A New Genus and New Combinations in Australian *Villarsia* (Menyanthaceae)

Nicholas P. Tippery and Donald H. Les

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs,
Connecticut 06269, U.S.A. nicholas.tippery@uconn.edu

ABSTRACT. Menyanthaceae species in Australia formerly belonging to the genus *Villarsia* Ventenat, which morphological and molecular data have shown to be paraphyletic, are provided with new combinations in *Liparophyllum* Hooker f. and the novel genus *Ornduffia* Tippery & Les: *L. capitatum* (Nees ex Lehmann) Tippery & Les; *L. congestiflorum* (F. Mueller) Tippery & Les, lectotypified here; *L. exaltatum* (Solander ex Sims) Tippery & Les; *L. exiguum* (F. Mueller) Tippery & Les; *L. lasiospermum* (F. Mueller) Tippery & Les, lectotypified here; *L. latifolium* (Bentham) Tippery & Les; *L. violifolium* (F. Mueller) Tippery & Les, lectotypified here; *O. albiflora* (F. Mueller) Tippery & Les, lectotypified here; *O. calthifolia* (F. Mueller) Tippery & Les, lectotypified here; *O. marchantii* (Ornduff) Tippery & Les; *O. parnassifolia* (Labillardière) Tippery & Les; *O. reniformis* (R. Brown) Tippery & Les; *O. submersa* (Aston) Tippery & Les; and *O. umbricola* (Aston) Tippery & Les.

Key words: Australia, *Liparophyllum*, Menyanthaceae, *Ornduffia*, *Villarsia*.

Menyanthaceae are a morphologically diverse family of aquatic and wetland plants in the order Asterales, consisting of 60 to 70 species that are distributed worldwide (Tippery et al., 2008). Two of the five genera, *Menyanthes* L. and *Nephrophyllidium* Gilg (= *Fauria* Franchet), are monotypic and restricted to the Northern Hemisphere. *Liparophyllum* Hooker f. (also monotypic) and *Villarsia* Ventenat (18 species) are found only in the Southern Hemisphere, and *Nymphoides* Séguier (40 to 50 species) is cosmopolitan in distribution.

Tournefort (1700) had recognized two genera (*Menyanthes* and *Nymphoides*) that Linnaeus (1753) combined under *Menyanthes* to include the emergent wetland species *M. trifoliata* L. and two floating-leaved species that currently are circumscribed within *Nymphoides*: *N. indica* (L.) Kuntze and *N. peltata* (S. G. Gmelin) Kuntze. Séguier (1754) validly published *Nymphoides* subsequently; however, the later synonym *Limnanthemum* S. G. Gmelin (1769) remained the accepted genus name for over 100 years (Grisebach,

1845; Mueller, 1875; Bentham & Hooker, 1876). Ventenat (1803) later segregated another genus, *Villarsia*, to accommodate the distinct South African species *V. capensis* (Houttuyn) Merrill.

Over the next century, many species were transferred between *Limnanthemum* and *Villarsia*, particularly in Australia, where taxa with either floating-leaved or emergent habit occur. Menyanthaceae species in Australia initially were designated under *Villarsia* (Brown, 1810; Don, 1837; Endlicher et al., 1837; Lehmann, 1845), although some were included under *Menyanthes* (Sims, 1807, 1810) or the gentianaceous genus *Swertia* L. (Labillardière, 1804–1805). In a comprehensive treatment of Menyanthaceae, Grisebach (1845) listed species of both *Limnanthemum* and *Villarsia* in Australia and provided morphological characters to distinguish the genera, including epipetalous glands, capsule dehiscence, floating leaves, and inflorescence architecture. However, Grisebach recognized only two species of Menyanthaceae in Australia, *L. geminatum* (R. Brown) Grisebach (= *Nymphoides geminata* (R. Brown) Kuntze) and *V. parnassifolia* (Labillardière) R. Brown. Many additional Australian species were designated subsequently by Mueller, under both *Limnanthemum* (Mueller, 1854, 1858) and *Villarsia* (Mueller, 1860, 1865, 1868). After noting that few characters could distinguish the genera, Mueller eventually transferred every menyanthaceous species in Australia to *Limnanthemum* (Mueller, 1875), including *Liparophyllum gunnii* Hooker f., an anomalous species for which Hooker (1847) had established a separate genus.

