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A note on leaf venation and the circumscription of *Tephrosieris* (Asteraceae–Senecioneae)

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Abstract: Molecular phylogenetic results had shown that *Tephrosieris*, a genus differentiated from its closest relatives by its pinnately veined leaves, also contains species with palmate leaf venation. This had led to the conclusion that leaf venation is a homoplasious character in the lineage containing *Tephrosieris*. We here take a closer look at leaf venation in *Tephrosieris* and other species of Asteraceae–Senecioneae. We found that leaf venation in *Tephrosieris* is distinct from leaf venation in *Jacobaea vulgaris* and *Senecio vulgaris*, which both have pinnately veined leaves as typical for most species of their respective genera, and that description of the leaves of *Tephrosieris* as pinnately veined is incorrect. Instead, leaf venation in *Tephrosieris* is very similar to that of upper cauline leaves of *Ligularia stenocephala*, a species with clearly palmately veined basal and lower cauline leaves. Both *L. stenocephala* and *Tephrosieris* are part of the *Ligularia–Cremanthodium–Parasenecio* (L–C–P) complex. We conclude that leaf venation in *Tephrosieris* is best regarded as derived from palmate leaf venation found in the large majority of species in the L–C–P complex, and presents no morphological obstacle to the circumscription of the genus.

Key words: Asteraceae, Compositae, heteroblasty, leaf venation, *Ligularia–Cremanthodium–Parasenecio* complex, *Nemosenecio*, palmate, pinnate, *Senecioneae*, *Sinosenecio*, *Tephrosieris*

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Introduction

Tephrosieris (Rchb.) Rchb., considered to contain 15 species by its last monographer (Cufodontis 1933) but more recently estimated to contain c. 50 species (Nordenstam 1978, 2007), is most closely related to *Nemosenecio* (Kitam.) B. Nord. and *Sinosenecio* B. Nord., a group of genera classified as subtribe *Tephrosieridinae* C. Jeffrey & Y. L. Chen by Jeffrey & Chen (1984) and recovered as a well-supported monophyletic group in a molecular phylogenetic analysis of *Senecioneae* (Pelser & al. 2007). This clade is part of a larger clade known as the *Ligularia–Cremanthodium–Parasenecio* complex (L–C–P

complex; Liu & al. 2006) which, besides *Tephrosieris*, *Nemosenecio* and *Sinosenecio*, contains *Cremanthodium* Benth., *Farfugium* Lindl., *Ligularia* Cass., *Ligulariopsis* Y. L. Chen, *Miricacalia* Kitam., *Parasenecio* W.W. Smith & Small, *Sinacalia* H. Rob. & Brettell and *Syneilesis* Maxim. as understood by Nordenstam & al. (2009). This complex in turn is part of *Tussilaginatae* s.str. (Nordenstam & al. 2009).

Tephrosieris, *Nemosenecio* and *Sinosenecio* have been differentiated, among other characters, using leaf morphology (Jeffrey & Chen 1984; Nordenstam 2007). Thus, *Tephrosieris* has been described as having pinnately veined, subentire or dentate leaves, *Nemosenecio* as hav-

