THE GENUS POTHOS L. (ARACEAE–POTHOEAE)
IN NEW GUINEA, SOLOMON ISLANDS AND AUSTRALIA

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SUMMARY

The genus *Pothos* L. is revised for the Australasian region. Twelve species are recognised. *Pothos albertisii* Engl. and *P. quinquevenosus* Alderw. are reduced to the synonymy of *P. papuanus* Becc. ex Engl.; *P. brevispatha* Ridl. and *P. ledermannii* Engl. & K. Krause are reduced to the synonymy of *P. versteegii* Engl.; *P. elegans* Engl. is reduced to the synonymy of *P. zippelii* Schott, and *P. brownii* Domin is reduced to the synonymy of *P. longipes* Schott. No new names are proposed. Illustrations are provided for previously unillustrated species. Aspects of morphology, architecture, and infrageneric and suprageneric relationships are briefly discussed.

INTRODUCTION

*Pothos* is a mainly tropical genus of about 70 species of climbing aroids occurring principally in the Indomalesian region, with lesser representations in China, western Oceania and Australia. One species, *P. scandens* L., extends from Central Malesia to India and Madagascar (Bogner, 1975). Fifty-three species are currently recognised for the Malesian region (Hay et al., 1995); however, the genus is in need of revision throughout the greater part of its range (but see Nicolson, 1987). *Pothos* was erected by Linnaeus for climbing aroids with bisexual flowers, and subsequently a great many climbing Araceae were brought to form an heterogeneous assemblage in this genus. Schott (1832, 1853) refined it into its present conceptualisation. *Pothos* was last revised as a whole by Engl (1905) who followed Schott (1853, 1860) in dividing it into two subgenera (as sections). Engl further divided the subgenera into a number of sections (as series), which division is not followed here.

Vegetative structure in *Pothos* is complex and, for the majority of species, not well understood (but see Boyce & Poulsen, 1994). Where known, the seedling shoot is filiform with much reduced leaves and long internodes. It is probably skototropic (shade-seeking) until a substrate for climbing is found (cf. Strong & Ray, 1975). Thereafter there is some shortening of internodes and development of foliage leaves. In early stages of establishment on the climbing substrate, juvenile foliage leaves are usually appressed to the substrate and may, in subgenus *Allopothos*, have morphology markedly and abruptly different from the adult form (heteroblasty). Attachment is by means of rather short spreading roots which arise near the nodes on the substrate side. Long, geotropic, feeder roots are also produced which may reach the

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ground. Shoot growth at this stage is monopodial. With maturity, lateral shoots are produced from dormant lateral buds on the monopodial climbing axis. These are generally plagiotropic, or, if apically orthotropic, soon spreading and not adherent. Lateral shoots may be highly ramified, especially in subgenus *Allopothos*, though definition of branch orders may be blurred by irregular apex abortion followed by substitution by irregular numbers of higher order laterals. Architecture in *Pothos* is to be the subject of another paper (Boyce & Hay, in prep.). Stem connection with the ground may be broken as the older parts of the stem die away, though feeder roots maintain soil contact. The climbing plant may therefore come to be defined as a hemiepiphyte, and most species are described as climbing or hemiepiphytic in the descriptions presented here.

The subgenus *Pothos* (section ‘Eupothos’ sensu Engler, 1905) has a remarkable characteristic leaf form shared with the satellite genus *Pothiodium* Schott (Philippines to Moluccas) and unknown elsewhere in the Araceae (though superficially similar conditions are found in some species of the tribe Monstereae, e.g. *Scindapsus perakensis* Hook. f.). In species of subgenus *Pothos* the petiole is highly modified into a flattened photosynthetic structure differing negligibly from the leaf blade in colour, texture, persistence, venation and strength of midrib, except in shape and insofar as the pattern of venation reflects that difference in shape. The leaves of subgenus *Allopothos* are, in contrast, quite ‘conventional’, with a sheathing petiole in which the wings of the sheath are commonly more membranous and shorter-lived than the leaf blade and an axis that is more robust than the midrib. There is also a distinct geniculum (pulvinus) at the apex of the petiole by the activity of which the poise of the blade is adjusted. This is reduced to the slightest articulation in subgenus *Pothos* and here the blade and flattened ‘petiole’ remain aligned during and after expansion.

In subgenus *Pothos* it can possibly be argued that, of external features, only position (between the stem and the ‘true’ leaf blade) and high length to width ratio (but that not in all cases – see *P. versteegii* Engl.) allow one to make this structure homologous to a (sheathing) petiole. The positional criterion is an important one, but the predominant blade-like special quality of the structure concerned indicates that the concept of mixed homology with blade and petiole better describes the homology of the structure than does an attempt at forcing it into one or other category (cf. Hay & Mabberley, 1991, 1994; Mabberley & Hay, 1994; Sattler, 1984, 1994). Use of the term petiole here requires one to acknowledge that the category ‘petiole’ is a fuzzy set (Rutishauser, 1993), with a blurred conceptual interface between it and (in this instance) ‘leaf blade’. This structure deserves detailed developmental study. It is, one is merely able to speculate at this stage, possibly an example of some sort of homoeotic transformation whereby the combination of developmental processes pertaining to leaf blade came not only to act out as the blade *per se*, but also to act out with positioning normally associated with the developmental process combinations (cf. Sattler, 1988, 1992) pertaining to petiole, which are themselves to some degree suppressed.

Inflorescence position is usually fairly constant within aroid genera and usually quite constant within species. However, there is a very considerable range of inflorescence position in both subgenera of *Pothos*, and quite frequently within species. There is a variably marked differentiation between sterile, adherent, monopodial, orthotropic, climbing shoots and fertile, free, monopodial or sympodial, plagiotropic,
often pendent lateral shoots. Such lateral shoots may flower terminally with a single inflorescence subtended by the last foliage leaf of the shoot and no cataphylls. This is apparently the usual case in *Pothos (Allopothos) rumphii* Schott. *Pothos (Allopothos) polysystachys* Engl. & K. Krause, and to a less well-developed extent *P. (Allopothos) cuspidatus* Alderw., show a complex, lax, leafless flowering branch system borne on the ends of much ramified leaf-bearing branches, while species such as *P. (Pothos) scandens* (which does not occur in the Australasian region) seems consistently to produce single lateral inflorescences subtended by cataphylls, arising in the axils of foliage leaves.

