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Cover images: 1. *Begonia holosericeoides* (female flower and habit) (Begoniaceae; Ardi *et al.*); 2. Abaxial cuticles of *Alseodaphne rhododendropsis* (Lauraceae; Nishida & van der Werff); 3. *Dipodium puspitae*, *Dipodium purpureum* (Orchidaceae; O'Byrne); 4. *Agalmyla exannulata*, *Cyrtandra coccinea* var. *celebica*, *Codonoboea kjellbergii* (Gesneriaceae; Kartonegoro & Potter).

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## ON THE EVOLUTION OF *DIPODIUM* R. BR.

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### ABSTRACT

O'BYRNE, P. 2014. On the evolution of *Dipodium* R. Br. *Reinwardtia* 14(1): 123 – 132. — *Dipodium* R. Br. (Orchidaceae), a genus of ca. 38 species, should be divided into an Australasian clade and a Malesian clade, based on morphological and geographic evidences. *Dipodium* section *Dipodium* and section *Leopardanthus* (Blume) O. Kuntze are re-defined to accommodate this change. An evolutionary scenario that explains this division is proposed. The lack of diversity of floral structure in the genus is probably caused by pollinator-specificity, while the diversity of plant form may be due to long-term environmental factors. An evolutionary explanation is suggested for the complex between *Dipodium fevrellii* J. J. Sm. and the hybrid *D. pandanum* Bailey in New Guinea. The complex in Java involving *D. pictum* (Lindl.) Rchb. f. and *D. scandens* (Bl.) J. J. Sm. is discussed, and the presence of a hybrid noted. In Borneo, the complex taxonomic situation caused by repeated inter-breeding of populations is noted.

**Key words:** *Dipodium*, evolution, inter-specific complex, hybrid, New Guinea, Orchidaceae, section *Dipodium*, section *Leopardanthus*.

### ABSTRAK

O'BYRNE, P. 2014. Evolusi *Dipodium* R. Br. *Reinwardtia* 14(1): 123 – 132. — Marga *Dipodium* R. Br. (Orchidaceae) yang mempunyai kurang lebih 38 jenis, seharusnya dibagi kedalam klad Australasian dan Malesian, berdasarkan bukti morfologi dan geografis. *Dipodium* seksi *Dipodium* dan seksi *Leopardanthus* (Blume) O. Kuntze dipertelakan ulang untuk mengakomodasi perubahan yang ada. Sebuah skenario evolusi yang menjelaskan pembagian ini telah diusulkan. Rendahnya keanekaragaman struktur pembungaan pada marga ini kemungkinan disebabkan oleh kekhususan polinator, sementara keanekaragaman bentuk tumbuhan kemungkinan disebabkan oleh faktor lingkungan. Penjelasan evolusi dianjurkan untuk jenis kompleks *Dipodium fevrellii* J. J. Sm. dan jenis hibrid *D. pandanum* Bailey di New Guinea. Jenis kompleks di Jawa meliputi *D. pictum* (Lindl.) Rchb. f. dan *D. scandens* (Bl.) J. J. Sm. dibahas dalam makalah ini, dan keberadaan jenis hibrid tersebut telah dicatat. Di Borneo, kondisi taksonomi yang kompleks disebabkan oleh persilangan antar populasi yang berulang.

**Kata kunci:** *Dipodium*, evolusi, inter-spesifik kompleks, hibrid, New Guinea, Orchidaceae, seksi *Dipodium*, seksi *Leopardanthus*.

## INTRODUCTION

*Dipodium* was established by R. Brown in 1810 for the Australian species *D. punctatum*. It currently has about 39 taxa, distributed from southern Indochina and Peninsular Thailand through the Malesian region to Palau (Caroline Islands), Queensland (Australia), Solomon Islands and New Caledonia and Vanuatu. *Dipodium* species show remarkable consistency in floral morphology, making it very difficult to determine species. This resulted in the genus gaining a reputation for being “difficult”, and most taxonomists avoided working on it. There have been no substantial taxonomic publications on the genus, other than O'Byrne (2013), which found 11 characters in the floral morphology that permit determination at species level. A full taxonomic revision of *Dipodium* section *Leopardanthus* (O'Byrne, in prep.) contains many new taxa, some of which are referred to in this paper.

