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A Review of the Taxonomy of the Genus *Echinacea*

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Echinacea (Asteraceae), a North American genus of 11 recognized taxa (McGregor 1968), is of great economic and scientific interest. Three species, *E. angustifolia* DC. var. *angustifolia, E. pallida* (Nutt.) and *E. purpurea* (L.) Moench, show potential pharmacological activity (Bauer et al. 1988a; Bauer and Wagner 1991). Hydroalcoholic extracts of the roots of these three taxa stimulate phagocytosis in vitro, but there are no conclusive human clinical trials to date that fully substantiate the immune stimulating effects of such extracts upon oral administration. Although these taxa have been subjected to extensive chemical characterization (Bauer et al. 1988b; Bauer and Remiger 1989; Bauer et al. 1988, 1989), the exact chemical identity of the active constituents is unknown (Awang 1999). There is historical documentation of the medicinal uses of *Echinacea* by the North American Plains Indians (Kindscher 1989). This ethnobotanical validation has certainly been a factor in the popular herbal use of *Echinacea,* which has skyrocketed over the last few decades. The market demand and the medicinal properties are responsible for the recent interest in this genus as a new specialty crop.

All species of *Echinacea* are herbaceous, perennial flowering plants of the composite family (Asteraceae). Generally, a basal rosette of petiolate leaves and one to several annual stems arise from an underground, perennial rootstock. A single taproot is characteristic of all species except for *E. purpurea,* which has a fibrous root system. The stems terminate in a long-lasting and mildly fragrant inflorescence. The disk flowers are attached to a conical, hemispherical or occasionally flattened receptacle. The disk itself may also be flattened, conical, or hemispheric. Surrounding the capitulum is an involucre of 3 to 4 series of imbricating bracts (phyllaries). Each disk floret is subtended abaxially by a modified bract, the palea, which protrudes beyond the 5-lobed corolla. The disk florets are protandrous and development and anthesis follow the typical centripetal pattern of development of the composite family. The whorls of sharply tipped palea give a distinctive look to the capitulum; indeed, the genus name is derived from the Greek word *echinos*, for hedgehog. Pubescence on the stems, leaves and bracts ranges from hispid, hirsute and strigose to glabrous and varies among the species. The sterile ray flowers have strap-shaped ligules with colors that range from white, pink, magenta and purple to yellow.

The majority of taxa are diploid (n = 11). *E. pallida* and some populations of *E. angustifolia* var. *strigosa* McGregor are tetraploid (n = 22) (McGregor 1968). A complete understanding of the reproductive biology and breeding system is lacking; the presumed sporophytic self-incompatibility system is not perfected in this genus. Every species of *Echinacea* self pollinates to some degree, *E. purpurea* more so than the others (McGregor pers. commun. 1997). A mixed breeding system has been recently demonstrated for *E. angustifolia* var. *angustifolia* (Leuszler et al. 1996).

In addition to its possible medicinal uses, *Echinacea* has enormous ornamental potential. *E. purpurea,* the only species for which ornamental cultivars have been bred, is both productive and profitable as a field grown specialty cut flower (Starman et al. 1995). In fact, *E. purpurea* is the only species of the genus which has been domesticated thus far. It is interesting to note that the cultivars of *E. purpurea* that are now in production as source materials for herbal extracts were actually developed for ornamental purposes. Com-

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mercial field plantings of the other species in the genus have been sown from generally unimproved, wild seed. Plant breeders have an important task and a number of challenges before them.

Between 1997 and 1998, there was a six-fold increase in the number of accessions from wild populations of *Echinacea* maintained by the USDA National Plant Germplasm System. Now at 134 total accessions, this is the only available collection in the world of the primary genepool for the genus. This preliminary collection represents a valuable starting source of genetic diversity for breeders. Harlan (1984) makes a point about the evaluation and utilization of wild germplasm that is relevant to the *Echinacea* situation, namely that "plant breeders are rarely familiar with wild relatives....and are often misled by inept taxonomies." Despite the widely cited and detailed monograph on the genus *Echinacea* by McGregor (1968), there are a number of misleading generalizations regarding the taxonomy that are being repeated in the scientific literature. There is also a tendency to omit designation of taxonomic varieties. The purpose of this article is to address the problems associated with these generalizations, to review the major macroscopic characters by which the taxa can be identified, to highlight some of the morphological characters that may be of interest to breeders and in which species they are found.

