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ON THE SUBMERSION OF DICRAURUS INTO IRESINE (AMARANTHACEAE)

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ABSTRACT

The two species of Dicraurus Hook. f. (Amaranthaceae) are shown to be more closely related to different species in Iresine L. than they are to one another. In addition, characters used to distinguish Dicraurus are more widespread within Iresine than was formerly thought, necessitating the merger of Dicraurus into Iresine. The two species as placed in Iresine are I. alternifolia S. Wats. and I. leptocladus (Hook. f.) Henrickson & Sundberg. Complete descriptions and distribution maps of the two species are included.

Key words: Amaranthaceae, Dicraurus, Iresine, plant systematics.

INTRODUCTION

The genus Dicraurus Hook. f., consisting of a single species, D. leptocladus Hook. f. (Fig. 1a), was separated from Iresine on the basis of four characteristics: sessile stigmas, subglobose seeds, broadly concave cotyledons, and alternate leaves (Bentham and Hooker 1880). The genus has been universally accepted from its inception [although Airy Shaw (1960) proposed Dicrairus as the correct spelling] and received a second species. D. alternifolius (Wats.) Uline & Bray, in 1896 (Fig. 1g). Standley (1915), however, did express doubts as to the validity of its recognition as a distinct genus. Studies in connection with the Chihuahuan Desert Flora revealed that other taxa of Iresine occasionally have alternate leaves, similar styles and seeds, and would appear to fit into Dicraurus. This stimulated an intensive study of the character states found within Dicraurus and Iresine to evaluate the relationships of the two genera. These studies indicate that the two species of Dicraurus appear to be more closely related to different species groups within Iresine than to one another and that their unique characteristics could easily be accommodated within Iresine.

No modern, comprehensive systematic treatment exists for Iresine. Standley (1917) recognized 32 species in North America but several more occur in South America. Within the tribe Gomphreneae, Iresine is characterized by having flowers arranged in small spikelets usually borne in broad, much-branched panicles. Calyces are terete, i.e., not laterally compressed, of separate sepals. The paired stigmas are subulate, borne on a short style. The androecium consists of a short basal tube bearing five, membranous, tapering filaments, typically alternating with
Fig. 1. *Iresine leptoclada* and *Iresine alternifolia*.—a–f. *I. leptoclada*.—a. Flowering branch showing branching, alternate leaves, inflorescences (Correll 30513).—b–c. Staminate flower (Muller 8432).—b. Outer view showing bractlets and woolly sepals.—c. View with sepals removed showing pistillodium and androecium with basal tube, five elongate filaments alternating with five hairy pseudostaminodia.—d–f. Pistillate flowers (from various collections).—d. Ovary showing style, stigmas, ovule, basal staminodial structure.—e. Adaxial view of sepal with abaxial wool attached.—f. Androecial structure showing true staminodia (alternate with sepals) that terminate with glandlike spheroidial structure alternating with hairy, nonglandular pseudostaminodia.—g–m. *I. alternifolia*.—g. Flowering branch showing larger alternate to subopposite leaves, branching of inflorescence (Carter 3211).—h–k. Staminate flower (from various collections).—h. Outer view of flower showing bract, bractlets, closed sepals, (note reduced amount of wool).—i. Inner view showing pistillodium, androecium with introrse anthers, staminodia.—j. Monothecal bilocular anther sac, adaxial (left) and abaxial (right) view.—k. Pseudostaminodia alternating with free filaments at rim of filament tube.—l–m. Pistillate flower (Carter 3211).—l. Cutaway view showing ovary, edge views of sepals and basal staminodia.—m. Androecial structure showing alternating staminodia (with spheroidial tips) and pseudostaminodia. (Scale in a also holds for g; scale in b holds for all flowers, c, d–e, h–j, l; scale in f holds for all staminodial structures, k, m.)

