

STAMEN VENATION IN THE WINTERACEAE

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SUMMARY

Stamen venation is described for all species of *Pseudowintera* and an interspecific hybrid; the single species of *Exospermum*, several species of *Belliolum*, *Drimys*, *Tasmannia* (syn. *Drimys* sect. *Tasmannia*) and *Zygogynum*, as well as one species of *Bubbia*. One, two and three-veined stamens were found in several taxa, in contrast to previous reports that invariably stamens have a single (median) vein. The presence of isolated, apparently vestigial, lateral veins in many stamens of some taxa, seems evidence there has been an evolutionary reduction from three- to one-veined stamens. In view of the antiquity of the Winteraceae, this lends support to the hypothesis of Bailey and Nast, that three-veined stamens are a primitive feature of the woody Ranales. No obvious correlation was found between stamen morphology and type of pollinator.

INTRODUCTION

Bailey & Nast (1943) noted that although they vary considerably in external form, the stamens of the Winteraceae have a single vein. They suggested that such stamens had evolved from a laminar three-veined stamen not differentiated into anther, connective and filament, which had two pairs of slender elongated pollen sacs, situated between the median and lateral veins, some distance from the lateral margins. Such stamens occur, for example, in the Degeneriaceae and Himantandraceae. Modifications from this type, leading to more conventional forms, were, they stated, found in the Magnoliaceae. See too, Canright (1952).

Bailey & Nast (1943) considered that the stamens of *Belliolum*, in which pollen sacs are some distance from the apex (figs. 8, 45-47), were closest to the primitive type in the Winteraceae. They envisaged two independent evolutionary trends. One led to broadly truncated stamens with transversely oriented apical pollen sacs, in *Bubbia*, *Exospermum*, *Pseudowintera* and *Zygogynum* (figs. 2-7, 10-44, 48-54, 60, 64-68). The other led to apically constricted stamens with laterally attached sub-apical pollen sacs in *Tasmannia* (syn. *Drimys* sect. *Tasmannia*) and *Drimys* (figs. 9, 55-59, 61-63). Cleared stamens of the above genera, excluding *Zygogynum*, were illustrated in their paper and it was recorded that the vein either extended throughout the stamen without branching, or there were one or more short branches directed towards the pairs of pollen sacs.

Subsequently, Tucker (1959) reported stamens had a single vein in *Drimys winteri* and I noted the same for *Pseudowintera axillaris* (Sampson, 1963), but Bhandari (1963) found that in *Pseudowintera colorata* although stamens are normally supplied with a single strand, rarely two traces may enter a stamen. He illustrated two examples of the latter category, but made no comment on the fact that in one of these illustrations, showing a median and a lateral vein, the lateral vein was present in only the upper two-thirds of the stamen and did not extend to its base (his fig. 2e). Vink (1970) reported that the stamens of *Tasmannia* (syn. *Drimys* sect. *Tasmannia*) have one trace at their point of insertion and noted there were one-veined stamens in *Zygogynum* (Vink, 1977).

In an important, frequently quoted paper, on floral anatomy, with emphasis on floral vascularization, Carlquist (1969) expressed doubt as to the primitiveness of many laminar stamens. He pointed out that investigators had ignored any relationship that might exist between stamen structure and pollination mechanisms. Thus, he suggested that flat three-trace stamens in *Musa* and other Zingiberales probably represent relatively recent adaptations to ornithophily. He cast doubt too on the primitiveness of laminar stamens in *Degeneria* and the Magnoliaceae and suggested they were specialized for beetle pollination. He stated: 'If one considers the 'ranalean' families with notably primitive wood structure, such as the vesselless . . . Winteraceae, one finds that stamens are not at all laminar, anther sacs are marginal, and only a single vein per stamen is present.'

The present investigation of stamen venation in the Winteraceae was initiated in the New Zealand endemic *Pseudowintera*, following the discovery of a natural interspecific hybrid (Sampson, 1980). Cleared stamens of the three species of *Pseudowintera*, from a variety of localities, revealed a surprising variation in stamen venation in some collections, but not in others. The study was therefore extended to other genera of Winteraceae. Stamens of all genera have been studied excepting the monotypic Madagascan plant *Takhtajania perrieri* (syn. *Bubbia perrieri*), known only from the type collection (Vink, 1978). Recent studies on pollination ecology (Thien, 1980, 1982; Thien et al., 1985; Gottsberger et al., 1980; Norton, 1980, 1984) have revealed a range of pollinators in the Winteraceae and provide a basis for determining whether type of stamen morphology seems linked with type of pollinator.

