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The unusual *Ondinea,* actually just another Australian water-lily of *Nymphaea* subg. *Anecphya (Nymphaeaceae)*

Abstract

Löhne C., Wiersema J. H. & Borsch T.: The unusual *Ondinea,* actually just another Australian water-lily of *Nymphaea* subg. *Anecphya (Nymphaeaceae).* – Willdenowia 39: 55-58. – Online ISSN 1868-6397; © 2009 BGBM Berlin-Dahlem.
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Based on recent findings of phylogenetic studies using character sets from all three genomic compartments and from morphology, *Ondinea purpurea* is transferred to *Nymphaea* and the new name *N. ondinea* is validly published. This change in classification implements the criterion that higher taxa should be monophyletic. Although, compared to other species of *Nymphaea,* the Australian *N. ondinea* appears to be phenotypically very different, most shifts in character states that led to its evolution (e.g., loss of perianth in some of the populations, decrease in stamen and carpel number) are rather quantitative. Several characters not only support a position of *Ondinea* within *Nymphaea* (such as an eusyncarpous gynoeceum with carpels less than 50 % fused), but also allow its unambiguous identification as a species of *Nymphaea*.

Additional key words: character state shifts, classification, phylogenetic hypothesis, monophyly, paraphyly, taxonomy

The generic name *Ondinea* was created by Hartog in 1970 for a newly discovered and "remarkable" member of the *Nymphaeaceae* endemic to the Kimberley region of Western Australia. This monotypic genus was considered unusual in its sagittate, mostly submersed mature leaves, apetalous flowers with a protruding floral base and supposedly exarillate seeds. A close relationship of *Ondinea* to the genus *Nymphaea* L. was suggested by Hartog (1970) and has been reinforced by studies of several other authors (Kenneally & Schneider 1983; Müller 1970; Schneider 1983; Schneider & Ford 1978; Schneider & al. 1995; Williamson & Moseley 1989).

This genus was included in a phylogenetic study of the *Nymphaeaceae* by Les & al. (1999), who sampled one species per genus. However, until recently the phylogenetic position of *Ondinea* was not investigated using data from a broad sampling of water-lily species. In contrast, our analyses of the order *Nymphaeales* have used extensive data sets of chloroplast DNA (Borsch & al. 2007; Löhne & al. 2007) and a detailed study of *Nymphaea* subg. *Anecphya* (Casp.) Conard incorporated both chloroplast and nuclear DNA data (Löhne & al. 2008). The results of these studies provide high support for *Ondinea* as a derived lineage within the genus *Nymphaea*. In fact, *Ondinea* is nested within one of two subgroups of the Australian water-lilies (*N.* subg. *Anecphya* sensu lato). The subgenus has been divided into a small-seeded group, *N.* subg. *Confluentes* S. W. L. Jacobs, and a large-seeded group, *N.* subg. *Anecphya* sensu stricto, by Jacobs & Porter (2007). The nested position of *Ondinea* within the small-seeded group of *N.* subg. *Anecphya* sensu lato is supported from both nuclear and chloroplast DNA (Löhne & al. 2008).

Morphological comparisons with *Nymphaea* species provide additional evidence for this phylogenetic position of *Ondinea*. The report of a petaloid subspecies of *Ondinea* by Kenneally & Schneider (1983) erased one of the original distinctions between the two genera. The violet colouration of these petals, exceptional among basal angiosperms according to Endress (2001),

