of 21 species were reported and are as follows: *A. albida* (Moq.) Griseb. (Borsch, 1998); *A. bettzickiana* (Li *et al.*, 1993); *A. caracasana* Kunth (Müller & Borsch, 2005b); *A. costaricensis* (Kuntze) Standl. (Borsch, 1998); *A. flavescens* Kunth (Borsch, 1998); *A. filifolia* (Hook.f.) J.T.Howell (Borsch, 1998); *A. galapagensis* (A.Stewart) J.T.Howell (Eliasson, 1988); *A. gracilis* M.Martens & Galeotti (Erdtman, 1966); *A. geniculata* Urb. (Eliasson, 1988); *A. maritima* (Mart.) A.St.-Hil. (Borsch, 1998); *A. olivacea* (Urb.) Urb. (Borsch, 1998); *A. paronychioides* (Perveen & Qaiser, 2002); *A. peruviana* (Moq.) Suess. (Borsch, 1998; Eliasson, 1988); *A. pycnantha* (Benth.) Standl. (Borsch, 1998); *A. reineckii* Briq. (Eliasson, 1988); *A. repens* (Mittre, 1963) and *A. sessilis* (Kajale, 1940; Li *et al.*, 1993; Liang *et al.*, 1978; Mittre, 1963; Perveen & Qaiser, 2002; Rao & Shukla, 1975).

Pollen grains of *Alternanthera* with deeply recessed pores were first classified as *Gomphrena*-type (Erdtman, 1966) but are further described as *Pfaffia*-type (Borsch, 1998). The pollen is characterized by having dodecahedric or spheroidal pollen. The pollen grains are small with size ranging from 10.9 μ m in *A. bettzickiana* (Li *et al.*, 1993) to 22.5 μ m in *A. pungens* (Bashir & Khan, 2003). For *A. sessilis*, the size of the pollen grains vary with locality; the largest (19.0 μ m) is from New Delhi (Rao & Shukla, 1975), followed by the pollen grains from China (16.7 μ m, Liang *et al.*, 1978;

14.4 μm; Li *et al.*, 1993) while the smallest are from Pakistan (13.59 μm, Perveen & Qaiser, 2002).

Alternanthera is reported as stenopalynous in terms of pore number (Borsch, 1998; Srivastava *et al.*, 1977). Most of the species are pantoporate and consisted of twelve to fourteen pores. Examples are, the pollen grains of *A. gracilis* (Erdtman, 1966); *A. flavescens, A. albida, A. costaricensis, A. filifolia, A. maritima, A. olivacea, A. peruviana* (Borsch, 1998); *A. repens* (Mittre, 1963); *A. sessilis* (Li *et al.*, 1993; Liang *et al.*, 1978; Mittre, 1963); *A. bettzickiana* and *A. nodiflora* (Li *et al.*, 1993). However, a few exceptions to this rule occurred when the number of pores was reported as 20–24 in the pollen grains of *A. paronychioides* from China (Li *et al.*, 1993) and six to nine in the pollen grains of *A. sessilis* also varies with locality. In the Upper Gangetic Plain (Rao & Shukla, 1975), it is reported as six but 3–3.2 in Pakistan (Perveen & Qaiser, 2002).

The pores of *Alternanthera* are covered by 20–60 ektexinous bodies which are closely adjoined in a mosaic-like pattern. The shape of the ektexinous body is rectangular, sinuous or elongated in outline with one to four distinct microspines attached onto it. The size of the ektexinous bodies is 1.5–4 times as long as broad. Most of the species from the New World such as *A. flavescens*, *A. albida*, *A. costaricensis*, *A. filifolia*, *A. maritima*, *A. olivacea*, *A. peruviana* (Borsch, 1998); *A. sessilis*, *A. philoxeroides*, *A. bettzickiana*, *A. nodiflora* (Li *et al.*, 1993); *A. nesiotes*, *A. galapagensis*, *A. peruviana*, *A. geniculata*, *A. reineckii* (Eliasson, 1988) and *A. caracasana* (Müller & Borsch, 2005b) having the above mentioned characters are named as pore of Type I.

Most of the sexine ornamentation of the pollen grains in *Alternanthera* conforms well to *Pfaffia*-type (Borsch, 1998; Eliasson, 1988). The sexine is metareticulate,

tectate, punctuate with unevenly distributed perforations. Both sides of the mesoporia are completely covered by tectum and therefore the collumellae could not be seen. A row of microspines is distally and regularly or irregularly arranged. However, the sexine pattern of the pollen of *A. sessilis* from India is distinctly different in being granulate (Rao & Shukla, 1975) or simplibaculate and devoid of spinules (Mittre, 1963).

Sexine ornamentation is an important character in pollen description even at the species level. An example is seen in the pollen grains of *A. philoxeroides* and *A. bettzickiana* which are somewhat distinct from those of *A. sessilis* and *A. nodiflora* in having a different number of spinules attached at the mesoporia (e.g. one to two rows in *A. bettzickiana*, one to three rows in *A. philoxeroides*, only one row in *A. sessilis* and *A. nodiflora*) (Li *et al.*, 1993).