Other authors, however, maintained the independence of *Liparophyllum* and established the boundary between *Limnanthemum* and *Villarsia* out of which current generic circumscriptions developed (Bentham & Mueller, 1869; Bentham & Hooker, 1876). The few characters that were used to distinguish between *Limnanthemum* and *Villarsia* included capsule dehiscence and inflorescence morphology, and *Liparophyllum* was differentiated by linear leaves and a lack of carpellary glands. Later, Kuntze (1891) further codified the assignment of species to genera when he transferred nearly all currently recognized species

in Australia to either *Nymphoides* or *Renealmia* Houttuyn (a *Villarsia* synonym and later homonym of *Renealmia* L. f.). Recent authors have maintained the separation of *Nymphoides* and *Villarsia* on morphological grounds that include vegetative habit and inflorescence architecture, and have supported the independence of *Liparophyllum*, which is unique among Menyanthaceae in having solitary flowers and linear leaves (Aston, 1973; Chuang & Ornduff, 1992; Cook, 1996).

Divisions among Menyanthaceae genera have been upheld in part because of their relatively discrete geographic ranges. Although *Nymphoides* species are found worldwide and *Villarsia* are relatively abundant in the Southern Hemisphere, there are few areas where both genera co-occur. Species of *Nymphoides* are absent from southwestern Australia, where over half of *Villarsia* species are endemic (Aston, 1973). In addition, *Menyanthes* and *Nephrophyllidium* are restricted to the Northern Hemisphere, which precludes any overlap in range with the Southern Hemisphere genera *Liparophyllum* and *Villarsia* (Cook, 1996).

Despite the general geographic and morphological distinctness of Menyanthaceae genera, several species of different genera are remarkably similar in their floral and seed morphology, which often have been considered as diagnostic (Grisebach, 1845; Aston, 1969; Chuang & Ornduff, 1992). Flowers in Menyanthaceae are yellow or white (rarely tinged with purple) and have either a dense covering of hair, e.g., *Menyanthes trifoliata*, *Nymphoides indica*, *Villarsia submersa* Aston, or lateral petal wings, e.g., *Nephrophyllidium crista-galli* (Menzies ex Hooker) Gilg, *Nymphoides cristata* (Roxburgh) Kuntze, *Villarsia capensis* (Tippery et al., 2008). Large seeds with smooth, elongate epidermal cells distinguish *Menyanthes* and *Nephrophyllidium* from the other genera, which have smooth to tuberculate seed surfaces that may be ornamented with trichomes, e.g., *Nymphoides peltata*, *Villarsia exaltata* (Solander ex Sims) G. Don, or a nutritive caruncle, e.g., *Nymphoides subacuta* Aston, *Villarsia latifolia* Benthham (Chuang & Ornduff, 1992). Although the distinctness of *Menyanthes* and *Nephrophyllidium* from the remainder of Menyanthaceae has been confirmed repeatedly (e.g., Nilsson, 1973; Chuang & Ornduff, 1992), morphological boundaries among the other genera have been obscured by a number of overlapping character states.

Phylogenetic analyses of the Asterales, conducted using both morphological and molecular data, have consistently resolved Menyanthaceae as monophyletic, within which *Menyanthes* and *Nephrophyllidium* are the sister clade to the remainder of the family (Olmstead et al., 2000; Soltis et al., 2000; Lundberg &

Bremer, 2003). An analysis of Menyanthaceae taxa using only morphological data (including pollen, seed, and flavonoid data) resolved the floating-leaved genus *Nymphoides* as monophyletic, except for *N. exigua* (F. Mueller) Kuntze, which lacks floating leaves (Tippery et al., 2008). In the same study, *Villarsia* resolved as a paraphyletic grade toward *Nymphoides*, and *Liparophyllum* was unresolved as either the sister taxon of *Nymphoides* or a lineage within the *Villarsia* grade. Phylogenetic analysis of morphological characters thus indicated that although *Nymphoides* is monophyletic, *Villarsia* does not comprise a morphologically coherent group (Tippery et al., 2008).

