Prickly Lettuce (*Lactuca serriola* L.) in Britain

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ABSTRACT

Lactuca serriola L. has cauline leaves which are either runcinate-pinnatifid or else unlobed, the latter being the more common in Britain; intermediate forms do not occur. The plants with pinnatifid leaves have a more restricted distribution in Britain, but are the commoner form in continental Europe. The

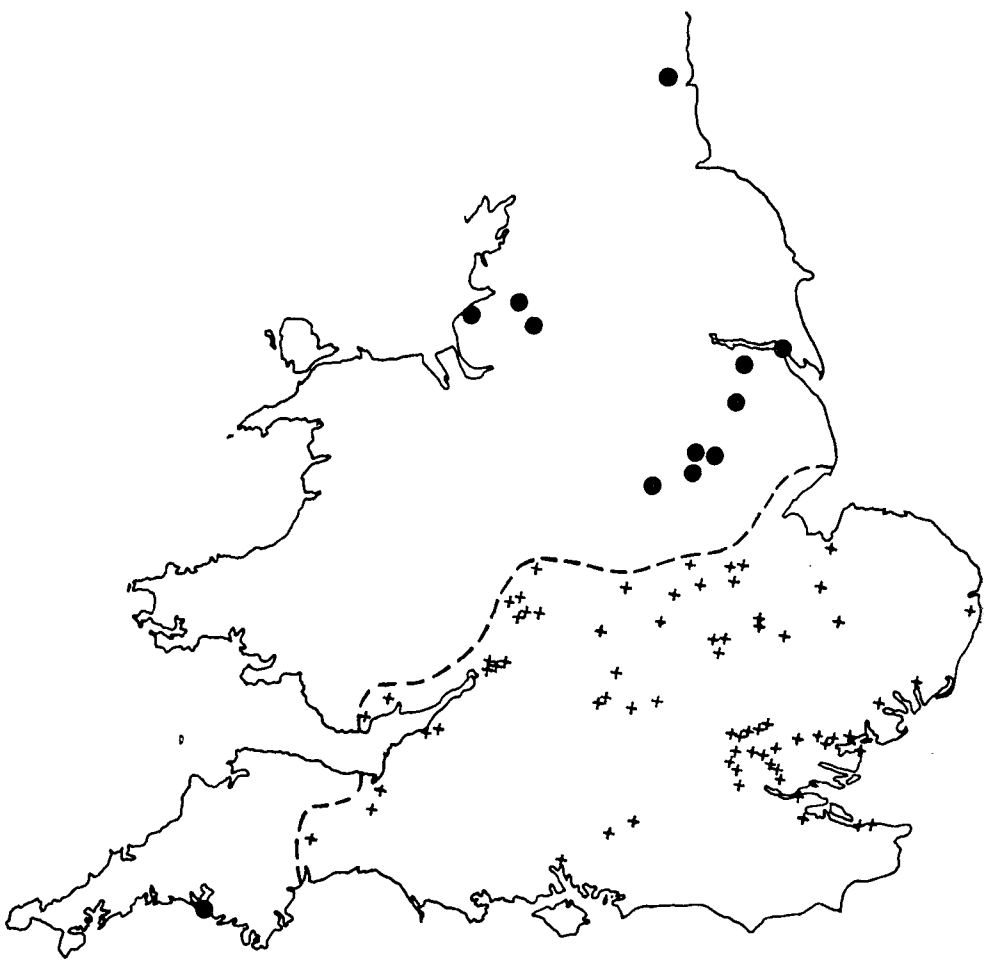

FIGURE 1. Location of *Lactuca serriola* sites studied (crosses) showing the limit of common occurrence in Britain (dashed line) and the occasional occurrences (circles) outside the limit. Data partly supplied by the Biological Records Centre.

taxonomic treatment of leaf-shape variation in *L. serriola* is revised; the pinnatifid-leaved form is given the name *L. serriola* L. forma *serriola* and the unlobed-leaved form is given the name *L. serriola* L. forma **integrifolia** (S. F. Gray) S. D. Prince & R. N. Carter, **comb. et stat. nov.**

The characters which distinguish *L. serriola*, *L. virosa* L. and *L. saligna* L. (the three wild British species) are reviewed and emphasis is placed on achene morphology. The geographical distribution and habitat preferences of the three species are described and a key to the British members of the genus *Lactuca*, including *L. sativa* L., is provided.

