

OXFORD UNIVERSITY EXPEDITION TO PAPUA NEW GUINEA, 1983

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INTRODUCTION

The 1983 Oxford University Botanical Expedition to Papua New Guinea aimed to investigate the reproductive isolation of the "entities" of *Drimys piperita* (Winteraceae) found on Mount Wilhelm, Simbu Province, Papua New Guinea (PNG). This species has been described taxonomically by Vink (1970) such that 39 entities are recognised in PNG. These show an almost complete intergradation of form, but are presumed to be reproductively isolated since the differences between them are consistent. It was decided to study the six reported entities on Mt. Wilhelm (4509m, 5° 05'S, 150° 05'E) since here they form a complex within which the individual members are relatively easily distinguished.

Members of the Winteraceae are felt to be primitive angiosperms and considerable work has been carried out concerning the development of reproductive structures in the family. However, no work had previously been carried out on the ecology of the species of the genus *Drimys*, and it was felt that any contribution of this type would be of value.

PERSONNEL

Leader: Michael Alexander Venables.
20 years of age.
Third year undergraduate at Wadham College studying BA Honours Botany.

Treasurer: Timothy Hamish Shepherd.
21 years of age.
Graduate of Wadham College, BA Honours Botany.

Home Agent: Dr. R.H. McCleery.
Department of Zoology, Oxford University.

ITINERARY

July 6th	Depart for PNG by Philippine Airlines, via Manila.
8th	Arrive Port Moresby.
11th	Internal flight to Lae. Following two and a half weeks spent in examination of herbarium specimens at the National Herbarium, and collecting equipment and supplies. One weekend spent working with forestry students from Unitech at Bulolo Forestry College, near Wau.
27th	Travelled by road to Kundiawa, Simbu Province, courtesy of Mr. Bob Johns of Unitech.
28th	Travelled by road to Keglsugl at the head of the Upper Chimbu Valley.
29th	Walked to Hut beside Lake Aunde, which acted as the base for studies during the next five weeks, hiring nine porters to carry equipment. Research carried out in the Pindaunde Valley with a three day trek over the summit to collect in the Upper Jimmi Valley.
August 31st	Returned by foot to Keglsugl.
September 1st	Returned to Lae by road. Following two weeks spent in Lae drying, sorting and packing specimens for return to the United Kingdom.
13th	Took bus to Madang for short excursion.
21st	Returned by road to Lae.
25th	Flight to Port Moresby.
28th	Intended to catch flight to Manila but plane delayed.
29th	Flight to Manila.
30th	Flight to Gatwick.
October 1st	Arrived in London.

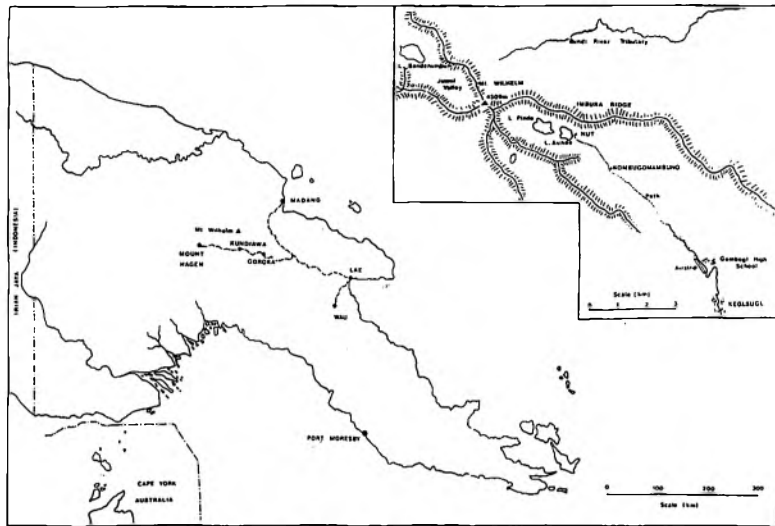


Figure 1: Papua New Guinea: inset Mt. Wilhelm & surrounding area.

RESULTS

The Expedition aimed to study the reproductive isolation of the entities of *Drimys piperita* found on Mt. Wilhelm. In the initial stages of planning considerable help was provided by Mr. R.F. Johns, Senior Lecturer in Forestry at the PNG University of Technology (Unitech) at Lae. In order to familiarise themselves with the material the members of the Expedition studied the available specimens at the Royal Botanic Gardens, Kew under the direction of Dr. C. Grey-Wilson and Dr. L.L. Foreman. In the March prior to departure a visit was made to the Rijksherbarium of the University of Leiden, the Netherlands, where Dr. W. Vink made available all collections and literature and gave much invaluable advice.

