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NORBERT KILIAN

Lactuca stebbinsii (Lactuceae, Compositae), a puzzling new species from Angola

Abstract

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A small perennial herb from marshy meadows in the highlands of SW Angola, only known from three 19th and early 20th century collections, is described as *Lactuca stebbinsii,* a species new to science, and illustrated. The taxonomic position of the unusual species with entirely beakless, apically truncate, pale brown, distinctly compressed and glabrous achenes within the *Lactuca-Prenanthes* line of the *Lactucinae* is discussed. The morphological features indicate a placement in *Lactuca* s.l. as the most plausible solution. Possible relationships are discussed but cannot be established yet.

Introduction

The *Lactuceae* are a predominantly holarctic tribe but a few genera are fairly well represented in tropical Africa, viz. *Lactuca* with some 30 species (Stebbins 1937a, Jeffrey 1966), *Crepis* with up to 28 species (Babcock 1947: 77, 326, but considerably less according to Jeffrey 1966), *Launaea* with some 20 species (Kilian 1997) and *Sonchus* with 14 species (Boulos 1973-74). Most species occur in grassland, open woodland and other types of open vegetation, often in a montane environment, and convergent evolution has led to the development of similar forms in different genera. In a group notoriously poor in diagnostic characters, this is a source of confusion, particularly when coupled to insufficient material. Owing to their general resemblance, a few gatherings from Angola had first been identified as *Launaea rarifolia* (Oliv. & Hiern) Boulos by Hiern (1898: 623 sub *Sonchus fischeri* O. Hoffm.) and Mendonça (1943: 152 sub *Sonchus welwitschii* (Scott Elliott) Chiov. ex Moore) before they were recognized by Jeffrey (1966: 466) as a hitherto undescribed species. Because of the lack of mature achenes Jeffrey (1966: 466) treated it provisionally as "*Launaea* sp. A". When the present author later revised the three collections cited (Jeffrey 1966: 466) in the course of his revision of *Launaea* (Kilian 1997), he also had at his disposal duplicates, which had not been seen by Jeffrey, of two of these collections. All plants (mostly a few on each sheet) were collected in an early state of flowering so that even capitula with older though still immature fruits are rare, except in one out of the six plants on the sheet of the collection *Welwitsch 3664* preserved at BM. In this plant, the terminal of the

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Fig. 1. *Lactuca stebbinsii* – a: habit, b: capitulum after anthesis, c-d: achene, ventral and dorsal view (c), lateral view (d). – Scale bars: a = 1 cm, b-d = 1 mm; drawings by Ingo Haas (a-b) and Michael Rodewald (c-d) after *Welwitsch 3664* (BM).

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few-flowered capitula, which is always the earliest to flower and fruit, had reached maturity. Its involucral bracts are spread out and the achenes had already fallen off. However, in an attached capsule, carrying the collection number written by the same hand as on the original labels, two achenes, one damaged, the other complete and with pappus, are preserved. Comparison with immature achenes and pappi of the mounted plants of this and the other specimens proved that the achenes in the capsule originate from the mounted plant. Apart from these three collections no further material could be traced and since civil war has made Angola largely inapproachable, more material cannot be expected to become easily available.

Taxonomic position

Indications for the placement in the *Lactuca-Prenanthes* line

Morphology of the mature achenes and pappi of *Welwitsch 3664* at BM (Fig. 1) prove that our species belongs to the crepidioid *Lactuceae* (comprising the subtribes *Sonchinae, Crepidinae*, *Lactucinae* and *Hieracinae,* see Bremer 1994) but also that it is definitely no *Launaea*. Although in fact similarly stout, truncate and compressed achenes with a smooth and glabrous epidermis and a homomorphic setaceous pappus occur in *Launaea* sect. *Pseudosonchus* (Kilian 1997), the ribbing pattern, funnel-shaped callose carpopodium and brittle pappus clearly distinguish our species from any *Launaea.* The latter two features rule out the *Sonchinae* in general, since their pappus bristles are always flexible and their carpopodia, though of various shapes, are never annular-callose. General as well as achene and pappus morphology strongly indicate that the species is instead a member of the subtribe *Lactucinae*.

Nevertheless, achenes similar to those of our species occur also among the *Crepidinae* in *Crepis,* in species groups classified as primitive by Babcock (1947). In *Crepis,* such achenes are never combined, however, with the type of few-flowered capitula as is present in our species and its involucre (number, shape, arrangement, colour and ornamentation of involucral bracts) is so entirely different from all *Crepis* that any relationship can safely be excluded.

