

of the inflorescence at an earlier stage show that the spathe itself emits a "minty" odour, while the sterile appendix of the spadix emits a rather different "soapy" one).

### Fruiting

The most salient finding of Shaw and Cantrell (1983) for Australian plants was that although wind-pollination and/or self-pollination did occur, by far the main part of the seed-set resulted from pollination by several kinds of insect. In my plants however I have never seen insects (other than thrips) in the spathal chamber, nor have I seen insect visitors to the male flowers, not even honey-bees.

Each season's earliest one or two inflorescences, and sometimes the last one or two as well, are sterile and soon wilt and rot. The others almost always mature a good complement (c. 100) of the red fruitlets. These are exposed almost exactly 4 months after flowering, when the spathal chamber tears in broad strips back down to its base and the peduncle curves back over towards ground level. The seeds (one per fruitlet) always appear to be well-formed, and a sample from the single fruit-head I tested gave 100 % germination.<sup>1</sup>

To resolve the discrepancy between the suggestion of a requirement for insect pollination and the lack of insect-visitors in Auckland I experimented on a number of mid-season inflorescences. All were kept in fine muslin bags from their earliest appearance. In

some the male part of the spadix was excised at the "open base" (female) stage. In the others the base of the spathal limb was plugged with cotton wool. Both treatments prevent pollen (self or other) from reaching the female flowers. In no case was any fruit set. Because bagged controls produced abundant fruit I conclude that my plants are largely or entirely self-pollinating. In agreement with this is that in the bagged controls it was not uncommon for some of the fruitlets to remain undeveloped. These were not placed in random over the cylindrical surface of the fruit, but occurred in a more or less vertical strip, as though pollen had not been able to fall down from above in that sector.

The question remains then: why isn't this plant spreading through the bush in company with *Zantedeschia*? I have not seen birds feeding on the infructescence of either species, but it seems reasonable to suppose that if blackbirds (say) have learnt to feed on *Zantedeschia* it would not be long before they took to the alocasia too. And Peter de Lange has reminded me that on Raoul I. (Kermadec Is.) the latter species is certainly spreading by seed — but how?

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<sup>1</sup> c. 50 seeds (removed from their fleshy covering), sown in a seed-tray outdoors, late winter; all germinated within 6 weeks.

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## How to look at *Macropiper* (Piperaceae)

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### Introduction

Molecular-taxonomic work on the Piperaceae has found that *Macropiper* comprises the major part of a basally-originating lineage (Jaramillo et al. 2008). Consequently, the suggestion is that it be reduced in rank, to coordinate with infrageneric status for another nine or so lineages in *Piper* broadly conceived. Names in *Piper* for *M. excelsum* and other

New Zealand macropipers are listed by de Lange (*New Zealand Journal of Botany*, in press).

A.C. Smith's revision of *Macropiper* (Smith 1975)<sup>1</sup> had concluded just the opposite, that generic status was fully deserved. The present article does not debate the merits of a change in rank; rather, it attempts to bring Smith's morphological observations, notably

those on inflorescence position, into harmony with the DNA results.<sup>2</sup>

### Taxonomic background

Jaramillo et al. (2008) found that the *Macropiper* lineage includes the kava plant, *Piper methysticum*, the best-known member of a small group of shrubby Malesian pipers.<sup>3</sup> The single shrubby species in Africa, *P. capense*,<sup>4</sup> was found to join with these species too.

The first true macropiper (*M. latifolium*) and *P. methysticum* were discovered in the Society Islands during Cook's first two voyages (Smith 1975; Nicolson & Fosberg 2004). Fifty or so years later F. A. W. Miquel placed the two together as the basis for his new genus *Macropiper*, simply because of their general vegetative similarity.<sup>5</sup> But to C. de Candolle, the next great *Piper* specialist (de Candolle 1869, 1923), this similarity was of much less importance than a difference in inflorescence position. *Macropiper* species (by then nearly all had been discovered) were seen to have one to several spikes clustered in the leaf axils or (in *M. excelsum* only) one to several spikes on a short axillary branched structure. In contrast, *P. methysticum*, like nearly all the Old World climbing pipers,<sup>6</sup> has the distinctive and somewhat perplexing "leaf-opposed" arrangement, where the petiole base and spike are on opposite sides of a node. It is an irony then that the DNA results mean we now have to try to homologize these two apparently very different inflorescence systems.

