

# A STUDY OF *CHAPTALIA* (ASTERACEAE: MUTISIEAE) IN CENTRAL, SOUTHERN, AND WESTERN TEXAS AND THE RESURRECTION OF *CHAPTALIA CARDUACEA*

Robert T. Harms

Plant Resources Center, The University of Texas at Austin, 1 University Station F0404, Austin, Texas 78712

**Abstract:** Recent authors have considered there to be just one species of *Chaptalia* in central, southern, and western Texas and have called it *C. nutans*, *C. nutans* var. *texana*, or *C. texana*. Field studies in Travis and Hays counties indicate the existence in that area of two populations with morphological, phenological, and behavioral differences, and revision of herbarium material shows that they correspond to two distinct taxa that occupy different but partially overlapping ranges in Texas and northern Mexico. Evidence is provided in support of their recognition as distinct species that correspond to *C. texana* and *C. carduacea*, both described by E. L. Greene. Descriptions of the two species and a revised key for *Chaptalia* in Texas are provided.

**Keywords:** Asteraceae, Mutisieae, Chaptalia, flora of Texas.

*Chaptalia* (Asteraceae: Mutisieae) occurs in Texas in the far eastern part (*C. tomentosa* Vent.) and, quite separately, in central, southern and western Texas (Fig. 1). The populations of central, southern and western Texas have been treated by all recent authors as a single taxon that has gone under varying names: *C. nutans* (L.) Pol. var. *texana* (Greene) Burkart (Burkart, 1944; Correll & Johnston, 1970), *C. nutans* (Simpson, 1978) and, most recently, *C. texana* Greene (Nesom, 1995, 2006a; Turner et al., 2003). However, intensive field observation from spring 2010 through spring 2011 on the morphology, behavior and phenology of two *Chaptalia* populations in Central Texas, one in Travis Co. and one in northern Hays Co., provides evidence that two taxa are present in this area. Review of literature and types indicates that one of these taxa corresponds to *C. texana* sens. strict. while the other can be referred to *C. carduacea* Greene, a name previously treated as a synonym of *C. texana* (Nesom, 1995) or *C. nutans* (Simpson, 1978). Data are presented to support this hypothesis. For ease of discussion, throughout I will refer to the two putative taxa by the E. L. Greene names mentioned above (Greene, 1906), even though their distinctiveness will be demon-

strated only once all the data are presented and considered.

## STUDY SITES

*C. carduacea*, northern Hays County: over 200 plants, all easily accessible, widely distributed over 50+ acres of previously ranched land on the Purola Preserve and Keyes Ranch, at latitude 30°17'18" N and longitude 98°09'57" W; elevations range from 298 to 335 m. The habitat of the species varies a great deal, including dense *Juniperus ashei* J. Buchholz thickets, shady hardwoods, scattered groves of live oak (*Quercus fusiformis* Small), steep creek banks, and open grassland, all on deep calcareous clay soil. Two plants from an open area were transplanted to pots in spring of 2010.

*C. texana*, Travis County in SW Austin: fewer than 100 plants, 32 easily accessible, on a west-facing hillside with rocky shallow calcareous soil near the mouth of an undeveloped canyon that enters Barton Creek, just west of Zilker Park at latitude 30°15'41" N and longitude 97°46'49" W; elevations ±148 m. The habitat is open juniper-oak woodland with numerous species typical of the eastern Edwards Plateau,

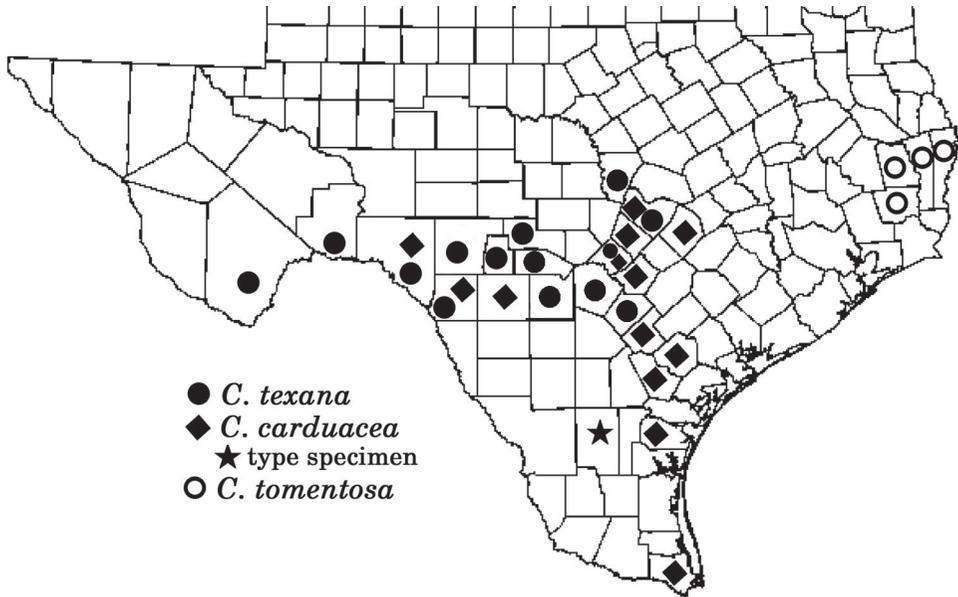


FIG. 1. Distribution of *Chaptalia* in Texas.

many *Juniperus ashei* having been removed several decades ago. Three plants from this group were moved to pots in spring of 2010.

#### METHODOLOGY

The two field populations and the transplanted plants were studied intensively, as described below, to ascertain which character-states and behaviors, if any, distinguish them. Character-states traditionally used to describe *Chaptalia* species were studied and either accepted as legitimate differentiae or rejected, based on observed variation within and between the two populations. Previously un-utilized characters were also studied, and several were found that present useful distinctions between the populations. Herbarium material was then studied to determine to what extent the conclusions based on the two populations are more broadly applicable.

**POPULATIONAL STUDIES.** Morphological details that did not require careful measurement, such as leaf form and size, were photographed and noted in the field in order

to determine ranges of variability. For this purpose, dozens of plants of both species were examined for structures that were fully developed and within the normal range for the plant, and noted or collected only if they extended ranges thus far established.

Specimens for detailed measurement were collected in the field and kept fresh until they could be imaged for measurement within 24 hours. Some of these specimens, often dissected but not flattened or compressed, were placed on the glass plate of an Epson Perfection 4800 flatbed scanner, and scanned at resolutions from 300 to 2400 dpi, and saved in TIFF or JPEG format. Measurements for these were made with digital scales approximating measurement accuracy to 0.1 mm. Details of some specimens were photographed and measured with a dissecting microscope equipped with a camera and using SPOT 4.6 software.

A subset of individuals (5 of *Chaptalia texana* and 5 of *C. carduacea*) was studied intensively as to phenology, behavior (capitular movements) and morphology from March 2010 to May 2011, primarily during the flowering and fruiting periods.

Potted adult plants were kept adjacent to each other during the period in various settings, including moving one of each species into a greenhouse to avoid a hard January freeze. Additionally, seedlings were produced for both species, from achenes from two extreme spring types: *Chaptalia texana* with well-developed, spreading ligules (presumably progeny of outcrossing, germinated late May 2010) and *C. carduacea* with greatly reduced ligules (presumably progeny of selfing, germinated mid March 2011). These had not yet flowered by late spring 2011.

Leaf length and width were determined in three ways: (1) for the longest leaf from among a group of neighboring plants; (2) for the longest leaves of a plant at the onset of anthesis in order to insure that the leaf size represents a fully mature leaf; (3) for all leaves except the youngest 4 for plants selected as representative of a group of plants in a ca. six-foot radius. Leaves collected as in 1 and 2 above were always the oldest and bottommost. Measurements were made for 93 *Chaptalia carduacea* and 47 *C. texana* plants, the latter showing overall less variation in morphology.