The following features are of diagnostic relevance for the position of our species within the *Lactucinae:* (1) a perennial herb with rosulate leaves, erect stems and paniculate synflorescence, (2) a narrow cylindrical, calyculate involucre with only five inner bracts, (3) involucral bracts tinged purplish with minutely papillose surface, (4) erect and (5) moderately few-flowered capitula (with 7-11 flowers), (6) yellow corollas, (7) truncate achene apex, hardly contracted below and little expanded into the pappus disk, (8) subfusiform and moderately but distinctly compressed achene body, (9) achene wall with seven unequal, rounded longitudinal ribs, partly prominent and partly divided by furrows, (10) achene surface entirely glabrous, pale-brown, (11) carpopodium almost funnel-shaped, (12) ovary wall with five principal strands, of which two are closely adjacent and fused in their basal part, and two supernumerary strands, (13) homomorphic white pappus, (14) brittle pappus bristles at base c. 4-5 cells in diameter.

The moderately few-flowered capitula as well as the minutely papillose, purplish tinged involucral bracts are present in several species groups of the *Lactuca-Prenanthes* line, and the habit is even less conclusive. Truncate, distinctly but moderately compressed, pale achenes, however, are not too common among the *Lactucinae,* but found in *Prenanthes,* in *Cicerbita* and in *Lactuca* s.l.

Generic concepts in the *Lactuca-Prenanthes* line

Since the generic concepts in the *Lactuca-Prenanthes* line have been continuously disputed since the early days of synantherology, some remarks seem appropriate here.

For the circumscription of *Lactuca* in particular three features have been strongly emphasized: (1) the presence or absence of an outer row of minute pappus hairs, (2) the presence or absence of a beak, and (3) the number of flowers per capitulum.

The number of flowers per capitulum has been used to separate *Scariola* (see e.g. Tuisl 1968), and, more recently, *Stenoseris* (Shih 1991) from *Lactuca.*

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The presence or absence of a beak played a major role in 19th century *Lactuceae* systematics and has been employed as an essential feature still in the more recent generic delimitation within the *Lactucinae* by Tuisl (1968) and Shih (1988) in favour of a narrower circumscription of *Lactuca.*

The presence of an outer minute pappus row was the main feature used by Beauverd (1910) to delimit *Lactuca* (without) and *Cicerbita* (with an outer row), later by Tuisl (1968) to delimit *Cephalorhynchus, Cicerbita* and *Steptorhamphus* (with) from *Lactuca, Scariola* and *Mulgedium* (without an outer row), by Feráková (1977) to keep *Mycelis, Cephalorhynchus, Cicerbita* and *Steptorhamphus* separate from *Lactuca,* inconsequently including, however, *L. tenerrima* Pourr. with an outer pappus in *Lactuca,* and more recently by Shih (1991), redefining *Cicerbita* and establishing *Chaetoseris* and *Stenoseris.* Already Stebbins (1937b) pointed out that for generic delimitation this character is as useless as the presence or absence of a beak, because it evidently separates closely related species such as *Lactuca tenerrima* and *L. perennis* L. Its taxonomic relevance has also been rejected by Jeffrey (1966) in his treatment of the African *Lactuca*. The homoplasy of the minute outer pappus row within the *Lactucinae* is further corroborated by the fact that, in contrast to what was known to Stebbins (1937b), it is also present in *Prenanthes* resp. *Notoseris,* as the species pair *Prenanthes amabilis* Balf. f. (without) and *P. somalensis* C. Jeffrey (with outer pappus) demonstrates.

The strongest support for Stebbins' view comes, however, from recent molecular analysis (Koopman & al. 1998). Based on the ITS 1 marker these authors demonstrated that the delimitation of *Lactuca* based on presence or absence of an outer pappus, presence or absence of a beak and the number of flowers per capitulum clearly conflicts with the molecular data. Consequently, separation of neither *Mycelis* nor *Cicerbita, Scariola* or *Mulgedium* has received any molecular support. The selection of species included in the analysis by Koopman & al. (1998) is still too small for a revised delimitation of *Lactuca* and related genera. Whether a narrower or broader concept of *Lactuca* is more appropriate will thus have to be shown by further molecular studies. For the time being it seems justified by the aforementioned initial results to operate with a wide concept of *Lactuca* in the sense of Stebbins (but with inclusion of Stebbins' redefined *Cicerbita* (Stebbins 1937b: 16)), and consequently to keep, e.g., the various tropical African species in *Lactuca,* as has been done by Jeffrey (1966), Dethier (1982), Pope (1992) and Jeffrey & Beentje (2000).

