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EXOSPERMUM STIPITATUM (WINTERACEAE): OBSERVATIONS ON WOOD, LEAVES, FLOWERS, POLLEN, AND FRUIT

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Introduction

The studies of Bailey and Nast (1943a, 1943b, 1944a, 1944b) reported on *Exospermum* van Tiegh. as part of a series of studies on anatomy of Winteraceae. Since that time, a study on flowers of the genus by Sampson and Tucker (1978) has appeared. That study was based upon liquid-preserved material and utilized scanning electron microscopy. Sampson and Tucker demonstrated that ovule placement in *Exospermum* is not laminar, as had been alleged. Bongers (1973) included *Exospermum* in a survey of foliar epidermis in Winteraceae.

In 1978, I was able to collect excellent material of *Exospermum stipitatum* (Baill.) van Tiegh. ex Pilg. from middle elevations of Mt. Panié, New Caledonia. Trees were in flower and permitted observations on details of flower opening and pollen presentation. From this material, liquid-preserved specimens upon which anatomical observations could be made were prepared.

Wood of these trees was also obtained at that time. Wood anatomy of *Exospermum* has not been described hitherto. Bailey (1944) did not include the genus in his survey of winteraceous woods, probably because no wood samples of *Exospermum* were to be found in wood collections at that time. Systematic anatomy of *Pseudowintera* Dandy wood has been studied by Patel (1974). The question of reaction wood in Winteraceae has been investigated more recently by Kuçera and Philipson (1977, 1978) and by Meylan (1981). Systematic wood anatomy of the genera of Winteraceae other than *Exospermum* is now being undertaken (Carlquist 1981, 1982).

The present study is designed to complement earlier studies on *Exospermum* and to offer comments on this genus and its relationships within Winteraceae.

Although a second species of *Exospermum, E. lecartii* van Tiegh., has been recognized by some authors, more recent information (Guillaumin 1942; Vink, cited in Sampson and Tucker 1978) supports recognition only of *E. stipitatum* within the genus.

Materials and Methods

From material of *Exospermum stipitatum* collected in the field, herbarium specimens (*Carlquist 15590,* RSA and other herbaria) were prepared. Por-

tions of flowers, stems, leaves, and bark were preserved in formalin acetic alcohol. The bark samples are now being studied by Katherine Esau and Vernon I. Cheadle with respect to phloem characteristics. A single fruit, probably from the preceding year, was also collected (Fig. 12).

Photographs of living material (Fig. 5–8, 10, 12) were taken with ordinary lenses and with Leitz "macro" lenses (Summar series). Such photographs are considered valuable in documenting details of floral morphology and in demonstrating stages in pollen presentation.

Wood samples were prepared by drying logs stripped of bark. Drying in the humid air of New Caledonia could only be initiated during the short term of field work there. Consequently, wood samples were enclosed in plastic bags with enough paraformaldehyde to prevent growth of fungi and bacteria; bagged wood samples were enclosed in cartons and sent via surface mail to Claremont. Upon arrival, woods were extracted, washed, and dried to equilibrium with air. The wood cylinder of *E. stipitatum* collected is 19.5 cm in diameter. Preparatory to sectioning, wood portions were boiled in water. Attempts to section *Exospermum* wood on a sliding microtome were not judged successful. The wide, thin-walled tracheids of this species (Fig. 3) collapsed during sectioning, no matter how sharp the knife. Moreover, tracheid walls in longitudinal sections showed a tendency toward shredding. Paraffin sectioning on a rotary microtome provided the only potential alternative by virtue of the reinforcement paraffin could offer. In order to section the wood in paraffin, however, softening was required. The softening technique employed four percent ethylene diamine. This represents a variant of the technique devised by Kukachka (1977) for a quite different purpose, the softening of excessively hard woods prior to sectioning on a sliding microtome. *Exospermum* wood was soaked in the ethylene diamine solution for a week. Samples were then washed and infiltrated by means of a tertiary butyl alcohol series. Paraffin with a melting point of 60 C was employed as an embedding medium. An additional treatment was necessary for proper sectioning, however. The paraffin pieces were trimmed and mounted on wooden blocks, as is usual in paraffin sectioning. Sections were cut until the face of the wood was entirely exposed. This cut surface was then exposed to water for 24 hr by inverting the wood block bearing the paraffin in a beaker containing a few mm of water. The beaker was placed in a refrigerator. While still cool, the soaked wood sample was sectioned at 12–16 μm. The sections were mounted and stained in a saturated solution of safranin in absolute ethyl alcohol. Wood macerations were prepared using Jeffrey's solution and stained in safranin.