COMMON MISREPRESENTATIONS

The most common misrepresentations about *Echinacea* deal with the natural range of the genus, which has implications regarding the suitability and adaptability for cultivation in different climates, and the usefulness of ligule color as a diagnostic taxonomic characteristic. These misrepresentations are addressed below.

Echinacea is not entirely a genus of the American Midwest, although the area of greatest species richness clearly lies in a band running from the Ozark Mountains of Missouri south through the east central grasslands of Oklahoma (Fig. 1). The genus as a whole is not exclusive to the Midwest or to the Great Plains, a common generic description that may be derived from the assumption that the range of the popular *E. angustifolia* var. *angustifolia* is descriptive for all species. The natural range of *Echinacea* is most accurately defined in broader terms as the Atlantic drainage region of the United States, extending into south central Canada (McGregor 1968). The southern United States is an important native area for this genus. Two of the species are endemics of the southeast, those being *E. tennesseensis* (Beadle) Small and *E. laevigata* (Boynton & Beadle) Blake, both of which are federally endangered. Half of the taxa have natural ranges that also extend well into the southern United States.

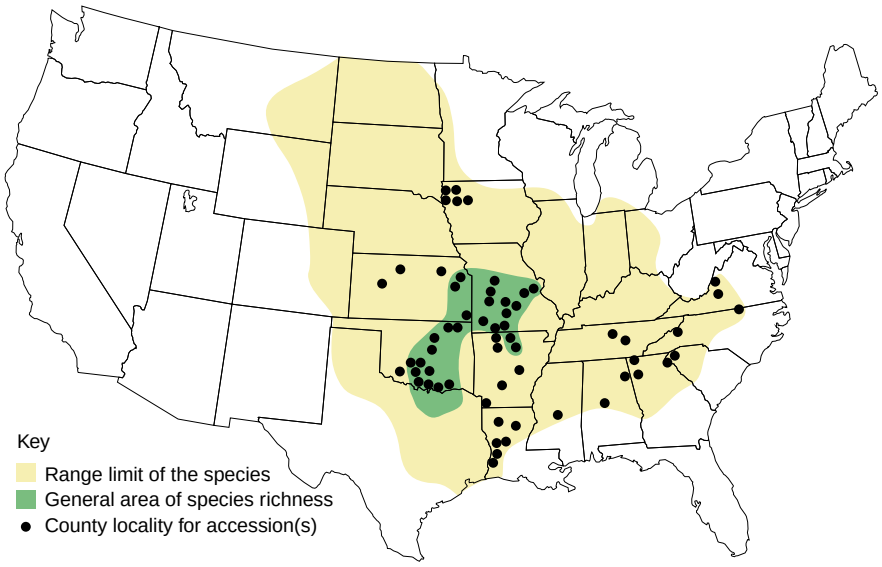

Fig. 1. The natural range of the genus *Echinacea* in the US. The outer solid line marks the limits for native populations; the inner dashed line marks the area of species richness. Accessions collected in 1997 and 1998 are mapped. Each dot may represent more than one accession.

The center of origin for *Echinacea* may well be the Ozark Mountains of Missouri and Arkansas. However, southeastern Oklahoma and the southern Appalachian Mountains as areas of diversity and speciation should not be overlooked. No native *Echinacea* populations have been discovered north or east of Pennsylvania and Virginia, although literature references to populations in Massachusetts and Maine, for example, are occasionally made without distinguishing these as probable introductions. A distinction between native and introduced populations is obviously important in any discussion of the evolution of the genus. The presence of naturalized populations in the northeastern US is a reflection of the adaptability of the genus rather than its potential or natural range. In addition to modern introductions, the existing range of the genus was impacted by the Native Americans who used and planted it; see the description of *E. angustifolia* var. *angustifolia*.

Another set of generalizations concerns ligule color. Misuse or misunderstanding of this diagnostic character is a likely factor in species misidentification and may result in the digging of rare endemics. The ligule is the strap-shaped part of the ray corolla of the composite inflorescence. Ligule color is generally a reliable character for distinguishing the yellow coneflower, *E. paradoxa* (Norton) Britton var. *paradoxa*, the only species with yellow ligules. For the other taxa of *Echinacea* ligule color is generally unreliable for a number of reasons. First, the color of the ligule is often developmentally dependent, being paler in the early stage of inflorescence development, darkening with maturation and anthesis, and fading with senescence. Therefore, one must clearly define the stage at which color is to be determined, notwithstanding the need to use a standard color system in order to avoid the subjective in the human evaluation of a physical character. The common names that refer to "pale" and "purple" coneflower are particularly misleading and ought to be avoided in the scientific literature.