Several species in the Australasian region appear variable as to the position of inflorescence, often with different arrangements on the same plant. *Pothos (Allopothos) brassii* B.L. Burtt is similar to *P. rumphii* in inflorescence position, but there may follow from out of the axil of the same subtending leaf base a second inflorescence bearing at the base of its peduncle a prophyll and one or more cataphylls. This second inflorescence may appear several months after the first. In *P. (Pothos) longipes* Schott, *P. (Pothos) papuanus* Becc. ex Engl., *P. (Pothos) hellwigii* Engl. and *P. (Pothos) zippelii* Schott there are instances where free lateral leafy shoots flower terminally without the peduncle bearing cataphylls. Then there are specimens where apparently terminal inflorescences on such shoots are subtended by cataphylls, suggesting that there may have been a truly terminal inflorescence in a previous season, or that the apex aborted (which appears to be a common occurrence in vegetative growth). In these same species there are also instances where inflorescences arise, subtended by cataphylls, in the axils of leaves well below the shoot apex and where inflorescences arise in the axils of the cataphylls and themselves bear cataphylls forming a short sympodial (foliage-) leafless flowering branch system. [A similar mode of inflorescence presentation has recently been documented for Bornean *P. (Allopothos) insignis* Engl. (Boyce & Poulsen, 1994).] In short there is great plasticity of branch system organisation in these species. This is taken further in *P. (Allopothos) falcifolius* Engl. & K. Krause in which inflorescences may be terminal on leafy shoots, may be borne in leaf axils subtended by cataphylls, may form short, sympodial, leafless flowering branch systems borne on leafy branches, or there may be apparently long-lived, perennial, leafless, dense but much-ramified flowering branch systems, each consisting of multiple sympodia, which arise (or persist until) on old, by now bare, lower parts of the shoot system, in a form of cauliflory. In this species, there is a reduction in inflorescence size corresponding to increase in complexity of the inflorescence branch system.

*Pothos* is rather uniform in floral morphology, and the only polytypic aroid genus to adhere for the most part to 'typical monocotyledonous' trimery, with six free tepals, six free stamens and a trilocular ovary with uniovulate locules. However, *P. falcifolius* has the tepals connate, with the flowers somewhat sunken in pits on the spadix, and four stamens (I have not seen material adequate for observation of the division of ovary). Flowers with connate tepals have also been reported for *P. remotiflorus* Hook. (Sri Lanka) by Nicolson (1987), who points out that this weakens one of the main distinguishing features of the very closely allied (to subgenus *Allopothos* – see also Grayum, 1992) *Pedicellarum* M. Hotta (Borneo). According to Boyce (pers. comm. – an account is in preparation) the very closely allied (to subgenus *Pothos* – see also
Grayum, 1992) *Pothoidium* has 6-stamine flowers, or occasionally shows reduction to a single whorl of three stamens, or the stamens are absent. The ovaries are unilocular or, in spadices with well-developed anthers, abortive and it appears that the plants may be functionally dioecious. The distal inflorescences of *Pothoidium* flowering branch systems also often have the spathe suppressed (Engler, 1990).

*Pothos* species in the Australasian region show a crowded arrangement of flowers on the spadix, typical for the Araceae, but in species of subgenus *Allopothos* 'series' *Goniuri* (sensu Engler, 1905), such as *P. remotiflorus*, *P. beccarianus* Engl. (Borneo) and *P. luzonensis* (Presl) Schott (Philippines), the flowers are distant. *Pedicellatum* not only has the flowers distant on the spadix, but also elevated on short pedicels - a feature unknown in any other bisexual-flowered aroid. Since in both *Pothos* series *Goniuri* and in *Pedicellatum* the flowers are bractless, as is characteristic of the family, it would seem that these conditions are derived, representing the 'drawing out' of the compact spadix of crowded sessile bractless flowers. It would be interesting to discover whether the phenoology of these examples of very loose spadices is similar to that in *Pothos* species with dense spadices (and in Araceae in general) where the entire spadix is first in female anthesis and then in male, rather than having each flower proceeding through anthesis individually (see Hay & Mabberley, 1991).

*Pothos brassii* and *P. hellwigii* have short blunt spadices (spherical in *P. hellwigii*) and anthesis takes place basipetally. In *P. longipes*, where the spadix is relatively long and tapering, anthesis is acropetal (sometimes amphipetal?) [cf. Araceae—Lasieae where basipetal spadix maturation is universal, as far as is known, regardless of spadix shape (Hay & Mabberley, 1991; Hay, 1992) and *Anthurium* where acropetal, amphipetal (from the middle) or diffuse maturation occur with some correlation to spadix shape (Croat, 1980)].

A note on dimensions: some species (especially of subgenus *Pothos*) may show much range in overall leaf size and petiole to blade ratio. Measurements given are taken from flowering lateral (non-adherent) shoots, focussing on the most developed leaf (i.e. with the largest blade), which is usually situated near midway between the base and the apex of the shoot. Basal and distal leaves on non-adherent shoots may be smaller in size and have larger petiole to blade ratios, while leaves on vigorous adherent shoots (which are not usually represented in herbarium material) may be considerably larger overall.

**POTHOS**

Rather to very slender, occasionally robust, often hemiepiphytic root-climbers usually with rather clearly differentiated, adherent, non-flowering and free flowering shoots, the latter of which may be highly ramified; flagelliform, leafless (cataphyll-bearing), skototropic 'foraging' shoots often produced; juvenile plants sometimes shingle-leaved (in subg. Allopothos; juveniles not described for most species and this feature not yet recorded for Australasian Pothos); internodes (except at beginning of branches) much longer than thick, with the nodes on free shoots occasionally bearing rudimentary roots hardened into spines; leaf blades simple, entire, very narrowly lanceolate to broadly ovate, often asymmetrical (subg. Allopothos), with reticulate venation, the primary lateral veins crossed on each side of the midrib within the margin by one or more intramarginal veins running ± from the base of and from about midway along the midrib to the apex or first to the distal margins and then to the apex; petiole either with a narrow, ± clasping membranous sheath and a conspicuous apical geniculum (subg. Allopothos), or broad, flattened and lamina-like and with a small apical articulation (subg. Pothos); inflorescences solitary and terminal on leafy branches or more usually arranged on lateral short shoots subtended by cataphylls, the short shoots usually simple with a single inflorescence or sometimes elaborated by sympodial branching into usually (foliage-)leafless, sometimes highly complex, compact or lax synflorescences bearing two to many inflorescences simultaneously or sometimes single inflorescences in series, synflorescences borne at the end of leafy branches or, when long-persistent, on older leafless parts of the stem (?sometimes arising there); spadices sessile or stipitate, tapering-cylindrical to spherical; spathes mostly rather inconspicuous, ovate to lanceolate, opening wide and held away from the spadix, often fully reflexed, white to green to purple-brown; flowers bisexual, with a perianth of usually 6, rarely 74, free tepals or the perianth completely united and the flowers sunken in pits on the spadix with the perianth forming an operculum, open in the centre, over the pit; stamens 6, rarely 4 (P. falcifolius), with flattened filaments and extrorse dehiscence; ovary trilocular, the locules uniovulate; stigma punctate, mostly sessile; fruit a 1–3-seeded berry ripening mostly yellow through to red, individually distinct and, relative to spadix, very large; seed large, exalbuminous; embryo macropodous.

