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Embryology and systematic position of *Psiloxylon* (Myrtales)

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Abstract. The embryology of *Psiloxylon*, a unique myrtalean genus endemic to Mauritius, was investigated to clarify its relationships to Myrtaceae *sensu stricto*, on the one hand, and to the continental African genus *Heteropyxis*, on the other. Embryologically *Psiloxylon*, which agrees with both in many features, is nevertheless more similar to *Heteropyxis* than to Myrtaceae. Indeed, *Psiloxylon* and *Heteropyxis* share two distinct apomorphies that are unknown in Myrtales: (1) an Allium type embryo sac (bisporic) and (2) anthers tetralocular at anthesis. This new embryological evidence, along with evidence from other sources, strongly suggests that *Psiloxylon* and *Heteropyxis* were derived as a single clade from a common ancestor with Myrtaceae, and favors the recognition either of a ditypic family Heteropyxidaceae (comprising *Psiloxylon* and *Heteropyxis*) close to Myrtaceae or, better, a ditypic subfamily Heteropyxidoideae within Myrtaceae.

Key words: Embryology; *Heteropyxis;* Myrtales; *Psiloxylon.*

Introduction

Psiloxylon Thouars ex Tul. is a unique myrtalean genus comprising only *P. mauritianum* (Hook. f.) Baill., which is endemic to Mauritius, an island in the western Indian Ocean. Historically, its relationships have been problematical, and the genus has been placed at various times in Lythraceae, Myrtaceae, a monotypic family-- Psiloxylaceae, generally in the order Myrtales, or even in various families in other orders; for a historical review of the taxonomic placement, see Schmid (1980). Recently, however, the debate about the affinities of *Psiloxylon* has centered on the question of whether it is more closely related to *Heteropyxis* Harvey, an endemic of southeastern Africa, or to Myrtaceae *sensu stricto*.

Schmid (1980), on the basis of a careful comparison of the known vegetative and reproductive features of the groups involved, concluded that the segregate families Psiloxylaceae (for *Psiloxylon*) and Heteropyxidaceae (for *Heteropyxis*) should be included in Myrtaceae. He assigned *Psiloxylon* into a new monotypic subfamily Psiloxyloideae, and *Heteropyxis* to one of the three remaining subfamilies, Leptospermoideae *sensu* Schmid. Subsequently, Thorne (1983) adopted a broadly defined Myrtaceae and placed *Psiloxylon* in Psiloxyloideae, but continued the placement of *Heteropyxis* in Heteropyxidoideae, whereas Dahlgren (1983) continued to accept Psiloxylaceae and Heteropyxidaceae as distinct families. The respective treatments of these two authors were reiterated subsequently in a joint paper (Dahlgren and Thorne, 1984). In contrast, Cronquist (1981, 1988) has consistently included both *Psiloxylon* and *Heteropyxis* in Myrtaceae, whereas Takhtajan (1986) has accepted Psiloxylaceae, but assigned *Heteropyxis* to Myrtaceae. Johnson and Briggs (1984), on the basis of phylogenetic (cladistic) analysis using their "CLAX" program, stated that "the shortest tree shows a branch leading to *Heteropyxis* and *Psiloxylon*, but a tree one step longer would associate *Heteropyxis* with the branch leading the Myrtaceae." Their result is, however, hardly conclusive as they admit, and instead seems indicative of the still uncertain relationships between *Psiloxylon, Heteropyxis*, and Myrtaceae

sensu stricto. We have undertaken our study to investigate the problem posed by Dahlgren and van Wyk (1988): "Whether *Psiloxylon* from Mauritius also belongs in Heteropyxidaceae must await further study."

In a previous paper (Tobe and Raven, 1987a), we reported the embryological features of *Heteropyxis* and showed that the genus, although doubtless closely allied to Myrtaceae, is distinct in possessing (1) a bisporic Allium type embryo sac, (2) a condition in which each of the two microsporangia of an anther half dehisces by its own longitudinal slits instead of by one slit common to both, and (3) an ovule and seed that have wings on both ends. A central objective of our investigation of the embryology of *Psiloxylon*, then, was to determine if the genus shares embryological apomorphies with Myrtaceae *sensu stricto* or with *Heteropyxis*.

A few embryological features of *Psiloxylon* were described by Schmid (1980), but most of them have not yet been reported. Our earlier studies of embryological features of a number of myrtalean groups (Tobe and Raven, 1983a, b, 1984a, b, c, d, e, 1987a, b, c) suggested to us that further elucidation of these features in *Psiloxylon* would be useful in evaluating its relationships with *Heteropyxis* and Myrtaceae *sensu stricto*.