MATERIALS AND METHODS

Flowers were preserved in formalin-acetic-alcohol. Undehisced and dehisced stamens were removed from them, cleared in 5% NaOH at 40°C for several days and stored in 50% ethyl alcohol. Unless noted otherwise, 10 stamens were removed from each of five open flowers of each collection.

Taxa examined: *Bellium* sp., Katrikoin Forest, New Caledonia (WELTU 13253); as there were only 4–9 stamens per flower, 50 stamens were obtained from 8 flowers. — *B. pancheri* (Baill.) v. Tiegh., near Plateau de Dogny, New Caledonia (WELTU 12308). — *Bubbia howeana* (F. v. Muell.) v. Tiegh., Mt Gower, Lord Howe

Island (WELTU 12311). — *Drimys winteri* J.R. & G. Forst. var. *chilensis* (DC.) A. Gray, cultivated, Victoria University of Wellington (WELTU 14475). — *D. grandensis* L.f. var. *mexicana* (DC.) A.C. Smith, Mt Tzoutehuitz, Chipas, Mexico (no voucher). — *Exospermum stipitatum* (Baill.) v. Tiegh., Katrikoin Forest, New Caledonia (WELTU 12126). — *Tasmania* sp. (syn. *Drimys piperita* Hook. f., entity indet.), Mt Wilhelm, Papua New Guinea (WELTU 14476). — *T. insipida* R. Br. ex DC. (syn. *Drimys insipida* v. Tiegh.), Doyle River State Forest, New South Wales, Australia (WELTU 13760). — *T. lanceolata* (Poir.) A.C. Smith (syn. *Drimys lanceolata* Baill.), cultivated, University of Tasmania. — *T. xerophila* (Parment.) M. Gray (syn. *Drimys piperita* Hook. f., entity 'xerophila'), Lake Mountain, Great Dividing Range, Victoria, Australia (WELTU 15397), stamens from immature buds. — *Zygogynum baillonii* v. Tiegh., Mt Koghi, New Caledonia, 30 stamens from 3 flowers. — *Z. baillonii* v. Tiegh., ridge between Mt Ouin and Mt Dzumac, New Caledonia (McKee 9781), 20 stamens from 2 flowers. — *Z. bicolor* v. Tiegh., Plateau de Dogny (McPherson 5873, MO), 50 stamens from 2 flowers. — *Z. pomiferum* Baill. subsp. *pomiferum*, Mt Do, New Caledonia (McPherson 2827, MO).

Unvouchered material of *Pseudowintera axillaris* (J.R. & G. Forst.) Dandy was collected from Orongorongo Valley, Rimutaka Range; Oakune Mountain Road, Tongariro National Park; Keith George Memorial Park, Hutt Valley and Akatarawa Ranges, Tararua Forest Park, North Island, New Zealand. *Pseudowintera colorata* (Raoul) Dandy was obtained from Puketitiri; Orongorongo Valley and Erua Forest, North Island; from Brown Cow Range, N.W. Nelson (WELTU 12949) and near Papatowai Stream, Owaka, Otago, South Island, New Zealand. Stamens/flowers varied from 8 to 17 in *P. axillaris* and from 10 to 18 in *P. colorata*. All stamens were examined from five flowers in each collection. *Pseudowintera traversii* (Buchanan) Dandy flowers were collected from N.W. Nelson, South Island at Mt Stevens; Boulder Lake; Brown Cow Range (WELTU 12948) and Goulund Downs. Flowers of this species have 4–9 stamens per flower, and all stamens were examined from five flowers of each collection (27–39 stamens/collection). In addition, all stamens were cleared from five flowers (47 stamens) of a natural hybrid, *P. colorata* × *P. traversii* (Sampson, 1980) from Brown Cow Range (WELTU 12950).