Distribution — About 70 species, from Madagascar to Indomalaysia, China, Oceania, and Australia.

Habitat — Mainly forest climbers from the lowlands to lower and mid-montane zones, in closed forest and in regrowth, but also sometimes lithophytic.

KEY TO THE SPECIES

1a. Petiole blade-like, without a sheath and with a slight apical articulation with the blade, occasionally much reduced (Subgenus Pothos) .......................... 2
b. Petiole sheathing for much of its length, conspicuously geniculate at the apex (Subgenus Allopothos) .......................................................... 8

2a. Petiole less than one sixth of the length of the blade .......... 6. P. versteegii
b. Petiole over one quarter of to exceeding the length of the blade .......... 3

3a. Spadix ± spherical ................................................. 4
b. Spadix ovoid to cylindrical ...................................... 5
4a. Apex of peduncle abruptly expanded at union with spadix  8. P. clavatus
b. Peduncle gradually thickened along its length .............. 7. P. hellwigii
5a. Spadix ovoid ...................................................... 6
b. Spadix cylindrical ................................................ 7
6a. Blade very narrowly lanceolate, c. 5 mm wide; spadix c. 3 mm diam. .......................... 12. P. gracillimus
b. Blade more or less elliptic, c. 1–3 cm wide; spadix c. 7 mm diam. .......................... 11. P. zippelii
7a. Spadix stipitate (very rarely sessile); petiole usually longer than the blade; Australia ......................... 9. P. longipes
b. Spadix sessile (very rarely stipitate); petiole usually shorter than to equalling the blade; Papuasia ..................................................... 10. P. papuanus
8a. Spadix stipitate (rarely sessile in P. rumphii which can then be distinguished by its robust dimensions) ................................................. 9
b. Spadix sessile ...................................................... 10
9a. Tepals free; robust plants with leaf blades to c. 50 cm long, broadly oblong-ovate; spadix to c. 17 cm long; inflorescence solitary, terminal 1. P. rumphii
b. Tepals united; leaf blades to c. 20 cm long, rather narrowly oblong-ovate; spadix to c. 4 cm long; inflorescences solitary or variously clustered, terminal or lateral ........................................... 5. P. falcifolius
10a. Inflorescences multiple, borne on lax (foliage-)leafless sympodial branch systems ......................................................... 3. P. polystachyus
b. Inflorescences solitary or paired, rarely few together ........................................... 11
11a. Inflorescence subtended by a bract held free of the proximate foliage leaf; spathe lanceolate, acuminate; New Guinea ........................................... 4. P. cuspidatus
b. Inflorescence not subtended by a bract, or bracts ± completely enclosed within the sheath of the proximate foliage leaf; spathe ovate, mucronate; Australia ........

Subgenus Allopothos


1. _Pothos rumphii_ Schott


Very robust and vigorous, sometimes smothering, moderately ramified climber reaching into the crowns of canopy trees, with rather poor differentiation between adherent and flowering shoots; leaf blades pendulous, rich green, glossy above, elliptic to oblanceolate, to very broadly ovate, c. 15–50 cm long, the tip somewhat acuminate to obtuse, ultimately with a flexuous filiform micro, the base acute to narrowly cordate; primary lateral venation diverging at c. 60–80°, crossed by usually three intramarginal veins on each side of the midrib, these arising from near the base of the midrib and running more or less to the leaf tip; petiole about half the length of the blade, sheathing almost or fully throughout its length to the geniculum, the wings of the sheath rather broad, persistent; inflorescence solitary, terminal, not subtended by cataphylls; peduncle about equalling the petiole of the subtending leaf, most of it within the sheath at flowering; spadix brownish green at flowering, long-cylindrical, c. 17 × 0.5 cm (fl., fresh), usually conspicuously stipitate with the stipe to c. 4 cm long, occasionally sessile or nearly so; spathe green, narrowly lanceolate, distally somewhat twisted, membranous, somewhat exceeding the spadix; flowers c. 2.5 mm diam., with 6 free tepals and 6 stamens; fruiting spadix considerable elongated, to c. 25 cm long, pendulous, often twisted; fruits ovoid, to c. 2.5 cm long, scarlet.

Distribution — Philippines and Celebes to Moluccas, New Guinea, Solomon Islands and Vanuatu. I observed this species in Vanuatu in 1989, but I am not aware of any herbarium material. Allied taxa further west (to Sumatra) may be conspecific with this. Although very widespread and common east of Wallacea, this species is not found in Australia.

Habitat — In lowland rain forest and regrowth. In New Guinea it is very common in the lowlands, especially in disturbed forests, often almost completely covering trees and hanging to the ground.

2. *Pothos brassii* B.L. Burtt — Fig. 1

Type: Australia, Queensland, Slopes of Thornton Peak, 15-iii-1932, *Brass 2311* (K holo; BRI iso).