## Traditional treatment of *Dipodium*

The relationship between *Dipodium* and related genera is unclear. Both Cameron *et al* (1999) and Stern and Judd (2002) placed *Dipodium* in subtribe *Cyrtopodiinae* and both showed that the *Cyrtopodiinae* is not a monophyletic group, but neither managed to resolve the relationships within the group. Pridgeon *et al.* (2009) placed *Dipodium* in tribe *Cymbidieae*, but did not comment on inter-generic relationships within the tribe and did not mention the infrageneric division into two sections.

The genus has traditionally been divided into section *Dipodium* and section *Leopardanthus* (Blume) O. Kuntze, which correspond roughly to the two geographic centres of diversity, Australasia and Malesia.

Section *Dipodium* has eleven species; nine endemic to Australia, one endemic to New Guinea, and *D. squamatum* (G. Forst.) R. Br. in Australia, New Caledonia and Vanuatu. They are homoge-

nous in habit; all are leafless plants with subterranean rhizomes and an erect flowering stem that has many persistent bracts (reduced leaves). They all have an annual growth cycle. It has long been assumed that they are holomycotrophic, but Dearnaley (2006) suggests that some may be indirect parasites on tree roots.

Section *Leopardanthus* has about 28 taxa, distributed from southern Indochina and Peninsular Thailand through the Malesian region to Palau (Caroline Islands), Queensland (Australia) and

Solomon Islands. All are leafy plants, but otherwise they are non-homogenous in habit. Three species are sympodial terrestrials (Fig. 1), with a disjunct distribution (Fig. 2). The remainder have traditionally been described as monopodial climbing plants (Fig. 3) and have a continuous distribution (Fig. 4). O’Byrne (2013) states that the division into terrestrial and climbing plants is an over-simplification, as climbing plants go through terrestrial and scrambling phases when immature. Horticultural experience supports this;

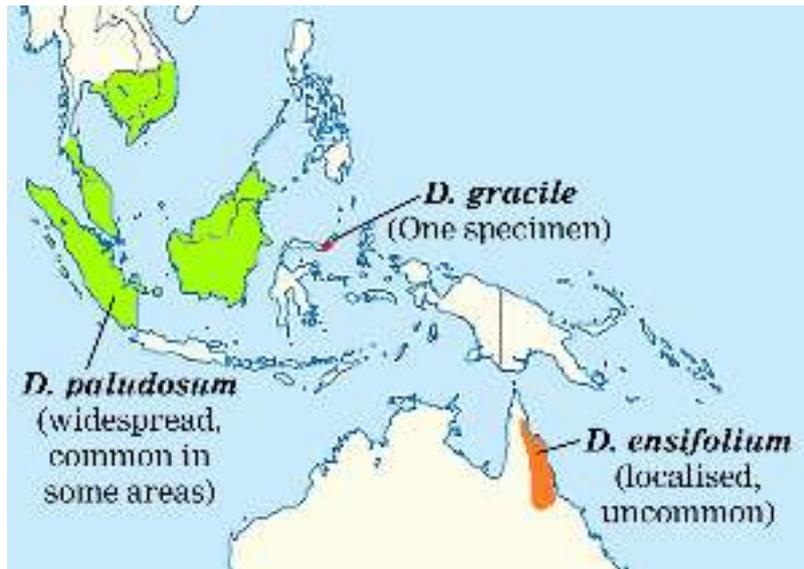


Fig. 1. *Dipodium paludosum* is one of the three leafy sympodial species traditionally described as “terrestrial”.

Fig. 2. Map showing the disjunct distribution of the three leafy sympodial *Dipodium* species.



Fig. 4. Map showing the continuous distribution of climbing *Dipodium* species.

Fig. 3. The majority of section *Leopardanthus* species have traditionally been described as monopodial climbing plants. Note the copious climbing roots on this *Dipodium fragrans*. Photo by P.T.Ong.

so-called “terrestrial” plants can be cultivated as epiphytes, and climbing phase specimens can be cultivated as terrestrials. Section *Leopardanthus* can have a seasonal growth cycle or can grow continuously; in some taxa these life-forms are interchangeable.

### **The origin and evolution of *Dipodium* (Fig. 5).**

If we consider *Dipodium* to be divided into Australasian and Malesian clades, then it is analogous to *Dendrobium*, where the division into two geographic clades is now well supported (Clements (2003); Schuiteman (in preparation); Wood (2006). It is reasonable to assume that both genera had similar origins and each developed into two clades through similar causes. This could mean, as suggested by Wood (2006) for *Dendrobium*, that *Dipodium* has an ancient origin and that the ancestral species was present on both the Australian and the Indian continental plates when (or shortly after) the ancient supercontinent of Pangea broke up. The ancestral species was probably not dissimilar to the modern-day *Dipodium ensifolium* F. Muell., a leafy sympodial terrestrial with a seasonal growth cycle. As the two continental plates drifted apart, the *Dipodium* populations on each plate developed separately, in isolation from each other. Consider the following scenario.