From discussions with the above-mentioned authorities it was decided that the first aspect of the problem to approach was the possibility that the different entities have varying ecological requirements. To this end it seemed best to make a series of observations of such ecological variables as soil-depth, -temperature, -water content, and -composition, altitude, aspect, and slope. Additionally it was intended to make a record of the minimum temperatures which the various entities are capable of withstanding. A further possibility is that different pollinators are active on the different entities, though this seemed somewhat unlikely because of the great similarity of the flowers. In order to determine the degree of interbreeding possible bagging experiments were to be performed and cross-pollinations executed. It is important to note that *D. piperita* is reported to be dioecious; this has critical consequences in terms of the breeding system. Finally, general observations were to be made on the growth habit and, as an ancillary study, a collection of roots to determine if they are mycorrhizal.

Since a hut is available in the Pindaunde Valley, near the village of Keglsugl it was decided that the investigations should be based there, with a short trip to collect in the Jimmi Valley.

On arrival in PNG a number of alterations had to be made to the proposed method of study. The most important of these was the total impossibility of obtaining max/min thermometers, as a result of which the investigation of minimum temperature had to be abandoned.

Before departure, a set of observation sheets on which results could be entered was made up. Altitude and aspect were determined from a map, slope with a klinometer. The observations on soil characteristics were determined as follows: depth using a crowbar and a 30 metre tape, temperature using a thermistor, type by observation and comparison with the notes of Wade & McVean (1969), and water content on an arbitrary scale of one (dry) to ten (saturated).

Bagging experiments were performed by tying a muslin bag securely over the inflorescences. Muslin was used since the mesh is fine enough to exclude potential insect vectors, and yet allows air to circulate, thereby preventing an increase in humidity and possible rotting. Cross-pollinations were performed by collecting male flowers of the entity in question and dusting the pollen from these over the stigmatic crests of emasculated female flowers. For this purpose the female flowers were carefully chosen as buds which were about to open, thereby precluding prior pollination and allowing development during the period of study. General observations were made for the duration of the five week period on the mountain, and collections made of aerial parts which were

dried and pressed for herbarium sheets. Spirit collections of flowers, fruits, roots and a series of wood chips were also made, the latter for the Rijksherbarium, Leiden.

Certain difficulties were encountered, in that, contrary to expectation, not all the entities were in flower during the period of study. Prior to travelling to the Pindaunde Valley a study was made at the National Herbarium at Lae of observed flowering times, which indicated that all might be expected to be flowering. However, during the investigation 'entity 9. montis-wilhelmi' was only seen with male flowers and fruits, and '8. crassipes' was not found in flower at all.

During the first two weeks of field work, 20 sets of ecological observations were made on various entities at 20 different sites. It soon became apparent that there was no significant difference between the various entities and consequently this analysis was abandoned. Indeed it was soon noted that, apart from the differences in the altitudinal range which is perhaps determined by frost tolerance, the entities did not vary at all in the ecological factors which determine the location of the adult plants. However, since there are habitat differences with relation to the associated species and the density of vegetation cover it seems likely that factors not measured in this study, possibly affecting seedling establishment, do play a part in determining the position of any given individual. Since plants of two entities may exist in close proximity and, on occasion in the same habitat, it does not seem likely that these factors effect reproductive isolation or, at least, not without the influence of other features of the ecology and breeding systems of the entities.

Bagging experiments were performed satisfactorily and since the fruits took longer to develop than indicated in the literature it was arranged that Mr J. Dua should send the developed fruits to the Botany Department, Oxford. Unfortunately this was not done and one of the more illuminating aspects of the study was not completed.

Since the quantitative data are not particularly informative it was decided that the best means of presenting the results is in the form of profiles of each entity. Plant communities follow those of Wade & McVean (1969). Details to be found in Vink (1970), and obtainable directly from herbarium specimens are omitted here.

'2. sub-alpina'

Field characters: bole grey - dark grey, smooth, diameter more than 20cm; young branches 4-5mm diameter, green - yellow; leaves upright, dull green, edged with red when young, rubbery texture; taste bitter and astringent, with strong

biting aftertaste; buds red to deep purple, petioles red; flowers, petals, and sepals red on underside, white on top; fruits fleshy, green to purple when unripe, red to black when ripe, ovoid; seeds black and very hard.

Growth habit: erect shrub up to 3m tall usually 1.5 - 2m; often suckering and with lignotubers.

Exists as scattered shrubs in lanslip vegetation or Danthonia grassland.

Associated spp.: Coprosma divergens, Detzneria tubata, Danthonia vestita, Haloragis microphylla.