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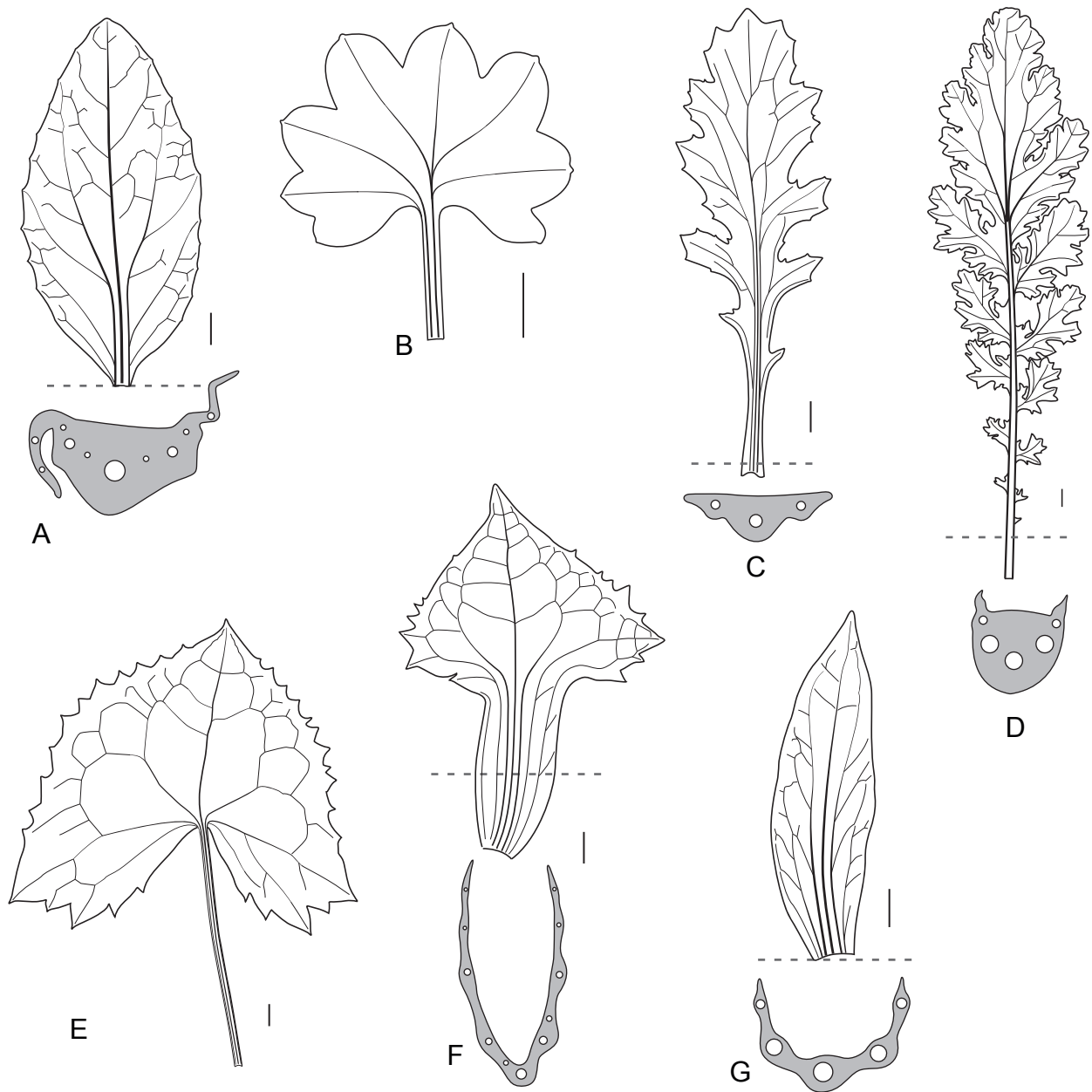


Fig. 1. Leaf shape and venation (abaxial leaf surface) and cross-sections (A, D, F, G; level of section indicated by dashed lines) of leaf bases. – A: *Tephrosieris integrifolia*; B: *T. newcombei*; C: *Senecio vulgaris*; D: *Jacobaea vulgaris*; E–G: *Ligularia stenocepala*; E: basal leaf; F: middle cauline leaf; G: upper cauline leaf. – Circles in cross-sections represent vascular bundles. – Scale bars: all 5 mm.

ing pinnately lobed or dissected leaves, and *Sinosenecio* as having palmately veined leaves (after exclusion of *S. hainanensis* (Chang & Tseng) C. Jeffrey & Y. L. Chen, with pinnately veined leaves, as *Hainanecio* Y. Liu & Q. E. Yang by Liu & Yang [2011]). Pinnate vs. palmate first-order vein topology represents the two major states of leaf venation in eudicotyledonous angiosperms, is not variable within species and has been used to describe higher-rank taxa (Hickey & Wolfe 1975). In the most recent molecular systematic study of *Tephrosieris*, aimed at further investigating its circumscription (Wang & al. 2009), it was found that *S. koreanus* (Kom.) B. Nord. and *S. newcombei* (Greene) J. P. Janovec & T. M. Barkley

fall into *Tephrosieris*. Accordingly, the two species have been combined into *Tephrosieris* as *T. koreana* (Kom.) B. Nord. & Pelser and *T. newcombei* (Greene) B. Nord. & Pelser by Nordenstam & Pelser (2011). On the other hand, *T. changii* B. Nord. was found to group outside *Tephrosieris*. Close relationships of *S. koreanus* and *S. newcombei* to *Tephrosieris* had been shown before by Golden & al. (2001), and a close relationship of *T. changii* to parts of *Sinosenecio* had been suspected by Jeffrey & Chen (1984). Beyond the relationships of the above two species of *Sinosenecio* to *Tephrosieris*, *Sinosenecio* has been shown to be non-monophyletic (Wang & al. 2009; Ren & al. 2017). Because *T. koreana* and *T. newcombei*

were considered to have palmately veined leaves (Wang & al. 2009), although Golden & al. (2001) described the venation pattern in *T. newcombei* (Fig. 1) as “clearly not strictly palmate”, Wang & al. (2009) concluded that characters used for the delimitation of *Nemosenecio*, *Sinosenecio* and *Tephroseris*, such as leaf venation, show widespread homoplasy.