INTRODUCTION

Lactuca serriola L. is a conspicuous plant of waysides and disturbed sites in south-eastern England. Its distribution (Fig. 1) is limited to the area south-east of a line from Exeter to Birmingham—taking in the part of South Wales bordering the Severn estuary—and south of the line from Birmingham to Boston on the east coast. Within this area it is most common in the counties bordering on London.

Only two other species of *Lactuca* are native in Britain—*L. virosa* L. and *L. saligna* L. However, all three species are members of the Section *Lactuca* Sub-section *Lactuca* (Feráková 1976) and have morphological similarities, so that it is difficult for the newcomer to the genus, even with the help of the keys and descriptions in modern Floras, to determine to which species a specimen belongs. Such difficulties are derived, at least in part, from published descriptions which underestimate phenotypic variation and neglect some useful characters, among them the existence of two relatively distinct leaf-shapes in *L. serriola*. Having examined approximately 70 sites in which *L. serriola* grows (Fig. 1) we are able to provide a more accurate description of the British material and an improved key to separate the British species of *Lactuca*.

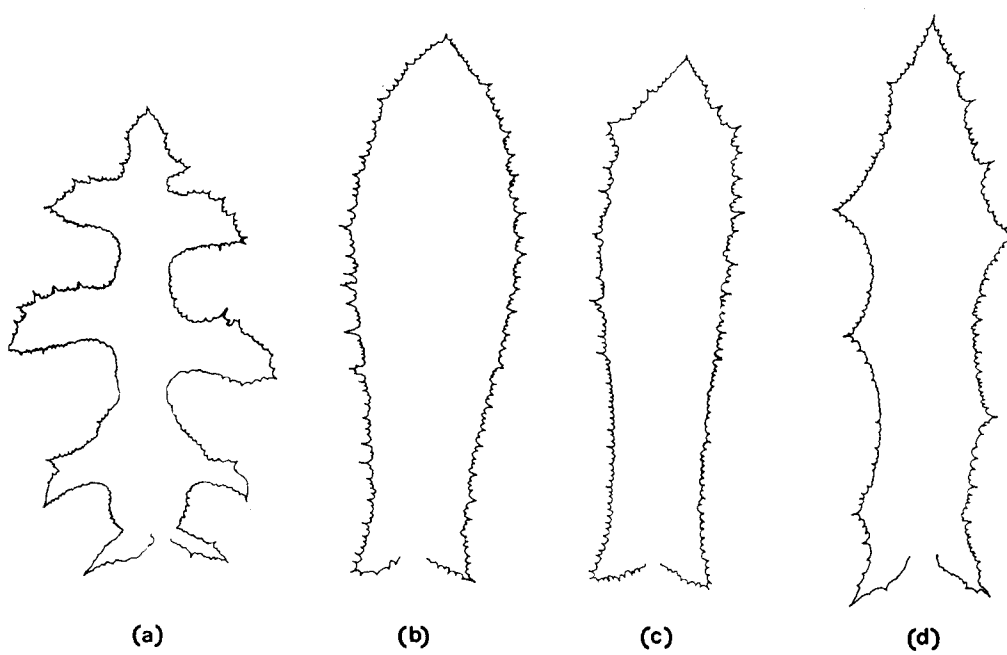

FIGURE 2. Outlines of cauline leaves of *Lactuca serriola* from Britain. (a) Runcinate-pinnatifid leaf of forma *serriola*; (b) and (c) unlobed leaves of forma *integrifolia*, (c) showing the triangular tip; (d) lobed leaf of a lateral stem of forma *integrifolia*.