The materials of flowers and leaves were embedded and sectioned according to the usual techniques without ethylene diamine, although the water-soaking technique described above was used. Mr. Vincent M. Eckhart prepared sections of leaves and flowers.

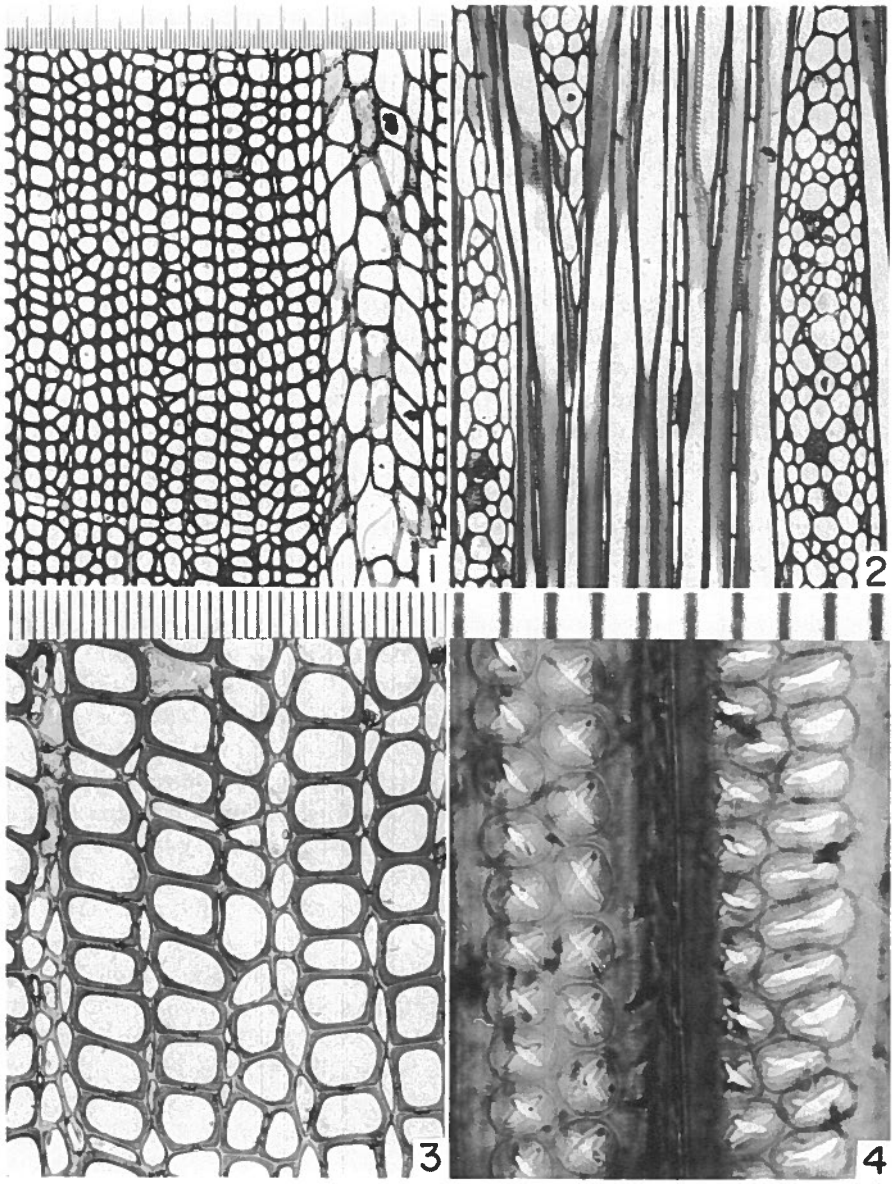
Pollen of liquid-preserved flowers was studied and photographed (Fig. 11) by the author using an AMR scanning electron microscope. A critical-point drying apparatus and palladium-gold spatter coating were employed for preparation of the pollen tetrads.