five smaller, membranous, glabrous to pubescent pseudostaminodia (Fig. 1k, 2c). Anthers are oblong, monothecal, and biloculed (Fig. 1j). Species range from perennial, erect to scandent, herbs to shrubs or small trees (reported to 12 m tall) with opposite leaves and perfect or unisexual flowers with plants sometimes being
polygamous or dioecious. They may be glabrous or be variously pubescent to woolly with a variety of uniseriate, multicellular, simple or variously branched, straight or variously bent, smooth or aculeate (i.e., prickled) hairs on stems, inflorescences and leaves. As in other members of the Gomphreneae, pistillate flowers develop a dense wool of multicellular hairs at the base of the calyx that aid in fruit dispersal. Fruit vary from subglobose with a thin, membranous pericarp and broadly oblong cotyledons to more lenticular, with a thicker, more brittle pericarp wall and narrower cotyledons.

RESULTS AND DISCUSSION

The two species of *Dicraurus* are dioecious, occasionally polygammo-dioecious shrubs and, except for the consistent (*D. leptocladus*) or occasional (*D. alternifolius*) alternate leaves, are similar in almost all respects to the dioecious, shrubby, more strongly vestitured species of *Iresine* (species 16 to 24 in Standley, 1917).

In addition to the features noted above, *Dicraurus* and the dioecious, shrubby, more strongly vestitured *Iresines* are also similar in certain minor features of the calyx and androecium. In most of these species, pistillate calyces are consistently shorter than staminate calyces. Pistillate calyces also tend to have sepals of uniform size. In contrast, the outer two sepals of staminate calyces are usually broader and three-veined while the inner sepals are narrower and one-veined. In staminate flowers the subulate filaments alternate with erect to incurved, mostly papillate to pubescent pseudostaminodia from one eighth to one third the filament length. Pistillate flowers all have a shallow disklike or cuplike androecial remnant subtending, but free from, the ovary that has 10 small teeth, five opposite the sepals (the staminodia) terminating in small glandlike, rounded tips, and five alternate the sepals (the pseudostaminodia) without rounded tips. In all these species, seeds are subglobose, with thin, light brown pericarp walls and their embryos have broadly oblong cotyledons about 0.7 mm wide.

In contrast, the herbaceous, dioecious *Iresines* (which are in a state of taxonomic chaos) have pistillate and staminate calyces of equal size. Pistillate flowers have only a five-toothed androecial remnant (the five pseudostaminal teeth are not present), and seeds are more lenticular in shape, with brittle, hard pericarp walls and embryo cotyledons are much narrower.

It becomes apparent that when Hooker established *Dicraurus*, he was contrasting the seed and embryo characteristics of *Dicraurus* with those of the herbaceous, dioecious *Iresines* rather than the shrubby dioecious *Iresines* with which they are basically identical in seed and embryo structures. Hooker’s statement that *Dicraurus* has sessile stigmas appears in error as the herbaceous, dioecious *Iresines* have much shorter styles than those of *Dicraurus leptocladus*. The only character used by Hooker that remains to distinguish *Dicraurus* from *Iresine* is that of alternate vs. opposite leaves. This was the only character used by Uline and Bray (1896) to justify the transfer of the second species (*D. alternifolius*) into the genus and it is the only character used by Schinz (1893), Standley (1917), and all subsequent authors in floristic treatments to distinguish *Dicraurus* from *Iresine*.

While *Dicraurus leptocladus* (Fig. 1a) consistently has alternate leaves, leaves of *D. alternifolius* (Fig. 1g) tend to be alternate only in distal portions of the stems, with some specimens showing no alternate leaves or nodes, others a mixture of opposite, subopposite and alternate nodes. Alternate nodes also occur in other
species of *Iresine*. Some herbarium specimens of the perfect-flowered, shrubby *I. angustifolia* Euphr. exhibit all alternate nodes while in other specimens all nodes are opposite. A mixture of opposite and alternate nodes similar to that found in *D. alternifolius* also occurs in *I. rotundifolia* Standl. from Puebla and Oaxaca (Fig. 2k). Elsewhere in the Amaranthaceae, alternate leaves is an important character used to distinguish the tribes Celosieae and Amarantheae from other primarily opposite-leaved tribes (Bentham and Hooker 1880; Standley 1917). This character is apparently not so taxonomically important in *Iresine* and *Dicraurus*. In light of this the relationships of the two species of *Dicraurus* to species of *Iresine*, as well as to one another, need reevaluation.

