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A MULTIVARIATE MORPHOMETRIC STUDY OF *HETEROTHECA INULOIDES* INCLUDING *H. LEPTOGLOSSA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the *Heterotheca inuloides* complex including *H. leptoglossa* was undertaken. The results of a cluster analysis and discriminant analyses on a matrix of 53 plants by 12 characters indicated that the four previously described varieties of *H. inuloides* warrant recognition: *H. inuloides* var. *inuloides*, *H. inuloides* var. *leptoglossa*, *H. inuloides* var. *rosei*, and *H. inuloides* var. *viridis*. The varieties are distinguished based on stem, leaf, and phyllary indument traits, extent of purple coloration of the apices of the phyllaries, and geographical distribution. The var. *leptoglossa* separates most strongly from the other varieties of *H. inuloides*, while var. *rosei* showed the weakest separation. Thus, a case for recognizing a species level *H. leptoglossa* could be made, a case for not recognizing var. *rosei* at all could also be made.

Heterotheca inuloides Cass. (including *H. leptoglossa* DC.) is a goldenaster species (Fig. 1) native to south-central Mexico and is heterocarpic and a member of *Heterotheca* sect. *Heterotheca* (Wagenknecht, 1960; Nesom, 1990; Semple, 1996; Nesom 2019). Wagenknecht (1960), treated *H. inuloides* and *H. leptoglossa* as separate species and recognized two varieties *H. inuloides* var. *inuloides* and *H. inuloides* var. *rosei* Wagenknecht. McVaugh (1983) recognized both species and varieties.

The division of *Heterotheca inuloides* into two varieties was reevaluated in a paper by Nesom (1990), wherein the two varieties described by Wagenknecht were retained and an additional variety, *H. inuloides* var. *viridis* Nesom, was described. Nesom (1990) recognized *H. leptoglossa* as a distinct species. Nesom (2019) subsequently treated the other varieties as separate species: *Heterotheca rosei* (Wagenk.) Nesom and *Heterotheca viridi*s (Nesom) Nesom. The four varieties or species of *H. inuloides* were distinguished based on geographical distribution, leaf and stem indument traits, and phyllary traits.

The geographic distribution outlined in literature for the varieties of *Heterotheca inuloides* is as follows: **var. *rosei*** is restricted to the western portion of the range of the species; **var. *inuloides*** is mainly found in the central portion of the range, although Nesom (1990) recorded specimens of this variety in all parts of the range of the species; **var. *viridis*** is normally found in the southern region in the states of Puebla and Oaxaca; **var. *leptoglossa*** is found primarily in Guanajuato and adjacent Querétaro and San Luis Potosí and disjunct in a small area of eastern Zacatecas and northwestern Querétaro.

According to Wagenknecht (1960), *Heterotheca inuloides* and *H. leptoglossa* could be distinguished by head size (with the heads of *H. leptoglossa* being smaller). Nesom (1990) separated the species based on phyllary indument traits, with the phyllaries of *H. leptoglossa* being less

glandular compared to those of *H. inuloides*. According to Nesom (1990, 2019), var. *inuloides* is distinguished based on a distinct purple coloration on the distal portion of the phyllaries and the presence of thick-based, non-glandular trichomes on the outer phyllaries. According to Wagenknecht (1960), var. *rosei* was distinguished from var. *inuloides* by having sparse, slender hairs on the phyllaries. Nesom (1990) used the trait of absence of non-glandular trichomes or non-glandular trichomes restricted to the distal third of the outer phyllaries to distinguish var. *rosei*. In his description of var. *viridis*, the main diagnostic traits used by Nesom (1990) were the absence of purple coloration and the presence of relatively thin-based, non-glandular trichomes on the outer phyllaries. Nesom (2019) used hair density on phyllaries, presence or absence of anthocyanin purplish color on the phyllary tips to over much of the phyllary, and presence and density of glandular hairs on the phyllaries to distinguish the four species/varieties of *H. inuloides* complex. All of these features are illustrated in Figs. 1-3.

Figure 1. *Heterotheca inuloides* Cass. var. *inuloides*, *La Duke & Jansen 399* OS.