Wood Anatomy and its Systematic Significance

The wood anatomy of *Exospermum stipitatum*, as seen in gross aspect, differs from that of *Zygogynum* Baill. in color. The pale straw color of *Exospermum* wood presumably derives from paucity of the resinlike deposits which give *Zygogynum* wood a reddish-brown color when it is dried.

Growth rings are absent in *Exospermum* wood (Fig. 1). Tracheids average 5758 μm in length; however, numerous tracheids are broken in macerations because of their fragility, so that a bias in favor of shorter tracheids (which may break less frequently than the long ones) is possible. Tracheids average 51 μm in diameter. Mean wall thickness is 4 μm (Fig. 3). Radial walls bear pits about 14 μm in diameter; overlap areas of tracheids (Fig. 4) bear two to three rows of pits. Of these, some are occasionally elongated (Fig. 4), but true scalariform pitting was not observed. No helical thickenings or trabeculae were observed on tracheids. Axial parenchyma is diffuse (Fig. 3) or in bands of one or two cells thickness (Fig. 1, near bottom). Rays correspond to Kribs's (1935) Heterogeneous Type I, although uniseriate rays and uniseriate portions of multiseriate rays contain few procumbent cells (Fig. 2). Multiseriate rays average 6812 μm in height. Multiseriate rays average 6.8 cells wide at their widest points. Borders are commonly present on pits between ray cells as seen in radial sections. A few small droplets of resinlike materials may be seen in ray cells (Fig. 1, 2). In the central portions of multiseriate rays, a few ethereal oil cells may be seen (Fig. 2, right). These cells have walls thinner than those of typical ray cells, and their size is larger.

With respect to wood features, *Exospermum* is entirely comparable to *Zygogynum* and to *Belliolum* van Tiegh. *Zygogynum bicolor* van Tiegh. (which grows with *E. stipitatum* in the Mt. Panié locality) and the Solomon Islands species of *Belliolum* have wide, thin-walled tracheids which match those of *Exospermum* (Carlquist 1981, 1982). Some collections of *Zygogynum* have only a few widened pits on tracheid overlap areas (Carlquist 1981) and thus match the conditions seen in *Exospermum*. Axial parenchyma is very much like that of some collections of *Zygogynum* and *Belliolum*. With respect to rays, however, the presence of ethereal oil cells, characteristic of *Exospermum*, has been noted in *Zygogynum* (Carlquist 1981) but not in *Belliolum* (Carlquist 1982). Thus the most numerous similarities in wood may be found between *Exospermum* and *Zygogynum*. This is not surprising in view of other similarities (stamen morphology, pollen ultrastructure) be-



Figs. 1–4. Wood sections of *Exospermum stipitatum (Carlquist 15590)*.—1. Transection; band of axial parenchyma near bottom.—2. Tangential section. Cells of uniseriate rays and uniseriate wings of multiseriate rays erect; a few ethereal oil cells in ray, right.—3. Transection. Wall of axial parenchyma cell in face view, above; note thin tracheid walls.—4. Pitting from overlap areas of tracheids in radial section. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, scale above Fig. 4 [divisions = 10 μm].)

tween the two genera. However, wood of *Bubbia* van Tiegh., presently under study by the writer, may yield as many similarities to the wood of *Exospermum*.

The lack of growth rings and the wideness of the tracheids seem related to the tropical climate, with moderately high moisture availability (and therefore moderately high transpiration) in the areas inhabited by *Exospermum*. If so, this is entirely comparable to similar features in woods of *Zygogynum* and *Belliolum* which occupy similar habitats (Carlquist 1981, 1982). The wood of *Pseudowintera* (Patel 1974), in contrast, seems to show adaptation to cooler climates in its growth rings and narrower tracheid diameter.

