

Splitting *Caldesia* in favour of *Albidella* (Alismataceae)

Author(s): Samuli Lehtonen

Source: Australian Systematic Botany, 30(1):64-69.

Published By: CSIRO Publishing

URL: <http://www.bioone.org/doi/full/10.1071/SB16050>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Splitting *Caldesia* in favour of *Albidella* (Alismataceae)

Samuli Lehtonen

Biodiversity Unit, University of Turku, FI-20014 Turku, Finland. Email: samile@utu.fi

Abstract. Phylogenetic analyses based on 10 molecular markers unquestionably support a sister relationship between *Albidella nymphaeifolia* and the *Caldesia oligococca* species group. The type species of the genus *Caldesia* is excluded from this monophylum. These results are unsurprising in the light of morphological characteristics, but require three new combinations in *Albidella* to render both *Albidella* and *Caldesia* monophyletic. These new combinations are provided here. Under the new circumscription, *Albidella* shows a disjunct distribution pattern, with one species in the Caribbean region and three species distributed from tropical Africa and along the margins of the Indian Ocean to Australia.

Received 22 March 2016, accepted 21 February 2017, published online 31 May 2017

Introduction

Caldesia Parl. and *Albidella* Pichon are small genera in the aquatic plant family Alismataceae (Les and Tippery 2013). *Albidella* has been considered either as monotypic genus from Cuba and Central America (Pichon 1946; Lehtonen and Myllys 2008), or it has been placed in *Echinodorus* Rich. (e.g. Rataj 1975; Haynes and Holm-Nielsen 1994; Lot and Novelo 1994), or even considered synonymous with *Caldesia* (Hutchinson 1959). However, generally, *Caldesia* is circumscribed as a purely Old World genus, although with an accepted fossil record from North America (Haggard and Tiffney 1997). This traditional circumscription of *Caldesia* brings together species possessing distinct fruit morphologies (Haggard and Tiffney 1997). The reniform fruits with crested to spiny ridges, present in the Palaeotropical *Caldesia oligococca* (F.Muell.) Buchenau species complex, are distinct from other *Caldesia*, but strikingly similar to the fruits of Neotropical *Albidella* (Lehtonen 2009). *Caldesia* can hardly be differentiated from *Albidella* by vegetative characters alone. Therefore, it was not surprising that morphology-based cladistic analysis resolved *Caldesia s.l.* as non-monophyletic by pairing *C. oligococca* with *Albidella* (Lehtonen 2009).

Phylogenetic analyses using molecular data have further increased our understanding of Alismataceae taxonomy, for example, by demonstrating that Limnocharitaceae is nested within it; however, the relationships of many genera have remained poorly resolved or unsupported (Chen *et al.* 2012; Les and Tippery 2013; Petersen *et al.* 2016; Ross *et al.* 2016). So far, only one molecular study has included both *Albidella* and *C. oligococca* in the same analysis (Chen *et al.* 2012). That study did not resolve them together, but *C. oligococca* was placed as sister to *C. parnassifolia* (L.) Parl., and *Albidella* remained as a rather distinct lineage of its own. However, this inference may have suffered from the poor quality of the published *Albidella* *matK* sequence (Les and Tippery 2013) and the paucity of data compatible with *Albidella* and *C. oligococca*

group in that study. Here, I have re-sequenced the *matK* gene from *A. nymphaeifolia* (Griseb.) Pichon, the *rbcL* gene from *C. parnassifolia*, and produced additional novel sequence data to complement previously published datasets, so as to test the morphologically sound hypothesis that the *C. oligococca* group actually belongs to *Albidella*.