Since *Chaptalia texana* and *C. carduacea* differ in the form of the leaf base, it was necessary to determine at what point to consider the narrowing of the lamina at the base to constitute a winged petiole. (See Definitions below.)

A difference in the color of older, post-anthesis ligules was noted: those of *Chaptalia carduacea* crimson, those of *C. texana* typically yellow. To insure that the yellowing of ligules was the result of age rather than an artifact of drying of a young specimen, only ligules of heads with lengthened achene beaks, a clear indicator of head maturity, were considered. In addition to the field populations, all Texas specimens in TEX/LL were examined for ligule color.

Voucher specimens of individuals from the sites representing typical phases of the two species are deposited at the Plant Resources Center (TEX, *Harms 100 to*

*106*). A web site with many results, details, and numerous images from the study can be found at <http://w3.biosci.utexas.edu/prc/CHAPT/CHAPT-top.html>.

HERBARIUM STUDIES. A total of 244 herbarium specimens, including types, of various species of *Chaptalia* deposited in TEX, LL, US, UTEP, and SRSC were examined, including 75 from Texas (including 65 of *C. texana*/*C. carduacea*; listed below) and 169 from Mexico (including 69 *C. texana* and 3 *C. carduacea*/*C. leonina* Greene). The JSTOR Plants website ([plants.jstor.org](http://plants.jstor.org)) was also consulted in search of additional type material not at the above-cited herbaria.

### Definitions

ANTHESIS: The period from the initial display of pistillate floret style branches until all pistillate floret style branches are enveloped by pappus bristles; generally 4–7 days. This is most apparent when the pappus of the peripheral florets is exerted from the involucre. The term is here applied to the capitulum as a whole, not individual florets.

HEAD ALIGNMENT (angle of the head to axis of the peduncle):

ERECT: 0°

ASCENDING: ± 45°

NUTANT: > 90° & < 150°

CERNUOUS: facing the ground or ± 180°

PHASE: A seasonal variation in floret morphology. Evidence for three phases was found: (1) Early spring; (2) Late spring; (3) Fall and winter.

PETIOLE: The basal portion of the leaf below an abrupt narrowing of the lamina, with a narrow margin nearly parallel to the midvein or slightly expanding toward the base and lacking the undulate margins and mucros typical of the lamina margin.

### FLORET MORPHOLOGY AND SPATIAL/ TEMPORAL DISTRIBUTION

Three series of florets are recognized in each head (Fig. 2, Table 1): (1) peripheral

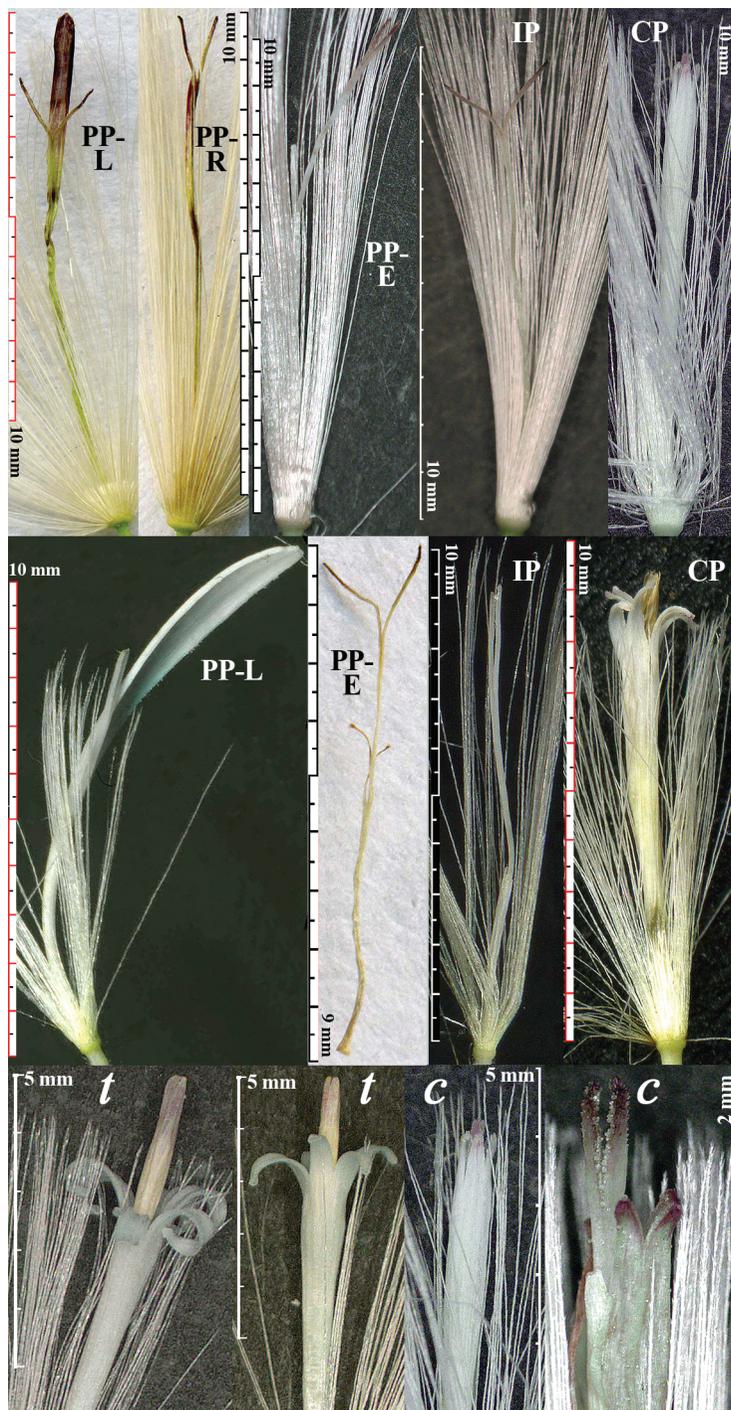


FIG. 2. Floret types. Top row *C. carduacea*; middle row *C. texana*; bottom row central florets. *t* = *C. texana*, *c* = *C. carduacea*, PP-L = peripheral pistillate (fully ligulate), PP-R = peripheral pistillate (reduced ligulate), PP-E = peripheral pistillate (eligulate long-tube), IP = inner pistillate (eligulate short-tube), CP = central perfect.

TABLE 1. Floret counts per head based on field population specimens; “n” is the number of heads analyzed. The parenthetical numbers in *Chaptalia carduea* for fall/winter reflect one atypical specimen with very few florets (but included in the average).

	<i>C. texana</i>				<i>C. carduea</i>			
	Spring (n=3)		Fall/Winter (n=4)		Spring (n=9)		Fall/Winter (n=5)	
	range	avg.	range	avg.	range	avg.	range	avg.
Peripheral pistillate	22–27	25	22–36	30	12–22	16	(1–) 11–21	14
Inner pistillate	54–62	58	57–95	71	17–50	34	(24–) 44–74	56
Central perfect	12–18	15	16–24	21	7–14	11	(6–) 12–16	12
total:	91–106	97	95–155	121	36–85	60	(31–) 75–107	82

pistillate florets, adjacent to the inner phyllaries; (2) inner pistillate florets; (3) central bisexual florets.

The **peripheral pistillate florets**, ca. 17–27% of the total, were observed to vary by season for both species (both wild and potted): ligulate in early spring, eligulate or with greatly reduced ligules in late spring and late summer through January. When eligulate, these corollas are typically morphologically similar to those of the inner pistillate florets but with a long two-lipped corolla tube greater than half the style length (and thus distinctly longer than the inner pistillate florets), but in some heads they are indistinguishable from the inner pistillate florets. In *Chaptalia texana* the lips were occasionally quite long with swollen tips similar to those of the central florets. Although in some instances it seemed arbitrary to distinguish between a highly reduced ligulate floret and an eligulate one with a long tube, the presence of two lips was interpreted as eligulate.

