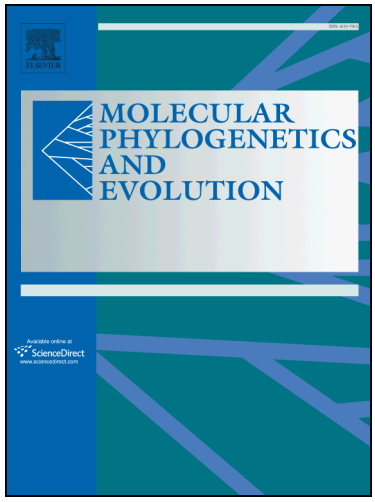

Out of southern Africa: Origin, biogeography and age of the Aizooideae (Aizoaceae)

Cornelia Klak, Pavel Haná ček, Peter V. Bruyns

PII: S1055-7903(16)30426-2
DOI: http://dx.doi.org/10.1016/j.ympev.2016.12.016
Reference: YMPEV 5695

To appear in: *Molecular Phylogenetics and Evolution*

Received Date: 1 August 2016
Revised Date: 7 December 2016
Accepted Date: 12 December 2016

Please cite this article as: Klak, C., Haná ček, P., Bruyns, P.V., Out of southern Africa: Origin, biogeography and age of the Aizooideae (Aizoaceae), *Molecular Phylogenetics and Evolution* (2016), doi: http://dx.doi.org/10.1016/j.ympev.2016.12.016

Out of southern Africa: Origin, biogeography and age of the Aizooideae (Aizoaceae)

Cornelia Klak,[a] Pavel Hanáček[b]& Peter V. Bruyns [a]

[a] *Bolus Herbarium, Department of Biological Sciences, University of Cape Town, 7701 Rondebosch, South Africa*

[b] *Department of Plant Biology, Mendel University in Brno, Zemědělská 1, 613 00 Brno, Czech Republic*

Author for correspondence, *Cornelia Klak, Cornelia.Klak@uct.ac.za*

Abstract

The Aizooideae is an early-diverging lineage within the Aizoaceae. It is most diverse in southern Africa, but also has endemic species in Australasia, Eurasia and South America. We derived a phylogenetic hypothesis from Bayesian and Maximum Likelihood analyses of plastid DNA-sequences. We find that one of the seven genera, the *fynbos*-endemic *Acrosanthes*, does not belong to the Aizooideae, but is an ancient sister-lineage to the subfamilies Mesembryanthemoideae & Ruschioideae. *Galenia* and *Plinthus* are embedded inside *Aizoon* and *Aizoanthemum* is polyphyletic. The Namibian endemic *Tetragonia schenckii* is sister to *Tribulocarpus* of the Sesuvioideae. For the Aizooideae, we explored their possible age by means of relaxed Bayesian dating and used Bayesian Binary MCMC reconstruction of ancestral areas to investigate their area of origin. Early diversification occurred in southern Africa in the Eocene-Oligocene, with a split into a mainly African lineage and an Eurasian-Australasian-African-South American lineage. These subsequently radiated in the early Miocene. For *Tetragonia*, colonisation of Australasia via long-distance dispersal from Eurasia gave rise to the Australasian lineage from which there were subsequent dispersals to South America and Southern Africa. Despite the relatively old age of the Aizooideae, more than half the species have radiated since the Pleiocene, coinciding with the large and rapid diversification of the Ruschioideae. The lineage made up of *Tetragonia schenckii* & *Tribulocarpus* split from the remainder of the Sesuvioideae already in the mid Oligocene and its disjunct distribution between Namibia and north-east Africa may be the result of a previously wider distribution within an early Arid African flora. Our reconstruction of ancestral character-states indicates that the expanding keels giving rise to hygrochastic fruits originated only once, i.e. after the split of the Sesuvioideae from the remainder of the Aizoaceae and that they were subsequently lost many times. Variously winged and spiky fruits, adapted to dispersal by wind and animals, have evolved independently in the Aizooideae and the Sesuvioideae. There is then a greater diversity of dispersal systems in the earlier lineages than in the Mesembryanthemoideae and Ruschioideae, where dispersal is mainly achieved by rain.

Keywords *Acrosanthes*, Ancestral area, divergence times, fruit-morphology, disjunctions, dispersal, phylogeny, *Tribulocarpus*.

1. Introduction

Earlier phylogenetic studies of the Aizoaceae using chloroplast (Klak & al., 2003) and nuclear markers (Thiede, 2004) showed that each of the four subfamilies (Aizooideae, Mesembryanthemoideae, Ruschioideae and Sesuvioideae) is monophyletic. For three of the subfamilies, the Mesembryanthemoideae (Klak et al., 2007), the Ruschioideae (Klak & Bruyns, 2012; Klak et al., 2013, Klak et al., 2015) and the Sesuvioideae (Hassan, et al., 2005; Thulin et al., 2012; Bohley et al., 2015), much denser sampling led to a better understanding of relationships within them. For the Aizooideae, Klak et al. (2003) sampled all currently recognized genera, but only nine of the 125 species and so phylogenetic relationships within the Aizooideae are the least understood in the family.

Klak et al. (2003) showed that the Aizooideae consisted of two major clades: one containing *Tetragonia* and *Gunniopsis* and one made up of *Acrosanthes*, *Aizoon*, *Aizoanthemum*, *Galenia* and *Plinthus*. The small genus *Tribulocarpus* S.Moore, formerly placed with *Tetragonia* in the subfamily Tetragonioideae, was found to be a close relative of the Sesuvioideae. Thulin & al. (2012) later confirmed this position and transferred a second species, *Tetragonia retusa* Thulin to *Tribulocarpus*. The two species of *Tribulocarpus* differ remarkably in their fruits: *T. retusus* (Thulin) Thulin & Liede has winged, simple fruits (as in many *Tetragonia* from southern Africa), while *T. dimorphanthus* has a compound, spiny fruit.

Seven genera and 125 species make up the Aizooideae. Over 70% of them occur only in southern Africa (Table 1, Klak et al., 2015), but 30 are endemic to Australasia, Eurasia and South America and one is cosmopolitan (Table 2). Revisions for the Southern African species of *Acrosanthes*, *Aizoon*, *Galenia*, *Plinthus* and *Tetragonia* were compiled by Adamson (1955, 1956, 1959a&b, 1961), for the Namibian species of *Aizoanthemum* by Friedrich (1957), for *Tetragonia* in South America by Taylor (1994) and for the endemic Australian *Gunniopsis* by Chinnock (1983). The subfamily is diverse, with annuals, perennials and geophytes and its members vary in size from small, prostrate or erect herbs to large shrubs. Characteristics of the Aizooideae, as well as the Sesuvioideae, are a basic chromosome number of n = 8, only slightly succulent leaves and flowers consisting of tepals, which are petaloid inside and sepaloid