Found at altitude of 3800m - 4200m. Flowered almost continuously. Female flowers never observed to have staminodes. Males have same number of carpels as females, but they are smaller, and sometimes these are fertile making the plant hermaphrodite. About 60-70% of the carpels become fruits. In living plants, some apices are commonly observed to be dead, whilst the leaves and older branches of some plants become coated in black mould of Antennula sp. If the buds are pierced they release a sweet sticky fluid. There were no signs of damage to the fruits still on the plants.

'8. crassipes'

Field characters: bole grey, rough and warty due to lenticels, more than 30cm in diameter; young shoots brown - yellow, occasionally red especially on suckers; more pachycaul than '2. sub-alpina'; young branches 4-10mm in diameter; leaves dull green, matt, upright, and often strongly recurved at the margins, especially when older; tough and brittle even when young; taste bitter with strong biting aftertaste; buds red; petals white on both sides, sepals white on upper surface, red below; fruits purple - black when ripe, ovoid; seeds black and very hard.

Growth habit: erect shrub to tree greater than 5m tall, though more usually 2-3m; sometimes suckering from base, sparsely branched. Found in well exposed sites in sub-alpine grassland that seems to be drier than other areas. Occasionally on the edge of the sub-alpine forest.

Associated spp.: Coprosma divergens, Dimorphanthera microphylla, Cyathea macgregorii, Haloragis microphylla, Rhododendron spp.

Found at altitude of 3650m-3850m. Only one plant found at end of flowering (female), fruiting heavily 60-70% of carpels becoming fruit. Many leaves damaged around the margins, even the younger leaves. No damage to the fruits on the plant.

'9. montis-wilhelmi'

Field characters: bole light grey to white, bark cracked; young branches 4-7mm in diameter, brown-black, yellow when very young; seedlings and runner shoots sometimes tinged red when young;

leaves horizontal when young, only shade leaf petioles red; sun forms are more ovate, shiny and bright green on the upper surface, less so below, recurved at margins when young; shade forms are duller, larger, darker, and more elliptic; taste bitter with only weak aftertaste; buds yellow-green; only male flowers seen, petals white on both sides; fruits red-maroon when ripe, almost spherical; seeds black and very hard.

Growth habit: erect shrub to 4m though more usually 2-3m tall. Runners sometimes from the base, seedlings very common especially near female plants. Only fully exposed sun forms seen flowering or fruiting. Found growing in a wide range of forest types, though most commonly in Upper Sub-alpine forest. Not restricted to the forest edge as previously thought, but only flowers in this location. One individual found growing outside the forest.

Associated spp.: very variable due to the wide altitudinal range but most commonly found are: Dimorphanthera microphylla, Vaccinium keysseri, Coprosma papuana, Pittosporum pullifolium, Rapanea vaccinioides. Found at altitudes of 3250m-3900m. Only males found flowering but females in heavy fruit, though no sign of young flower buds. Fruiting moderate to heavy, greater than 50%. One plant found heavily infected with Cladomyza angustifolia, a climbing parasite of the Loranthaceae, and almost dead. Some herbivore damage noted.

'25. heteromera'

Field characters: no distinct bole, diameter not more than 5cm, bark very black, except on the youngest parts, young branches 5-6mm diameter; leaves horizontal, bright green and glossy especially on the upper surface, fairly tough but not brittle, taste variable sometimes with biting aftertaste; buds red tinged when young, almost white prior to opening; petals white, sepals pale green, tinged or edged with pink; inflorescences arranged horizontally around stem; carpels green; fruits fleshy, black-red when ripe, oblong, slightly curved, and flatter along stigmatic side; seeds black and hard.

Growth habit: sparsely branched scrambling shrub, lacking a main stem; runners abundant spreading a clone over a considerable area. Up to 3m tall though not self-supporting at this height. No seedlings found. Found as an understory shrub inside the Lower Sub-alpine forest, rarely reaching the canopy or becoming exposed at the forest margin.

Associated spp.: Dimorphanthera microphylla, Harmsiopanax sp., Cyathea percrassa, Senecio sp. (tree form), Amaracarpus caeruleus. Found at altitudes of 3400m-3560m. Flowered almost continuously, male flowers having rudimentary

carpels which may function as nectaries. Fruits never found on these plants. Many female plants have staminodes, but never form fertile pollen. Inflorescence horizontal. Fruiting heavy, over 60%. Leaves often eaten and leaf miners common.

'32. cordata'

Field characters: bole not distinct; young branches brown; leaves horizontal, leathery but brittle and somewhat glossy with a bright green upper surface, midrib on lower surface red, whilst lamina is pale green and glabrous; taste bitter with biting aftertaste; buds yellow green; petals and sepals white on both surfaces, petiole at 45° to stem but flowers upright, carpels green; fruits black when ripe; seeds brown and hard.