When eligulate outer florets were first encountered in the spring 2010 all inner florets were removed from a head for study, leaving only those at the periphery. The results showed that these differed from inner eligulate florets in tube length. Subsequently all eligulate heads were dissected in such manner that peripheral and inner florets were placed into separate groups for examination.

A late spring shift toward an eligulate phase was first noted in mid April 2011 with a *Chaptalia texana* plant in cultivation that

had earlier produced several heads with large showy ligules. Heads of both species in the wild were then inspected and were seen to have undergone the same phase shift, with ligules absent or greatly reduced. Although the trigger for this shift is not clear, it seems unlikely that it was due to increasing soil dryness given that it also occurred in well-watered cultivated plants. A review of earlier images and data from May 2010 indicate that this shift had occurred with *C. carduea* in Hays County and had gone unnoticed at that time. I had largely stopped dissecting heads, and the population with no ligulate florets discovered in May was treated as a new morphological form at that time.

**Inner pistillate florets**, ca. 56–68% of the total, have corolla tubes typically minutely two-lipped, less than half the length of the style, and did not vary by season.

The perfect **central florets**, ca. 15–18% of the total, are zygomorphic, with 5 lobes distributed 2 plus 3 on two lips atop a floral tube that widens toward the top. In spring phase the lobes spread prominently, almost appearing actinomorphic; the anther tube is exerted, with clumps of pollen pushed forth by the thick style branches. In fall phase, the floret lobes remain erect and the anther tube remains hidden; the style branches are only sometimes exerted, and although no pollen clumps appear, there seem to be a few grains limited to the style branches (i.e., not on the pistillate floret styles).

Virtually all inflorescence components continue to grow from the onset of anthesis



FIG. 3. *C. carduacea* diurnal head alignment on day 3 (spring).

to just prior to dispersal, especially the ligules, achene beaks, pappus bristles, phyllaries, and peduncles, all of which continue to increase in length. The use of phyllary form and dimensions of immature heads for identification may be difficult. Pappus bristles lengthen up to 2 mm or more after the onset of anthesis, so that ranges in bristle length should have been correlated with length of achene beak, but this was not done. Lengths given pappus bristles throughout this article are always for those of mature achenes with fully elongated neck.

PHENOLOGY AND NODDING PHENOMENA

This study began when notable differences in nodding behavior and visual prominence of ligulate corollas were noted between the two central Texas populations during spring flowering, and so the morphology and behavior of the heads were studied intensively. Although both species exhibit the familiar ‘nodding’ behavior of *Chaptalia nutans*, the degree and duration for the two is different. Spring nodding behavior was closely monitored for one plant of each species in cultivation under identical conditions of exposure and moisture for almost a year. The results matched the behavior of the wild populations being studied and are summarized here.

Nodding behavior includes both daily cycles during anthesis and day-to-day changes along the course from pre-anthesis to achene dispersal. The latter changes are outlined below. As to the daily cycles, during the few days of anthesis, the head begins the

day in a lower position, rises by midday to a higher position, then falls to a lower position again by late afternoon (Figs. 3, 4). The amount of movement and the midday position vary by species, as outlined below.

Although the *Chaptalia carduacea* plant monitored for nodding was from a population with reduced (not visible) ligules, field observation of a large population of plants with small, but visible ligules (largest noted for this species), indicated that there was no difference in the relatively short period of erect alignment. On any given day very few plants had erect heads. By contrast the

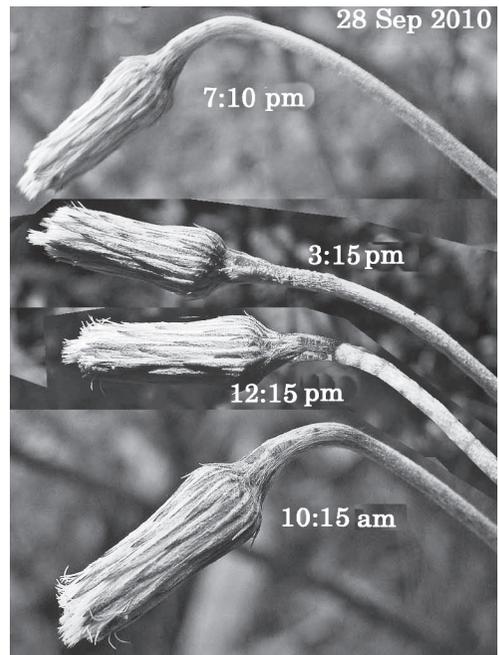


FIG. 4. *C. texana* diurnal head alignment (fall phase).



FIG. 5. Head orientation: *C. carduacea* (left) vs. heliotropic *C. texana*.

population of *C. texana* had many plants with erect heads during the peak flowering period.

***Chaptalia carduacea* (spring):**

*The head remains closed and the ligules distally-directed (and hidden in the monitored specimen) during the entire bloom cycle. It is:*

- nutant on day 1 of anthesis;
- erect at midday for very short period on days 2–3 of anthesis, Fig. 3;
- ascending at midday on day 4 of anthesis;
- cernuous at midday during most of fruiting period (16 days);
- rising just prior to dispersal (day 23) and erect at dispersal (day 24).

Diurnal head alignment during anthesis undergoes a change of  $(30^\circ -) 45^\circ - 90^\circ (- 115^\circ)$  between midday position and early morning/evening position until day 9.

The heads are *not heliotropic* (Fig. 5).

***Chaptalia texana* (spring):**

Days 3–7 of anthesis are marked by fully extended ligules, retroflexed together with the inner phyllaries and visually prominent. The head is:

- nutant on day 1 of anthesis (day 2 was not recorded);

cernuous early on day 3 of anthesis, later in the day ascending;

erect at midday on days 4–5 of anthesis, nearly erect (ca.  $20^\circ$ ) on day 6;

ascending on day 7;

nutant at midday during most of fruiting period (17 days);

rising to nearly erect (ca.  $20^\circ$ ) at dispersal, day 28;

Diurnal head alignment during anthesis undergoes a change of  $30^\circ - 45^\circ (- 90^\circ)$  between midday position and early morning/evening position until day 10.

The heads are *heliotropic* during early anthesis, but as the peduncle matures remain directed toward the strongest light source (i.e., do not change position at dark). (Fig. 5).

The most significant differences in overall spring capitulum behavior can be summarized as follows: *Chaptalia carduacea*, ligules always distally-directed, even hidden, daily movement cycle of head generally 45–90 degrees, heads in fruit cernuous, heads not heliotropic; *C. texana*, ligules reflexed and prominent on days 3–7, daily movement cycle of head generally 30–45 degrees, heads in fruit nutant, heads heliotropic.



FIG. 6. *C. texana* diurnal ligulate floret cycle (spring).

Fall diurnal nodding behavior was closely observed only for *Chaptalia texana* and closely matched that of the spring heads, although no ligules were visible (Fig. 4) Winter heads of two *C. carduacea* plants exhibited extreme rotation of the peduncle, one ca.  $230^\circ$  and one  $380^\circ$  (a complete loop, down and up to erect), but this was not typical of that species.

Closely related to the diurnal head alignment is the unique opening and closing of *Chaptalia texana* heads, due to the movement of the ligulate peripheral florets, during anthesis for ca. 5 successive days. Initially the ligules are more or less the length of involucre, but these lengthen rapidly and by day 3, during the day, only slightly longer, they reflex outward, pushing the inner phyllaries with them. (Phyllaries not adjacent to ligules are not reflexed.) By late afternoon they are already closing and at dusk they are fully closed, the phyllaries straight, and this position is maintained until early morning, when the opening process is repeated (Fig. 6). By day 7 the ligules have more than doubled their length. By day 9 they curve inward, their orientation essentially constrained by surrounding pappus.

Flowering season for the two taxa overlaps greatly, but *Chaptalia texana* tends to reach peak bloom earlier. Based on the population studies and herbarium records, *C. carduacea* is known to flower in all months except June through August, with peak bloom from mid-March through late April, while *C. texana* is known to flower in all months except May through July, with peak bloom from early March through early April.

