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THE GENUS ACANTHOXANTHIUM (DC.) FOURR. REVIVED

D. Löve

Boulder, Colorado, U.S.A.

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Summary. The genus *Acanthoxanthium* (DC.) Fourr. is revived. A comparison is made on basis of morphology and anatomy between this genus and *Xanthium* L. The taxa of *Acanthoxanthium* are reviewed critically. The are: *A. spinosum* (L.) Fourr. with subsp. *spinosum* and subsp. *catharticum* (H., B. & K.) D. Löve, and *A. ambrosioides* (Hook. & Arn.) D. Löve. Two other taxa, previously referred to the *Acanthoxanthium* complex, *X. argenteum* Widder and *X. canescens* (Costa) Widder, are excluded as presently non-existent.

Resumen. En esta nota se hace una revisión del género *Acanthoxanthium* (DC.) Fourr., que se separa del género *Xanthium* L. basándose en sus diferencias morfológicas y anatómicas. Se revisan críticamente los taxones de *Acanthoxanthium*: *A. spinosum* (L.) Fourr. con subsp. *spinosum* y subsp. *catharticum* (H., B. & K.) D. Löve, y *A. ambrosioides* (Hook. & Arn.) D. Löve. Otros dos taxones, que habían sido referidos anteriormente al complejo *Acanthoxanthium, X. argenteum* Widder y *X. canescens* (Costa) Widder, se excluyen de esta revisión por no existir en la actualidad.

INTRODUCTION

The generic name *Xanthium* was known already before Linnaeus adopted it in 1753 (Dioscorides, according to Tournefort, 1700), but *Acanthoxanthium* was first used by De Candolle in 1836 as a name for a section of the genus *Xanthium* L.

The section *Acanthoxanthium* DC. is characterized first and foremost by the presence of tripartite spines in the leaf axils. Such spines are entirely absent in the section *Euxanthium* DC. There are also differences in leaf-shape, the leaves of *Acanthoxanthium* usually being lanceoid-triangular-ovoid in outline with a prolonged midlobe and the lobes sometimes toothed or deeply cut so as to give the whole leaf a nearly pinnatifid or laciniate appearance. The leaves of *Euxanthium* are broadly cordate in outline, often cuneate at the base. Its 3-5 lobes are toothed but rarely deeply cut. DE CANDOLLE (1836) also pointed out the difference in the so-called «beaks» (*rostra*) of the fruits, *Euxanthium* usually having two, coarse, hooked «beaks», *Acanthoxanthium* sometimes a single one, other times two, then usually unevenly long ones, but both straight.

Most later botanists have followed DE CANDOLLE's (1836) division of the genus *Xanthium* L. into sections. Only FOURREAU (1869) was bold enough to distinguish them as separate genera, which he called *Xanthium* Tourn. and *Acanthoxanthium* DC. Prod. (in sect.). He did so in a little known paper, *Catalogue des plantes qui croissent le long du cours du Rhone,* and it seems to have been mostly overlooked or ignored by later scientists. The specialist on the genus *Xanthium,* WIDDER, did not agree and criticized FOURREAU (WIDDER, 1923, 1935, 1964) for going too far. WIDDER (especially 1935, 1964) was of the opinion that there was far less distinction between DE CANDOLLE's two sections than the «enormous cleft» between *Xanthium* and other related genera such as *Ambrosia, Iva, Franseria,* and *Hymenoclea.* He did, in spite of these firm convictions, agree to raise the two sections to subgeneric status (WIDDER, 1964): subgenus *Xanthium* and subgenus *Acanthoxanthium* (DC.) Widder. This had been suggested already by D. LÖVE & DANSEREAU (1959) but an —unfortunately— illegitimate transfer was made. WIDDER corrected this mistake.

In my further studies of the genus *Xanthium* L. s. lat. I have now reached the conclusion that a distinction into subgenera is not enough, and I have come to agree with FOURREAU (1869) that a separation into distinct genera is valid. FOURREAU (l. c.) gave no reason whatsoever, simply used the DE CANDOLLE section-names in a generic sense, and —ironically— it is WIDDER (1935) who has furnished us with the best evidence, morphological and anatomical, for the distinction into genera. His claim (WIDDER, 1964) that similar traits (especially «Sprossfolge», i. e. sequence of branching) has not led to a splitting up of the genus *Viola* can not be taken seriously. Rather, there is no doubt that *Viola* is a very heteromorphus genus which on morphological, anatomical and cytogenetical basis would really benefit from being split.

COMPARISON BETWEEN XANTHIUM AND ACANTHOXANTHIUM

To delimit a genus used to be, and in part still is, far more sujective than even the delimitation of species. But with the arrival of biosystematic concepts (cf. MAYR, 1942, 1969; A. LÖVE, 1963), the task has become much simpler and more logical and reasonable. It can now be based on genetics, cytology, and even mathematics (LEGENDRE, 1972). The most important distinction between genera is the existence of an absolute sterility barrier: «Whereas hybridization is possible between species of a genus, hybridization between genera should be excluded» (A. LÖVE, 1963). Between species, the formation of sterile hybrids (crossability) can be permitted, but between genera, the barrier should be absolute.

So it is between taxa of *Xanthium* and *Acanthoxanthium*. In spite of attempts (BITTER, 1908; WIDDER, 1923, 1925, 1932), all experiments to cross members of these two groups have failed and natural hybrids have never been observed or reported. Crosses within *Xanthium* s. str. are easily produced and natural hybrids abound (cf. for instance: SENNEN in PAU, 1905; SENNEN, 1912, 1916; WIDDER, 1923 to 1964; MILLSPAUGH & SHERFF, 1923; D. LÖVE & DANSEREAU, 1959; MCMILLAN, 1973, 1974, 1975a, 1975b). Hybrids between species of *Acanthoxanthium* have apparently not yet been definitely reported, but research on this group, native to South America and increasingly widespread as a weed, has been nowhere as exhausting as on *Xanthium* s. str.