INFRASPECIFIC VARIATION

All the plants in the 70 wild populations of *L. serriola* can be assigned without difficulty to one of two distinctive forms characterized by the shape of the cauline leaves, which may be either unlobed (Fig. 2b), often with a triangular tip (Fig. 2c), or else pinnatifid (Fig. 2a); both leaf-shapes have irregularly denticulate to dentate, spinose-ciliate margins. These two forms have been found together in some of the sites but no intermediates were found. The leaf shapes are maintained in cultivation and are undoubtedly inherited. Feráková (1970) described similar variation in leaf-shape in other species of *Lactuca*.

The absence of intermediate leaf-shapes suggests either that the plant is an inbreeder or that a single gene controls leaf-shape. In fact both explanations appear to apply to *L. serriola*. The structure of the *Lactuca* floret is such that self-pollination normally occurs, although cross-pollination can be achieved artificially. Clearly there are no absolute barriers to cross-pollination,

TABLE 1. INFRASPECIFIC VARIATION IN RATE OF DEVELOPMENT OF *LACTUCA SERRIOLA*

Origin	Experiment 1,* 1975				Experiment 2,* 1976
	Stage of development (No. of plants)			Days from planting to first flower	Date of 50% capitula shedding
	Rosette	Bolted	Flowering		
British collections					
Waltham Abbey, Bucks., v.c. 24	14			171	23 July
Aylesbury, Bucks., v.c. 24	12	6		150±28	25 July
Oxford, Oxon., v.c. 23	14	3		121±67	
Pershore, Worcs., v.c. 37	18			187±26	
Bedford, Beds., v.c. 30	17	1		167±42	
Rugby, Warks., v.c. 38	16	2		127±20	
Peterborough, Northants., v.c. 32	18			181±48	
Tixover, Rutland, v.c. 55b	6	12		111±6	
Southampton, S. Hants., v.c. 11	17	1		156±67	
Continental European collections					
Godollo, Hungary	14	3		184±16	
S. Slovakia, Czechoslovakia	18			189±13	
Liège, Belgium	16	2		166±22	
Berlin, E. Germany	17			167±19	
Warsaw, Poland		17	1	74±2	
Erevan, U.S.S.R.	6	4		114±14	
Portugal		16		82±12	
Lund, Sweden	18			190	19 August

* Experiment 1. 18 plants of each collection grown in 7·5cm pots in glasshouse, minimum temperature 15° C. Sown 25 April. Stage of development assessed 30 June. Mean days to opening of first flower and 95% confidence limits.

Experiment 2. 5 plants of each collection sown in field plots at Dytchleys, Essex, October 1975. Capitula counted each day after first opening, 50% shedding estimated from curve of accumulated number against time.

but in *L. sativa* natural cross-pollination of varieties grown in adjacent rows does not exceed 2·87% (Thompson *et al.* 1958). On the other hand, Lindqvist (1958) has proposed that leaf-lobing in *L. serriola* is controlled by two alleles at a single locus—pinnatifid leaves being dominant and unlobed leaves recessive; he also found a dominant allele which determines an 'oak' leaf-shape in Italy but we have not found any plants with leaves of this type in Britain. Lindqvist examined specimens from Harwich and Romford and found them to be homozygous for the recessive and dominant alleles respectively. Since in the many populations we have examined there were no intermediate leaf-shapes, it seems reasonable to accept that the difference is a result of a single gene,

In an attempt to encourage cross-pollination, two 250 × 350 mm trays each containing 15 plants. some with pinnatifid leaves and others with unlobed leaves, were kept in the open throughout the flowering period and the leaf-shapes of their progeny were examined. In all cases the maternal leaf-shape was maintained. Under these particularly favourable conditions for cross-pollination, the failure to detect pinnatifid-leaved plants among the progeny of unlobed-leaved female parents (as would have been expected given the genetic system proposed by Lindqvist) suggests that, although there are no absolute barriers to natural cross-pollination, it is nevertheless an extremely rare occurrence. Our failure to detect segregation of leaf-shapes in these, or in any other of our collections of pinnatifid-leaved plants, suggests that, like those examined by Lindqvist, they are homozygous for the alleles controlling leaf-shape.