Materials and Methods

The only species of the genus, *Psiloxylon mauritianum* (Hook. f.) Baill., endemic to Mauritius, was studied. Our investigation was principally based on materials preserved in FAA (5:5:90, using 50% ethanol), comprising functionally staminate flowers (*Guého & Lecordier s.n. in 1983*, no voucher), pistillate flower buds and fruits (*Guého & Lecordier s.n. in 1982*, Mauritius Herb. 20131, MO; *Guého s.n. in 1983*, no voucher), and supplemented by seeds from an herbarium collection (*Lawrence 1075*, MO). Flowers with stamens are apparently bisexual, but the gynoecium is rudimentary containing many abortive ovules, so they are functionally staminate. Pistillate flowers lack stamens. For microscopic observations, seven functionally staminate flowers, 30 pistillate flowers, five young fruits, and five mature seeds were sectioned.

Flower buds and fruits in various stages and dry mature seeds (which also had been soaked in FAA) were dehydrated through a *t*-butyl alcohol series and embedded in Paraplast with a melting point of 56-58°C. Embedded fruits and seeds were softened by a mixture of a 10:3:90 glycerol:10% Aerosol OT:water before sectioning (Schmid and Turner, 1977; see also Tobe and Raven, 1987a). Serial sections, cut 6-8 μm thick on a rotary microtome, were stained with Heidenhain's hematoxylin, safranin, and fast green FCF, and were mounted with Entellan. The number of cells in mature pollen grains was examined by staining with 1% acetocarmine, as was done elsewhere (Tobe and Raven, 1984a, 1987a). Scanning electron microscopic observations on seeds were made following the standard technique and using a JSM-25S (JEOL).

Observations

The following descriptions are based on functionally staminate flowers (Anther and microspores), or on pistillate flowers.

Anther and Microspores

The anther is tetrasporangiate (Fig. 3). The wall structure prior to maturity comprises five or six layers, i.e., an epidermis, an endothecium, two or three middle layers, and a tapetum (Fig. 1). Since the middle layers share their developmental origin with both the endothecium and the tapetum (Fig. 1), anther wall formation conforms to the Basic type (see Davis, 1966, p. 10). During maturation both the epidermis and the middle layers collapse, while the endothecium develops fibrous thickenings. The tapetum is glandular and its cells become two-nucleate before degeneration (Fig. 2). Thus, the mature anther wall is composed only of the fibrous endothecium (Fig. 4).

Meiosis in a microspore mother cell is followed by simultaneous cytokinesis (Fig. 2). The arrangement of the microspores in the resultant tetrad, on the basis of the examination of 50 randomly selected examples, is always tetrahedral. Pollen grains are two-celled at the time of shedding (Fig. 5). Nuclei of both generative and vegetative cells are faintly stained by acetocarmine (Fig. 5); the generative cell is spindle - shaped when viewed on longitudinal axis.

The anther dehisces by longitudinal slits. Two microsporangia of one theca (i.e., a lateral half of the anther) are widely separated from each other by a broad zone of connective tissue. Each microsporangium opens by its own longitudinal slit (Fig. 3, 4),