Evidence bearing on this question comes from analysis of additional characters such as vestiture. *Dicraurus* and the dioecious, woody species of *Iresine* are quite variable in vestiture. Most *Iresine* species, as well as *D. alternifolius*, have uniseriate, multicellular, usually basally bent or geniculate trichomes with distinct aculeate processes on their surfaces (Fig. 3b–d). The distal portions of the trichomes may be either straight, and the vestiture sericeous (*D. alternifolius*—Fig. 3b) or the trichomes may be variously bent or contorted forming a more villous vestiture (*I. rotundifolia*—Fig. 3d). *Dicraurus leptocladus*, in contrast, has appressed, equally two-branched, dolabriform, aculeate trichomes (Fig. 3a), a type otherwise not known in *Iresine*. Other species of *Iresine*, however, have branched trichomes. *Iresine pringlei* S. Wats. and *I. stricta* Standl. have stellately branched trichomes with subequal, usually nonaculeate radii (Fig. 3e). Trichomes of *I. schaffneri* S. Wats. are two-branched and aculeate but the branches are very unequal in length and one branch is typically distinctly forked or further branched (Fig. 3c). While there is no exact match of the distinctive, equally two-branched trichomes of *D. leptocladus* (Fig. 3a) in *Iresine*, *Iresine* has such a wide diversity of simple and branched trichomes that the distinctive trichomes of *D. leptocladus* could easily be accommodated with the variation found in *Iresine*.

Within *Iresine*, *D. alternifolius* appears to be most similar to *I. rotundifolia* (Fig. 2k–r). Both are dioecious shrubs of arid habitats. In both, vestiture consists of basally bent, aculeate hairs, though the hairs are often more crinkled in *I. rotundifolia* (Fig. 3b, d). Both have relatively small, thick, occasionally alternate leaves with secondary veins slightly raised beneath. *Iresine rotundifolia*, however, tends to have less-branched inflorescences with flowers clustered in reduced glomerules (Fig. 2l) rather than in open panicles of pedunculate spikes. The reduced pseudostaminodia also tend to be lacking in male flowers of *Iresine rotundifolia* (Fig. 2n), though this is not consistent.

Relationships of *Dicraurus leptocladus* in *Iresine* appear less obvious. In its consistently alternate leaves it has no equal in *Iresine*. In its two-branched hairs and more lance-ovate leaves it is most similar to *I. schaffneri* (Fig. 2a–j) a species found in the southern Chihuahuan Desert. This species, however, has larger, opposite leaves, unequally branched trichomes, longer styles, staminate flowers

q. Pistil showing style, stigmas, basal staminodial complex.—r. Androecial complex showing staminodia (with spheroidal processes) alternating with glabrous pseudostaminodia. (Scale in a also holds for k; scale in b holds for all flowers in c, e-f, g-i, m-q; scale in j also holds for d, r.)
Fig. 3. Leaf trichomes (abaxial surface) of *Iresine* spp. — a. *I. leptoclada*. Appressed dola-briform hairs with equal length arms covered with aculeate processes. (Pringle 345). — b. *I. alternifolia*. Hairs are basally decurved and have distinct aculeate processes. (Carter 3914). — c. *I. schaffneri*. Hairs are branched with one arm long, the others short and often secondarily branched. All radii are aculeate. (Rzedowski 23178). — d. *I. rotundifolia*. Hairs are variously crinkled, aculeate. (Sundberg et al. 2484). — e. *I. pringlei*. Vestiture consists of stellate trichomes with several basal cells, nonaculeate radii. (Purpus 2756). (Scale holds for all trichomes.)

with narrow, lanceoloid sterile pistillodia, and more aggregated inflorescences borne on very long peduncles (Fig. 2a–j). It agrees, however, with *D. leptoclados* in most other features and, of all known species of *Iresine*, shows the greatest similarity with *D. leptoclados*. In the character of green mid stripes on pistillate sepals, *D. leptoclados* approaches *I. pringlei*, a species with stellately branched trichomes.