Leaf Anatomy

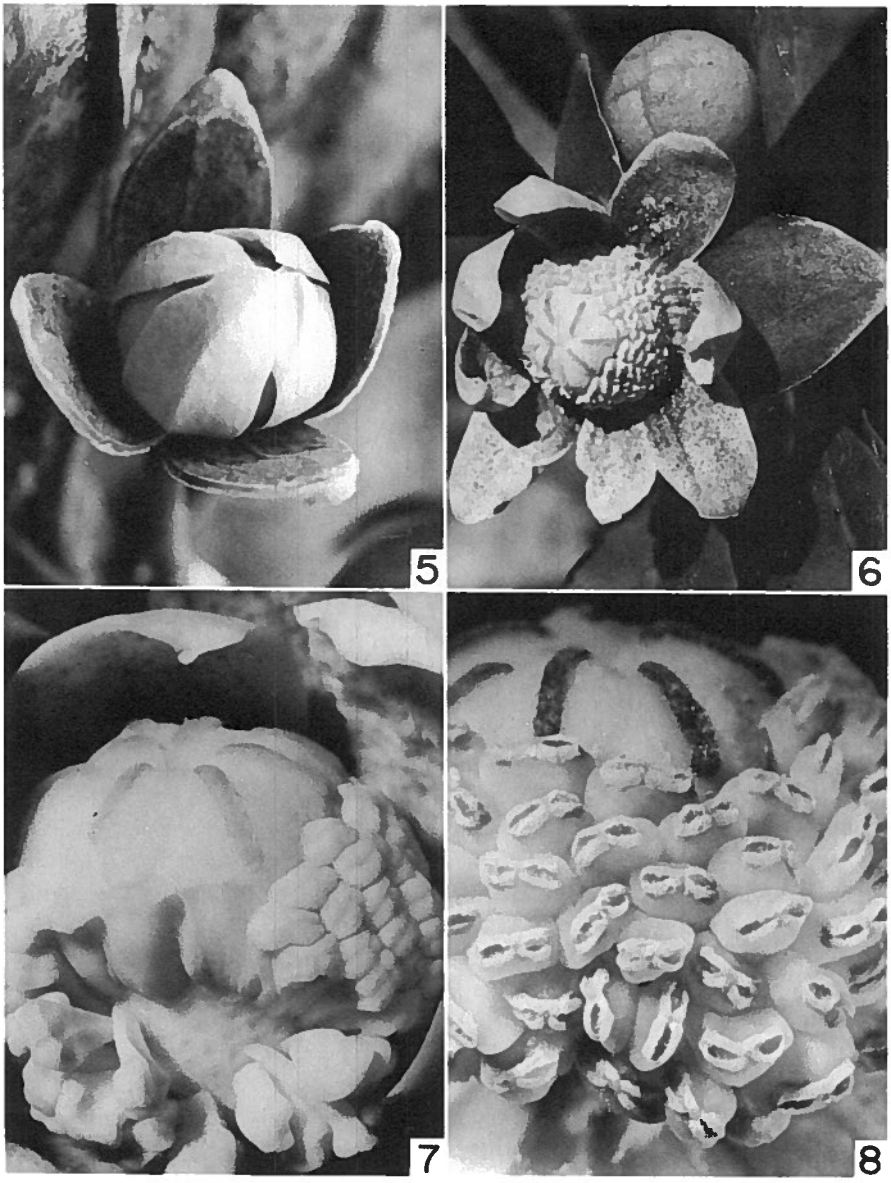
Bailey and Nast (1944a) reported on the vascularization of leaves of *Exospermum*. The peculiar circles of bundles in petioles and in midribs of leaves which they described are also present in my material. Bailey and Nast (1944b) report that leaf veins in *Exospermum* bear sclerenchyma. This was confirmed in my material on the basis of liquid-preserved material (Fig. 9). Small veins lack sclerenchyma.

Various degrees of wall thickening of leaf mesophyll cells were reported by Bailey and Nast (1944b) for *Exospermum*. The collection named *E. lecartii* possessed the beginnings of sclereid formation, "a reticulately thickened mesophyll." In *E. stipitatum,* Bailey and Nast report a thin-walled mesophyll in which more or less isodiametric sclereids are scattered. In my material (Fig. 9), sclereid nests occur in mesophyll and midrib, but very infrequently. The occurrence within a single species of various types of sclereid development is not surprising. Possible explanations include variation of individuals within the species, position of leaf (sun versus shade leaf), and age of leaf.