As Australia drifted slowly north-east, it became drier and more arid, and *Dipodium* responded by becoming subterranean and developing holomycotrophy or indirect parasitism as their energy source. This enabled them to reduce water-loss by reducing the leaf area; in most modern day species, the leaves are vestigial, present only as non-photosynthetic scales at the stem base. Since their stems are short-lived (their only function is to support the inflorescence), these species never developed the ability to produce adventitious roots along the stems.

The Indian continental plate drifted northwards until it collided with Eurasia. The *Dipodium* population travelled across the collision zone and then spread south-east through what is now Myanmar into Thailand and Malaysia. Somewhere on this journey, they encountered a barrier of rainforest and responded by developing the ability to climb up tree trunks. In order to do this, they need adventitious roots along the stems and these are present in copious quantities in all members of the Malesian clade. Once they had adapted to living in rainforest, the Malesian clade were able to spread south-east through the island chains, eventually reaching Caroline Islands, Australia and the Solo-

mon Islands, the outer limits of their present-day distribution.

The main binary morphological difference between the two *Dipodium* clades is therefore not the presence or absence of leaves (section *Dipodium* has reduced leaves on the stem), but the presence or absence of adventitious roots along the stem. Section *Dipodium* lacks adventitious roots at stem nodes; section *Leopardanthus* possesses them. This enables us to resolve the sectional position of the two of the “leafy terrestrial” taxa traditionally placed in *Leopardanthus*. The Australian *Dipodium ensifolium* F. Muell. does not form adventitious roots at stem nodes, and therefore belongs in the Australasian clade, despite the presence of green leaves. *Dipodium gracile* Schltr. from Sulawesi is known only from the type (destroyed), but the protologue does not mention adventitious roots and Schlechter stated it was closer to *D. ensifolium* than *D. paludosum* (which is in section *Leopardanthus*). *Dipodium gracile* is therefore tentatively placed in Section *Dipodium*, becoming its northernmost member and the only species outside Australasia.

### ***Dipodium* Sections redefined; summary**

#### **Section *Dipodium***

Australasian Clade. 13 species. Distribution: Australia (11 species, 10 endemic), 1 extending to New Caledonia and Vanuatu, New Guinea (1 endemic), Sulawesi (1 endemic). Terrestrial. Sympodial. Stems with green leaves (2 species) or leaves reduced to scales/bracts. Stems without adventitious roots at nodes. Column apex not yellow.

**Section *Leopardanthus*** (Blume) O. Kuntze in Post & Kuntze, *Lexicon Gen. Phanerog.*: 179 (1904).

Malesian Clade. ca. 26 taxa. Distribution: Indochina, Malaysia, Indonesia, Philippines, Caroline Islands (1 taxon), New Guinea (3 taxa, 1 endemic), 1 taxon extending to Australia and Solomon Islands, Louisiade Archipelago (1 endemic). Adult phase either sympodial terrestrial (1 species) or monopodial climbing. Leafy. Stems with adventitious roots at nodes. Column apex yellow (3 exceptions).

#### **Pollinators, conservation of floral structure, and the significance of flower color**

The flowers of all *Dipodium* species are unusually consistent in size, shape and structure, especially when compared to the great diversity of floral form found in genera of similar evolutionary