It becomes apparent that *Dicraurus*, as now recognized, is intimately related to *Iresine* and cannot even be distinguished on the basis of alternate vs. opposite leaves as alternate leaves also occur in other species of *Iresine*. Most of the other characters found in *Dicraurus* also occur in *Iresine*, and while *Dicraurus leptoclados* has some unique characteristics, a number of equally unique characters occur in other species of *Iresine*. We believe recognition of *Dicraurus* as a distinct genus, based on these few autapomorphic characteristics, is unsupportable and, as the two constituent species appear to be more closely related to different species of *Iresine* than to each other, the genus as it now stands is polyphyletic and thus unacceptable. We therefore adopt the following nomenclature, including one new combination.

**Iresine leptoclada** (Hook. f.) Henrickson & Sundberg, comb. nov.


Spreading to erect, weak-stemmed, divaricately branched shrubs 0.2–1.5 m tall, often growing within and receiving support from other shrubs; young stems gray to buff colored, closely appressed villous-tomentose with 2-branched, aculeate hairs 0.3–0.8 mm long, tardily glabrate, 1.1–1.5(–2.0) mm in diameter 3 dm below tip, longest internodes 15–22 mm long; older stems rust-brown to gray, axillary fascicles of leaves absent. Leaves alternate; petioles 1–3 mm long, winged, vestitured as leaves; leaf blades ovate to narrowly ovate, sometimes elliptical, ob-lanceolate, (5–)10–19(–24) mm long, (3–)4–10(–13) mm wide, acute, apiculate to obtuse-rounded at tip, broadly, sometimes obliquely cuneate to somewhat round-ed, with margins decurrent on petiole, at margins entire to somewhat sinuate, appressed sericeous on both surfaces with 2-branched, aculeate, hairs 0.3–0.8(–1.1) mm long, dull green throughout often lighter green beneath due to increased vestiture, sometimes turning reddish before abscissing. Inflorescences terminating long-shoot branches, of narrowly to broadly conical, alternately branched panicles (4–)7–15(–27) cm long, (1.5–)4–8(–15) cm wide, rachis often leafy at base of lateral branches, vestitured as stems, lateral branches divergent 65–80 degrees, (0.7–)1–4(–7) cm long; flowers crowded or scarcely overlapping on short lateral spicate shoots 0.5–1.7 cm long, borne on short peduncles 0.5–6 mm long. Bracts ovate, 0.8–1.2 mm long, strongly cupped, membranous except at base and along brief midvein, obtuse to acute at tip, glabrous to variously villous with nonaculeate hairs, persistent. Paired bracteoles orbicular to orbicular-ovate, (1–)1.3–2.4 mm long, rounded to acute at tip, similarly membranous except at base and along weak midvein, weakly villous distally in pistillate flowers, more uniformly villous with simple, nonaculeate hairs 0.2–0.5 mm long in staminate flowers, persistent. Staminate flowers caducous; sepals oblong, oblong-ovate, lanceolate, (1.5–)2.0–2.3(–2.5) mm long, 0.7–1.1 mm wide, outer 2 usually broader than inner 3, 1-veined, often green, rarely reddish along midvein with broad membranous margins, obtuse at tip, glabrous inside and at thickened base with curved, crinkled, often aculeate trichomes 0.4–1.2 mm long where exposed outside; stamens joined to basal cuplike disk 0.7–1 mm wide; filaments subulate, (1.2–)1.6–2.5(–2.8) mm long; anthers oblong, 0.6–0.8 long, 0.2 mm wide; staminodia linear, linear-lan-ceolate, (0.25–)0.3–0.6(–0.9) mm long, often inflexed when dry, consistently papillate-pubescent marginally. Pistillodium 1.0–1.6(–2.0) mm long, style bilobed, 0.15–0.2 mm long, body somewhat compressed, ovoid above a narrow base, 0.7–1 mm long, 0.4–0.7 mm wide; perfect flowers similar but pistil with stigmas to 0.6 mm long and sepals with longer hairs. Pistillate flowers persistent; sepals oblong-lanceolate to lanceolate, (1.2–)1.4–1.8 mm long, 0.3–0.5 mm wide, all equal in width, 1-veined, acute at tip, broadly membranous, entire at margins, glabrous inside, densely woolly outside with slender nonaculeate wavy hairs 1–5.2 mm long with longest hairs near sepal base; staminal disk saucer-shaped, 0.4(–0.7) mm in diameter; staminodia (0.13–)0.25–0.35(–0.55) mm long, tapering to a capitate tip, glabrous, pseudostaminodia tapering, 0.2–0.4 mm long, mostly shorter than staminodia, moderately papillate-pubescent marginally; pistil 1.9–2.3 mm
Iresine leptoclada can be distinguished from all other Iresines by its consistently alternate, lance-ovate to ovate, relatively small leaves, and its distinctive equally two-branched, aculeate, appressed trichomes. In habit it is also somewhat distinctive in having very slender, weak stems and it reaches its maximum heights only when growing among other shrubs. It is occasionally reported as trailing over other bushes. As in other dioecious Iresines, pistillate flowers are smaller than staminate flowers. Unlike most other species, however, the pistillate sepals are uniform in width and tend to be thicker and slightly green along the midvein. Occasional plants have perfect flowers (e.g., G. C. Nealley s.n.).

