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Taxonomic treatment of Cichorieae (Asteraceae) endemic to the Juan Fernández and Desventuradas Islands (SE Pacific)

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The evolutionary origin and taxonomic position of *Dendroseris* and *Thamnoseris* (Cichorieae, Asteraceae) are discussed in the light of recent molecular systematic studies. Based on the previous development of a robust phylogenetic framework, we support the inclusion of the group as a subgenus integrated within a new and broad concept of the genus *Sonchus*. This approach retains information on the evolutionary relationships of the group which most likely originated from an adaptive radiation process; furthermore, it also promotes holophyly in the subtribe Hyoseridinae (formerly Sonchinae). Consequently, all the former *Dendroseris* and *Thamnoseris* species must be transferred to *Sonchus*. A preliminary nomenclatural synopsis of the proposed subgenus is given here, including the new required combinations.

Introduction

Adaptive radiation on oceanic islands has yielded spectacular and explosive *in-situ* diversification of plants (Carlquist 1974: 22–23), which often differ significantly from the common habits among their respective taxonomic relatives on continents. Consequently, they are recognized as distinct, often endemic, genera, and there has been much debate about whether or not generic recognition is warranted. Asteraceae have produced some of the most striking examples of plant radiation on islands (for a general view, *see* Carlquist 1974, Bramwell 1979, Givnish & Sytsma 1997, Stuessy & Ono 1998, Levin 2000: chapter 2).

Within the tribe Cichorieae, the most prominent cases occur on the Canary Islands (NE Atlantic Ocean), and on the Juan Fernández Islands (SE Pacific Ocean) (Crawford *et al*. 2009). In the former archipelago, radiation involves the genus *Tolpis* (Crawford *et al*. 2006), but particularly the woody *Sonchus* alliance (Kim *et al*. 1999). On the Juan Fernández Islands, the endemic genus *Dendroseris* is represented by a dozen narrow endemic species showing peculiar growth forms within the tribe: sparsely branched or palmiform rosette trees, and succulent rosette shrubs. Radiation in this group appears to be completed with the current monotypic genus *Thamnoseris* from the nearby Desventuradas Islands (San Ambrosio

and San Félix Islands). These taxa have been the subject of numerous biological, systematic, and biogeographic studies over several decades (e.g., Skottsberg 1956, Carlquist 1967, Sanders *et al*. 1983, Crawford *et al*. 1987, Sanders *et al*. 1987, Spooner *et al*. 1987, Pacheco *et al*. 1991, Crawford *et al*. 1992, Sang *et al*. 1994, Kim *et al*. 1996b, Stuessy *et al*. 1998, Kim *et al*. 2007, Crawford *et al*. 2009, Heads 2011). At present, the most common opinion is that they are the result of recent adaptive radiation (but *see* Moreira-Muñoz 2011: 169, and Heads 2011), causing gigantism and a somewhat whimsical diversification of reproductive structures. The origin of this enigmatic spectacular group remains vague, but molecular phylogenetic studies provided convincing evidence of its position within the subtribe Hyoseridinae (formerly Sonchinae). In the present paper, we introduce and discuss the taxonomic history of the group and make a nomenclatural proposal in the light of recent molecular phylogenetic studies.

Taxonomic history

The first report of the Cichorieae endemic to the Juan Fernández Islands was by Don (1832), who coined the name *Dendroseris macrophylla* for a South American plant. Don however made no annotation on the specific locality or provenance area of the material, and he included no indication of the arborescent habit in the concise description. Nevertheless, the author was clearly aware of the particular plant form, because the name "*Dendroseris*" indicates a tree-like plant. One year later, Decaisne (1833) published a full report on the plants collected on the largest of the Juan Fernández Islands (Masatierra) by Carlo G. Bertero, including seven new species of the group subordinated to the new generic name *Rea*. In the publication, he emphasized the uniqueness of the woody stem among Cichoreae (also present in several representatives of the woody *Sonchus* alliance in the Canary Islands), and provided a detailed and sound description of the main morphological characters within the new genus. He pointed out that achene shape (trigonous to compressed and winged), the alveolate receptacle (sometimes frimbiate) and the pappus composed of stiff, rough uneven hair constituted the main differences from the Canarian endemics. Hooker and Arnott (1835) reduced *Rea* to *Dendroseris* and made the necessary combinations, accepting a total of seven species.