Fig. 1. *Pothos brassii* B.L. Burtt (*Hay 7053*). a. Flowering branch; b. venation; c. apex of spadix; d. flower. — Scale: bar: to a = 2 cm; to b & c = 5 mm; to d = 2.5 mm.
Slender, not highly ramified, hemiepiphytic rain forest and gallery forest climber on the lower parts of trees and on rocks, the branchlets having the leaves arranged very obviously in two ranks; leaf blade elliptic, slightly to distinctly falcate, c. 12 × 5 cm, the midrib impressed above; leaf base acute to obtuse, minutely auriculate; primary lateral veins diverging at c. 60–80°, subparallel, running into an intramarginal vein c. 8 mm from the margin and a submarginal vein c. 3 mm from the margin; petiole shorter than the blade, sheathing for most of its length with the sheath usually not quite reaching the geniculum; wings of sheath more or less persistent, eventually becoming fibrous; inflorescence solitary or paired, terminal on leafy ultimate branchlets; peduncle exceeding the petiole of the subtending leaf, green (drying black), with c. 4 short cataphylls at its base (from the axil of one of which the second inflorescence may arise) usually hidden in the leaf sheath, or the first inflorescence without cataphylls and the second arising (with a minute prophyll and short cataphylls) in the axil of the subtending leaf; spathe reflexed, green, broadly ovate, c. 2 cm long, the tip mucronate for c. 3 mm; spadix sessile, with the base of the spathe margins somewhat decurrent (c. 3 mm) on the peduncle, oblong-ovoid, ivory white, to c. 2 cm long (fresh); flowers c. 1.7 mm diam., with 6 free tepals and 6 stamens, with the anthers fully exserted from the tepals at and after anthesis; fruit ovoid, orange to orange-red, c. 1.3 cm long.

Distribution — Australia, endemic to and locally common in tropical Queensland between Daintree and Bellenden Ker.

Habitat — In rain forests from the lowlands to c. 1200 m altitude.

Note — Seedlings are recorded as thread-like, with a series of gradually larger leaves. Juveniles are observed not to have a shingle-leaved phase, but to succeed gradually to adult leaf form.

Selected other specimens seen — AUSTRALIA. Queensland, Daintree River, Brass & White 278 (BRI, K, LAE); Noah Point, Cape Tribulation National Park, Hay 7053 (NSW); Daintree River, Flecker 7071 (BRI, QRS); McDowell Range, Hyland 3792 (BRI, QRS); E slope of Mt Bellenden Ker, Hyland 5351 (BRI, QRS); VCL Noah, Hyland 8287 (BRI, L, LAE, QRS); between McDowell Range and Bloomfield, Gold Hill nr China camp, Tracy 14800 (BRI, QRS); McDowell Range, between Daintree and Bloomfield Rivers, Webb & Tracy 10855 (BRI, K, L).


Tall slender climber or hemiepiphyte; leaf blades lanceolate, somewhat oblong and falcate, rather stiff, the tip acuminate, the base acute, c. 12–16 × 2–4 cm; petiole 2–5 cm long, prominently geniculate at the apex, sheathing for most of its length, the sheath persistent; primary lateral veins diverging at c. 30–60°, intramarginal veins one on each side of the midrib, submarginal; inflorescence a lax, compound, much-ramified, sympodial synflorescence, the modules consisting of a prophyll, 3 or 4 cataphylls, a terminal inflorescence and a relay bud in the axil of the last cataphyll — the lower cataphylls sometimes with similar modules in their axils; synflorescence cataphylls lanceolate, 6–12 mm long; peduncle very slender, c. 2–4 cm long, subtended by a cataphyll almost as long; spathe 3.5–4 cm long, ovate-lanceolate, acumi-
Fig. 2. *Pothos cuspidatus* Alderw. (*Lam* 1566). a. Fruiting branch; b. vegetative branch; c. venation; d. infructescence. — Scale bar: to a & b = 2 cm; to c & d = 1 cm.
nate, about twice the length of the spadix; spadix sessile, cylindrical, to c. 2 cm long, c. 3 mm diam. (fl., dry); flowers c. 1.6 mm diam.; tepals 6, free; stamens 6; fruit globose, c. 5 mm diam.

Distribution — Northeastern New Guinea; known only from the type collection. Habitat — Lower montane rain forest.

Notes — 1. This species is evidently closely related to P. cuspidatus (q.v.), differing in the less markedly cuspidate leaf and spathe, the somewhat longer spadix, the smaller globose fruit and in the much-ramified synflorescence.

2. The illustration cited above shows a rather more highly ramified synflorescence than that in the type specimen. Possibly there was a second sheet which did not survive the wartime damage to Berlin.

4. Pothos cuspidatus Alderw. — Fig. 2


Very slender, highly ramified climber or hemiepiphyte, the branchlets having the leaves interspersed with a greater number of cataphylls; leaf blades ovate-lanceolate to lanceolate, rather abruptly acuminate into prolonged 'drip tips', the base acute to somewhat obtuse, highly variable in size on a branch, c. 6–12.5 × 1.5–4 cm (sometimes much smaller on ultimate branchlets); primary lateral veins diverging at 45–75°, intramarginal veins one on each side of the midrib, submarginal; petiole slender, about 1/4 the length of the blade, to 2.5 cm long, very narrowly sheathing to the geniculum; inflorescence solitary, terminal on ultimate leafy branches but subtended by one or more narrow cataphylls to 1.7 cm long; peduncle very slender, 1–2 cm long; spadix sessile, oblong, to 1 × c. 0.3 cm (fl., dry); spathe ovate below, subulate, to 3 × 0.4 cm; flowers c. 1.6 mm diam., with 6 free tepals and 6 stamens; fruit elongate-obovoid, 1–1.2 × c. 0.5 cm (dry).

Distribution — Known only from northern Irian Jaya in the Idenburg River area. Habitat — The lower montane zone (presumably in forest). Further details are lacking.

Note — Close to P. polystachyus. Similar features to those which distinguish P. polystachyus and P. cuspidatus are found together in P. falcifolius (q.v.), with intermediates in that case. Further collections may allow the former two poorly known species to be united.

Other specimen seen — INDONESIAN NEW GUINEA. Idenburg River, Bernhard Camp, Brass 12100 (L).