#### MORPHOLOGICAL DIFFERENCES BETWEEN THE TAXA

The strong behavioral differences between the two populations noted in the previous section strongly suggested that two separate taxa are involved. A detailed look at morphological characteristics of the two populations, followed by study of herbarium material, clearly demonstrated consistent morphological differences as well. The most notable of these differences are discussed here; these and others are highlighted in the species descriptions at the end of the paper.

The basal rosettes of the two taxa are rather different (Fig. 7). *Chaptalia carduacea*



FIG. 7. Basal rosettes (*C. carduacea* on left; *C. texana*, right).

forms visually denser rosettes due to the fact that the leaves are mostly epetiolate or subpetiolate (mature petioles up to 40 (extreme 60) mm. long, with ca. half of all leaves sessile, Fig. 8); the bottommost leaves in a dense rosette tend to be those that develop a petiole. *C. texana* rosettes are rarely as dense, in part due to the facts that the leaves are essentially always petiolate (mature petioles 18–65 mm long, very rarely

less, Fig. 8) and seem to be relatively short-lived (Fig. 7).

The phyllaries differ between the two taxa (Fig. 9). Although narrow in both taxa, those of *Chaptalia carduacea* are distinctly broader and stiffer. The bases of the innermost phyllaries in this taxon are of two widths (ca. 1.1 mm and ca. 1.8 mm) and the outer phyllaries are commonly over 1.5 mm wide; the stiffness of the phyllaries

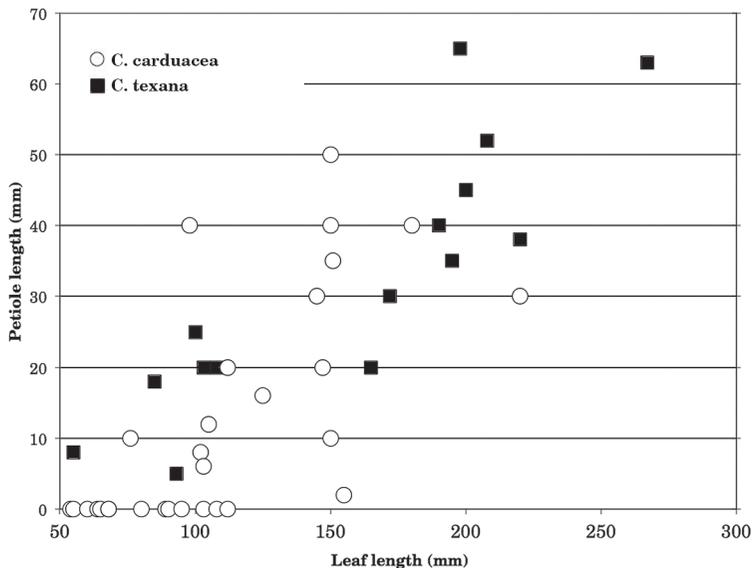


FIG. 8. Leaf length plotted against petiole length, data from field populations, plants selected from different sites (30 leaves for *C. carduacea*; 15 for *C. texana*).



FIG. 9. Phyllaries (abaxial view).

is due to a thick midrib that extends to the tip (midrib ca. 0.23 mm thick when measured 3 mm below the phyllary tip, Fig. 10). In contrast, the phyllaries of *C. texana* are distinctly narrower; the innermost series are all less than 1 mm wide, and the outermost less than 1.5 mm wide. The midrib is much less notable and the phyllary tip is more flexible (midrib ca. 0.1 mm thick at a point 3 mm below the tip, Fig. 10).

There are many differences in the details of the florets, as noted in the descriptions below. Although the total number of heads analyzed was small (14 *Chaptalia carduacea* and 7 *C. texana*, all from field populations), the range of total numbers of florets per head appears to be quite different (*C. carduacea*, 36–107; *C. texana*, 91–155; combining for all phases, Table 1). The dimensions of the well-developed spring ligulate florets are also quite different. The typical spring ligulate floret in *C. carduacea* has a ligule (ca. 5 mm) shorter than the tube (ca. 7 mm), while in *C. texana* the ligule (ca. 8 mm) is longer than the tube (ca. 5 mm).

As noted in the previous section, the ligules are prominent and reflexed for several days in *C. texana*, while always enclosed within the stiff erect phyllaries in *C. carduacea* (Fig. 11). Although white in both taxa at anthesis, the spring ligulate corollas become yellowish with age in *C. texana* and crimson

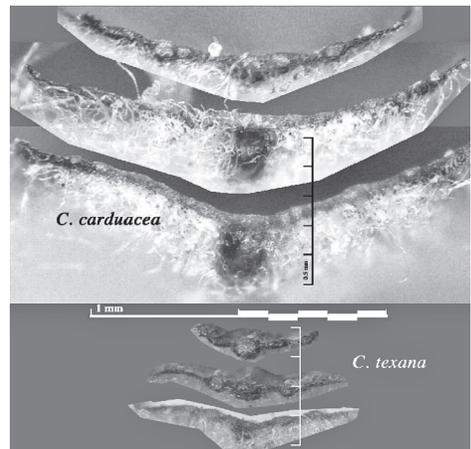


FIG. 10. Cross sections of longest (innermost) phyllary tips at 1 mm, 2 mm, 3 mm.



FIG. 11. *C. carduacea* (left): innermost phyllaries remain stiffly erect and only the tips of the ligules spread beyond the phyllaries if positioned between them. *C. texana*: ligules reflexing outward for most of their length together with the phyllary tips.

in *C. carduacea*; the only exception to this pattern in Texas was found in *C. texana* specimens from Medina Co., which have crimson corollas with age (as do virtually all Mexican *C. texana* specimens).

Pappus details also differ (Figs. 12, 13). Based on data from field populations, in *Chaptalia carduacea* the pappus bristles number 135–203 per achene (average 174) and are 10.4–14.1 mm long (average 12.0) at maturity, while in *C. texana* the bristles number 76–124 (average 100) and are 9.3–10.6 mm long (average 9.8) at maturity.

#### GEOGRAPHICAL DISTRIBUTION AND HABITAT

Nesom (1995) gives a total geographical range for *Chaptalia texana* sens. lat. from southern, central and western Texas and extreme southern New Mexico, southward in Mexico to Jalisco, state of México, Puebla and Oaxaca (and with an outlier in Baja California Sur). All *Chaptalia* specimens from this region at TEX-LL, which has a very strong collection for Texas and north-eastern Mexico, plus specimens from US, SRSC and UTEP, were studied to see which represented each of the taxa here recognized.

Within Texas, a pattern of overlapping but different ranges emerges (Fig. 1). Both taxa occur in the southern and eastern Edwards Plateau, but from there *Chaptalia carduacea* extends southward into South Texas, where *C. texana* does not occur, while *C. texana* is found westward into the Trans-Pecos, where *C. carduacea* does not occur. In the study populations, although both occur in similar vegetation types, there seemed to be a clear difference in soil preference, with *C. carduacea* restricted to deeper soils (although shallow soils are common at that site) and *C. texana* the opposite. Scattered substrate data mentioned on herbarium specimens supported this potential difference but were not conclusive.