OBSERVATIONS

In this paper, 'vein' refers to tracheary elements (tracheids) visible in cleared stamens (fig. 1). Material was not sectioned to determine the occurrence of phloem in these veins.

There is a dramatic increase in the size of stamens from the beginning of anthesis to the time of pollen liberation. In *Pseudowintera* the increase is more than two-fold (see fig. 21 in Sampson, 1980) but the pollen sacs themselves do not increase in size. A similar enlargement of stamens has been reported in *Belliolum* (Carlquist, 1983), *Exospermum* (Carlquist, 1982), and *Zygogynum* (Carlquist, 1981). Carlquist (1981) noted that this swelling of stamens involved a water imbibition mechanism, which

forces flowers open, in contrast to drying mechanisms which are believed responsible for opening flowers in many angiosperms. He noted that in *Belliolum*, *Exospermum* and *Zygogynum* the petals too swell by water intake as the flower opens and suggested that starch in parenchyma cells of petals and stamens is hydrolysed to sugar, osmotically inducing water flow into these organs (Carlquist, 1982, 1983). All Winteraceae which have been studied are protogynous (excepting dioecious *Tasmannia* species).

Pseudowintera

Most stamens have a single (median) vein terminating in the connective near their distal end. This vein usually gives off lateral branches near its tip, each of which terminates near a pair of pollen sacs (fig. 1). These laterals may, or may not, branch (figs. 2, 3). Sometimes there is only one lateral branch from the median vein (fig. 4). Only *P. colorata* had some stamens with a single, unbranched vein (fig. 5).

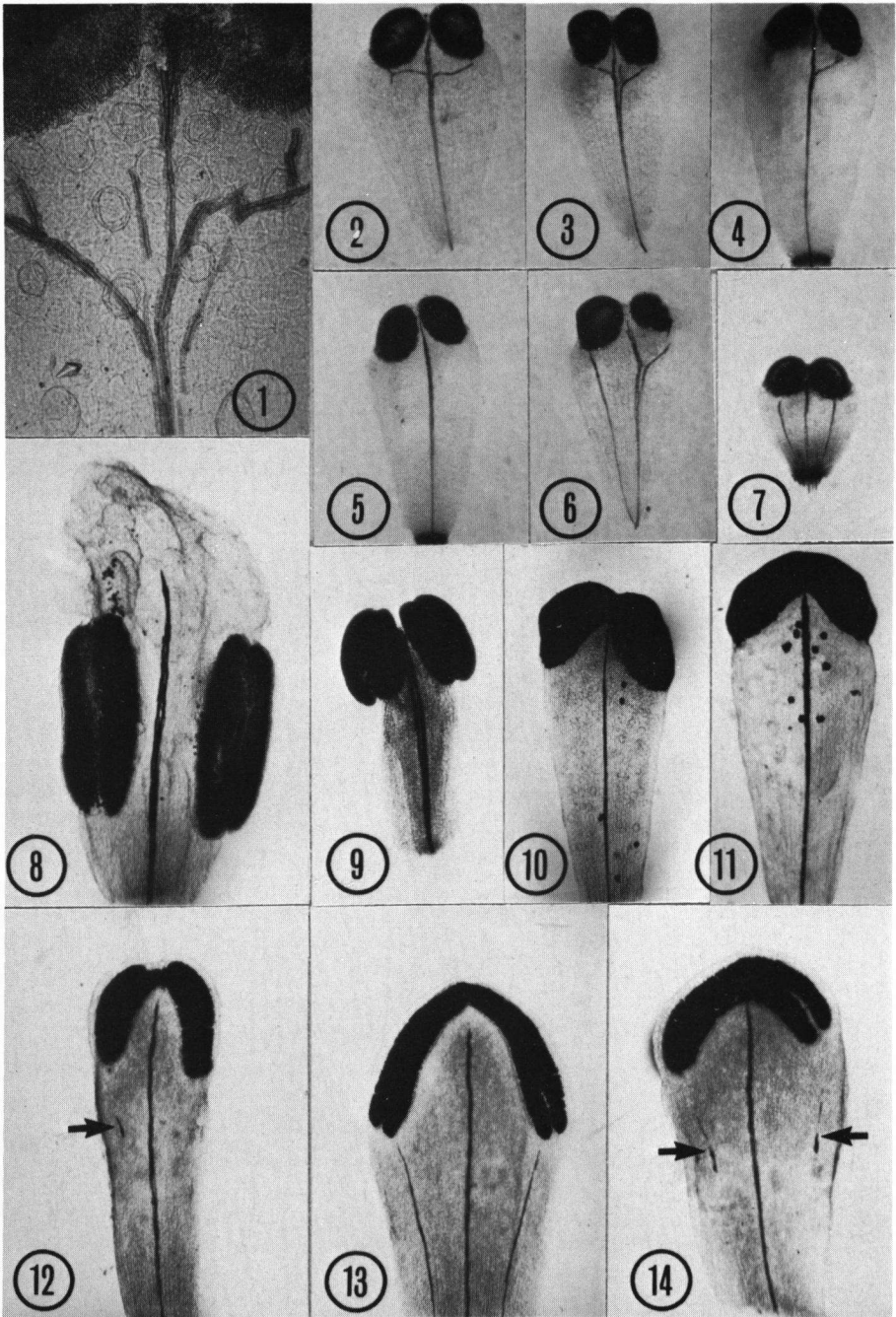
P. axillaris – In all collections some two-veined stamens were found. In one instance the veins joined near the base of the stamen (fig. 6). Of a total of 247 stamens examined, 8 (3%) had two veins. One stamen was three-veined for most of its length but the veins fused near its base (fig. 15).