New *Dendroseris* species were described in the 2nd half of the 19th century and the early 20th century (R. A. Philippi 1870, Johow 1896, Skottsberg 1922) and approximately a dozen species (*see* below) were completed, some of which were merely treated as varieties of other species by Johow (1896). Federico Philippi (1875) segregated the monotypic genus *Thamnoseris* for a plant endemic to the Desventuradas Islands (*T. lacerata*) based on the presence of a non-branched style (which would constitute a novelty among the Cichorieae). Some years later, Reiche (1910: 6) conserved the name, but indicated the presence of very short style arms in this plant. Skottsberg (1953) divided the genus *Dendroseris* into four genera: *Dendroseris*, *Rea*, *Phoenicoseris*, and *Hesperoseris*, mainly based on palynological characters, but that notion was not frequently followed. Carlquist (1967) and Sang *et al*. (1994) found no anatomical or molecular phylogenetic evidence, which satisfactorily supported such a segregation.

The soundness of the *Dendroseris* species as a taxonomic group has never been questioned; however, its position within the Cichorieae has been somewhat unstable. De Candolle (1838) ranked all the species known at the time (combined under the generic name *Rea*) within the subtribe Hieracieae, but Bentham (1873) coined the name Dendroserideae for a subtribe comprising *Dendroseris* and the Hawaiian *Fitchia* (the latter currently placed in the tribe Coreopsideae), because of their common arborescent life form. Stebbins (1953) redefined the group as the subtribe Dendroseridinae, accepted until recent times (Bremer 1994), comprising *Dendroseris* and *Thamnoseris* as exclusive members. Jeffrey (1966), on the other hand, proposed the two genera to be allied to *Sonchus*. Recently, Kim *et al*. (1996b, 2007), in molecular phylogenetic studies of *Sonchus* and related genera, showed that the subtribal rank of Dendroseridinae is not supported since *Dendroseris* is deeply embedded within the Sonchinae (Fig. 1). In addition, the genus *Thamnoseris*, endemic to the Desventura-