The species is almost confined to the Chihuahuan Desert from trans-Pecos Texas (Pecos, Presidio, Brewster cos.) to eastern Chihuahua, Coahuila, north-eastern Durango, northern Zacatecas to central San Luis Potosi with one collection from central Nuevo León (Fig. 4). It occurs on both limestone and igneous-rock substrates in foothills, alluvial fans, local rocky outcroppings, arroyo margins mostly among mixed desert scrub, to Agave and izotal zones but occasionally in oak-juniper woodlands or in finer valley silts with Larrea from (500-)1000 to 1800 m. Flowering occurs from (August-) September to November with fruit sometimes persisting until February.


Iresine pulchella M. E. Jones. Contr. W. bot. 18:34. 1934. TYPE: Mexico, Baja California del Sur, Cayuca Ranch, (Loreto), Sierra Giganta, 23 Oct. 1930. M. E. Jones s.n.. Lectotype (here designated) POM!, isotypes US (2 sheets)

Spreading to erect, divaricately branched, free-standing shrubs 0.5–2(–3) m tall; young stems buff colored, closely villous-tomentose with appressed, basally curved, aculeate hairs 0.2–0.4 mm long, mostly 3–4(–5) mm in diameter 3 dm below tip, longest internodes 2.3–5.7 cm long; older stems light brown to gray, short-shoot spurs sometimes developing. Leaves mostly opposite below, more subopposite to alternate above; petioles 2–10(–14) mm long, closely villose-tomentose as young stems, terete below, canaliculate distally; leaf blades ovate, broadly ovate-orbicular, ovate-deltate to oblong-ovate, (9–)13–30(–39) mm long, (7–)11–22(–34) mm wide, obtuse, rounded to acute, sometimes apiculate at tip, rounded, commonly truncate, occasionally somewhat cordate but broadly, sometimes unevenly cuneate with margins decurrent along distal petiole at base, at margins entire to unevenly undulate or crisped, mostly bicolored, dull green, sparsely villose with basally bent, somewhat appressed to curved hairs 0.4–0.9 mm long, subglabrate above, more buff-gray, densely, closely villose-tomentose, usually more persistently vestitured beneath, soft, flexuous, flat or more thickened with midvein and secondary veins impressed above and raised beneath, sometimes turning red before abscissing. Inflorescences mostly terminating long-shoot stems, branches, at times ter-
minating short shoots, narrowly to broadly, largely alternately branched panicles (3–)4–8(–12) cm long, (2.2–)3–7(–9) cm wide, but smaller on short shoots; peduncles-rachis densely villous-tomentose as stems but with hairs 0.2–1.5 mm long; flowers sessile or on pedicels to 0.4 mm long; bracts ovate, membranous except at very base, strongly cupped, 0.8–1.2 mm long and wide, obtuse to rounded at tip, entire, variously villous at tip and base or glabrous; paired bracteoles similar, larger, 1.1–1.6 mm long, 0.8–1.3 mm wide, glabrous to sparsely