In the course of evolution from some common early ancestor, *Xanthium* and *Acanthoxanthium* have developed along morphologically different lines, especially as far as the structure of leaves and burs are concerned.

Xanthium-taxa always grow erect with stiff stems and branches, whereas in *Acanthoxanthium* there are taxa which sometimes have weak, thin and decumbent stems (*ambrosioides*).

In *Xanthium,* the main nerves in the leafblade are usually five in number. The blade varies in having 3-5 more or less distinct, toothed lobes, but is always ± palmatilobate. Both surfaces of the leaf are usually equal in color and sparsely strigose.

In *Acanthoxanthium,* the nerves of the leafblade ordinarily number three (two of the original five being suppressed). If it is three-lobed, the top-lobe is usually deeply cut and in some taxa this has led to a pinnate appearance of the leaves (*catharticum, ambrosioides*). In *spinosum,* the side lobes are at times almost absent and the blade lanceolate. The upper and lower surfaces of the blade differ in color due to the presence of various kinds of hairs from strigose to silky and felted. The hairiness also extends to the upper stems and branches as well as the burs.

Xanthium has no coarse spines or thornes in the leaf axils, whereas the presence of 1-3-furcate, stiff, yellowish spines of varying length is the character identifying the *Acanthoxanthium*-group as a whole.

The origin of these axial spines has been disputed. LINNAEUS (1753) defined them as stipules, some of which are transformed into axial fruits («spinae trifurcatae sunt stipulae, quarum altera fit fructus»). But, stipules are on the whole not found in the *Asteraceae.* Others, as for instance KITTEL (1884) and BRAUN (1853), considered them aborted or transformed leaves, but this does not tally with their occasional transformation into floral structures. WIDDER (1935) has furnished us with an excellent, critical review of the abovementioned and many following theories on this phenomenon all the way up to 1926. Then, he himself made a thourough study of the origin of the axial spines and the differences in the floral development within *Xanthium* s. lat. He reached the conclusion that the axial spines in *Acanthoxanthium* are actually a kind of bracts which occasionally revert to leafy shoots in some aberrant taxa, but develop into involucral bracts in normal plants:

«a) The spinal shoots are usually situated on each side of the axial shoot in most of the *Acanthoxanthia,* i. e. are developed on the right and the left side respectively at the base of the axial shoot.» (WIDDER, 1935, fig. 27b, plate III.)

«b) In the inflorescence, the spinal shoots are represented by female heads, so that female heads take the place of one, or further up [the stem] both shoots.»

«c) The transformation from spinal shoot to female flower is perfect: both are homologous, which can be seen in the not rarely appearing gradual transformation from one to the other.» (WIDDER, 1935, fig. 20.)

...«g) *X. spinosum inerme* has indeed in place of the spinal shoot leafy shoots which often sit 'in the axils' of small leaves (figs. 29b, c, plate IV).» (Translated from German, WIDDER, 1935: 354-355.)

In respect to the inflorescence, WIDDER (1935) made the following observations: «The male inflorescences look similar in *Xanthium* and *Acantho-*

xanthium». They terminate the main axis, but, WIDDER (1935: 345) concludes:

«The male inflorescence in *Euxanthium* is a *manyflowered, bracteate, simple head.* The inflorescal spindle carries, after some involucral bracts, floral bracts in the axil of each of which a male flower is positioned. The main axis of the plant is terminated by such a floral head, the *Euxanthia* are, thus, bi-axial in the male sex.»

«The male inflorescence of the *Acanthoxanthium* is a *manyheaded, often non-bracteate, composite head* which consists of singleflowered, sometimes bracteate, sometimes non-bracteate heads. These can be assumed to have arisen from a manyflowered, bracteate, simple head (similar to that of *Euxanthium*) into a pseudo-terminally positioned flower; a further developmental step leads over a general disappearance of the involucre to the 'single flower standing in the axil of a floral bract', which no longer can be distinguished from a *Euxanthium* head. Thus, in the male sex, *Acanthoxanthium* is tri-axial.»

«The outer similarity between the simple male heads in *Euxanthium* and the composite male heads in *Acanthoxanthium* is, thus, a convergence appearance.»

The arrangement and structures of the female heads in the two groups are also quite different. WIDDER (1935: 348) made the following statements:

«In respect to the female flowers, *Euxanthium* is a tri-axial plant, whereas *Acanthoxanthium* is a quadri-axial one. The two groups are, thus, definitely different as regards the sequence of branching leading to the female flowers.»

In spite of the fact that the female head consists of two florets only, WIDDER (1935) states that it does not differ from other few-flowered composite heads. The rim of the receptacle with only two florets (sitting in the axil of floral bracts) is circularly protracted whereby each of the two floral bracts are prolonged lengthwise so that they are finally «fused» to the pitcher-shaped receptacle with the exception of their very tips, which remain free. In this manner, a body is formed, the outer wall of which is shaped by the head-axis (receptacle), the inner wall by the two floral bracts. The spines on the outside of the head are fused involucral bracts, arranged in distinct spirals (2/5) but with their tips free and turned into hooked spines. The beaks are formed by the free tips of the floral bracts, fused on the inside, but forming the free beaks at the top.

In *Xanthium,* there is a gradual transformation from the true, leafy involucral bracts on the peduncles to «involucral spines» on the heads, whereas in *Acanthoxanthium* all the bracts from the leafaxil up are turned into thorns in the axils or spines on the fruting head. The floral bracts are absent and the involucre carries 0-2 prominent, thorn-like spines at the top. These beaks, if two, are usually unequal in length, always straight and never hooked as in *Xanthium.*

It should be added here that the appearance of the spines on the female heads and the shape of the burs is quite different in the two groups.