Growth habit: a scrambling sparsely branched shrub. Seedlings of various ages found. First leaves petiolate and ovate, only later leaves becoming cordate. Found in the understory of the Cloud forest scrambling up to 4m, but never emergent. Altitude ranges from 3000m-3250m. Flowered continuously. Female flowers have only carpels developing to fruit. Many leaves eaten and infected with leaf miners.

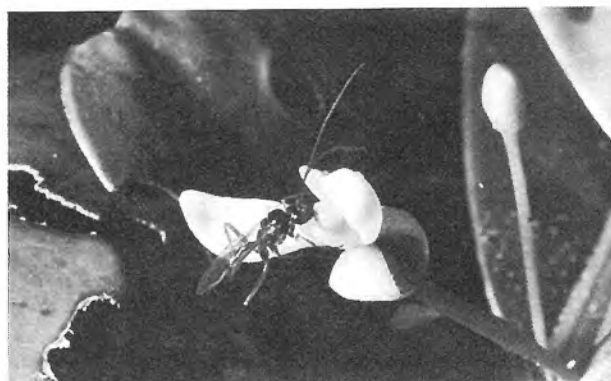


Figure 2: Male Ichneumonid wasp on flower of Drimys piperita entity 25, heteromera. Four times actual size.

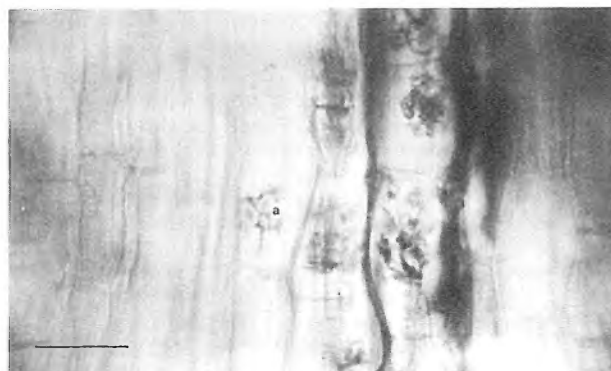


Figure 3: Section through root of Drimys piperita, showing infection by mycorrhizal fungus, a - arbuscule. Scale bar 50µm.

Other observations

Three consecutive days and a short period at night were spent observing flowers on 'entity 25. heteromera' in an attempt to determine what acts as the pollinating agent. During this period one fly was observed to visit the flowers though this was probably a chance visit since the individual spent about as much time on the leaves as the flowers and showed no great preference for the latter. An insect subsequently identified from a photograph (figure 2.) as a male Ichneumonid wasp was also observed to visit but this was deemed unlikely to be a particularly efficient pollinator due to the extreme lack of hairs on the body. Finally an unidentified beetle was seen crawling over the plant and occasionally visiting the flowers, but since it did not leave the plant for the duration of the three day study it also seems to be a poor pollinator.

Similar observations were carried out on 'entity 32. cordata' for one day in the Cloud forest. Contrary to the notes of Thien (1980) there was little evidence of any great insect activity, with the exception of the large number of small flies attracted by the presence of the researchers.

Research was also carried out on the floral structure of the flowers, largely that of 'entity 25. heteromera'. It was seen that several types of flower existed viz. with carpels alone, carpels and staminodes, carpels and stamens, and stamens alone. Dissections were carried out on those having carpels and stamens, and it was found that of 47 carpels examined only 11 had any ovules (usually only one or two), whilst the carpels of the entirely female flowers all had many ovules. Thus the apparently hermaphrodite flowers of this entity are effectively male. This is supported by the observation that these plants were never seen bearing fruit.

Observations were made on the carpels and these indicated that the stigmatic crest is initially green and fleshy, producing a liquid that collects on the receptacle, presumably nectar. As the carpels become older the stigmatic crest turns red and dries out. Generally carpels in this condition contain a large number of seeds in the early stages of development.

Once the Expedition had returned to Oxford the collections of roots were checked for the presence of nycorrhizae, using a simple staining technique. All the entities were found to possess vesicular-arbuscular infections (figure 3.). At present samples of soil collected at the same time as the roots are being analysed in an attempt to determine the identity of the infecting fungus on the basis of spore morphology.

DISCUSSION

Attention should be drawn to the existence of seedlings in entities '9. montis-wilhelmi', and '32. cordata', whilst none was seen of the other entities, reproduction being predominantly by means of runners in the case of '25. heteromera', and suckers in the case of '2. sub-alpina' and '8. crassipes'.