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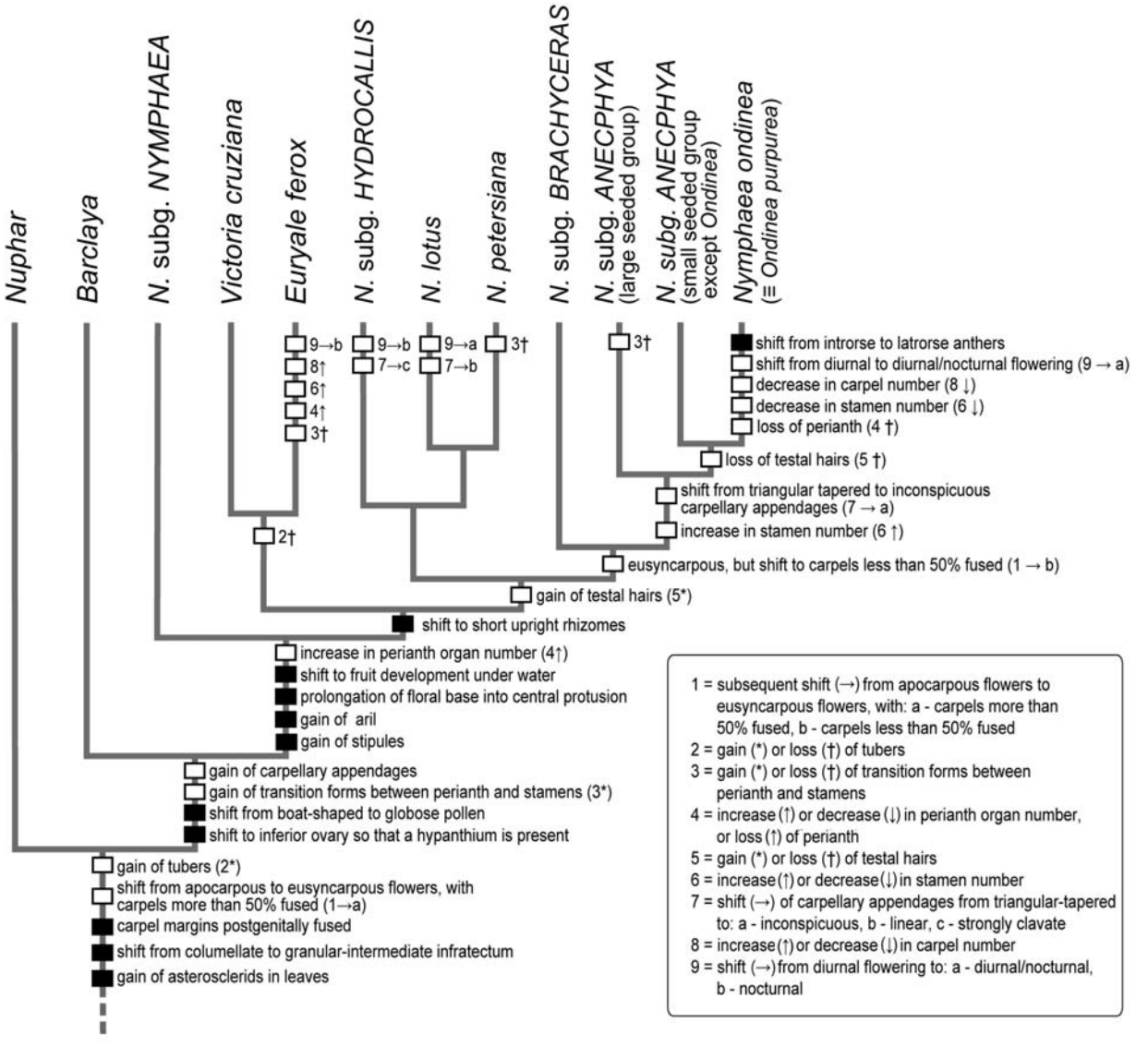


Fig. 1. Shifts in phenotypic characters during evolution of the core water-lilies *(Nymphaea, Euryale, Victoria, Ondinea).* – This figure shows a simplified tree based on the results of Borsch & al. (2008, see fig. 6 there), illustrating unambiguous character changes (regardless of using accelerated or delayed transformation settings) with unique shifts (apomorphies) displayed as black boxes and shifts that occurred more than once (homoplasies) shown as white boxes. Most features appearing on the branch to *Ondinea* are quantitative or homoplastic, and five character state changes were reconstructed to have happened since the evolution of the common ancestor of tropical *Nymphaea* species (incl. *Ondinea*).