In *Xanthium,* the burs vary enormously in size between different taxa and are usually ovoid in shape, very rarely cylindrical. The beaks are coarse, cone-shaped and have a distinct furrow on the inner side. They are hardly ever straight, and never thornlike. The spines thicken gradually from the hooked apex towards the much wider base.

In *Acanthoxanthium,* the burs are usually cylindrical in shape, rarely ovoid. The beaks are straight and very similar to the thorns in the axils. The spines on the burs are extremely fine and almost equally thick from the «swan's neck» hook at the apex to the suddenly widening base on the fruiting body.

In spite of all the above-mentioned differences, WIDDER (1923, 1935, 1964) did not think there was a reason for separation into the two distinct genera *Xanthium* L. and *Acanthoxanthium* (DC.) Fourr.

The only later scientist to support FOURREAU (1869) was the American palynologist WODEHOUSE (1928). He discovered tha the pollen grains of the two taxa differ in morphology. Those of *Xanthium* have relatively smooth grains with rudimentary projections on the exine, while those of *Acanthoxantium* have more distinct projections. He even claimed (WODEHOUSE, 1928: 187) that: «In fact, the morphology of these plants themselves, as well as the pollen grains, show considerably more difference between these two sections of *Xanthium* than exists between the genera *Franseria, Ambrosia,* and *Acanthambrosia.*» But, although he advocated the splitting of the genus *Xanthium* in two, he later reflected that because it would leave *Acanthoxanthium* with a single species (*spinosum*) in North America, it might be more convenient to keep *Xanthium* as the only genus (cf. WODEHOUSE, 1935), even if in so doing «the classification no longer reflects the true relationship, which should be the ultimate aim of all classification» (WODEHOUSE 1928: 189).

We ourselves have now looked at the pollen of the two groups in the

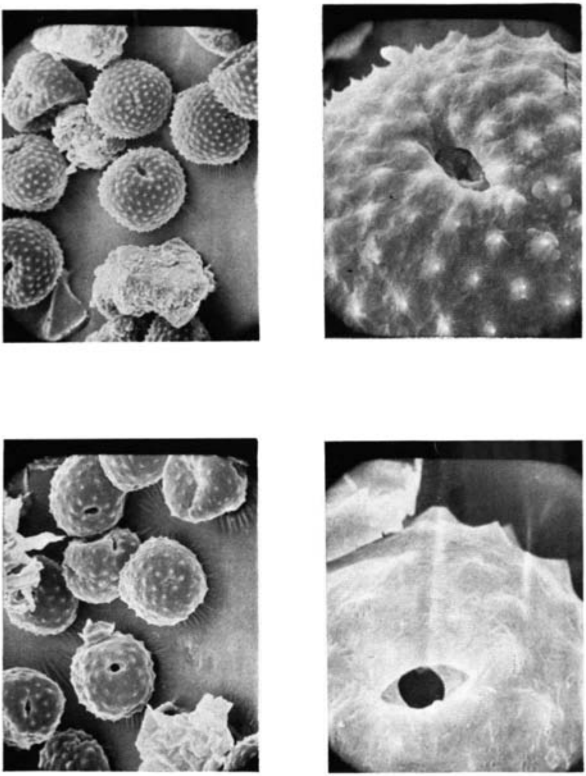

Fig. 1.—Scanning Electron Microscope photos of *Xanthium* pollen. Above, left: pollen of *Xanthium strumarium* L. (x 1140), right: its pore (x 5750). Below, left: pollen of *Acanthoxanthium spinosum* (L.) Fourr. (x 1140), right: its pore (x 5750). Photo W. H. Reid.

scanning electron microscope (with kind assistance from Dr. W. H. REID, University of Texas at El Paso, Texas, U.S.A.). The pollen is indeed different, but those of *Xanthium* are not as smooth as WODEHOUSE and I myself had seen them in an ordinary light microscope. The *Xanthium* pollen have a dense cover of minute tubercles, which seem to disappear in the light microscope, whereas *Acanthoxanthium* pollen have fewer and more pronounced protuberances, which are visible also at lower magnification. The shape of the pores also seem to differ slightly in the two types as well (Fig. 1).

I agree fully with WODEHOUSE (1928) that *the ultimate aim of classification is to reflect true relationship between taxa.* A break in relationship is indicated by the existence of a sterility barrier, and knowing that the pollen of the two groups discussed here are different in morphology helps in part to explain this barrier. It may not only be genetic in nature, but in addition mechanical. It could be that pollen from one group is unable to germinate on the stigmas of the other.

Henceforth, when using the generic name *Xanthium,* it will therefore mean only this genus in the restricted sense, excluding any species or taxon belonging to *Acanthoxanthium.*

THE SPECIES OF ACANTHOXANTHIUM (DC.) FOURR.

When FOURREAU in 1869 raised *Acanthoxanthium* to generic status, the only species he transferred was *Xanthium spinosum* L., which thus must be named *Acanthoxanthium spinosum* (L.) Fourr. Even if he did not quote his basionym in his tersely worded catalogue but only listed the species as «*Acanthoxanthium spinosum* (L.)» on p. 110, there can be no doubt that he used the Linnaean species as a basis. Dr. A. CRONQUIST, New York Botanical Garden, New York, agrees with me in this interpretation. FOURREAU'S (l. c.) publication of *Acanthoxanthium* clearly meets the requirements of Article 32 of the International Code of Nomenclature (1972), the transfer of *spinosum* just barely does so. But no well-informed botanist will doubt that FOURREAU meant anything else than LINNAEUS' *Species Plantarum* 1753, and thus, nobody should object to the legality of FOURREAU'S transfer.

Acanthoxanthium spinosum (L.) Fourr. is the only species of that genus which is met with almost all over the world in temperate and tropical areas, where it has become a serious weed problem in many places, especially sheep- and cattle-raising districts. In Argentine folk medicine, a concoction on its roots is used es a diaphoretic, diuretic and coleretic according to AMORIN & ORFILA (1972). From its present distribution it is hardly possible to deduct with any certainty its true center of origin. Both South America and the steppes north of the Black Sea have been suggested (cf. WIDDER, 1923).