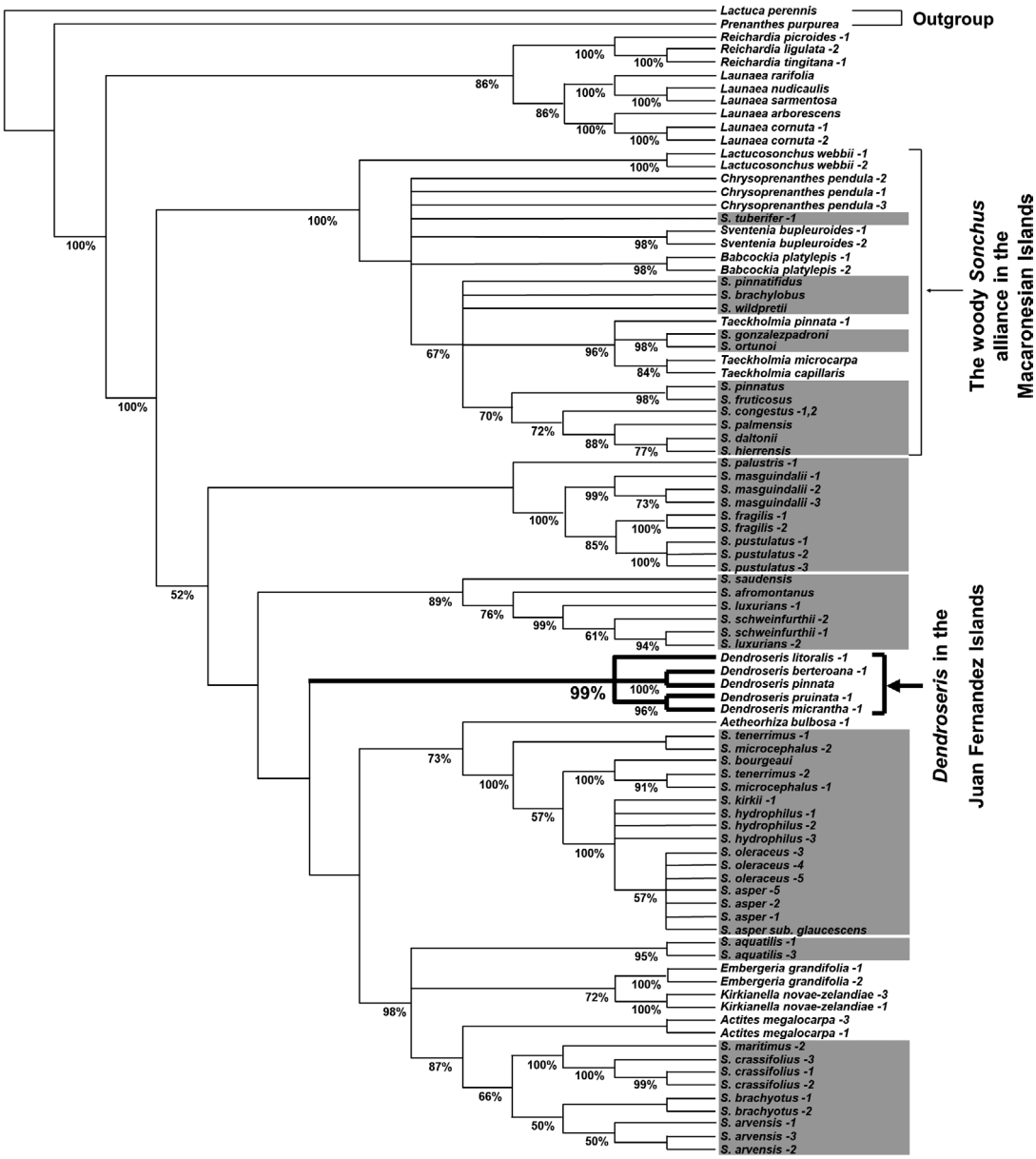

Fig. 1. Strict consensus tree of *Sonchus s. lato* based on the combined ITS and cpDNA dataset (slightly modified from figure 3 in Kim *et al.* 2007). Bootstrap supports are shown below branches and the paraphyletic genus *Sonchus* (*S.*) is shown in gray boxes.

das Islands, turned out to be sister to *Dendroseris* (Jeffrey 1966, Kim *et al*. 1996b; B. G. Baldwin pers. comm. based on DNA molecular analysis). These findings were acknowledged and subsequently adopted in the treatment of Cichorieae by Lack (2007), who included *Dendroseris* and *Thamnoseris* within the subtribe Sonchinae. More recently Kilian *et al*. (2009), also taking into account the findings of Kim *et al*. (1996b, 2007), integrated *Dendroseris* and *Thamnoseris* into the same subtribe and placed both taxa within a broader *Sonchus*. Consequently, the names *Dendroseris* and *Thamnoseris* were considered to be synonymous to *Sonchus*. Kilian *et*

al. (2009) also proposed a re-circumscription of the subtribe, which was named Hyoseridinae.

Origin of the *Dendroseris* group: taxonomic rank and position

The most intriguing question regarding the systematics of *Dendroseris–Thamnoseris* concerns the origin of these noteworthy species within the tribe Cichorieae. Skottsberg (1956) considered the group as a relict. However, in a painstaking anatomical study, Carlquist (1967) found evidence that growth forms in *Dendroseris* were derived from an herbaceous ancestry, by means of anomalous secondary growth, and envisaged the group as originating from a common stock on the Juan Fernández Islands. The discovery of the tetraploid condition, based on the uniform n = 18 meiotic chromosome number (Sanders *et al*. 1983, Spooner *et al*. 1987, Crawford *et al*. 1987), and its evident holophyly (= monophyly *s*. *str*.; Ashlock 1971) greatly strengthen the hypothesis of Carlquist (Crawford *et al*. 1992, Sang *et al*. 1994). In addition, Crawford *et al*. (1987, 1992) found little allozyme divergence and minimal cpDNA restriction site variation among the species, which is concordant with rapid speciation resulting from an adaptive radiation process probably occurring on the Islands.

