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Australian spinifex grasses: new names in *Triodia* for *Monodia* and *Symplectrodia*

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The Australian spinifex grasses comprise an endemic radiation (69+ species) of morphologically and ecologically distinctive plants. Many species are long-lived hummock-forming perennials that bristle with needle-like leaves. Ecologically, they resemble sclerophyll shrubs rather than grasses (Rice & Westoby 1999). They are widespread in dry communities, especially the eremaean and monsoonal (savannah) biomes, where they often dominate the landscape, particularly on oligotrophic (sandy and skeletal) substrates. Across nearly one-third of the continent, spinifex plays a dominant role in structuring communities and their fire regimes, directly influencing the habitat dynamics of many animals, including endangered species (Allan & Southgate 2002, Brown *et al.* 2009, Dickman *et al.* 2011).

Taxonomically, spinifex grasses have always been recognised as a natural group and molecular phylogenies strongly support their monophyly (Mant *et al.* 2000, Toon *et al.* 2015). The sister group relationship is uncertain (Peterson *et al.* 2010, Toon *et al.* 2015) but is most likely a pair of African and Asian genera (*Aeluropus* and *Odyssea*, Soreng *et al.* 2015) that occur in similar environments to spinifex. Currently, spinifex grasses are classified as subtribe Triodiinae in Poaceae subfam. Chloridoideae, tribe Cynodonteae, together with the above two genera of subtribe Aeluropodinae (Soreng *et al.* 2015).

As many as four genera have been recognised in Triodiinae—*Triodia* (1810), *Plectrachne* (1929), *Monodia* (1985) and *Symplectrodia* (1985)—and diagnosed using characters of the glumes, lemmas and spikelet structure (Jacobs 2004, Lazarides 1997). *Plectrachne* was distinguished from *Triodia* by having a lemma with three deep lobes, each with an awn, and glumes much longer than the florets excluding awns (Lazarides 1997: table 1). However, as the number of species included in *Plectrachne* grew (ultimately to 18), the two genera were found to be very heterogeneous in these features. As the morphological diagnosis proved to be unworkable, Lazarides (1997) formally sank *Plectrachne* into *Triodia*. Subsequent molecular phylogenetic analysis (Mant *et al.* 2000) supported this decision by finding both *Triodia sens. str.* and *Plectrachne sens. str.* to be paraphyletic and the phylogeny also showed that the characters used to distinguish the genera were homoplastic. Meanwhile, three new species had been discovered in the monsoonal tropics and were found to have spikelets that differed in number and arrangement of florets, and their fertility, from those in *Triodia sensu* Lazarides (1997). *Monodia*, known only from the Kimberley region of north-western Australia including the environs of the Mitchell Plateau, was diagnosed and named for its single-flowered spikelet and sterile prolongation of the rachilla (Jacobs 1985). In the same year, Lazarides (1985) described *Symplectrodia* with two species, both occurring in restricted areas of the Arnhem Land plateau. Subsequently, a comprehensive treatment of the whole spinifex group (as tribe Triodieae) in the *Flora of Australia* recognised three genera: *Triodia s.l.* (including *Plectrachne*), *Monodia* and *Symplectrodia*, totalling 68 species (Anonymous 2005, Lazarides *et al.* 2005, Nightingale *et al.* 2005, Nightingale & Weiller 2005).

Recently, we carried out a new molecular phylogenetic analysis of the spinifex group to test a hypothesis that historical shifts in leaf anatomical traits related to C_4 photosynthesis, and water relations might have been a key innovation leading to the radiation of the group into the monsoonal tropics (Toon *et al.* 2015). Sampling was more comprehensive than in the previous study by Mant *et al.*, including 66 of 69 described species and adding sequences of the *matK* gene (chloroplast DNA) to the nuclear ITS sequences that had been used by Mant *et al.* (2000). This presented an opportunity to test the generic classification more rigorously. *Plectrachne* was confirmed as non-monophyletic, being scattered throughout the spinifex clade. Both *Symplectrodia* and *Monodia* were nested deeply within the spinifex clade, with their inclusion supported by multiple nodes with high statistical support. Moreover, the

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two *Symplectrodia* species were paraphyletic within a clade including two *Triodia* species. In other words, *Triodia*, even in the broader circumscription including *Plectrachne* (*sensu* Lazarides *et al.* 2005), is rendered paraphyletic if *Monodia* and *Symplectrodia* are recognised as separate genera. Toon *et al.* (2015) concluded that both genera should be sunk into *Triodia*.

