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

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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 caputula 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).
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, Lacticinae 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 Lacticinae.

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 Lacticinae: (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 papilllose, 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 Lacticinae, 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, Stenoserus (Shih 1991) from Lactuca.
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 Cephalorhynchos, Cicerbita and Steptorhamphus (with) from Lactuca, Scariola and Mulgedium (without an outer row), by Ferákóvá (1977) to keep Mycelis, Cephalorhynchos, Cicerbita and Steptorhamphus separate from Lactuca, consequently including, however, L. tenerrima Pourr. with an outer pappus in Lactuca, and more recently by Shih (1991), redefining Cicerbita and establishing Chaetoseris and Stenososeris. 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).
Indications for the placement within the \textit{Lactuca-Prenanthes} line

The achenes of our species show some similarity with \textit{Prenanthes}; when compared to those of \textit{P. purpurea} \textit{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 \textit{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 \textit{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 \textit{Prenanthes} in achen features are accompanied by other differences, which make its initially suspected (Kilian 1997: 419) affinity with \textit{Prenanthes} very unlikely. In our species (1) the pappus consists of thinner rays than would be usual for \textit{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 \textit{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 \textit{Lactucinae}, similar to the situation in the \textit{Sonchinae} (Kilian 1997), an evolutionary trend led from the original achen type with five principal bundles (as in all \textit{Prenanthes}, \textit{Noto-seris} and \textit{Nabalus}, cf. Stebbins 1940: 63, Milstead 1964: 60) to a progressive reduction with four, three or two principal bundles in \textit{Lactuca} \textit{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 \textit{Nabalus}, however, deviate by secondarily increased numbers of supernumeraries (Stebbins 1940: 63, Milstead 1964: 60), and surprisingly \textit{N. altissimus} (L.) Hook. (as \textit{Prenanthes altissima} L.) has been found in a recent molecular analysis actually to group with the \textit{Crepidaeae}, in a clade together with \textit{Taraxacum}, \textit{Dubyaea} and \textit{Youngia} (Whitton & al. 1995). In \textit{Lactuca}, the original achen type with five principals is also present, though rarely, e.g. in the Sino-Himalayan \textit{L. porphyrea} (Marq. & Shaw) Stebbins and \textit{L. disciformis} (Mattf.) Stebbins (Stebbins 1940: 48). Whereas these species have no supernumeraries as is usual in \textit{Lactuca}, two supernumeraries are present in \textit{L. lesserti}ana with otherwise only four principals (Stebbins 1940: 58).

The achenes of \textit{Lactuca} \textit{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 antorse papillae (Stebbins 1937a-b, 1939, Jeffrey 1966). Glabrous and almost glabrous achenes are, however, known, e.g., from the scandent afromontane \textit{L. stipulata} Stebbins and pale achenes are present in the \textit{L. stipulata} group (Stebbins 1940) and in several SW Asian species.
(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 dispersal 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 acheniis omnino erostratis, truncatis, modice compressis, glabris et pallidis differt. Clarissimo G. Ledyard Stebbins, Jr. hane speciem dedicavi.
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 cartilaginous 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

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