Figure 2. Stem hairs and leaf variation in *Heterotheca inuloides*. **A.** Mid stem, var. *inuloides*, *Roe et al 1532* WIS. **B.** Upper mid stem, var. *viridis*, *Roe & Roe 1989* WIS. **C.** Var. *rosei*, *Powell & Edmondson 862* TEX. **D.** Upper mid stem, var. *leptoglossa*, *Henrickson & Lee 17524* TEX. **E.** Lower mid stem, var. *leptoglossa*, *Powell & Edmondson 562* TEX. **F.** Rosette leaves, var. *inuloides*, *Roe et al. 1532* WIS. **G.** Mid stem and leaves, var. *rosei*, *Diaz Luna 7502* TEX. **H.** Upper mid stem and leaves, var. *viridis*, *Davidze 9623* TEX. Scale bars = 1 cm.

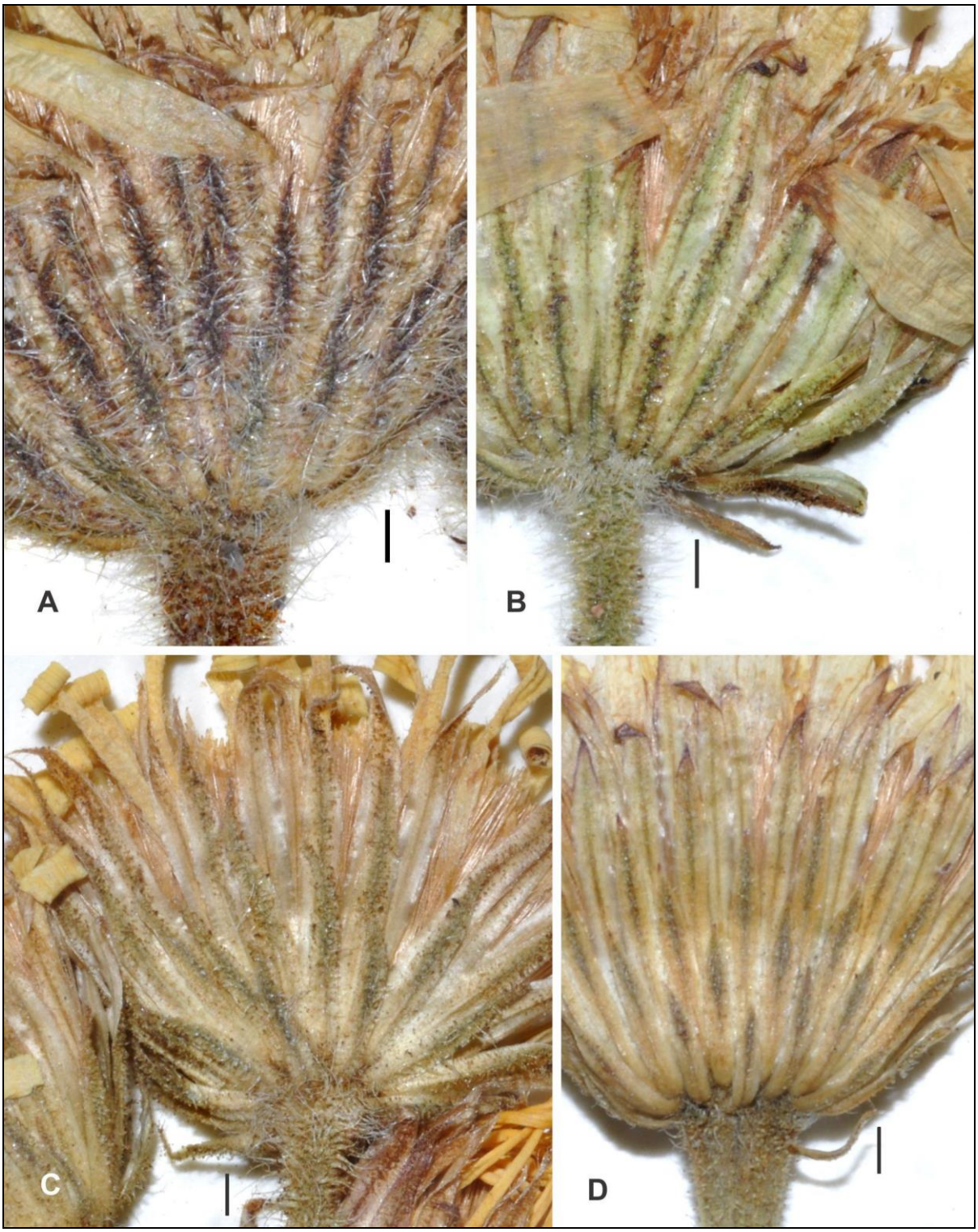

Figure 3. Involucre and phyllary variation in *Heterotheca inuloides*. **A.** Var. *inuloides*, *Marcks & Marcks 1139* WIS. **B.** Var. *viridis*, *Soule & Loockerman 2657* TEX. **C.** Var. *rosei*, *Rinehart 7332* TEX. D. Var. *leptoglossa*, *Rzedowski 38673* TEX. Scale bars = 1 mm.

The purpose of this investigation was to statistically examine the four varieties/species of *Heterotheca inuloides* to determine which traits are most useful in distinguishing these varieties/species and to determine if there are in fact four distinct varieties/species or if there is merely a continuum or cline following geographical distribution. *Heterotheca leptoglossa* was included for comparison and to determine its morphological relationship to *H. inuloides*. Following our conclusions, *H. leptoglossa* is referred to as *H. inuloides* var. *leptoglossa* R.E. Cook & Semple in the remainder of this paper.

MATERIALS AND METHODS

Herbarium specimens were borrowed and examined from herbaria in the USA (WIS, MIN, OS, TEX, NY, and SD; Thiers, continuously updated). These herbaria were selected because they are where specimens collected in large numbers in the assumed ranges of the taxa were believed to be located. Of the 174 herbarium specimens obtained, 63 specimens were selected for inclusion in the multivariate analyses. All complete specimens available at the correct stage of development were measured for this study. The distribution of these specimens in Mexico is shown in Fig. 4. Of the 63 specimens scored, 53 specimens were included in the canonical analyses, while the others were excluded do to missing data, e.g. immature or too mature heads. The key to taxa in Nesom (2019) was used to identify all specimens included in this study.

