Astartoseris (Cichorieae, Asteraceae), a new, systematically isolated monospecific genus accommodating Lactuca triquetra endemic to Lebanon and Cyprus

Authors: Kilian, Norbert, Hand, Ralf, Hadjikyriakou, Georgios N., Christodoulou, Charalambos S., and Dagher-Kharrat, Magda Bou

Source: Willdenowia, 47(2) : 115-125

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.47.47203

Willdenowia
Annals of the Botanic Garden and Botanical Museum Berlin-Dahlem

NORBERT KILIAN[1*], RALF HAND[1], GEORGIOS N. HADJIKYRIAKOU[2], CHARALAMBOS S. CHRISTODOULOU[3] & MAGDA BOU DAGHER-KHARRAT[4]

Astartoseris (*Cichorieae, Asteraceae*), a new, systematically isolated monospecific genus accommodating *Lactuca triquetra* endemic to Lebanon and Cyprus

Abstract: The taxonomy of *Lactuca triquetra*, a scoparious subshrub of localized distribution and uncertain generic placement, is assessed. The taxon was described in the early 19th century from Lebanon and more than 100 years later also discovered on Cyprus. Referring to new molecular phylogenetic results published elsewhere, morphological characters, in particular of the achenes, are reconsidered. It is inferred from the available evidence that the diploid species represents an orphan lineage, which diverged from its ancestors already in the Middle Miocene, when the *Cichorieae* subtribes *Crepidinae* and *Lactucinae* started diversifying. Both molecular and morphological data indicate that the species holds a position mediating between both subtribes. The taxonomic conclusion is drawn to place the species in a new genus of its own, *Astartoseris*. The taxon is illustrated and a comprehensive description, distribution map and brief ecological characterization are provided. Its threat status in both countries is assessed for the first time.

Key words: *Asteraceae*, *Compositae*, *Lactucinae*, *Crepidinae*, *Astartoseris*, phylogenetics, taxonomy, new genus, Mediterranean region, Cyprus, Lebanon

Article history: Received 6 April 2017; peer-review completed 6 June 2017; received in revised form 16 June 2017; accepted for publication 22 June 2017.

Citation: Kilian N., Hand R., Hadjikyriakou G. N., Christodoulou Ch. S. & Bou Dagher-Kharrat M. 2017: *Astartoseris* (*Cichorieae*, *Asteraceae*), a new, systematically isolated monospecific genus accommodating *Lactuca triquetra* endemic to Lebanon and Cyprus. – Willdenowia 47: 115–125. doi: https://doi.org/10.3372/wi.47.47203

Introduction

Among the early collections from the Levant, specimens of a scoparious, almost leafless subshrub, unmistakable for its conspicuously triangular stems and lilac-blue-flowered, lactucoid capitula, were brought to Europe by Jacques-Julien Houtou de Labillardière in 1788 and subsequently described as *Prenanthes triquetra* Labill. in 1809. Much later, in 1937, the species was also discovered and collected in Cyprus by A. Syngrassides (Meikle 1985). No evident allies of the species are known and with respect to its generic classification no consensus has been reached. Therefore the species has been treated as a member of either *Prenanthes* L. (Meikle 1985), *Scariola* F. W. Schmidt (Mouterde 1978; Tohmè & Tohmè 2007) or *Lactuca* L. (Boissier 1875; Greuter 2006+). Meikle (1985) remarked on its obscure generic status and that "further work on the tribe *Lactuceae* may find a better home for it".

It was in 2003 when the first author generated first DNA sequences of this peculiar, taxonomically isolated species in his attempt to resolve the phylogeny of the *Lactuca* alliance. Quite unexpectedly, however, the case became intriguing. While more and more sequences of members of the *Lactuca* alliance were added to the analyses over

---

1 Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany; *e-mail: n.kilian@bgbm.org (author for correspondence); r.hand@bgbm.org
2 Antifonitis str. 10, 4551 Trachoni Lemesou, Cyprus; e-mail: alakati@cytanet.com.cy
3 Department of Forests, 26 Louki Akrita, 1414 Nicosia, Cyprus; e-mail: floracy@primehome.com
4 Laboratoire Caractérisation Génomique des Plantes, Faculté des Sciences, Campus Sciences et Technologies, Université Saint-Joseph, Mar Roukos Mkalles, Lebanon; e-mail: magda.boudagher@usj.edu.lb

time, the sister-group relationships of *Lactuca triquetra* changed repeatedly, but always with the effect that it was never found nested within any of the other terminal clades. Only years later, after a comprehensive sampling of the entire subtribe *Lactucinae* and its related taxa had been achieved, did it become evident that *L. triquetra* is an early diverging orphan lineage somehow mediating between the subtribes *Lactucinae* and *Crepidinae.* While the corresponding comprehensive phylogeny has been published elsewhere (Kilian & al. 2017), the aims of this article are (1) to re-examine the morphological characterization of *L. triquetra*, in particular the achene ribbing pattern in the context of the molecular phylogenetic results, because it was shown by Stebbins (1940) and has been confirmed by the data accumulated since that different patterns have evolved in the two subtribes; (2) to draw the taxonomic conclusions; and (3) to investigate its distribution, ecology and threat status in both countries of occurrence.

Material and methods

Plant material — This study is based on an extensive survey of all populations of the species in Cyprus and of many in Lebanon in particular during recent years, on plants cultivated in the Botanic Garden Berlin as well as on the specimens preserved at the herbaria B, BEI, CYP, G, JE, P and W, the personal herbarium of G. Hadjikyriakou and digital images of specimens from E, FI, G-DC, G-BOIS and K. The samples of *Lactuca triquetra* used in the molecular phylogenetic analysis by Kilian & al. (2017) and shown in Fig. 3 and 4 are vouchered by the following specimens: LAC-276 = *Cubr 38916* (B), LAC-277 = *Hand 5731* (B), LAC-278 = *Hand 5730* (B), LAC-285 = *Bou Dagher-Kharrat* (B100517440) and LAC-286 = *Bou Dagher-Kharrat* (B100517439); see Appendix.

Micromorphology — For scanning electron microscopy, achenes were mounted onto SEM stubs on double-sided sticky tape, coated with 20 nm Au-Pd using an Emitech K550 sputter-coater and examined using a Philips SEM 515. Stem cross-sections were hand-cut from stem portions embedded in elder pith and documented using a WILD M5 optical reflected-light microscope equipped with a digital camera. Achene anatomy was studied on toluidin blue stained permanent preparations of transverse and longitudinal microtome sections (3 μm) prepared according to the following method: the achenes were soaked in a mixture (6:1) of 10 % aqueous solution of sulfosuccinate and 96 % ethanol at 4 °C for 24 h, then dehydrated in an 1:1, 3:7, 1:9 incremental series of sulfosuccinate/ethanol for 24 h each, finally twice dehydrated in pure 96 % ethanol for 45 min, subsequently soaked for 6 weeks in commercial hydroxyethylmethylacrylate (Kulzer Technovit 7100 and Kulzer Solidifier No. 1, 100 ml : 1 g) at 4 °C before final embedding in a 1:15 mixture of these reagents.