Unlobed-leaved plants occasionally bear leaves with very slight lobing (Fig. 2d). These are generally found on the lateral stems arising from the base of the plant. However, the indentations are shallow and unlobed leaves are always to be found elsewhere on the plant.

Most Floras correctly describe the runcinate-pinnatifid leaf-shape, but either neglect to mention the unlobed leaf-shape or suggest that it is uncommon. In our experience, however, unlobed-leaved plants are much the commoner; of the 70 sites examined only 8 contained pinnatifid-leaved plants, and only at Aylesbury was the population composed exclusively of such plants.

Infraspecific variation can be demonstrated in a number of physiological characters and an example is given in Table 1. For the collections listed there, there is less variation among the British plants than there is among those from continental European sites—for example the range in mean number of days to flowering in the Continental plants is 74 to 189 days compared with 111 to 187 days in the British plants. The experiments so far have not been sufficiently extensive to establish any correlation of phenological variation with the climate at the site of origin, except that the British collection which flowers most rapidly is from a site near the northern limit (Tixover, v.c. 55b). The British material examined is likely to be more representative of the variation among British plants than are the few available Continental collections of continental European plants as a whole and so it is probable that the range of variation present on the Continent is even more extensive than we have found so far.

Apart from the different leaf-shapes, there is relatively little genetic variation in morphology between British collections of *L. serriola*, but there is great phenotypic plasticity. Under favourable conditions plants are commonly 1·8m high with 10 or more lateral branches from the base reaching almost the same height and together bearing 2,000 capitula, whereas plants growing under unfavourable conditions may be as little as 0·15m high with a single stem and 20 capitula. Such small plants are often found on compacted ground or in dense grass swards near stands of taller *L. serriola* plants. Most Floras, e.g. Clapham (1962), underestimate the maximum height: the range for British plants in the wild is (0·15–) 0·3–1·9 (–2·1)m.

COMPARISON OF *L. SERRIOLA*, *L. VIROSA* AND *L. SALIGNA*

The three members of the genus found wild in Britain are easily identified when fruiting, although it is also possible to identify non-fruiting, and even vegetative plants. A list of the most useful diagnostic features is given in Table 2. The characters are based on plants growing in the wild, and remain constant in cultivation.

The achenes (cypselae) we have examined from populations of each species have no primary dormancy and on shedding in late summer will germinate as soon as the soil surface is wet. The rate of germination declines during the winter but increases during mild periods and again in the spring. Young plants of all three species form rosettes which can be identified once the first true

TABLE 2. COMPARISON OF DIAGNOSTIC CHARACTERS OF *L. SERRIOLA*, *L. VIROSA* AND *L. SALIGNA*

	L. serriola	*L. virosa*	*L. saligna*
Overwintering rosette	Leaves oblong-obovate, unlobed or, later in development, indented, green	Leaves oblong-obovate, unlobed, broader than *L. serriola*, grey-green, often with maroon veins	Leaves pinnatifid, green. Rosette often with prostrate, spreading lateral stems each terminated with a smaller leafy rosette
Stem leaves	Unlobed or runcinate-pinnatifid, flat	Unlobed or pinnatifid, margins undulate	Lower stem leaves runcinate-pinnatifid, upper linear-lanceolate, flat
	Prickly, particularly on underside of main veins	Prickly, particularly on underside of main veins	Few stiff hairs only on underside of main veins
	Leaves held twisted at the base, often all arranged in the same vertical plane, the white stem and midribs giving a 'herring-bone' pattern visible from a distance	Some leaves twisted at base, but not all arranged in the same vertical plane	Leaves not obviously twisted
Height	Up to 2·1m	Up to 2·5m	Less than 1m
Bracts	Spreading auricles	Auricles clasping stem	Auricles clasping stem
Colour	Leaves often glaucous with white midrib	Leaves green, often with maroon patches especially along veins	Leaves green
	Stems whitish	Stems maroon	Stems whitish
	Inflorescence green	Inflorescence tinged maroon	Inflorescence green
Inflorescence shape	Inflorescence branches (as distinct from lateral stems) arising only from upper half of stem, erect	Inflorescence branches arising from lower part of stem as well as upper part, large and spreading	Inflorescence essentially a single stem with tightly clustered capitula on short branches
Achenes	Olive-grey, mottled	Maroon	Olive-grey, mottled
	(2·8–)3–4(–4·2) × 0·8–1·3mm	(4–)4·2–4·8(–5·2) × (1–)1·3–1·6(–1·7)mm	2·8–3·5 × 0·7–1·2mm
	Broadest ⅔–¾ from base	Broadest in middle	Broadest ⅔–¾ from base
	Margins narrow	Margins broad	Margins narrow
	Very bristly on the sides where it narrows into the beak and on the faces above, bristles simple	Bristles mainly on the faces near the beak, palmate	No bristles
	5–7(–8) ribs	(6–)7–8(–9) ribs	7–10 ribs
	Beak equalling or slightly shorter than achene	Beak much shorter than achene	Beak longer than achene
Life cycle	Annual or winter annual	Winter annual or biennial	Annual or winter annual