Materials and methods

The sequence data used in the present study were largely produced and published by Les *et al.* (1997), Davis *et al.* (2004), Petersen *et al.* (2006), Lehtonen and Myllys (2008), Chen *et al.* (2012), Les and Tippery (2013), Cuenca *et al.* (2016) and Ross *et al.* (2016). The data matrix used by Chen *et al.* (2012) was downloaded and supplemented by querying additional data from GenBank and producing novel sequences (Table 1). The *matK* gene of *A. nymphaeifolia* published in Lehtonen and Myllys (2008) was re-sequenced from the original DNA extraction, using a different set of polymerase chain reactions (PCRs) and sequencing primers (1R_KIM and 3F_KIM; Dunning and Savolainen 2010). The new *matK* sequence had high quality, unlike the original one, and the poor quality of which may have compromised earlier inferences. The novel *rbcL* sequences were amplified and sequenced using primers 1F (Fay *et al.* 1997) and 1204R (Olmstead and Palmer 1994). For the other newly produced sequences, primers used by Chen *et al.* (2012) were applied. All the sequencing reactions were performed at Macrogen Inc. (Seoul, South Korea, or Amsterdam, Netherlands). This resulted in a data matrix of 10 genetic markers and 55 taxa. *Butomus umbellatus* L. was used as an outgroup.

The sequence data were aligned using default settings in MAFFT, ver. 7.029b (Kato and Standley 2013), without manual manipulations. The alignments, as well as resulting trees, are available in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S20397>, accessed 4 January 2017). Initially,

Table 1. Taxa sampled

Analysed taxa and genetic markers with GenBank accession codes. Loci marked with an asterisk were taken from the data published by Ross *et al.* (2016), available at figshare.com (DOI:10.6084/m9.figshare.1407422). New and updated sequences are in bold

Taxon	ITS	psbA	rbcL	matK	rpoB	rpoC1	trnK 5'intron	trnK 3'intron	cob	atp1
<i>Albidella acanthocarpa</i>	HQ456396	—	HQ456501	HQ456460	—	—	—	—	—	—
<i>Albidella nymphaeifolia</i>	EF088077	KX980066	KU499837	EF088125	KX980072	KX980078	—	—	KX980058	KX980052
<i>Albidella oligococca</i>	HQ456397	*	AY277799	AY952427	*	*	—	—	DQ859129	AY277800
<i>Alisma canaliculatum</i>	DQ339081	JF975413	JF781042	AB040179	JF781090	JF781105	JF781026	JF781011	—	—
<i>Alisma gramineum</i>	JF780979	JF975412	JF781041	JF781067	—	—	—	—	JF780993	JF781002
<i>Alisma nanum</i>	JF780978	JF975411	JF781040	JF781066	—	—	—	—	—	—
<i>Alisma plantago-aquatica</i>	JF780977	JF975410	L08759	JF781065	JF781089	JF781104	JF781025	JF781010	DQ859125	AF197717
<i>Alisma triviale</i>	DQ339086	*	*	*	*	*	—	—	—	—
<i>Astonia australiensis</i>	AY335952	*	HQ456499	HQ456457	*	*	AY335996	—	—	—
<i>Baldellia alpestris</i>	HQ607769	—	—	—	—	—	—	—	—	—
<i>Baldellia ranunculoides</i>	DQ339092	JF975421	DQ859163	HQ456458	*	*	HQ456458	—	DQ859127	DQ859092
<i>Baldellia repens</i>	DQ339091	—	—	—	—	—	—	—	—	—
<i>Burnatia enneandra</i>	—	JN547808	JN547809	JN547814	JN547810	JN547811	JN547813	JN547812	JN547807	JN547806
<i>Butomopsis latifolia</i>	HQ456395	*	KC355437	HQ456459	*	*	HQ456459	—	—	—
<i>Butomus umbellatus</i>	JF780965	JF975415	AY149345	AY952416	JF781091	JF781106	JF781027	JF781012	DQ916649	HQ317974
<i>Caldesia grandis</i>	DQ207881	JF975417	JF781043	JF781068	JF781093	JF781108	JF781029	JF781014	JF780995	JF781004
<i>Caldesia parnassifolia</i>	JF780984	JF975416	KU499838	EF088140	JF781092	JF781107	JF781028	JF781013	JF780994	JF781003
<i>Damasonium alisma</i>	JF780988	JF975419	U80678	JF781070	—	—	—	—	—	—
<i>Damasonium minus</i>	JF780987	JF975418	JF781063	JF781069	*	*	—	—	—	—
<i>Damasonium polyspermum</i>	JF780989	JF975420	JF781064	—	—	—	—	—	—	—
<i>Echinodorus amaronicus</i>	—	*	HQ456503	*	*	*	*	*	KU642238	KU642441
<i>Echinodorus berteroi</i>	EF088087	KX980068	KU499839	EF088134	KX980069	KX980079	—	—	KX980060	KX980053
<i>Echinodorus cordifolius</i>	EF088078	KX980067	DQ859164	EF088126	KX980071	KX980082	—	—	KX980059	—
<i>Echinodorus grandiflorus</i>	EF088086	KX980065	U80679	EF088113	KX980070	KX980081	—	—	KX980056	—
<i>Echinodorus horizontalis</i>	EF088050	KX980061	KU499840	EF088099	—	KX980080	—	—	—	KX980050
<i>Echinodorus cf. osiris</i>	EF088094	—	DQ859165	—	—	—	—	—	—	—
<i>Echinodorus</i> sp. 1	JF780980	JF975422	JF781044	JF781071	JF781094	JF781109	JF781030	JF781015	JF780996	JF781005
<i>Echinodorus</i> sp. 2	JF780981	JF975423	JF781045	JF781072	—	—	—	—	—	—
<i>Echinodorus</i> sp. 3	JF780982	JF975424	JF781046	JF781073	JF781095	JF781110	JF781031	JF781016	JF780997	—
<i>Helanthis bolivianum</i>	EF088060	KX980064	KU499841	EF088109	KX980074	KX980076	—	—	KX980054	—
<i>Helanthis parvulum</i>	HQ456399	—	HQ456504	HQ456463	—	—	HQ456463	—	—	—
<i>Helanthis tenellum</i>	EF088056	KX980062	—	EF088105	—	KX980075	KX980084	KX980083	KX980055	KX980051
<i>Helanthis zombiense</i>	EF088072	KX980063	—	EF088120	KX980073	KX980077	—	—	KX980057	—
<i>Hydrocleys nymphoides</i>	JF780985	JF975425	JF781047	JF781074	JF781096	JF781111	JF781032	JF781017	DQ859139	DQ859103
<i>Limncharis flava</i>	JF780986	JF975426	JF781048	JF781075	JF781097	JF781112	JF781034	JF781018	DQ859142	DQ859106
<i>Limnophyton angolensis</i>	JF780991	JF975427	JF781049	JF781076	—	—	—	—	—	—
<i>Limnophyton</i> sp. 1	—	JF975428	JF781050	—	—	—	—	—	—	—