5. Pothos falcifolius Engl. & K. Krause — Fig. 3


Moderately robust hemiepiphytic climber often with root-thorns at the nodes; leaf blade ovate to elliptic to elliptic-lanceolate, somewhat falcate when narrow, mid-
Fig. 3. *Pothos falcifolius* Engl. & K. Krause (Mack 509). a. Fruiting branch showing 'cupular' perianth; b. vegetative branch; c. venation. — Scale bar: to a & b = 2 cm; to c = 1 cm.
dark green abaxially and adaxially, rather stiffly chartaceous, 10–28 cm long, 2–11 cm wide, the tip acute to gradually or abruptly acuminate, the base acute to obtuse to somewhat auriculate; midrib clearly off-centre, prominent abaxially, flush or impressed adaxially, primary lateral veins diverging at 45–85°, intramarginal veins 1 or 2, continuing more or less the length of the blade from the base or running to margin and replaced by another about midway up blade; petiole 2.5–9 cm long, sheathing up to or just short of the geniculum, sheath persistent; inflorescence solitary and terminal on free leafy shoots or on sympodial, leafless, cataphyll-bearing, simple branch systems borne among the leaves (initially?) to (later?) complex ?perennial branch systems borne on older parts of the stem; spadix 2–4 cm long, c. 2 mm diam. (fl., dry) to c. 6 cm long and c. 7–8 mm diam. (fr., dry), tapering; spathe white, oblong-lanceolate, deflexed, usually persisting into fruit, c. 2.3–7 cm long; flowers c. 1 mm diam., somewhat distant, sunken in pits in the spadix, perianth united into an operculum with a central pore over the floral pit; stamens 4, the anthers at the mouth of the perianth at anthesis; fruiting perianth c. 4–5 mm diam., spreading, with the margins split into irregular segments, forming a cupule beneath the fruit; fruit with watery pulp, ovoid to subcylindric, 1–2 cm long, ripening yellow through orange to dark red; seed 1 or 2 per fruit, dark brown.

Distribution — Widespread in western parts of New Guinea.

Habitat — Forested areas from the lowlands to mid-montane rain forest up to about 2200 m altitude.

Note — Apparently a rather widespread and variable but under-collected species. The sunken flower with four stamens and the perianth united into an operculum, markedly asymmetric leaf blades and the spines formed at the nodes from adventitious roots are distinctive. The latter character is otherwise known only in Pothos armatus C.F.C. Fisch. (NW India).

Other specimens seen — INDOONESIAN NEW GUINEA. Japen-Biak, Sumberbaba, nr Serui, Aet & Idjan 841 (L); Idenburg R., 6 km SW of Bernhard Camp, Brass 13030 (L); Wondiwoi Mts, Wandammen Peninsula, BW 13337, BW 13634, BW 13712 (all L); Sorong, Main 443 (L); Vogelkop, Tohkiri Mts, Aifat R. valley, van Royen & Sleumer 7245 (L). — PAPUA NEW GUINEA. Gulf Prov., Mt Bosavi, N side, Jacobs 8779, 9483 (both L); East Sepik Prov., Wagu, Ambunti, Hoogland & Craven 10354 (K, L); West Sepik Prov., Amanab, Imonda Patrol Post, LAE 52888 (L, LAE); Madang Prov., Crater Mt, Mack 509 (NSW); Southern Highlands Prov., Habomo Rest House, 6.5 mi W of Mt Ne, Tari, NGF 32077 (L, LAE); Western Prov., Kiunga, NGF 48482 (BRI, K, L, LAE, SING).

Subgenus Pothos


6. Pothos versteegii Engl. — Fig. 4


Fig. 4. *Pothos versteegii* Engl. (*Ledermann 8333*). a. Flowering branch; b. venation; c. articulation of petiole and blade; d. inflorescence and subtending cataphylls; e. flowers. — Scale bar: to a = 2 cm; to b & d = 1 cm; to c = 7 mm; to e = 2.5 mm.

Slender hemiepiphytic climber with free lateral flowering shoots; leaf blades dull green, darker adaxially, narrowly ovate to oblorg to ovate somewhat obovate, very variable in size on a single shoot, absent on early leaves of a sympodial module, to 8–17 × 2–6 cm, the tip somewhat acuminate, the base tapering, acute to slightly retuse; primary lateral veins diverging from the midrib at c. 30–60°, intramarginal veins 1 or 2 (or 3) on each side, where more than one, the first arising near the base of the blade and running distally to the margin, the second arising about midway and running to the tip; petiole flat and lamina-like, linguiform to narrowly lanceolate and up to 6 × 1 cm when blade absent, otherwise very much reduced, 1/6th to 1/20th of length of the blade, to 5 mm wide; inflorescence solitary (at any one time) on leafless, perennial, sympodial, repeatedly-flowering, condensed short shoots in distal leaf axils (these persisting after leaf fall and some inflorescences thus on otherwise naked stem), 1–4 per leafy flowering shoot, subtended by a series of cataphylls, the longest to c. 8 mm long; peduncle slender, to c. 2.5 cm long, mostly rather abruptly (?up)curved near the base; spadix creamy white to yellowish, sessile, subspherical to ovoid, 4–7 × 3–4 mm (fl., dry); spathe creamy white to yellowish, ovate, 2–3 × 4–5 mm, reflexed, tip mucronulate; flowers c. 1.5 mm diam., with 6 free tepals and 6 stamens; fruit red when ripe, small, c. 3.5 × 3 mm, subglobose to ovoid, minutely beaked.

Distribution — Endemic to New Guinea, recorded rather sporadically and not in eastern parts of Papua New Guinea.

Habitat — Lowland to lower montane rain forest.

Note — A species easily distinguished by the very reduced petiole, small spadix and small fruits.

Other specimens seen — INDONESIAN NEW GUINEA. Sande-Flusse, Pulle 360 (L). — PAPUA NEW GUINEA. East Sepik Prov., Ambunti, Wagu, Hoogland & Craven 10404 (LAE); Western Prov., Kiunga, LAE 51738 (L), & 5 mi NW of Kiunga, LAE 51862 (L); Western Prov., Yat, NGF 31973 (LAE); Western Prov., Kiunga, W of airstrip, NGF 34132 (L, LAE).


Pothos hellwigii var. latifolius Lauterb., Bot. Jahrb. 45 (1911) 358. — Type: New Ireland, Nebumai, Peekel 239 (B†?, holo).

