

A multidisciplinary study of the genus *Althenia* (Potamogetonaceae)

Мультидисциплинарное исследование рода *Althenia* (Potamogetonaceae)

Sokoloff D. D.¹, Degtjareva G. V.¹, Fomichev C. I.¹, Remizowa M. V.¹, Samigullin T. H.², Severova E. E.¹, Valiejo-Roman C. M.², Volkova O. A.¹, Macfarlane T. D.³

Соколов Д. Д.¹, Дегтярева Г. В.¹, Фомичев К. И.¹, Ремизова М. В.¹, Самигуллин Т. Х.², Северова Е. Э.¹, Вальехо-Роман К. М.², Волкова О. А.¹, Макфарлен Т. Д.³

¹ Biological Faculty, M. V. Lomonosov Moscow State University, Moscow, Russia. E-mail: sokoloff-v@yandex.ru

² A. N. Belozersky Institute of Physico-Chemical Biology, M. V. Lomonosov Moscow State University, Moscow, Russia

³ Western Australian Herbarium, Department of Biodiversity, Conservation and Attractions, Perth, Australia. E-mail: terry.macfarlane@dbca.wa.gov.au

¹ Биологический факультет Московского государственного университета имени М. В. Ломоносова, г. Москва, Россия

² НИИ Физико-химической биологии имени А. Н. Белозерского Московского государственного университета имени М. В. Ломоносова, г. Москва, Россия

³ Гербарий Западной Австралии, г. Перт, Австралия

Summary. Taxonomy, molecular phylogenetics, developmental reproductive morphology and anatomy and palynology of *Althenia* are discussed.

Key words. *Althenia*, molecular phylogenetics, reproductive morphology and anatomy, taxonomy.

Реферат. В работе рассмотрены систематика, молекулярная филогенетика, морфолого-анатомическое строение и развитие репродуктивных органов и палинология видов рода *Althenia* в объеме мировой флоры.

Ключевые слова. Молекулярная филогенетика, морфолого-анатомическое строение, род *Althenia*, систематика.

Tomlinson et Posluszny (1976) treated *Althenia* Petit with two species in Eurasia and Africa as one of four genera of submerged aquatics comprising the family Zannichelliaceae. This view was followed by subsequent authors. Molecular phylogenetic data confirmed monophyly of Zannichelliaceae in its traditional circumscription but placed the clade together with *Potamogeton* L. and its segregate genera *Groenlandia* J. Gay and *Stuckenia* Börner (Les et al., 1997, Ross et al., 2016), so that Zannichelliaceae is currently placed in synonymy of Potamogetonaceae (APG IV, 2016). A recent study (Ito et al., 2016) using a nuclear (phyC) and several plastid (matK, ndhF, rbcL, rpoB, rpoC1) markers demonstrated that *Althenia* is nested within the Australasian (Australian and New Zealand) *Lepilaena* J. Drumm. ex Harvey. As a result, the two genera were combined under the name *Althenia*. As currently circumscribed (Macfarlane et al., 2017), the genus *Althenia* includes nine species, of which six are endemic to Australia (*A. australis* (J. Drumm. ex Harvey) Muell., *A. cylindrocarpa* (Körn. ex Müll. Berol.) Asch., *A. hearnii* T. Macfarlane et D. D. Sokoloff, *A. marina* (E. L. Robertson) Y. Ito, *A. patentifolia* (E. L. Robertson) T. Macfarlane et D. D. Sokoloff, *A. preissii* (Lehm.) Muell.), one (*A. bilocularis* Kirk) grows in Australia and New Zealand and two (*A. orientalis* (Tzvel.) García-Murillo & Talavera and *A. filiformis* Petit) occur in the Old World and are not recorded from Australasia.

The molecular phylogenetic study of Ito et al. (2016) did not include specimens of *A. marina* and *A. hearnii* and did not explore potential infraspecific variation in molecular characters. Our study filled these gaps. The inferred placement of the two previously unsampled species fits perfectly their morphological characters. In particular, the south-western Western Australian endemic *A. hearnii* is strongly supported as sister to *A. orientalis* plus *A. filiformis*, further supporting the ideas of Ito et al. (2016) that the lineage of *A. orientalis* and *A. filiformis* appeared in Eurasia and Africa (where it ranges from southern Siberia – Kipriyanova, Romanov, 2015 – to South Africa and south-western Europe) through a long-distance dispersal event from

Australia. These three species (*A. hearnii*, *A. orientalis*, *A. filiformis*) share an interesting morphological feature (synapomorphy), namely the ascidiate carpels with a polysymmetric circular stigma. The bilateral symmetry of their carpels (manifested in the one-sided attachment of the ovule, the occurrence of two vascular bundles and slightly unequal rates of growth of the ventral and the dorsal side early in development) cannot be seen without a dissection in anthetic flowers. All other species of *Althenia* and the outgroup, *Zannichellia*, possess stigmas that are clearly monosymmetric at anthesis. Our data are of interest with respect to the general trends of carpel evolution in angiosperms, as (externally) polysymmetric carpels are found in some ancient angiosperms such as Hydatellaceae and Chloranthaceae.

Our phylogenetic framework suggests that the monoecy that characterizes the lineage of *A. orientalis* and *A. filiformis* is likely derived from dioecy that characterizes the related species *A. hearnii*, *A. marina*, *A. cylindrocarpa* and usually *A. preissii*. The dioecy in these species is often of a specialized form (with a dimorphism between male and female plants and with the occurrence of peculiar filiform terminal structures in male inflorescence units). The inferred switch from dioecy to monoecy and from obligate outcrossing to frequent selfing (Cook, Guo, 1990) clearly increased the potential for a long-distance dispersal in *A. orientalis* and *A. filiformis*, especially as these are annual plants. The switch to monoecy appeared along with a dramatic decrease in the number of anther thecae (from 6 to 1), and although direct quantitative data are lacking, apparently with a strong decrease of the pollen to ovule ratio.

Our molecular phylogenetic and morphological data suggest that the species diversity of Australian *Althenia* is still underestimated. Apart from the possibility of the occurrence of cryptic species, at least one morphologically well-defined species has to be described. This species (*A. tzvelevii* T. Macfarlane et D. D. Sokoloff, nom. prov.) has clear morphological similarities with *A. bilocularis* and *A. patentifolia*, but differs from them in being monoecious. Molecular phylogenetic data place all three species in a clade.

Althenia is unusual among angiosperm genera (especially taking into account the relatively low species diversity) in possessing four clearly distinct palynotypes. These types can be distinguished by a combination of two binary characters, the biaperturate vs. omniaperturate condition and the type of exine ornamentation. General considerations suggest that the omniaperturate condition was derived from the biaperturate in at least two lineages, each time with a conserved type of exine ornamentation. However, based on our molecular phylogenetic data, the evolutionary history of pollen characters was more complex. As with some other investigated characters, the evolution of palynotypes is apparently homoplastic in *Althenia*.

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