The End of *Pseudodracontium* N.E. Br.

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ABSTRACT

The aroid genus *Pseudodracontium* N.E. Br. is reduced to *Amorphophallus* Bl. ex Decne. New names and a new key to taxa of the former *Pseudodracontium* are presented. A discussion on its phylogenetic position within *Amorphophallus* is given.

KEY WORDS

Amorphophallus, *Pseudodracontium*, taxonomy, Thomsonieae, Araceae, phylogeny.

INTRODUCTION

The genus *Pseudodracontium* was established by N.E. Brown in 1882. He introduced one new species, *P. anomalum* N.E. Br., and transferred *Amorphophallus lacourii* Lind. & André to *Pseudodracontium*. The first mentioned species was chosen as the lectotype species by Nicolson (1967). Subsequent years saw the addition of several new names in *Pseudodracontium*. These were dealt with taxonomically in a revision of the genus by Serebryanyi (1995) which left a total of 6 accepted species, 4 of which were newly introduced in that revision. After the revision only one new name was published in relation to *Pseudodracontium*, namely *Amorphophallus glaucophyllus* Hett. & Serebryanyi (Hetterscheid, 2006): Because it was already then strongly suspected by the authors that *Pseudodracontium* would soon be transferred to *Amorphophallus*, this new species, clearly a member of "*Pseudodracontium*", was published as a species of *Amorphophallus*.

Pseudodracontium has always been thought to be very closely related to *Amorphophallus* and both genera solely make up the tribe Thomsonieae. Thomsonieae is now regarded to be the sister group of Caladieae (incl. Zomicarpeae; Cabrera et al., 2008; Cusimano et al., 2011).

PSEUDODRACONTIUM AND *AMORPHOPHALLUS*

Hetterscheid (1994) already suggested that *Pseudodracontium* may well be a part of *Amorphophallus* instead of its sister genus. This was based on morphological observations which resulted in a small suite of apomorphies for *Amorphophallus* + *Pseudodracontium*, whereas without *Pseudodracontium* there was no single character to be found for a monophyletic *Amorphophallus* (Hetterscheid, 1994; Serebryanyi, 1995). The monophyly of *Pseudodracontium* itself was never disputed and strongly supported by a suite of morphological (near-) autapomorphies (Serebryanyi, 1995; Van der Ham & Van Heuven, 2001; Van der Ham et al., 1998, 2000, 2005). The most obvious ones are: unilocular thecae, slender filaments (fully free or more or less connate to form a slender column, Fig. 1b), appendix with recognizable staminodial structure (Fig. 1c), pollen with "polar caps" (smooth