According to WIDDER (1923), fruits of *spinosum* have been found in Pliocene layers in the South American pampas by AMEGHINO and SPEGAZZINI, and these fruits are said to be preserved in a museum in La Plata (cf. also AMORIN & ORFILA, 1972). Most other species and forms related to *spinosum* in Portugal and Spain are of comparatively late date, definitely post-Columbian. LINNAEUS (1753) also gave Portugal («Lusitania») as the only then known area of his *X. spinosum*, but added a note that according to LOEFLING, it was a native of and migrating from «America». QUER (1784) stated that PLUKENET in 1696 in his «Almagestum» referred to «*Xanthium lusitanicum spinosum*» as spreading into Castillean Spain from Portugal along the river Tajo. DE CANDOLLE (1856), on the other hand, gave southern France, Italy, «maritime Austria» (now the Trieste-Istria-area of the Adriatic), Hungary and «Podolia» (now southwestern Ukraine) as its native area, whence it should be introduced to South America. This is probably the basis for IHNE's (1880) and KÖPPEN's (1881) opinions that *spinosum* originated north of the Black Sea in southern Russia.

However, all European pre-Columbian reports on and of *Xanthium* seem to refer exclusively to *X. strumarium* L. and moreover to ist subsp. *strumamium*. FONT QUER (1962) states that *Xanthium* as known to DIOSCORIDES (cf. WALLROTH, 1844) was *X. strumarium*, not *A. spinosum*. Pollen and fruits of *X. strumarium* have been found in Central and North Europe all the way back to Late Glacial time (ZOLLER, 1960; LANGE, 1968; OPRAVIL, 1968; JÁRAI-KOMLODI, 1968; FLORIN, 1969). A report of a fossil *spinosum* fruit from Bulgaria has proved to be of modern origin (TURRILL, 1923; cf. STOJANOFF in WIDDER, 1937).

There can, thus, be no doubt that *spinosum* has arrived in Europe only after 1600 and rapidly dispersed eastwards from Portugal, where it was first noted. Soon it became established all around the Mediterranean and Black Seas where the growing conditions are similar to those in its native South America. From these places, it has also spread into other tropical and temperate areas of the world, but is only occasional and rarely persistent in colder areas. Even if not yet known for sure, a daylength factor may be involved. BITTER (1908) observed two forms in cultivation in Germany, a spring-flowering form (*spinosum* fma. *precocius* Widder) and a fall-flowering one (*spinosum* fma. *spinosum* Widder). In northern Europe, *spinosum* rarely reaches flowering stage; but it may also need more heat to develop flowers. Contrary to this, LONA (1946) and MCMILLAN (1975a) have found indications for day-neutrality in *A. spinosum.* If it is, even only at times, day-neutral, this may be why it has spread so easily as a weed, and then only temperature could be its limiting factor.

Some extremes or aberrants in respect to size and shape of leaves and size, shape and number of spines have been given Latin names, but are of no real taxonomic value. Obviously belonging to *A. spinosum* (L.) Fourr. are: *X. parvifolium* DC. from South America, apparently described on immature specimen, *X. brachyacanthum* DC., a short-spined specimen from Brasil, *X. xanthocarpum* Wallr., immature specimens with «golden-spined» female heads (a common appearance in immature specimens of *spinosum*) from eastern North America, *X. spinosum* var. *synacanthum* Widder with malformed axillary spines, *X. spinosum* var. *inerme* Bel. the axillary spines of which are replaced by short-branches with leaves, *X. spinosum* var. *pseudinerme* Widder in Parodi with only some spines replaced by leaves, and *X. spinosum* var. *laciniatum* (Scheuerm. & Thellung) Widder, with laciniate, deeply lobed leaves instead of the normal three-lobed to entire ones. *X. medium* Noss. has only one spine instead of three in the leaf-axils, and has been excluded as an abnormality in the Russian flora (Flora U.S.S.R., vol. 25). None warrant transfers or even taxonomic distinction.

The next taxon in the *Acanthoxanthium* group to be described was the South American *X. catharticum* H., B. & K. from Ecuador (at Quito; HUMBOLDT & alii, 1820). It has since been found all along the Pacific side of the Andes and penetrating somewhat into west-central Andean Argentina. So far, it does not seem to have spread outside of South America, and according to WIDDER (1923) reports of this species from Europe belong under other species.

It is very similar to *A. spinosum* in general, but the leaves of *catharticum* are more broadly lanceolate-ovate in outline and the front lobe is usually deeply toothed giving the blade an almost pinnatifid appearance at times. In respect to the hairiness of the leaf surfaces, the strigose hairs on the green upper surface are more evenly distributed and not only concentrated along the midrib (especially at the tip of the leaf) as in *A. spinosum* itself. The underside is gray from a mat of strigose hairs. The *spinosum* fruit is only lightly hairy at the apex, but that of *catharticum* is densely woolly-hairy, particularly toward the top, and the rather short beak(s) are often more or less hidden among the hairs (Fig. 2). In the specimens we have seen from Ecuador and Chile, the size of the fruits was within the same range as that of *A. spinosum,* but some Argentine floras (CABRERA in CORREA, 1971; BURKART, 1974) indicate slightly larger measures (*spinosum* 8-10 x 3-5 mm, *catharticum* 9-13 x 3-4 mm), but this is not borne out in the illustrations in the Flora of Patagonia (CABRERA, l. c.). As WIDDER (1923) does not give any measures for the fruits of *spinosum*, it is hard to judge his opinion, but the illustrations of the fruits (WIDDER, l. c., plate IV) in his monograph show very similar size ranges.