### Homology of the inflorescences

We can start from the following premise. Since the "leaf-opposed" arrangement is nearly universal in the Old World climbing pipers,<sup>7</sup> that is, in what seems at least on geographical grounds to be the most likely sister group to (*Macropiper* + *P. methysticum* + *P. capense*), it ought to be regarded as primitive. So we need to understand how the leaf-opposed condition, as in *P. methysticum*, might have been transformed into the axillary condition of *Macropiper*.

In New Guinea I was able to examine the wild progenitor of kava, *P. subbullatum* (syn. *P. wichmannii*). The existing descriptions of it, and the herbarium material that I had seen, gave a very inadequate idea of its architecture. I saw that the trunks and branches of *P. subbullatum* are differentiated in a way not seen in the macropipers. The vegetative (sterile) erect stems grow more or less erect and straight, and bear their leaves (which have conspicuously sheathing petioles) in a spiral. From the axils of these leaves horizontal fertile branches are produced. These have leaves set in two rows, with a spike opposite each leaf-base. The spike develops from the apical bud, and, through outgrowth of each axillary bud at the shoot tip, the

initially terminal position of the new spike becomes a leaf-opposed one.

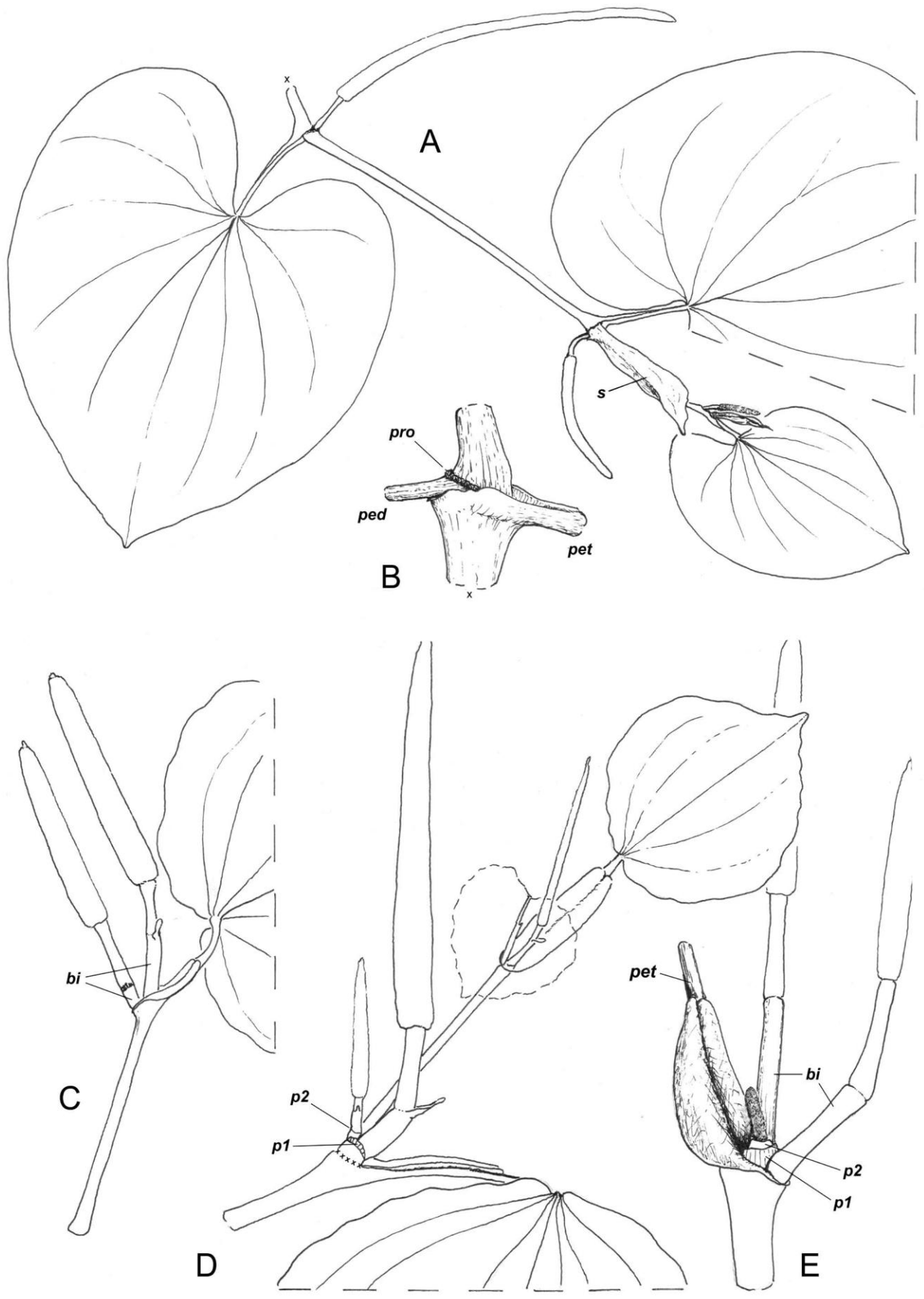
The leaves of the fertile branches lack a petiole sheath; instead, the prophyll (circular bract around the base of all axillary shoots)<sup>8</sup> seems to have been converted into a cap-like stipule. As in *Ficus*, this surrounds the apical part of the shoot and is shed as that part of the shoot grows out (Fig. 1 A, B). These fertile branches have a relatively limited capacity for further growth once the spikes have been matured – that is, there is little axillary regrowth from the lower nodes once the spikes have matured.