We have conducted an updated phylogenetic analysis of combined nucleotide (nuclear ribosomal ITS [nrITS], *rbcL*, *matK*, and *trnK* introns) and structural (encoded *matK/trnK* indels and nrITS secondary structure) molecular data, using the methods outlined in Tippery and Les (2008) and Tippery et al. (2008). In addition to previously reported sequences (Tippery et al., 2008), we obtained new molecular data for one *Villarsia* specimen from South Africa: *V. goldblattiana* Ornduff (*Rebello 2008113001*, NBG), and two specimens from Western Australia: *V. submersa* (Hort & Crawford 1845, PERTH) and *V. violifolia* F. Mueller (*Ornduff 9342*, UC; GenBank accession numbers EU342366–EU342370, FJ546980–FJ546982). The resulting phylogeny (Fig. 1) produced a congruent topology but showed better-resolved interspecific relationships than the tree generated strictly from morphological data (Tippery et al., 2008). *Nymphoides* was strongly supported as monophyletic, whereas *Villarsia* resolved as three separate clades, one of which also contained *Liparophyllum* (Fig. 1). The two larger *Villarsia* clades consisted entirely of Australian taxa, and the other clade contained only the three South African species. Each of the Australian clades included taxa from both the eastern and western floristic regions of that continent (Takhtajan, 1986). The phylogeny depicted here (Fig. 1) represents a complete sampling of *Villarsia* species worldwide. It should be noted that separate analyses have resolved another species, *V. cambodiana* Hance from Southeast Asia, within *Nymphoides*, where we recommend its transfer (Tippery et al., 2010).

Although the clades of *Villarsia* that were resolved in the combined data analysis have never been suggested on the basis of morphology alone, several morphological characters nonetheless support them as separate, internally cohesive groups. Species in the clade that includes the anomalous, floating-leaved species *V. submersa* are united by their remarkably similar seeds that are ellipsoid with a subterminal hilum (Chuang & Ornduff, 1992). Seeds of most

Figure 1. Phylogenetic relationships in Menyanthaceae, reconstructed using molecular data (nrITS, *matK*, *rbcL*, *trnK* introns, and nrITS secondary structure), with analyses as described by Tippery and Les (2008) and Tippery et al. (2008). Topology represents the single most-parsimonious tree; nodal values indicate parsimony bootstrap and Bayesian posterior probability support, above and below each branch, respectively. Names shown represent previously circumscribed *Villarsia* taxa. Revised generic circumscriptions proposed in this paper are depicted at right.

species in the clade are smooth, although some taxa (e.g., *V. albiflora* F. Mueller, *V. calthifolia* F. Mueller) have seeds that are densely covered with acuminate trichomes. In addition, species in the clade all have substantially more ovules per placenta than other *Villarsia* species (Tippery et al., 2008). The South African species, which form a second clade, are characterized by the most deeply fimbriate petal margins and the fewest seeds per capsule of any *Villarsia* (Ornduff, 2001; Tippery et al., 2008).

The third clade resolved by the combined data analysis is quite heterogeneous taxonomically and consists of species with varied growth habit, inflorescence architecture, and seed morphology (i.e., *Liparophyllum gunnii*, *Nymphoides exigua*, several *Villarsia* species). Nonetheless, subsets of the taxa within this clade share a number of distinctive traits that are found nowhere else in Menyanthaceae. Among the traits are inflorescences that are few flowered (*L. gunnii*, *N. exigua*, *V. violifolia*) or congested (*V. capitata* Nees ex Lehmann, *V. congestiflora* F. Mueller) and various distinguishing seed features that include sparse trichomes (*V. exaltata*, *V. lasiosperma* F. Mueller), a smooth testa with indistinct epidermal cells (*N. exigua*, *V. capitata*, *V. latifolia*, *V. violifolia*), or a nutritive caruncle (*V. congestiflora*, *V. exaltata*, *V. latifolia*, *V. violifolia*). None of these features occurs in the other *Villarsia* clades (Aston, 1969; Chuang & Ornduff, 1992; Tippery et al., 2008). Furthermore, all taxa in this otherwise diverse clade are distinct from other *Villarsia* in having between five and 10 ovules per placenta (Tippery et al., 2008).