occurs elsewhere in *Nymphaeales* only in *N.* subg. *Anecphya* and subg. *Brachyceras* (Casp.) Conard. Additionally, these two subgenera share with *Ondinea,* alone among the *Nymphaeaceae,* the character state of partially fused carpels (see Schneider 1983: 375). According to Borsch & al. (2008) the eusyncarpous gynoecia with carpels less than 50 % fused, common to these three groups, appears to be derived within the family (Fig. 1). The presence of stigmatic fluid also unites *Ondinea* with *Nymphaea.* Within *Nymphaea,* the very inconspicuous to almost absent carpellary appendages in *Ondinea* are most similar to those of *N.* subg. *Anecphya* (Borsch & al. 2008: see char. no. 48 & 50). Water-lilies have evolved several kinds of carpellary appendages probably in relation to specializations in floral biology, and their extreme reduction must have occurred in a common ancestor of *N.* subg. *Anecphya* and *Ondinea*.

Schneider & Ford (1983) found the seeds of *Ondinea* to be arillate, in contrast to the original report by Hartog (1970), and within *Nymphaeaceae* they most closely match those of *Nymphaea* in their overall morphology. The gain of an aril was hypothesized by Borsch & al. (2008) to have happened in conjunction with the adaptation of fruits developing under water (Fig. 1). When compared to seeds of various *Nymphaea* subgenera illustrated by Wiersema (1987) and Jacobs & Porter (2007), *Ondinea* seeds compare best, in their lon-

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gitudinally ridged glabrous surfaces, with those of either *N.* subg. *Lotos* (DC.) Conard (usually ridged, but sometimes with hairs) or the *Confluentes* (small-seeded) group of *N.* subg. *Anecphya* (sometimes ridged, usually without hairs). Earlier in the evolution of water-lilies, testal hairs were gained in a common ancestor of the tropical subgenera of *Nymphaea* including *Ondinea*. The subsequent loss of testal hairs occurred in a common ancestor of *Ondinea* and the small-seeded group of *N.* subg. *Anecphya* (Fig. 1). Thus, the position of *Ondinea* within the Australian radiation of *Anecphya* species as inferred at the species level by nuclear and plastid sequence data (Löhne & al. 2008) is also confirmed by morphological evidence.

Ondinea has also been separated from *Nymphaea* by its predominately submersed sagittate mature foliage, but similar foliage characterizes *N. oxypetala* Planch. of *N.* subg. *Hydrocallis* (Planch.) Conard and juvenile leaves of a number of *Nymphaea* species, being often associated with lotic environments (Wiersema 1987) such as are inhabited by *Ondinea*. Indeed, juvenile sagittate leaves of *N. hastifolia* Domin, the species judged closest to *Ondinea* among those sampled in molecular studies (Löhne & al. 2008), are the basis for its specific epithet. A number of water-lily species of various lineages develop submerged leaves when light conditions become limiting, as with cultivated tropical taxa during the winter in the northern hemisphere (Borsch, Wiersema, Löhne, pers. obs.), indicating that shifts from floating to submerged leaves are easily possible and in some cases may be environmentally induced modifications. The floating leaves sometimes produced by *Ondinea* (Wilson 2009) are reminiscent of sagittate-leaved *Nymphaea* such as *N. belophylla* Trickett and *N. potamophila* Wiersema of *N.* subg. *Hydrocallis* (Wiersema 1987). The extreme reduction in floral size and floral organ number seen in *Ondinea* is also approached in some *Nymphaea;* for example, comparable numbers of flower parts were recently described for the small-flowered *N. minuta* K. C. Landon & al. (2006) of *N.* subg. *Brachyceras*. Extremely small flowers also occur in small plants of *N. micrantha (N.* subg. *Brachyceras)* that arise from proliferating leaf buds.