Slender but often very vigorous climber or hemiepiphyte with pendulous, free, lateral flowering branches well differentiated from the adhering shoots; leaf blades dark green above, paler below, ovate-lanceolate to ovate (usually absent from early leaves of a sympodial module), c. 8–12 × 2–4 cm, the tip not or somewhat acuminate, the base mostly rounded; intramarginal veins mostly 2 on each side of the midrib, one
basal and running to the margin, one from about midway up the blade, running to the
tip; petiole usually considerably shorter than the blade, 1/7 to 2/3 its length, the
distal part somewhat to distinctly auriculate, subtriangular (when short) to subparallel-
sided (when longer); inflorescence solitary or rarely paired, borne on leafless con-
densed short shoots (these rarely with 1 or 2 reduced blade-bearing leaves) in the
axils of usually only the most distal leaves, or less commonly terminal on the leafy
shoot, or rarely on older leafless parts of the stem, the short shoots sometimes with
scars of previous flowering, subtended by series of cataphylls, the longest and last to
3 cm long; peduncle to 7 cm long, deep purple-black, gradually thickening from
the base up more or less evenly throughout its length (cf. P. clavatus), slightly curved;
spadix sessile, spherical, yellow, 0.6–1.3–1.8 cm diam. (fl., dry); spathe broadly
ovate, emarginate-tipped, mucronulate, reflected, dark green to dark purple, slightly
longer than the spadix; flowers c. 1.1 mm diam. (dry), with 6 free tepals and 6 stam-
ens; fruit ripening deep red, to 2.5 cm long (fresh), ovoid.

**Distribution** — Widespread and common in New Guinea, with fewer records in
the Bismarck Archipelago and Solomon Islands.

**Habitat** — Lowland rain forest, secondary regrowth and lower montane rain forest
to c. 1000 m altitude.

**Note** — This species and _P. clavatus, P. longipes, P. papuanus_ and _P. zippelii_,
which follow, are evidently very closely related. The great majority of collections can
be ascribed to one or other of these with confidence. However, there are occasional
collections which appear to fall somewhere between _P. clavatus_ and _P. hellwigii, P._
_hellwigii_ and _P. zippelii, P. zippeli_ and _P. papuanus_, and _P. papuanus_ and _P. longi-
pes_. Of these, _P. clavatus_ is geographically confined to western Irian Jaya, _P. longi-
pes_ is disjunct from all the rest, endemic to Australia. _Pothos hellwigii, P. papuanus_
and _P. zippelii_, however, are mainly sympatric and wide-ranging in New Guinea and
Solomon Islands. Whether the intermediate specimens indicate incomplete separation
of these species (and so suggest their preferable recognition as varieties or subspe-
cies) is not yet clear.

**Selected other specimens seen** — **INDONESIAN NEW GUINEA.** Mt Carstensz, camp Vla, _Boden Kloss s.n._ (BM, K); Meremi, Manokwari, _BW 9806_ (BRI, L, LAE); Vogelkop, Segior, _BW 15295_
(K, L); Tubun, N of Lake Ajamaru, _BW 15355_ (K, L, LAE); Tafelberg Forest Reserve, 2 km N of
Manokwari, _Nicolson 1579_ (B, K, L); Vogelkop, Steenkool-Tembuni Rd, _van Royen 4030_ (K, LAE).
— **PAPUA NEW GUINEA.** Western Prov., Lower Fly R., E bank opposite Surt Is., _Brass 8242_
(BRI, L); Milne Bay Prov., Normanby Is., _Vaikaiuna, Brass 25609_ (L); Central Prov., Kanosia,
_Carr 11565_ (BM, K, L, SING); Central Prov., Koitaki, _Carr 12116_ (BM, K, L, SING); Morobe
Prov., nr Butibum R., c. 6 mi N of Lae, _Hartley 11897_ (BRI, K, L, LAE); Gurakor, _LAE 62235_
(BRI, K, L, LAE); North Solomons Prov., Bougainville Is., Taki Village, Toiumompu Plantation,
_NGF 16403_ (BRI, L, LAE); Central Prov., Mori R., Abau, _NGF 19641_ (BRI, K, L, LAE, NSW,
SING); W New Britain Prov., Kandrian, Pule R., _NGF 27249_ (BRI, K, LAE); Milne Bay Prov.,
Raba-Raba subdist., Binigini-Maneau track, _NGF 28802_ (BRI, K, L, LAE); Central Prov., Edevu,
Brown R., _NGF 30841_ (BRI, K, L, LAE, NSW, SING); North Solomons Prov., Bougainville Is.,
Pavairi, _NGF 31092_ (BRI, K, L, LAE); Morobe Prov., Busu logging area, _NGF 32724_ (BRI, K, L,
LAE, NSW, SING); Central Prov., Mori R., _NGF 41828_ (L, LAE); Morobe Prov., Bupu R., 12 mi
N of Lae, _NGF 43681_ (BRI, K, L, LAE); Morobe Prov., track 6 mi S of Gabensis, _NGF 47741_
(BRI, K, L, LAE, NSW); W New Britain Prov., Kandrian, _Nicolson 1538_ (K, L, LAE); N Solomons
Prov., Bougainville, Siwai, _Waterhouse 196_ (BRI, LAE, NSW). — **SOLOMON ISLANDS.** NW Fauro
Is., Barahono, _BSIP 13858_ (K, LAE); N Choiseul Is., Wasile R., _BSIP 17385_ (K, L, LAE, SING).

_Pothos clavatus_ Engl., Bull. Soc. Tosc. Ortic. 4 (1879) 266, in Becc., Malesia 1 (1883) 261, t. 16, f. 1–4; Pflanzenz. 21 (IV. 23B) (1905) 31. — Type: New Guinea, Sorong, _Beccari P. P. 487_ (B lecto; Fl isolecto, selected here; the more widely distributed of the two syntypes).

Slender climber or hemiepiphyte with well differentiated, adherent, non-flowering and free, lateral flowering branches; leaf blades dark green, rather fleshy, narrowly ovate to ovate to oblong-ovobovate, c. 6.5–10 × 2–4.5 cm, the tip acute to somewhat acuminate, the base rounded; primary lateral nerves diverging at 40–60°, intramarginal veins 2 or 3 on each side of the midrib; petiole lamina-like, shorter than the blade, 3–5 × 1.1–1.5 cm, distally emarginate to auriculate; inflorescence solitary, in the axils of distal leaves, borne on condensed short shoots and subtended by cataphylls, the last and largest oblong, c. 2 × 1 cm; peduncle rather thick, thickening gradually from the base and then very abruptly expanded at junction with spadix and there c. 1 cm diam., c. 4 cm long, blackish purple; spadix ± spherical, c. 1.4 cm diam.; spathe broadly ovate, reflexed, c. 1.2 × 1 cm; flowers c. 1.2 mm diam., with 6 free tepals and 6 stamens; fruit ovoid, c. 1.1 cm long, ripening red.