From liquid-preserved material, I was able to determine that 12 or 13 layers of mesophylla are characteristically present in the Mt. Panié plant (Fig. 9). The mesophyll is not markedly differentiated, and no palisade in the ordinary sense of the word could be said to occur. A differentiation of the layer beneath the adaxial epidermis is apparent, however. Cells in this layer are somewhat larger than are other mesophyll cells. This subepidermal layer also has fewer chloroplasts than do the other mesophyll layers. Thus a kind of hypodermis can be said to be present.

Floral Anatomy and Opening of the Flower

The four outer petals of *Exospermum* (Fig. 6, above) are united except at their tips. They break apart as the first event in opening of the flower (Fig. 5). Trees of *Exospermum stipitatum* vary with respect to petal color.



Figs 5–8. Views of flower of *Exospermum stipitatum (Carlquist 15590)*.—5. Opening flower, four outer petals unfolded.—6. Habit of open flower presenting pollen; bud above.—7. Dissection (some stamens dislodged) of flower just after opening, stigmas receptive.—8. Center of flower with anthers presenting pollen, stigmas no longer receptive. (Fig. 5, ×1.3; Fig. 6, ×1.0; Fig. 7, 8, ×4.0.)

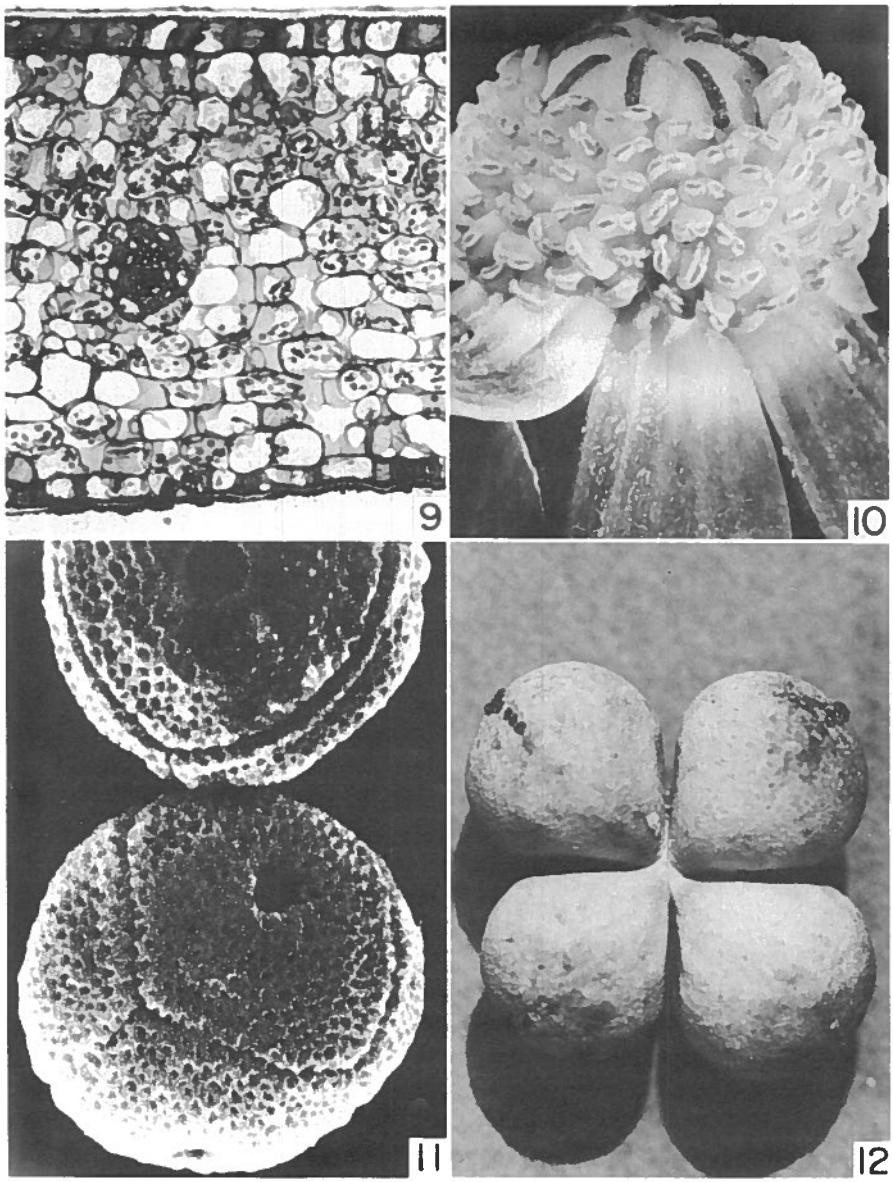
In the flower illustrated, the outer petals were yellow overlaid with purple, the inner petals yellow with a sparse overlay of purple. Flowers the petals of which were entirely yellow could be observed on trees in the population I saw in 1978, a determination made easy by the dropping of petals in large quantities. Variation in flower color may correlate with the probably cantharophilous nature of *Exospermum* flowers, because color and pattern variation is of neutral selective value in a flower not pollinated by insects which respond to particular colors and patterns. Although a pollinator has not yet been found on *Exospermum,* the flowers are probably pollinated by beetles according to Thien (1980). When they are open, flowers of *Exospermum* very strongly emit an odor which may be described as "burnt orange." This scent persists for two years in flowers which have been dried.