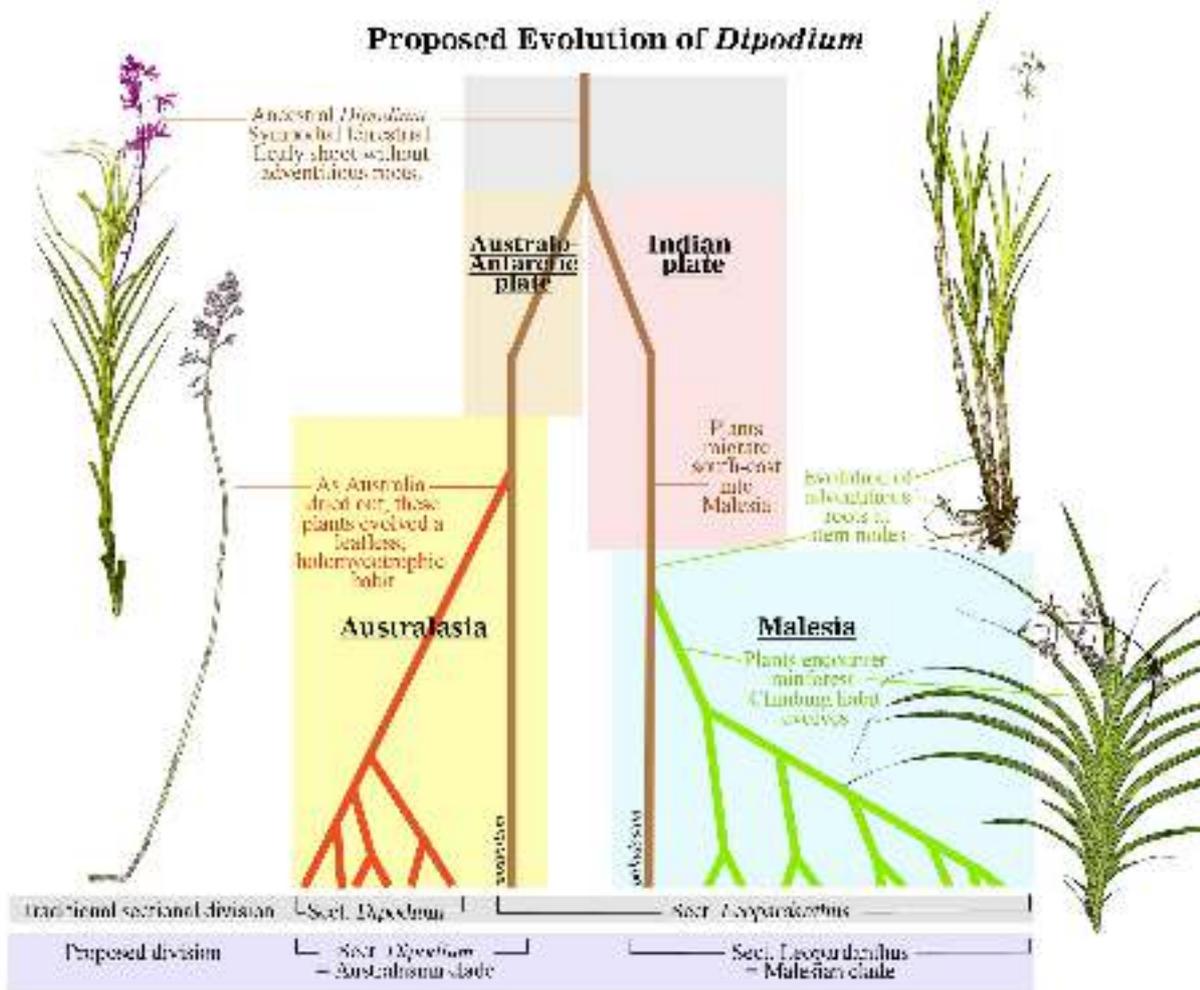


Fig. 5. Diagram summarising the proposed evolution of *Dipodium*, the development of different plant habits, and the infrageneric division into sections.

age, such as *Dendrobium*. Despite the long period of geographically-enforced separate development, there is hardly any difference in the flowers of the Australasian and Malesian clades. The simplest explanation for such highly conserved floral morphology is that from an early stage in its evolutionary history, the ancestral *Dipodium* was producing flowers that were a perfect match with its pollinator and neither flower nor insect have undergone major external changes since then.

This does not mean that there has been no evolution of floral form since the time of the ancestral *Dipodium*, just that the evolutionary changes have been minor. The only visible difference between flowers of the Australasian and Malesian clades is the colour of the column apex. No species in the Australian clade have a yellow column apex, while most species in the Malesian clade (and all the successful ones) have a bright yellow column tip (Fig. 6). The evolutionary paths of the pollinating insects in Australasia and Malesia have diverged, but only slightly. The *Dipodium* species in the two

areas have co-evolved along with the pollinators, resulting in a minor floral difference in flower colour between the two clades. The highly-conserved yellow column apex in the Malesian clade must be a pollinator-attractant, while the pollinators of the Australasian clade do not require yellow on the column to attract them to the flowers.