A detailed multivariate morphometric analysis of a sufficiently large enough sample set as to include representatives of all morphological variants was undertaken to quantitatively determine how distinct each of the four species/varieties were from each other. In order for this to be accomplished, a data matrix of specimens scored for many floral and vegetative traits was constructed. This matrix was then subjected to univariate and multivariate analyses, including clustering, canonical variate analysis, stepwise discriminant analysis and classificatory discriminant analysis.

A list of the major and possible minor distinguishing traits for the taxa was created. All of the characters scored and their abbreviated variable names are listed in Appendix 1. Characters marked with an asterisk were not included in the canonical analysis as they were one of a pair of characteristics that had a correlation coefficient of $| r | > 0.7$, they were used in assigning the specimens to their *a priori* groups, or a significant number of plants were missing these traits making analysis unrepresentative. Replicates of five measurements for each trait were obtained per plant (if present) and averaged. The measured specimens were selected based on the suitability of their stage of development and geographical distribution from all of the specimens available. Measurements were made on structures at the same stage of development and position on the plant regardless of the actual age of the plant.

Membership in *a priori* groups was based on the morphological traits included in the key in (Nesom 2019). Geographical locations of all collections were determined and mapped (Fig. 4) using Google Earth Pro 2025.

SYSTAT 10 for Windows (SPSS Inc., 2000), SAS Version 8.01 (SAS Institute Inc., 2000) and Microsoft Excel 97 (Microsoft Corporation, 1996) were used for all statistical, cluster, canonical and discriminant analyses of the data. Characters used to determine *a priori* groups: upper and lower leaf indument traits, and outer phyllary indument traits and purple colouration, were not included in the canonical analyses to avoid circular logic.

Cluster analysis of the 63 specimens using average linkage on squared Euclidean distances (UPGMA) and all of the measured characteristics standardized with mean (x) equal to zero and standard deviation (SD) equal to one were calculated and graphed for the examination of this species. Clustering is used to determine the relative similarity of the *a priori* groups using unweighted characteristics.