Results and Discussion

Morphological characterization — Being a scoparious, almost leafless, xerophytic subshrub (Fig. 1A, D) with small capitula of only 5 cyanic florets with long (fertile part 4.8–5.8 mm) anther tubes (Fig. 2D), *Lactuca triquetra* is a fairly conspicuous species. It, moreover, shows two morphological peculiarities, which diagnose it well:

(1) Stems with a distinct triangular cross-section (Fig. 2A): triquetrous axes otherwise occur scattered in angiosperms but also in pteridophytes (see *Psilotum* Sw.). In the *Cyperaceae* they are a common state, but occurrences seem to exist in some other families, as judged from an IPNI (2016) search for epithets beginning with “triquet” and subsequent random verification through the protologues. Usually, however, triquetrous axes seem to be present only in single species of a family, and also in the tribe *Cichorieae* we know of no other species with triquetrous axes. Phylogenetic investigations in the *Cyperaceae* genus *Eleocharis* R. Br. indicate that shifts between different stem cross-section shapes (circular, 3-, 4-, 5-angular) occur frequently (Hinchliff & Roalson 2009). This may imply that a rather limited set of mutational steps are responsible for the different states. Nothing is known about the ecological significance of different cross-section shapes (Hinchliff & Roalson 2009), and altogether non-circular stem cross-sections seem to be a field largely untouched by research. In *Lactuca triquetra*, the angles are very prominent and the sides are often even somewhat concave. Taken into account that the plants are most of the time almost leafless, the triangular stems are the major organ for photosynthesis. A stem angle always concurs with the singular leaf trace in the axes and terminates in the midrib of the corresponding leaf or bract. The alternate leaves have a divergence angle of somewhat more than 120°, rotating counter-clockwise and spiralling around the axis. So the midrib and leaf trace of every fourth leaf is finally situated over the left edge of the first leaf. In contrast, the perennial and lignifying bases of the stems are cylindric. A transitional state is illustrated in Fig. 2B, C.

(2) Ribbing pattern of its achenes (Fig. 2E–G): the achene wall of *Lactuca triquetra* is composed of five segments, as is common and plesiomorphic for the tribe and family (Kilian & al. 2009a). These correspond to the five principal longitudinal ribs, which can be clearly seen in a cross-section of the basal third of the achene (Fig. 2G). In the middle third of the achene, where the wall patterns are fully developed, each segment shows 5–7-plets of ribs fairly similar in size, the achene wall thus has 25–35 longitudinal ribs altogether (Fig. 2F). This feature is very odd in the subtribe *Lactucinae*, where the achene wall segments otherwise have 3-plets of ribs, namely the principal rib accompanied by one, usually narrower and less prominent, secondary rib on either side, adding to at most 15 longitudinal ribs altogether. Its ribbing pattern morphologically links *L. triquetra* to the subtribe *Crepidinae*, where such a pattern is frequently found (Stebbins 1940).

Fig. 1. *Astartoseris triquetra* – A: habitat and habit of a plant on serpentinite between Foinikaria and Prastio, Cyprus; B: same plant with one basal branch at base removed (arrow) and tap root (arrow) excavated, measuring c. 3 cm in diam. at top; C: same plant, cross-section of removed basal branch measuring 11 mm in diam., showing at least four annual rings (arrow indicating first one); D: plant growing in crevices of limestone rock at Hamat, Lebanon. – A–C photographed by G. Hadjikyriakou on 14 Oct 2011 (A) and on 17 Nov 2016 (B, C); D photographed by Magda Bou Dagher-Kharrat on 16 Nov 2008.

Karyology — The species is a diploid with a chromosome number of 2*n* = 18 (Kilian & Hand 2004) and has a nuclear genome size of 1C = 18.56 pg (Bou Dagher-Kharrat & al. 2013). This chromosome number is within the range of basic chromosome numbers of the *Lactucinae* (*x* = 9 and *x* = 8) but outside those of the *Crepidinae* (from *x* = 8 to *x* = 3) (Kilian & al. 2009a). The nuclear genome content is near the lower end of the medium size class (>1.4–3.5 pg). Several diploid species, both in the *Lactucinae* and *Crepidinae,* show a similar value (e.g. *Cicerbita muralis* (L.) Wallr., *Crepis aurea* (L.) Cass., *C. capillaris* (L.) Wallr., *C. foetida* L., *Lactuca viminea* (L.) J. Presl & C. Presl and *L. virosa* L., but many more show higher values or are in the upper size class (GSAD 2013).

Phylogeny and divergence time estimation — Recent molecular phylogenetic analyses of the subtribe *Lactucinae* and its closest relatives revealed incongruent tree topologies for nrITS and non-coding plastid DNA loci with respect to *Lactuca triquetra* (Kilian & al. 2017). The species is nested in the *Lactucinae* clade in the nrITS phylogeny (Fig. 3) but in the *Crepidinae* clade in the plastid DNA phylogeny (Fig. 4). In both phylogenies, *L. triquetra* holds a very isolated position. In particular, it is distant in the nrITS phylogram from *Lactuca* even in its widest sense. The genus *Prenanthes* (with its only species *P. purpurea* L.) and *L. triquetra* in a polytomy with the *Faberia* lineage are consecutive sisters to all other *Lactucinae* in the nrITS phylogram, and as is also indicated by the branch lengths correlated to the number of nucleotide substitutions, *L. triquetra* and *P. purpurea* are by no means close relatives. Apart from the fact that both species have few-flowered capitula with cyanic florets, also morphologically, in particular with respect to the achenes, both have low affinity to each other.

The molecular findings for *Lactuca triquetra* strongly resemble the case of *Faberia* Hemsl., a genus chiefly restricted to SW China. Both are found in an early diverging position in the *Lactucinae* in the ITS phylogeny but more deeply nested within the *Crepidinae* in the plastid DNA phylogeny (Fig. 3 and 4). The members of *Faberia*, however, uniformly have a chromosome number of 2*n* = 34 and the genus evidently has an allopolyploid origin. Because of the different distribution of basic chromosome numbers in the *Crepidinae* and the *Lactucinae*, it has been assumed that the ma-