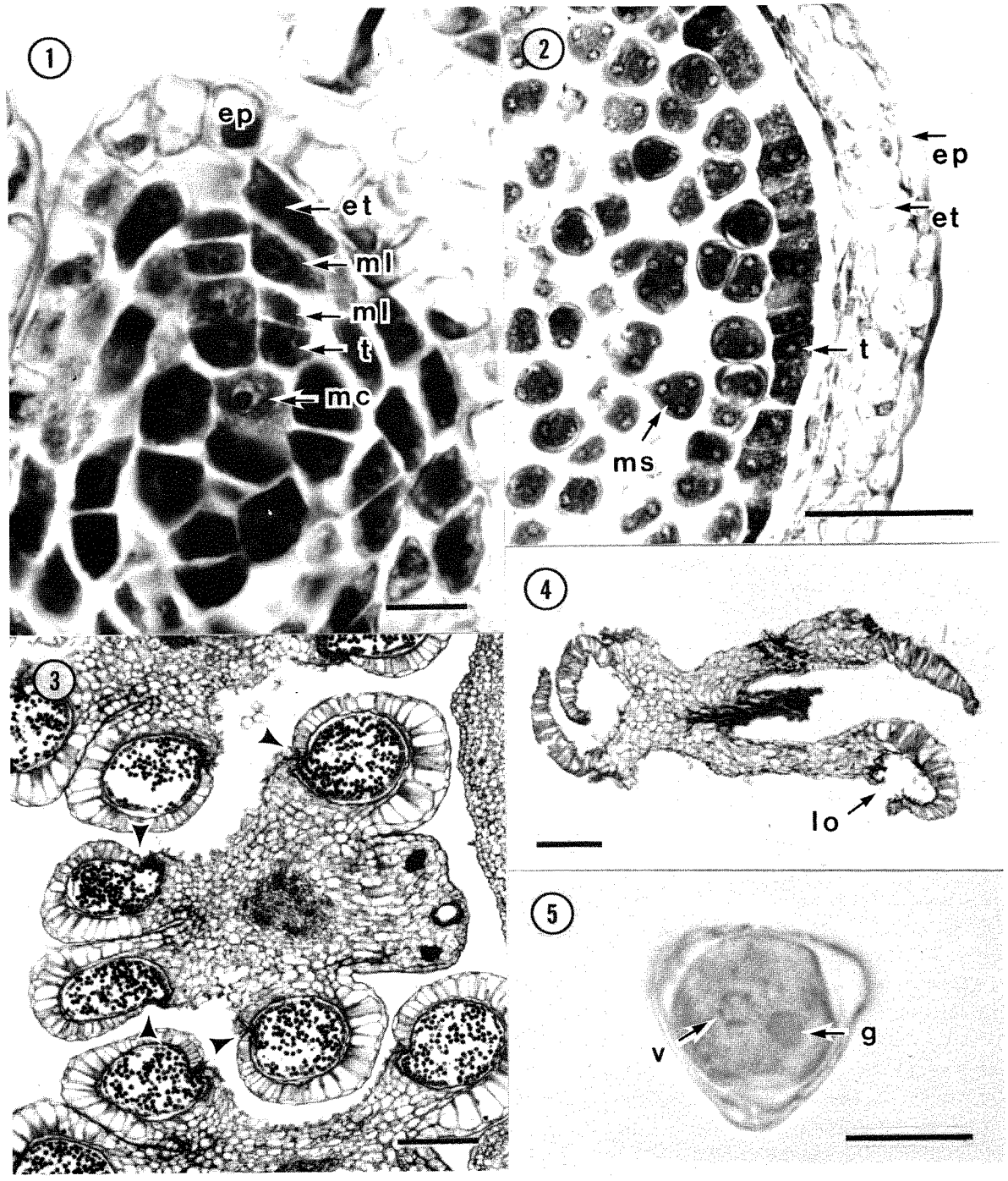

Fig. 1-5. Development of anthers and microspores in functionally staminate flower of *Psiloxylon mauritianum*. Fig. 1. Transverse section (TS) of young microsporangium showing wall structure. Fig. 2. Longitudinal section of older microsporangium. Fig. 3. TS of anther just before dehiscence. Note that the two microsporangia of the theca are opening independently by separate slits (arrowheads) and not by a common slit. Fig. 4. TS of old dehisced anther, one theca above, the other below. Fig. 5. Acetocarmine-stained mature pollen showing two-celled condition. Abbreviations: ep=epidermis; et=endothecium; g=nucleus of generative cell; lo=anther locule left by a single microsporangium; mc=microspore mother cell; ml =middle layer; ms=microspore in telophase of meiosis II; t =tapetum; v=nucleus of vegetative cell. Scale bars, respectively, 10, 50, 200, 200, 10 μm.

instead of opening by one slit common to both microsporangia of the same theca. Therefore, the anther is tetralocular at anthesis, not bilocular as described earlier (Schmid, 1980). During and after pollen grain dispersal, the wall of each microsporangium is usually recurved so that the microsporangium loses its locule structure; however, as seen in Fig. 4, rarely the locule may remain as it was , clearly demonstrating that each microsporangium opened by its own longitudinal slit.

Integuments and Ovular Orientation

The ovule is bitegmic (Fig. 7, 14), as reported by Schmid (1980). Both the inner (ii) and outer (oi) integuments are consistently two cell layers thick and formed exclusively from cells derived from dermal cells of the ovule primordium. The growth of the oi exceeds that of the ii, so that it becomes much longer than the ii (Fig. 7), and the micropyle is always formed by both integuments.

The ovule is hemi-campylotropous, with the micropylar tip nearer the funicle than is the chalazal end (Fig. 11). Although Schmid (1980) described the ovules of *Psiloxylon* as anatropous, we did not see any that we would consider strictly anatropous.

Megagametophyte and Nucellus

The archesporium is always one-celled (Fig. 6). The archesporial cell divides periclinally to form a primary parietal cell and a sporogenous cell. The primary parietal cell further divides to form a parietal tissue of four or five layers, whereas the primary sporogenous cell develops directly into a megaspore mother cell (Fig. 7). Thus, the ovule of *Psiloxylon* is crassinucellate, as reported by Schmid (1980). The megaspore mother cell undergoes meiosis I to give rise to a dyad rather than a tetrad of megaspores. The upper dyad cell degenerates, whereas the lower dyad cell functions and increases its volume (Fig. 8). Thereafter, by three successive nuclear divisions, meiosis II and two mitoses, the functional dyad develops into a two- (Fig. 9), four- (Fig. 10), and eight-nucleate embryo sac (Fig. 12, 13). Therefore, *Psiloxylon* has a bisporic, Allium type embryo sac. Of the eight nuclei in the embryo sac, the three antipodal cells soon degenerate (Fig. 12, 13), so that the mature embryo sac is composed of only five nuclei in four cells: an egg cell, two synergids, and two polar nuclei in the central cell. The two polar nuclei usually fuse to form a single central nucleus.