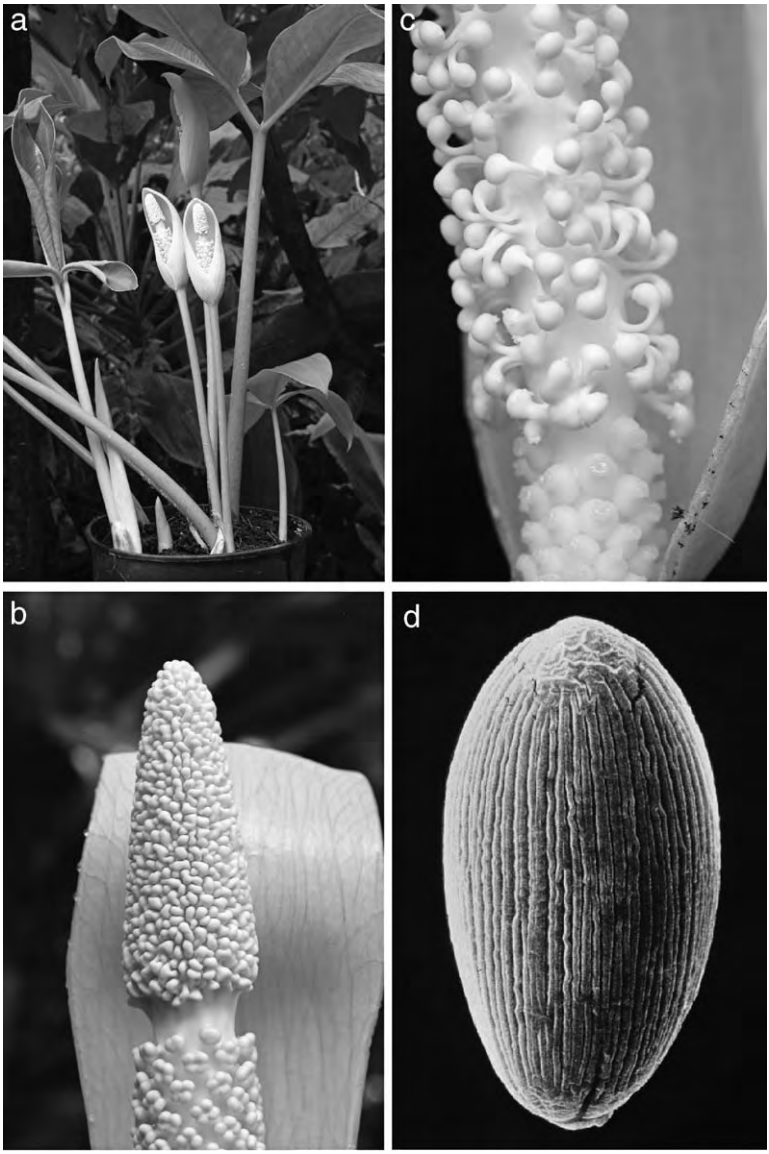

Plate 1. 1a. *Amorphophallus lacourii* group. Habit. 1b. *Amorphophallus lacourii* group. Male flowers. 1c. *Amorphophallus pseudoharmandii* Appendix. 1d. *Amorphophallus macrophyllus* Pollen with polar caps.

or irregularly structured polar areas, fig. 1d).

We have always been puzzled by the retention of seemingly juvenile leaf architecture in many adult plants of *Pseudodracontium* taxa (fig 1a). In almost all taxa the central main segment of the leaf is considerably less complex than the lateral ones, and there is a general morphocline from more complex to rather simply divided leaf laminas (or the reverse). In some specimens the leaf remains fully juvenile with only three, very large, leaflets in adult plants, as is seen in seedlings, also in many

other *Amorphophallus* species. In nearly all seedlings ever observed by us (several hundred) the first seedling leaf lacks the central segment (leaflet) entirely.

The polar caps of the pollen grains appear to be a retained non-adult phase of pollen formation. Looking at the inflorescence, we observe a few characters that may be seen as "plesiomorphic" for *Amorphophallus* at large, like the appendix wall with fully developed staminodes and the long, free or partly fused filaments. We hypothesize that the morphogenic pathways of several phenotypic characters in *Pseudodracontium* is deregulated. It may well be that the chaotic molecular and morphological patterns display an evolutionary phase *Pseudodracontium* is going through whereby (past and ongoing) hybridisation (see also paragraph 3.1) may well have been the onset of the deregulation. Heterochrony seems to be part of this deregulation, leading to adult plants with partly juvenile morphologies.

Pseudodracontium as a group within *Amorphophallus* is considered to be closely related to *A. longituberosus* (Engl.) Engl. & Gehrm. and its immediate allied species *A. albispathus* Hett., *A. coudercii* (Bogn.) Bogn. and *A. tenuispadix* Hett. This group turned up again and again in morphology-based attempts to unravel the phylogeny of *Amorphophallus*. In these analyses *Pseudodracontium* species were always associated with the aforementioned group as a sister group. Even in chemical analyses of the scent of species in this alliance (Kite & Hetterscheid, 1997; Kite et al., 1998), traces of a compound (4-methoxyphenetyl alcohol, or "anise oil") unique to it, were found in *P. lacourii* (Lind. & André) N.E. Br. and *P. fallax* Serebryanyi. This seemed to strengthen the suggested relationship. The trouble with all full-morphology-based phylogeny reconstructions of *Amorphophallus* was that no statistically relevant support for this grouping could be found, not even applying the Implied Weighing procedure of the TNT program of Goloboff et al. (2004; Hovenkamp & Hetterscheid, 2008). The species group of *A. longituberosus* reappeared in all analyses but never associated with *Pseudodracontium*.