While revising *Tephroseris* for a work in preparation by the first author, it became evident that leaf venation cannot really be described as pinnate when compared to leaf venation patterns in, e.g., *Jacobaea* Mill. and *Senecio* L. Also, pinnate leaf venation appears to be rather rare in the *Ligularia*–*Cremanthodium*–*Parasenecio* complex. Within the *L–C–P* complex, *Cremanthodium* has been described as having palmately, pinnately or parallel-veined leaves (Liu & Illarionova 2011), *Farfugium* as having palmately veined leaves (Nordenstam 2007), *Ligularia* as having palmately or pinnately veined leaves (Liu & Illarionova 2011), *Ligulariopsis* as having pinnately veined leaves (Nordenstam 2007), *Miricacalia*, *Sinacalia* and *Syneilesis* as having palmately veined leaves (Nordenstam 2007; *Sinacalia*: palmately veined or nearly so) and a clearly non-monophyletic *Parasenecio* (Ren & al. 2017) as usually having palmately veined leaves (Nordenstam 2007). The *Parasenecio* segregates, *Japonicalia* C. Ren & Q. E. Yang and *Taimingasa* (Kitam.) C. Ren & Q. E. Yang, appear to have palmately veined leaves.

The aim of this paper is to examine leaf venation in *Tephroseris* in order to find out whether the genus indeed contains species with either pinnately or palmately veined leaves, as claimed in the literature (Wang & al. 2009). For this purpose, we will compare leaf venation in *Tephroseris* with leaf venation in species of *Senecio* L. and *Jacobaea* Mill. with clearly pinnately veined leaves, and with a species of *Ligularia*, representing the *L–C–P* complex, with clearly palmately veined leaves.

Material and methods

Origin of plant material

Jacobaea vulgaris Gaertn.: Germany, Mainz, Johannes Gutenberg-Universität Mainz, campus, waste ground, 29 Aug 2019, K. Bohley & J. W. Kadereit s.n. (MJG).

Ligularia stenocephala (Maxim.) Matsum. & Koidz.: Germany, Mainz, Johannes Gutenberg-Universität Mainz, Botanic Garden, cultivated material, 29 Aug 2019, K. Bohley & J. W. Kadereit s.n. (MJG).

Senecio vulgaris L.: Germany, Mainz, Johannes Gutenberg-Universität Mainz, campus, waste ground, 29 Aug 2019, K. Bohley & J. W. Kadereit s.n. (MJG).

Tephroseris integrifolia (L.) Holub: Germany, Mainz, Johannes Gutenberg-Universität Mainz, Botanic Garden, cultivated material, 29 Aug 2019, K. Bohley & J. W. Kadereit s.n. (MJG) (grown from seed collected at Germany, Kyffhäuser, 3 Jun 2018, J. W. Kadereit s.n.).

Tephroseris newcombei (Greene) B. Nord. & Pelsler: Canada, Queen Charlotte Islands, c. 20 miles S of Moresby Logging Camp, 29 Jul – 2 Aug [without year], Calder, Savile & Taylor 23075 (H).

Leaf shape and leaf venation as visible on the lower leaf surface were observed with a Leitz Elvar (Leitz, Germany) dissecting microscope at 3.2× magnification. For *Tephroseris newcombei* these observations were made on herbarium material; for all other species on freshly collected and carefully pressed leaves. Cross-sections of leaf bases were obtained by hand with a razor blade using freshly collected leaves, and cross-sections were observed with a Leitz Laborlux S microscope (Leitz, Germany) at 25× magnification.

Results

Leaf shape and leaf venation (lower leaf surface) and leaf base cross-sections are shown in Fig. 1. *Senecio vulgaris* (Fig. 1C) and *Jacobaea vulgaris* (Fig. 1D) have pinnately veined leaves with one primary vein with lateral veins departing at more or less regular intervals toward the leaf tip. The petiole of *S. vulgaris* contains three vascular bundles and the petiole of *J. vulgaris* contains five vascular bundles. In contrast, clearly three primary veins enter the leaf in *Tephroseris integrifolia* (Fig. 1A) and more than five vascular bundles can be seen in cross-section. In *T. newcombei* (Fig. 1B), described as palmately veined in the literature, more than one primary vein can be seen entering the leaf. *Ligularia stenocephala* has clearly palmately veined basal leaves (Fig. 1E). The upper cauline leaves of this species have three primary veins, and five vascular bundles are visible in cross-section (Fig. 1G). In middle cauline leaves (Fig. 1F), several primary veins and several vascular bundles can be seen.