(continued next page)

Table 1. (continued)

Taxon	ITS	psbA	rbcL	matK	rpoB	rpoC1	trnK 5'intron	trnK 3'intron	cob	atp1
<i>Limnophyton</i> sp. 2	JF780992	JF975429	JF781062	JF781077	JF781098	JF781113	JF781033	JF781019	JF780998	JF781006
<i>Luronium natans</i>	DQ333093	*	U80680	HQ456465	*	*	HQ456465	—	HQ317976	HQ317983
<i>Ottelia acuminata</i>	KP676565	JF975430	AY952435	AY952432	JF781099	JF781114	JF781035	JF781020	JF975477	JF975482
<i>Ranalisma humile</i>	HQ456402	*	U80681	HQ456466	*	*	—	—	HQ317977	HQ317984
<i>Ranalisma rostrata</i>	JF780983	JF975431	JF781051	JF781078	JF781101	JF781116	JF781037	JF781022	JF780999	JF781007
<i>Sagittaria graminea</i>	JF780971	JF975437	JF781057	JF781084	—	—	—	—	—	—
<i>Sagittaria guayanensis</i>	JF780968	JF975434	JF781054	JF781081	—	—	—	—	JF781001	JF781009
<i>Sagittaria isoetiformis</i>	JF780976	JF975442	JF781061	JF781088	—	—	—	—	—	—
<i>Sagittaria latifolia</i>	JF780975	JF975441	L08767	JF781087	JF781103	JF781118	JF781039	JF781024	DQ978243	DQ508948
<i>Sagittaria lichuanensis</i> 1	JF780966	JF975432	JF781052	JF781079	JF781102	JF781117	JF781038	JF781023	JF781000	JF781008
<i>Sagittaria montevidensis</i>	JF780974	JF975440	JF781060	JF781086	—	—	—	—	—	—
<i>Sagittaria natans</i>	JF780969	JF975435	JF781055	JF781082	—	—	—	—	—	—
<i>Sagittaria potamogetifolia</i>	JF780972	JF975438	JF781058	JF781085	—	—	—	—	—	—
<i>Sagittaria pygmaea</i>	JF780973	JF975439	JF781059	—	—	—	—	—	—	—
<i>Sagittaria trifolia</i>	JF780970	JF975436	JF781056	JF781083	—	—	—	—	—	—
<i>Sagittaria wuyiensis</i>	JF780967	JF975433	JF781053	JF781080	—	—	—	—	—	—
<i>Stratiotes aloides</i>	KX166964	*	AB004896	AB002576	JF975527	JF975545	AY870382	AY874448	KU642251	KU642455
<i>Wiesneria triandra</i>	AY335953	*	U80682	HQ535983	*	*	—	—	—	—