leaves are fully expanded. In *L. serriola*, the rosette leaves are oblong-obovate and bright green; the first are always unlobed but, in pinnatifid-leaved plants, those appearing later may have indentations. In *L. virosa* they are broader and grey-green, often with maroon patches on the veins and lamina. In *L. saligna* they are bright green and pinnatifid from an early age; well-grown rosettes may have prostrate lateral stems spreading radially, each terminated with a smaller rosette of leaves. Autumn- and spring-germinated *L. serriola* and *L. saligna* plants normally flower in the following summer and are therefore winter or spring annuals. Autumn-germinated *L. virosa* plants are normally winter annuals, but occasionally poorly-grown plants behave as biennials passing the first summer as rosettes, as do spring-germinated plants.

The species are easily distinguished from each other when the leafy stems extend in early summer, prior to flowering. The leaves of *L. serriola* have a broad, white midrib, the same colour as the

stem. The midribs are twisted at the base such that the laminas lie in the same vertical plane, in two rows which are on opposite sides of the white stem (Hegi 1928). This results in a characteristic herring-bone pattern readily seen from a distance. The undersides of the midribs bear large, regularly spaced, spines. In *L. virosa*, the lower cauline leaves are unlobed while the upper leaves may be either unlobed or pinnatifid. Although the midribs are often twisted at the base causing the laminas to be held vertically at right-angles to the axis of the stem, the laminas are still arranged spirally around the stem and not orientated into two rows as they are in *L. serriola*. The stems are maroon, in marked contrast to the other two species. In *L. saligna*, the lower cauline leaves are runcinate-pinnatifid and the segments are very narrow. The upper leaves are linear-lanceolate, with no lobes and no spines on the underside of the midrib. The whole plant rarely exceeds 0·5m in height, whereas the other species often approach 2m.

The inflorescences have characteristic shapes. The branches of the *L. serriola* inflorescence are held upright and many terminate at approximately the same height, producing a sub-corymbose panicle. Well-grown *L. virosa* plants have large inflorescence branches which spread and create an asymmetric, diffuse panicle. In *L. saligna* they are contracted to give clusters of capitula along the spike-like inflorescence.

Ripe achenes provide an easy and reliable means of identification, but about these there is a degree of confusion in some Floras. Plate 4 illustrates achenes of each species; clearly there are differences in shape, size and the presence of bristles on the upper parts of the achenes; another character is the colour—olive-grey, mottled with lighter and darker patches in *L. serriola* and *L. saligna*, deep maroon in *L. virosa*. Exact dimensions of the achenes are given in Table 2. The achenes of *L. virosa* are both longer and broader than those of the other two species; they are more oval in outline and have a broad, wing-like border. Only *L. serriola* and *L. virosa* have bristle-like appendages on the upper part of the achenes. These bristles are very obvious in *L. serriola* since they are colourless and contrast with the olive-grey achene, and are particularly numerous on the sides of the achene where it narrows into the beak. Maroon bristles which have a palmate structure are a constant character in *L. virosa*. The length of the beak (the distance from the insertion of the pappus to the point where achene pigmentation starts) also differs between the species: in *L. saligna* the beak is longer than the achene, in *L. serriola* it is about the same length, and in *L. virosa* it is shorter. Using the colour, size, bristles and beak-length it is possible to identify each of the wild species.