Because there is a good deal of variation in amount of hairiness on the fruits, and in the shape and hairiness of the leaves also in *A. spinosum* itself, sometimes making it look very close to *catharticum*, it seems to me better to regard *catharticum* as a geographically limited extreme of the Linnaean taxon, and I suggest it be lowered to subspecific rank as

A. spinosum (L.) Fourr. subsp. **catharticum** (H., B. & K.) D. Löve, nov. stat., based on *Xanthium catharticum* H., B. & K., *Nova Gen. Spec.*: 274, 1820.

Hybridization between the subspecies is indicated at least in one specimen from Quillota (prov. Valparaíso, Chile; coll. Bridges, Herb. Hofmuseums, Vienna; cf. WIDDER, 1923).

The specific epithet *catharticum,* referring to the medical properties of this plant (sudorific and cathartic), must be considered valid, even if WALLROTH (1844) preferred to call it *X. armatum* because HUMBOLDT had used this name on herbarium sheets and in correspondence sent to WILLDENOW before he described the plant under the name *X. catharticum* (HUMBOLDT & alii, 1820).

The third taxon in the *Acanthoxanthium* group to be described was also from South America: *X. ambrosioides* Hook. & Arn. in HOOKER, 1841. It is indigenous, probably endemic, to the central Argentine plains of Patagonia and only found as a rare, ephemeral weed outside of the pampas in a few European localities to where it was apparently brought with hides and wool (WIDDER, 1923). It does not seem to persist.

This taxon differs in several respects from the two previous ones, first and foremost in size and growth habit. Whereas *spinosum* and *catharticum* both grow erect or ascending with stiff stems and branches and reach a height of up to and over 50-100 cm., *ambrosioides* has thin and weak stems, decumbent at least in their lower portion and rarely exceeding 20-30 cm.

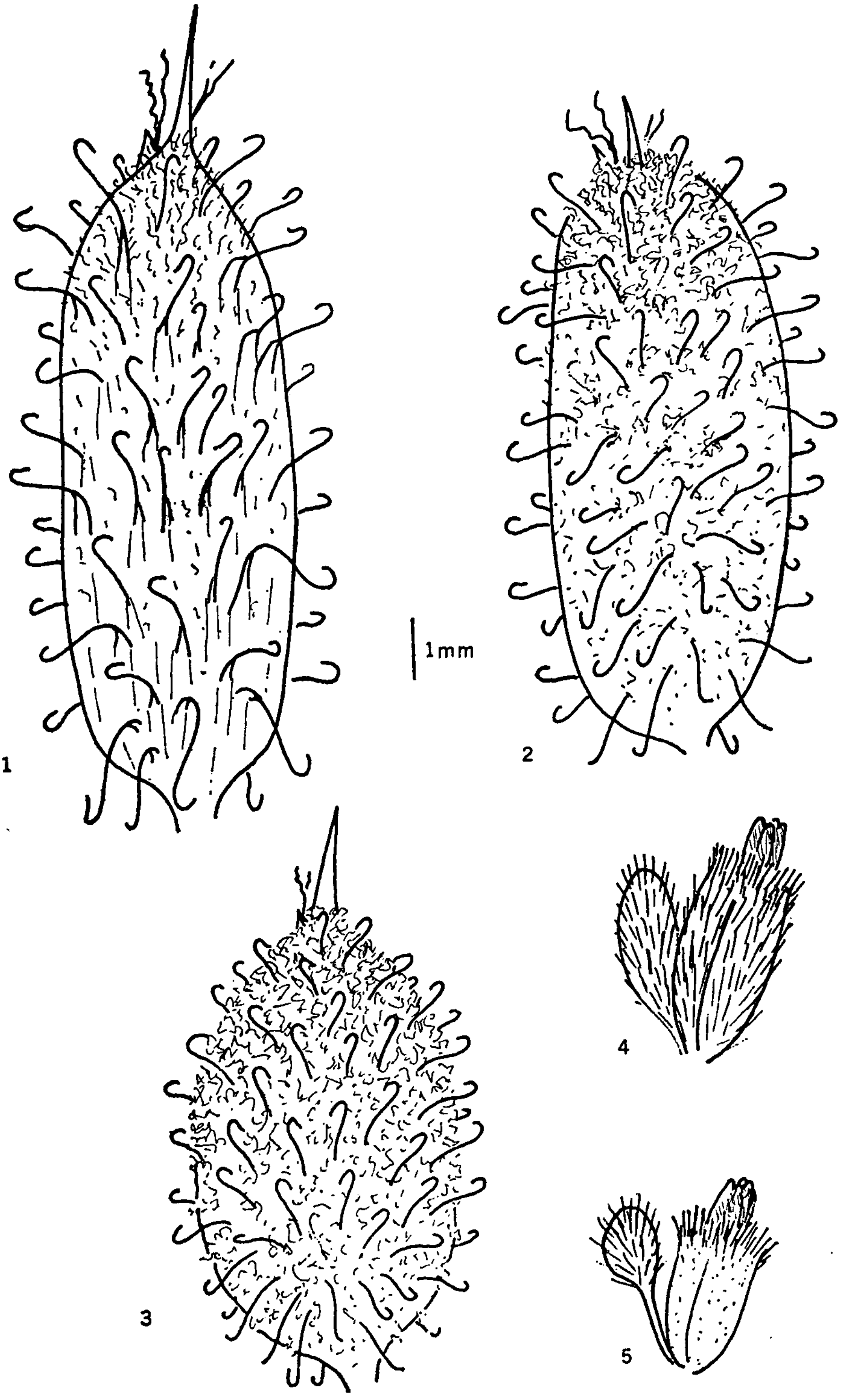

Fig. 2.—Burs and male flowers of *Acanthoxanthium*. 1, bur of *A. spinosum* subsp. *spinosum*; 2, bur of *A. spinosum* subsp. *catharticum*; 3, bur of *A. ambrosioides*; 4, male flower of *A. spinosum*; 5, male flower of *A. ambrosioides*.

in height. Its fruits are much smaller and broader (7-8 mm. x 4-5 mm.) than those of the other two (8-13 mm. x 3-4 mm.). They are entirely covered with a web of filted hairs in which the two beaks, if short, almost disappear. Sometimes, one of the beaks is prominently developed, being almost as long as the fruiting body. The spines on the fruit are short, but not different from those of the other taxa (Fig. 2).

