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

Authors: Cornelia Löhne, John H. Wiersema, and Thomas Borsch
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Abstract

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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 gynoecium 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-
itudinally ridged glabrous surfaces, with those of either N. subg. Lotos (DC.) Conard (usually ridged, but sometimes with hairs) or the Confluences (small-seeded) group of N. subg. Anechphya (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. Anechphya (Fig. 1). Thus, the position of Ondinea within the Australian radiation of Anechphya 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 characteristics 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 Domín, 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 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. Anechphya, 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 Rehnnel & 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; Albach 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 *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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