Analyses of molecular data clearly indicate that *Villarsia* is paraphyletic as currently circumscribed (Fig. 1; Tippery et al., 2008). Consequently, in order to recognize groups that are meaningful phylogenetically, it will be necessary to revise the current taxonomy to reflect monophyletic genera. This objective can be achieved either by expanding *Nymphoides* to include all of *Villarsia* and *Liparophyllum*, or by subdividing *Villarsia* among the three clades that resolve in phylogenetic analyses (Fig. 1). Under the former scenario, the defining morphological features of *Nymphoides*, namely floating leaves that support a lax inflorescence, would no longer be diagnostic for the genus. In addition, the inclusion of morphologically diverse species under *Nymphoides* could precipitate a concomitant condensation of *Menyanthes* and *Nephrophyllidium* into a single genus so that Menyanthaceae genera would remain equivalently diverse. Alternatively, the latter scenario of subdividing *Villarsia* would preserve the distinctness of *Nymphoides* as well as provide unifying morphological traits for the separate *Villarsia* clades. Under neither scenario would the genus name *Villarsia* apply

to any taxon in Australia, because the type species *V. capensis* belongs to the isolated South African clade (Fig. 1). In our opinion, optimal clarity would be achieved by retaining *Nymphoides* as currently circumscribed (except for *N. exigua*), while subdividing *Villarsia* among the clades that were identified by the molecular and morphological data analyses.

Here we revise the nomenclature for species that formerly belonged to *Villarsia*. The genus name remains associated with *V. capensis* and the other two South African species, *V. goldblattiana* and *V. manningiana* Ornduff. For the morphologically diverse group that includes *Liparophyllum gunnii*, *Nymphoides exigua*, and several *Villarsia* species, the genus *Liparophyllum* is expanded to include all species resolving within the clade. Lastly, we establish a new genus to accommodate the third group of *Villarsia* species, which is separated from other taxa in the phylogenetic analysis by a well-defined, strongly supported branch (Fig. 1; Tippery et al., 2008). The appropriate taxonomic combinations, including emended descriptions of the genera *Liparophyllum* and *Villarsia*, are provided below.

TAXONOMIC TREATMENT

- 1. *Liparophyllum* Hooker f.**, London J. Bot. 6: 472. 1847. TYPE: *Liparophyllum gunnii* Hooker f., London J. Bot. 6: 473. 1847.

Aquatic or wetland annual or perennial herbs. *Radical leaves* erect, with sheathing bases; sessile and linear (*Liparophyllum gunnii*) or petiolate with ovate or ellipsoid laminae, margins entire to crenate-dentate. *Inflorescence* paniculate; flowers 1 to 3 per node or congested into dense, sessile or subsessile capitula (*L. capitatum* (Nees ex Lehmann) Tippery & Les, *L. congestiflorum* (F. Mueller) Tippery & Les), or the whole inflorescence consisting of 1 to 5 flowers (*L. exiguum* (F. Mueller) Tippery & Les, *L. gunnii*, *L. violifolium* (F. Mueller) Tippery & Les). *Calyx* persistent, divided into 5 lobes; *corolla* yellow or white, gamopetalous, 5-lobed, rotate, throat fimbriate, margins entire or serrulate; *stamens* 5, alternate with corolla lobes, inserted on the corolla tube at the junction of the lobes; anthers 2-celled, sagittate, introrse; *ovary* unilocular with 2 parietal placentae; base surrounded by 5 glands (absent in *L. gunnii*); style solitary with 2 stigmas; *ovules* 5 to 10 per placenta. *Capsule* dehiscent into 4 valves, adnate to calyx at the base only (*L. gunnii*, *L. lasiospermum* (F. Mueller) Tippery & Les) or for more than 1/4 of length, of equal length or longer than the calyx; *seeds* 0.7–3 mm diam., orbicular or ellipsoid, smooth or sparsely covered with trichomes (< 1 trichome per

epidermal cell; *L. exaltatum* (Solander ex Sims) Tippiery & Les, *L. lasiospermum*), hilum terminal (angle between major axis and hilum with vertex at seed center < 30°; angle approaches 30° in *L. exaltatum* and *L. latifolium*), caruncle present (*L. congestiflorum*, *L. exaltatum*, *L. latifolium*, *L. violifolium* (Bentham) Tippiery & Les) or lacking.