In the male flower, the supporting floral bract is petioled and has a small, roundish lamina, but in *spinosum* and *catharticum* these bracts are sessile and lanceoid or obovoid in shape (Fig. 2).

The leaves of *ambrosioides* are smaller than those of the preceding taxa, measuring 20-30 mm. x 10-18 mm., in contrast to 30-40 x 7-10 mm. for *spinosum* and 70-120 x 20-30 mm. for *catharticum*. The *ambrosioides* lamina is ovoid in outline and deeply pinnatifid with broadly lobate segments, densely sericeous below and lightly so above. In *spinosum,* the leaves are much longer than broad, usually entire to faintly three-lobed, in *catharticum,* sometimes almost pinnatifid, but with lanceolate slender lobes (Fig. 3).

The epithet *ambrosioides* was apparently chosen because the leaves resemble those of for instance *Ambrosia trifida,* even if WALLROTH objected to this as a «non-sensical name» and preferred to call it *X. eriocarpon* (red-fruited) in the descriptive part of his monograph (p. 242), but *leucocarpon* (white-fruited) in the list of species on p. 229! (WALLROTH, 1844).

In view of the above described differences between *ambrosioides* and *spinosum* (incl. *catharticum*) we feel it is prudent to keep it as a separate species of the genus *Acanthoxanthium* until more is known about its crossability or interfertility with the latter. Its proper name will therefore be:

Acanthoxanthium ambrosioides (Hook. & Arn.) D. Löve, nova comb., based on *Xanthium ambrosioides* Hook. & Arn. in J. Hooker, *Journ. of Botany,* 3: 310, 1841.

Two more taxa within the *Acanthoxanthium* have been given species names by WIDDER (1923).

Xanthium argenteum Widder was based on two herbarium sheets (one in Vienna University Herbarium, the other in Berlin-Dahlem), both seemingly from the same plant and collected at the same time in Nuble, Chile. One sheet (Berlin-Dahlem) was annotated «*X. catharticum* Phillips 1888». The specimens are incomplete, lacking roots, mature flowers and fruits. The main characteristic separating them from *catharticum* is the hairiness, which on the *argenteum*-specimens is denser, longer, and more silvery on both

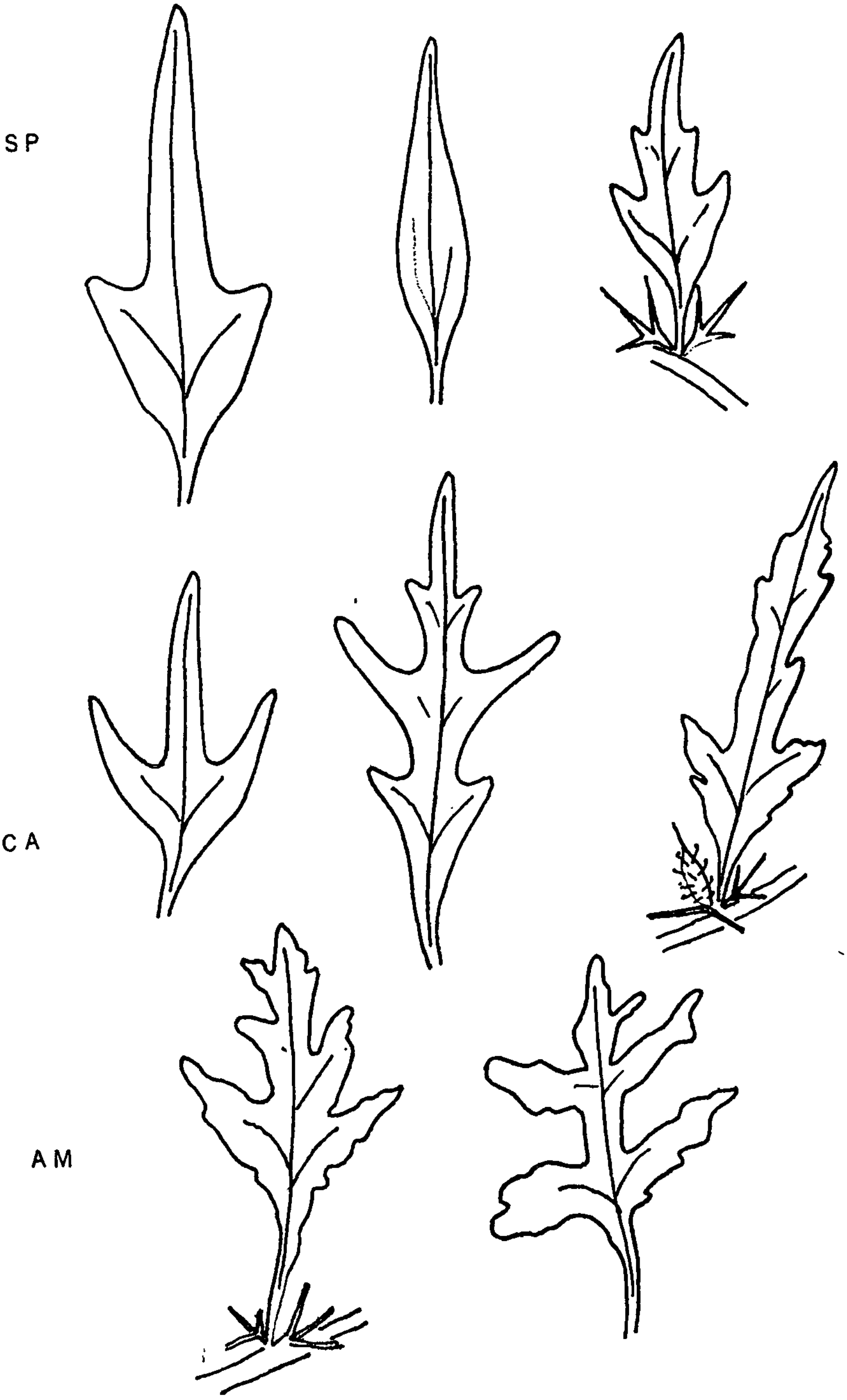

Fig. 3.—Leaf-types of *Acanthoxanthium*. SP: *A. spinosum* subsp. *spinosum*; CA: *A. spinosum* subsp. *catharticum*; AM: *A. ambrosioides*.

