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 Cichorieae (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 Canary 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 Coreopsis-ideae), because of their common arborescent life form. Stebbins (1953) redefined the group as 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 Sonchiae (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.

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.*

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.

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**Outgroup**

**The woody Sonchus alliance in the Macaronesian Islands**

**Dendroseris in the Juan Fernandez Islands**
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 matK 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 Fernandean 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., Kathirarachchi 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 matK dataset) which, according to
these results, should be proposed as a new sub-
genus 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 classifica-
tions 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 evolution-
ary 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 radia-
tion process (just as in the woody *Sonchus* alli-
ance in the Canary Islands) within the *Sonchus*
group. Furthermore, we avoid subjective consid-
erations 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 com-
binations for the species in the clade.

**Taxonomic treatment**

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

1875. — *Dendroseris* D. Don subg. *Eudendroseris* Skottsb.,
( Arts. 21, 22). — *Dendroseris* D. Don subg. *Phoenicoseris*
— *Dendroseris* D. Don subg. *Rea* (Bertero ex Decne.) Skot-
tsb., Nat. Hist. Juan Fernández (Botany) 2: 201. 1922. —
*Phoenicoseris* (Skottsb.) Skottsb., Nat. Hist. Juan Fernández
Juan Fernández (Botany) 2: 788. 1953. — *Dendroseris* D.
Don subg. *Schizoglossum* (Skottsb.) Carlquist, Brittonia 19:

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

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

*Dendroseris macrophylla* D. Don in Philos. Mag. Ann. Chem. 11: 388. 1832. [syn. subst.]; *non* *Sonchus macrophy-

*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.
*litoralis* Kirk, Trans. New Zealand Inst. 26: 265. 1893; *ne*
21. 1907.

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

1833. [syn. subst.]; *non* *S. 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*

1833. [basion.]. — *Dendroseris marginata* Hook. & Arn.,
Compan. Bot. Mag. 1: 32. 1835. — *Dendroseris macrophylla*
1896.

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

1896. [syn. subst.]; *non* S. *giganteus* Shuttlew. ex Rouy, Fl.
Fr. 9: 203. 1905. — *Hesperoseris gigantea* (Johow) Skottsb.,

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

[basion.]. — *Dendroseris berteroana* (Decne.) Hook. & Arn.,
1896. — *Phoenicoseris berteroana* (Decne.) Skottsb., Nat.
Hist. Juan Fernández (Botany) 2: 787. 1953.
Sonchus phoeniciformis S.-C. Kim & Mejías, nom. nov.


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


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


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


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


Doubtful taxon


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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