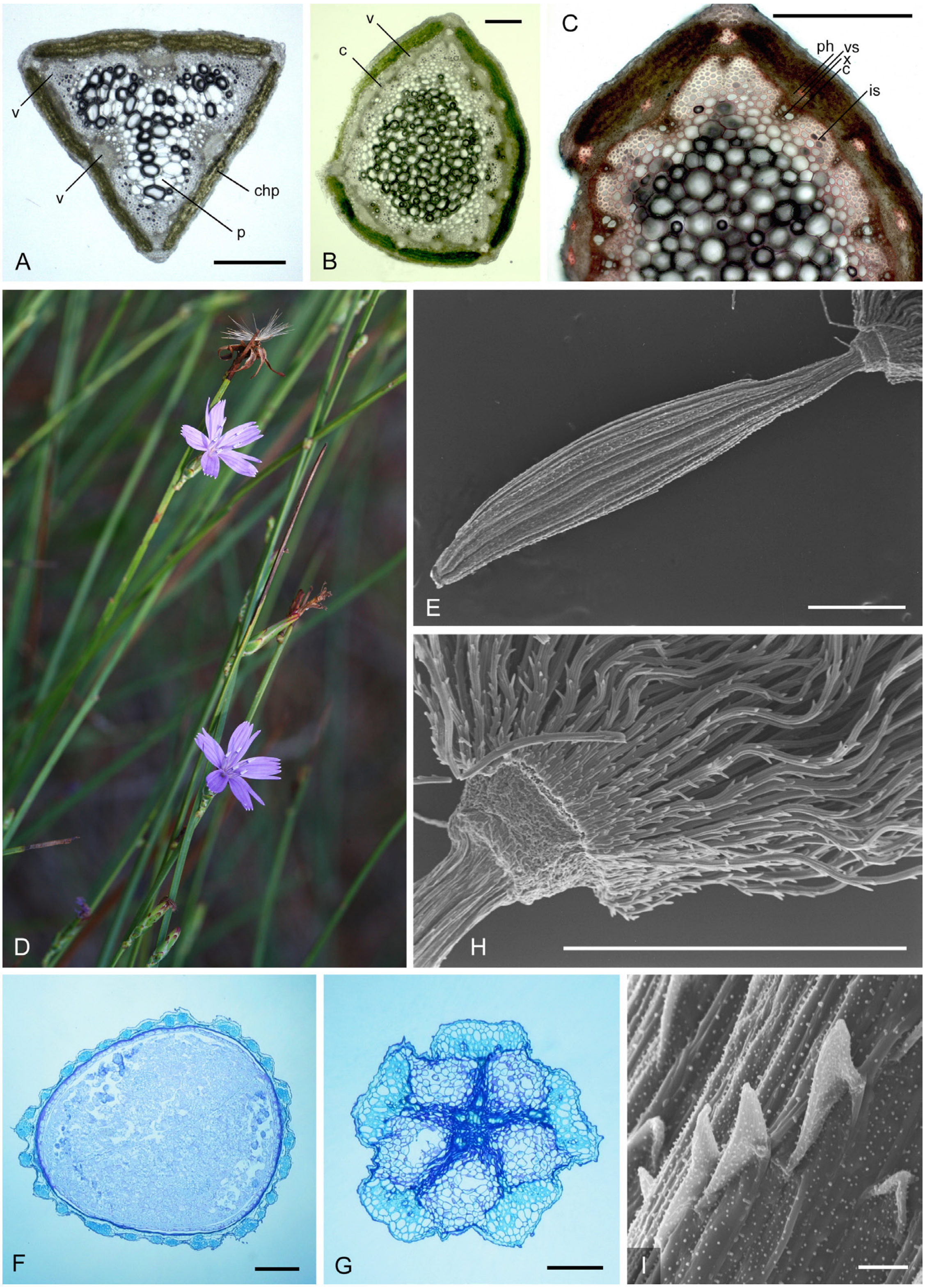

Fig. 2. *Astartoseris triquetra* – A: cross-section of first year's triquetrous shoot, showing six vascular bundles (v); B: cross-section of shoot in transition zone between first year's shoot and lignified axis with secondary growth, showing 15 vascular bundles (v), a closed cambium cylinder (c) and start of secondary growth; C: detail view of cross-section of transition zone shoot; D: flowering capitula; E: scanning electron microscopy (SEM) image of an achene; F: achene cross-section in middle third, showing ribbing pattern; G: achene cross-section near base, showing five wall segments; H: SEM image of achene apex with pappus; I: SEM image of achene epidermis. – v = vascular bundle; x = xylem; c = cambium; ph = phloem; vs = vascular sclerenchyma; is = intervascular sclerenchyma; p = pith; chp = chlorophyllous parenchyma. – Scale bars: A–C = 5 mm; E, H = 1 mm; F, G = 0.1 mm; I = 10 µm. – A–C from a plant cultivated at BG Berlin from *Hand 5730*; D photographed by Christodoulos Makris near Foinikaria, Cyprus, on 13 Oct 2007; E–I first published in Willdenowia 34: 442, fig. 1. 2004, from *Buttler 32460* (B).

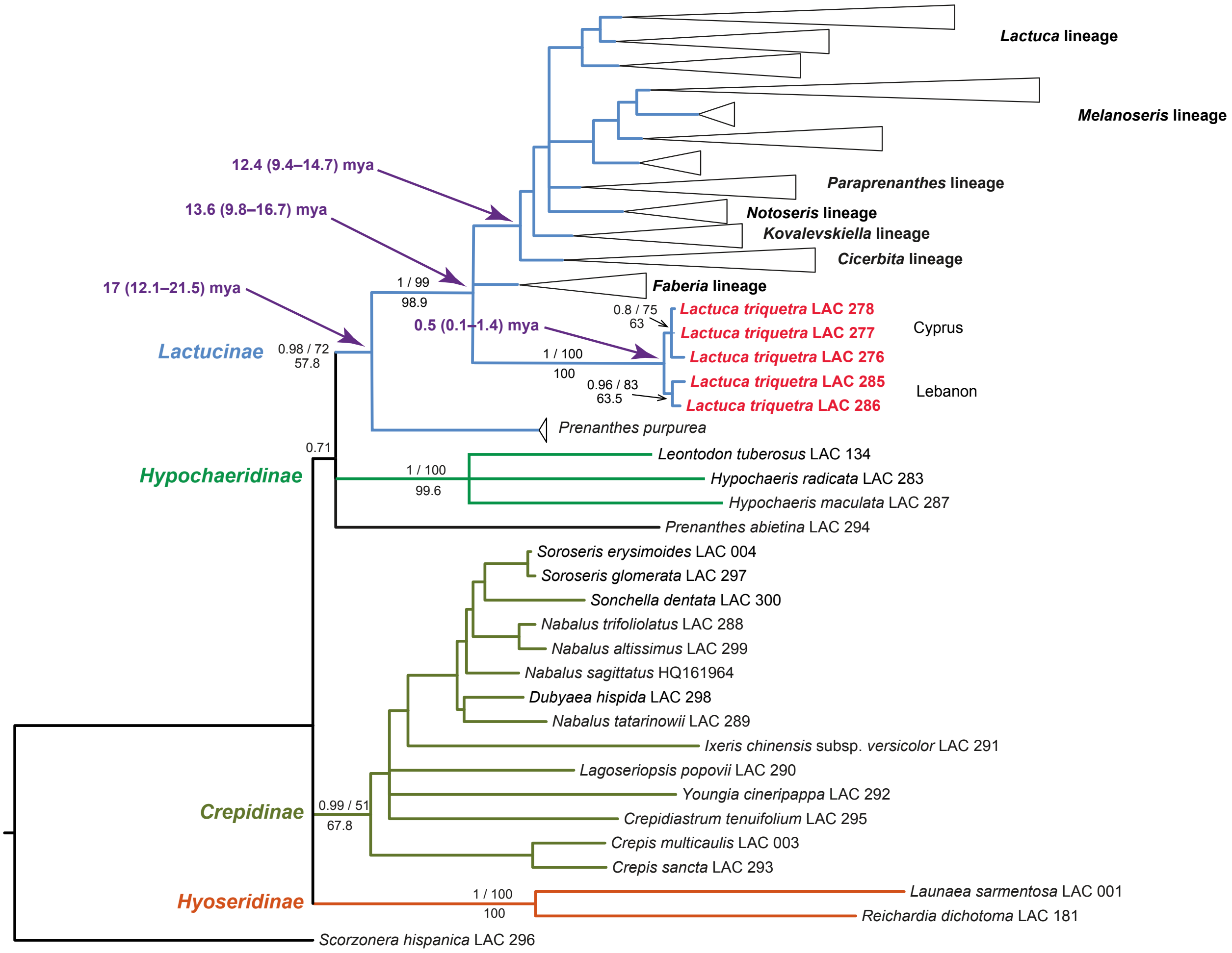

Fig. 3. Majority consensus phylogram of *Lactucinae* from Bayesian analysis based on nrITS data set and focusing on phylogenetic position of *Lactuca triquetra*; adapted from Kilian & al. (2017). Support values (Bayesian posterior probability / Maximum Likelihood Bootstrap; second line: Maximum Parsimony Jackknife) for relevant branches; ages of relevant nodes as median heights (in purple) obtained with relaxed molecular clock dating using BEAST (Drummond & Rambaut 2007).

ternal ancestor of *Faberia* (with 2*n* = 16) was contributed by the *Crepidinae* and its paternal ancestor (with 2*n* = 18) by the *Lactucinae* (Liu & al. 2012, 2013; Wang & al. 2013). In the case of the diploid *L. triquetra* with 2*n* = 18 chromosomes and a rather low genome size, karyology therefore provides no indication for reticulate evolution. The finding of crepidinoid achenes with 5–7-plets of ribs combined with the lactucinoid, cyanic, few-flowered capitula in *L. triquetra* are nevertheless a conspicuous morphological equivalent to the incongruent gene trees with the placement of the taxon in the *Crepidinae* based on the maternally inherited plastid DNA and in the *Lactucinae* based on the biparentally inherited nrITS DNA.