surfaces of the leaves, rather than short and strigose. WIDDER stated that in other respects these specimens do not differ from Bolivian plants of *catharticum* which he had seen.

As far as we have been able to establish, no other specimens similar to WIDDER's *argenteum* have again been collected in Chile or elsewhere, and its present existence seems very much in doubt. Until further verification, it seems preferable to exclude this taxon as a species and simply regard it as an ephemeral extreme-type of *catharticum* in respect to hairiness. It was most likely a mutant or some sort of double-recessive for a single gene, which did not survive, but happened to be collected and described during its short existence.

The second of WIDDER's (1923) species, *X. canescens* (Costa) Widder, poses a similar problem. Two specimens are known: one from near Barcelona (in Herbarium Petersburg, now Leningrad), the other from Bédarieux (Hér.), France, sent to WIDDER, unnamed, by SENNEN. The Leningrad specimen is named *X. spinosum* var. *canescens* by COSTA and was described as such by COSTA in 1864. It is also distinguished from *spinosum* by the hairiness, which covers both sides of the leaves making them appear uniformly grey. In spite of the fact that the plants were found only in France and Spain, WIDDER (1923) was convinced that they were of S. American origin, because some *ambrosioides* had also been found at Bédarieux.

However, no specimens similar to these have since been found, neither in France, Spain or South America. Dr. FOLCH (Barcelona, in litt.), considers the Barcelona specimen «un simple *X. spinosum* malformado» and not worthy of taxonomic recognition. Like in the case of *argenteum* from Chile, it may have been an occasional extreme in hairiness in a population of *spinosum* which was accidentally picked up and named by a botanist. Until it is again confirmed by new finds, this taxon is apparently better excluded.

ACANTHOXANTHIUM (DC.) Fourr.

Differs from *Xanthium* L. by the presence of 1-3 furcate thorn-like spines in the leaf axils; smaller, more cylindrical fruits with 0-2 straight, thorn-like «beaks» and very fine spines, hooked like «swan's necks» at the apex; longish leaves, green above, grey from hairiness below, three-nerved, entire, three-lobate or pinnatifid.

Key to the taxa of Acanthoxanthium (DC.) Fourr.

A. Erect or ascending annuals with stout, stiff stems and branches reaching 50-100 cm. in height or more; leaves 3-4 times as long as broad; male flowers with supporting lanceoid or obovoid floral bracts; burs, excluding the beak, 8-13 x 3-4 mm.

A. spinosum (L.) Fourr.

a. Leaves 3-4 times as long as broad, entire or three-lobate at the base, the midlobe sometimes ± toothed or indented, rarely laciniate. Strigose hairs concentrated along the midrib, esp. near the tip, along the upper surface of the lamina. Native to South America, worldwide weed in tropical and temperate areas.

A. spinosum subsp. **spinosum**

aa. Leaves about 3 times as long as broad, three-lobate, the midlobe always deeply indented, sometimes giving the leaf a pinnatifid appearance. Strigose hairs on the upper side of the lamina dispersed over the entire surface. Along the Pacific side of South America, penetrating into W. Patagonia, Argentine.

A. spinosum subsp. **catharticum** (H., B. & K.) D. Löve

AA. Decumbent annuals with thin, weak stems and branches, not more than 20-30 cm. tall; leaves about twice as long as broad, pinnatifid; male flowers with a stipitate floral bract with a roundish lamina; fruits small, 7-8 x 3-5 mm. Endemic to Patagonia, Argentine.

A. ambrosioides (Hook. & Arn.) D. Löve

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BIBLIOGRAPHY

Amorin, J. L. & E. Orfila (1972) Cepa Caballo, *Xanthium spinosum* Linné (Compositae), maleza utilizada en la medicina popular Argentina. *Farmacobotânica, Pub. Técn.* No. **11:** 155-169.

Bitter, G. (1908) Ueber Verschiedenheiten in der Entwicklungsdauer bei *Xanthium*-Rassen. *Abh. Naturwiss. Ver. Bremen* **19:** 290-297.

BRAUN, A. (1853) Das Individuum der Pflanze in seinem Verhältniss zur Species. *Abh. Königl. Akad. Wiss. Berlin* **97**: 1-106.

BURKART, A. (1974) Flora ilustrada de Entre Ríos (Argentina). Parte VI. Dicotiledones Metaclamideas. *Col. cient. INTA* **6**: 328-332.

CORREA, M. N. (1971) Flora Patagonica. Parte VII. Compositae. *Col. cient. INTA* **3**: 131-134.

COSTA, A. P. (1864) *Introducción a la flora de Cataluña.* Barcelona.

DE CANDOLLE, A. P. (1836) *Xanthium* L. *Prodromus Syst. Nat. Reg. Veg.* **5**: 522-524.

FLORIN, M.-B. (1969) Late glacial and pre-boreal vegetation in central Sweden. I. Records of pollen species. *Svensk Bot. Tidskr.* **62**: 143-187.