The archipelago presents an age range from one to four million years (Stuessy *et al*. 1984) and the estimated divergence times are less than 2.6 million years for all *Dendroseris* species (Crawford *et al*. 1992). The identification of the ancestor(s) of the *Dendroseris* group is problematic, and is reflected in its variable taxonomic position within the tribe Cichorieae. Based on a very limited sampling of tribe Lactuceae, Whitton *et al*. (1995) provided the first molecular evidence (cpDNA restriction site analysis) that *Dendroseris* is closely related to *Sonchus* and *Sventenia*. Later, molecular phylogenetic studies based on nrDNA ITS sequences (Kim *et al*. 1996b, 2007) put forward the possibility that the group shares the most recent common ancestor with *Sonchus* subgenus *Sonchus* sections *Maritimi* and *Arveneses*, and some other Pacific island endemics such as *Kirkianella*, *Embergeria* and *Actites*. However, that relationship was not statistically supported, having a bootstrap value of 52%. Additional phylogenetic study based on *mat*K cpDNA sequence provided very little resolution with regard to the origin of *Dendroseris* (Kim *et al*. 2007). Nevertheless, both nuclear and chloroplast genomes strongly suggest that *Dendroseris* is deeply embedded within *Sonchus*. Based on the ITS phylogeny, it is conceivable that the ancestor(s) of *Dendroseris* came from the western Pacific, since the presence of native representatives in South America is highly questionable (Reiche 1910, Boulos 1974: fig. 27). Recently, it has been hypothesized that this and other Asteraceous groups from the Fernandezian flora might constitute the remnant of ancient biotas related to the Pacific plate and the Cretaceous plateau (Heads 2009, Moreira-Muñoz 2011), which would have persisted by successive colonization of volcanic islands along the south Pacific. This theory clearly conflicts with the numerous genealogical analyses by the group discussed above, but there is some controversy in this respect (Heads 2011).

One significant and consistent finding based on the molecular phylogenetic studies by Kim *et al*. (1996a, 1996b, 1999, 2007) involves the highly paraphyletic nature of the currently circumscribed genus *Sonchus*. This genus and 12 other genera (i.e., *Actites*, *Aetheorhiza*, *Babcockia*, *Chrysoprenanthes*, *Dendroseris*, *Embergeria*, *Kirkianella*, *Lactucosonchus*, *Sventenia*, *Taeckholmia*, *Thamnoseris* and *Wildpretia*) represent the core radiated group of the Hyoseridinae (formerly Sonchinae). Of the 12 other genera, all but two (*Dendroseris* and *Taeckholmia*) can be considered monotypic and they are deeply embedded within genus *Sonchus* (Fig. 1).

The lack of strong taxonomic or phylogenetic support for segregation of the above genera highlights the necessity of amalgamating them into a large *Sonchus* genus, which will also promote holophyly in the group (e.g., Kathriarachchi *et al*. 2006, Richter *et al*. 2009, Chase & Reveal 2009). Moreover, Kim *et al*. (2007) stressed the convenience of identifying clades at subgeneric rank in a revised classification of the subtribe. The *Dendroseris* group is a well-supported clade within the Hyoseridinae (bootstrap support of 99% based on the combined ITS and cpDNA *mat*K dataset) which, according to