Distribution — New Guinea, confined to western Irian Jaya.

Habitat — Lowland rain forest and fresh-water swamp forest.

*Other specimens seen* — **INDONESIAN NEW GUINEA.** Ramoi, _Beccari P. P. 329_ (Fl); Sorong, nr Remu, _Pleyte 723_ (L); Rufei R., _N of Sorong, van Royen 3153_ (L); Radjah Ampat, Waigei Is., _van Royen 5252_ (L).

9. Pothos longipes Schott


_Pothos australasicus_ F. Muell., Fragm. Phytogr. Austr. 1 (1858) 62; Schott, Bonplandia 7 (1859) 104. — Type: Australia, Queensland, Pine River, _Hill s.n._ (MEL lecto, selected here; see below).

_Pothos loureirii_ ('loureirii') auct. non Presl: Bentham, Fl. Austr. 7 (1878) 158, in synonym.


_Pothos brownii_ Domin, Feddes Rep. 10 (1911) 58; Biblioth. Bot. 20 (85, 4) (1915) 501; F. M. Bailey, Compr. Cat. Queensland Pl. (1913) 579. — Type: Australia, Queensland, Rockingham Bay, _Dallachy s.n._ (K lecto; MEL isolecto, selected here; see below).

Slender climber or hemiepiphyte with well differentiated, adherent, climbing shoots and free, lateral flowering branches, very variable as to vigour; leaf blades elliptic to narrowly lanceolate, rather glossy dark green above, 1.5–15 cm long, 3–15 mm
wide, somewhat acuminate-tipped, the base rounded; primary lateral veins diverging at c. 30–40°; intramarginal veins 1 or 2 (or 3) on each side of the midrib; petiole usually exceeding the blade in length, oblanceolate, 2–12 cm × 4–14 mm, distally rounded to truncate to strongly auriculate; inflorescence solitary or less commonly paired, in the axils mostly of distal leaves of a flowering branch and subtended by cataphylls, less commonly terminal on leafy branchlets; peduncle c. 2–5 cm long; spadix yellow to purplish, to c. 6 cm long, sessile or more usually stipitate with the stipe to c. 3 cm long and sometimes subequaling the spadix in length (particularly in individuals of very slender dimensions); spathe ± lanceolate, c. 1.5–4 × 0.5–0.9 cm, wide opening to reflexed, purple-black to greenish; flowers c. 1.3 mm diam., with 6 free tepals and 6 stamens; fruit ovoid, 8–13 mm long, red when ripe.

Distribution — Eastern Australia, from northeastern Queensland to the New South Wales North Coast region.

Habitat — In rain forest at low altitudes in the southern part of the range, extending, in warmer latitudes, into montane forest to c. 1000 m altitude.

Notes — 1. Engler (1905) grouped this species with P. cylindricus Presl in his series Longipedes, separated from the other three series of subg. Pothos by the presence of foliage leaves on the ultimate flowering branches between the basal cataphylls and the terminal inflorescence. Engler (1879) had made a similar grouping earlier but without there erecting formal supraspecific taxa at that rank. In other series the inflorescence is immediately subtended by cataphylls, and is considered lateral to the leafy branch that bears it. This distinction breaks down in P. longipes where one may find in the same specimen inflorescences immediately subtended by cataphylls and borne laterally on a leafy shoot, and inflorescences with foliage leaves between the spathe and the cataphylls. It may thus be said that the inflorescence is lateral or terminal in this species, or one may say that inflorescences are always terminal on the shoots that bear them and that leaves may or may not develop on those shoots. To describe them as lateral in a strict sense requires the cataphylls to be included in the concept of inflorescence, but virtually identical cataphylls must be deemed ‘vegetative’ when there is one or more foliage leaves between them and the spathe and the inflorescence is terminal. Distinction between terminal and lateral inflorescences can be somewhat arbitrary in such highly ramified plants in which inflorescence position impacts so insignificantly on vegetative architecture.

2. Pothos longipes is evidently closely related to P. papuanus (q.v.), differing from it chiefly in the petiole usually longer than the blade (though this is rarely the case in P. papuanus, and rarely not the case in P. longipes), and in the usually stipitate spadix (though likewise this is rarely the case in P. papuanus and rarely not the case in P. longipes). There is rather wide geographical disjunction between the two, and some ecological differentiation: tolerance of cooler climate in P. longipes.

3. In first describing P. australasicus, Mueller (l.c.) cited "in silvis densis circum Moreton Bay. Hill & Mueller." No specimen explicitly collected by Hill & Mueller together has been located, and I conclude that the specimen cited above, collected by Hill at Pine River (which empties into Moreton Bay) and annotated with this name by Mueller, is eligible to be selected as lectotype. It is sterile, but vegetatively it matches P. longipes perfectly. A fertile specimen at K, collected by Mueller from the same locality is annotated P. longipes in Schott’s hand, but not annotated by Mueller.
4. In the protologue of *P. brownii*, Domin (I.c.) cited, in addition to his own collections (n.v.; presumed to be in Prague), three earlier collections by Dallachy, Fitzalan and Nernst. Prior to Domin, all of these were identified with *P. longipes* by Bentham (I.c., but as the incorrectly interpreted *P. loureiroi*, with *P. longipes* as a synonym), the second also by Engler (II.cc.). Any one would serve as lectotype.