As a phylogenetically isolated, monospecific taxon, *Lactuca triquetra* appears well comparable to other orphan lineages such as the Caucasian "*Prenanthes*" *abietina* (Boiss. & Balansa) Kirp. (see Fig. 3 and 4 and Kilian & al. 2017) or *Avellara* Blanca & C. Díaz from the Iberian Peninsula (Fernández-Mazuecos & al. 2016). Apparently they all diverged at rather early stages in the diversification of the *Chondrillinae-Crepidinae-Hyoseridinae-Hypochaeridinae-Lactucinae* main clade of the *Cichorieae* in their present subtribes during the Middle Miocene (Kilian & al. 2009a, 2017; Tremetsberger & al. 2013).

Divergence time estimation by Kilian & al. (2017) based on the nrITS dataset revealed that the *Lactuca triquetra* lineage diverged from its ancestors in the *Lactucinae* around 13.6 mya (95 % HPD 9.8–16.7 mya) (see Fig. 3). Based on the plastid DNA dataset, a similar estimate of 13.5 mya (95 % HPD 9–17.9 mya) was revealed for its divergence from the common ancestors in the *Crepidinae* (see Fig. 4). The lineage is thus younger than *Prenanthes purpurea* and has emerged little earlier than or roughly around the same time as the core *Lactucinae* sensu Wang & al. (2013), the clade including the lineages *Cicerbita* Wallr. to *Lactuca*. The split between the *L. triquetra* populations in Cyprus and Lebanon, in contrast, occurred comparatively late: around 0.5 mya (95 % HPD 0.1–1.4 mya) to 0.8 mya (95 % HPD 0.1–1.9) according to the same nrITS and plastid DNA analyses (Fig. 3, 4). Such disjunctions between the Mediterranean parts of the Levant (i.e. Lebanon, neighbour-

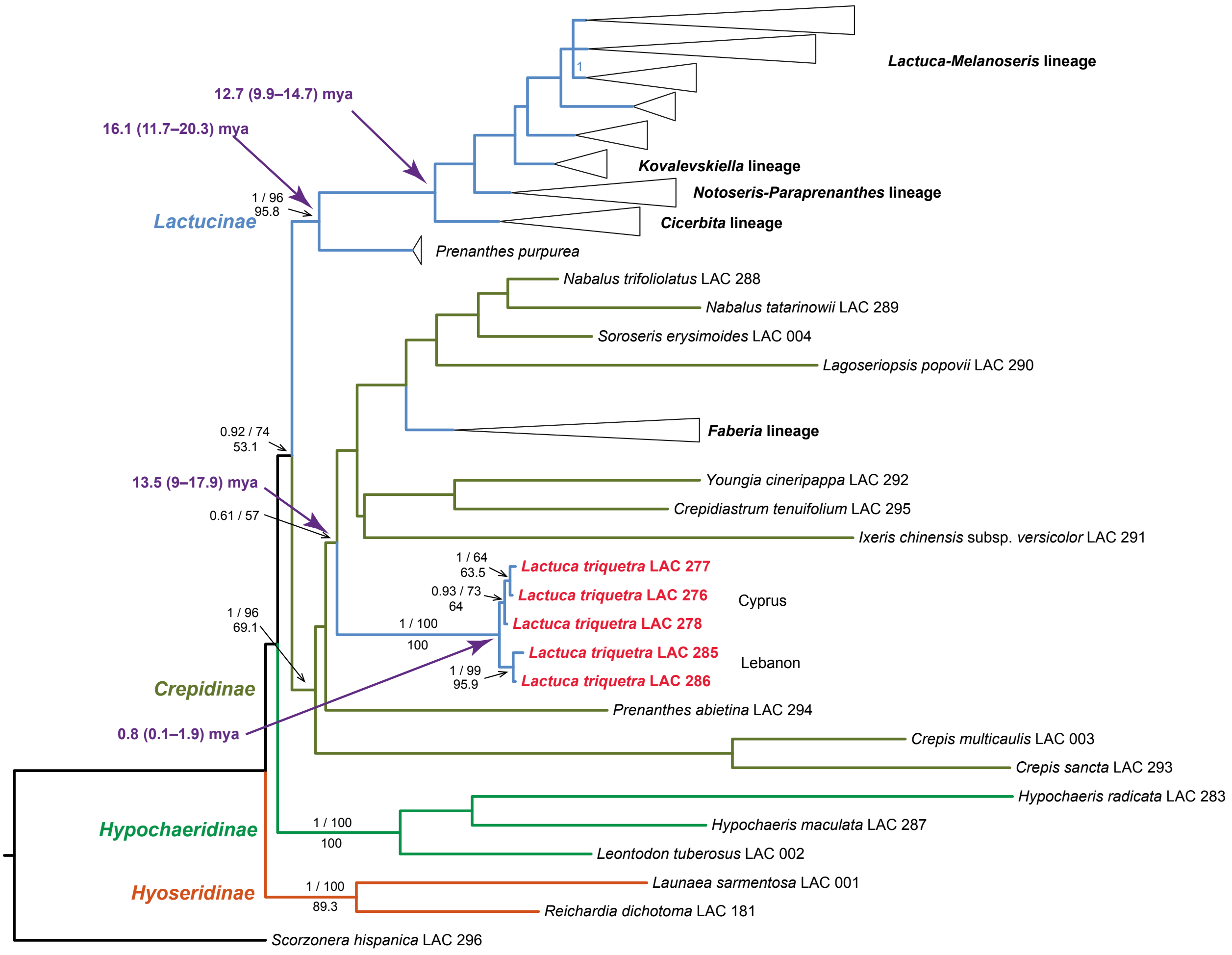

Fig. 4. Majority consensus phylogram of *Lactucinae* from Bayesian analysis based on plastid DNA data set and focusing on phylogenetic position of *Lactuca triquetra*; adapted from Kilian & al. (2017). Support values (Bayesian posterior probability / Maximum Likelihood Bootstrap; second line: Maximum Parsimony Jackknife) for relevant branches; ages of relevant nodes as median heights (in purple) obtained with relaxed molecular clock dating using BEAST (Drummond & Rambaut 2007).

ing parts of Syria, and Israel) to the island of Cyprus can be found in many species, e.g. *Acer obtusifolium* Sm., *Echium judaeum* Lacaita, *Tordylium carmeli* (Labill.) Al-Eisawi and *Trigonella berythea* Boiss. & C. I. Blanche. No comparable studies on divergence time estimation seem to exist.

Although both trees show a congruent phylogenetic structure that places the Cyprus and Lebanon plants in two different clades with good statistical support, we have failed to find morphological discontinuities between them. The most conspicuous difference seems to be the occurrence on different substrates in both parts of the distribution area (see below).

Classification — The appropriate taxonomic conclusion from the evidence provided is to place *Lactuca triquetra* in a new genus of its own. Its subtribal affiliation remains questionable in the light of its incongruent positions in the gene trees and morphological intermediacies. However, in view of the stronger affinity to the *Lactucinae* expressed in its overall morphology as well in its karyology, we treat it as a member of the *Lactucinae*.