The pollinators in *Dipodium* are not known, but there are two relevant records, both from Australia. Bernhardt & Burns-Balogh (1983) reported the removal of pollinia from *Dipodium punctatum* (Sm.) R. Br. by a female leafcutter bee (*Chalicodoma derelicta*) and Jones (1988) observed wasps removing pollinia from *D. stenochilum* O. Schwarz. Note that removal of pollinia does not automatically equate with being a pollinator; Ling (2011) and Ong (2011) both report stingless bees (*Trigona sarawakensis*) collecting pollinia from orchid flowers without causing pollination.



Fig. 6. Most species in the Malesian clade have a bright yellow column tip. Left to right: *Dipodium bicallosum* J.J.Sm., *Dipodium purpureum*, *Dipodium conduplicatum* J. J. Sm.

It is possible to write a list of characters that the pollinators of *Dipodium* must possess:

- A medium to large size flying insect that is long-lived and travels long distances.
- Belongs to an old insect group that currently occurs throughout Malesia and Australasia.
- Possesses some degree of colour vision.

Solitary bees (*eg.* leafcutter bees) and solitary wasps (*eg.* parasitoid wasps of subfamily *Eumeninae*) fulfill the criteria for being pollinators in *Dipodium*. Honeybees (*Apis* sp.) and bumblebees (*Bombus* sp.) are excluded because they are not native to Australia.

Unusually in *Orchidaceae*, flower colour is a conserved character in all *Dipodium* species except for *D. pandanum* (O'Byrne, 2011). Furthermore, most species share the same colour palette; white to cream tepals with pink to purple spots. Several species have yellow tepals with red spots. Only a small number of species deviate from these colour palettes and they are all rare, *i.e.* not very successful. This level of colour-conservation must be linked to pollinator-attraction. It also implies that the pollinators are likely to be attracted to and capable of pollinating, different *Dipodium* species. This means that hybrids between *Dipodium* species should occur; the remaining part of this paper deals with this issue.

### New Guinea and the *Dipodium pandanum* complex

The island of New Guinea has 5 *Dipodium* species. *Dipodium elatum* J. J. Sm. is in section *Dipodium*; the other 4 species are in section *Leopardanthus* and arrived in New Guinea from Malesia. One of these, *Dipodium brevilabium* Metusala & O'Byrne, occupies an isolated position in the section, while the other three form

the *Dipodium pandanum* complex. The species involved are *D. fevrellii* J. J. Sm., *D. pandanum* Bail. and *D. brassii* O'Byrne (in prep.). Their distributions are shown in Fig. 7. *Dipodium* section *Leopardanthus* would have reached New Guinea by island-hopping to the south-east (from modern-day Maluku) while the island was being pushed in the opposite direction.

New Guinea arrived at its present position only recently in geological time, having been pushed to the north-west by the northward drift of Australia. The Louisiade Archipelago, which was originally part of mainland New Guinea, got left behind and became a chain of isolated islands.

*Dipodium brassii* is the only species found in the Louisiade Archipelago and is endemic there. Although it is possible that it arose *in-situ* by reversion, its glabrous midlobe flanks are caused by a fundamentally different bud-development to the other New Guinea *Leopardanthus* taxa, all of which have hairy midlobe flanks. It is more likely that the ancestor of *D. brassii* island-hopped to New Guinea from the north-east and occupied the whole island before the Louisiade Archipelago became isolated. *Dipodium brassii* (or its immediate ancestor) was probably the first *Leopardanthus* to reach New Guinea and although it has been replaced by more vigorous competitors on the mainland, it has survived on isolated islands that the competitors never reached.

O'Byrne (in prep.) shows that *Dipodium fevrellii* is widely distributed across the Malesian islands (Fig. 7). It is one of the most easily recognised species in the section, with red-spotted bright yellow sepals and petals (Fig. 8) and a red-marked white midlobe which has stiff bristle-like hairs on its flanks. (Fig. 9). In New Guinea, it is found only in the west of the island, where it is often hard to distinguish from the rather variable

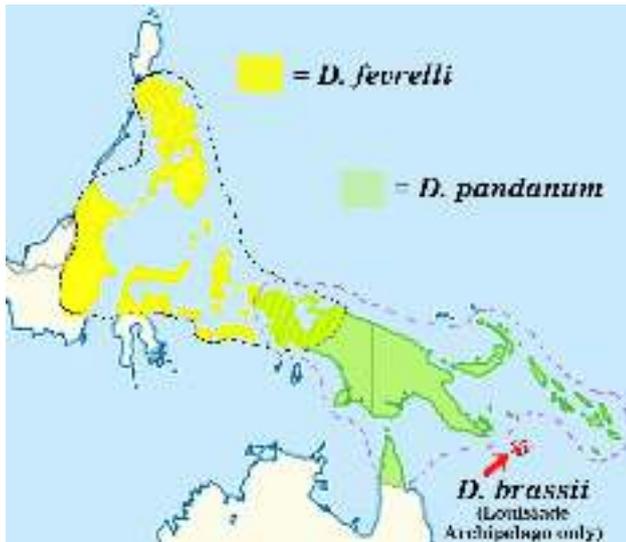


Fig. 7. Map showing the distribution of the three species in the *Dipodium pandanum* complex.