villous outside, midvein obscure. Staminate flowers caducous; sepals oblong-ovate, (1.5–)1.8–2.4 mm long, 0.8–1.2 mm wide, membranous, rarely chlorophyllous medially, somewhat chartaceous to indurated at curved base, all 1-veined or with 2(–3) sepals with 3 more or less parallel, distinct veins (visible when wetted), obtuse, erose at tip, glabrous inside and at gibbous base outside, variously villous outside above base with hairs 0.2–1.5 mm long; staminal disk thickened, 0.5–0.7 mm in diameter; filaments membranous, subulate, 1–1.5 mm long; anthers oblong, (0.5–)0.7–1 mm long, 0.2–0.3 mm wide (wet); staminodia linear-lanceolate, 0.2–0.4 mm long, consistently papillate-pubescent marginally from tip to base, often inflexed when dry; pistillodium 0.6–1.0 mm long; style bilobed, 0.25–0.3 mm long, body somewhat compressed, obovoid or more ovate above a cylindrical base, 0.45–0.8 mm long, 0.45–0.6 mm wide; perfect flowers similar but pistil with styles about 0.6 mm long and sepals with longer hairs. Pistillate flowers persistent;
sepals oblong-elliptical to oblong-ovate, 1.3–1.8(–2.4) mm long, 0.6–0.9(–1.3) mm wide, all 1 veined or inner 3, narrower sepals or all sepals with 3 more or less parallel veins, obtuse, erose at tip, glabrous inside, densely woolly outside with slender, wavy hairs 1–4.5 mm long, with longest hairs near sepal base; basal staminal disk 0.4–0.7 mm in diameter; staminodia (0.08–)0.1–0.28 mm long, glabrous, tapering to a capitate head, pseudostaminodia (0.06–)0.1–0.24 mm long, longer or shorter than staminodia, tapering to a narrow tip, glabrous (in 9 of 16 collections) or papillate-pubescent marginally; pistil 0.85–1.9 mm long; styles 0.2–0.3 mm long; stigmas 0.5–0.9(–1.0) mm long, papillate, spreading. Seeds 1.0–1.1 mm in diameter; testa membranous; embryos 2–2.2 mm long; radicle cylindrical, 0.8 mm long, cotyledons oblong-elliptical, acute-obtuse, 1.2 mm long, 0.7 mm wide. Based on 17 pistillate, 10 staminate, 1 perfect collections (Fig. 1g–m).

Iresine alternifolia is characterized by its shrubby, divaricately branched habit, by its relatively small, ovate, hairy leaves that tend to be alternate on the upper stems and also tend to develop in axillary clusters and on distinct short-shoot spurs, and by its dioecy. Trichomes are unbranched, aculeate, mostly bent at the base—a type widespread in Iresine.

The species occurs in the Sonoran Desert region both in Sonora north of Guaymas and in south-central Baja California (Fig. 4) in mesic, northerly facing canyons in the volcanic Sierra Gigantea and on several islands in the Gulf of California from (25–)90–1200 m elevation. Flowering occurs from (September–)October until January with fruit persisting into February.

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LITERATURE CITED