A second reason to avoid using ligule color as a diagnostic character is that a geographical color cline exists for a number of the species. The ligules of *E. pallida* during mid-anthesis are nearly white in the most southern portion of its range, and take on a much deeper pink color in the north (McGregor 1968). *E. laevigata* is another species, the populations of which have very pale pink to white ligules at their most southerly boundaries and which are distinctly darker at northern latitudes, reaching a deep magenta color in some populations. The author has observed whole populations of *E. angustifolia* var. *angustifolia*, *E. paradoxa* (Norton) Britton var. *neglecta* McGregor and *E. sanguinea* Nutt. that are very pale pink to white in ligule color during anthesis. *E. pallida* is so designated because its pollen is white, not because its ligules are pale, yet it continues to be described as being *the* taxon having pale-colored ligules. In *E. sanguinea*, the disk corollas and the palea tips are blood red in color while the ligules can be quite pale.

There are two much more taxonomically useful characteristics of the ligule: the ratio of its length to width, and the ratio of its length relative to the width of the disk. This is reviewed below for each species. Obviously, with a genus as variable as this one, there will be exceptions to these features as well.

The taxonomic misconceptions are further compounded by the fact that many of the taxa are similar phenotypically and can be difficult to distinguish without familiarity with the morphological variation among them. The existence of hybrid swarms complicates this situation, especially in south central Missouri and southeastern Oklahoma. There has been no complete molecular systematic study of *Echinacea*, although restriction site investigations of the chloroplast genome suggests a close relationship among taxa (Urbatsch and Jansen 1995). Despite the very fine work of Bauer and colleagues as cited above on the identification of chemical constituents, no complete systematic chemotaxonomic study of this economic genus has been conducted. No doubt this is due, in part, to the previous lack of available material for study.

SUMMARY OF THE GENUS BY SPECIES

Ligule color, when given, is for reference to ornamental potential and is described for the period when approximately half of the florets have passed through anthesis. The reader should refer to McGregor (1968) for a complete metrical treatment of the macroscopic characters. These observations are of wild populations; variations may occur in cultivation.

E. angustifolia DC. var. *angustifolia*

This is a prairie forb that apparently thrives in the mixed and tallgrass habitats and dry, calcareous soils in which it grows. It is one of several species in the genus that has a compact growth habit, attaining 0.5 m in

maximum height. Ligules are reflexed and broad relative to their length, that length being shorter than or equal to the width of the disk. Pollen color is bright yellow. These three simple macroscopic characters taken together, i.e., the short plant height, the short and broad, reflexed ligule, and the yellow pollen color, can be used to easily distinguish *E. angustifolia* var. *angustifolia* from *E. pallida,* despite reports to the contrary. The latter species is generally taller and has narrow and long ligules and white pollen. However, identification can be difficult among wild populations on the eastern edge of the range of *E. angustifolia* var. *angustifolia*, where it overlaps the range of *E. pallida* and where intermediate colonies exist. This is discussed in detail by McGregor (1968). Flowering of wild populations of *E. angustifolia* var. *angustifolia* generally occurs in June and July. This species has a hispid or hirsute pubescence, usually unbranched stems, and linear to lanceolate leaves.

The native range of *E. angustifolia* var. *angustifolia* is from south central Texas through the Great Plains north to Saskatchewan, Canada. It is the only species of the genus that is native to Canada. There is ample ethnobotanical evidence for the widespread use of this species as a favored medicinal plant of the Plains Indians (Kindscher 1989). An important point to add is that the Comanche women traditionally collected seed of this species and distributed the seed throughout their buffalo hunting grounds so as to have this useful medicinal plant at their disposal (T. Whitewolf pers. commun. 1997). The Comanche people originally ranged from Wyoming to Texas. Although more evidence from oral histories and tradition is needed, the broad distribution of this species throughout the plains region of the United States may be the result of its ethnic usage and human dispersal rather than that of natural modes of seed distribution, which for this genus include water and possibly birds and mammals.

Chemically, this species is well studied. Roots contain alkylamides and caffeic acid derivatives (Bauer et al. 1988, 1989; Bauer and Remiger 1989; Bauer and Wagner 1991).