sequences were concatenated into three datasets according to their genomic origin (nuclear, mitochondrial, plastid). These datasets were analysed under Bayesian and parsimony frameworks, to investigate possible incongruence in the phylogenetic information between the genomes. This was followed by a total evidence analysis (Kluge 1989), with all the data simultaneously analysed under Bayesian and parsimony frameworks. Parsimony analyses were run with TNT (Goloboff *et al.* 2008), by repeating 10 000 random addition sequences, each followed by 50 ratchet iterations (Nixon 1999), using default options and holding up to 10 trees from each replicate. Jackknife support was measured by running 1000 pseudoreplications, each analysis repeating 100 random addition sequences followed by 50 ratchet iterations and holding a single tree per replicate. The default deletion probability of 36% was used for character removal. Gaps were treated as missing data.

Bayesian analyses were undertaken in MrBayes, ver. 3.2.6. (Ronquist *et al.* 2012). The optimal data partitioning and evolutionary models were selected with PartitionFinder (Lanfear *et al.* 2012). The following three partition schemes were tested: (1) all DNA fragments together, (2) all DNA fragments separately, (3) DNA fragments grouped according to their genomic origin (nuclear: ITS1, ITS2, 5.8S; plastid: *matK*, *psbA*, *rbcL*, *rpoB*, *rpoC1*, *trnK3*, *trnK5*; mitochondrial: *atp1*, *cob*). The last partition scheme was selected on the basis of Bayesian information criterion, with GTR+I+G model supported as the best model for each data block. This data-partition scheme and model selection was used in the Bayesian inference. Two simultaneous runs of four chains and 10 million generations were performed, sampling every 1000th tree. The first 25% of samples were discarded as burn-in, and a majority-rule consensus tree was constructed from the remaining trees.

Results and discussion

Analyses of data according to their genomes revealed only a few incongruent nodes with support (PP > 0.9, jackknife > 75; not shown). These included the slightly variable position of *E. grandiflorus* within *Echinodorus* in Bayesian trees and a few derived nodes inside of *Sagittaria* with varying resolution in parsimony as well as in Bayesian trees. Since all the supported incongruence was located very close to the tips of the phylogeny and did not involve *Albidella* or *Caldesia*, it is concluded that data concatenation into a single supermatrix can be justified. The following discussion is, therefore, based on the total evidence trees.

Albidella nymphaeifolia and two representatives of the *C. oligococca* species group, *C. oligococca* and *C. acanthocarpa*, were resolved as a fully supported clade by both Bayesian and parsimony analyses of concatenated data (Fig. 1). This clade was not resolved as closely related to *Caldesia s.s.*, exemplified by *C. grandis* and the type species *C. parnassifolia* in the present study. These results differ from those obtained by Chen *et al.* (2012), who resolved *C. oligococca* as a member of *Caldesia* and distinct from *Albidella*. It is assumed that this different result stems from the paucity of overlapping data in the analyses by Chen *et al.* (2012), because they used only ITS and (a poor quality) *matK* sequences from *Albidella*, and lacked ITS data from *C. oligococca*. Hence, their inference of this