Nesom (1995) reports that *Chaptalia texana* sens. lat. “probably” occurs in extreme southern New Mexico, based on *C. C. Parry et al. 674* (US!) labeled “Mexican Boundary Survey, chiefly in the Valley of the Rio Grande, below Doñana.” Based on TEX-LL specimens, literature, on-line databases, and a review of the UTEP *Chaptalia* holdings, the species is not otherwise known from southern New Mexico or the immediately adjacent parts of Texas (a report in the SEINET on-line

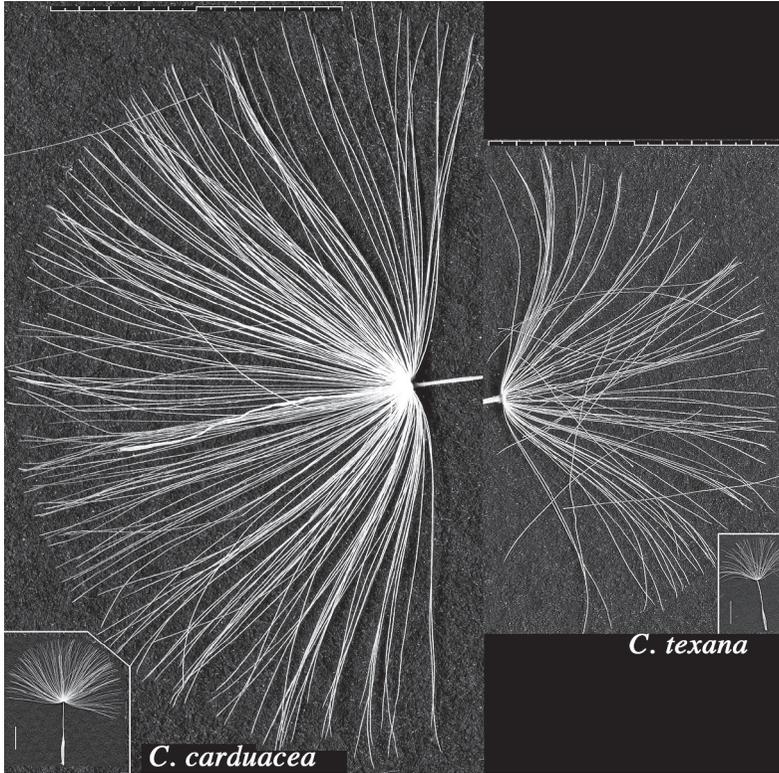


FIG. 12. Pappus at maturity as verified by long achene beaks (inserts).

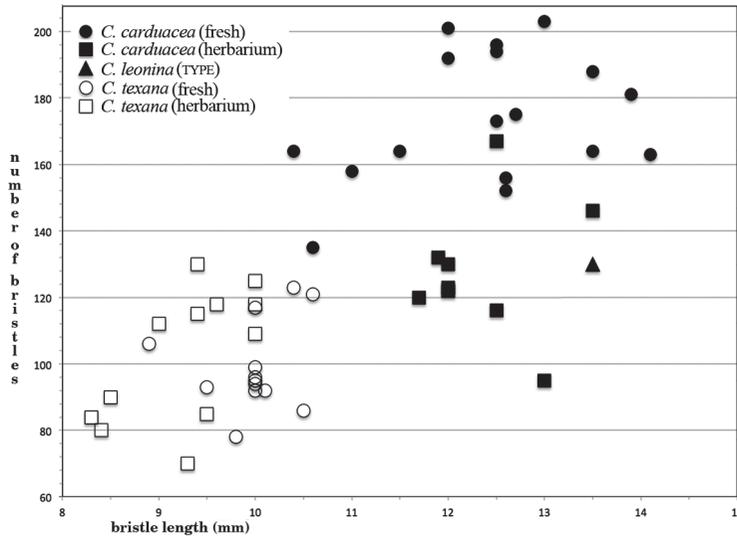


FIG. 13. Average pappus bristle length plotted against number of bristles. 17 achenes from different locations at the study sites and at different dates were selected for each taxon (plus 1 from an herbarium specimen for *C. leonina*).

database <<http://swbiodiversity.org/seinet/index.php>> of *C. texana* from southern New Mexico (Worthington 31834-A (UTEPI!)) was based on a misidentification of *Leibnitzia lyrata* (D. Don) G.L. Nesom). Given that the Mexican Boundary Survey labels were often extremely general, it seems very possible that the Parry collection was not from New Mexico.

No Mexican material referable to *Chaptalia carduacea* was found at TEX-LL. All TEX-LL Mexican specimens cited by Nesom (1995) as *C. texana* are indeed that species in the strict sense. However, the type of the *C. leonina* Greene from Monterrey, Nuevo León, Mexico (*E. Palmer* 764; holotype, US!; isotypes, US!, NY (image at JSTOR Plants!)) is referable to *C. carduacea*. Additionally, Pringle 10169 (US; April 2, 1906) from Monterrey has phyllaries and pappus that permit its identification as *C. carduacea*. The duplicate collection Pringle 10169 (LL) is *C. texana*. The occurrence of *C. carduacea* in extreme northeastern Mexico (near the Texas border) is to be expected (but is not confirmed) given its presence very near the Mexican border in Cameron Co, Texas (*Runyon* 1596, TEX). The Monterrey locality shows that it may well occur in at least scattered form from extreme southern Texas across coastal plain of northern Tamaulipas southwestward to the base of the Sierra Madre Oriental in Nuevo León.

## DISCUSSION

The previous sections show that two taxa exist that differ in morphology, capitular behavior, phenology and geographical distribution, and perhaps soil type preference. It would seem very unlikely that observed differences are merely environmentally induced variation, because the suites of characters common to both field and potted, transplanted plants do not vary in the same "direction." For instance, *Chaptalia texana* has, compared to *C. carduacea*, larger leaves, peduncles and ligulate florets, and a greater number of florets and a longer period of

anthesis, but also shorter pappus, fewer pappus bristles and thinner and narrower phyllaries. Although the geographical ranges are different, there is broad overlap in the eastern and southern Edwards Plateau, with no indication of significant intergradation in this area. These facts, taken in the context of the species delimitations currently used in this genus (Nesom, 1995), clearly support the recognition of the two taxa as separate species. Indeed, based on a very preliminary examination of *Chaptalia nutans* (sensu Nesom 1995), *C. texana* appears closer to that species by virtue of their shared linear lanceolate phyllaries and larger number of florets than it is to *C. carduacea*. In comparing the quantitative differentiae for *C. nutans* and *C. texana* given in Nesom 1995, and allowing for the separation of values obtained for *C. carduacea*, we find a continuum from lower values for *C. nutans* to higher values for *C. texana* sens. strict. (style branch length, achene body width – conceivably a consequence of the significantly larger number of florets per head) or overlapping values (phyllary length). And, as Nesom notes (p. 165), "even though the two taxa are clearly differentiated over most of their ranges, apparent intermediates occur in Edo. México, Puebla, and Oaxaca, where their geographic ranges appear to interdigitate." And since "they also are separated ecologically, with *C. texana* occurring in inland, relatively arid habitats and *C. nutans* typically in tropical ones," (Nesom p. 165) it is conceivable that they are only varietally distinct.

As previously noted, the spring heads of both species produce three series of florets: peripheral pistillate, inner pistillate, and central morphologically bisexual. In the spring, the peripheral pistillate florets of *Chaptalia texana* and *C. carduacea* both produce well developed ligules; in *C. texana* these are visually prominent and reflexed, while in *C. carduacea* they are much less prominent because they are erect and partially to completely hidden by the erect involucre. Thus, spring heads in both species are clearly trimorphic. But in the late spring

and fall phases of both species, when the peripheral florets are typically eligulate, having elongated tubular florets that are similar to florets of the inner pistillate series except for their greater length, the term trimorphic might still be technically correct, but not in the sense as it is commonly used in the current literature. (Although one can generally determine the presence or absence of ligules with pressed specimens, the discovery of elongated tubular peripheral florets without dissecting the entire head is generally not feasible.) In fall/winter phase heads with purely dimorphic florets, in the strictest sense, were observed with both species. Nesom (1995) noted that "some heads of *Chaptalia texana* completely lack ligulate pistillate flowers, but this does not appear to be correlated with geography or season..." The current study demonstrates that, at least in central Texas, there is a strongly seasonal aspect to this variation.