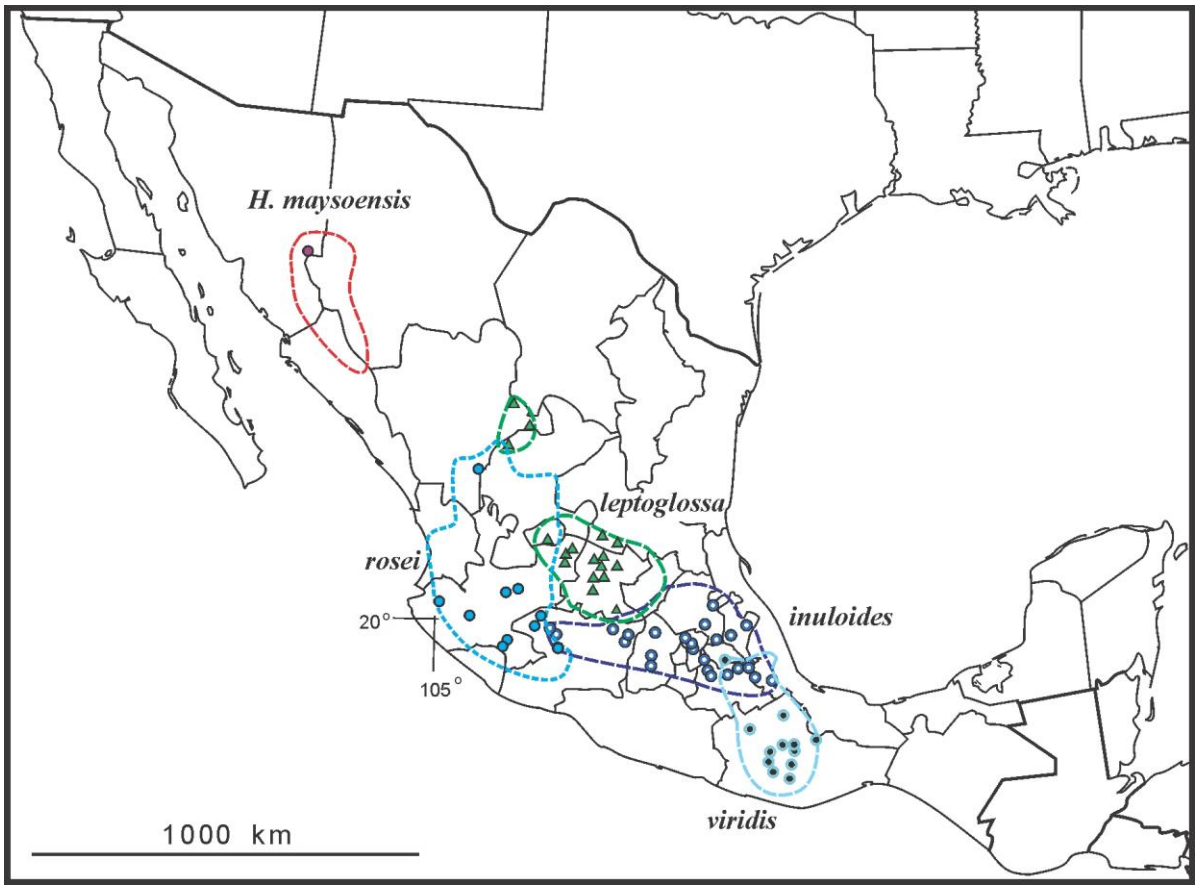

Figure 4. Distribution of 63 specimens of *Heterotheca inuloides* (including *H. leptoglossa*) examined in the multivariate analyses of 53 specimens: var. *inuloides* (white dots with black and blue outlines), *var. leptoglossa* (green triangles) var. *rosei* (bright blue dots with black outlines), and var. *viridis* (dark blue dots with light blue outlines). One specimen of *H. mayoensis* (red dot) was also scored but not included in the analyses. Ranges have been modified from Nesom (2019); symbols are similar to those used by Nesom (2019).

A Pearson's Correlation was performed to identify pairs of characters with a high degree of correlation ($| r | > 0.7$) and one member of each pair was then excluded from further statistical analyses. The data set was standardized with the x=0 and SD=1 to eliminate biases due to the relative differences in magnitude of some of the characters. Stepwise discriminant analysis was used to select a subset of characters which best demonstrated the differences between the *a priori* groups. Discriminant statistical analyses (including tests for equality of group centroids, Wilk's lambda, Pillai's Trace and Hotelling-Lawley Trace and Geisser assignment probabilities) were performed on the data matrix using the characters identified by the step-wise discriminant analysis. The Geisser assignment probabilities are a measure of the reliability of the *a posteriori* classification of the specimens relative to the *a priori* groupings and the strengths of alternative placements of the specimens. Correct *a posteriori* classification with low assignment probabilities may indicate weak group separation. These analyses were then used to determine the most suitable rank for the statistically distinct groups of plants.