*Macropiper* species too have a vegetative framework of erect shoots with spiralled, sheathing-petiole leaves. However, there is no regular production of fertile lateral branches. Instead, the higher parts of the vegetative shoots begin to dichotomize through simultaneous outgrowth of their tip's terminal and axillary buds. Eventually, these distal branches become fertile through production of axillary systems, these consisting of one or more terminal spikes, each situated (in *M. excelsum* at least) at the apex of a single internode. The apex of each of these "basal internodes", at the base of the spike's peduncle, carries a much-reduced leaf. In all macropipers except *M. excelsum* the basal internode is very short (if present at all) and is usually completely hidden by the sheathing petiole. Depending, presumably, on the position of the shoot in the plant's canopy, and on the vigour of the plant, the terminal internode as well as the basal internode may become fertile, thus ending vegetative extension of that branch (Fig. 1C).

In *M. excelsum* the first-produced spike of the axillary system is often accompanied by a second spike. This comes not from outgrowth of a bud in the axil of the reduced leaf, but from one low down on the basal internode, situated laterally and included by the basal internode's prophyll. Since it is itself an axillary shoot its base too is ringed by a prophyll (Fig. 1D, E).

Thus the fertile branches in the axils of an *M. excelsum* stem can be interpreted as the much-reduced equivalent of the fertile lateral branches of *P. methysticum* but with basipetal rather than acropetal production of spikes. Note too that the stipules of the *P. subbullatum* fertile system are lacking; an immature inflorescence in this plant is protected by the sheathing leaf base.

For *M. latifolium*, which has a number of nearly sessile spikes per axil, a close developmental study would be required to determine whether the spikes are produced as above or whether they come from a number of buds all truly axillary in the parent node. Similarly, with only dry material of the solitary-spiked *M. puberulum* to hand, I have not been able to tell whether the spike is truly sessile or whether it might have a very short, prophyll-ringed, basal internode.