these results, should be proposed as a new subgenus within the new broader generic concept *Sonchus*. This approach may be controversial to some botanists who emphasize the interest of accepting paraphyletic groups in classifications (e.g., Carpenter 1993, Grant 2003, Hörandl 2006, Hörandl & Stuessy 2010). The main justification for their view lies in the argument that paraphyly is a transitional stage in the evolution of taxa, and to include paraphyletic groups in classifications therefore retains the information content for evolutionary relationships (Hörandl & Stuessy 2010). However, without intending to make any general assessment of the different classification criteria, in this case we strongly believe that the recognition of a broadly defined *Sonchus* and the subsequent delimitation of subgenera within it is the most consistent option from an evolutionary standpoint, and we fulfill any requirement of monophyly. Taking this approach, we feel that the *Dendroseris–Thamnoseris* group can easily be seen as the result of an insular adaptive radiation process (just as in the woody *Sonchus* alliance in the Canary Islands) within the *Sonchus* group. Furthermore, we avoid subjective considerations referring to which taxa at generic rank are worth being preserved, as well as potential transfers of species epithets among them; thus we also attempt to avoid superfluous combinations and to promote long-term nomenclatural stability. Consequently, herein we propose a new subgenus *Dendroseris*, as well as all the new required combinations for the species in the clade.

Taxonomic treatment

Sonchus subg. ***Dendroseris*** (D. Don) S.-C. Kim & Mejías, *comb. nova*

Dendroseris D. Don *in* Philos. Mag. Ann. Chem. 11: 388. 1832. — *Rea* Bertero *ex* Decne., Arch. Bot. (Paris) 1: 513. 1833. — *Thamnoseris* F. Phil., Anales Univ. Chile 47: 189. 1875. — *Dendroseris* D. Don subg. *Eudendroseris* Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 200. 1922, *nom. inval.* (Arts. 21, 22). — *Dendroseris* D. Don subg. *Phoenicoseris* Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 201. 1922. — *Dendroseris* D. Don subg. *Rea* (Bertero *ex* Decne.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 201. 1922. — *Phoenicoseris* (Skottsb.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 787. 1953. — *Hesperoseris* Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 788. 1953. — *Dendroseris* D. Don subg. *Schizoglossum* (Skottsb.) Carlquist, Brittonia 19: 101. 1967.

Type: *Sonchus splendens* (D. Don) S.-C. Kim & Mejías.

Sonchus splendens S.-C. Kim & Mejías, *nom. nov.*

Dendroseris macrophylla D. Don *in* Philos. Mag. Ann. Chem. 11: 388. 1832. [syn. subst.]; *non Sonchus macrophyllus* Willd., Sp. Pl., ed. 4 [Willdenow] 3: 1519. 1803.

Sonchus brassicifolius S.-C. Kim & Mejías, *nom. nov.*

Dendroseris litoralis Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 204. 1922. [syn. subst.]; *non S. oleraceus* L. var. *littoralis* Kirk, Trans. New Zealand Inst. 26: 265. 1893; *nec S. littoralis* (Kirk) Cockayne, Rep. Bot. Surv. Kapiti Island: 21. 1907.

Sonchus sinuatus S.-C. Kim & Mejías, *nom. nov.*

Rea macrantha Bertero *ex* Decne., Arch. Bot. (Paris) 1: 514. 1833. [syn. subst.]; *non Sonchus macranthus* Poir., Encycl. (Lamarck) Suppl. 3: 289. 1813. — *Dendroseris macrantha* (Bertero *ex* Decne.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 202. 1922.

Sonchus marginatus (Bertero *ex* Decne.) S.-C. Kim & Mejías, *comb. nova*

Rea marginata Bertero *ex* Decne., Arch. Bot. (Paris) 1: 519. 1833. [basion.]. — *Dendroseris marginata* Hook. & Arn., Compan. Bot. Mag. 1: 32. 1835. — *Dendroseris macrophylla* D. Don var. *marginata* Johow, Estud. H. Juan Fernández: 71. 1896.