Selected other specimens seen (this species has been collected on very numerous occasions) — Australia. — Queensland: foot of Mt Bartle Frere, nr Josephine Ck, Blake 9807 (BRI, K, L); Mt Glorious, *Blake 12686*; Montville, *Blake 15389* (BRI, K); Jarra Ck, nr Tully, *Blake 19710* (BRI, K, L); Mossman, entrance to Mossman Gorge, *Blake 19755* (BRI, K); Upper Parrot Ck, Annan R., *Brass 20179* (BRI, K, L); Daintree R., *Kajewski 1432* (BRI, K); d’Aguilar Range nr Mt Glorious, *Moriarty 873* (BRI, K); Fine R., von Mueller s.n. (K); Pt Mackay, *Nernst s. n. (K)*; Mt Glorious, *Nicolson 1381* (K, L, LAE); Mt Wolvi, c. 15 km NE of Kin Kin, *Sharpe 4534* (BRI, NSW); Davies Ck, *Webb & Tracy 5375* (BRI, NSW). — New South Wales: Dorrigo, *Boorman s. n.* (L, NSW); Hastings R., *Cunningham s. n.* (BM, K); *Fraser s. n.* (BM, NSW); E Dorrigo Plateau, Never Never Ck, *Melville 3389* (K, NSW); Tweed Range, Wiangaree State Forest, c. 13 mi NE of Kyogle, *Schodde 5617* (BRI, K, L, NSW);


Vigorous slender climber or hemiepiphyte with well differentiated adherent climbing shoots and free lateral flowering shoots; leaf blades narrowly elliptic to (ob)lanceolate, the tip tapering to a point but hardly acuminate, the base rounded, c. 6–12 × 1.2–3.5 cm; primary lateral veins diverging at c. 30°, intramarginal veins 2–5 on each side of the midrib, the inner ones arising about midway along its length; petiole c. 1/3 the length of to equalling the blade, distally truncate to strongly auriculate, rarely rounded, c. 4–8 cm long, to c. 2 cm wide; inflorescence solitary or occasionally clustered (to three together), rarely terminal on a leafy shoot, more usually lateral on a (sometimes sympodially branched) short shoot in distal leaf axils and subtended by cataphylls, the last and longest of these c. 3 cm long; peduncle mostly rather robust, gradually increasing in thickness distally, to c. 9 cm long, purple-black; spadix sessile, very rarely shortly stipitate, cylindric to somewhat tapering, blunt-tipped, usually more than six times as long as thick, 2–4 × 0.3–0.4 cm (fl., dry); spathe pale green to purplish brown, reflexed, oblong-ovate to oblong-lanceolate, 1/3 to
about 4/5 the length of the spadix, to c. 4 × 1.2 cm; flowers yellow, c. 1.1 mm diam., with 6 free tepals and 6 stamens; fruit ovoid, ripening through yellow to deep red, to 2 × 0.9 cm.

Distribution — Widespread in New Guinea and Solomon Islands.

Habitat — Lowland and lower montane rain forest and regrowth.

Note — *Pothos papuanus* manifests a wide range of vigour, with *P. quinquevenosus* and *P. albertisii* falling within the range. The young shoots and fruits are reported to be edible after cooking. A single collection from near Jayapura, *McKee 1911*, has a stipitate spadix and much resembles the Australian *P. longipes* Schott (q.v.).


11. Pothos zippelii Schott


Slender climber or hemiepiphyte with well differentiated adherent climbing shoots and free lateral flowering branches; leaf blades elliptic to ovate, the tip somewhat to very acuminate, the base rounded, c. 6–12 × 2–3.5 cm; primary lateral veins diverging at c. 30–45°, intramarginal veins 2 or 3 on each side of the midrib; petiole lamina-like, about 1/4–2/3 of the length of the blade, to c. 1.4 cm wide, distally rounded to slightly (to pronouncedly) auriculate; inflorescence solitary, rarely clustered, rarely terminal, or more usually subtended by cataphylls on condensed short shoots in the axils of distal leaves; peduncle slender, sometimes gradually thickening distally, to c. 10 cm long; spadix sessile to minutely stipitate, ovoid-cylindric, about
twice as long as thick, to c. 1–2.5 cm long; spathe oblong-ovate to lanceolate, 1.2–3.5 × 0.6–0.8 cm, reflexed; flowers c. 1.1 mm diam., with 6 free tepals and 6 stamens; fruit obovoid, 6–9 mm long, red when ripe.

Distribution — Moluccas to New Guinea and Solomon Islands. Some incomplete material from Sulawesi may be of this species.

Habitat — Lowland to lower montane rain forest.

Other specimens seen — INDONESIAN NEW GUINEA. Biak, Sorido airstrip, Brongersma s.n. (L); 2 km N of Manokwari, Nicolson 1576 (B, BM, BRI, L, LAE); Biak Is., 1 km NW of Mokmer airport, Nicolson 1593 (B, K, L, LAE); Vogelkop, Steenkool to Tembuni Rd, van Royen 4030 (L).

— PAPUA NEW GUINEA. Gulf Prov., N side Mt Bosavi, Jacobs 8986 (L); North Solomons Prov., Bougainville, Buin, Mollo-hito, Kajewski 1808 (BM, BR); West New Britain Prov., Hoskins, SE slopes Mt Uluwun, LAE 58597 (L, LAE); West New Britain Prov., 2 mi W of Fullerborn Harbour, NGF 31481 (L, LAE). — SOLOMON ISLANDS. Santa Ysabel, Pilema Bay, BSIP 6496 (LAE).


Very slender diminutive climber or hemiepiphyte; leaf blades very narrowly lanceolate, c. 5–9 cm long, c. 3–7 mm wide, the apex attenuate, the base rounded; primary lateral veins diverging at c. 20°, intramarginal veins 1 or 2 on each side of the midrib; petiole lamina-like, c. 1/4–1/3 of the length of the blade, c. 1.5–3 cm long, c. 3–4 mm wide, rounded to somewhat auriculate distally; inflorescence solitary on condensed short shoots in the axils of distal leaves; peduncle very slender, to c. 3.5 cm long, subtended by cataphylls, the last and longest very narrowly lanceolate, c. 1–1.5 cm long; spadix sessile, sub-spherical to ovoid-cylindric, c. 3–7 × 3–4 mm; spathe ovate-lanceolate, 6–8 × 4–5 mm, green; flowers green, c. 1.2 mm diam., with 6 free tepals and 6 stamens; fruit ovoid to elliptic-obovoid, c. 1 cm long, cherry red.

Distribution — Endemic to New Guinea; known from only three very widely scattered sites.

Habitat — Lowland hill forest.

Note — This species is clearly closely related to P. zippelii Schott, differing principally in its very diminutive and slender stature. The very scattered distribution may indicate that this is a rare and/or very easily overlooked plant. Alternatively, the distribution may simply suggest that this is a sporadically arising depauperate form of P. zippelii; however, there are as yet no linking intermediates.

Other specimens seen — INDONESIAN NEW GUINEA. Idenburg R., Bernhard Camp, Brass 13876 (BRI, L). — PAPUA NEW GUINEA. Gulf Prov., Vailala R., Wade s.n. (K).

SPECIES EXCLUDENDAE


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