E. angustifolia DC. var. *angustifolia* is an obvious candidate for the selection of cold hardiness because it has adapted to northern climates. McGregor (1968) reported that *E. angustifolia* var. *angustifolia* is the only species in the genus with sclereid cells in the pith, and that all hybrids with this species maintain this character, which is potentially useful in breeding for stem strength.

***E. angustifolia* DC. var *strigosa* McGregor**

This is a taxonomic variety of *E. angustifolia* which has not been recognized in the literature or studied beyond its taxonomic identification. *E. angustifolia* DC. var. *strigosa* is an endemic that runs in a narrow band from south central Kansas through central Oklahoma and northeastern Texas. It is characterized and distinguished from its closest relative, *E. a*. var. *angustifolia*, by the presence of a strigose, rather than hirsute pubescence, frequency of branching, a wider disk and darker (reddish) ligules. These morphological characters, hybridization studies, and the species' distribution, which follows the eastern edge of *E. a.* var. *angustifolia*, and the western edge of *E. atrorubens*, led McGregor (1968) to the suggestion that this taxon is derived from hybridization between the latter two species. McGregor (1968) also found tetraploid colonies of this species, more frequently in its southern segment.

Southeastern Oklahoma is a geographical area where hybridization has been occurring and where the taxonomy of these taxa is incompletely understood (R. McGregor pers. commun. 1997). Hybridization between *E. paradoxa* var. *neglecta*, both varieties of *E. angustifolia* and *E. atrorubens* may account for some of the variation that is typical of this region.

***E. atrorubens* Nutt.**

E. atrorubens is an endemic found in a narrow region running north to south along the eastern grasslands of Texas, Oklahoma (west of the Ouachita Mountains), and Kansas. This species, except for its taxonomic features, is essentially unstudied. In habit it has a tall, sturdy, unbranched flowering stem that grows to about 0.9 m in height, normally without lodging. The inflorescence is characterized by very broad ligules that are shorter or equal to the length of the head, which are very strongly reflexed, and which are a deep magenta or reddish purple color. *E. atrorubens* is relatively early in flowering late May and June.

A potentially useful character of *E. atrorubens* is its large seed head. Wild seed (technically, the achene) of a number of *Echinacea* species has entered the commercial market not only as a propagule but as a source of medicinally active constituents, despite the fact that there are no clinical studies to directly support this

latter usage. Potentially active compounds such as cichoric acid have been extracted from the "flowers" of *E. purpurea* (Bauer and Wagner 1991), which may include the achenes in varying stages of development. Also, it has been documented that the Lakota ate the green fruit of *E. angustifolia* var. *angustifolia* (Kindscher 1989). Presumably, either the ethnobotanical usage, documented for this one species and extended to the others, or unpublished chemical profiling of the achene has been justification for its inclusion in commercial products. If medicinal value for the achene is eventually demonstrated, then breeding and selection for large achenes and seed heads that can be mechanically harvested will be desirable.

***E. laevigata* (Boynton & Beadle) Blake**

E. laevigata is one of the two federally endangered species of *Echinacea*. It is closely related to *E. purpurea* (McGregor 1968) and is found at the eastern edge of the geographic range of the genus, in the Appalachians and piedmont running from Virginia through the Carolinas to the northeast corner of Georgia. Its distinctive characteristics are a glabrous, ovate leaf, long narrow rays that droop and a tall, usually unbranched flowering stem that can reach a meter in height. It is this latter characteristic coupled with a wide range of ligule color, which in some populations varies from white to deep magenta, that may make it a good candidate for ornamental breeding as a long stemmed cut flower. The ligule is much like that of *E. pallida* in shape, being long and thin relative to the width of the disk, and drooping. *E. laevigata* flowers in June. The presence of alkamides has been demonstrated in this species (Bauer and Wagner 1991).

