Telopea 12(3) 419–423

New combinations in *Zostera* (Zosteraceae)

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Abstract

Systematic studies have clarified interspecific relationships in *Zostera*, but also allow for different but phylogenetically compatible classifications. Recently, several new species have been assigned to the genus *Heterozostera*, which some prefer to retain as a subgenus within *Zostera*; thus, if this taxonomic interpretation is followed, appropriate names do not exist in *Zostera*.To address this problem, we provide three new combinations (***Zostera chilensis, Z. nigricaulis*** and ***Z. polychlamys***) for species from Chile and Australia, that have been described in *Heterozostera.* We also present a brief account of the conflicting classifications available for Zosteraceae.

Introduction

By analysing both molecular and morphological data, Les et al. (2002) demonstrated that *Heterozostera* is nested phylogenetically within *Zostera*. The DNA and morphological cladograms presented by Les et al. (2002) are consistent with a number of options for maintaining monophyletic taxa within Zosteraceae, and there have been at least three ways proposed for resolving the classificatory problem:

(i) recognise one genus, *Zostera* (with two or three subgenera), treating *Heterozostera* as a synonym of the former genus;

(ii) recognise three genera, namely, *Zostera, Heterozostera* and *Nanozostera*; or

(iii) recognise two genera, namely, *Zostera* and *Nanozostera* (including *Heterozostera*).

Tomlinson and Posluszny (2001) adopted option (ii) by elevating the former *Zostera* subgenus *Zosterella* Aschers. to generic rank as *Nanozostera*, an approach that has not yet been widely followed. In our estimation, this option appears to be the least optimal because it introduces a new name for a taxon already widely recognised as a subgenus and would require the unnecessary abandonment of taxonomic names that have been in use for more than a century. Furthermore, the proposed genera would be difficult to delimit morphologically; e.g., a morphological phylogenetic analysis depicted the three taxa as an unresolved polytomy (Les et al. 2002). It also seems excessive to segregate the less than 15 total species as three separate genera with rather weak morphological distinctions.

 ISSN0312-9764

Consequently, Les et al. (2002) proposed that only one genus should be recognised, namely *Zostera* (option [i], above). Their recommendation was made because that option provided the highest level of nomenclatural stability and avoided a proliferation of names within this small group of morphologically similar plants.

Phylogenetic analyses by Tanaka et al. (2003) resolved the same basic clades as those found by Les et al. (2002). These authors did not advocate adoption of a specific classification, but suggested yet another option (iii), which was to merge subgenus *Zosterella* and the genus *Heterozostera* under the name of the recently described *Nanozostera*. However, that option would not be valid nomenclaturally, given that such a merger would require the use of the oldest name available at the rank of genus. In this case, that name would be *Heterozostera* (named by Hartog in 1970) rather than *Nanozostera* (named by Tomlinson & Posluszny in 2001).

Phylogenetic analyses by Kato et al. (2003) also mirrored the results of Les et al. (2002), by recovering essentially the same three clades of *Zostera* species. However, those authors advocated the adoption of the 'option (iii)' classification suggested by Tanaka et al. (2003), i.e., two genera (*Zostera*, *Nanozostera*), with *Heterozostera* merged within the latter. Consequently, these authors also failed to recognise the nomenclatural priority of the name *Heterozostera* at the genus level. Further nomenclatural confusion is evidenced by their proposed establishment of only two subgenera within *Nanozostera* (*Heterozostera*, *Zosterella*), neither representing the required autonym (i.e., subgenus *Nanozostera*) which would be established by the presence of the type species of the genus. In any case it is clearly evident that option (iii) should not be considered for classification of *Zostera* species because it is invalid nomenclaturally.

Kuo (2005) published a revision of *Heterozostera*, using morphological and anatomical characters to distinguish four taxa from what originally had been considered a single species (*Heterozostera tasmanica*). This work followed the classification option (ii), retaining *Heterozostera* as one of the four generic segregates advocated by Tomlinson and Posluszny (2001). However, no rationale for following that particular classification was provided. As a result, Kuo (2005) named three new species of *Heterozostera*, that, if they are to be treated as species of *Zostera,* currently lack combinations in that genus.