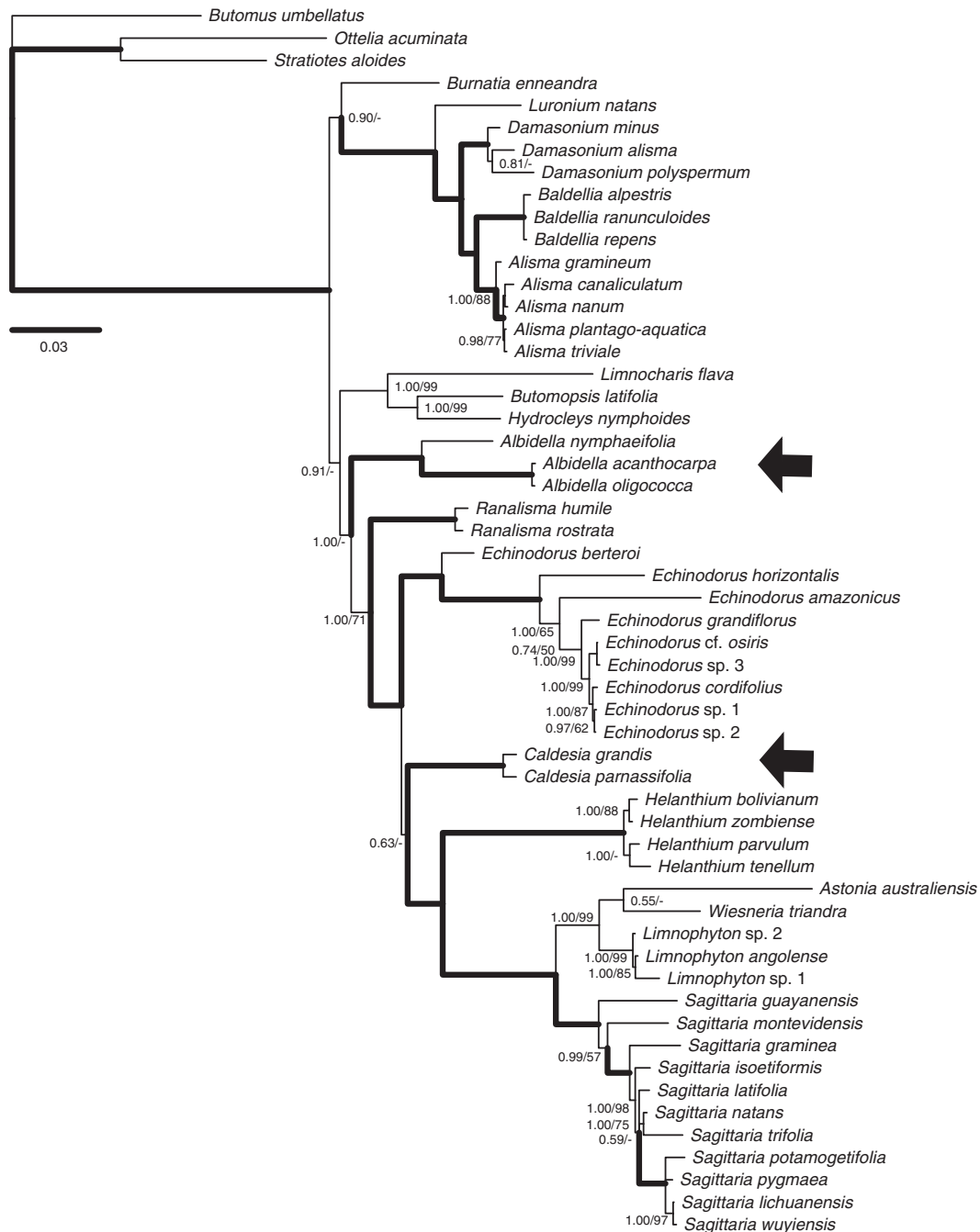


Fig. 1. Phylogeny of Alismataceae. Bayesian major-rule consensus tree based on simultaneous analysis of 10 molecular markers. Posterior probabilities/parsimony jackknife support values are shown beside the branches; thick lines indicate full support (PP = 1.00/jackknife = 100). *Albidella* and *Caldesia* are indicated.

particular relationship was entirely based on the compromised *matK* data.