In the taxonomic treatment, the range of variation of quantitative characters is expressed as mean (in bold face), the statistically normal range of variation (i.e. minus to plus one standard deviation) and the maximum and minimum values (in parenthesis). These were calculated using the aforementioned statistical packages.

RESULTS

A clustering analysis using average linkage on squared Euclidean distances (UPGMA), was obtained. The cluster tree for this algorithm shows poor separation of the groups with no distinct groupings with the exception of most of the specimens of *H. inuloides* var. *leptoglossa* (Fig. 5). The remaining branches contained a mixture of several different varieties although there were some clusters of 5-9 specimens of the varietal *a priori* groups.

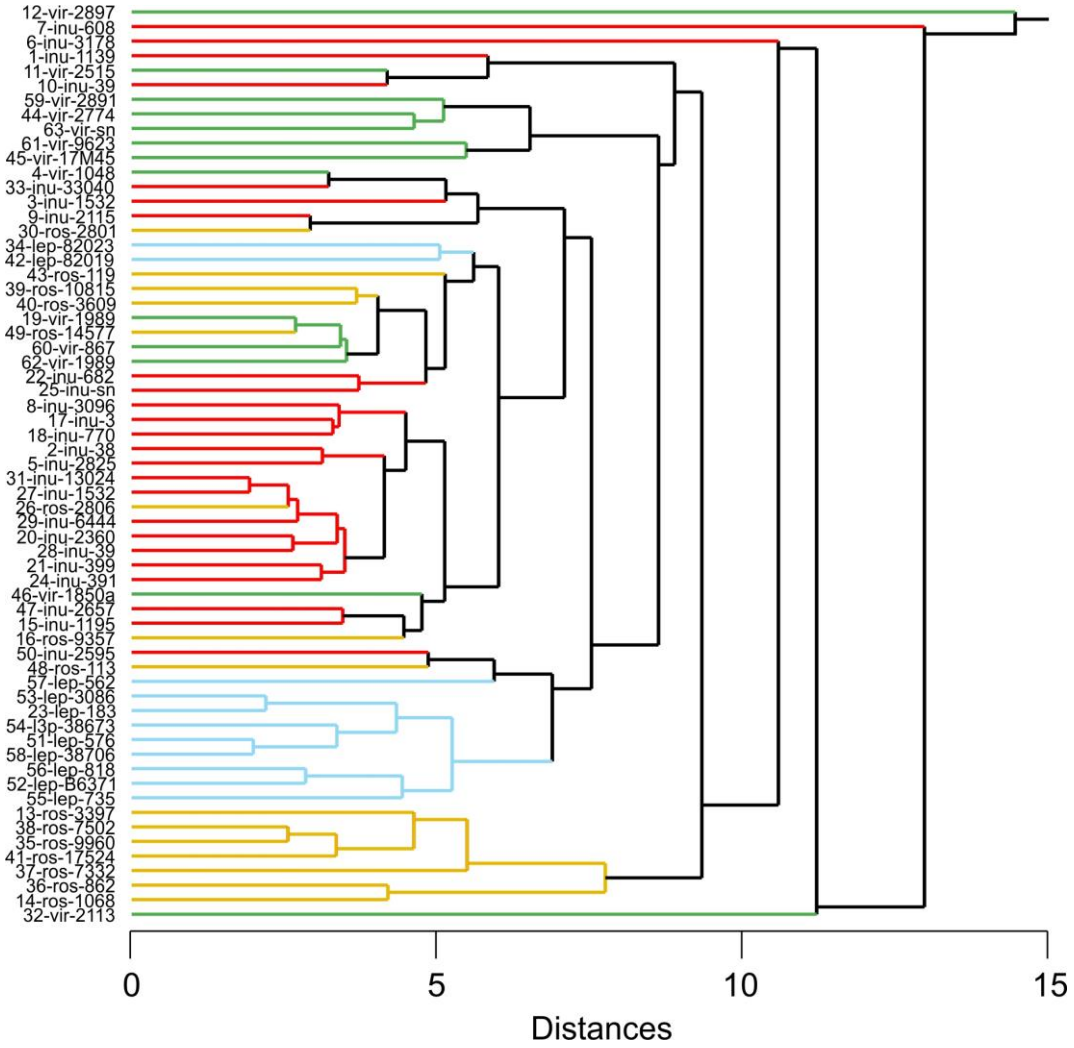

Figure 5. UPGMA cluster analysis of 63 specimens of *Heterotheca inuloides*: red lines for var. *inuloides* specimens, blue lines for var. *leptoglossa* specimens, yellow-orange lines for var. *rosei* specimens, and green lines for var. *viridis* specimens.

As the characters used to determine membership in the *a priori* groups cannot be included in the discriminant analysis; all traits scored are listed in Appendix 1 and means and standard deviations for all characters by variety are presented in Appendix 2. Ranges of leaf and phyllary indument traits and phyllary apex colouration are shown in box plots in Fig 6 (A-F). As can be seen in Fig. 6, the upper leaves of var. *leptoglossa* usually have considerably more hairs and less glands than the other three recognized varieties of *H. inuloides*. On the distal portions of the phyllaries (Figure 6 D), var. *leptoglossa* also has significantly fewer glands on average, while both it and var. *rosei* have significantly fewer hairs on average than the other two varieties of *H. inuloides*.