The work of Vink, which was largely based on herbarium material, has been fully substantiated by this study, and a number of field characters added which should aid identification of fresh material. Although each entity has its own distinctive character which is easily recognised, it is extremely difficult to formulate these features in a means which is readily appreciable to those who have not encountered the plant. During the study only one individual was found that was of dubious identity, and it was later considered to be an hybrid of '9. montis-wilhelmi' with '25. heteromera' (MAV & THS 21).

It was observed that although both '9. montis-wilhelmi' and '25. heteromera' will grow within the Sub-alpine forest only the latter ever flowered in this location. Those individuals of the former found in the forest not only did not flower but they also showed a differing leaf morphology, closer to that of '25. heteromera' than those of the same entity flowering on the margins of the forest.

As to the reproductive biology it is impossible to draw any concrete conclusions. However, given the unusually high frequency of fruiting and the low level of insect activity there is at least some indication that apomixis may be the predominant method of fruit and seed production. The bagging experiments would have established this point but the results are unfortunately unavailable. The other possibility is, of course, wind pollination but in view of the floral structure of highly fleshy stamen filaments and inwardly directed stigmatic surface unspecialised for the reception of wind-borne pollen this seems, at best, unlikely.

Consequently, one is led to the view that the entities studied reproduce by a combination of vegetative propagation, apomixis, and, in the case of '2. sub-alpina' self-fertilisation. Apparently pollination does occasionally take place, and when this is between entities it can lead to hybrids of the type noted above. Hybridization is probably limited by the tendency for the vegetatively reproducing entities to grow in clumps, reducing the likelihood of foreign pollen reaching the stigmatic surface.

No animal was ever observed eating or dispersing the fruits though a large number of birds were in the locality, and, perhaps as a consequence of this, seedlings were generally found in close proximity to a female plant of the same entity.

If the conclusions drawn above are a true reflection of the situation pertaining in the field then this goes some way to providing an explanation of the taxonomy of the species. It may well be a complex of microspecies capable of reproducing both sexually and asexually, somewhat like Rubus (Rosaceae) in Europe, for example. In order to establish this view definitively, many more experiments would have to be performed but this investigation does at least indicate the direction further research should take.

ACKNOWLEDGEMENTS

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We are also grateful to all those people who helped with both the organisation of the Expedition and the various problems that arose in Papua New Guinea. It is not possible to mention everyone but we would like to give our special thanks to the following: Dr. R.H. McCleery (Home Agent), Mr. F. White (Scientific Advisor) and Drs. D.J. Maberley and K. Hardie (preparation of mycorrhizae) of Oxford University; Drs. W. Vink and M.M.J. van Balgooy of the Rijksherbarium, University of Leiden; Professor N.M. Wace of the Dept. of Biogeography and Geomorphology, Australian National University; Dr. David Frodin and Professor Dick Moreton of the University of Papua New Guinea; Dr. J. Ismay, DPI, Port Moresby; Dr. Ted Henty and Karl Kerenga of the Dept. of Forests, Lae; Professor David Wigston, Sue Jones, Professor Bob and Sue Day, Dr. Tom Vigus, Jack Fenton, the Architecture Dept., and most especially for making everything so easy, our field agent Bob Johns, all of the PNG University of Technology; all those at the Gembogl High School; and lastly James Garky Titiko and Josep Nama Dua who cared for the two of us for five weeks whilst on Mt. Wilhelm.

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ACCOUNTS

INCOME

Oxford University Funds	
Anonymous Trust	200.00
Alexander Allan Paton Fund	200.00
Gilchrist Trust	150.00
University Chest	250.00
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The Biological Council	150.00
British Petroleum Ltd.	100.00
Colour Library Books Ltd.	250.00
The Explorer's Club (Youth Activities Fund)	1277.12
The Mount Everest Foundation	600.00
The Oxford Society	60.00
The Royal Geographic Society	200.00
The Vincent Wildlife Trust	250.00
Wadham College	70.00
Wadham College Students' Union	260.00
Personal Contributions	600.00
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Interest on deposit account	5.16
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EXPENDITURE

i) In U.K.	
Research fee	174.64
Prospectus	80.57
Stationery	60.96
Postage & telephone	53.47
Travel (Leiden)	67.83
Travel (PNG)	1710.00
Insurance	102.50
Equipment	81.65
Camera extras	145.12
ii) In P.N.G.	
Accommodation	475.00
Employment	167.00
Internal travel	284.00
Food	790.00
Administration	65.90
Miscellaneous	186.00
iii) Predicted Expenditure Report	150.00
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Cash in hand	27.64
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