In the megaspore mother cell stages (Fig. 7), the nucellus is small with the megaspore mother cell surrounded by three or four layers of nucellar tissue (Fig. 7, 14). However, during megasporo- and megagametogenesis, the nucellus, particularly in the micropylar half, increases in size by cell enlargement, rather than by division of its constituent cells. The nucellus is not straight but slightly curved so that the chalaza is not directly opposite the micropyle (Fig. 11). An hypostase is not differentiated in either the ovule or during later stages of seed development.

Fertilization, Endosperm and Embryo

Pollen tube entry leading to fertilization is porogamous. Endosperm formation is of the Nuclear type (Fig. 15), but wall formation occurs only in a small area around the proembryo or embryo (Fig. 16). Although clearly present initially, endosperm appears to be scanty throughout seed development, and the mature seed lacks it completely (Fig. 18).

We did not pursue embryogenesis in detail due to a lack of appropriate fruits. Nevertheless, based on the limited information available, we can say that proembryos and embryos (Fig. 15, 16) develop normally and are unlikely to have any unusual structure. The embryo in the mature seed has a short suspensor and is straight with two equal-sized cotyledons (Fig. 18). The hypocotyl is not particularly swollen, a feature seen in some genera of Myrtaceae (Landrum and Stevenson, 1986), and is nearly the same size as the cotyledons. Polyembryony was not observed.

Mature Seed and Seed Coat

Although mature seeds are more or less diverse in shape and size, they lack wings and are generally reniform (Fig. 17); they are 0.6–0.8 mm long and 0.4–0.5 mm in diameter. In cross section, the mature seed is basically circular like the ovule (Fig. 14) and young seed (Fig. 16). (The somewhat flattened condition of the seed shown in Fig. 18 is an artifact.). The seed coat surface is scalariform-reticulate, as defined by Schmid (1980).

The mature seed coat is made up of a two-layered testa and a single-layered tegmen (Fig. 20). The latter, although somewhat obscure in the young seed (Fig. 19), is derived from the inner cell layer of the ii, the outer cell layer having been completely crushed early in seed development. Cells of the exotesta are enlarged both