*Dipodium pandanum*. *Dipodium pandanum* is the most common section *Leopardanthus* in New Guinea. It is unique in the genus because of the variation in tepal colour (Fig. 10). Since flower colour is a conserved character in all other *Dipodium* species, this level of colour variation points to a hybrid origin for *D. pandanum*. The species also shows variation in sidelobe length and an abnormally high degree of variation in the quantity and nature of hairs on the midlobe flanks and the simplest explanation for this is hybridization between a species with glabrous flanks and another with hairy flanks. There are only two possible parents of this hybrid; *D. brassii* (purple-spotted creamy-white tepals, short side lobes, glabrous



Fig. 8. *Dipodium fevrellii*. Photo by R. Kusumawati.

midlobe flanks) and *D. fevrellii* (red-spotted yellow tepals, long sidelobes, hairy midlobe flanks).

A hypothetical scenario that accounts for these observations is that *D. brassii* occupied New Guinea before the Louisiade Archipelago became isolated and before the relatively young volcanic island chain of New Britain, Bougainville and the Solomon Islands emerged. After the Louisiade Archipelago became isolated, *D. fevrellii* (or its immediate ancestor) invaded New Guinea from the west. Since the two species have the same pollinators, they hybridized, forming *D. pandanum*. The hybrid displaced both parent species and occupied New Guinea, later spreading through a newly emerged New Britain to Bougainville and the Solomon Islands and (only recently) crossing the Torres Straits to Australia. *Dipodium fevrellii* has probably invaded New Guinea several times, each time hybridizing with



Fig. 9. The lip of *Dipodium fevrellii*. Arrows point to the rows of bristle-like hairs. Photo by R. Kusumawati.



Fig. 10. Variation in tepal colour in *Dipodium pandanum*. A: Solomon Islands, photo by P. J. Cribb. B: *alba*-form, Indonesian Papua, photo by F. Handoyo. C: Indonesian Papua, showing the influence of *D. fevrellii*, photo by E. F. de Vogel. D: Papua New Guinea, photo by P. O'Byrne.

the native *Dipodium* population. The existence of pure-form *D. fevrellii* in the west of the island is an unhybridized population from the most recent invasion. The cline of *D. pandanum* forms that is found from west to east is due to the percentage of *D. fevrellii* in the population; plants in the west have the highest percentage and thus the most bristles amongst the hairs on the midlobe; plants in the Solomon Islands have the lowest percentage, and thus the midlobe flanks are covered in long soft hairs, not bristles. Fig. 11 shows some of the lip variation in *D. pandanum* and the lips of both parents.

Although *D. pandanum* may be of hybrid origin, it has been in existence for a long time, has a widespread population and is stable in the eastern part of its range. Therefore, this paper does not propose any taxonomic change to its specific status. In the western part of the range, the population seems to contain many F<sub>2</sub>, F<sub>3</sub> (*etc.*) hybrids, which cannot be readily distinguished from each other, or from the putative parents. It is beyond the scope of this paper to resolve their status, so they are all treated as *D. pandanum*, but their existence is noted. For similar reasons, this paper does not propose to change the specific status of *D. fevrellii*. The species is widespread and easily-recognised across the whole of its range except in western New Guinea, where repeated hybridization events apparently caused it to merge with *D. pandanum*. If it were reduced to synonymy under *D. pandanum*, it would become impossible to identify these hybrids; it makes no taxonomic sense to make such a change.

#### **Java & the *Dipodium scandens* – *D. pictum* complex**

*Dipodium scandens* (Bl.) J. J. Sm. and *D. pictum* (Lindl.) Rchb. f. are the two earliest names in section *Leopardanthus*. Both species are confined to West Java, where *D. pictum* is known only from the type and *D. scandens* is still found in scattered populations (O'Byrne, in prep). Both species have been widely misinterpreted, partly because of poor protologues (*D. pictum* is a mixture), but also because a hybrid between the two species is more common than either parent. In books and photos of Javanese orchids, this hybrid has invariably been referred to as "*D. pictum*". The confusion probably originated with J. J. Smith (1924), who illustrated 2 different taxa under *D. pictum*, but chose the wrong one for publication. The published illustration shows the hybrid; the unpublished one is *D. pictum*.