1. ***Liparophyllum capitatum*** (Nees ex Lehmann) Tippiery & Les, comb. nov. Basionym: *Villarsia capitata* Nees ex Lehmann, Pl. Preiss. 1: 365. 1845. *Limnanthemum capitatum* (Nees ex Lehmann) F. Mueller, Fragm. 9: 40. 1858. *Renalmia capitata* (Nees ex Lehmann) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: "In paludosis ad flumen Canning, Perth," Nov. 1841, *L. Preiss 1956* (holotype, LD; isotypes, B, G [2 sheets], GOET, L [3 sheets], M not seen, MEL [2 sheets], NSW, S, STR).

Villarsia involocrata Hooker, Icon. Pl. viii. 725. 1845. TYPE: Australia. Western Australia: Swan River, *J. Drummond 7* (holotype, K; isotype, MEL).

Typification. Duplicates of *Preiss 1956* are lodged in herbaria in Europe and Australia, although few of these bear more than cursory label information. Preiss specimens that were owned by Lehmann reside at LD (Stafleu & Cowan, 1983); indeed, the label of their *Preiss 1956* specimen bears locality information, apparently written by Preiss, matching the protologue: "In paludosis ad fl. Canning (Perth), Novbr. 41," with an additional note: "Flor. flavi." The species name appears above, clearly written by Nees. Although there are numerous duplicates of *Preiss 1956*, the provenance of the LD specimen and its annotation by both Preiss and Nees leave little doubt that it should be regarded as the holotype.

2. ***Liparophyllum congestiflorum*** (F. Mueller) Tippiery & Les, comb. nov. Basionym: *Villarsia congestiflora* F. Mueller, Fragm. 6: 141. 1868. *Limnanthemum congestiflorum* (F. Mueller) F. Mueller, Syst. Census Austral. Pl. 90. 1882. *Renalmia congestiflora* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: Murchison River, s.d., *A. F. Oldfield s.n.* (lectotype, designated here, MEL).

Typification. In the original description of *Villarsia congestiflora*, Mueller (1868) designated two specimens, both collected by Oldfield: "Ad fluvios Swan-River et Murchison-River. Oldf." Three Oldfield specimens annotated by Mueller reside at MEL. Two of these (MEL 872 and 873) give only the locality "Near Perth" written by Oldfield, with another label on which Mueller wrote "Swan River." The third specimen (MEL 874), which we have selected as the

lectotype, is the only one whose original label (written by Oldfield) matches the published text, and furthermore it represents the most morphologically complete specimen of the three.

3. ***Liparophyllum exaltatum*** (Solander ex Sims) Tippiery & Les, comb. nov. Basionym: *Menyanthes exaltata* Solander ex Sims, Bot. Mag. 26: 1029. 1807. *Limnanthemum exaltatum* (Solander ex Sims) F. Mueller, Fragm. 9: 165. 1875. *Renalmia exaltata* (Solander ex Sims) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. New South Wales: 28 Apr.–5 May 1770, *J. Banks & D. C. Solander s.n.* (lectotype, designated by Aston, 1969: 44, BM; isotype, NSW not seen).
4. ***Liparophyllum exiguum*** (F. Mueller) Tippiery & Les, comb. nov. Basionym: *Limnanthemum exiguum* F. Mueller, Fragm. 1: 40. 1858. *Villarsia exigua* (F. Mueller) Hooker f., Bot. Antarct. Voy., Vol. 3, Fl. Tasman. 2: 368. 1859. *Nymphoides exigua* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Tasmania: "Wet muddy places in brackish water, South Port," s.d., *A. F. Oldfield s.n.* (holotype, K).
5. ***Liparophyllum lasiospermum*** (F. Mueller) Tippiery & Les, comb. nov. Basionym: *Villarsia lasiosperma* F. Mueller, Fragm. 6: 137. 1868. *Limnanthemum lasiospermum* (F. Mueller) F. Mueller, Fragm. 9: 165. 1875. *Renalmia lasiosperma* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: Swamps at King George Sound, Albany, Oct. 1867, *F. Mueller s.n.* (lectotype, designated here, MEL).