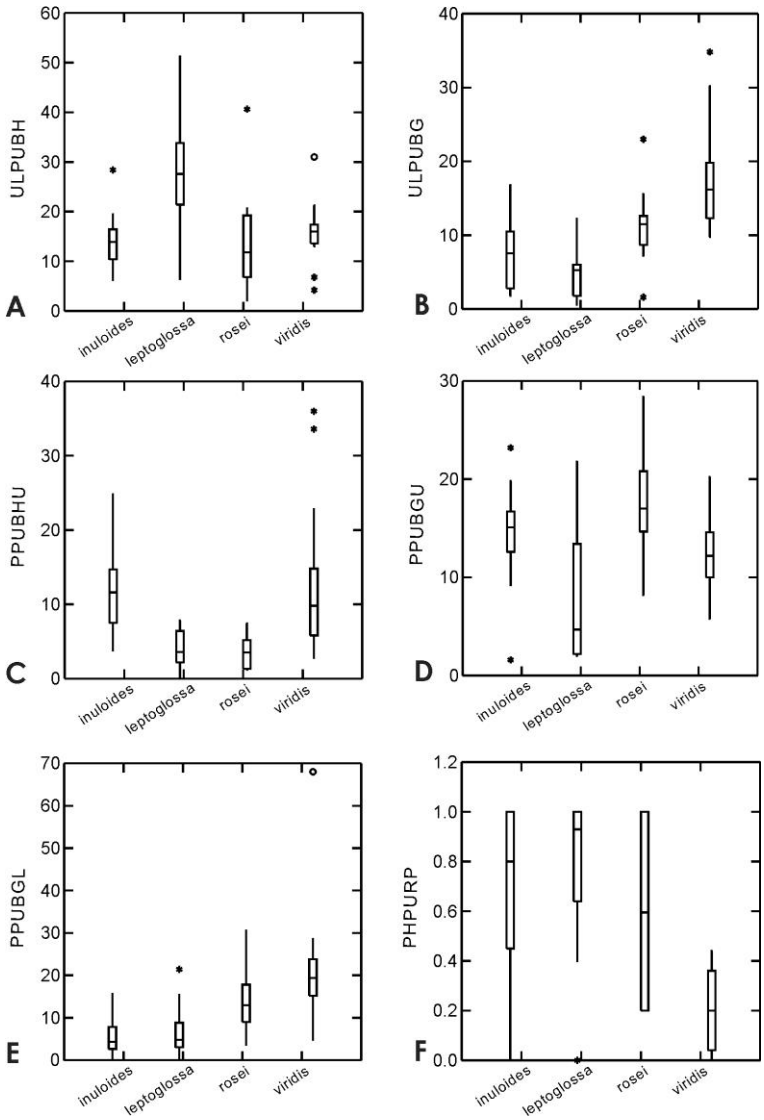

Figure 6. SYSTAT Box plots of leaf and phyllary indument traits and phyllary apex colouration in varieties of *Heterotheca inuloides*. **A.** Upper leaf hair density (UPUBH). **B.** Upper leaf gland density (ULPUBG). **C**. Outer phyllary hair density (distal third; PPUBHU). **D.** Outer phyllary gland density (distal third; PPUBGU). **E.** Outer phyllary gland density (proximal third; PPUBGL). **F.** Amount of anthocyanin along distal phyllary margins; 0-1 scale (PHPURP).

A step-wise discriminant analysis including all of the 53 specimens was performed using 15 characteristics to determine which characters were most useful in separating the putative taxa. Only the 7 characters with the highest F-values were selected to perform a complete discriminant analysis due to the small sample size of *Heterotheca inuloides* var. *rosei* (N=8). The selected characters in order of decreasing order of discriminatory power (F-to-remove) were upper leaf length (7.31), ray floret strap length (6.60), upper leaf length from widest point to tip (5.88), number of disc florets (5.46), and upper leaf width (2.51). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all four varietal groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated that the largest separations were between var. *inuloides* and var. *viridis* (7.186) and between var. *inuloides*

and var. *leptoglossa* (6.637); the smallest separations were between var. *inuloides* and var. *rosei* (1.795) and var. *leptoglossa* and var. *rosei* (2.411). Statistical summaries of all characters including mean, standard deviation and range can be found in Appendix 2 and Appendix 3.

In the Classificatory Discriminant Analysis of 53 specimens of the four varietal level *a priori* groups (var. *inuloides*, var. *leptoglossa*, var. *rosei*, and var. *viridis*), percents of correct *a posterori* assignment to the same *a priori* group ranged from 56-92%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. Eleven of the 12 specimens of var. *leptoglossa* (92%) included *a priori* in the analysis were placed *a posteriori* into var. *leptoglossa*: 6 specimens