There are clear indications from my observations during this study that self-fertilization and/or apomixis may be involved in reproduction in these two species, and this clearly merits further study. (This issue was addressed for *Chaptalia* more generally in Burkart 1944, Vuilleumier 1969 and Nesom 1983.) In the spring, the inner pistillate florets have their styles exposed only for the first three days or so of capitular anthesis; at the same time, the central florets are producing abundant pollen from exerted anther tubes. The styles of the all pistillate florets were observed to have numerous pollen grains on them, although no flying insect visitors were ever noted during many hours of observation. The pistillate florets produced abundant fertile achenes, and it seems likely that this was due to pollen from the central florets (assuming that the achenes were produced sexually). (The central florets also produce abundant fertile achenes.) Even more suggestive are some observations on late spring and fall/winter heads of both species. While the early spring central florets have spreading corolla lobes and are longer than the

other florets, allowing the produced pollen to stand somewhat above the plane of the pistillate flowers, in the fall the central florets have erect lobes (thus, a more closed structure), are shorter, and generally produce little or no obvious pollen. In these fall heads, the pistillate florets produce, as in the spring, prominent exerted styles, but pollen was not observed on these styles. An isolated mid-winter greenhouse *C. carduacea* plant (not at the study site) with no apparent pollen produced a full set of achenes that were subsequently germinated, producing many more seedlings than could have been from central florets (meaning, that is, that at least some of the achenes were produced by the pistillate florets). This is a strong indication of apomixis, although more observations are obviously needed. For the same reasons it also seems likely that the achenes produced by the fall/winter central florets are (at least in part) the result of apomixis or cleistogamy. One of the prime characters said to distinguish North American *Chaptalia* from *Leibnitzia* (cf. Nesom's key for Mutisieae, 2006b, p. 71) is the presence of later season cleistogamous flowers in the latter, although Nesom 1995 does recognize the heads of *Chaptalia* sect. *Lieberkuhna* as "alternating between chasmogamous and cleistogamous modes" (p. 156). Clarifying the situation of these *Chaptalia* species (and others) would be interesting from the standpoints of both reproductive biology and systematics.

#### TAXONOMY

Descriptions of the two species are given below. Where images are cited, these are online images at JSTOR Plants <plants.jstor.org>. Character-states that differ significantly between the two species are highlighted in *italic bold*. Synonymy only includes names directly relevant to this study of Texas populations

*Chaptalia carduacea* Greene, Leaflet Bot. Observ. 1:191. 1906. TYPE: UNITED STATES.



FIG. 14. Involucres at anthesis (left) & in fruit: cylindrical vs. subconical (& twisted).

Texas: Duval Co., San Diego, 1885, M.B. Croft 35 (HOLOTYPE: US!; Isotypes: MICH (image!), NY (image!)).

*Chaptalia leonina* Greene, Leafl. Bot. Observ. 1:193. 1906. TYPE: MEXICO. Nuevo León: Monterrey, 17–26 Feb 1880, E. Palmer 764 (HOLOTYPE: US!; Isotypes: US!, NY (image!), GH (image!)).

Acaulescent evergreen PERENNIAL HERB forming a **dense basal rosette**, typically flat on the ground, with one or more flowering stalks (Fig. 7). LEAVES **epetiolate or with short petioles** (Fig. 8), obovate to elliptic with undulate, mucronulate margins, more strongly lobed toward the bottom, new leaves erect with ample moisture, apex acute with a small mucro, the base cuneate in overall form, LEAF BLADE **4.5–20 (–26) cm long (avg. 11.6 cm), 1.5–4 (–6) cm wide, L/W ratio (1.5–) 2–6 (–7)** (Fig. 5); LEAF SURFACE adaxially glabrescent, abaxially tomentose, pinnate venation with primary lateral veins visible on both surfaces; PETIOLE **0–40 (–62) mm (roughly half were sessile)**. PEDUNCLE ebracteate or rarely with 1 or 2 small bracts just below the head, densely woolly, asymmetrically thickened ca. 5 mm below the head, **at anthesis 5–23 cm (avg. 12 cm), at dispersal 5–34 cm (avg. 19 cm)**; INVOLUCRE **cylindrical, slightly narrowing from base to top in fruit (by  $\pm 25\%$ ), expanding from anthesis through fruit c. 1 mm in length, c. 1.5 mm in width** (FIG. 14); PHYLLARIES in 6 unequal series,

**imbricate, subulate and subulate-linear**, abaxial surface densely lanate between the dark crimson midrib and margins where exposed, **rather stiff by virtue of a thick midrib which continues to the tip (ca. 0.23 mm thick 3 mm from the tip; Fig. 10)**, innermost phyllaries 15–20 mm long (avg. 17.7 mm), **of two widths,  $\pm 1.1$  mm  $\phi$   $\pm 1.8$  mm, outer phyllaries commonly greater than 1.5 mm wide** (Fig. 9); RECEPTACLE foveolate, naked, flat, slightly concave in the center, then becoming strongly convex at dispersal. FLORETS **36–107**, more numerous in fall/winter phase (Tables 1, Fig. 2); EARLY SPRING PISTILLATE LIGULATE FLORETS **10–12.5 mm (avg. 11.5 mm), of which the ligule is ca. 5 mm, tube ca. 7 mm, turning crimson with age**; REDUCED LIGULATE FLORETS with style **10–11.6 mm (avg. 11 mm), of which corolla 7.9–9.3 (avg. 9), ligule 1.5–2 mm long, 0.15–0.5 (avg. 0.3 mm) wide**; PERIPHERAL PISTILLATE LONG—TUBULAR FLORETS (**4.5–)5.3–9.2 mm (avg. 6.6 mm)**, asymmetrically 2-lipped, longer lip 0.5–2mm, **tips not swollen**; INNER PISTILLATE FLORETS **9.9–11.2 mm (avg. 10.5 mm), tube 3.6–5 mm (avg. 4.6 mm), lips < 0.5 mm**; CENTRAL PERFECT FLORETS 9–12 mm (avg. 11 mm), width at apex 0.5–0.8 mm, **spring floret lobes spreading, tip acute (not swollen)**. PAPPUS **10.4–14.1 mm (avg. 12 mm), number of bristles 135–203 (avg. 174)** (Figs. 12, 13), covered (9–12 per mm) with antrorse

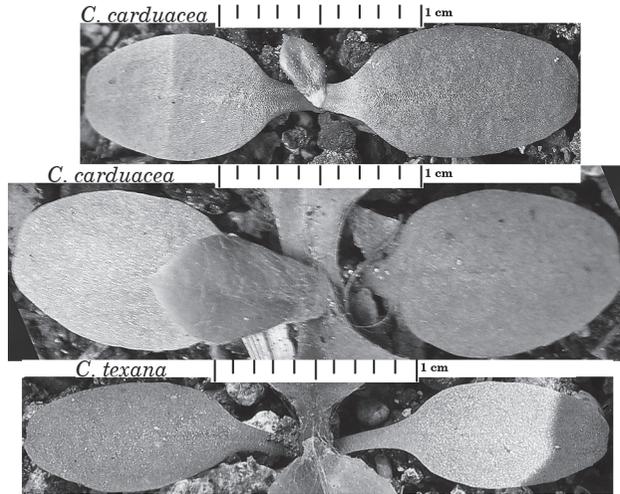


FIG. 15. Cotyledons on May 25. Planted April 17. Lower two germinated on April 25.

barbs 0.05–0.07 mm long; ACHENE fusiform, body 5–8 mm long,  $\pm 1$  mm wide, beak 1–1.6 times longer than body, covered with papillate trichomes  $< 0.1$  mm long. COTYLEDONS **elliptic, less than twice as long as wide, with a petiolar region ca. 2 mm** (Fig. 15). FLOWERING *all months except August; peak bloom mid March to late April*.

DISTRIBUTION: Southeast central Texas from Bastrop Co. west to the Devils River and south to the lower Rio Grande Valley; and south into Mexico; reported from Nuevo León (as *C. leonina* Greene); in deeper soils, often well shaded (Fig. 1).