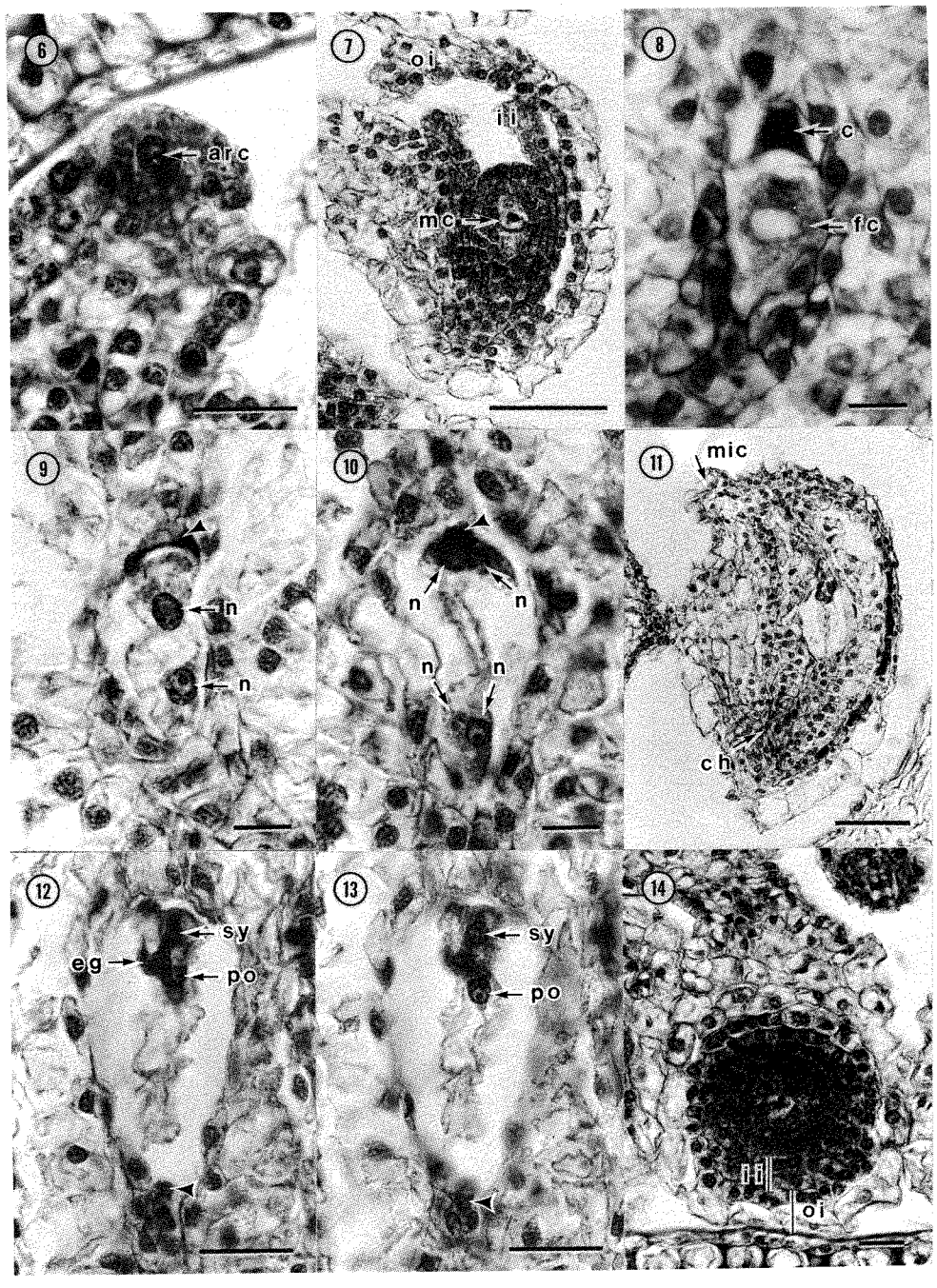

Fig. 6-14. Development of ovules and megagametophytes of pistillate flower of *Psiloxylon mauritianum*. Fig. 6. Longitudinal section (LS) of ovule primordium with one-celled archesporium. Fig. 7. LS of young ovule with megaspore mother cell, both integuments clear. Fig. 8. LS of young ovule with dyad cells, the upper degenerating, the lower functioning to form an embryo sac. Figs. 9, 10. LSs of two- and four-nucleate embryo sacs. Arrowhead indicates remnant of crushed upper dyad cell. Fig. 11. LS of mature ovule. Figs. 12, 13. Two successive LSs of eight-nucleate mature embryo sac with degenerating antipodal cells (arrowheads). Fig. 14. Transverse section of mature ovule, showing integuments and nucellus. Abbreviations: arc=archesporial cell; c=micropylar dyad cell; ch=chalaza; eg=egg cell; fc=functional dyad cell; ii=inner integument; mc=megaspore mother cell; mic=micropyle; n=nucleus of embryo sac; oi=outer integument; po=polar nucleus. Scale bars, respectively, 20, 50, 10, 10, 10, 50, 20, 20, 20 μm.