ACHENE CHARACTERS OF *L. SATIVA*

L. sativa, the cultivated lettuce, exists in many varieties and all of the 31 we have examined have achenes shaped like those of *L. serriola*, although in most cases they are somewhat larger ((3·2–) 3·5–4(–5) × (1–)1·2–1·5mm). Their colour is either olive-grey, as in *L. serriola* (and commercially referred to as 'black-seeded'), or colourless ('white-seeded'); and there is a range from those with no bristles to some with large, simple bristles identical with those of *L. serriola*. The *L. virosa* achene-type, with palmate bristles, is not found in *L. sativa*.

HABITATS

L. serriola behaves as a ruderal in Britain. It is most commonly, though not always, found in places where large amounts of earth have been moved; new housing estates and the verges of new roads are typical sites. Very occasionally it is reported from natural habitats such as shingle banks, but in the main it is confined to places affected by man's activities. It is never found on waterlogged ground although it may occur on the well-drained sides of dykes in low-lying districts. It is not found on acid peat although it grows well on fen peat; it is rarely found on skeletal calcareous soils.

L. virosa is more usually found in naturally unstable habitats, such as sand-dunes and cliff-ledges, although it is also found on gravel workings, quarries, industrial estates and roadside verges. It is frequently found on chalk and oolitic limestone and can occur at woodland margins. It is found further north than *L. serriola*, reaching the River Tweed and possibly the Firth of

Forth. *L. saligna* is known to us only on one sea wall in W. Kent (v.c. 16), although colonies have been reported at Rye, E. Sussex (v.c. 14) up to 1975 and at Seasalter, E. Kent (v.c. 15). *L. saligna* has not been found at the inland sites near Earith, Hunts. (v.c. 31) for a number of years and is probably extinct there.

NOMENCLATURE

Linnaeus made no mention of *Lactuca serriola* in the first edition of *Species Plantarum* (1753). He first published the name in *Centuria II Plantarum* (1756), validating it by reference to several earlier descriptions. Also in 1756 he published the name *Lactuca scariola* in *Flora Monspeliensis*, but he did not describe it or refer to any earlier description; this omission was corrected when the work was later reprinted in *Amoenitates Academicae* IV (1759) and *L. scariola* appears in the second edition of *Species Plantarum* (1762). The existence of two Linnaean names for the same plant inevitably gave rise to confusion, both being used by nineteenth century authors, but *L. serriola* is the correct name having the earlier valid publication (Stearn 1973).

Taxonomists have long distinguished *L. serriola* plants having unlobed leaves from those having pinnatifid leaves. Several early authors described them as altogether different plants, e.g. Ray (1690), although Magnol had earlier (1676) referred to them as variants of the same taxon. There are good reasons for according these leaf-shape variants taxonomic recognition and in our opinion the appropriate rank is that of forma. Whereas the pinnatifid-leaved plant is the less common variant in Britain (having a particularly restricted south-eastern distribution), on the Continent it is the more abundant of the two. The arguments for this treatment of polymorphic variation in general are presented by Valentine (1975).

Linnaeus treated the pinnatifid-leaved form of *L. serriola* as typical, referring in *Centuria II Plantarum* (1756) to *Lactuca sylvestris laciniata*, Morison, *Hist.* **3**: 58, S7, t.2, f.17 (1715), which is a pinnatifid-leaved plant as both the description and the illustration show. The only *L. serriola* specimen in **LINN** (labelled *L. scariola*) is a pinnatifid-leaved plant. This argument is supported by the fact that *L. serriola* var. γ in *Centuria II Plantarum* (1756) is an unlobed-leaved plant based on *Lactuca sylvestris annua costa spinosa, folio integro colore caesio*, Morison, *Hist.* **3**: 58, S7, f. 15 (1715).