*Dipodium scandens* and *D. pictum* have totally different flowers, different lip shapes and different stipes. The hybrid, *Dipodium javanicum* (O'Byrne, in prep), is intermediate between the parents in each of these (Fig. 12). It is being described at specific status because it has formed a stable population that has been in existence for at least one hundred years.

There are other, unknown taxa in the Javanese complex. The photograph in Comber (1990) labelled "*D. scandens*, West Java, 820 m." shows a taxon from Gunung Halimun that is neither *D. scandens* nor *D. javanicum*. It probably represents another hybrid; the influence of *D. scandens* on the lip shape is clear. I have seen no herbarium material that matches this photo.

#### **Borneo**

The Australasian section *Dipodium* never reached Borneo; here, all taxa belong to section *Leopardanthus*. Apart from a few distinct, uncommon (*i.e.* not very successful) species, the situation in Borneo is extremely complicated. The best-known species is *Dipodium purpureum* J. J. Sm. (Fig. 13), but *D. fragrans* O'Byrne & Vermeulen (Fig. 14), *D. paludosum* (Griff.) Rchb. f. (Fig. 15) and *D. puspitae* O'Byrne (in prep) (Fig. 16) are also widespread across the island, while pockets of *D. fevrellii* can be found in the east. All these taxa probably share the same pollinators and should be capable of interbreeding. It is hardly surprising that many Borneo *Dipodium* specimens cannot be placed under any of these existing names and appear to be intermediates between two or more of these species. With the few exceptions mentioned above, *Dipodium* in Borneo is in a state of population-flux, with new populations constantly emerging, then inter-breeding with neighbouring populations to produce new hybrids. This has probably been going on for tens or hundreds of millennia, with frequent invasions of species from neighbouring territories preventing the emergence of a stable population. O'Byrne (in prep) attempted to produce a specific level taxonomy using traditional morphological methods, but the results are unsatisfactory; it will require an inspired DNA analysis to fully resolve the relationships between these constantly changing populations.

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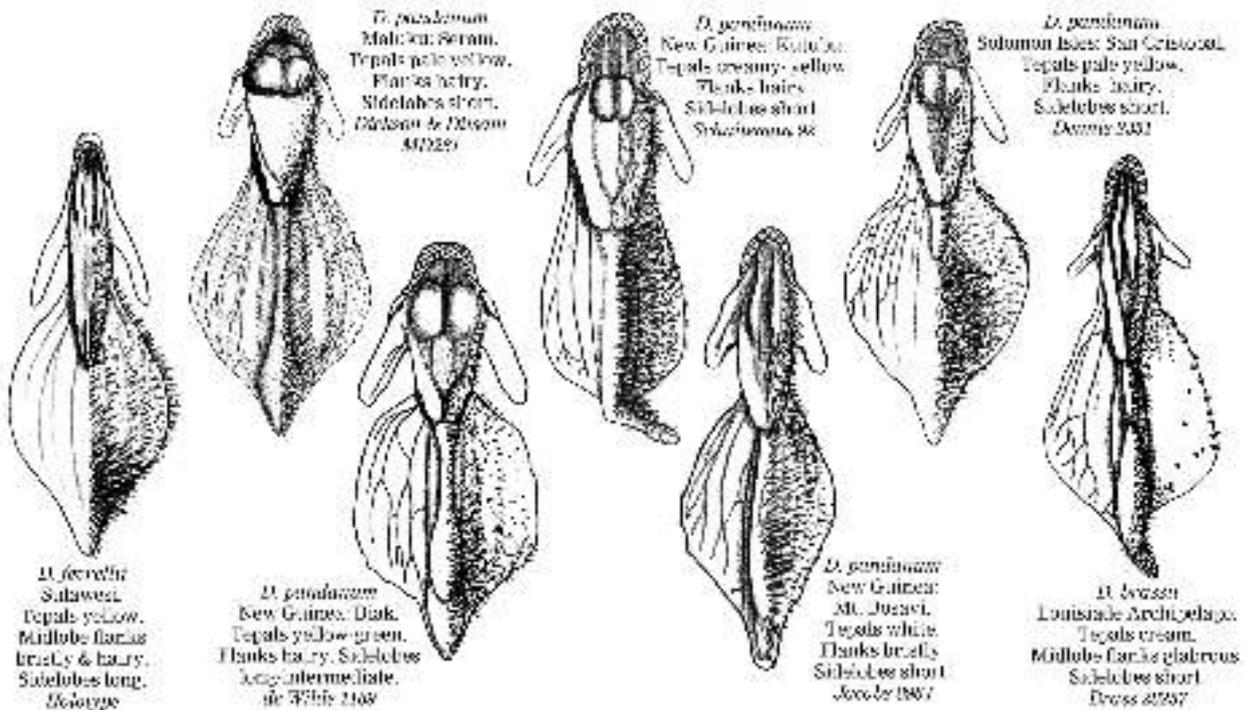