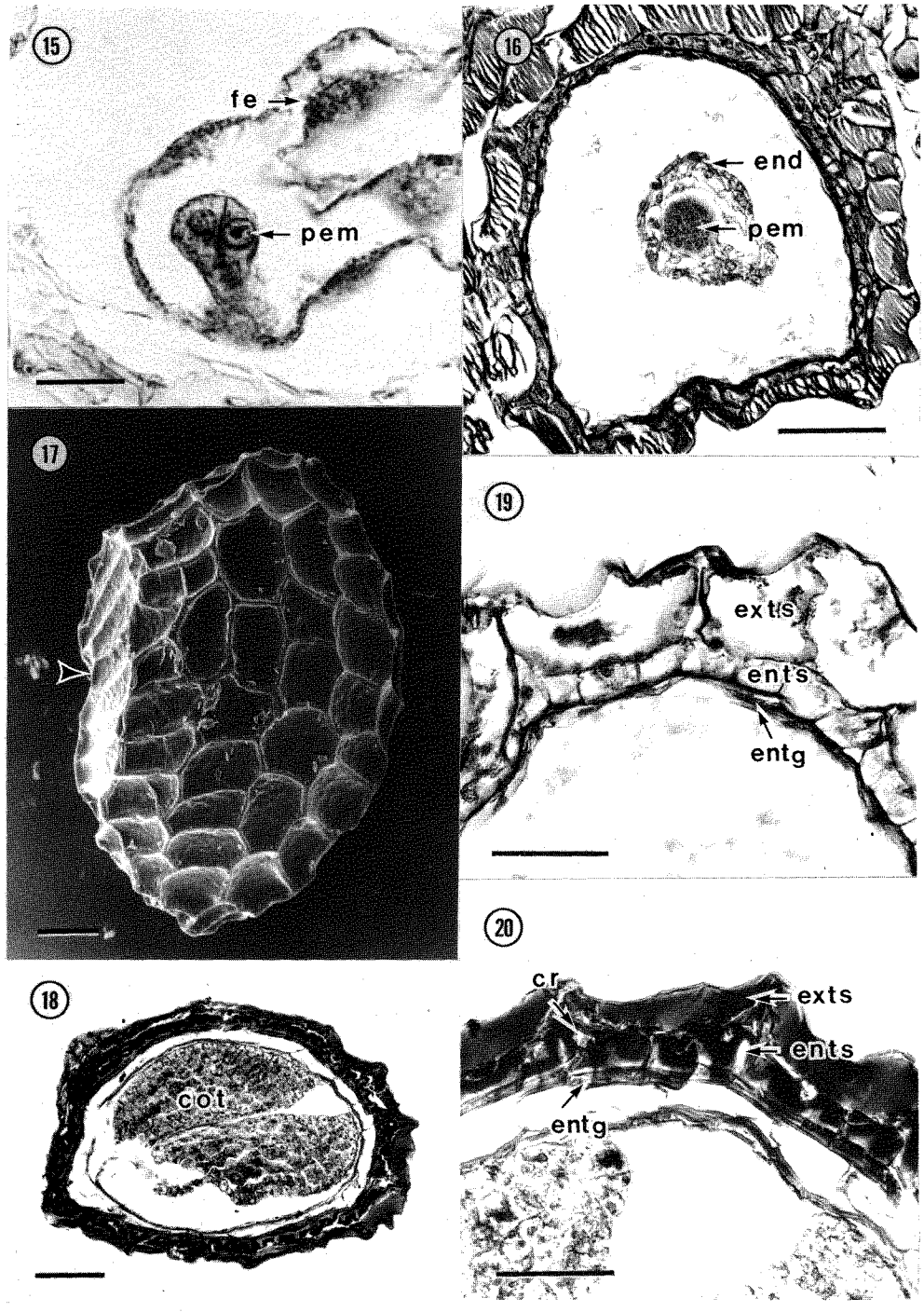

Fig. 15-20. Development of endosperm, embryo and seed coat in fruit of *Psiloxylon mauritianum*. Fig. 15. Longitudinal section of young seed with three-celled proembryo and free endosperm nuclei. Fig. 16. Transverse section (TS) of older seed with globular proembryo and cellular endosperm. Fig. 17. SEM of mature seed showing lateral view. Arrow indicates position of raphe. Fig. 18. TS of mature seed. Note that seed is exalbuminous. Fig. 19, 20. TSs of young and mature seed coat composed of two-layered testa and one-layered tegmen. Abbreviations: cot=cotyledon; cr=crystal; end=cellular endosperm; entg=endotegmen; ents=endotesta; exts=exotesta; fe=free endosperm nucleus; pem=proembryo. Scale bars, respectively, 20, 100, 100, 100, 50, 50 μm.

tangentially and longitudinally and become tanniferous; those of the endotesta are elongate longitudinally, the inner tangential and radial walls become extremely thick, and they contain crystals. Cells of the endotegmen are nearly collapsed at maturity but persist as a thin layer (Fig. 20).

Discussion

Psiloxylon clearly shares with other Myrtales a characteristic combination of eight embryological features: (1) anther tapetum glandular, (2) ovule crassinucellate, (3) inner integument of two cell layers, (4) micropyle formed by both integuments, (5) antipodal cells ephemeral, (6) endosperm formation of the Nuclear type, (7) mature seed exalbuminous, and (8) pollen two-celled when shed (Tobe and Raven, 1983a, 1984a). This confirms a myrtalean affinity for *Psiloxylon,* as generally agreed on the basis of other lines of evidence (see Dahlgren and Thorne, 1984; Johnson and Briggs, 1984; Raven, 1984).

In the context of Myrtales, *Psiloxylon* further agrees with both Myrtaceae *sensu stricto* and *Heteropyxis* in many specific embryological features: anther wall development conforming to the Basic type, endothecium developing fibrous thickenings, ovule archesporium one-celled, nucellar cells surrounding the embryo sac enlarged before they are absorbed, nucellus not straight, suspensor of embryo short, embryo possessing two equally developed cotyledons, and cells of the outer layer of the ii crushed during seed development (i. e., fibrous exotegmen lacking; for data on Myrtaceae and *Heteropyxis* see Tobe and Raven, 1983a and 1987a, respectively). This embryological relationship supports the close affinities between these groups that have been suggested by their sharing secretory cavities, sunken styles, and other common features (see Schmid, 1980; Dahlgren and Thorne, 1984; Johnson and Briggs, 1984).

We observed no embryological features that linked either *Psiloxylon* and Myrtaceae *sensu stricto* on the one hand or *Heteropyxis* and Myrtaceae *sensu stricto* on the other. In contrast, there are significant embryological features that do link *Psiloxylon* and *Heteropyxis*. Indeed, *Psiloxylon* shares with *Heteropyxis* two of the three characteristic and clearly apomorphic features (Tobe and Raven, 1987a) by which *Heteropyxis* is distinguished from Myrtaceae *sensu stricto*: (1) a bisporic Allium type embryo sac, and (2) anthers tetralocular at anthesis, not bilocular, since the two microsporangia of each theca are remote from one another and open by individual longitudinal slits instead of by a slit common to both.