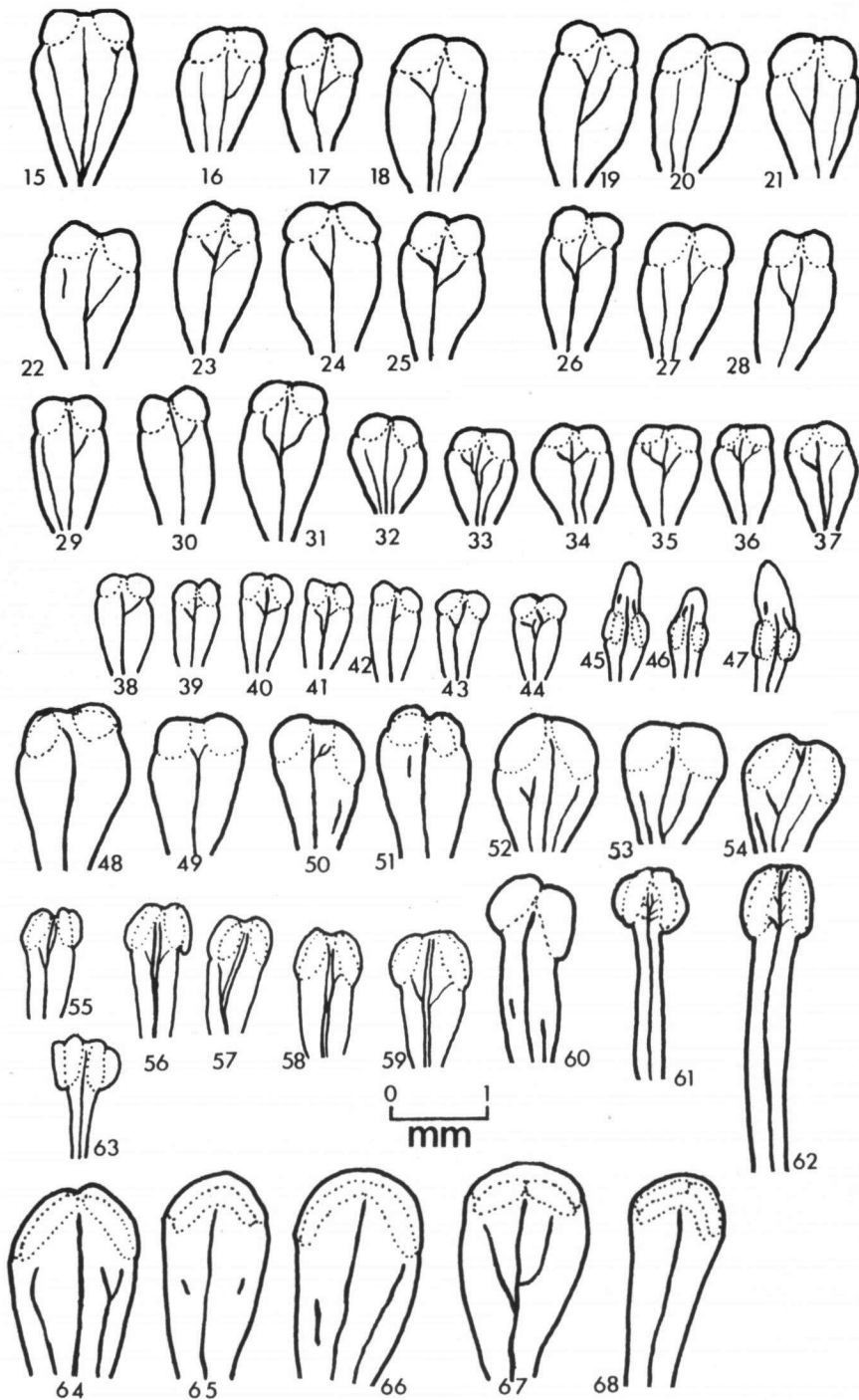
P. colorata – Some two-veined stamens were present (11 in a total of 382, i.e., c. 3%). In contrast to the previous species, a number of stamens had isolated, apparently vestigial, veins lateral to the median vein (figs. 21, 22). Such stamens, in this and other taxa (see on), were not sectioned to establish if they were linked via procambial tissue to another vein. Two three-veined stamens were found (Owaka collection) with similar venation to fig. 7 (*P. traversii*) except that in one stamen all three veins dichotomised near their tips and in the other only the median dichotomised. A surprising feature of stamen venation was its variability from collection to collection. For example, figs. 16–31 illustrate stamens from a single flower in the Akatarawa collection, in which there is considerable variation in venation. On the other hand, most stamens (88%) in the Erua collection had a single (median) unbranched vein.