Molecular analyses of *Amorphophallus* + *Pseudodracontium* published to date (Grob et al., 2002, 2004; Sedayu et al., 2010) strongly support the sister-group relationship of *Pseudodracontium* to the *A. longituberosus* group within *Amorphophallus* and thus confirms the earlier morphology-based hypotheses. More recent molecular analysis (Randomized Axelerated Maximum Likelihood [RAxML]) by the second author using the markers ITS1, FLint2, rbcL and matK and applied to ca. 130 species of *Amorphophallus* (incl. *Pseudodracontium*) again strongly supports the aforementioned grouping of *Pseudodracontium* in *Amorphophallus* (Claudel et al., in prep., Hetterscheid & Claudel, in prep.) but expands it with a small strongly supported clade of 3 (possibly only 2) species (*A. saraburiensis* Gagn., *A. scutatus* Hett. & T.C. Chapman and *A. tenuistylis* Hett.). This group of the *Amorphophallus* species mentioned + *Pseudodracontium* is part of a larger and strongly supported clade of the "Continental Asia-II"-clade of Sedayu et al. (2010).

In the light of all evidence discussed above it is here decided to reduce the genus *Pseudodracontium* to the synonymy of *Amorphophallus*. The necessary new combinations and one new name are presented below. The tribe Thomsonieae will become monotypic.

THE "SPECIES"-PROBLEM IN "*PSEUDODRACONTIUM*" AND A PROVISIONAL NEW KEY TO THE TAXA

Species Number in *Pseudodracontium*

Serebryanyi (1995) recognized 6 species in *Pseudodracontium* and provided an identification key. In subsequent years, many more collections of *Pseudodracontium* species were made by many botanists and studied by the first author morphologically. It turned out that many species-defining character combinations proposed by Serebryanyi can no longer be used. Many character combinations that were used to define particular species prove to be more widespread and recombined with

other characters to form an ever more complex of combinations blurring almost all conventional species borders in the "genus".

Molecular analyses by the second author (Claudel at al., in prep.) also show huge overlap in characters between "taxa" as well as suggesting extensive hybridization (particularly in ITS1 analyses).

As a result there is a strong conviction that the number of species of *Pseudodracontium* is overstated. In the forthcoming *Amorphophallus* treatment in the Flora of Thailand (Hetterscheid, in press) a key to the taxa of "*Pseudodracontium*" is presented, which is duplicated here (see below) using the new combinations and new name in *Amorphophallus*.

Five New Combinations and One New Name in *Amorphophallus*

As a result of the transfer of all *Pseudodracontium* species to *Amorphophallus*, five new nomenclatural combinations and one new name in *Amorphophallus* are presented here (names considered heterotypic synonyms by Serebryanyi in 1995 are not recombined; for invalidly published names and full synonymy, see there). The new nomenclatural combinations do not mirror taxonomic opinion of the authors on the biological reality of the taxa carrying these names. The taxonomy of this group of "species" is not finished yet (Hetterscheid, in prep.). The introduction of a species group incl. *A. lacourii* as presented in the key in the next paragraph (3.3) mirrors this uncertainty and must be considered a preliminary opinion and not a definitive one as yet.

Amorphophallus fallax (Serebryanyi) Hett. & C. Claudel, **comb. nov.** Basionym: *Pseudodracontium fallax* Serebryanyi, Blumea 40(1)(1995): 221, fig 1. - Type: Vietnam, Vungtau-Con Dao special district, limestone hills c. 10 km E of Vung Tau port, near Mount N. Chau Vien, 300 m. alt., SE slope, 100 m. below Jesus Christ momument, in thickets, 28 May 1989, *Serebryanyi 8908* (holotypus, MHA, spiritcoll.).

Amorphophallus kuznetsovii (Serebryanyi) Hett. & C. Claudel, **comb. nov.** Basionym: *Pseudodracontium kuznetsovii* Serebryanyi. Blumea 40(1)(1995): 226, fig. 2. 1995 - Type: from a plant cultivivated in Hortus Botanicus Leiden, the Netherlands, 15 July 1992, *Hetterscheid H.AM.165-T* (holotypus, MHA, spiritcoll.) - orig. coll. Vietnam, Xuen Moc Reserve, easternmost part of the Dong Nai province, *Kuznetsov s.n.*, 1991.

Amorphophallus lanceolatus (Serebryanyi) Hett. & C. Claudel, **comb. nov.** Basionym: *Pseudodracontium lanceolatum* Serebryanyi, Blumea 40(1)(1995): 230, fig 4a, b. - Type: from a plant cultivivated in Hortus Botanicus Leiden, the Netherlands, 15 July 1992, *Hetterscheid H.AM.179-T* (holotypus, MHA, spiritcoll.) - orig. coll. Vietnam, Xuen Moc Reserve, easternmost part of the Dong Nai province, *Kuznetsov s.n.*, 1991.