Astartoseris N. Kilian, Hand, Hadjik., Christodoulou & M. Bou Dagher-Kharrat, **gen. nov.** – Type: *Astartoseris triquetra* (Labill.) N. Kilian, Hand, Hadjik., Christodoulou & Bou Dagher-Kharrat

Diagnosis — Scoparious subshrub with triangular branches and spiculiform synflorescences; capitula with 5 lilac-blue florets; achenes with 5 main sections in the middle third differentiated into 5–7-plets of longitudinal ribs rather similar to each other, therefore with 25–35 ribs (instead of up to 15 ribs as is usual in the *Lactucinae*).

Etymology — The generic name of female gender is a compound of the Greek name “Astarte” (Αστάρτη) for the ancient Levant goddess *ʿAthtartu* (Ugaritic) or *ʿštrt* (Phoenician) and “seris” (σέρις), the classical Greek name for salad (more precisely for *Cichorium* species, Liddell & al. 1940). Worship of Astarte spread to Cyprus. Often she was equated with Aphrodite, whose mythical place of birth has been localized in Cyprus since ancient times.

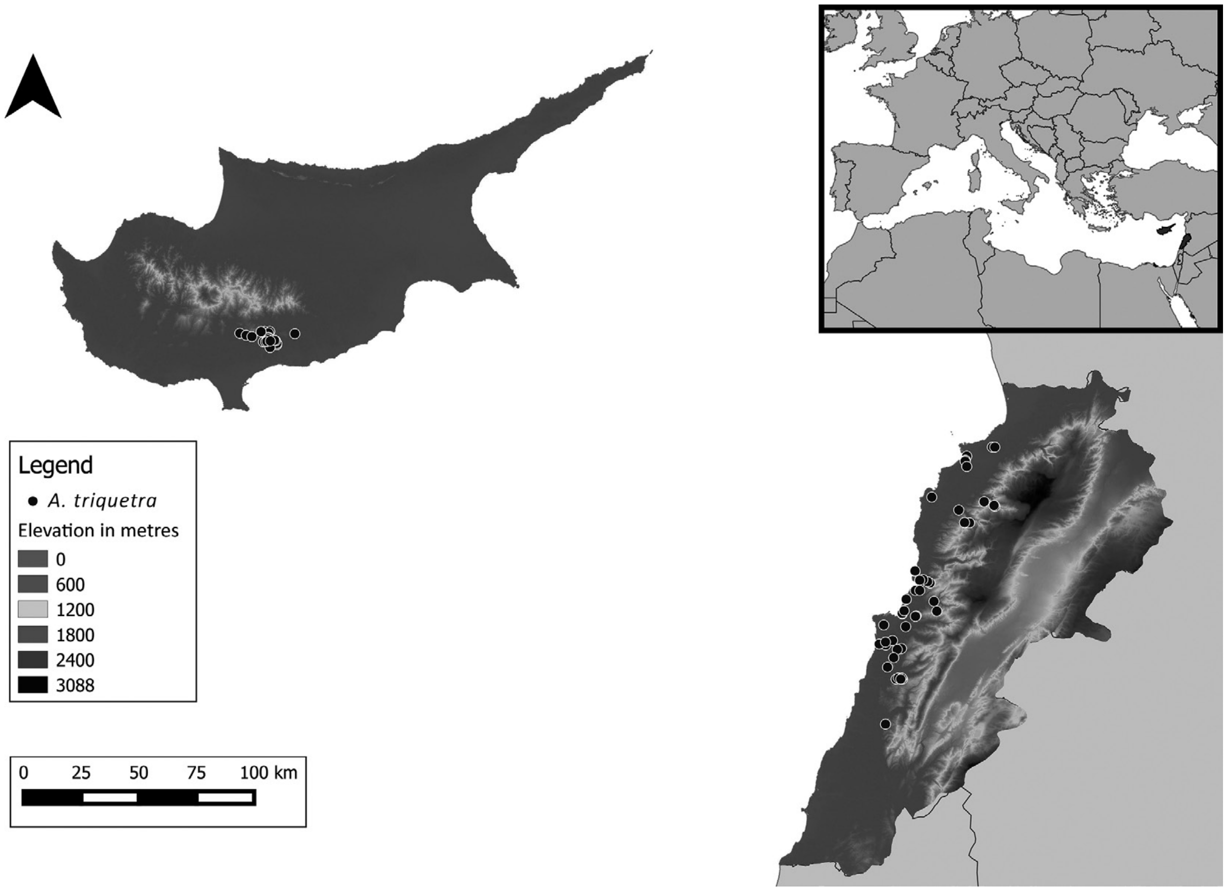

Fig. 5. Distribution of *Astartoseris triquetra* based on material seen and field observations (see Appendix).

Astartoseris triquetra (Labill.) N. Kilian, Hand, Hadjik., Christodoulou & Bou Dagher-Kharrat, **comb. nov.** ≡ *Prenanthes triquetra* Labill., Icon. Pl. Syr. 3: 4, t. 2. 1809 ≡ *Phaenopus triqueter* (Labill.) DC., Prodr. 7: 176. 1838 ≡ *Chondrilla triquetra* (Labill.) Steud., Nomencl. Bot., ed. 2, 1: 354. 1840 ≡ *Lactuca triquetra* (Labill.) Boiss., Fl. Orient. 3: 819. 1875 ≡ *Scariola triquetra* (Labill.) Soják in Novit. Bot. Delect. Seminum Horti Bot. Univ. Carol. Prag. 1962: 46. 1962. – **Lectotype (designated here):** [Lebanon, s. loc.], "ad montium radices", [1787], *J. J. H. de Labillardière s.n.* (FI006679; isolectotype: K00815010).
[– *Lygodesmia triquetra* (Labill.) D. Don in Edinburgh New Philos. J. 6: 311. 1829, nom. inval. (McNeill & al. 2012: Art. 35.2)].

Typification — It is evident from the protologue of *Prenanthes triquetra* that the description was based on material collected by the author and the only other indication of the material given is "Habitat in Libano ad montium radices". According to Stafleu (1968), Jacques-Julien Houtou de Labillardière's journey to Syria and Lebanon in 1787–1788 was promoted by Louis-Guillaume Lemonnier, professor of botany at the Jardin du Roi, Paris, and the main set of plants was retained by him, as part of his personal herbarium. Lemonnier's herbarium was acquired in 1803 by Benjamin Delessert. With Delessert's herbarium it finally became part of the collection of the Conservatoire et Jardin botaniques de la Ville de Genève (G). Some specimens, however, were kept by Labillardière. After his death Labillardière's herbarium was acquired by Philipp Baker Webb and is now part of the Webb herbarium at Herbarium Universitatis Florentinae (FI). This apparently happened with Labillardière's material of *P. triquetra.* No specimen is preserved at G (pers. comm. Laurent Gautier, Head Curator, Oct. 2016), while a specimen is present in the Webb herbarium, on which the text of the protologue written in Labillardière's hand is mounted. The basal part of this specimen well matches the excellent illustration of the species by Pierre-Jean-François Turpin in the protologue (Labillardière 1791–1812 [part 3 : t. 2. 1809]). A further specimen is present at K. The FI specimen is selected here as the lectotype of the name *P. triquetra*.