P. traversii – Venation was as variable in this species as in *P. colorata*, with one- (110), two- (15) and three-veined (3) stamens. In three collections there was a wide range in venation (figs. 1, 7, 32–37), but in the Goulard Downs material, only single-veined stamens with limited branching were present. As in *P. colorata* some stamens had isolated lateral veins.

P. colorata × *P. traversii* – In this natural hybrid, while stamens resembled *P. traversii* in being smaller than those of *P. colorata*, they had a less extensive venation (figs. 38–44) than *P. traversii* stamens collected in this region (figs. 32–37). This reduced venation more closely resembled that of *P. colorata* stamens in this locality.

Fig. 1–14. All figures show cleared stamen(s) in lateral extrorse view (1: × 82; 2–14: × 14). – *Pseudowintera traversii* (Boulder Lake), portion of a stamen. – 2 & 3. *P. axillaris* (Akatarawas). – 4 & 5. *P. colorata* (Brown Cow). – 6. *P. axillaris* (Akatarawas). – 7. *P. traversii* (Brown Cow). – 8. *Belliolum pancheri* (WELTU 12308). – 9. *Drimys winteri* (WELTU 14475). – 10. *Exospermum stipitatum* (WELTU 12126). – 11. *Zygogynum baillonii* (McKee 9781). – 12–14. *Z. pomiferum* subsp. *pomiferum* (McPherson 2827). – Arrows in fig. 12 and fig. 14 indicate isolated veins.





Bellium

In *B. pancheri*, all stamens possessed a single median vein which extended beyond the level of the pollen sacs into the lower part of the sterile distal portion of the stamens (fig. 8). The veining showed varying degrees of 'doubling', in which there were two closely approximated groups of tracheary elements (fig. 8). Some stamens had a median strand which had this double nature throughout its length, others had the 'doubling' confined to the distal region and others lacked it entirely. The unidentified *Bellium* sp. which has very small flowers (c. 8 mm diameter) and stamens, had a single median unbranched vein per stamen, without signs of 'doubling'. In some stamens the vein continued almost to the tip. Three stamens had lateral isolated tracheary elements distal to the pollen sacs (figs. 45–47) suggesting that the species had evolved from one with more extensively vascularized stamens.