Both *Chaptalia carduacea* and *C. leonina* were published by Greene in the same publication, and thus either name could be applied to this species from a priority point of view. However, *C. carduacea* is the obvious choice because its type is from within the known Texas range of the species, while the inclusion of the type of *C. leonina* within the species as understood in Texas, even though likely and therefore treated as such here, requires further study.

Texas specimens examined:

**Bastrop Co.:** ca. 1.5 airmiles NW of jct. TEX 17 and FM 1209 NW of Bastrop, McKinney Roughs Tract,  $30^{\circ} 8' 23''$  N  $97^{\circ}$

$26' 53''$  W, elev. 430–440', 19 May 1996, W. R. Carr & P. McNeal 15394 (TEX); **Bee Co.:** 12 mi. E of Beeville, 27 Mar 1963, D. S. Correll 27022 (LL); **Cameron Co.:** Loma Alta, elev. 30', 13 Mar 1937, R. Runyon 1596 (TEX, US); **Comal Co.:** ca. 1 km WNW Startzville, "Deer Haven,"  $29^{\circ} 51' N 98^{\circ} 17' W$  elev. 950–1100, 26 April 1987, C.S. Lieb & V. J. Roessling, Jr. 752 (UTEP); **Goliad Co.:** Goliad, 1 Mar 1927, Rev. C. B. Williams H6 (TEX); Goliad, 8 April 1900, H. Eggert s.n. (US); **Guadalupe Co.:** SE of Seguin, ca. 3/4 air mi. WSW mouth of Mill Cr. at Guadalupe R., on N-facing slope, Bill Kutac farm;  $29^{\circ} 32' 40'' N 97^{\circ} 49' 46'' W$ , 10 Mar 1990, W. R. Carr 10306 (TEX); **Hays Co.:** Purola Preserve, along Deadman's Creek,  $30^{\circ} 17' 18.48'' N 98^{\circ} 09' 56.94'' W$ , elev. 980 ft., 5 May 2010, R.T. Harms 101 (TEX), 5 May 2010, R.T. Harms 102 (TEX), 24 Oct 2010, R.T. Harms 105 (TEX), 4 Dec 2010, R.T. Harms 106 (TEX); **Karnes Co.:** 1 mi. SSE of Cres School, 15 Mar 1953, J. C. Johnson 53-889 (TEX); **Kinney Co.:** along US hwy 90, roadside park 6 mi. E of Brackettville, 29 March 1990, R. D. Worthington 18376 (UTEP); 7 air km NE of Brackettville; 3.3 road mi. NE of jct Ranch Rd. 384 w/ RR 674 (at Lindsey Cr. and RR 384) elev. 1210', 13 Apr 1983, C. S. Lieb 354 (TEX); **Nueces Co.:** Corpus Christi, 27.8006

N 97.3964 W, elev. 5.6', 6 Apr 1905, S. M. Tracy 8959 (TEX, US); **Travis Co.:** Austin, 9 Nov 1940, B. C. Tharp s.n. (TEX); **Uvalde Co.:** Canyon of Sabinal, June 1885, J. Reverchon (US); Uvalde, 30 Apr 1928, E. J. Palmer 33636 (LL); S of Utopia, off Hwy 183. W bank of Sabinal R. belev.ow dam, Tom Smith's Ranch at county road crossing of Sabinal R.), 10 May 1982, L. J. Dorr & K. C. Nixon 2213 (TEX); **Val Verde Co.:** ca. 18 mi. N of Del Rio; 2 mi. S along US 277, jct w/ US 377, 25 Mar 1995, B. L. Turner 95-34 (TEX).

**Chaptalia texana** Greene, Leaf. Bot. Observ. 1:191. 1906. *Chaptalia nutans* (L.) Polak. var. *texana* (Greene) Burkart, Darwiniana 6.569. 1944. TYPE: UNITED STATES. Texas: "rocky, sparsely wooded ground in western Texas," Oct 1890, G.C. Neally 297 (HOLOTYPE: US!).

Acaulescent evergreen PERENNIAL HERB forming a *sparse basal rosette*, typically flat on the ground, with one or more flowering stalks (Fig. 7). LEAVES *typically petiolate* (Fig. 8), obovate to elliptic (less commonly ovate) with undulate, mucronulate margins, more strongly lobed toward the bottom, somewhat erect when young, apex acute with a small mucro, the base cuneate in overall form, LEAF BLADE *5.5–27 cm long (avg. 17 cm), 2–6 cm wide, L/W ratio 2.5–5.5 (–8)* (Fig. 5); LEAF SURFACE adaxially glabrescent, abaxially tomentose, pinnate venation with primary lateral veins visible on both surfaces; PETIOLE (5–) *18–65 mm (all but 3 were at least 18 mm)*. PEDUNCLE ebracteate or rarely with 1 or 2 small bracts just below the head, densely woolly, asymmetrically thickened ca.5 mm below the head, *at anthesis 11–28 cm (avg. 21 cm), at dispersal 20–46 cm (avg. 33 cm)*; INVOLUCRE *cylindrical to subconical, narrowing from base to top, especially in fruit (by 40–50%)*, expanding from anthesis through fruit 0–2 mm in length, 1–4 mm in width (FIG. 14); PHYLLARIES in 6 unequal series, *linear lanceolate, subimbricate*, abaxial surface densely lanate between the crimson to green midrib and margins where exposed,

*tips acute and flexible (ca. 0.1 mm 3 mm from the tip*; Fig. 10), innermost phyllaries 12.3–17.5 mm long (avg. 15 mm), *of uniform width, not exceeding 1 mm, outer phyllaries not exceeding 1.5 mm* (Fig. 9); RECEPTACLE foveolate, naked, flat, slightly concave in the center, then becoming strongly convex at dispersal. FLORETS: **91–155**, more numerous in fall/winter phase (Tables 1, Fig. 2); EARLY SPRING PISTILLATE LIGULATE FLORETS **11–13.2 mm (avg. 12.6 mm)**, *of which ligule is ca. 8 mm, tube ca. 5 mm, with age turning yellow (most Texas populations) or crimson (Medina Co. Texas populations and Mexican populations)*; REDUCED LIGULATE FLORETS *with style 7.6 mm, corolla tube 5 mm, ligule 2.2 mm*; PERIPHERAL PISTILLATE LONG-TUBULAR FLORETS **8–8.5 mm w style, tube 4.5–5.2 mm**, asymmetrically 2-lipped, longer lip 1–2 mm, *often with swollen tips*; INNER PISTILLATE FLORETS **8.8–9.5 mm (9.2 mm), tube 3.1–3.8 mm (3.6 mm)**, lips < 0.5 mm; CENTRAL PERFECT FLORETS 8.8–12 mm (avg. 11 mm), width at apex 0.8–0.9 mm, *spring floret lobes reflexed or curled, tapering to a swollen tip*. PAPPUS **7.6–10.6 mm (average 9.8 mm), number of bristles 70–130 (avg. 100)** (Figs. 12, 13), covered (9–12 per mm) with antrorse barbs 0.06–0.1 mm long; ACHENE fusiform, body 4.5–7 mm long, ± 1 mm wide, beak 1.2–2 times longer than body, covered with papillate trichomes < 0.1 mm long. COTYLEDONS **elliptic, ca. twice as long as wide, with a petiolar region ca. 3.5 mm** (Fig. 15). FLOWERING in *all months; peak bloom early March to early April*. DISTRIBUTION. Southeast Edwards Plateau in central Texas southwest through the S. Trans-Pecos, and into the mountains of Mexico; reported from New Mexico [Parry et al. 674 (US), Mexican Boundary Survey], but the only more recent voucher from New Mexico [Worthington 31834 (UTEP)] has been determined as *Leibnitzia lyrata* (D. Don) G.L. Nesom); in well mulched but shallow rocky calcareous soils, typically well shaded (Fig. 1).