Prenanthes has posed problems regarding its delimitation from *Cicerbita* on the one hand and from *Lactuca* on the other hand. Some clarifying notes have been contributed by Stebbins (1937b, 1939), chiefly emphasizing for *Prenanthes* the larger basal diameter of the pappus bristles, the lack of an apical constriction and of an expanded pappus disk, not or only slightly compressed achenes and the similar shape and regular arrangement of the five main ribs of the achenes. Recently Shih (1987) attempted to make *Prenanthes* more homogeneous and excluded the species with reddish-brown, many-ribbed (i.e. with well developed secondary ribs) achenes as a separate genus *Notoseris* and also reinstated the mainly N American *Nabalus,* a treatment more recently maintained by Sennikov (2000). *Prenanthes* in this strict sense thus comprises only species with truncate, pale achenes with five regular main ribs and thick pappus bristles. Sennikov (1997) and Sennikov & Illarionova (1999) added as a further diagnostic feature that the *Prenanthes* achenes lack longitudinal furrows between the little raised ribs. However, a clearly furrowed achene wall is actually present at least in *P. subpeltata* Stebbins of the disjunctly distributed *P. yakoensis* group, which comprises the SE Asian *P. scandens* Benth. & Hook. f. and *P. yakoensis* Jeffrey and the tropical E African *P. subpeltata.*

It should also be noted in this context that the scandent, high-montane *P. subpeltata* is the only species of *Prenanthes* sensu Shih (1987) present in Africa, since *P. amabilis* Balf. f. from Socotra and *P. somalensis* C. Jeffrey (as well as their possible Asian sister species *P. khasiana* C. B. Clarke from E India and N Burma) would have to be placed for their many-ribbed reddish brown achenes in *Notoseris,* and since the former endemic so-called *"Prenanthes"* on the Canary Islands has correctly been reclassified as *Sonchus pendulus* (Sch. Bip.) Sennikov (Sennikov & Illarionova 1999).

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Indications for the placement within the *Lactuca-Prenanthes* line

The achenes of our species show some similarity with *Prenanthes;* when compared to those of *P. purpurea* L., which provides the type of the generic name, they show similar general shape, colour, epidermis texture and morphology of the pappus disk. Apart from lesser similarities in carpopodium morphology, the achenes of *P. purpurea*, however, differ strongly in ribbing pattern, which is much more regular, with five lesser raised main ribs and (almost) without secondary ribs. The achenes of our species have furrows between the ribs but even if compared with the exceptionally furrowed *P. subpeltata* Stebbins, the regular five-ribbed achenes (each main rib accompanied by two secondary ribs) of the latter are strikingly different from those of our species. Moreover, the differences of our species from all *Prenanthes* in achene features are accompanied by other differences, which make its initially suspected (Kilian 1997: 419) affinity with *Prenanthes* very unlikely. In our species (1) the pappus consists of thinner rays than would be usual for *Prenanthes* (Stebbins 1937b: 13); (2) the capitula are erect at anthesis and (3) yellow-flowered, whereas they are usually pendent and purplish-bluish-flowered in *Prenanthes*.

The morphology of the achenes (Fig. 1c-d) of our species needs further consideration. The ribs are prominent in the basal two thirds and flattened in the apical third. The achene is longitudinally somewhat asymmetrical, approximately elliptical in cross section, dorsiventrally differentiated and distinctly but still moderately compressed (cross section of 1.2 × 0.5-0.6 mm). The ribbing pattern appears irregular and arbitrarily but actually follows a clear order: there are two lateral ribs which are thicker than the others but less prominent than the adjacent smaller ribs, and three or two median ribs respectively on either side between the lateral ribs. The three dorsal and two ventral ribs are not evenly distributed over the surface of either side and are different in size and prominence. The ribbing pattern of the ovary wall at anthesis, studied on a sample cleared and fixed in Hoyer's solution under the compound microscope, corresponds to the vascularization of the ovary wall (see Stebbins 1940: 55-64, Kilian 1997: 44-47): five principal bundles that continue into the corolla and two supernumerary bundles without continuation outside the achene can be observed. Two of the principal bundles, a lateral and a median one, are partly fused in the basal part and run otherwise closely adjacent in a (sub)lateral position, two further principal bundles hold a median position on either side, the fifth is the opposite lateral bundle. The two supernumeraries run between either lateral and a median principal and fuse at the achene apex each with a median principal bundle.