The flowers of *Exospermum* are protogynous, as are all Winteraceae with bisexual flowers. The stigmas of the flowers illustrated in Fig. 7 are receptive; the anthers of this flower have not opened yet. Later, when anthers are open and presenting pollen (Fig. 6, 8, 10), stigmas are nonreceptive, as indicated by their darkened color. This color may represent the presence of tannins. Sampson and Tucker (1978) figure a flower with dark stigmas but unopened anthers; the darkened color of stigmas in that flower seems premature, perhaps owing to the fact that their photograph represents a pickled flower.

The stamens of *Exospermum* are often skewed in orientation (Fig. 8), a fact which may be related to the crowding of stamen primordia. The anther sacs do not open wide; the pollen thereby is not shed rapidly. The thick appearance of the anther sacs is confirmed when one looks at sectioned material: a minimum of three endothecium layers surrounds each anther sac, and four or five can be seen in places. Pollen tends to fall in masses onto the surfaces of the inner petals (Fig. 10, below).

In *Zygogynum* (Carlquist 1981) and *Belliolum* (Carlquist 1982), opening of flowers is accompanied by a swelling of petals and stamens. This can be readily seen for *Exospermum* also in the photographs shown here. The open flower in Fig. 6 is much larger in volume than the accompanying bud. The stamens in Fig. 8 show a vast increase in volume over the stamens illustrated in Fig. 7, in which the filaments are tapered. The opening of the flower is thus a matter of rapid imbibition of water, accompanied by increase in cell size.

A mechanism for rapid imbibition of water by stamens and petals was suggested by study of *Exospermum* flowers. Parenchyma cells of petals and stamens of a bud just prior to anthesis contain numerous small starch grains. One can hypothesize that by hydrolysis, starch is coverted to sugar, osmotically inducing inflow of water into petals and stamens. Thereby these organs swell and the flower opens. The large number and small size of the



Figs. 9–12. Anatomy of *Exospermum stipitatum (Carlquist 15590)*.—9. Transection of lamina, showing vein sheathed in fibers.—10. Center of flower presenting pollen, pollen visible on inner petal surfaces.—11. Scanning electron micrograph of pollen tetrads showing small diameter of depressions in exine.—12. Fruit, viewed from above, showing that carpels separate in fruit. (Fig. 9, magnification scale above Fig. 3; Fig. 10, ×2.2; Fig. 11, ×1600; Fig. 12, ×2.5.)

starch grains would seem to correlate with a quick but massive production of sugar. Significantly, perhaps, the carpels, which do not change in bulk as the flower opens, are devoid of starch grains.

All organs of the flower of *Exospermum* contain ethereal oil cells. The carpels, as noted by Sampson and Tucker (1978), contain nests of sclereids. The petals also contain nests of sclereids. Sclereids are notably absent from the stamen. One can hypothesize that a correlation exists between the marked and rapid increase in volume of the stamens and the absence of sclereids. The petals increase proportionately less in bulk as the flower opens than do the stamens.

The presence of sclereids may have the effect of deterring phytophagous insects, as postulated earlier (Carlquist 1969). Ethereal oil cells very likely also have this effect.