The first post-Linnaean reference to an unlobed-leaved plant was by Allioni (1785) who gave it the name *L. augustana*; but this plant had no prickles (Lindqvist 1960) and is not found in Britain. Gray (1821) described a variety of *L. virosa* with unlobed leaves and called it var. *integrifolia*; this was based on *Lactuca sylvestris folio non-laciniato* Ray (1690), the description of which agrees with unlobed-leaved *L. serriola*. Although there is no Ray specimen labelled with this name there is one in the herbarium of the Rev. Adam Buddle, now incorporated in the Sloane Herbarium (H.S. 118 folio 2, **BM**), and this is definitely unlobed-leaved *L. serriola*. In his introduction to the third edition of Ray's *Synopsis* (1724), Dillenius acknowledged Buddle's herbarium, stating that 'it is of great value in determining the plants of the *Synopsis*'. Because many of the older British Floras, e.g. Bentham (1865), suggested that all unlobed-leaved forms of *Lactuca* should be assigned to *L. virosa*, there has been much confusion among British botanists over the correct name of the unlobed-leaved form of *L. serriola*, and many pre-1910 herbarium specimens were wrongly named (e.g. in **BM**). Around 1920 the error was realized and varietal names of Continental origin were adopted (e.g. Druce 1913, Little 1931, Lousley 1933); however none of these were published as early as Gray's var. *integrifolia*. We now propose a name for the unlobed-leaved plant and give the synonymy of both forms.

Lactuca serriola L. forma *serriola*
L. scariola var. *vulgaris* Bischoff, *Beiträge Flora Deutschlands und der Schweiz*, 189 (1851)
L. scariola var. *typica* Rouy, *Flore de France*, **9**: 198 (1905)
LECTOTYPUS: Herb. Linn. 950.3 (**LINN**)

Lactuca serriola L. forma **integrifolia** (S. F. Gray) S. D. Prince & R. N. Carter, **comb. et stat. nov.**
L. virosa var. *integrifolia* S. F. Gray, *Natural Arrangement of British Plants*, **2**: 417 (1821)
L. scariola var. *integrata* Grenier & Godron, *Flore de France*, 320 (1850)
L. scariola var. *integrifolia* Bogenhard, *Flora von Jena*, 269 (1850)
L. scariola var. *integrifolia* Bischoff, *Beiträge Flora Deutschlands und der Schweiz*, 189 (1851)

L. dubia Jordan, *Pugillus Plantarum Novarum*, 119 (1852)

L. integrata (Grenier & Godron) A. Nelson, *New Manual of Botany of the Central Rocky Mountains*, 596 (1909)

LECTOTYPUS: *A. Buddle*, H.S. 118 folio 2 (**BM**)

KEY TO BRITISH SPECIES OF *LACTUCA*

1 Cauline leaves entire, margins not spinose-ciliate; involucral bracts appressed to the ripe achenes .. .. *L. sativa*

1 Cauline leaves pinnatifid or, if not lobed, margins spinose-ciliate; involucral bracts patent or reflexed at maturity

2 Midrib on underside of cauline leaves glabrous or sparsely hispid, without spines; inflorescence narrow with capitula tightly clustered on short branches; ripe achenes not bristly at apex .. .. *L. saligna*

2 Midrib on underside of cauline leaves spinose; inflorescence a broad panicle; ripe achenes bristly at apex

3 Ripe achenes (4−)4·2–4·8(−5·2) × 1·3–1·6(−1·7)mm, maroon; stem maroon; upper stem leaves undulate and, if held vertically, not all in one plane *L. virosa*

3 Ripe achenes (2·8−)3–4(−4·2) × 0·8–1·3mm, olive-grey; stem and midribs of leaves whitish; upper cauline leaves flat, held vertically, often all in one plane

4 Cauline leaves deeply runcinate-pinnatifid .. .. *L. serriola* forma *serriola*

4 Cauline leaves undivided or shallowly lobed .. .. *L. serriola* forma *integrifolia*

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