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

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Source: Willdenowia, 39(1) : 55-58

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.39.39104
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The unusual *Ondinea*, actually just another Australian water-lily of *Nymphaea* subg. *Anecphya* (*Nymphaeaceae*)

Abstract


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),
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-

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).
When considering a separate Ondinea from Nymphaea, it is argued that the character 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 Nymphaeae 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 Nymphaeae. 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 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; Alback 2008). One of the arguments advocated by those in favour of recognizing paraphyletic taxa (e.g., Hörandl 2006) is that all taxa...
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 Pseudolysimachium Opiz into Veronica L. (Plantaginaceae, Lamiales) and explained that characters used to define Pseudolysimachium 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.

Acknowledgements

The authors wish to thank Surrey W. L. Jacobs (Royal Botanic Gardens, National Herbarium, Sydney) and C. Barre Helliquist (Massachusetts College of Liberal Arts, Department of Biology, North Adams) for long-standing collaboration in water-lily research, for providing plant material and for fruitful discussions on the status of Ondinea. We also thank the two reviewers for valuable comments on the manuscript.

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