Apart from *Psiloxylon* and *Heteropyxis* but within Myrtales, the Allium type embryo sac is also known in Alzateaceae (*Alzatea* Ruiz & Pavõn only) (Tobe and Raven, 1984c), and the anther tetralocular at anthesis in Rhynchocalycaceae (*Rhynchocalyx* Oliver only) (Tobe and Raven, 1984b). In spite of these similarities, *Psiloxylon* and *Heteropyxis,* on the basis of many lines of evidence, have no direct relationships either to *Alzatea* or to *Rhynchocalyx*, (see Dahlgren and Thorne, 1984; Johnson and Briggs, 1984; Tobe and Raven, 1984b, c). It seems, therefore, that the Allium type embryo sac and an anther tetralocular at anthesis have evolved independently in *Alzatea* and *Rhynchocalyx*, respectively, and do not indicate affinities between those genera and *Psiloxylon* or *Heteropyxis*.

It has been suggested previously that *Psiloxylon* and *Heteropyxis* are directly related because they share the following synapomorphies: spiral phyllotaxy, noninflexed stamen, and tricarpellate gynoecium (Johnson and Briggs, 1984). It now seems probable that both the Allium type embryo sac and the tetralocular anther at anthesis were acquired by the common ancestor of *Psiloxylon* and *Heteropyxis*, rather than evolving independently in the two genera. These two additional embryological synapomorphies, taken together with those presented by Johnson and Briggs (1984), suggest even more strongly that *Psiloxylon* and *Heteropyxis* are closely related.

In apparent contradiction to this suggestion, and more in agreement with that of Schmid (1980), the features of wood anatomy, leaf anatomy, and pollen morphology of these groups suggest a rather isolated position for *Psiloxylon* and a relatively close relationship between Myrtaceae and *Heteropyxis*. According to van Vliet and Baas (1984), *Psiloxylon* exhibits a distinctive combination of wood anatomical features that include, for example, chambered crystalliferous fibers, which are lacking in Myrtaceae. *Psiloxylon* agrees with Oliniaceae (*Olinia* Thunb. only) and Lythraceae in retaining a low level of specialization in ray structure. Keating (1984) has indicated that the midrib and midvein configuration in *Psiloxylon* is unique enough to support the concept of its belonging to a separate family, and, on the other hand, that the histological fea-

tures of *Heteropyxis* leaves support the inclusion of the genus within Myrtaceae. Furthermore, according to Patel *et al.* (1984), pollen of *Psiloxylon* is parasyncolpate, like that of some Myrtaceae, but differs from the parasyncolpate taxa of Myrtaceae by having unusually large apocolpia and larger rugulate elements on the equator; in contrast, the pollen of *Heteropyxis*, which may be syn-, parasyn-, or longicolpate, or a combination of these, closely resembles the pollen of syn- and parasyncolpate taxa of Myrtaceae. The phylogenetic analysis by Johnson and Briggs (1984), however, concludes that most or all of the distinctive features of *Psiloxylon* are autapomorphies. In other words, the coincidences in contrasting features between *Heteropyxis* and Myrtaceae are symplesiomorphies and do not indicate a close phylogenetic affinity.

Embryologically, there also are several differences between *Psiloxylon* and *Heteropyxis*. The ovule of *Psiloxylon* is hemi-campylotropous, rather than hemitropous as in *Heteropyxis*; the mature seed of *Psiloxylon* lacks wings on both ends, a characteristic feature of *Heteropyxis* (see Tobe and Raven, 1987 a). These distinct embryological features also appear to represent autapomorphies in the respective genera; they do not appear to provide a basis for negating a hypothesis of very close relationship between *Psiloxylon* and *Heteropyxis*. Gaps in various characters between *Psiloxylon* and *Heteropyxis* seem to indicate that they separated from each other early in their common evolutionary line, as discussed by Johnson and Briggs (1984).

In conclusion, the new embryological evidence supports the concept of a close mutual relationship between *Psiloxylon* and *Heteropyxis*, rather than between *Heteropyxis* and Myrtaceae. *Psiloxylon* and *Heteropyxis* seem most likely to have diverged as a single clade from a common ancestor of Myrtaceae (for additional relevant discussion, see Johnson and Briggs, 1984; Tobe and Raven, 1987 a). To reflect this, it seems best of combine *Psiloxylon* and *Heteropyxis* into a single group. They could logically be treated as a distinct ditypic family Heteropyxidaceae, but they are so closely related to Myrtaceae in their secretory cavities, sunken styles, common embryological features (discussed above), and some other synapomorphies presented by Johnson and Briggs (1984) that we favor their inclusion within that family, as a subfamily Heteropyxidoideae.

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Literature Cited

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. 2nd ed. New York Bot. Gard., New York.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nord. J. Bot. **3:** 119-149.