Bubbia

The single species examined, *B. howeana*, had stamens with a venation resembling the range of types found in *Pseudowintera*. These included one-, two- and three-veined stamens as well as stamens with isolated veins (figs. 48–54).

Drimys

Most stamens of *D. granadensis* and *D. winteri* had a central vein of two closely aggregated groups of tracheary elements, which were often joined in the lower part of the stamen (fig. 9). A few stamens with branches from this central region were found in both *D. granadensis* (figs. 55–57) and *D. winteri* (figs. 58, 59).

Exospermum

With one exception, all stamens of *E. stipitatum* had a single unbranched median vein (fig. 10). One stamen had two short lateral veins, one of them isolated (fig. 60).

Tasmannia

The four species studied had a single vein, which in *T. insipida* (fig. 62) and *T. lanceolata* (fig. 61) gave off several short lateral branches towards each pair of pollen sacs, before dichotomising at its tip. *Tasmannia piperita* had some stamens with a similar venation, but in many stamens (46%), although the vein bifurcated near its tip, there were no lateral branches. In *T. xerophila* all stamens had a single unbranched vein (fig. 63).

Fig. 15–68. All figures depict cleared stamens in lateral extrorse view. Dotted lines indicate boundaries of pollen sacs. All figures are to the same scale. — 15. *Pseudowintera axillaris* (Akatarawas). — 16–31. *P. colorata* (Akatarawas), all stamens are from a single flower. — 32–37. *P. traversii* (Brown Cow), all stamens are from a single flower. — 38–44. Natural hybrid *P. colorata* × *P. traversii* (WELTU 12950), all stamens are from a single flower. — 45–47. *Bellium* sp. (WELTU 13253). — 48–54. *Bubbia howeana* (WELTU 12311). — 55–57. *Drimys granadensis* var. *mexicana*. — 58 & 59. *D. winteri* (WELTU 14475). — 60. *Exospermum stipitatum* (WELTU 12126). — 61. *Tasmannia lanceolata*. — 62. *T. insipida* (WELTU 13760). — 63. *T. xerophila* (WELTU 15397). — 64–68. *Zygogynum pomiferum* subsp. *pomiferum* (McPherson 2827).

Zygogynum

Zygogynum baillonii (fig. 11) and *Z. bicolor* had all stamens vascularized by a single unbranched median vein. In contrast, stamens of *Z. pomiferum* subsp. *pomiferum* displayed considerable variation in stamen venation (figs. 12–14, 64–68). Venation ranged from one to three veins per stamen, including isolated lateral veins (fig. 14). Of the 50 stamens examined, 15 were three-veined, 4 were two-veined and the remainder had a single vein. Nearly 50% of the stamens (24) had isolated strands of apparently vestigial tracheary elements.

DISCUSSION

Results of this study seem to support the hypothesis of Bailey & Nast (1943) that three-veined stamens are a primitive feature of the woody Ranales, at least with reference to the Winteraceae. Although three-veined stamens do not predominate in any one species, they were found in some species at least, in three genera (*Bubbia*, *Pseudowintera* and *Zygogynum*). Furthermore, the hypothesis is strengthened by the existence of some stamens with what appears to be isolated vestiges of the two lateral veins, in these genera and in *Bellium* and *Exospermum*. It could hardly be argued that three-veined and two-veined stamens have evolved from single-veined ones, in view of the presence of such isolated veins. Nor could such veins be considered an occasional teratological feature, as they are so abundant in some species.

Carlquist (1969) has emphasised the pitfalls in using the principle of vascular conservatism as a phylogenetic tool and commented that angiosperms 'are sufficiently efficient in evolution of structure and ontogeny that the simplest and most orderly form of a vein system can be expected to be achieved within a few generations.' His article did not include, however, mention of isolated floral vascular tissue. Such tissue is not uncommon in some woody Ranales. For example, all tepals of *Laurelia novae-zelandiae* (Monimiaceae) I examined, had isolated vascular strands near their periphery. This feature, as well as the variable nature of the venation, seemed to indicate the tepals had evolved from the more richly veined bracts (Sampson, 1969).