We make no evaluation of the validity of the new *Heterozostera* species proposed by Kuo (2005); however, we continue to advocate that any species related phylogenetically to the clade containing the former *Heterozostera tasmanica* should be assigned to the genus *Zostera*. A more detailed rationale for our preference is provided in Les et al. 2002), but is summarised here.

The generic distinction of *Zostera* and *Heterozostera* has been disputed, mainly because of the uncertainty of the reliability of apparent diagnostic taxonomic characters. Several taxonomists have remarked on the difficulty of separating the morphologically similar *Zostera* and *Heterozostera* (Aston 1973; Jacobs & Williams 1980). Aston (1973) and Phillips and Meñez (1988) essentially followed Hartog (1970) who distinguished the two genera based on a distinction between monopodial rhizomes as found in *Zostera* compared to sympodial (unbranched) rhizomes in *Heterozostera.* However, Tomlinson (1982) and Soros-Pottruff and Posluszny (1995) have shown that this often-cited sympodial feature is erroneous and should not be used to distinguish the genera. Robertson (1984) followed Tomlinson's (1982) recommendations and considered both *Heterozostera* and *Zostera* as having monopodial, herbaceous rhizomes. Instead, she relied on the difference in cortical vascular bundle number (employed as the secondary key character by Hartog 1970) and retinacule shape to separate the genera. However, Yip (1988) later showed that overlap exists in the number of cortical bundles in *Zostera* (2–4) and *Heterozostera* (2–12). Therefore *Heterozostera*, as circumscribed originally by Hartog (1970), cannot be supported.

Although Soros-Pottruff and Posluszny (1995) clarified the rhizome type in *Heterozostera* and *Zostera* (both monopodial), their clarification provided for a new method of distinguishing between the taxa, namely, an undulating growth pattern that, in the family, is apparently unique to *Heterozostera*. Soros-Pottruff and Posluszny (1995) also included the presence of wiry, erect stems, a tendency toward increased cortical vascular bundles, and lack of vascularisation in retinacules as additional features that separate *Heterozostera* from *Zostera*. Les et al (2002) added retinacule morphology as another useful diagnostic feature, which is described as lanceolate in *Heterozostera* and triangular to suborbicular in *Zostera* (Roberts 1984). Within Zosteraceae, Hartog (1970) described the retinacules as elongate, hence long (2.5–14 mm long) in *Phyllospadix*, moderately long (2–3 mm) in *Heterozostera* and either short (0.5–1.75 mm) or absent in *Zostera*. The longer (>2 mm) retinacules of *Heterozostera* appear to effectively separate it from *Zostera* (<1.75 mm) without overlap.

Even though some of the distinctions made between *Heterozostera* and *Zostera* in past treatments have proven to be flawed, a modified set of characters could be used effectively to separate these taxa taxonomically. In addition to these distinctions, Kuo and McComb (1998) suggest that *Heterozostera* is probably a hexaploid, a unique ploidy level in the family. Hence, the major issue with *Heterozostera* is not whether it is distinct taxonomically, but rather which taxonomic rank is most appropriate given the observed differences. Are undulating rhizomes, additional vascular bundles, and long, unvascularised retinacules sufficient to separate *Heterozostera* and *Zostera* at the generic level?

The circumscription of ranks (genera, sections, species) always involves some subjectivity, but greater objectivity can be achieved by the satisfaction of phylogenetic criteria that taxa should represent monophyletic groups (Judd et al. 1999). Morphological data alone cannot effectively answer this question because of their low resolving power. If the topology of the majority rule consensus tree (Les et al 2002) is used as a guideline, then *Heterozostera* must either be combined with *Zostera*, or four separate genera of Zosteraceae recognised to avoid paraphyletic taxa.