Pollen and its Systematic Significance

Pollen tetrads of the Mt. Panié *Exospermum stipitatum* are shown in Fig. 11. This scanning electron micrograph clearly reveals two characteristic features: the fine polygonal pattern of the exine (muri), and the nonprotuberant nature of the germ pore. As the illustrations of Bailey and Nast (1943a), Lobreau-Callen (1977), and Praglowski (1979) show, the patterning of *Exospermum* exine shows the smallest polygons of any genus of Winteraceae. The next finest polygons may be seen in *Zygogynum*. Both *Exospermum* and *Zygogynum* have some duplibaculate muri, whereas muri in the remaining genera of Winteraceae are all simplibaculate (Lobreau-Callen 1977). The germ pores in *Exospermum* and *Zygogynum* are not bulging. Thus, *Exospermum* most closely resembles *Zygogynum* in its pollen morphology, and this is perhaps a valid indicator of relationships of *Exospermum*. The genus with the pollen most similar to that of *Exospermum* and *Zygogynum* is *Belliolum*. *Exospermum, Zygogynum,* and *Belliolum* pollen tetrads may accommodate changes in volume by depression or expansion of the distal walls of the tetrad. In genera with bulging germ pores, such as *Drimys* J. R. & G. Forst., the germ pore, or the thin circular exine plate around the germ pore, may serve to accommodate volume changes.

Morphology and Significance of Fruit and Carpels

The fruit of *Exospermum stipitatum* is illustrated in Fig. 12. Notable in its morphology is the fact that the carpels are quite separate from each other in fruit. This feature is one which distinguishes *Exospermum* from *Zygogynum*. The discussions of van Tieghem (1900) and Smith (1943) accurately describe the nature of the fruit. Carpel number in fruits varies. Sections of the mature fruit showed little difference from the nature of the carpel at

anthesis in terms of the types of cells present. Nests of sclereids are present at both stages, separated by thin-walled parenchyma. In fruit, parenchyma cells are somewhat enlarged compared to parenchyma cells in carpels at anthesis. In addition, the sclereid nests become somewhat larger by virtue of sclerification of cell walls on parenchyma cells adjacent to the smaller sclereid nests seen in carpels at anthesis. Thus the fruit of *Exospermum* differs from fruits of either *Zygogynum* or *Bubbia*. In *Bubbia,* according to the species I know and descriptions of Smith (1943), carpels become reddish to purplish at maturity and contain fewer sclereids than in *Exospermum*; the fruits of *Exospermum* are yellowish. In *Zygogynum,* the syncarpous fruit may be yellowish or purplish at maturity, but it has an outer region, which breaks away, revealing the greenish inner pulp containing the seeds. The outer region is rich in large sclereid nests, whereas in the inner zone, sclereid nests are smaller and more distant from each other.

One may note that in flower, the carpels of *Exospermum* are closely appressed to each other although not united. The stigmas run the length of the exposed carpel faces at this stage (Fig. 6, 10). In fruit, the surfaces appressed during anthesis are exposed. At anthesis no stigmatic surface is formed where it would be inaccessible to a pollinator.

In a matter related to the above, I have hypothesized (1969) that carpels in *Tasmannia* R. Br., which have a stigmatic crest running the length of the carpel, are correlated with accessibility to a pollinator and with unisexuality of the flower, whereas the restricted stigmas of *Drimys* (s.s.) carpels correlate with the fact that numerous carpels in a whorl enclose a central space inaccessible to a pollinator, a space along which no stigmatic surfaces occur. I have also hypothesized (1969) that the large stigmatic crest of *Degeneria* Bailey & Smith might be related to the fact that flowers of this genus have only a single carpel, and that large carpellary surface and large number of ovules compensate for the presence of only a single carpel. If these hypotheses are true, the *Tasmannia*-type and *Degeneria*-type of carpels may not necessarily be the relicts of a leaflike condition which some workers tend to claim. Instead, both increase and decrease in stigmatic surface may have occurred relevant to floral biology, and before literally interpreting the *Tasmannia*-type carpel as a living relict of the origin of angiospermy, we should consider how it is adapted to the biology of the flower in which it is located. There is often a tendency for morphologists to select a particular genus and then interpret all features of its flowers, or in this case, carpels, as primitive (or specialized); in each taxon, we may expect a mix of primitive and specialized features, relating to adaptation. Structures do not persist as historical relicts but rather represent features adaptive at the present time (for extant species).