Assuming that the isolated veins do not have a conductive function, unless of course they are linked to other veins by procambial tissue, it is difficult to envisage a function for them. Their sporadic occurrence within the stamens of many taxa would seem to indicate they have no great selective value. They are mostly too small to give any appreciable extra strength to the stamen and in any case, stamens of the Winteraceae seem robust organs, which would not need any strengthening from the vascular tissue. The vascular instability shown by stamens of many Winteraceae seems surprising in view of the antiquity of the group, which is now believed to extend further back in the fossil record than any other angiosperm family extant (Walker et al., 1983). Ehrendorfer et al. (1979) have made a detailed study of variation in the polymorphic species *Drimys brasiliensis* and have commented on its genetic significance.

There is obviously some correlation between broad truncate stamens and a more elaborate venation. Conversely, more 'conventional' stamens in the family, with long

narrow filaments, terminal anthers and narrow connectives, as in *Tasmannia insipida*, each have a single vein with small branches near its distal end. It seems no coincidence that *Zygogynum pomiferum* subsp. *pomiferum*, which has exceptionally broad stamens, has many with two and three veins and nearly 50% with isolated veins, whereas *Z. baillonii* and *Z. bicolor*, which have comparatively narrow, less truncate stamens, are invariably vascularized by a single unbranched vein. It should be noted that there can be marked differences in stamen morphology in a single flower. For instance, the broadest stamens of *Z. pomiferum* subsp. *pomiferum* (figs 13, 14) are closer to the petals, than narrower, less truncate and, in general, less richly veined stamens (fig. 12).

In the present state of our knowledge of pollination ecology in the Winteraceae, there seems to be no obvious correlation between pollinator and stamen type. *Drimys brasiliensis* subsp. *brasiliensis* and *D. granadensis* var. *mexicana*, which have similar stamens, are both pollinated by Diptera and Hymenoptera. Flowers of *D. brasiliensis* are pollinated also by thrips (Thysanoptera) and those of *D. granadensis* by Hymenoptera (Gottsberger et al., 1980; Thien, 1982). *Tasmannia piperita* entities *heteromera*, *montis-wilhelmi* and *polymera*, which have stamens rather similar in form, though with longer filaments, are chiefly pollinated by flies (Thien, 1980, 1982). Flowers remain functional for up to 10 days in this species and in *Drimys brasiliensis*. It is possible too, that some species of *Tasmannia* may be wind-pollinated in view of the large fraction of *Tasmannia* pollen which has been recorded in regional pollen rain in Australia (Macphail, 1974). Flowers of *Pseudowintera*, with their quite different stamens, are pollinated too by thrips, flies (Diptera) and to a lesser extent beetles (Coleoptera) as well as by larvae (caterpillars) of geometrid moths. *Pseudowintera* is almost completely self-incompatible and the caterpillars can be transferred from one plant to another by wind, as they hang on threads up to a metre or more in length (Norton, 1980, 1984). Flowers are functional for many days. It is possible too that some wind-pollination occurs in this genus (Norton, 1980; Godley & Smith, 1981). Contrasting with these examples, *Zygogynum*, with stamens of some species not too dissimilar in form and venation from those of *Pseudowintera* and *Bubbia* (compare figs. 32, 52, 64), has a floral life-span of two days only, with a female phase on the first and a male phase on the second day. Pollination is by beetles and moths and the inner petals close over the flower at the end of the first day (Thien, 1980; Thien et al., 1985). Despite their short life-span, stamens of *Zygogynum* do not seem less robust than those of other genera. *Exospermum* too, has short-lived flowers, pollinated by beetles (Thien et al., 1985). Although their stamens are distinctly different from other genera, the two species of *Bellium* which have been investigated (*B. crassifolium* and *B. pauciflora*) are like *Pseudowintera* and *Drimys brasiliensis* in being pollinated by thrips (Thien, 1980).

What then is the archetypical stamen and archetypical pollinator in the Winteraceae? On the basis of Bailey & Nast's hypothesis, the presence of apparent vestiges of lateral veins in some stamens of *Bellium*, the antiquity of the Coleoptera, the presence of beetle pollination in woody Ranales with leaf-like, three-veined stamens e.g. *Degeneria* (Thien, 1980), one is tempted to speculate that the archetypical stamen in

the Winteraceae most nearly resembled that of *Belliolum*, but was broader and three-veined with non-marginal pollen sacs and pollination was by beetles!

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