Here we formally synonymise *Monodia* and *Symplectrodia* under *Triodia*, thus combining all the species of spinifex into a single genus comprising subtribe Triodiinae. This decision raises the question of how *Triodia* can be diagnosed in its new, broader circumscription. The spinifex grasses have always been recognised by their highly developed scleromorphy and xeromorphy, with tough, needle-like leaves resulting from the in-rolling of the leaf blades (at least in dry conditions) and crypsis of stomata in deep grooves. Although these characters occur elsewhere within the family (e.g. *Spartina*: Maricle *et al.* 2009, now *Sporobolus*: Peterson *et al.* 2014), they remain the best morphological characters for diagnosing *Triodia s.l.*, in combination with reproductive characters (Jacobs 2004). Other features considered to be characteristic of spinifex, such as the hummocky growth habit, often abundant leaf sclerenchyma, production of resin by the leaf sheaths and the restriction of stomata to the adaxial leaf surface (epistomatous anatomy), are found in some but not all species and cannot be used to unambiguously diagnose the genus. In other words, there is no known morphological synapomorphy for *Triodia s.l.*; however, there is strong molecular support for the clade (Toon *et al.* 2015).

Within the genus, it has long been recognised that epistomatous leaf anatomy correlates with resin production and these traits have been used to define an informal group of species known as the "softs". With minor exceptions, this group forms a clade that originated late in the evolution of the Triodiinae and it appears that these traits were adaptations that evolved after spinifex diversified into the monsoonal biome (Toon *et al.* 2015). The complementary group, known as "hards", is characterised by amphistomatous leaves (stomata on both adaxial and abaxial surfaces) and absence of resin, and is therefore paraphyletic, with these traits representing the ancestral condition in the genus. All species can be identified using the keys and descriptions in the *Flora of Australia*, volume 44B (Anonymous 2005, Lazarides *et al.* 2005, Nightingale *et al.* 2005, Nightingale & Weiller 2005), bearing in mind that the three species treated there under *Monodia* and *Symplectrodia* now have the combinations under *Triodia* listed below. Species described more recently (Armstrong 2009, Barrett & Barrett 2011) are diagnosed in those papers. The types in CANB of all three species of *Monodia* and *Symplectrodia* were examined by MDC and JM, as well as the specimens used by Lazarides in his taxonomic treatments, including his types. All three new names were checked against the taxonomic databases APNI (1991 onwards) and IPNI (2012 onwards), to verify that the combinations did not already exist in *Triodia*.

Taxonomy

Triodia Brown (1810: 182). Type: *T. pungens* Brown (1810: 182)

Plectrachne Henrard (1929: 132). Type: *P. schinzii* Henrard (1929: 134).
Symplectrodia Lazarides (1985: 273). Type: *S. lanosa* Lazarides (1985: 275).
Monodia Jacobs (1985: 659). Type: *M. stipoides* Jacobs (1985: 659).

Triodia gracilis (Lazarides) Crisp & Mant, *comb. nov.*

Basionym:—*Symplectrodia gracilis* Lazarides (1985: 276).
Type:—AUSTRALIA. Northern Territory: Darwin & Gulf District: c. 7.5 miles SE of Mt Gilruth, 133°10′E, 13°07′S, 28 February 1973, *Lazarides 7919* (holotype CANB!, isotypes BRI, DNA, K, L, US).

Triodia lanosa (Lazarides) Crisp & Mant, *comb. nov.*

Basionym:—*Symplectrodia lanosa* Lazarides (1985: 275) Type:—Northern Territory: Darwin & Gulf District: Mt Gilruth area, 12°58′S, 133°10′E, 2 June 1978 *Dunlop 4874* (holotype NT, isotypes BRI, CANB!, DNA, K, NSW).

Triodia stipoides (S.W.L.Jacobs) Crisp & Mant, *comb. nov.*

Basionym:—*Monodia stipoides* Jacobs (1985: 659).

Type:—AUSTRALIA. Western Australia, *C.R.Dunlop 5233* (holotype CANB!, isotypes BRI, DNA, NT, PERTH).

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