***E. pallida* (Nutt.) Nutt.**

E. pallida is the only tetraploid in the genus (n = 22) with the exception of occasional tetraploid colonies of *E. angustifolia* var. *strigosa* (McGregor 1968). This species is generally characterized by long, rarely branching flowering stems up to 0.9 m in height, with drooping or reflexed and slender ray flowers significantly longer than the width of the disk. Typically, this species has white pollen. However, the distinction between *E. pallida* and the closely related *E. sanguinea* at the southern boundary of its range (discussed under *E. sanguinea*) and from *E. simulata* to the east, is a matter of taxonomic controversy. Regarding the range overlap with *E. simulata*, there is an area of intergradation that is roughly one county wide which occurs in the Ozarks of north central Arkansas (P. Hyatt pers. commun. 1998) and south central Missouri. Some wild populations in this zone are of a "mixed pollen color" character, i.e., they are composed of individuals with pure white, bright yellow, and a clearly intermediate, soft yellow colored pollen. McGregor (1968) discovered sterile triploids in this area which he characterized as having an ochre-like, pale yellow pollen color (McGregor pers. commun. 1997). This interesting area of hybridization is unfortunately also an area frequented by root diggers and wild seed collectors. The flowering period of *E. pallida* follows a cline running south to north, May to July (McGregor 1968).

E. pallida is one of the three species under study as a medicinal plant. Its roots contain a number of polyacetylenes that with a few exceptions have not been found in any of the other species of the genus to date (Bauer et al. 1988b; Bauer and Wagner 1991).

***E. paradoxa* (Norton) Britton var. *neglecta* McGregor**

This species is a narrow endemic found in the Arbuckle Mountain region of south central Oklahoma. It is characterized by strigose pubescence, a glossy, lanceolate to elliptical leaf, and drooping ray flowers that are, much like *E. pallida*, longer than they are wide and longer than the width of the disk. They are white to pink or light purple in color. This botanically unstudied species is of unknown medicinal value and could be easily confused with *E. pallida* by a wild harvester with no taxonomic background; digging of this taxon has been a problem in south central Oklahoma. Strigose pubescence, bright green stems and yellow pollen are characteristic of *E. paradoxa* var. *neglecta* and serve to distinguish it from *E. pallida*. Its closest putative relatives are *E. paradoxa* var. *paradoxa* and *E. atrorubens.*

E. paradoxa* (Norton) Britton var. *paradoxa

This is the only yellow coneflower of the genus, and is endemic to the Ozark Mountains of Missouri and Arkansas. It has the same strigose pubescence, bright green stems and yellow pollen that characterize *E.*

paradoxa var. *neglecta*. Polyacetylenes identical to those found in *E. pallida* have been identified in its roots, as well as echinacoside, a caffeic acid derivative found in *E. angustifolia* var. *angustifolia* (Bauer and Foster 1991). In the wild, *E. paradoxa* var. *paradoxa* tends to grow in the same localities as *E. pallida* or *E. simulata* and hybridization in these mixed wild populations apparently occurs (author, pers. obs.).

This species and its hybrids have ornamental value. It generally flowers in June.

***E. purpurea* (L.) Moench**

Although the natural range of *E. purpurea* is quite broad, in the wild it is truly a plant of the ecotone, preferring the shaded edges of savannas and glades and open woodlands with partial sun exposure. Characterized by a classic discontinuous distribution, as is the genus as a whole, it is found in scattered prairie remnants of the south from Louisiana to North Carolina, and from Oklahoma and Kansas through the Midwest to Ohio, Kentucky, and Tennessee. The wild populations of *E. purpurea* in Louisiana and Mississippi are particularly striking in terms of pigmentation; the ligules are deep lavender and contrast dramatically with bright orange tipped paleae. Both soil pH and genetics may factor into ligule color, and any genetic component underlying the coloration of these populations is worthy of selection for ornamental value. *E. purpurea* flowers from late June through September.

E. purpurea is probably the most widely used and is certainly the most widely cultivated medicinal species of the genus. All parts of the plant are harvested, including the flowering heads for polysaccharides and cichoric acid (a caffeic acid derivative) and the roots for cichoric acid and various alkylamides. The polysaccharides, caffeic acid derivatives and the alkylamides are three chemical classes of constituents that are implicated in the immunostimulatory effect of this species and others (Bauer and Wagner 1991); see Bone (1997) for a good general review of these studies.

E. purpurea is a host of the aster yellows phytoplasma (Stanosz and Heimann 1997) which is a notable problem in cultivation (J. Simon pers. commun. 1998). Selection of thick pubescence to discourage leafhoppers may be achieved by working with accessions of wild populations from the western segment of the species range, as a general tendency toward the glabrous occurs to the east. Also, the transfer of an insect-deterrent pubescence from other taxa, particularly *E. tennesseensis*, which has a dense, hirsute hair type and phenological compatibility is a possibility. Such transfers have been successful for other crop plants (Harlan 1984).