Sampson and Tucker (1978), while conceding my correlations hold in the case of unisexuality of the *Tasmannia* flowers, are skeptical about inacces-

sibility of the carpel faces in a *Drimys* flower as a selective factor in stigmatic crest restriction in *Drimys*. They point out that some *Tasmannia* flowers have numerous carpels, so that the long stigmatic crests of *Tasmannia* do not correlate with carpel number. I would like to point out several features of *Drimys* and *Tasmannia* flowers. Some of the observations below relate to field studies upon *Tasmannia piperita* (Hook. f.) Miers on Mt. Kinabalu, Sabah, in 1978.

Where carpels in *Tasmannia* are more than two in number, they are not arranged simply in a cycle, as they are in *Drimys*, with stigmatic crests facing each other. Rather, they are splayed so that stigmatic crests are, in fact, accessible. This point is noted by Sampson and Tucker. One may add that were stamens present in the same flowers as fertile carpels in *Tasmannia*, stamens would render the stigmatic surfaces inaccessible, so that one cannot compare *Tasmannia* with *Drimys* without taking into account the unisexuality of flowers in the former genus. If unisexuality is derived in Winteraceae, the long stigmatic crest also may be derived, therefore.

In most species of *Tasmannia*, carpels are one or two. In some entities of *T. piperita*, carpels may be as many as 15 in number (Vink 1970). However, the reproductive system of the *T. piperita* entities may not be an ordinary one at all, and must be taken into account. The occurrence of locally distinct populations (the "entities" of Vink), numerous yet difficult taxonomically, in *T. piperita* is one indication that apomixis may be occurring. Another more persuasive line of evidence may be found in the high proportion of female to male plants. In the Kinabalu population of *T. piperita*, the ratio of females to males is 11 to one, strongly suggestive of facultative apomixis. If *T. piperita* is markedly apomictic, inaccessibility of the stigmatic crests of female flowers would not be a selective factor. One could even imagine that carpel number (and thereby fecundity) could increase in a *Tasmannia* population with facultative apomixis. Certainly one should suspect this possibility, rather than imagine that carpel number in *Tasmannia* was primitively large. Therefore in analyzing the selective value of long stigmatic crests, we do not need to take into account larger carpel numbers as being a necessary accompaniment of *Tasmannia*-type carpels with long crests—very likely this was not true.

From photographs and dissections of *Drimys winteri* Forst. flowers in cultivation in southern California, I note that the carpels in the cycle are at very narrow angles, so that at their bases, a very narrow crevice likely to be inaccessible to pollinators is indeed present. This may be related to the bisexual nature of flowers in the genus *Drimys* (s.s.). Because of the numerous stamens in *Drimys* flowers, the carpels cannot be splayed out from each other as they are in a *Tasmannia* female flower with more than one carpel. Even in those *Drimys* species with few carpels, the narrow angle of carpels still obtains because stamens are present in all flowers of *Drimys*

(s.s.). A very low carpel number is very likely not the primitive condition within *Drimys* (s.s.). One can hypothesize five or more carpels as primitive within *Drimys*. If this is true, the occurrence of five or more carpels must be the condition in which restriction of stigmatic crests is judged to have (or not have) a selective value. Thus, the citation by Sampson and Tucker of a similar range in carpel number in *Tasmannia* and *Drimys* does not at all vitiate my hypotheses.

The recent studies on reproductive biology of *Drimys brasiliensis* Miers by Gottsberger, Silberbauer-Gottsberger, and Ehrendorfer (1980) are relevant. The pollinators they cite (chiefly beetles, secondarily flies) do not have long tongues, and thus could not reach into the narrow spaces between the carpels without actually climbing between the carpels. Climbing between the carpels is certainly not possible for at least some of the beetles they figure; at the very least, nectar would be inconspicuous, as well as less accessible, if it were formed at the base of long stigmatic crests of carpels formed within a cycle of *Drimys*-type carpels. Thus I feel that the facts of morphology, pollination biology, and reproductive biology tend to support my hypothesis on the correlations of long versus short stigmas in Winteraceae.

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