Description — *Subshrub* (Fig. 1A, D), scoparious, largely leafless, glabrous, to c. 80 cm tall, many-branched from woody rootstock and with a strong taproot (Fig. 1B). *Branches* stiff, erect to curved-erect, woody at base and with roundish cross-section (Fig. 1C), otherwise conspicuously acute-triangular to winged-triangular, slender, green to glaucous green (Fig. 1A). *Leaves* crowded to rosulate at base of young shoots from woody axes, narrowly spatulate, acute to acuminate, 1.5–7 × 0.2–1 cm, usually perished at anthesis, at first consecutive nodes of shoots linear-spatulate to linear and soon reduced to linear bracts. *Synflorescence* spiculiform, capitula single or in small clusters at nodes of terminal portion of branches. *Capitula* with 5 florets, sessile or on 1–5 mm long peduncles (Fig. 2D) covered by bracts similar to and grading into outer involucral bracts. *Involucre* 11–14 mm long, narrowly cylindric; involucral bracts with a distinct scarious margin often tinged purplish, especially towards tip; outer involucral bracts ovate-acute, to c. 4(–7) mm long; inner involucral bracts 5, linear-lanceolate, 11–14 mm. *Florets* with pale lilac-blue corolla, anther tube white with pale lilac-blue connectives and apical appendages, pollen white, style lilac-blue; corolla tube 7–9 mm long, apically pubescent on outside, ligule 10–11 mm long, 3.2–3.8 mm wide; anther tube with fertile part 4.8–5.8 mm long, basal appendages 0.6–0.9 mm long, apical appendages 0.6–0.8 mm long. *Achenes* 4.5–5.5 mm long, narrowly subfusiform (Fig. 2E), with largest diameter in upper third and tapering more strongly towards apex than base, somewhat compressed; main ribs 5 (Fig. 2G), each at least in middle third usually accompanied on either side by 2 or 3 secondary ribs similar in size to main rib, forming 5–7-plets, thus achene altogether with 25–35 ribs (Fig. 2F); epidermis cells on their surface with numerous minute, globular to subcylindric papillae and with an apically protruding, triangular, subacute to acute tip (Fig. 2I); achene apex subcuspidate below pappus disk; carpophore annular, smooth. *Pappus* 6–7 mm long, persistent, of numerous scabrid bristles (Fig. 2H), near base mostly 5–7 cells in diam.

Distribution, ecology and phenology — The distribution of the species is restricted to a small area in southwestern Cyprus and western Lebanon (Fig. 5).

In Lebanon, *Astartoseris triquetra* occurs in the western part of the Mount Lebanon range from the coastline up to 1100 m (Fig. 5). In some locations it is present on the calcareous bedrock (e.g. Hamat region), while in others it occurs also on cliffs under *Pinus brutia* Ten. trees (e.g. Baabda region). Flowers are seen from September until November; ripe achenes can be found from October until December. Freshly collected seeds germinate after 15 days at 10 °C with very high germination rates.

In Cyprus, *Astartoseris triquetra* is restricted to Lemesos forest (Fig. 5), one of the largest occurrences of Upper Cretaceous serpentinites at lower and medium altitudes of the island. Typically, the species flourishes at the bottom of stream beds situated in very open *Pinus brutia* forests between c. 150 and 750 m above sea level. In some places it dominates vegetation of the stream beds forming dense thickets. Water runs in winter and spring only, and in some places the species is accompanied by hygrophilous taxa such as *Epipactis veratrifolia* Boiss. & Hohen. On the other hand, *A. triquetra* is able to colonize the neighbouring dry, often semi-shaded slopes, but the population density is much lower there. Meikle's (1985) information about occurrences "on chalky cliffs" is not based on his own field observations and may be a misinterpretation. Such occurrences cannot be excluded considering the complicated geological mosaic of the Lemesos forest, but need corroboration. However, recent surveys failed to locate any population on calcareous bedrocks. Lemesos forest is well known for its remarkable flora, namely the local serpentine endemics *Alyssum chondrogynum* B. L. Burtt, *Dichoropetalum kyriakae* (Hadjik. & Alziar) Hand & Hadjik. and *Euphorbia lemesiana* Hadjik. & al., and the characteristic serpentinophilous *Centaurea cyprensis* (Holub) T. Georgiadis otherwise present only on the Akamas peninsula. The isolated occurrence of *A. triquetra* underlines the phytogeographical significance of Lemesos forest. The plant flowers in September and October. Ripe achenes can be found until December. Among Cypriot *Asteraceae*, it is one of the few strictly autumnal bloomers. Occasional sightings showed that *Astartoseris triquetra* is pollinated by various insect species such as small *Apidae* and the bee fly *Phthiria* Meigen, 1803 (*P.* cf. *gaedii* Wiedemann in Meigen, 1820; det. Christodoulos Makris; for photographs see Kilian & al. 2009b).

Threat status — The threat status of *Astartoseris triquetra* is evaluated here for the first time. On Cyprus it is evaluated as Near Threatened (NT) according to IUCN criteria (2012). It is close to qualifying as Vulnerable (VU) because two of the three requirements for classification in this category are fulfilled: its extent of occurrence (EOO) is approximately 38 km^2 (criterion B1 and/or B2) and the number of locations is fewer than 10 (B1a and/or B2a), but no decline or extreme fluctuations occur. In Lebanon its status is evaluated as Endangered (EN) B1ab(i,ii,iii)+2ab(i,ii,iii) based on its limited area of distribution and the ongoing threats, such as urbanization and browsing. Its EOO is approximately 1602 km^2 and its area of occupancy (AOO) is estimated to 144 km^2. The appropriate global status is therefore assessed as Vulnerable (VU).

Acknowledgements

The authors would like to thank Christodoulos Makris (Lemesos) for the determination of pollinators and photographs of the species, Karl Peter Buttler (Frankfurt am Main) for providing specimens collected in Cyprus, Michael Meyer and his team of gardeners (Berlin) for the successful cultivation of the species, Christoph Dietrich (Berlin) for technical assistance in the morphological lab, Michael Rodewald (Berlin) for graphical assistance, and two anonymous reviewers and the Editor for their critical scrutiny and valuable comments.

References

Boissier E. 1875: Flora orientalis **3.** – Basel & Genève: H. Georg.

Bou Dagher-Kharrat M., Abdel-Samada N., Douaihy B., Bourge M., Fridlender A., Siljak-Yakovlev S. & Brown S. C. 2013: Nuclear DNA C-values for biodiversity screening: case of the Lebanese flora. – Pl. Biosystems **147:** 1228–1237.

Drummond A. J. & Rambaut A. 2007: BEAST: Bayesian evolutionary analysis by sampling trees. – BMC Evol. Biol. **7:** 214.

Fernández-Mazuecos M., Jiménez-Mejías P., Martín-Bravo S., Buide M. L., Álvarez I. & Vargas P. 2016: Narrow endemics on coastal plains: Miocene divergence of the critically endangered genus *Avellara* (*Compositae*). – Pl. Biol. 18: 729–738.

Greuter W. (2006+): *Compositae* (pro parte majore). – In: Greuter W. & Raab-Straube E. von (ed.): *Compositae*. Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. – Published at http://ww2.bgbm.org/EuroPlusMed/ [accessed Dec 2016].

GSAD 2013: Genome Size in *Asteraceae* Database. – Published by the Universitat de Barcelona, the Institut Botánic de Barcelona, and Consejo Superior de Investigaciones Científicas (CSIC). – Published at http://asteraceaegenomesize.com/

Hinchliff C. E. & Roalson E. H. 2009: Stem architecture in *Eleocharis* subgenus *Limnochloa* (*Cyperaceae*): evidence of dynamic morphological evolution in a group of pantropical sedges. – Amer. J. Bot. **96:** 1487–1499.

IPNI 2016: The International Plant Names Index. – Published at http://www.ipni.org [accessed Dec 2016].

IUCN 2012: IUCN Red List categories and criteria: version 3.1, ed. 2. – Gland & Cambridge: IUCN. – Published at http://www.iucnredlist.org/technical-documents/red-list-documents

Kilian N., Gemeinholzer B. & Lack H. W. 2009a: Tribe *Cichorieae*. – Pp. 343–383 in: Funk V. A., Susanna A., Stuessy T. & Bayer R. (ed.), Systematics, evolution, and biogeography of the *Compositae*. – Vienna: International Association for Plant Taxonomy.