Typification. Mueller (1868) listed several of his own collections in the description of *Villarsia lasiosperma*: "In paludibus aqua pura repletis prope urbem Albany, ad bases montium Willyung et montes Porongorup versus. F.M." Three specimens at MEL were interpreted by Aston (1969) to represent syntypes, although curiously none of their labels matches the published text exactly: "Forest swamps north of Albany, Oct. 1867," with an apparently later label "Swamps at King George's Sound, Oct. 67" (MEL 875); "Swamps in the rear of Mt. Melville, Oct. 67," two packets apparently containing seeds, with a later label "Swamps at King George's Sound (fresh water), Oct. 67" (MEL 16493); "Heath swamps north of Albany, Oct. 1867," with the same text reproduced on a later label (MEL 16494). We have selected the first of these (MEL 875) to be the lectotype, because it is the most morphologically complete specimen and

its locality description most closely matches the text of the original publication.

6. *Liparophyllum latifolium* (Benth) Tippery & Les, comb. nov. Basionym: *Villarsia latifolia* Benth, Enum. Pl. (Endlicher) 81. 1837. *Limnanthemum latifolium* (Benth) F. Mueller, Fragm. 9: 164. 1875. *Renealmia latifolia* (Benth) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: "King George's Sound," s.d., *C. Hügel s.n.* (holotype, W).

7. *Liparophyllum violifolium* (F. Mueller) Tippery & Les, comb. nov. Basionym: *Villarsia violifolia* F. Mueller, Fragm. 6: 138. 1868. *Limnanthemum violifolium* (F. Mueller) F. Mueller, Syst. Census Austral. Pl. 90. 1882. *Renealmia violifolia* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: Don River, s.d., *T. C. Maxwell s.n.* (lectotype, designated here, MEL).

Typification. Mueller (1868) listed several localities and collectors in the original description of *Villarsia violifolia*: "Ad fluvios Tweed et Don's River; Oldf. Maxw. Prope urbem Hamden, Clarke." Three specimens at MEL, clarified by Aston (1969), conform to the description: "S. W. Austr." collected by Clarke (label in Mueller's hand; MEL 16489); "Plts. matted, fl. yellow, Tweed R. W. Aust." collected by Oldfield (MEL 16490); "Don River, S. W. Aust." collected by Maxwell (labels written by Mueller; MEL 16491 and 16492). Of these, the most complete specimen is the collection by Maxwell, specifically MEL 16491, which we designate as the lectotype.

II. *Ornduffia* Tippery & Les, gen. nov. TYPE: *Villarsia reniformis* R. Brown, Prodr. Fl. Nov. Holland. 437. 1810 $\equiv$ *Ornduffia reniformis* (R. Brown) Tippery & Les.

Genus foliis simplicibus, inflorescentia diffusa paniculataque, lobo corollino quoque alam medianam carenti, capsula fundo solum ad calycem adnata, seminibus non carunculatis *Villarsiae* Ventenat simile, sed ab eo marginibus loborum corollinarum integris serrulatisve, ovulis ad quamque placentam plus quam 10, seminibus ellipticis hilo subterminali differt.

Aquatic or wetland perennial herbs. *Radical leaves* erect or floating, petiolate, with sheathing bases; laminae simple, ovate or ellipsoid, margins entire to crenate-dentate. *Inflorescence* paniculate; flowers 1 to 3 per node. *Calyx* persistent, divided into 5 lobes; *corolla* yellow or white, gamopetalous, 5-lobed, rotate, throat fimbriate, margins entire or serrulate; *stamens* 5, alternate with corolla lobes, inserted on the corolla tube at the junction of the lobes; anthers 2-celled,

sagittate, introrse; *ovary* unilocular with 2 parietal placentae; base surrounded by 5 glands; style solitary with 2 stigmas; *ovules* 11 or more per placenta. *Capsule* dehiscent into 4 valves, adnate to calyx only at the base; *seeds* 0.5–1.9 mm diam., ellipsoid, smooth or densely covered with trichomes (one per epidermal cell; *O. albiflora* (F. Mueller) Tippery & Les, *O. calthifolia* (F. Mueller) Tippery & Les, *O. marchantii* (Ornduff) Tippery & Les, *O. umbricola* var. *beaugleholei* (Aston) Tippery & Les), hilum subterminal (angle between major axis and hilum with vertex at seed center $> 30^\circ$), without a conspicuous caruncle.

Etymology. We have chosen the generic name *Ornduffia* to honor the late Robert Ornduff (1932–2000), who contributed immensely to the study of reproductive system ecology and evolution in Menyanthaceae, and *Villarsia* in particular.

1. *Ornduffia albiflora* (F. Mueller) Tippery & Les, comb. nov. Basionym: *Villarsia albiflora* F. Mueller, Fragm. 2: 21. 1860. *Limnanthemum albiflorum* (F. Mueller) F. Mueller, Syst. Census Austral. Pl. 90. 1882. *Renealmia albiflora* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: Perth, s.d., *A. F. Oldfield s.n.* (lectotype, designated here, MEL).

Typification. Mueller (1860) indicated two collections in the description of *Villarsia albiflora*: "In stagnis prope oppida Perth et Hampden. Clarke et Oldfield." Aston (1969) located two corresponding Oldfield specimens at MEL: "Fl. white, Hampden, W. A." (MEL 16430) and "Perth, W. Aust." (MEL 16447). We designate the latter specimen (MEL 16447), which has more leaves and flowers, as the lectotype.

2. *Ornduffia calthifolia* (F. Mueller) Tippery & Les, comb. nov. Basionym: *Villarsia calthifolia* F. Mueller, Fragm. 6: 140. 1868. *Limnanthemum calthifolium* (F. Mueller) F. Mueller, Fragm. 9: 164. 1875. *Renealmia calthifolia* (F. Mueller) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: Porongorup, Oct. 1867, *F. Mueller s.n.* (lectotype, designated here, MEL).

Typification. The original description of *Villarsia calthifolia* (Mueller, 1868) listed the locality "In rivulis et in summitatibus rupestribus montium Porongorup. F. M." Aston (1969) identified three Mueller specimens that she considered syntypes: "Porongorup" (MEL 16480); "Summit of the Porongorup. Cor. yellow. Oct. 67" (MEL 16481); and "Porongorup" (NSW 90574). None of the specimens

represents an entire plant, but the most complete combination of leaf and inflorescence occurs on one of the Melbourne sheets (MEL 16481), which we designate as the lectotype.

- 3. **Ornduffia marchantii** (Ornduff) Tippet & Les, comb. nov. Basionym: *Villarsia marchantii* Ornduff, Syst. Bot. 15: 216–220. 1990. TYPE: Australia. Western Australia: Wet soil in deep shade of *Trymalium* thicket, below Wansbrough Walk on N side of Porongorup Range, elevation 450 m, 15 Nov. 1983, R. Ornduff 9323 (holotype, PERTH).
- 4. **Ornduffia parnassifolia** (Labillardière) Tippet & Les, comb. nov. Basionym: *Swertia parnassifolia* Labillardière, Nov. Holl. Pl. 1: 72, t. 97. 1805. *Villarsia parnassifolia* (Labillardière) R. Brown, Prodr. Fl. Nov. Holland. 457. 1810, as “*V. parnassifolia*.” *Limnanthemum parnassifolium* (Labillardière) F. Mueller, Fragm. 9: 165. 1875. *Renealmia parnassifolia* (Labillardière) Kuntze, Revis. Gen. Pl. 430. 1891. TYPE: Australia. Western Australia: In terra Van-Leeuwin, s.d., J. J. H. Labillardière s.n. (lectotype, designated by Aston, 1969: 37, FI; isotypes, BM, MEL, NSW).
- 5. **Ornduffia reniformis** (R. Brown) Tippet & Les, comb. nov. Basionym: *Villarsia reniformis* R. Brown, Prodr. Fl. Nov. Holland. 457. 1810. TYPE: Australia. Tasmania: Port Dalrymple, s.d., W. Paterson s.n. (lectotype, designated by Aston, 1969: 50, BM).
- 6. **Ornduffia submersa** (Aston) Tippet & Les, comb. nov. Basionym: *Villarsia submersa* Aston, Muelleria 2: 19. 1969. TYPE: Australia. Western Australia: Boyanup, 9 Sep. 1953, R. D. Royce 3778 (holotype, PERTH; isotype, MEL).
- 7. **Ornduffia umbricola** (Aston) Tippet & Les, comb. nov. Basionym: *Villarsia umbricola* Aston, Muelleria 2: 53. 1969. TYPE: Australia. South Australia: ca. 4 mi. direct line ESE of Myponga, betw. Myponga & Hindmarsh Valley, 18 Dec. 1966, H. I. Aston 1531 (holotype, MEL; isotypes, AD not seen, K not seen, NSW).
- 8. **Ornduffia umbricola** var. **beaubleholei** (Aston) Tippet & Les, comb. nov. Basionym: *Villarsia umbricola* var. *beaubleholei* Aston, Muelleria 2: 55. 1969. TYPE: Australia. Victoria: 1.3 mi. W of Dergholm, along the rd. to Penola, 15 Dec. 1965, H. I. Aston 1445 (holotype, MEL; isotypes, AD not seen, BM not seen, K not seen, MEL not seen, NSW, PERTH).

III. **Villarsia** Ventenat, Choix Pl. t. 9. 1803, nom. cons. TYPE: *Villarsia ovata* (L. f.) Ventenat, Choix Pl. t. 9. 1803, typ. cons., = *Menyanthes ovata* L. f., Suppl. Pl. 133. 1781, = *V. capensis* (Houttuyn) Merrill, J. Arnold Arbor. 19: 360. 1938. *Renealmia capensis* Houttuyn, Handl. Pl.-Kruidk. 8: 335. 1777.

Aquatic or wetland perennial herbs. *Radical leaves* erect, with sheathing bases; petiole with ovate or ellipsoid laminae, margins entire to crenate-dentate. *Inflorescence* paniculate; flowers 1 to 3 per node. *Calyx* persistent, divided into 5 lobes; *corolla* yellow, gamopetalous, 5-lobed, rotate, throat fimbriate, margins deeply fimbriate; *stamens* 5, alternate with corolla lobes, inserted on the corolla tube at the junction of the lobes; anthers 2-celled, sagittate, introrse; *ovary* unilocular with 2 parietal placentae; base surrounded by 5 glands; style solitary with 2 stigmas; *ovules* 1 to 4 per placenta. *Capsule* dehiscent into 4 valves, adnate to calyx only at the base; of equal length or shorter than the calyx; *seeds* 1.5–2.5 mm diam., orbicular, smooth or with bulliform protuberances, hilum terminal (angle between major axis and hilum with vertex at seed center > 30°), without a conspicuous caruncle.

KEY TO GENERA OF MENYANTHACEAE WORLDWIDE

- 1a. Leaves trifoliate; inflorescence an erect raceme with > 10 flowers. *Menyanthes*
- 1b. Leaves simple; inflorescence lax, or if erect, then capitate, paniculate, or consisting of < 5 flowers. 2
- 2a. Leaves erect, their margins distinctly crenate; pollen grains subprolate to prolate; seeds with distinct, narrowly elongate epidermal cells, their surface smooth. *Nephrophyllidium*
- 2b. Leaves floating, or if erect then margins entire, dentate, or indistinctly crenate; pollen grains peroblate to suboblate; seeds with indistinct or orbicular epidermal cells, their surface smooth, roughened, tuberculate, or possessing trichomes 3
- 3a. Plants submersed with floating leaves (emergent in mudflat forms or when crowded); inflorescence lax, the flowers in pairs or umbellate, supported by 1 or more floating leaves, or erect and paniculate with > 10 flowers occurring in pairs *Nymphoides*
- 3b. Plants submersed (*O. submersa*) or emergent, with erect and/or floating leaves; inflorescence erect or lax; if erect, then either capitate, paniculate with flowers arising singly (rarely paired), or consisting of ≤ 5 flowers; if lax, then never supported by a floating leaf (*O. submersa*) 4
- 4a. Corolla lobe margins fimbriate; each placenta with 1 to 4 ovules; seeds orbicular, > 1.5 mm diam. *Villarsia*
- 4b. Corolla lobe margins entire or serrulate; each placenta with ≥ 5 ovules; seeds ellipsoid, or < 1.4 mm diam. if orbicular 5
- 5a. Each placenta with 5 to 10 ovules; inflorescence capitate, paniculate, or reduced to ≤ 5 flowers; seeds lacking trichomes on some or all epidermal cells; if trichomes absent, then either margins of

- epidermal cells inconspicuous (under 100× magnification) or seed caruncle present. . . *Liparophyllum*
- 5b. Each placenta with ≥ 11 ovules; inflorescence always paniculate with > 10 flowers; seeds bearing a trichome on each epidermal cell or, if trichomes absent, then margins of epidermal cells conspicuous; seed caruncle absent *Ornduffia*

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