**Fig. 1.**

**Fig. 1. A & B (opposite) *Piper recessum* (a shrubby "true piper" from montane New Guinea). A: Fertile shoot (distal 3 nodes) with stipule (*s*), fully expanded, beginning to detach. Shoot apex with very immature spike, exceeded by the convolute stipule. [x 2] B: Close-up of lowermost node of A. *ped* = peduncle; *pet* = petiole; *pro* = prophyll, seen here as a raised and thickened rim, partly concealed by sheathing base of petiole. [x 5] Drawn from *ROG 10131*, AK 281794, New Guinea.**

**Fig. 1. C, D & E (opposite) *Macropiper excelsum*. C: Arrangement of two spikes terminating the growth of a branch, the slightly larger central one being (as usual) that of the axillary shoot. Note the reduced leaf (or its scar, as on left) between peduncle and shoot apex, and the basal internodes (*bi*) of the terminal and axillary fertile shoots. [x 2] D: Terminal portion of fertile shoot. At lowermost node: xxxx indicates part of sheathing petiole removed to show base of axillary shoot, the prophyll of this (*p1*) appearing as a drying, partly-encircling membrane, and itself enclosing a minute axillary shoot, whose prophyll (*p2*) is a mere line. Distal node with a fully developed axillary shoot. Concealing leaf blade shown dashed. [x 2] E: Node showing sheathing base of petiole (*pet*) enclosing bases of two fertile shoots. Prophyll of axillary shoot (*p1*) shown dashed, enclosing base of minute spike axillary on it, with prophyll *p2*. Basal internodes (*bi*) of the terminal and axillary fertile shoots. [x 5] C and E drawn from *Macropiper excelsum* subsp. *excelsum* (Gribblehurst Park, Sandringham; not vouchered). D drawn from *Macropiper excelsum* subsp. *peltatum* (cult. 6 Ward Tce, Sandringham, not vouchered).**

It is satisfying to have made this rationalization even if no obvious ecological correlates between the two kinds of inflorescence architecture come to mind. Perhaps it is significant, though, that tropical macropipers and the subtropical ones (*M. excelsum* subsp. *psittacorum*, *M. hooglandii*, *M. melchior*) have completed the putative reduction whereas the temperate *M. excelsum* has not.

#### Footnotes:

1. *Macropiper* has nine species, distributed from Micronesia, Santa Cruz Is. and Vanuatu to SW Pacific (Lord Howe I., Norfolk I., New Zealand) and east across the Pacific Ocean region to the Society and Marquesas Is. (Smith (1975). It is absent from Australia and New Caledonia. Note the vicariance with the shrubby Old World pipers (see 3 below).

2. Smith came close to anticipating the conclusions of the present article. In particular, his statement that in *Macropiper* "all the inflorescences are solitary and terminal at inception" (Smith 1975: 5) is the key to interpreting the fertile structures of *Piper* in the broad sense.

3. *Piper methysticum* is a near-sterile ancient cultivar widespread in the Pacific Ocean region. Its presumed progenitor, *P. subbullatum* (also known, especially in the anthropological literature, by the later name *P. wichmannii*) is found in the Philippine Is., New Guinea, the Solomons and possibly Vanuatu (although wild plants here may be garden relicts?). Also in this

group, although not sampled in the molecular study, would be several shrubby spp. from montane New Guinea (Gardner 2003).

4. *Piper capense* Africa has relatively few *Piper* species. This is the only shrubby one; it has subsucculent branches and leaf-opposed spikes with hermaphrodite flowers. See the image at <http://www.mozambiqueflora.com>

5. The name seemingly referred to the (relatively) large size of the leaves of these two species. But the shrubby habit might have also played a part in the naming; they are described (in Latin) as "shrubs or subshrubs", whereas the woody South American species are described only as "subshrubs".

6. The cultivated kava itself is generally not fertile, so that specimens and illustrations of it are mostly of the vegetative shoot and thus show only leaves with sheathing bases; but sometimes spikes are shown as appearing with such leaves, suggesting a juvenile fertility.

7. The New Guinean climber *P. versteegii* appears to be the single exception, but even its inflorescence system can be rationalized in terms of an erect shoot/fertile lateral shoot kind of architecture (Gardner, *Blumea* in press).

8. Working out the various arrangements in *Piper* and *Macropiper* is facilitated by a distinction between the axillary and terminal branches. The base of the first internode of an axillary stem is always wholly or partially ringed by a very low, near-translucent bract, the prophyll. This is absent from terminal shoots and is therefore absent from the base of any internode that bears a (pedunculate) spike.

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