Kilian N. & Hand R. 2004: *Lactuca triquetra* (Labill.) Boiss. – Pp. 441–444 in: Hand R. (ed.), Supplementary notes to the flora of Cyprus IV. – Willdenowia **34:** 427–456.

Kilian N., Hand R. & Raab-Straube E. von (general ed.) 2009b+. *Cichorieae* Systematics Portal. – Published at http://cichorieae.e-taxonomy.net/portal

Kilian N., Sennikov A., Wang Z.-H., Gemeinholzer B. & Zhang J.-W. 2017: Sub-Paratethyan origin and Middle to Late Miocene principal diversification of the *Lactucinae* (*Compositae*: *Cichorieae*) inferred from molecular phylogenetics, divergence-dating and biogeographic analysis. – Taxon 66: 675–703.

Labillardière J.-J. H. de 1791–1812: Icones plantarum Syriae rariorum. – Paris: Prevost.

Liddell H. G., Scott R., Stuart Jones, H. & McKenzie R. 1940: A Greek-English lexicon. A new edition [ed. 9]. – Oxford: Clarendon Press.

Liu Y., Chen Y.-S. & Yang Q.-E. 2013. Generic status, circumscription, and allopolyploid origin of *Faberia* (*Asteraceae*: *Cichorieae*) as revealed by ITS and chloroplast DNA sequence data. – Taxon **62:** 1235–1247.

Liu Y., Deng T. & Yang Q.-E. 2012: Karyology of the genus *Faberia* (*Cichorieae – Asteraceae*) and its systematic implications. – Nordic J. Bot. **29:** 365–371.

McNeill J., Barrie F. R., Buck W. R., Demoulin V., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Marhold K., Prado J., Prud'homme van Reine W. F., Smith G. F., Wiersema J. H. & Turland N. J. (ed.) 2012: International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. – Königstein: Koeltz Scientific Books. – Regnum Veg. **154.**

Meikle R. D. 1985: Flora of Cyprus **2.** – Kew: Royal Botanic Gardens.

Mouterde P. 1978: Nouvelle flore du Liban et de la Syrie **3.** – Beyrouth: Dar El-Machreq.

Stafleu F. A. 1968: Labillardière and the Levant. – Pp. v–xv in: Labillardière J.-J. de, Icones plantarum Syriae rariorum. – Lehre: Cramer [reprint of the orig. ed. 1791–1812].

Stebbins G. L. 1940: Studies in *Cichorieae*: *Dubyaea* and *Soroseris*. Endemics of the Sino-Himalayan region. – Mem. Torrey Bot. Club **19(3):** 1–76.

Tohmè G. & Tohmè H. 2007: Illustrated flora of Lebanon. – Beirut: National Council for Scientific Research.

Tremetsberger K., Gemeinholzer B., Zetzsche H., Blackmore S., Kilian N. & Talavera S. 2012: Divergence time estimation in *Cichorieae* (*Asteraceae*) using a fossil-calibrated relaxed molecular clock. – Organisms Diversity Evol. **13:** 1–13.

Wang Z.-H., Peng H. & Kilian N. 2013: Molecular phylogeny of the *Lactuca* alliance (*Cichorieae* subtribe *Lactucinae*, *Asteraceae*) with focus on their Chinese centre of diversity detects potential events of reticulation and chloroplast capture. – PLoS ONE **8(12):** e82692.

Appendix: Specimens studied and own observations

Cyprus: Akrounta, 1.8 km above, at road to Dierona, brook in serpentine area E of a distinctive bend, alt. 250 m, 34°46'42.45"N, 33°05'14.04"E, 21 Oct 2003, *R. Hand 4009* (B); ibid., 23 Sep 2010, *R. Hand 5731* (B); Fountanoudin, Lemesos Forest, rocky streamside in open *Pinus brutia* forest, alt. 600 m, 34°49'33°07'E, 5 Nov 1990, *G. Hadjikyriakou 1002* (herb. Hadjikyriakou); Gerasa, valley above road to Kalo Chorio 1.2 km N of Apsiou junction, alt. 470 m, 34°48'40"N, 33°00'E, 12 Oct 1998, *K. P. Buttler 32460* (B; also cultivated at BG Berlin as acc. 033-08-99-10 and preserved as *Cubr 38916* at B); Dierona, 5.3 km S of village on road to Akrounta, alt. 590 m, 34°49'N, 33°05'45"E, 12 Oct 1998, *K. P. Buttler 32466* (B); ibid., 28 Apr 1999, *R. Hand 2939* (B); Kyparissia river, Lemesos forest, on rocks and cliffs along banks of river, alt. 500 m, [34°47'N, 33°06'E], 22 Oct 1989, *G. Hadjikyriakou 351* (herb. Hadjikyriakou); ibid., 22 Oct 1989, *G. Hadjikyriakou 722* (CYP); ibid., on rocky ground by streamside, alt. 500 m, [34°47’13.47”N, 33°07’00.49”E], 11 Sep 1991, *C. S. Christodoulou 1228* (CYP); c. 2 km SSW of Dierona (not on road), brook valley above road to Akrounta, dry rivulet, alt. 610 m, 34°48'29"N, 33°05'03"E, 23 Sep 2010, *R. Hand 5730* (B; also cultivated at BG Berlin as acc. 237-90-10-10 and preserved as *Cubr 49479* at B); Apsiou, Lemesos forest, at stream crossing track NE of Amirou monastery, alt. 480 m, 34°47'59"N, 33°02'47"E, 23 May 2013, *R. Hand & G. Hadjikyriakou* (*obs.*); 500 m N of Apsiou village, rocky streamside in open *Pinus brutia* forest, alt. 470 m, [34°48'36.31"N, 33°01'28.83"], 23 Sep 2016, *G. Hadjikyriakou 7459* (herb. Hadjikyriakou); ibid., 23 Sep 2016, *C. S. Christodoulou & G. Hadjikyriakou 6512* (CYP); 1 km E of Amirou monastery, rocky streamside in open *Pinus brutia* forest, alt. 390 m, [34°48'02.10"N, 33°02'48.58"], 23 Sep 2016, *G. Hadjikyriakou 7460* (herb. Hadjikyriakou); ibid., 23 Sep 2016, *C. S. Christodoulou & G. Hadjikyriakou 6513* (CYP).