Discussion

Leaf venation in *Tephroseris* (*T. integrifolia*), described as pinnately veined in the literature (Jeffrey & Chen 1984; Nordenstam 2007), clearly is different from pinnate leaf venation as seen in *Senecio* (*S. vulgaris*) and *Jacobaea* (*J. vulgaris*). Whereas in the latter two species the leaves have one primary vein with lateral veins departing at more or less regular intervals toward the leaf tip (Fig. 1C, D), and thus are pinnately veined, *T. integrifolia* clearly has three veins entering the leaves (Fig. 1A). This difference is evident both from the venation pattern recognizable on the leaf surface and from leaf anatomy as seen in cross-sections. The cross-section of the petiole of *J. vulgaris* (Fig. 1D) shows, as is typical for *Asteraceae* (Stevens 2001+), that the primary vein of its leaves contains an arc of five vascular bundles, and three vascular bundles can be seen in *S. vulgaris* (Fig. 1C). In *T. in-*

tegrifolia, however, cross-sectioned at a similar position, clearly additional lateral vascular bundles can be seen (Fig. 1A), and these correspond to the additional veins entering the leaf from its very base.

It therefore seems clear that description of leaf venation in *Tephrosieris integrifolia* as pinnately veined is inaccurate. Leaf venation in all other species traditionally included in *Tephrosieris* is very similar to that seen in *T. integrifolia*, and only in species with a distinct petiole is it more difficult to see that more than one vein enters the leaf blade (Kadereit, pers. obs.). Leaf venation seen in *T. newcombei* (Fig. 1B), described as palmately veined by Wang & al. (2009) but as “clearly not strictly palmate” by Golden & al. (2001), can easily be derived from the *T. integrifolia* pattern by stronger outward curvature of the veins entering the leaf base, which probably is related to the somewhat reniform shape of the leaf blade of this species. Thus leaf venation pattern in *Tephrosieris*, i.e. including *T. koreana* and *T. newcombei*, is essentially uniform and does not fall into two categories that could be described as pinnate or palmate.

The leaf venation pattern seen in *Tephrosieris* does not easily fit into what is considered and illustrated as pinnately and palmately veined in the literature (Hickey & Wolfe 1975; Walls 2011; Sack & Scoffoni 2013). Interestingly, instead of resembling pinnately veined leaves of *Jacobaea* and *Senecio*, the leaves of *T. integrifolia* are similar to the upper cauline leaves (Fig. 1G) of *Ligularia stenocephala* (Maxim.) Matsum. & Koidz. *Ligularia* is a member of the *L–C–P* complex with either palmately or pinnately veined leaves (Liu & Illarionova 2011), and *L. stenocephala* has clearly palmately veined basal and lower cauline leaves (Fig. 1E). The upper cauline leaves of this species, however, clearly show three primary leaf veins entering the leaf at its very base (Fig. 1G). While the similarity between basal leaves of *T. integrifolia* and upper cauline leaves of *L. stenocephala* is evident in the venation pattern recognizable on the leaf surface, there exists a difference in leaf anatomy because only five vascular bundles are visible in the cross-section at the base of an upper cauline leaf of the latter species (Fig. 1G). However, in more transitional leaves a little further down the axis, a pattern similar to *T. integrifolia* can be seen with additional vascular bundles lateral to the five bundles of the central vein (Fig. 1F). In *L. stenocephala*, the two very different leaf morphologies seen in one individual are the endpoints of heteroblastic change of leaf morphology along the axis, i.e. ontogenetic change, as very commonly seen in angiosperms, where such heteroblastic change often consists of reduction of morphological complexity (Troll 1939). Although phylogenetic relationships are not well resolved in the *L–C–P* complex (Liu & al. 2006; Pelser & al. 2007; Wang & al. 2009; Ren & al. 2017), the predominance of palmate leaf venation in the complex (and indeed in *Tussilaginatae* s.str.) make it likely that the condition seen in *Tephrosieris* is derived. If correct, the presence in *T. integrifolia* of only leaves with

several veins entering from the very base can then be interpreted as resulting from a phylogenetic loss of lower cauline leaves. In the context of discussing the evolution of flowering phenologies, reduction in number or loss of leaves observed in early-flowering genotypes has been referred to as “deletion” by Diggle (1999).

When the leaves of *Tephrosieris*, examined in detail in *T. integrifolia* and *T. newcombei*, are considered homologous with the upper cauline leaves of *L. stenocephala*, they could be named palmate-derived. If this interpretation is correct, leaf venation pattern within the *L–C–P* complex may be less variable than described because the pattern seen in *Tephrosieris*, and described as pinnately veined, fits into the presumable ancestral, palmately veined condition of the *L–C–P* complex.

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