In the *Lactucinae,* similar to the situation in the *Sonchinae* (Kilian 1997), an evolutionary trend led from the original achene type with five principal bundles (as in all *Prenanthes, Notoseris* and *Nabalus,* cf. Stebbins 1940: 63, Milstead 1964: 60) to a progressive reduction with four, three or two principal bundles in *Lactuca* s.l. by fusion of a corresponding number of principals and accompanied by successive loss of all supernumeraries (Stebbins 1940: 58, 64). The species of *Nabalus,* however, deviate by secondarily increased numbers of supernumeraries (Stebbins 1940: 63, Milstead 1964: 60), and surprisingly *N. altissimus* (L.) Hook. (as *Prenanthes altissima* L.) has been found in a recent molecular analysis actually to group with the *Crepidinae,* in a clade together with *Taraxacum, Dubyaea* and *Youngia* (Whitton & al. 1995). In *Lactuca,* the original achene type with five principals is also present, though rarely, e.g. in the Sino-Himalayan *L. porphyrea* (Marq. & Shaw) Stebbins and *L. disciformis* (Mattf.) Stebbins (Stebbins 1940: 48). Whereas these species have no supernumeraries as is usual in *Lactuca,* two supernumeraries are present in *L. lessertiana* with otherwise only four principals (Stebbins 1940: 58).

The achenes of *Lactuca* s.l. are usually more or less compressed with two lateral ribs that are clearly thicker than the others, they are beaked or unbeaked but usually contracted below the pappus disk, they are pale or reddish or brownish or black and the ribs are usually scabrous of acute antrorse papillae (Stebbins 1937a-b, 1939, Jeffrey 1966). Glabrous and almost glabrous achenes are, however, known, e.g., from the scandent afromontane *L. stipulata* Stebbins and pale achenes are present in the *L. stipulata* group (Stebbins 1940) and in several SW Asian species

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(Tuisl 1968), moderately compressed and not or scarcely beaked achenes are found in some species, among them, e.g., the Asian *L. brunoniana* (DC.) Franch., the African *L. tysonii* (Philipps) C. Jeffrey, *L. lasiorhiza* (O. Hoffm.) C. Jeffrey and again *L. stipulata*.

The comparison reveals that the achenes of our species actually have more in common with those of *Lactuca* s.l. than with those of *Prenanthes* s.str. and the same holds true also regarding the pappus and other features such as flower colour, posture of the capitula and leaf shape.

Relationships

Within *Lactuca,* our species shows a fairly primitive ovary wall vascularization, and should therefore be regarded as a rather ancient element of the genus. When looking out for possible relatives, we have to take into consideration that the ancestors of the tropical African species migrated from Asia via S Arabia into E Africa and have radiated and spread from there to the south and west of the continent. *Lactuca* s.l. has its greatest diversity in the Sino-Himalayan region, and it has been assumed by Stebbins (1940) that the Central Asian/Sino-Himalayan region may represent the centre of origin for the *Lactucinae* and *Crepidinae* in particular and the *Lactuceae* in general. This assumption still has some plausibility (Whitton & al. 1995). Migration of *Lactuceae* into Africa probably took place in a rather remote pluvial period as may be assumed, e.g., from the E African presence of disjunctly distributed hygrophilous high-montane scandent species in *Lactuca* and *Prenanthes*, since at least in the latter case the vicariance with Sino-Himalayan taxa is evident. This makes it likely that the migration into Africa took place already in a rather early period of the phylogeny of the *Lactucinae*.

The scandent *Lactuca stipulata* group, which is chiefly distributed on volcanoes bordering the E African rift valley system (Stebbins 1937a) and of which no non-African allies are known, is worth further considerations. Since there is little doubt that the species are all closely related, the range of achene shapes within this group is remarkable. From the moderately compressed and apically hardly constricted type in *L. stipulata* Stebbins we find a series leading to the distinctly flattened and beaked type in *L. glandulifera* Hook. f. at the other end of the scale (see Stebbins 1937a: fig. 8 and Jeffrey 1966: fig. 3). This case illustrates that a relatively small group of even ecologically similar species comprises a considerably amount of the achene variation of the entire genus in its wide circumscription. Similar though less obvious series can be found in other African species groups (see Jeffrey 1966: fig. 2-3). Among African species, *L. stipulata* is the one with the least compressed and beaked achenes and approaches in this respect the achenes of our species, without, however, actually matching them.