However, the approach taken recently by Tomlinson and Posluszny (2001), seems unnecessarily excessive. Tomlinson and Posluszny (2001) proposed the adoption of a new genus *Nanozostera* to accommodate species in *Zostera* subgenus *Zosterella*. They provided no new data, but essentially echoed the results of Soros-Pottruff and Posluszny (1995) as the basis of their generic segregation. Because neither study analysed phylogenetic relationships, the conclusions were based on perceived morphological incongruities. However, the morphological cladistic analyses of Les et al. (2002) indicate that none of the genera recognised by Tomlinson and Posluszny is particularly well-defined morphologically, especially when compared to the genus *Phyllospadix*. *Nanozostera* is defined by only two morphological synapomorphies, *Zostera* (sensu stricto) by three synapomorphies, and *Heterozostera* by four synapomorphies. In perspective, *Zostera noltii* and *Z. japonica* are differentiated from the other members of *Zostera* subgenus *Zosterella* also by only two synapomorphies, yet have never been considered as separate genera. This level of differentiation is miniscule when compared to *Phyllospadix* which is separated from these taxa by 19 morphological apomorphies. Comparatively, the low level of morphological differentiation would support the merger of *Heterozostera*, plus *Nanozostera*, into a single genus (*Zostera*) and with the family consisting of the latter genus and *Phyllospadix*.

The pattern of nucleotide divergence is similar proportionately; e.g., with *Phyllospadix* differing substantially from all other Zosteraceae (21.8–26.7%) and none of the remaining taxa exhibiting more than 16.8% (mostly <8.0%) nucleotide divergence (Les et al. 2002). Although relative nucleotide divergence can provide interesting evolutionary insights, we believe that major taxonomic distinctions (such as delimitation of genera) should rely principally on morphological characters if any practical utility is to be achieved.

In summary, the phylogenetic analyses of Zosteraceae by Les et al. (2002) resolved the same four clades using molecular or morphological data, either singly or in combination. Although each clade could be recognised as a distinct genus in a cladistic sense, doing so would, in our opinion, create several highly similar and weakly differentiated genera. However, phylogenetic analyses of Zosteraceae by several groups of researchers consistently demonstrate no support for the circumscription of *Heterozostera* as proposed originally by Hartog (1970). If that genus is to be retained, it must also be redefined to include *Zostera* subgenus *Zosterella* if phylogenetic integrity is to be maintained. In such an instance, the generic name *Heterozostera* would have nomenclatural priority.

Our suggestion is to recognise only two genera in Zosteraceae, namely *Zostera* and *Phyllospadix*, which we believe to most usefully depict the major phylogenetic lineages within this family as these two genera are well differentiated at both the morphological and molecular levels. The three subclades within *Zostera* should continue to be recognised as subgenera, namely as *Zostera* subg. *Zostera*, subg. *Heterozostera* and subg. *Zosterella*.

Here we provide the new combinations that are necessary for the implementation of this option (i.e. option i).

New combinations (*Zostera* subgenus *Heterozostera*)

Zostera chilensis (J.Kuo) S.W.L.Jacobs & D.H.Les **comb. nov.**

Basionym: *Heterozostera chilensis* J. Kuo (2005; 126–127).

Type: Chile: Aldea, Puerta, Coquimbo Province, drift, January. 1997, *H. Kirkman and M. Edding* (holo.: US; iso: K, MEL).

This is the name that should be used for all Chilean specimens previously treated as *Heterozostera* (mostly as *H. tasmanica*).

Zostera nigricaulis (J.Kuo) S.W.L.Jacobs & D.H.Les **comb. nov.**

Basionym: *Heterozostera nigricaulis* J. Kuo (2005; 110–124).

Type: Australia: South Australia: Kangaroo Island, site 91, 21 November 1977, *H. Kirkman* (CSIRO 1988) (holo: AD; iso: PERTH).

This is the most widespread and common of the new species and most Australian references to *H. tasmanica* from the eastern States refer to this species.

Zostera polychlamys (J.Kuo) S.W.L.Jacobs & D.H.Les **comb. nov.**

Basionym: *Heterozostera polychlamys* J.Kuo (2005; 124–126)

Type: Australia: Western Australia: Flinders Bay, drift, 11 December 1990, *H. Kirkman* (CSIRO 1751; CMM 260, 261) (holo: CANB; iso L, MEL, PERTH).

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Manuscript submitted 07 April 2008, accepted 30 June 2009