Lebanon: s loc., “ad montium radices” [1787], *J. J. H. de Labillardière s.n.* (FI006679, K000815010); Mont Liban, 1832, *N. Bové 433* (W 1889-173516); Mont Liban, *N. Bové 434* (G-DC GDC00453869, P03767653, P03767654, P03767655); s.loc., 1837, *P. M. R. Aucher-Eloy 3346* (G-DC GDC00453866); s.loc., 1837, *P. M. R. Aucher-Eloy 3353* (G00308988, G-BOIS G00334047, G-DC GDC00453867, P03767643, P03767644); Arissa [= Harissa, 33°59'N, 35°39'E], July 1833, *P. M. R. Aucher-Eloy 327* (W 1889-171469); Deir el Konir [=? Deir el-Qamar, near Beit-ed-Dine, 33°42'N, 35°34'E], 8 Aug 1864, *G. E. Post* (BEI); Ghazir à Beit Kachbo [ancient couvent et maisons S de Ghazir, au-dessus de Ma’meltein, 34°00'51.12"N, 35°39'28.44"E], 20 Apr 1859, *C. Gaillardot* (JE, P03767645, p.p., W 1889-65315); au-dessus de Choueifat [Shuwayfat; côte, E de l’aéroport, N de Khaldé, 33°48'36.72"N, 35°29'32.28"E], rochers calcaires, alt. 250 m, 5 Nov 1957, *H. Pabot* (G00308981); beyond Shwaifat / Shoufat [= Choueifat, 33°49'N, 35°31'E], 28 Nov 1958, *M. Sloane 101* (BEI); Roum, from Sidon, alt. c. 600 m, 33°33'N, 35°31'E, 15 Sep 1957, *T. D. Maitland 181* (W 1960-5250); Choueifat [33°49'N 35°31'E] nr. Beirut, 500 ft, hard limestone rocks, *P. H. Davis 9833* (E00481428); Choueifat [33°49'N 35°31'E], among calcareous rocks, 24 Jan 1943, *P. H. Davis 5197* (E00481429); Dlepta [Kesrouan, vers Ghazir et Ghosta] à Ghazir [34°00'42.84"N, 35°40'49.8"E], 27 Oct 1948, *P. Mouterde 9420* (G00308983); prope Ghazir in m. Libano [34°01'N, 35°39'E], *C. Gaillardot* (P03767659); Aleib [N Deir-el-Qamar] to Souk-el-Gharb [33°47'43.44"N, 35°34'43.68"E], 9 Sep 1899, *G. E. Post* (BEI); Bchela [entre Mayfouq et Douma, 34°12'09.72"N, 35°49'29.28"E], alt. 1200 m, 26 Apr 1959, *P. Mouterde 12183* (G00308985); Hakel [paleontological site 12 miles NE of Byblos = Jebeil, 34°14'36"N, 35°48'08"E], Jul 1931, *Frère L. Arsene s.n.* (P04314027, P04314028); Nahr el Kelb [33°57'16"N, 35°35'51"E], Jun–Jul 1846, *E. Boissier* (G-BOIS G00334048) Nahr el Kelb, ad rupes [33°57'16"N, 35°35'51"E], 2 Nov 1878, *E. Peyron* (G00308979); Nahr el Kelb [33°57'16"N, 35°35'51"E], 3 Nov 1893, E. Peyron (P03767649, P03767650); Nahr el Kelb [33°57'16"N, 35°35'51"E], 30 Oct 1951, *H. Pabot* (G00308987); Nahr el Kelb [33°57'16"N, 35°35'51"E], 20 Feb 1952, *H. Pabot* (G00308976); Nahr el Kelb [33°57'16"N, 35°35'51"E], Nov 1953, *H. Pabot* (G00308977); Nahr el Kelb [33°57'16"N, 35°35'51"E], 3 Oct 1933, *P. Mouterde 2814* (G00308982); Nahr el Kelb [33°57'16"N, 35°35'51"E], 20 Apr 1951, *P. Mouterde 10156* (G00308986); Nahr el Kelb, versant rocheux [33°57'16"N, 35°35'51"E], Nov 1938, *J. E. Vidal L 06* (P04135484); “Fleuve du Chien” [= Nahr el Kelb, 33°57'16"N, 35°35'51"E], *C. I. Blanche 190* (P03767651, P03767652); in rupestribus calcariis infra Anubin alt. 3000 ped. [= below Qannoubine = Deir Qannubin = ancient monastery, in direction to Dimane and Hasroune, 34°15'28.2"N, 35°56'22.98"E], alt. 1000 m, 31 Jul 1855, *C. G. T. Kotschy 366* (E00481430, G-BOIS G00334046, P00750405, P00750406, W0049844, W0049843, W 1889-289114); Fontes des rochers calcaires de la rive gauche du Nahr-el-Kelb entre le pont et le moulin du couvent de Marc Joussef, au N de Beyrouth [33°57'16"N, 35°35'51"E], 18 Oct 1857, *C. Gaillardot 276* (B, G00308989, G00308990, JE, P03767646, P03767647, P03767648, P04312168, P04390381, P04402075, W 1889-56440); dans la fissures de rochers calcaires à pie de la rive gauche du Fleuve du Chien [= Nahr el Kelb] entre le pont et le moulin du couvent de Marc Joussef, au N de Beyrouth [33°57'16"N, 35°35'51"E], 18 Oct 1857, *C. Gaillardot 2019* (B, E00481425, G-BOIS G00334050, JE, P03767660, P03767661, P03767658, W0049842, W0049841); ad Berytum (Beirût), in rupestribus vallis fluvii Nahr el-Kelb [33°57'16"N, 35°35'51"E], 5 May 1910, *J. Bornmüller & F. Bornmüller Iter Syriacum II 12060* (B, G00308994, W 1912-4067); Beyruth, 1863–1864, *B. T. Lowne* (E00481427); Schluchten bei Brummana [E of Beirut, between Beit Méri and Ba’abdate, 33°54'N, 35°38'E], alt. 650 m, Jul 1897, *J. Bornmüller Iter Syriacum I 321* (B); bei Brumana, auf Kalk, alt. c. 700 m [33°54'N, 35°38'E], 10 Oct 1895, *E. Hartmann 38* (JE); vers Jall-ed-Dib [Banlieue de Beyrouth sur la route de Tripoli, 33°54'34.92"N, 35°34'54.48"E], 18 Nov 1950, *P. Mouterde 10024* (G00308984); monte Torbol [Turbol, c. 34°26'N, 35°56'E] près Tripoli, May–Jul 1846, *E. Boissier* (G-BOIS G00334049); Bouar [village côtier, proche de l’embouchure du Nahr Ibrahim et de l’Aquaibé, 34°02'48.12"N, 35°37'54.48"E], 10 Apr 1949, *P. Mouterde 9497* (G00308980); Beitmeri [= Beit Mery, 33°52'N, 35°35'43"E], ad rupes, 25 Sep 1878, *E. Peyron 67* (G00308978); Suq el Gharb, mountains above, 33°47'33"N, 35°33'45"E, 17 Sep 1899, *G. E. Post* (G00308993); Souk el Gharb [33°47'33"N, 35°33'45"E], Nov 1900, *B. V. D. Post* (G00308992); Saida, rochers au Sud de Deir Me Khallés, vallée de Nahr aoule, 22 Jun 1854, *C. Gaillardot* (JE); Vallée de Dein Mekhalles, Nov 1850, *C. Gaillardot* (JE); près de Ain Sindiane, sur la route de Tripoli à Dimane [34°16'13.02"N, 35°54'04.02"E], 5 Oct 1864, *C. I. Blanche 3509* (BEI, E00481426, G-BOIS G00334029, JE, P03767656, P03767657); l’Est de Ghazier, rochers calcaires [34°01'08"N, 35°39'45"E], 19 Oct 1861, *C. Gaillardot* (JE); de Deir El Qarnar [= 33°42'03.24"N, 35°33'38.16"E] à Beit Ed Din [= 33°41'59.28"N, 35°34'47.28"E] [33°41'47"N, 35°34'33.5"E], 18 Sep 1927, *R. Gombault 96* (P03278847, P03278848, P03278849); Ainab [33°45'57"N, 35°32'55"E], 14 Sep 1959, *Edgecombe 493* (BEI); Ainab [33°45'57"N, 35°32'55"E], 27 Oct 1963, *Edgecombe A-1681* (BEI); 3 km N of Jounie [= Jounieh, Juniyah, 33°59'N, 35°38'E], limestone rocks, W slope, 13 Dec 1967, *H. Stutz 2943* (BEI); Hamat, 34°18'09.86"N, 35°40'51.58"E, alt. 145 m, 24 May 2014, *M. Bou Dagher-Kharrat* (B100517440); Baabda, 33°50'07.22"N, 35°32'49.96"E, alt. 305 m, 15 Jul 2014, *M. Bou Dagher-Kharrat* (B100517439).

Willdenowia
Open-access online edition www.bioone.org/loi/will
Online ISSN 1868-6397 · Print ISSN 0511-9618 · Impact factor 0.680
Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin