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Source: Willdenowia, 37(1) : 283-296

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

URL: https://doi.org/10.3372/wi.37.37117

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NORBERT KILIAN & BIRGIT GEMEINHOLZER

Studies in the *Compositae* of the Arabian Peninsula and Socotra – 7. *Erythroseris,* a new genus and the previously unknown sister group of *Cichorium (Cichorieae* subtribe *Cichoriinae)*

Abstract

Kilian, N. & Gemeinholzer, B.: Studies in the *Compositae* of the Arabian Peninsula and Socotra – 7. *Erythroseris,* a new genus and the previously unknown sister group of *Cichorium (Cichorieae* subtribe *Cichoriinae).* – Willdenowia 37: 283-296. – ISSN 0511-9618; © 2007 BGBM Berlin-Dahlem. doi:10.3372/wi.37.37117 (available via http://dx.doi.org/)

Two species of Socotra Island and N Somalia, respectively, known as *Prenanthes amabilis* and *P. somaliensis,* are identified by molecular (ITS and *matK*) and morphological analyses as the closest relatives to *Cichorium,* hitherto considered an isolated genus of the tribe *Cichorieae*. To accommodate these two species, the new genus *Erythroseris* is established, the new combinations *E. amabilis* and *E. somalensis* are validated, and the basionym *Tolpis somalensis* is neotypified. Morphological differences and accordances between *Cichorium* and *Erythroseris* are discussed. It is concluded from the micromorphological results that the scaly pappus of *Cichorium* is homologous with the setaceous pappus as present in *Erythroseris.* A key to the species, illustrations of achenes, pappus and pollen, and a distribution map of the new genus are given.

Key words: *Asteraceae,* systematics, nr DNA ITS, cp DNA *matK,* phylogeny, micromorphology, Somalia, Yemen.

Introduction

From the easternmost extension of Africa two species of *Prenanthes* L. are known. One is from the island of Socotra, situated on the continental shelf c. 230 km E off the coast of Gees Gwardafuy [Cape Guardafui], and was discovered and described in the late 19th century (Balfour 1882, 1888). The other is from N Somalia, from c. 300-400 km W of Gees Gwardafuy, and was twice independently described in the 20th century (Fries 1925, Jeffrey 1966). In the course of his studies in the *Cichorieae* subtribe *Lactucinae,* the first author doubted their placement in *Prenanthes* and initially hypothesized their affinity to the E Asian genus *Notoseris* Shih of subtribe *Lactucinae* (Kilian 2001: 74). One year later, after he had the opportunity to study and collect the Socotran species in the field, his molecular phylogenetic analyses based on ITS sequences pointed in an entirely unexpected direction, indicating an affinity of the Socotran species to *Cichorium* L. Since the second author has been working specifically on the molecular phylogeny of the *Cichorium* alliance, the two have collaborated to elucidate further the relationships of the Socotran species and its Somali relative.

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Material and methods

Plant material. – The investigation is based on field studies by the first author on the island of Socotra, Yemen, and on herbarium material from the herbaria B, CAS *(Notoseris),* HUH *(Notoseris),* K, UPS (abbreviations according to Holmgren & Holmgren 1998-) and the personal herbarium of Bruno Mies (Duisburg); the material at K has been consulted using online high-resolution images accessed via Aluka (2007-).

Molecular analyses. – We used 36 taxa for the phylogenetic analyses of the nuclear marker, including representatives from throughout the *Cichorieae,* and a reduced dataset of 21 taxa for the chloroplast analysis. Most sequences were taken from GenBank/EMBL/DDBJ, but for 9 taxa sequences were obtained from herbarium specimens or field-collected leaf material dried and stored in silica gel. The relevant data for the source of the sequences are presented in Table 1.

DNA was isolated from silica-gel dried or herbarium material by use of the DNeasy kit (Qiagen GmbH, Germany). Amplifications of the Internal Transcribed Spacer region (ITS1, 5.8S rDNA, ITS2) was carried out by using primer ITS-A and ITS-B (Blattner 1999), and, if necessary, primer ITS-C and ITS-D (Blattner 1999) or ITS-SF and ITS-SR (Blattner & al. 2001). For *matK* fragment amplification, primer *trnK* 710F, *trnK*2R (Johnson & Soltis 1995) and AST-1R (Garcia-Jacas & al. 2002) were utilized as well as the *Cichorieae*-specific primers *matK*-RL, *matK*-iF and *matK*-iR (Fehrer & al. 2007). PCR conditions and sequencing were the same for ITS and *matK*.

The PCR mix contained 0.1-0.2 µg of DNA, 0.15 units of Taq DNA polymerase, 2.50 µl 10x buffer, 1 µl dNTP, 1 µl Q-solution (all Qiagen GmbH, Germany) and 0.25 µl of each primer (50 pmol/µl), adding up with H_2O to a total of 12.5 µl. An initial denaturation step at 95 °C for 3 min was followed by 32 cycles of annealing at 52 °C for 30 sec., extension at 70 °C for 45 sec. and denaturation at 95 °C for 30 sec., and a final extension at 70 °C for 8 min. The PCR products were purified with the QIAquick PCR purification kit (Qiagen GmbH, Germany) and served as templates for cycle sequencing with the DTCS-Quick-Start-Kit (Beckman-Coulter). A Beckman-Coulter CEQ 8000 automated sequencer was used to generate the data.

Sequences were aligned manually using BioEdit 7.0.5.2 (Hall 1999). The alignment is available online in the electronic supplement to this paper (www.bgbm.org/willdenowia/willd37/kilian+gemeinholzer.htm). Phylogenetic relationships were reconstructed with maximum parsimony analyses (MP), using PAUP* 4.0b10 (Swofford 2003), and Bayesian inference (BI) analyses, using Mr Bayes 3.1.2. (Ronquist & Huelsenbeck 2003). For the MP analyses heuristic searches were conducted (10 000 random sequence additions and no more than 100 trees saved per replicate, tree bisection-reconnection [TBR], branch swapping, and the MULTREES option in effect). Confidence limits for trees were assessed by performing 10 000 replicates of bootstrapping (Felsenstein 1985) using equal weighting, TBR swapping, MULTREES on and holding only 10 trees per replicate. The BI analyses was carried out calculating four simultaneous chains of two million generations by partitioning the ITS dataset into ITS1, the 5.8S rDNA, and ITS2 with tree sampling trees every 1000 generations to reduce memory space (lset nst=6, rates=invgamma and unlink statefreq=all, revmat=all, shape=all, pinvar=all and default prior settings were applied). Stationary position was reached after 18 000 generations the first 20 000 generations were discarded as burn-in determined from plotting log-likelihood values against generation time. The *matK* dataset was running unpartitioned. The Bayesian Markov chains reached stationary position after about 12 000 generations. Also 20 000 generations were discarded as burn-in. The consensus trees with posterior probabilities were generated in PAUP* 4.0b10.

Micromorphology. – Pollen grains, achenes and pappus 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 scanning electron microscope. The pollen, obtained from dry flowers, had been acetolysed according to a standard technique (see Kilian & Miller 2000) before.

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Table 1. List of taxa and the sources of the sequences or of the plant material, respectively, used in the molecular phylogenetic analyses. – 1 = Fehrer & al. (2007), 2 = Gemeinholzer & al. (2005), 3 = Lee & al. (2003), 4 = Lohwasser & al. (2004), 5 = Tremetsberger & al. (2005), 6 = Kiers & al. (2000).

	ITS	**Ref.**	***matK***	**Ref.**
Agoseris retrorsa (A. Gray) Green	AJ633461	2	AJ633250	1
Andryala integrifolia L.	AJ633384	1	AJ633166	1
Arnoseris minima (L.) Schweigg. & Körte	AJ633444	2	AJ633162	1
Cichorium bottae Deflers	AF118919	6	–	–
Cichorium calvum Asch.	AF118914	6	–	–
Cichorium endivia L.	AJ633452	2	–	–
Cichorium intybus L.	AJ633456	2	AJ633131	1
Cichorium pumilum Jacq.	AJ633454	2	–	–
Cichorium spinosum L.	AJ633448 & AJ633455	2	–	–
Crepis vesicaria subsp. *taraxacifolia* (Thuill.) Thell.	AJ633371 (as subsp. *haenseleri*)	2	AJ633154	1
Erythroseris amabilis (Balf. f.) N. Kilian & Gemeinholzer (= *Prenanthes amabilis* Balf. f.)	Socotra, *Kilian & al. YP 2369* (B) – EU046557	–	id. – EU046562	–
Erythroseris somalensis (R. E. Fr.) N. Kilian & Gemeinholzer (≡ *Prenanthes somaliensis* C. Jeffrey)	Somalia, *Thulin 10795* (UPS) – EU046558	–	–	–
Hyoseris radiata L.	AJ633299	2	AJ633215	1
Hypochaeris glabra L.	AJ627264	5	AJ633232	1
Hypochaeris radicata L.	AJ633310	2	AJ633231	1
Lactuca saligna L.	AJ633336	2	AJ633238	1
Lactuca sativa L.	AJ633337	2	cult. Bot. Gard. Cluj, 7/03, *Napoca 681* (GAT) – EU046561	–
Microseris borealis (Bong.) Sch. Bip.	AJ581725	4	AJ633246	1
Notoseris s.l. sp.	China, Yunnan, Gaoligong Shan, 2130 m, *Li Heng 13207* (CAS 1029897) – EU046559	–	–	–
Notoseris psilolepis C. Shih	China, Guizhou, 850-1300 m, *Sino Amer. Exp. 1379* (CAS 772751) – EU046560	–	id. – EU046565	–
Pilosella argyrocoma (Fr.) F. W. Schultz & Sch. Bip.	AJ633395 (as *Hieracium argyrocoma*)	1	AJ633176	1
Pilosella echioides (Lumn.) F. W. Schultz & Sch. Bip.	AJ633397 (as *Hieracium echioides*)	1	AJ633177 (as *Hieracium echioides*)	1
Pilosella officinarum Vaill.	AY879161 (as *Hieracium pilosella*)	2	–	–
Pilosella pseudopilosella (Ten.) Soják	AJ633390 (as *Hieracium pseudopilosella*)	2	–	–
Pleiacanthus spinosus (Nutt.) Rydb.	AJ633464	2	AJ633244	1
Prenanthes purpurea L.	AJ633343	2	Switzerland, Kanton St Gallen, Alt. St. Johann SG Churfirsten, 1407 m, cult. Bot. Gard. Zürich *190 W 32/03* (GAT) – EU946563	
Reichardia intermedia (Sch. Bip.) Samp.	AJ633304	2	AJ633281	1
Rhagadiolus stellatus (L.) Gaertn.	AJ633298	2	AJ633225	1
Schlagintweitia intybacea (Jacq.) Griseb.	AJ633430	2	–	–
Scorzonera angustifolia L.	AJ633488	2	AJ633278	1
Scorzonera crispatula (DC.) Boiss.	AJ633486	2	AJ633276	1
Sonchus oleraceus L.	AJ633306	2	AJ633279	1
Stephanomeria diegensis Gottlieb	AF473618	3	AJ633245	1
Tolpis barbata (L.) Gaertn.	AJ633434	2	AJ633206	1
Youngia denticulata (Houtt.) Kitam.	AJ633293	2	–	–
Youngia japonica (L.) DC.	AJ633294	2	AJ633140	1

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Results

Molecular analyses. – Results from analyses of nuclear ITS region, and plastid *matK* gave congruent results concerning the placement of the two species under consideration as sister group to *Cichorium.* Analysis of ITS resulted in phylogenies with higher bootstrap percentage support (BP). The plastid coding *matK* was less informative. Not all accessions sampled were sequenced for ITS and *matK* due to problems with PCR amplification in some taxa.

ITS: Results were obtained from 37 accessions. Representatives throughout the *Cichorieae* were included in the analysis and *Scorzonera* was chosen as outgroup. No evidence for multiple rDNA repeat types were observed. The length of the ITS region ranged from 554 bp to 644 bp. Unambiguous alignment in some cases was problematic due to the high variability of this region. A total of 672 characters were included in the analysis of which 264 (39 %) were parsimony informative. The heuristic search resulted in two most parsimonious trees with 1232 steps (CI [consistency index] = 0.476; RI [retention index] = 0.672). The strict consensus tree with bootstrap percentages greater than 50 and posterior probabilities is presented in Fig.1.

The ITS tree confirms the monophyly of *Prenanthes somaliensis* and *P. amabilis* with 98 % BP and 1.0 % posterior probabilities (PP). Both species form a well supported clade being a sister group to the monophyletic *Cichorium* with 100 % BP, well nested within the subtribe *Cichoriinae.*

matK: Not all accessions sampled for the ITS region were sequenced for *matK* due to problems with PCR amplification, also known from other taxa of this tribe (e.g., Samuel & al. 2006). In total 21 taxa were included in the analysis and *Scorzonera* was again chosen as outgroup. The length of the analysed *matK* region varied from 440 bp to 978 bp. Insertions and deletions were coded each as single event. A total of 994 bp characters were used for the analyses, of which 64 bp characters (0.6 %) were parsimony informative resulting in only partly resolved trees. The heuristic search generated two most parsimonious tree with 220 steps (CI = 0.873 and RI = 0.71). The 50 % majority rule consensus tree with bootstrap percentages greater than 50 and posterior probabilities is presented in Fig. 2.

The tree obtained with *matK* is less resolved than the ITS tree due to the lower variability of the amplified region. Incongruent patterns in the topology of both trees do not affect the placement of *Prenanthes amabilis* as sister to *Cichorium,* which is well nested within the *Cichoriinae*, but are present in other parts of the tree, most likely due to chloroplast capture in early stages of evolution, e.g. between ancestors of *Tolpis, Arnoseris* and *Hyoseris*.

The position of *Prenanthes purpurea,* which provides the type of the name *Prenanthes,* is in both trees far remote from our two species in question. In both trees *P. purpurea* appears as sister group to the *Lactucinae,* however, with low or even no bootstrap support and low posterior probabilities.

Larger data samples (Gemeinholzer, Enke, Bachmann & Kilian, in prep.) confirm the placement of *Prenanthes amabilis* and *P. somaliensis* in the *Cichoriinae* far away from *P. purpurea* and provide better supported groupings. Both markers corroborate the position of *Notoseris* as a member of subtribe *Lactucinae,* thus disproving the initial hypothesis of a relationship of the two species close to this genus.

Micromorphology. – The achenes of both *Prenanthes* species are largely similar. Both are cylindrical, thus not compressed (Fig. 3A, D as *Erythroseris*), reddish brown with antrorse papillae (Fig. 3F), have 5 main ribs accompanied by a ± weaker secondary rib on either side (Fig. 4B as *Erythroseris*), and a truncate apex (Fig. 3B, E), in so far resembling the achenes of *Notoseris*. At the basis of the achenes of the two *Prenanthes* species, however, the ribs are only partly fused and somewhat incurved (Fig. 4A). The achenes of *Notoseris,* in contrast, have the cylindrical to funnel-shaped carpopodium, which is so characteristic for the *Lactuca* alliance.

The pappus consists of rather strong bristles (of more than 20 cells in diameter, Fig. 3C) of the same length and at the margin a few or some tiny bristles are present (Fig. 3B-C, E). Comparative analysis of the scaly pappus of *Cichorium* and the setaceous pappus of the *Prenanthes* species pair reveals interesting accordances: (1) the pappi of both consist of a marginal series of

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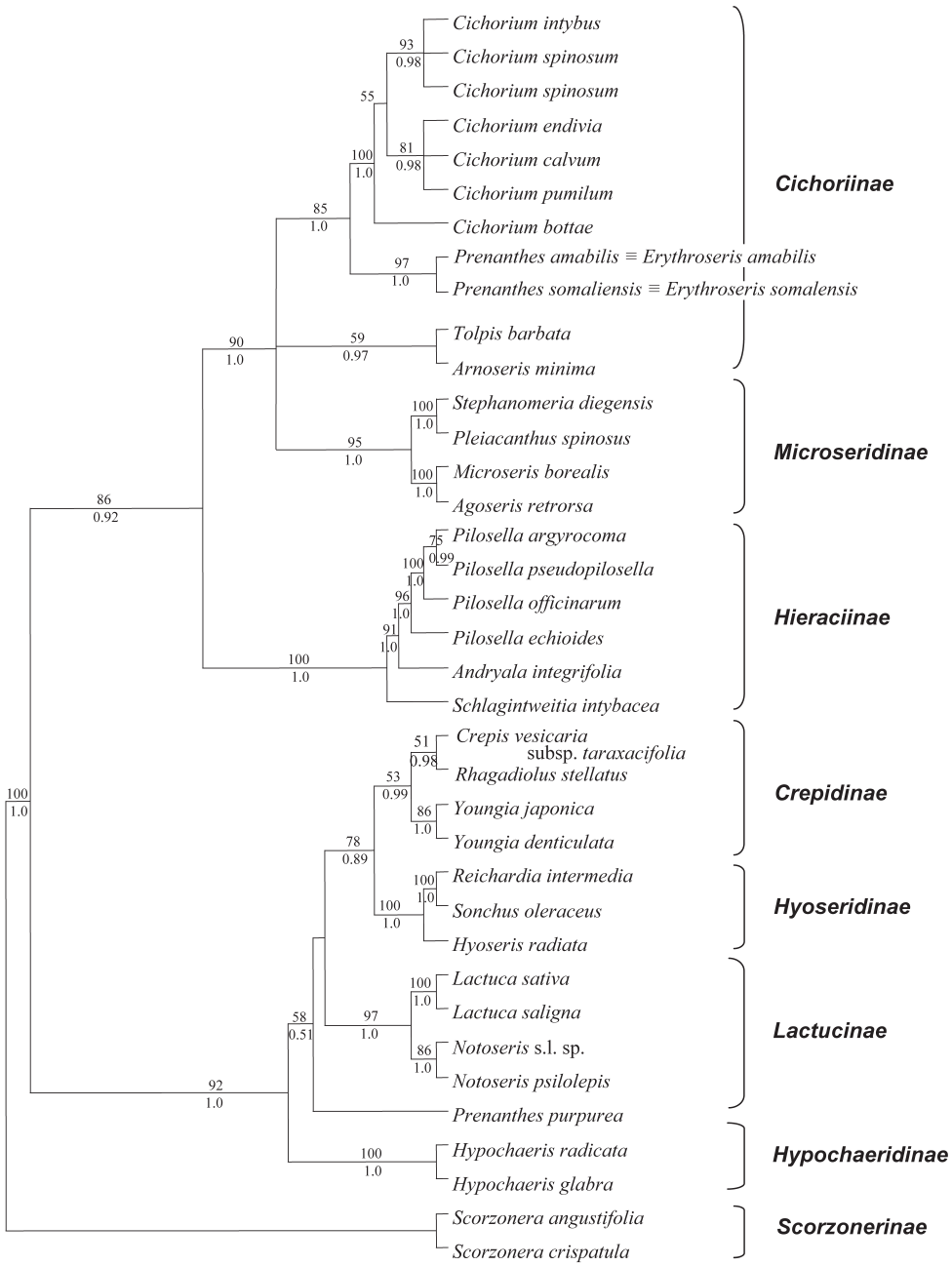


Fig. 1. Strict consensus tree of the two most parsimonious trees of the rDNA ITS analysis. Bootstrap percentages greater than 50 are given above the branches and posterior probabilities above 0.50 are depicted below.

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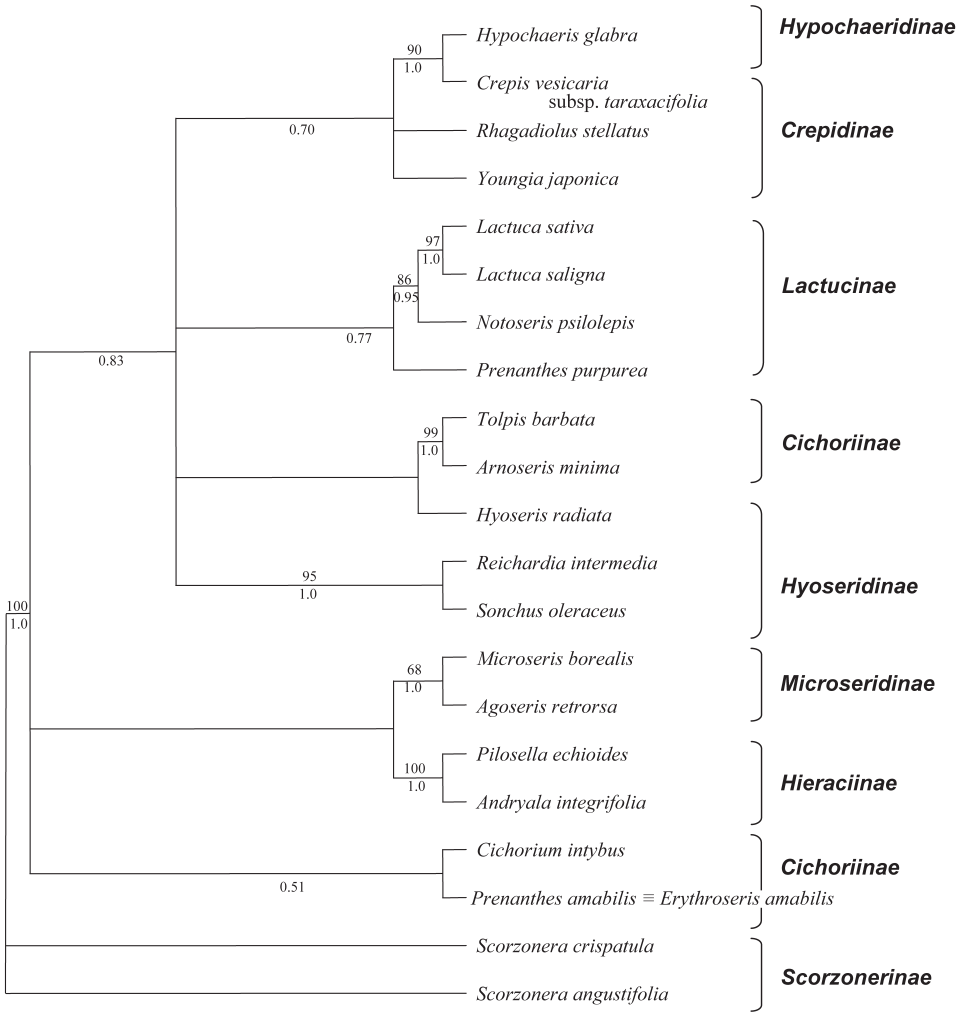


Fig. 2. Strict consensus tree of the two most parsimonious trees from the plastid *matK* analysis. Bootstrap percentages greater than 50 are given above the branches and posterior probabilities above 0.50 are depicted below.

smaller and thinner elements (Fig. 4G; in *C. bottae* only one series, perhaps the outer, is present, Fig. 4F), (2) the inner and marginal pappus elements of both are composed of the same longish type of cells (compare Fig. 3C and 4G), and (3) the pappus elements are basally not clearly separated from each other (compare Fig. 3C and 4F-G), in the two *Prenanthes* species (see Fig. 3C), e.g., the inner and marginal elements are laterally variously united at their bases.

The pollen is echinolophate, tricolporate, with medium wide polar thickenings and spines that are globose and perforate basally whereas conical and non-perforate distally (Fig. 4C-D); it is of the *Cichorium* type sensu Blackmore (1986), the *Taraxacum* type of older authors, which is the predominant pollen type in the *Cichorieae.*

Both species are micromorphologically as well as macromorphologically (see, Taxonomy, below) closely related and as a species pair well delimited.

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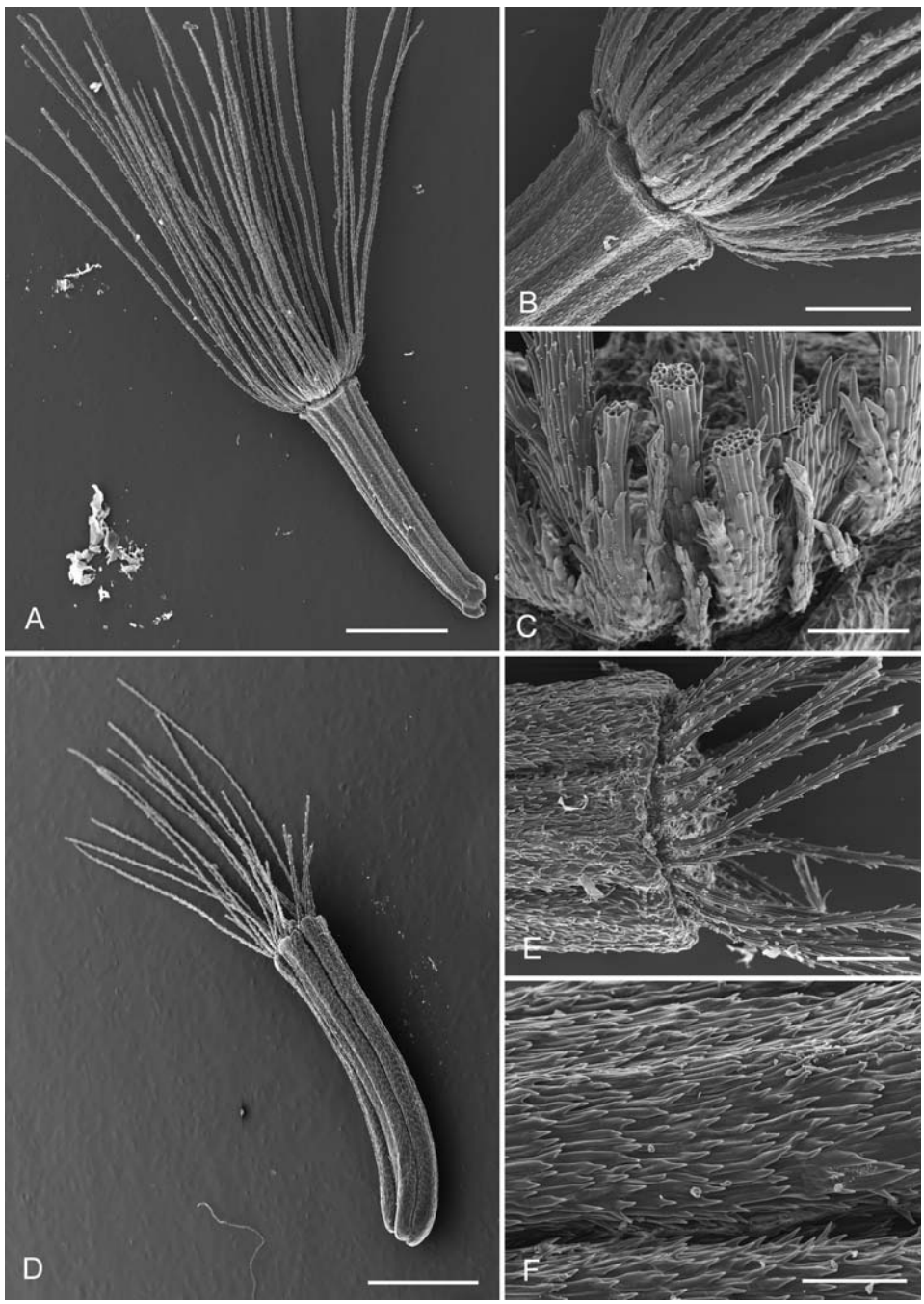


Fig. 3. *Erythroseris,* achenes and pappus – A-C: *E. somalensis,* achene, overview (A), achene apex and pappus basis (B), marginal minute bristles and basis of inner bristles, partly broken to show bristle diameter (C); D-F: *E. amabilis,* achene, overview (D), achene apex and pappus basis (E), detail of achene epidermis with antrorse papillae (F). – Scale bars: A, D = 1 mm, B = 400 µm, C = 80 µm, E = 200 µm, F = 100 µm; A-C from *Thulin 4260* (UPS), D-F from *Kilian & al. YP3739* (B).

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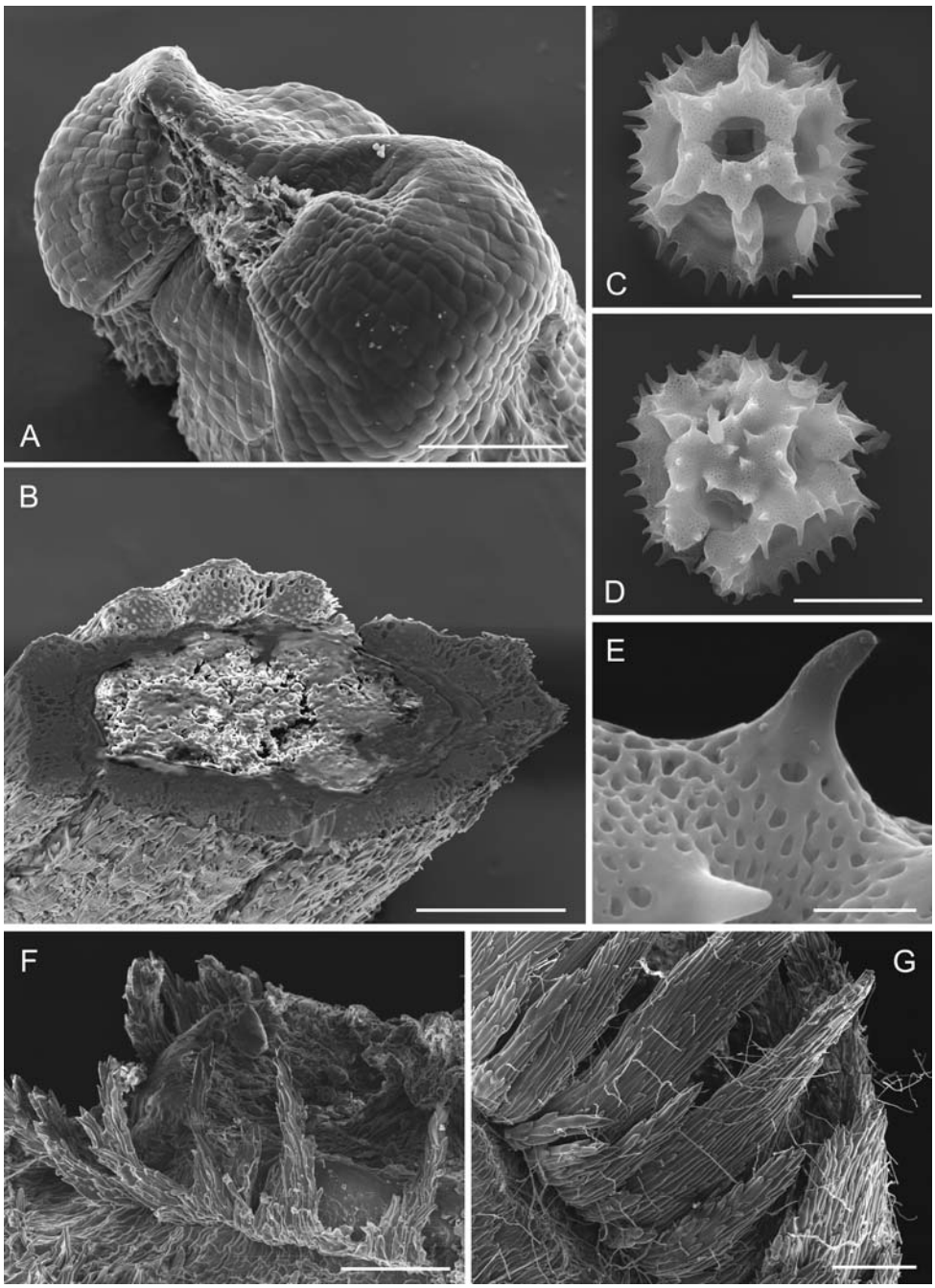


Fig. 4. A-E *Erythroseris,* achenes and pollen – A: *E. somalensis,* achene, carpopodium; B-E: *E. amabilis,* achene, cross section in middle third (B), pollen (C-D), equatorial view (C), polar view (D), spine in detail (E). – F-G *Cichorium* pappi, details – F: *C. bottae;* G: *C. pumilum,* thread-like structures representing fungi hyphae. – Scale bars: A, G = 100 µm, B = 200 µm, C-D = 20 µm, E = 2 µm, F = 90 µm; A from *Thulin 4260* (UPS), B-E from *Kilian & al. YP3739* (B), F from *Kilian 4884* (B), G from *Raus 8683* (B).

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Discussion

The attempts for a natural classification of the *Cichorieae* are hampered, perhaps more than in any other tribe of the *Compositae,* by the notorious poverty of taxonomically relevant features combined with a high rate of homoplasy as a result of extensive parallel character evolution. Utilization of DNA marker sequencing has proven helpful to decide between competing phylogenetic hypotheses and systematic classifications based on morphological characters. The combination of methodologies has essentially been improving our understanding of the phylogeny of the tribe (Gemeinholzer, Enke, Bachmann & Kilian, in prep.).

Prenanthes, previously a genus of some 40 species spanning a geographical area from Central and S Europe across Africa and Asia to North America (Tomb 1977: 1070), provides a particular dramatic example. Modern re-evaluation of *Prenanthes* dates back to Shih (1987), who not only re-established *Nabalus* Cass. for chiefly the North American members, but also removed other E Asian members from *Prenanthes* into the new genus *Notoseris* on morphological analyses. Sennikov (2000) and Sennikov & Illarionova (2000) morphologically further narrowed down the circumscription of *Prenanthes.* Sennikov & Illarionova (2001) then, however, returned to the former very wide circumscription of *Prenanthes,* arguing with the similar achene anatomy and morphology of all *Prenanthes* segregates. In contrast to the last conclusion of these authors, recent molecular analyses (Gemeinholzer, Enke, Bachmann & Kilian, in prep.) have proven that *Nabalus* is entirely unrelated to *Prenanthes* and actually a member of the *Crepidinae* (as indicated previously by Whitton & al. 1995). Ongoing work (Kilian & Gemeinholzer in prep.) and the molecular analyses presented in the present paper show that, moreover, the former *Prenanthes* species segregated as *Notoseris* are well nested in subtribe *Lactucinae,* whereas the two E African species treated in the present paper are members of subtribe *Cichoriinae.* What is left of *Prenanthes,* appears in a sister group relationship to either *Lactucinae* or *Hypochaeridinae,* possibly reflecting patterns of ancient hybridization with other members of the tribe.

Considering the traditional concept of *Prenanthes,* one reason appears essential for this fate: *Prenanthes* s.l. united species with apically truncate, non-compressed, basically cylindrical achenes with 5 main ribs (or more, then hardly differentiated ribs). This, however, is a plesiomorphic character combination in the tribe, present in all major clades, and it was combined in the traditional concept of *Prenanthes* with a prevalence of cyanic (purplish to bluish) flower colour. It is thus no surprise that the *Prenanthes* fragments in the four subtribes, where they have been placed according to the molecular data, are nested each in a more or less basal position (Gemeinholzer, Enke, Bachmann & Kilian, in prep.).

The two *Prenanthes* species considered here, form, according to the morphological as well as the molecular data, a closely related species pair, which is clearly separated from but represents the closest relative to *Cichorium,* which was considered as an isolated genus of the *Cichorieae* (Bremer 1994, Kiers 2000, Lack 2006). The recognition of the two species under study as a separate genus, described as *Erythroseris* below, is therefore the appropriate taxonomic conclusion.

The genus *Cichorium,* centred in the Mediterranean region, extends with the endemic *C. bottae* Deflers into the highlands of the SW Arabian Peninsula. *C. bottae* has been found in all molecular analyses (nuclear and chloroplast marker sequence analyses as well as AFLP fingerprint analysis) in a basal position and as sister group to the rest of *Cichorium* (Kiers 2000). Geography thus poses no problems to the assumption of a common ancestry of *Cichorium* and *Erythroseris*.

Cichorium is a clearly delimited, in general appearance very uniform and easily recognizable genus, the species of which are fairly similar to each other, both regarding morphological and molecular characters (Kiers 2000), hence indicating sudden and rather recent speciation. The combination of the following four features is perhaps most characteristic of this genus: (1) comparatively thick peduncles of those capitula that are not sessile and clustered in the leaf axils, (2) bright blue flowers, (3) the minute, (1-)2-seriate, irregularly scaly pappus, and (4) the sturdy, obovoid to subcylindrical and faintly ribbed achenes.

It is in particular due to the difficulties to homologize its scaly pappus (Bremer 1994: 168) that *Cichorium* has been considered an isolated genus in the *Cichorieae.* Comparative scanning

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electron microscopic analysis of the scaly pappus of *Cichorium* and the setaceous pappus of the two *Erythroseris* species (Fig. 3A-E, 4F-G), however, makes the morphological transition between both evident. Being composed of the same cell types, taking the same place on the achene and being similarly arranged in two irregular rows (except *C. bottae* and *C. calvum*), the scaly pappus of *Cichorium* can safely be regarded as homologous with the setaceous pappus of *Erythroseris.* This conclusion receives particular support from the fact that the inner and marginal elements of the *Erythroseris* pappus are laterally variously united at their bases. Considering that the lateral extension and reduced length constitute the main differences between the pappus scales and bristles, proximal unification morphologically mediates between bristle and scale shape.

As in *Erythroseris,* the involucre of *Cichorium* is of either 5 or 8 inner involucral bracts, a feature, however, not uncommon in the tribe, and capitula are rather few-flowered (with 5-c. 25 flowers), the receptacle is naked, the flowers are cyanic, the pollen grains are largely similar also with respect to the size of the polar thickenings (compare Kiers 2000: 16, fig. 2.2, Blackmore 1986: 3106, fig. 15-16).

The main differences between *Erythroseris* and *Cichorium* are (1) in the habit: the aerial parts of *Cichorium* are entirely herbaceous, whereas the two species of *Erythroseris* are a basally woody perennials and a shrub respectively; (2) in the involucre: the inner involucral bracts are in their lower half strongly indurate at maturity in *Cichorium,* but remain flexible, herbaceous in *Erythroseris;* (3) in flower colour: bright blue in *Cichorium,* but pale purplish bluish in *Erythroseris;* (4) in the achenes: obovoid or sturdy obcolumnar to sturdy subcylindrical and chiefly basally faintly ribbed (Kiers 2000: 12-14, fig, 2.1a-f) in *Cichorium,* but slender cylindrical and with 5 prominent main ribs in *Erythroseris* (Fig. 3A-B, D-F, 4B); (4) in the pappus: with minute scales and marginal bristle-like scales (see Kiers 2000: 12-15, fig. 2.1a-h; Fig. 4G) in *Cichorium,* but with long inner bristles and minute marginal bristles in *Erythroseris* (Fig. 3A-E).

Taxonomy

Erythroseris N. Kilian & Gemeinholzer, **gen. nov.**
Type: *Erythroseris amabilis* (Balf.f.) N. Kilian & Gemeinholzer

Genus *Cichorio* L. cognatum, a quo habitu fruticoso vel herbaceo caudice lignoso (nec suprateranne omnino herbaceo), floribus pallide lilaceo-caesiis (nec caeruleis), achaeniis gracile cylindricis costis longitudinalibus quinque costis secundariis lateralibus duobus concomitatis (nec obovatis usque ad crasse subcylindricis et basaliter indistincte costatis), pappo achaeniorum ± 2-seriato, setis 4-5 mm longis et setulis marginalibus minutis composito (nec squamulis irregularibus minutis et setis marginalibus minutissimis composito vel omnino destituto) differt.

Description. – Low basally woody perennial rosette herb or intricately branched shrublet of up to 0.6 m height. *Leaves* with white-lanose axils, ± fleshy, obovate to oblanceolate or elliptic in outline, shallowly sinuate-dentate to pinnately lobed, up to c. 10 × 5 cm, crowded or rosetted at the base of each innovation, scattered and reduced in size along the flowering axes. *Capitula* disposed in a synflorescence terminating the basally rosette-leafy innovations, with 5-c. 25 flowers. *Involucre* narrowly cylindrical, of 5 or 8 inner involucral bracts. *Receptacle* flat to somewhat concave, c. 1-2 mm in diameter, epaleate. *Flowers,* when fresh, with purplish bluish ligule, anther tubes and styles. *Pollen* echinolophate, tricolporate, with medium wide polar thickenings. *Achenes* cylindrical to slightly attenuate from apex to base, 1.7-2.3 mm long, with 5 longitudinal main ribs and each accompanied by a less conspicuous secondary rib on either side (sometimes incompletely so), surface scabrid by antrorse, linear scales with acute and somewhat spreading tip, reddish brown, apex truncate, basis, straight to oblique, with ribs incurved and attachment area central. *Pappus* c. 4-5 mm long, of c. 20-40 fragile, cream to straw-coloured, strong (> 20 cells in diameter) scabrid bristles, marginally with some or almost without additional very short (< 0.5 mm) bristles.

Etymology. – The name *Erythroseris* is composed of the ancient Greek σεριϛ (seris) for lettuce and εργθρο- (erythro) for red, the latter referring to the reddish hue in the achene and flower col-

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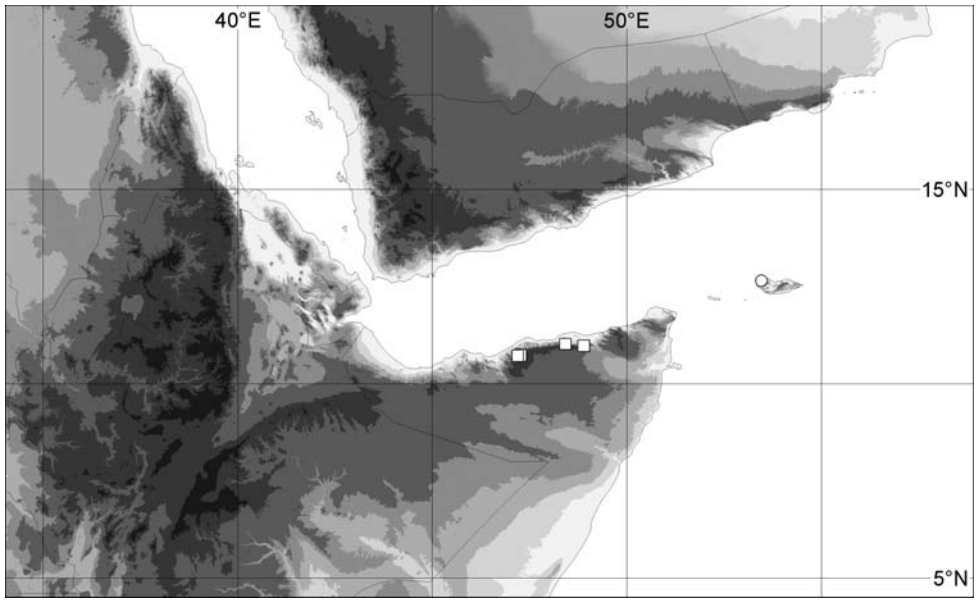


Fig. 5. Distribution of *Erythroseris – E. somalensis* (squares) and *E. amabilis* (circle). – Georeferenced map generated with DIVA-GIS (Hijmans & al. 2005) using an adaptation of the SRTM 90 m digital elevation data (CGIAR-CSI 2004).

our of its species and at the same time to the "Erythraean Sea" of the ancient Greeks, which did not only include the Red Sea but also the Indian Ocean, on escarpments to which the genus occurs, and the Arabian Gulf (see, e.g., Huntingford 1980).

Distribution. – The genus comprises two species restricted to localised areas of the sea- and north-facing limestone escarpments in N Somalia and the Yemeni island of Socotra, respectively (Fig. 5).

Key to the species of *Erythroseris*

1. Basally woody perennial rosette herb, with herbaceous synflorescence; involucre with 5 inner involucral bracts, ± greenish, ± glabrous . . . . . *E. amabilis*
– Small, intricately branched shrub to 0.6 m; involucre with ≥ 8 inner involucral bracts, purplish, pubescent of glandular and simple hairs . . . . . *E. somalensis*

Erythroseris amabilis (Balf.f.) N. Kilian & Gemeinholzer, **comb. nov.** ≡ *Prenanthes amabilis* Balf.f. in Proc. Roy. Soc. Edinburgh 11: 842. 1882. – Holotype: Yemen, Socotra, on the rocks south-west of Galonsir, at an elevation over 1500ft, 2.-3.1880, *I. B. Balfour, Cochleburn & Scott 311* (two sheets K 000251826! & K 000251827!, see http://www.kew.org/herbcat/ getImage.do?imageBarcode=K000251826 and …=K000251827)

Ic. – Fig. 3D-F, 4B-E; Balfour (1888: t. 48 [draw., habit + details]); Miller & al. (2004: 256 [col., habit] as *Prenanthes amabilis*).

Distribution. – The species has only been collected from and is apparently restricted to the upper N-NE facing escarpment, at 500-650 m, of the Ma'alah plateau, W Socotra, where it grows in open ground in the crevices of the limestone (Fig. 4). For its limited area of occupancy it has been classified as Endangered (EN B2 a biii, IUCN 2001) by Miller & al. (2004: 510).

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Additional specimens seen. – YEMEN: SOCOTRA: Entrance to the top plateau of Jebel Ma'alli above Qaisu, 5.7 km S of Qalansiyah, 510 m, 12°38.81'N, 53°27.74'E, lithosol from limestone, in shady cleft, 22.2.1999, *B. Mies 1462, 1463* (B, herb. B. Mies); near Ma'ala Plateau, uppermost part of the escarpment, immediately below 12°38'50.4"N, 53°27'45.4"E, limestone, 550 m, 30.3.2002, *N. Kilian & al. YP2369* (B); Ma'ala plateau, upper part of westernmost ascent from Wadi Galansia, rocky limestone slopes, 550-650 m 12°39'26.7"N, 53°26'24.3"E, 6.3.2003, *N. Kilian & al. YP 3739* (B).

Erythroseris somalensis (R. E. Fr.) N. Kilian & Gemeinholzer, **comb. nov.** ≡ *Tolpis somalensis* R. E. Fr. in Acta Horti Berg. 8: 271. 1925. – Holotype: Somalia, "bei Meid, Gebirgsregion Sérrut", 1800 m, 4.1875, *J. M. Hildebrandt 1445* (B, destroyed); neotype (designated here): Somalia, escarpment between Mait and Erigavo, E of Mt Surud, 1950 m, rocky slope with *Juniperus procera* and *Dodonea,* perennial, hanging from rocks, 9.2.1982, *M. Thulin 4260* (UPS!).
= *Prenanthes somaliensis* C. Jeffrey in Kew Bull. 18: 434. 1966. – Holotype: Somalia, Al Hills, Sugli, 10°58'N, 48°53'E, 5000ft, 13.11.1929, *C. L. Collenette 269* (K 000251824!, see http://www.kew.org/herbcat/getImage.do?imageBarcode=K000251824).

Note. – While Jeffrey's name of 1966 has to be used in *Prenanthes,* because the combination based on Fries's earlier name would result in a "confusingly similar" binomial and is thus not available (Art. 53.3, ICBN, McNeill & al. 2006), Fries's name has to be taken up for the combination in the new genus *Erythroseris*. To replace the destroyed holotype of Fries's basionym a flowering and fruiting specimen from the same mountain range preserved in Uppsala is designated here as neotype.

Ic. – Fig. 3A-C, 4A; Jeffrey (1966: 435, fig. 1) = Thulin (2006: 486, fig. 327 [draw., habit + details] as *Prenanthes somaliensis*).

Distribution. – The species is restricted to the sea-facing limestone escarpment of the highest N Somali mountain range, between Cerigaabo and Maydh in the region Sanaag (Fig. 5), where it occurs at altitudes of 1300-1950 m on rocks in evergreen bushland with *Buxus* or *Juniperus* forest (Beentje in Thulin 2006: 486).

Additional specimens seen. – SOMALIA: SANAAG: Escarpment between Ceerigabo and Maydh, below Tabah Pass, 10°45'N, 47°16'E, 1850 m, open *Juniperus* forest with *Cadia,* on limestone, hanging from rocks, 2.2.2002, *M. Thulin 10795* (UPS); ibid., 10°44'N, 47°16'E, 2200 m, 1.2. 2002, *M. Thulin 10793* (UPS); escarpment SE of Laasqoray, near Moon, 11°01'N, 48°25'E, 1300 m, evergreen bushland on limestone, 18.1.1995, *M. Thulin & al. 9154* (UPS).

Acknowledgements

Valuable comments by Henk Beentje and a second, anonymous referee on a previous version of this paper are gratefully acknowledged. We thank the curators of CAS and HUH, and Mats Thulin (UPS) and Bruno Mies (Essen) for the loan of herbarium specimens, as well as Christian Zidorn for the supply of DNA material. Special thanks are due to Jana Bansemer, Jonas Zimmermann and Holger Zetzsche (Berlin, molecular laboratory), Monika Lüchow (Berlin, scanning electron microspcopy) and Michael Rodewald (Berlin, digital image processing and layout) for their excellent technical assistance.

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