Les and Tippery (2013), Petersen *et al.* (2016) and Ross *et al.* (2016) performed further phylogenetic analyses on the Alismataceae; however, they excluded both *Albidella nymphaeifolia* and *Caldesia s.s.* from their analyses and, therefore, were not able to test the monophyly of broadly defined *Caldesia*. Beyond the non-monophyly of *Caldesia s.l.*,

the present results are mostly congruent with those of previous molecular studies. *Alisma* L., *Baldellia* Parl., *Luronium* Raf. and *Damasonium* Mill. are supported as a monophyletic group, as well as *Astonia* S.W.L.Jacobs, *Limnophyton* Miq., *Wiesneria* Micheli and *Sagittaria* L. However, the Bayesian analysis resolved *Astonia* as sister to *Wiesneria*, unlike the parsimony analysis and Chen *et al.* (2012), which resolved *Astonia* as sister to *Limnophyton*. In the Bayesian analysis, *Burnatia* Micheli

was resolved as sister to the *Luronium*–*Damasonium*–*Baldellia*–*Alisma* clade, whereas parsimony analysis resolved it as sister to the rest of Alismataceae. Both positions are different than in Chen *et al.* (2012); however, none of these results is well supported. The relative positions of *Caldesia parnassifolia* and *Albidella* (*Caldesia*) *oligococca* also differ from Chen *et al.* (2012). This incongruence is probably caused by the *C. parnassifolia* *rbcL* sequence Chen *et al.* (2012) used (AY169494). This sequence is apparently problematic, because it contains stop codons and does not align very well with the new sequence produced here (KU499838). Phylogenetic position of *Helanthium* Engelm. ex J.G.Sm. remained unclear in Chen *et al.* (2012), whereas Les and Tippet (2013) and Ross *et al.* (2016) resolved it as the closest relative of *Echinodorus* Rich. & Engelm. ex A.Gray. This differs from the results of the present analyses, where *Helanthium* is strongly supported as sister to *Astonia*–*Wiesneria*–*Limnophyton*–*Sagittaria* clade.

These findings require the transfer of *C. oligococca* and related species from *Caldesia* to the previously monospecific *Albidella*. After this transfer, *Albidella* contains the following four species and *Caldesia*: *C. parnassifolia*, *C. reniformis* (D.Don) Makino, *C. grandis* Sam. and *C. janaki-ammaliae* Guha & M.S.Mondal. The fossil species *C. brandoniana* Haggard & Tiffney from the Early Miocene of North America (Haggard and Tiffney 1997) belongs to *Caldesia*.

Taxonomy

Albidella Pichon, *Notul. Syst. (Paris)* 12: 174 (1946)

Type: Albidella nymphaeifolia (Griseb.) Pichon.

Annual or perennial hydrophytes from short rhizomes, glabrous. Leaves floating or submersed; floating leaves petiolate, ovate, deeply cordate at the base, the apex round-acute, the pellucid markings present as lines or dots; submersed leaves sessile, linear. Inflorescence overtopping the leaves, erect, pyramidal panicle, whorls with 3 branches or 3 flowers. Flowers small, bisexual, pedicellate; petals 3, white, 1–6 mm long; stamens 6–9; carpels 5–12. Achenes reniform, laterally compressed, bearing 4 dorsal-lateral longitudinal ribs crested with blunt tubercles or spiny outgrowths.

Under this circumscription, the genus includes four species, one from Central America and Cuba, and three distributed in the Palaeotropics from tropical Africa and along the margins of the Indian Ocean to Australia. The Palaeotropical taxa are often recognised at varietal level only and further taxonomic studies are required to verify their taxonomic status. Detailed descriptions of the taxa can be found in Haynes and Holm-Nielsen (1994), den Hartog (1957) and Symoens (1984).

Albidella nymphaeifolia (Griseb.) Pichon, *Notul. Syst. (Paris)* 12: 175 (1946)

Alisma nymphaeifolium Griseb., *Cat. pl. Cub.* 218 (1866); *Echinodorus nymphaeifolius* (Griseb.) Buchenau, *Bot. Jahrb. Syst.* 2: 483 (1882); *Helanthium nymphaeifolium* (Griseb.) Small, *N. Amer. Fl.* 17: 45 (1909) (as '*Helianthium*').

Type: Cuba, 1865, *Wright 3196* (lecto: K!, *fide* Rataj (1975)), islecto: BM!, G!, GH, K!, MO, NY, S, US!).

Distribution: Mexico, Belizé, Guatemala, Cuba (Haynes and Holm-Nielsen 1994).

Albidella oligococca (F.Muell.) Lehtonen, *comb. nov.*

Alisma oligococcum F.Muell., *Fragm.* 1: 23 (1858); *Caldesia oligococca* (F.Muell.) Buchenau, *Bot. Jahrb. Syst.* 2: 479 (1882).

Type: Australia, Upper Victoria River, *s.d.*, *F. Mueller* (lecto: MEL 501493, *fide* Jacobs (2004)).

Distribution: Java and northern Australia in Western Australia, the Northern Territory and Queensland (den Hartog 1957).

Albidella acanthocarpa (F.Muell.) Lehtonen, *comb. nov.*

Alisma acanthocarpa F.Muell., *Fragm.* 1: 23 (1858); *Caldesia acanthocarpa* (F.Muell.) Buchenau, *Bot. Jahrb. Syst.* 2: 479 (1882); *Caldesia oligococca* var. *acanthocarpa* (F.Muell.) Hartog, *Fl. Males., Ser. 1, Spermat.* 5: 322 (1957).

Type: 'In stagnis ad flumen Victoriae ejus ostium versus.' *F. Mueller* (syn: MEL 0501476A).

Distribution: northern Australia, in the Northern Territory and Queensland (den Hartog 1957).

Albidella glandulosa (Thwaites) Lehtonen, *comb. nov.*

Alisma glandulosum Thwaites, *Enum. Pl. Zeyl.* 332 (1864); *Caldesia oligococca* var. *echinata* Hartog, *Fl. Males., Ser. 1, Spermat.* 5: 322 (1957).

Type: Sri Lanka, *Thwaites 2318* (BM!).

Alisma apetalum Wall., *Numer. List [Wallich]* n. 4996. (1831–1832), nom. inval., nom. nud.

Distribution: tropical Africa, India, Sri Lanka, Indo-China, Java (Symoens 1984).

Acknowledgements

This study was financially supported by the Finnish Cultural Foundation.

References

- Chen L-Y, Chen J-M, Gituru RW, Temam TD, Wang Q-F (2012) Generic phylogeny and historical biogeography of Alismataceae, inferred from multiple DNA sequences. *Molecular Phylogenetics and Evolution* **63**, 407–416. doi:10.1016/j.ympev.2012.01.016
- Cuenca A, Ross TG, Graham SW, Barrett CF, Davis JI, Seberg O, Petersen G (2016) Localized retroprocessing as a model of intron loss in the plant mitochondrial genome. *Genome Biology and Evolution* **8**, 2176–2189. doi:10.1093/gbe/evw148
- Davis JI, Stevenson DW, Petersen G, Seberg O, Campbell LM, Freudenstein JV, Goldman DH, Hardy CR, Michelangeli FA, Simmons MP, Specht CD, Vergara-Silva F, Gandolfo M (2004) A phylogeny of the monocots, as inferred from *rbcL* and *atpA* sequence variation, and a comparison of methods for calculating jackknife and bootstrap values. *Systematic Botany* **29**, 467–510. doi:10.1600/0363644041744365
- den Hartog C (1957) Alismataceae. In 'Flora Malesiana Ser.1 Vol.5'. (Ed. CGGJ Van Steenis) pp. 317–334. (Noordhoff-Kolff N.V.: Jakarta, Indonesia)
- Dunning LT, Savolainen V (2010) Broad-scale amplification of *matK* for DNA barcoding plants, a technical note. *Botanical Journal of the Linnean Society* **164**, 1–9. doi:10.1111/j.1095-8339.2010.01071.x
- Fay MF, Swensen SM, Chase MW (1997) Taxonomic affinities of *Medusagyne oppositifolia* (Medusagynaceae). *Kew Bulletin* **52**, 111–120. doi:10.2307/4117844

- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786. doi:10.1111/j.1096-0031.2008.00217.x
- Haggard KK, Tiffney BH (1997) The flora of the early Miocene Brandon Lignite, Vermont, USA. VIII. *Caldesia* (Alismataceae). *American Journal of Botany* **84**, 239–252. doi:10.2307/2446086
- Haynes RR, Holm-Nielsen LB (1994) The Alismataceae. *Flora Neotropica Monograph* **64**, 1–112.
- Hutchinson J (1959) 'The Families of Flowering Plants. Monocotyledons, vol. 2.' (Clarendon Press: Oxford, UK)
- Jacobs SWL (2004) Lectotypification of *Alisma oligococcum* F.Muell. (Alismataceae). *Telopea* **10**, 839.
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**, 772–780. doi:10.1093/molbev/mst010
- Kluge AG (1989) A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* **38**, 7–25. doi:10.2307/2992432
- Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**, 1695–1701. doi:10.1093/molbev/mss020
- Lehtonen S (2009) Systematics of the Alismataceae – a morphological evaluation. *Aquatic Botany* **91**, 279–290. doi:10.1016/j.aquabot.2009.08.002
- Lehtonen S, Myllys L (2008) Cladistic analysis of *Echinodorus* (Alismataceae): simultaneous analysis of molecular and morphological data. *Cladistics* **24**, 218–239. doi:10.1111/j.1096-0031.2007.00177.x
- Les DH, Tippery NP (2013) In time and with water ... the systematics of alismatid monocotyledons. In 'Early Events in Monocot Evolution'. (Eds P Wilkin, SJ Mayo) pp. 118–164. (Cambridge University Press: New York, NY, USA)
- Les DH, Cleland MA, Waycott M (1997) Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophyly. *Systematic Botany* **22**, 443–463. doi:10.2307/2419820
- Lot AH, Novelo AR (1994) Alismataceae. In 'Flora Mesoamericana. Vol. 6. Alismataceae a Cyperaceae'. (Eds G Davidse, MS Sousa, AO Chater) pp. 3–8. (Universidad Nacional Autónoma de México, Missouri Botanical Garden and The Natural History Museum: London, UK)
- Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**, 407–414. doi:10.1111/j.1096-0031.1999.tb00277.x
- Olmstead RG, Palmer JD (1994) Chloroplast DNA systematics: a review of methods and data analysis. *American Journal of Botany* **81**, 1205–1225. doi:10.2307/2445483
- Petersen G, Seberg O, Davis JI, Stevenson DW (2006) RNA editing and phylogenetic reconstruction in two monocot mitochondrial genes. *Taxon* **55**, 871–886. doi:10.2307/25065682
- Petersen G, Seberg O, Cuenca A, Stevenson DW, Thadeo M, Davis JI, Graham S, Ross TG (2016) Phylogeny of Alismatales (monocotyledons) and the relationship of *Acorus* (Acorales?). *Cladistics* **32**, 141–159. doi:10.1111/cla.12120
- Pichon M (1946) Sur les Alismatacées et les Butomacées. *Notulae Systematicae, Herbier du Museum de Paris. Phanerogramie, Paris* **12**, 170–183.
- Rataj K (1975) Revision of the genus *Echinodorus* Rich. *Studie Čsav* **2**, 1–156.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**, 539–542. doi:10.1093/sysbio/sys029
- Ross TG, Barrett CF, Gomez MS, Lam VKY, Henriquez CL, Les DH, Davis JI, Cuenca A, Petersen G, Seberg O, Thadeo M, Givnish TJ, Conran J, Stevenson DW, Graham SW (2016) Plastid phylogenomics and molecular evolution of Alismatales. *Cladistics* **32**, 160–178. doi:10.1111/cla.12133
- Symoens J-J (1984) Alismataceae. *Flore du Cameroun* **26**, 3–26.

Handling editor: Russell Barrett