Fig. 11. Lip variation in *D. pandanum*, and the lips of *D. fevrellii* and *D. brassii*.

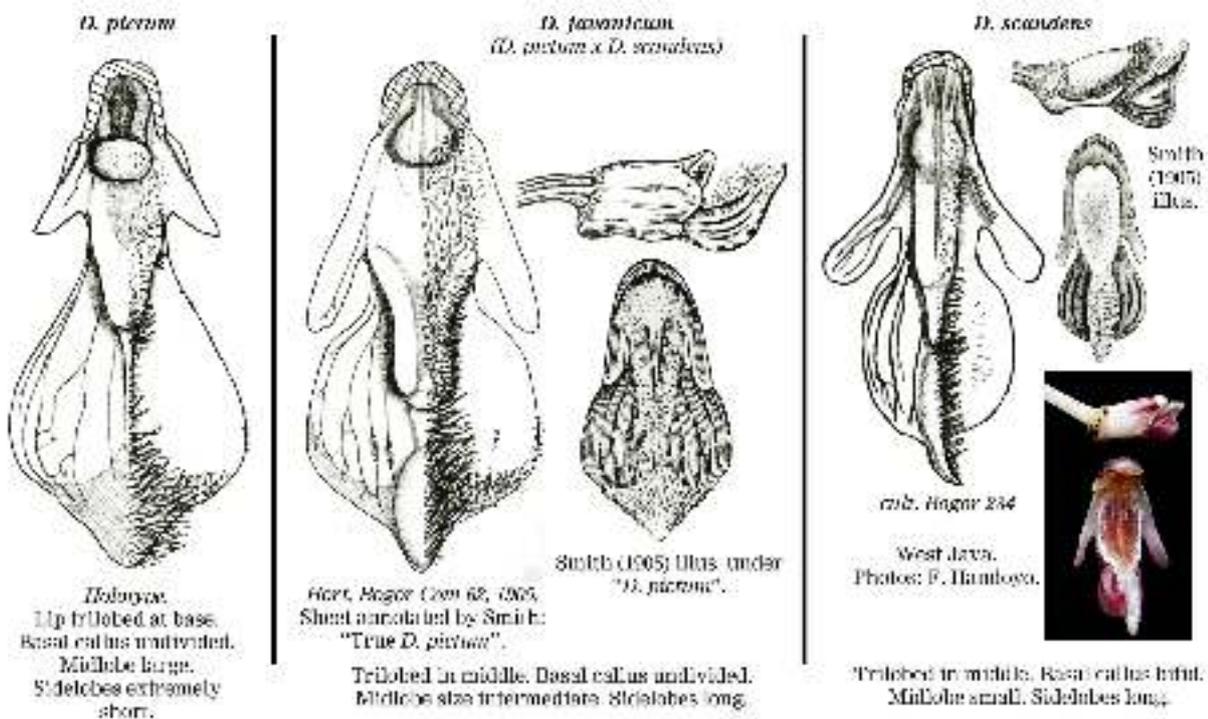


Fig. 12. Lip and column of *Dipodium javanicum*, lip of *D. pictum*, lip and column of *D. scandens*. Four of the drawings after Smith (1905). Photos by F. Handoyo.



Fig. 13. *Dipodium purpureum* from Sabah, Borneo.



Fig. 14. *Dipodium fragrans* from Central Kalimantan, Borneo. Photo by F. Handoyo.



Fig. 15. *Dipodium paludosum* from Pahang, Peninsular Malaysia.



Fig. 16. *Dipodium puspitae* holotype from Jambi, Sumatra. The flowers of this species are hard to distinguish from *D. paludosum*; the most obvious differences are in plant habit.

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