Amorphophallus latifolius (Serebryanyi) Hett. & C. Claudel, **comb. nov.** Basionym: *Pseudodracontium latifolium* Serebryanyi, Blumea 40(1)(1995): 231, fig. 4c, d. - Type: from a plant cultivivated in Hortus Botanicus Leiden, the Netherlands, 7 August 1991, *Hetterscheid H.AM.167-T* (holotypus, MHA, spiritcoll.) - orig. coll. Thailand, Kanchanaburi prov., Thong Pha Phum, Kwai River valley, alt. 100 m., steep hillslope covered in bamboo, 2 July 1985, *Dransfield JD 6219 p.p.*

Amorphophallus macrophyllus (Gagn. ex Serebryanyi) Hett. & C. Claudel, **comb. nov.** Basionym: *Pseudodracontium macrophyllum* Gagn. ex Serebryanyi, Blumea 40(1)(1995): 232, fig. 5. - Type: Thailand, Kanchanaburi prov., Wang Kanai, 200 m. alt., in crevices of limestone rocks, 15 May 1927, *Kerr 12866* (holotypus, K).

Amorphophallus pseudoharmandii Hett. & C. Claudel, **nom. nov.** - Syn.: *Pseudodracontium harmandii* Engl., Bot. Jahrb. 25 (1898): 15. - Type: Cambodia, Compon Chnang, June

1875, *Godefroy s.n.* "in Exped. Dr. Harmand" (holotypus, P).

The new name proposed here is made necessary because of the existence of the name *Amorphophallus harmandii* Engl. & Gehrm, in Pflanzenr. (IV, 23C) (1911) 83 - Type: Cambodia, Compon Chnang, 6 June 1875, *Godefroy 144* "in exp. Harmand" (p.p., only the inflorescences) (holotypus, P). To complicate matters both the holotype and isotype (B) of *A. harmandii* are a combination of inflorescences of *A. harmandii* and leaves of *A. pseudoharmandii*, which apparently got mixed. The holotype of *A. pseudoharmandii* is a full flowering specimen.

KEY TO THE TAXA OF THE FORMER GENUS *PSEUDODRACONTIUM*, NOW *AMORPHOPHALLUS*

1a. Leaf blade bright pale bluish gray (not resulting from a wax layer); appendix with a ridged-grooved staminodial pattern, tops of staminodes distinctly separated; stigma depressed to slightly hemispheric, 1.5 mm in diam., bright yellow, strongly echinate-scabrate; style 0.4 mm long . . . . . *A. glaucophyllus*

1b. Leaf blade green, with or without variegation, or with a greenish blue wax layer; appendix with a ridged-grooved, papillate, or more or less brain-like staminodial pattern, or rarely almost to entirely smooth (this usually in reduced appendices); staminodes congested or the tops separated; stigma off-white 2

2a. Plants often flowering before leaf development; stigma disciform, 2 mm diam., with a distinct central depression, surface nearly smooth or slightly corrugated, or minutely echinate; style almost nil; appendix always fully developed, never reduced, staminodial structure of the appendix a mixture of terete, rod-like staminodes with orbicular tips and two or a few more staminodes fused resulting in short ridges, these often slightly sinuous, sometimes appendix with deeper longitudinal cracks independent from the staminodial structure . . . . . *A. macrophyllus*

2b. Stigma depressed or hemispheric, 0.4–1.5 mm, with or without a central depression; style very short or distinct; flowering mostly alongside developing leaves or after leaf development; appendix sometimes reduced, staminodial structure of appendix papillate, papillate-brain-like or brain-like 3

3a. Staminodial structure of appendix largely papillate, tops of staminodes orbicular or very short elongate (with fusion of 2 or 3 neighboring staminodes) and then often slightly sinuous; stigma 1–2 mm diam . . . . . *A. pseudoharmandii*

3b. Staminodial structure of appendix for the larger part brain-like, with several staminodes fused into longer, strongly sinuous brain-fold-like ridges, more rarely with progressed fusion to form a shallowly corrugate or smooth surface (often in reduced appendices), or papillate but with scattered, small groups of a few fused staminodes, forming short convolutions; stigma 0.4–1 mm diam . . . . *A. lacourii* group (incl. *A. lacourii*, *A. kuznetsovii*, *A. fallax*, *A. lanceolatus* and *A. latifolius*).

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