Another character that was considered to separate *Ondinea* from *Nymphaea* is the former's extremely long-projecting floral base. Schneider (1983) hypothesized this feature to be an adaptation heightening the level of the stigmatic fluid, thereby improving pollination effectiveness. The overall analysis of floral character evolution in water-lilies (Fig. 1; Borsch & al. 2008) indicates the prolongation of the floral base into a central protrusion to have occurred in the common ancestor of the *Nymphaea* clade, which includes *Euryale-Victoria* and *Ondinea*. The tissue identity of this central protrusion (i.e. axial tissue or receptacle) is, however, not fully understood; therefore the conservative term 'floral base' is used (see char. 17 in Borsch & al. 2008). The further prolongation in *Ondinea* is likely an adaptation influenced by the reduced stigmatic surface area of *Ondinea* and under strong selective pressures to improve fertility. Thus, despite the seeming phenotypic distance of *Ondinea* from the other water-lilies, the only clearly autapomorphic character state change that remains is the shift from introrse to latrorse anthers (Fig. 1).

Whereas DNA sequence data from all three genomic compartments reveal *Ondinea* in a derived position, nested within *Nymphaea* subg. *Anecphya,* with high statistical support (Borsch & al. 2007; Löhne & al. 2007, 2008; Borsch & al. 2008), the situation is not as clear for the *Euryale-Victoria* clade. The latter has been found nested within *Nymphaea* based on combined plastid DNA sequence data (Löhne & al. 2007). Such a position has been confirmed with mitochondrial and especially nuclear data but is still not well supported (Borsch & al. 2008). Ongoing work (Borsch, Löhne, Wiersema, work in progress) will be necessary to confirm whether the plastid tree of Löhne & al. (2007) resembles the organismic tree of core *Nymphaeales*. Thus, in contrast to *Ondinea,* nomenclatural adjustments for *Euryale* and *Victoria* would be premature at this time.

Given the above described evidence, it is no longer appropriate to treat *Ondinea purpurea* as a taxon distinct from *Nymphaea*. Due to the existence of the earlier name *N. purpurea* Rehnelt & F. Henkel (in Henkel & al. 1907) its specific epithet cannot be transferred to *Nymphaea*. We therefore validly publish the following new names to accommodate it within the water-lily genus:

Nymphaea ondinea Löhne, Wiersema & Borsch, **nom. nov.** ≡ *Ondinea purpurea* Hartog in Blumea 18: 413. 1970. – Holotype: Australia, Western Australia, Kimberley District, Kurunundalo [or Kurunundalu], 15.4. 1968, *W. Leutert 108* (CANB 171930; isotypes: CANB [5 sheets]).

Nymphaea ondinea subsp. ***petaloidea*** (Kenneally & E. L. Schneid.) Löhne, Wiersema & Borsch, **comb. nov.** ≡ *Ondinea purpurea* subsp. *petaloidea* Kenneally & E. L. Schneid. in Nuytsia 4: 362. 1983. – Holotype: Australia, Western Australia, Kimberley District, Mitchell Plateau, 21.1.1982, *E. L. Schneider s.n.* (PERTH; isotypes: CANB, K, NY, PERTH, TEX).

Nymphaea ondinea subsp. *petaloidea* is retained at the rank of subspecies because of its morphological distinctions (Jacobs & Porter 2007) and, although slight, its geographical separation from the apetaloid subspecies.

Moreover, this study adds empirical data to the ongoing discussion of whether or not to accept paraphyletic taxa (Stevens 2006; Hörandl 2006; Albach 2008). One of the arguments advocated by those in favour of recognizing paraphyletic taxa (e.g., Hörandl 2006) is that all taxa

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have to be recognizable by phenotypic characters. Morphologically deviating species within a genus, for example, can therefore be classified in their own, distinct genera. We argue that the question of "being different" strongly depends on the depth of investigation. The case described in this study shows how a few shifts of predominantly quantitative, and presumably highly adaptive, features can produce a very different phenotypic appearance *(Nymphaea ondinea)*. More thorough investigation reveals apomorphies for successively deeper nodes, and allows for identification of the monophyletic taxon *(Nymphaea* including *Ondinea)* on morphological grounds. Similar arguments were provided by Albach (2008), who reclassified *Pseudolysimachion* Opiz into *Veronica* L. *(Plantaginaceae, Lamiales)* and explained that characters used to define *Pseudolysimachion* were strongly homoplastic. We believe that the case of *Ondinea* provides a further good example favouring a monophyly-based classification above the species level (such as genera and families) as stable, predictive and at the same time practical.

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