The achene variation among the scandent *Lactuca* species also implies that a possible ally of our species does not necessarily need to have similarly truncate achenes. Beaked achenes are usually the result of a selection in an environment that makes long-distant dispersal an advantage. Our species, in contrast, seems restricted to marshy meadows. In two of the three known localities the meadows are at the riverbank and probably seasonally inundated but otherwise dry, as must be assumed from the somewhat fleshy leaves. Restriction of the species to this type of habitat suggests disperal by water rather than wind. An interpretation of the non-beaked achene as a result of the selection in this particular environment should therefore be considered. However, I have failed to discover among the African or Asian species one which may be regarded with some plausibility as an relative of our species.

Lactuca stebbinsii N. Kilian, **sp. nova** – Fig. 1
Holotypus: Angola, district Huilla, 14-16°S, 3800-5500', in pratis junta ripas riv. Lopollo, 12.1.859, *Welwitsch 3664* (BM!; isotypi: BR!, G!, K!, M!).

Herba nudicaulis perennis a ceteris *Lactucae* speciebus africanis habitu similibus achaeniis omnino erostratis, truncatis, modice compressis, glabris et pallidis differt. Clarissimo G. Ledyard Stebbins, Jr. hanc speciem dedicavi.

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Perennial herb, flowering up to c. 40 cm high, with a strong, ± tuberous(?) taproot, with a basal leaf rosette on a very short caudex and a slender, ascending-erect flowering stem or with a few stems; stems leafless except for a few bracts at the distantly situated nodes. *Leaves* somewhat fleshy and, as the stem, glaucous green (Gossweiler in sched.); *rosette leaves* up to 9(-13) cm long and 0.5-1.3 cm wide, narrowly oblanceolate or narrowly lanceolate to linear-lanceolate and strongly tapering into a narrow to almost petiole-like, finally semiamplexicaul base, margin almost entire to inconspicuously sinuate-dentate of minute cartilagineous teeth, apex ± acute; leaf axils somewhat woolly and leaf base ± pubescent with multicellular trichomes; *cauline leaves* already at the lowest node of the flowering stem strongly reduced in size and ± bract-like, linear-lanceolate, acuminate, with semiamplexicaul base. *Flowering stems* often branching already from the lower nodes, branches slender and ascending-erect, like the main stem terminated by a slender, few-capitulate synflorescence. *Peduncles* ± ascending-erect, thin, up to a few cm long, with a few bracts passing over into the outer involucral bracts. *Capitula* erect, with c. 7-11 flowers. *Involucre* slender-cylindrical, 8-10 mm long; outer involucral bracts 5-7, narrowly lanceolate, the longest ones less than half the length of the inner involucral bracts; inner involucral bracts ± 5, linear-lanceolate with narrow scarious margin, often with a purplish tinge, towards the tip very minutely papillose. *Flowers* with a golden yellow (Gossweiler in sched.), 10-12(?) mm long corolla, with few trichomes at the transition between the shorter tube and longer ligule; anther tube c. 4 mm long. *Achenes* slightly fusiform with the maximal diameter above the middle, 4.8 mm long, distinctly but moderately compressed (1.2 mm wide and 0.5-0.6 mm thick), with 7 unequal, rounded and only partially and irregularly prominent longitudinal ribs, straw-coloured, surface entirely glabrous and smooth, apically truncate with a little expanded pappus disk, basally with an almost funnel-shaped rather than cylindrical c. 0.1-0.2 mm long carpopodium. *Pappus* 4(-6?) mm long, of c. 50-60 stiff, barbellate, brittle bristles, with c. 4-5 cells in diameter at base and with barbs becoming longer towards the pappus base, evoking the impression of the presence of an outer row of minute pappus elements.

Distribution and ecology

Lactuca stebbinsii is known from three localities at the southern edge of the SW Angolan highlands. According to the collectors' labels it occurs in grassland on waterlogged soil at altitudes between about 1300 and 1800 m. Welwitsch (in sched. 3664) reports that it grows "in varzeas (meadows) along the banks of the Lopollo stream, plentiful but very quickly disappearing" (English translation after Hiern 1898). The flowering material was collected in late October and December, during the rainy season, which lasts from November to April.

Additional specimens seen

ANGOLA: Marsh on edges of Humpata plateau [c. 15°S, 13°20'E] above Huilla, 5300', *H.H.W. Pearson 2663* (K); Benguella [today: Bié], in wet grassy meadows between forte Princeza Amelia [c. 14°S, 16°25'E, 1550 m] & Rio Kubango, 28.10.1905, *Gossweiler 2187* (BM, COI, K).

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