Dahlgren, R. and R. F. Thorne. 1984. The order Myrtales: circumscription, variation, and relationships. Ann. Missouri Bot. Gard. **71:** 633-699.

Dahlgren, R. and A. E. van Wyk. 1988. Structures and relationships of families endemic to or centered in southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. **25:** 1-94.

Davis, G. L. 1966. Systematic Embryology of the Angiosperms. John Wiley and Sons, New York.

Johnson, L. A. S. and B. G. Briggs. 1984. Myrtales and Myrtaceae -- a phylogenetic analysis. Ann. Missouri Bot. Gard. **71:** 700-756.

Keating, R. C. 1984. Leaf histology and its contribution to relationships in the Myrtales. Ann. Missouri Bot. Gard. **71:** 801-823.

Landrum, L. R. and D. Stevenson. 1986. Variability of embryos in subtribe Myrtinae (Myrtaceae). Syst. Bot. **11:** 155-162.

Patel, V., J. J. Skvarla, and P. H. Raven. 1984. Pollen characters in relation to the delimitation of Myrtales. Ann. Missouri Bot. Gard. **71:** 858-969.

Raven, P. H. 1984. The order Myrtales: a symposium. Ann. Missouri Bot. Gard. **71:** 631-632.

Schmid, R. 1980. Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae. Taxon **29:** 559-595.

Schmid, R. and M. D. Turner. 1977. Contrad 70, an effective softener of herbarium material for anatomical study. Taxon **26:** 551-552.

Takhtajan, A. 1986. Floristic Regions of the World. Univ. California Press, Berkeley.

Thorne, R. F. 1983. Proposed new realignments in angiosperms. Nord. J. Bot. **3:** 85-117.

Tobe, H. and P. H. Raven. 1983a. An embryological analysis of the Myrtales: its definition and characteristics. Ann. Missouri Bot. Gard. **70:** 71-94.

Tobe, H. and P. H. Raven. 1983b. The embryology of *Axinandra zeylanica* (Crypteroniaceae) and the relationships of the genus. Bot. Gaz. (Crawfordsville) **144:** 426-432.

Tobe, H. and P. H. Raven. 1984a. The number of cells in the pollen of Melastomataceae. Bot. Mag. (Tokyo) **97:** 131-136.
Tobe, H. and P. H. Raven. 1984b. The embryology and relationships of *Rhynchocalyx* Oliv. (Myrtales). Ann. Missouri Bot. Gard. **71:** 836-843.
Tobe, H. and P. H. Raven. 1984c. The embryology and relationships of *Alzatea* Ruiz and Pav. (Myrtales). Ann. Missouri Bot. Gard. **71:** 844-852.
Tobe, H. and P. H. Raven. 1984d. The embryology and relationships of Oliniaceae. Plant Syst. Evol. **146:** 105-116.
Tobe, H. and P. H. Raven. 1984e. The embryology and relationships of Penaeaceae (Myrtales). Plant Syst. Evol. **146:** 181-195.
Tobe, H. and P. H. Raven. 1987a. Embryology and systematic position of *Heteropyxis* (Myrtales). Amer. J. Bot. **74:** 197-208.
Tobe, H. and P. H. Raven. 1987b. The embryology and relationships of *Crypteronia* (Crypteroniaceae). Bot. Gaz. (Crawfordsville) **148:** 96-102.
Tobe, H. and P. H. Raven. 1987c. The embryology and relationships of *Dactylocladus* (Crypteroniaceae)and a discussion of the family . Bot. Gaz. (Crawfordsville) **148:** 103-111.
Van Vliet, G. J. C. M. and P. Baas. 1984. Wood anatomy and classification of the Myrtales. Ann. Missouri Bot. Gard. **71:** 783-800.

Psiloxylon 屬(桃金孃目)植物的胚胎學研究以及系統分類地位

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Psiloxylon 是桃金孃目裡獨特的一屬植物，特產於模里斯島。爲確切了解其與狹義之桃金鑲科和非洲大陸所產 *Heteropyxis* 屬之親緣關係，特進行本胚胎學研究。*Psiloxylon* 有許多胚胎學特徵與上述二者相似，但較爲接近 *Heteropyxis* 屬。*Psiloxylon* 與 *Heteropyxis* 屬共具兩項明顯的衍生型特徵(apomorphies)：(1)一個雙孢葱型(bisporic Allium type)胚囊及(2)雄蕊花藥四室，此爲桃金孃目植物所未見。此一胚胎學新證據以及其他證據均強烈顯示 *Psiloxylon* 和 *Heteropyxis* 爲起源於與桃金孃科共同祖先的一個分支單元(clade)。因此我們可以視 *Heteropyxis* 爲包含 *Psiloxylon* 和 *Heteropyxis* 二型的科，而與桃金孃科有近緣關係；或最好將 *Heteropyxidoideae* 視爲桃金孃科中的一個具有兩型的亞科。