Sonchus lobatiflorus S.-C. Kim & Mejías, *nom. nov.*

Dendroseris gigantea Johow, Estud. H. Juan Fernández: 69. 1896. [syn. subst.]; *non S. giganteus* Shuttlew. *ex* Rouy, Fl. Fr. 9: 203. 1905. — *Hesperoseris gigantea* (Johow) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 788. 1953.

Sonchus berteroanus (Decne.) S.-C. Kim & Mejías, *comb. nova*

Rea berteroana Decne., Arch. Bot. (Paris) 1: 515. 1833. [basion.]. — *Dendroseris berteroana* (Decne.) Hook. & Arn., Compan. Bot. Mag. 1: 32. 1835. — *Rea pinnata* Bertero *ex* Decne. var. *insignis* Johow, Estud. H. Juan Fernández: 71. 1896. — *Phoenicoseris berteroana* (Decne.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 787. 1953.

Sonchus phoeniciformis S.-C. Kim & Mejias, *nom. nov.*

Rea pinnata Bertero *ex* Decne., Arch. Bot. (Paris) 1: 516. 1833. [syn. subst.]; *non S. pinnatus* Aiton *in* Hort. Kew. (ed. 1) 3: 116. 1789. — *Dendroseris pinnata* (Bertero *ex* Decne.) Hook. & Arn., Compan. Bot. Mag. 1: 32. 1835. — *Phoenicoseris pinnata* (Bertero *ex* Decne.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 787. 1953.

Sonchus regius (Skottsb.) S.-C. Kim & Mejías, *comb. nova*

Dendroseris regia Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 205. 1922. [basion.]. — *Phoenicoseris regia* (Skottsb.) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 787. 1953.

Sonchus micranthus (Bertero *ex* Decne.) S.-C. Kim & Mejías, *comb. nova*

Rea michrantha Bertero *ex* Decne., Arch. Bot. (Paris) 1: 518. 1833. [basion.]. — *Dendroseris micrantha* Hook. & Arn., Compan. Bot. Mag. 1: 32. 1835.

Sonchus neriifolius (Hook. & Arn.) S.-C. Kim & Mejías, *comb. nova*

Rea neriifolia Bertero *ex* Decne., Arch. Bot. (Paris) 1: 517. 1833. [basion.]. — *Dendroseris neriifolia* Hook. & Arn., Compan. Bot. Mag. 1: 32. 1835. — *Rea leucantha* Bertero *ex* DC., Prodr. (DC.) 7: 243. 1838, *nom. nud.* (Art. 32.1)

Sonchus pruinatus (Johow) S.-C. Kim & Mejías, *comb. nova*

Dendroseris micrantha var. *pruinata* Johow, Estud. H. Juan Fernández: 69. 1896. [basion.]. — *Dendroseris pruinata* (Johow) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 207. 1922. — *Rea pruinata* (Johow) Skottsb., Nat. Hist. Juan Fernández (Botany) 2: 788. 1953.

Sonchus laceratus (Phil.) S.-C. Kim & Mejías, *comb. nova*

Rea lacerata Phil., Bot. Zeitung (Berlin) 28: 499. 1870. [basion.]. — *Thamnoseris lacerata* (Phil.) F. Phil., Anales Univ. Chile 47: 190. 1875. — *Dendroseris lacerata* (Phil.) Hemsl., Rep. Voy. Challenger, Bot. 1: 99. 1885. — *Thamnoseris lobata* I. M. Johnst., J. Arnold Arbor. 16: 445. 1935.

Doubtful taxon

Dendroseris mollis (Bertero *ex* Decne.) Hook. & Arn., Hook. Comp. Bot. Mag. 1: 32. 1835. — *Rea mollis* Bertero *ex* Decne., Arch. Bot. (Paris) 1: 519. 1833. [basion.].

The description of this species seems to be exclusively based on vegetative material. The plant described has hoary, velutinous, oval leaves (Johow 1896, Reiche 1910), which would differ from those of the remaining species in the genus, being basically glabrous. According to Johow (1896: 67) the presence of a *Dendroseris* species with this kind of leaves in the typical locality is doubtful; probably the material was mistaken for a *Dendroseris*.

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