FONT QUER, P. (1962) *Plantas medicinales, el Dioscorides renovado.* Barcelona.

FOURREAU, P. J. (1869) Catalogue des plantes qui croissent spontanement le long du cours de Rhône. *Ann. Soc. Linn. Lyon,* Ser. 2, **17**: 89-200.

HOOKER, J. D. (1841) *Journal of botany, being a second series of the botanical miscellany* **3.** London, 446 pp.

HUMBOLDT, F. A. von, A. BONPLAND & C. S. KUNTH (1820) *Voyage aux régions équinoctiales du Nouveau Continent, fait en 1799-1804, partie 6, Botanique. Sect. 3, Nova genera et species plantarum* **4.** Paris.

IHNE, N. (1880) Studien zur Pflanzengeographie: Verbreitung von *Xanthium strumarium* und Geschichte der Einwanderung von *Xanthium spinosum. Ber. Oberhess. Ges. Natur. Heilk.* **19.**

JÁRAI-KOMLODI, M. (1968) The Late Glacial and Holocene flora of the Hungarian great plain. *Ann. Univ. Scient. Budapest Rolando Eötvös Nom., Sect. Biol.* **9-10**: 199-225.

KITTEL, M. B. (1844) Taschenbuch der Flora Deutschlands **2.** Nuernberg.

KOEPPEN, F. T. (1881) Zur Verbreitung des *Xanthium spinosum* L., besonders in Russland. *Beitr. Kenntn. Russ. Reiches, 2. Ser.,* **4.**

LANGE, E. (1968) Zur Vorkommen von *Xanthium strumarium* L. in Mitteleuropa. *Feddes Repert.* **77**: 57-60.

LEGENDRE, P. (1972) The definition of systematic categories in biology. *Taxon* **21**: 381-406.

LINNAEUS, C. (1753) *Species plantarum.* Holmiae.

LONA, F. (1946) Sul contemporamento fotoperiodico di alcune specie di *Xanthium. Nuovo Giorn. Bot. Ital. nov. ser.* **43**: 635-656.

LÖVE, Á. (1963) Cytotaxonomy and generic delimitation. *Regnum Veg.* **27**: 45-51.

LÖVE, D. & P. DANSEREAU (1964) Biosystematic studies on *Xanthium*: taxonomic appraisal and ecological status. *Canad. J. Bot.* **37**: 173-208.

MAYR, E. (1942) *Systematics and the origin of species.* New York.

——— (1969) *Principles of systematic zoology.* New York.

MCMILLAN, C. (1973) Partial fertility of artificial hybrids between Asiatic and American cockleburs (*Xanthium strumarium* L.). *Nature* **249**: 183-186.

——— (1974) Experimental hybridization in *Xanthium strumarium* of American complexes with diverse photoperiodic adaptation. *Canad. J. Bot.* **52**: 849-859.

——— (1975a) The *Xanthium strumarium* complexes of Australia. *Austral. J. Bot.* **23**: 173-192.

——— (1975b) Experimental hybridization of *Xanthium strumarium* (Compositae) from Asia and America. I. Responses of F_1 hybrids to photoperiod and temperature. *Amer. J. Bot.* **62**: 41-47.

MILLSPAUGH, C. F. & E. E. SHERFF (1919) Revision of the North American species of *Xanthium. Field. Mus. Nat. Hist. Publ.* 204, *Bot Ser.* **4, 2:** 1-52.

OPRAVIL, E. (1963) *Xanthium strumarium* L. aus mittelalterlichen Fundstellen in Ostrava. *Preslia* **35:** 327-329.

PAU, C. (1905) Plantes observées dans l'Ampourdan. *Bol. Soc. Aragonesa Cienc. Nat.* **4:** 303-333.

QUER, D. J. (1784) *Flora Española* **4.** Madrid.

SENNEN, Fr. (1912) Quelques formes nouvelles ou peu connues de la flore de Catalogne, Aragon, Valence. *Bol. Soc. Aragonesa Cienc. Nat.* **11:** 177-215.

———— (1916) Liste des plantes observées aux alentours d'Igualada. *Bol. Soc. Aragonesa Cienc. Nat.* **15:** 94-105.

TOURNEFORT, J. P. (1700) *Institutiones Rei Herbariae.* Paris.

TURRILL, W. B. (1923) *Xanthium spinosum* in Neolithic deposits in Bulgaria. *Kew Bull.* **1923:** 190-191.

WALLROTH, C. F. W. (1844) Monographischer Versuch ueber die Gewächs-Gattung *Xanthium* Diosc. *Wallroths Beiträge zur Botanik* **1:** 219-244.

WIDDER, F. J. (1923) Die Arten der Gattung *Xanthium.* Beiträge zur einer Monographie. *Feddes Repert.* **20:** 1-222.

———— (1925) Uebersicht über die bisher in Europa beobachteten *Xanthium*-Arten und Bastarde. *Feddes Repert.* **21:** 273-305.

———— (1932) Kreuzungsversuche mit *Xanthium*-Sippen. *Mitt. Naturwiss. Vereins Steiermark* **68:** 1-8.

———— (1935) Vergleichende Morphologie einiger *Xanthium*-Sippen. *Beih. Bot. Centralbl.* **54, A:** 321-368.

———— (1937) Ueber Afrikanischen *Xanthium*-Arten. *Feddes Repert.* **41:** 272-284.

———— (1964) Die Veränderlichkeit von *Xanthium spinosum. Phyton* **11:** 69-82.

WODEHOUSE, R. P. (1928) Pollen grains in the identification and classification of plants. I. The Ambrosiaceae. *Bull. Torrey Bot. Club* **55:** 181-198.

———— (1935) *Pollen grains.* New York.

ZOLLER, H. (1960) Pollenanalytische Untersuchungen zur Vegetationsgeschichte der insubrischen Schweiz. *Denkschr. Schweiz. Naturf. Ges.* **83:** 40-156.