Texas specimens examined:

**Mexican boundary survey, chiefly in the valley of the Rio Grande, below Doñana:** Locale not verifiable, (no date), *C.C. Parry et al. 674* (US (2 sheets)); **W. Texas:** Expedition from Western Texas to El Paso, N. Mexico., 1849, *C. Wright 414* (US); **Bandera Co.:** around old Murphy's cabin; Lost Maples (Sabinal Canyon) State Nat'l Area Growing on grassy slopes, 16 Mar 1975, *Smith & S. Osburn 444* (LL); Love Creek Nature Preserve. 10 mi E of Media, on Hwy 337. 29° 47.44' N 99° 26.86' W elev. 2000', 12 Mar 2001, *G. Denny & S. Harvey 86* (TEX); **Bexar Co.:** Rich soil ravines, Helotes, 4 Apr 1919, *E. Schulz 126* (US); Ravine 20 miles N. of San Antonio, 14 March 1920, *E. Schulz 62* (US); N of I-410 immediately W of cleared San Antonio River corridor, San Antonio Missions NHP. N29°19.424', W098°27.289' ±17.8 ft., Elev. 540 ft., 25 April 2002, *W. R. Carr 20783* (TEX); **Brewster Co.:** Lower Cattail Canyon, Chisos Mtns, 29 August 1936, *O. E. Sperry* (SRSC); Upper Cattail Falls, Chisos Mts., 3 Aug 1937, *B. H. Warnock 323* (TEX); Northeast slopes above lower Window Trail, Basin, Big Bend National Park, 7 Apr 1967, *A. M. Powell & S. Sikes 1526* (TEX, SRSC); Big Bend National Park. In Oak Canyon below the Window, 9 Jan. 1964, *D. S. Correll & H. B. Correll 30608* (LL); Pulliam Canyon, Chisos Mts., 1 Apr 1939, *V. L. Cory 44047* (TEX); above lower Window Trail, Basin, Big Bend Nat'l Park, 7 Apr 1967, *A. M. Powell & S. Sikes 1526* (LL); **Comal Co.:** New Braunfels, May 1846, *F.J. Lindheimer 446* (US); New Braunfels, July 1847, *F.J. Lindheimer 446* (US); W edge of New Braunfels, Landa Park, 17 Apr 1966, *D. S. Correll 32505* (LL); **Edwards Co.:** 13 1/4 mi. SE of Rocksprings, 19 Apr 1942, *V. L. Cory 38949* (TEX); 1.7 mi. N of Kinney Co. line along Hwy. 2523, SW-most part of Edwards Co., 25 Mar 1995, *B. L. Turner 95-31B* (TEX); **Kerr Co.:** ca. 13 mi. SW of Kerrville (along Lamb Cr.), 13 Oct 1967, *D. S. Correll 35085* (LL); **Kinney Co.:** Anacacho Ranch, West-facing canyon on W side of Anacacho Mts., 1 Apr 1965, *D. S. Correll & H. B. Correll 30781* (LL); **Medina**

**Co.:** Geronimo Creek, 19 Apr 1926, *E. R. Bogusch 807* (LL); 3 air km ENE of Mico 29° 32' 0" N 98° 54' 0" W elev. 1180–1220', 19 Mar 1983, *C. S. Lieb & V. J. Roessling, Jr. 306* (TEX); **Real Co.:** Barksdale, Oct., Nov. 1927, *Dry Creek School 6553* (TEX); 11.5 mi. N of Leakey, Hwy 83; on Edwards Plateau, above Rio Frio, 16 Apr 1957, *K. L. Chambers 1144* (LL); canyon below Russell Springs on private ranch ca. 8.3 air miles NE of Camp Wood, 29° 41' 43" N 98° 54' 07" W, elev. 600 ft., 27 Aug 2010, *R.T. Harms 103* (TEX); **Terrell Co.:** 20 miles N of Dryden, 1 November 1958, *B. H. Warnock & M. C. Johnston 17256* (SRSC); 20 miles N of Dryden, 1 November 1958, *B. H. Warnock & M. C. Johnston 17256* (SRSC); on the Mexican side of the Rio Grande a few miles downstream from San Francisco Canyon, 6 Apr 1976, *M. Butterwick & S. Osburn 2257* (LL); Oasis Ranch Preserve (TNC), on rocky slopes and bottom of steep-sided canyon on S side of Independence Creek, ca. 3.5 airmiles E to ESE of jct. Independence Creek Rd. and TX 349, upcanyon from 30°27.364' N, 101°46.051' W. elev. 2000–2200', 5 Apr 2001, *W. R. Carr 19495* (TEX); **Travis Co.:** Austin, Slope D, 22 Nov 1923, *R. H. Painter s.n.* (TEX); Hills west of Austin, 18 Mar 1908, *H. H. York s.n.* (TEX); West of Dam, 5 Nov 1897, *collector unknown s.n.* (TEX); Near Austin, 1 Mar 1943, *B. C. Tharp 43Q106* (TEX); Austin, 30 Mar 1939, *B. C. Tharp s.n.* (TEX); Travis County, 2 Mar 1938, *E. Brackett s.n.* (TEX); Walnut Creek Metropolitan Park. Pflugerville W Quad, 29 Sep 1995, *P. D. Turner 249* (TEX); Martins Ford Road, Ca. 10 mi. NW of Austin, 27 Mar 1949, *C. M. Rogers 6729* (TEX); 4 mi. W of Austin, 11 Mar 1955, *B. Anderson 3* (TEX); canyon that enters Barton Ck. from S, just WSW of Zilker Pk., Austin, 30° 15' 40.6" N 97° 46' 48.5" W, elev. 483', 21 Mar 2010, *R.T. Harms 100* (TEX), 23 Oct 2010, *R.T. Harms 104* (TEX); **Val Verde Co.:** Mouth of Pecos River, 19 March 1947, *B. H. Warnock & R. McVaugh 47217* (SRSC); San Felipe Springs in Del Rio, below main springs, elev. ca. 1000', 24 Nov 1984, *B. Ertter*

*et al* 5516 (TEX); hwy 90 at Pecos R. bridge, E side at overlook, ca. 29° 42' N 101° 21' W elev. 1300', 16 March 1997, R. D. Worthington 26181 (UTEP); Amistad National Recreation Area: Canyon 6 along Devil's R. just upstream and southwest of Big Satan Canyon. UTM: 14R 310323.77855 3282306.02924, 9 Oct

2003, Jackie M. Poole 4913 (TEX, SRSC); **Wilson Co.:** W side of San Antonio River floodplain, Rancho de las Cabras NHS, ca. 0.8 airmiles SSE of St. Rt. 97 bridge over San Antonio River. N29°05.992', W098°09.995' ±24.3 ft. Elev. 400–420 ft., 26-Mar-2002, W.R. Carr 20514 (TEX).

#### ARTIFICIAL KEY FOR CHAPTALIA IN TEXAS

1. Ligules of peripheral florets with a purple midstripe beneath at anthesis; disk florets (functionally staminate; ca. 25) more than twice as numerous as internal pistillate florets (5–11); SE Texas coastal plain . . . . . *C. tomentosa*
1. Ligules of peripheral florets when present uniformly cream colored on both sides at anthesis; internal pistillate florets much more numerous than disk (perfect) florets; central, south and west Texas . . . . . 2
2. Phyllaries flexible, linear-lanceolate, subimbricate, ± 1 mm wide in the middle (Fig. 9); pappus 7.6–10.5 mm long (Figs. 12, 13); ligules of spring florets extending beyond the phyllaries, spreading outward from the involucre at midday and closing in the evening (Figs. 6, 11); heads heliotropic (Fig. 5). . . . . *C. texana*
2. Phyllaries rigid, subulate and subulate-linear, imbricate, typically greater than 1.5 mm wide in the middle (Fig. 9); pappus 10.5–14.1 mm long (Figs. 12, 13); ligules of spring florets, when visible, barely extending beyond the phyllaries and blocked from spreading outward by stiff phyllary tips (Fig. 11); heads not heliotropic (Fig. 5) . . . . . *C. carduacea*

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