***E. sanguinea* Nutt.**

The historical range of *E. sanguinea* is from eastern Texas and western Louisiana north into Arkansas and southeastern Oklahoma. *E. sanguinea* is not cold hardy (McGregor 1968). Although it generally flowers in May, wild populations in southern Louisiana will bloom well into August.

This species can be difficult to distinguish from *E. pallida*, especially where its northern range overlaps the southern boundary of the latter, because there are close phenotypic similarities between these two. Heights of both can approach 0.9 m and the ligule of *E. sanguinea*, like that of *E. pallida*, is long and narrow and can be very pale in color. Qualitatively, *E. sanguinea* is the more delicate of the species, having more narrow rays and more slender stems (McGregor 1968). One character not noted in the McGregor monograph is that the disk corolla of *E. sanguinea* is a blood red color, whereas that of *E. pallida* is very pale (L. Urbatsch pers. commun. 1997). However, this character, as for ligule color, may be developmentally dependent and may not hold true for *E. pallida* in some parts of its range, especially where its populations intergrade with those of *E. simulata*. Some taxonomists make a geographical distinction, placing *E. sanguinea* south of the Red River in Louisiana, and *E. pallida* to the north, but there are clear exceptions to this rule. What is agreed is that *E. sanguinea* is always found in more acidic, sandy soils and open pine woodlands.

***E. simulata* McGregor**

The range of this species runs from south central Missouri east through Tennessee and northern Georgia. It is phenotypically very similar to *E. pallida* from which it is primarily distinguished based on ploidy level ($n = 11$), pollen size and pollen color. The strictly white pollen color of *E. pallida*, as described by McGregor, may not be a reliable character in the area where the two species overlap, i.e. south central Missouri. *E. simulata* has ornamental potential in that the ligule color varies dramatically from pale pink to deep magenta

in many of its populations, and it is remarkably fragrant. Ornamental, purple colored stems are also found in this species, as well as in *E. purpurea*. There is an undescribed, glabrous race of this taxon found in a few isolated prairie barrens of northeastern Alabama and northwestern Georgia.

This species is coming under the digging pressure of its close relative, *E. pallida*, probably due to misidentification. The medicinal value is unknown; however, alkamides similar to those of *E. angustifolia* var. *angustifolia* and ketoalkenynes similar to those of *E. pallida* have been identified in the roots of *E. simulata* (Bauer and Foster, 1991).

***E. tennesseensis* (Beadle) Small**

E. tennesseensis was the second plant to be officially listed by the U.S. Fish and Wildlife Service as an endangered species (U.S. Department of the Interior 1979). Although McGregor had considered it to be possibly extinct at the time of the publication of his monograph (McGregor 1968), five populations in a 14 mile radius in central Tennessee are extant and have been the subject of a careful recovery plan (Currie and Somers 1989). In fact, *E. tennesseensis* may soon be ready for downlisting to threatened status (A. Shea pers. commun. 1997).

This species is unique from all others in the genus in that its rays neither droop nor reflex backward, but spread up and outward to form an inverted cup-shaped corolla. Ligule color varies from white to rose and purple. Its flowering occurs from June through September and is similar to that of *E. purpurea. E. tennesseensis* has ornamental value because of its compact habit, the multiplicity of flowering stems arising from a single rootstock, and its range of ray flower pigmentation. The medicinal value of this species is unknown. Alkamides identical to those found in the roots of *E. angustifolia* var. *angustifolia* have been identified in ethanolic extracts of the roots (Bauer et al. 1990).

CONCLUDING REMARKS

This paper was intended to provide a brief overview of the taxonomy of the genus *Echinacea*, and to highlight the macroscopic characters most useful for species identification. Another objective was to clarify the misrepresentations that have appeared in the literature, and to provide some preliminary guidelines for breeders interested in this economic genus. This review will hopefully also serve to educate a broader audience and help to prevent the digging of rare endemics, by providing a simplified version of the taxonomic descriptions. Wild harvesting is a potentially serious problem; the in situ conservation of the genus *Echinacea* is a growing concern among American scientists engaged in the monitoring of wild populations. Much research is needed in breeding and horticulture, and breeding for secondary metabolites will remain a challenge until the active constituents are unequivocally identified. Agricultural production is essential, however, and supports conservation by directly addressing the issue of supply.

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