with 93-99% probabilities; 1 specimen with 87% probability, and 4 specimens with 72-79% probability. One specimen of var. *leptoglossa* included *a priori* was placed *a posteriori* into var. *viridis* with 41% probability (35% into var. *rosei*, and 22% into var. *inuloides*); *Henrickson B6371* TEX-LL from the disjunct portion of the range in eastern Zacatecas; annotated by Nesom in 1990 as *H. leptoglossa*. Eight of the 10 specimens of var. *viridis* (80%) included *a priori* were placed *a posteriori* into the var. *viridis* group: 1 specimen with 100% probability, 3 specimens with 97-98% probability, 2 specimens with 88% and 77% probabilities, 1 specimen with 67% probability, and 1 specimen with 42% probability. Two specimens of var. *viridis* included *a priori* were placed *a posteriori* into var. *inuloides* with 59% and 44% probabilities. Sixteen of the 22 specimens of var. *inuloides* (73%) included *a priori* were placed *a posteriori* into var. *inuloides*: 3 specimens with 90-99% probability, 3 specimens with 80-82% probabilities, 3 specimens with 70-76% probabilities, 3 specimens with 64-69% probabilities, 2 specimens with 55% and 58% probabilities, and 1 specimen with 46% probability. Six specimens of var. *inuloides* included a priori were placed *a posteriori* into other varieties: 3 specimens into var. *viridis* with 71%, 70%, and 56%; 2 specimens into var. *rosei* with 84% and 69%; and 1 specimen into var. *leptoglossa* with 57% probability. Five of the 8 specimens of var. *rosei* (56%) included *a priori* were placed *a posteriori* into var. *rosei*: 1 specimen with 96% probability, 2 specimens with 63% and 60% probabilities, and 2 specimens with 59% and 50% probabilities. Four specimens of var. *rosei* were placed *a posteriori* into other varieties: 2 specimens with 71% and 48% into var. *leptoglossa*; 1 specimen with 87% into var. *inuloides*, and 1 specimen into var. *viridis* with 50% probability.

A canonical analysis was performed as part of the discriminant analysis. A plot of the canonical variant scores on the first and second, and first and third axis (CAN 1, CAN 2 and CAN3) for the putative taxa examined in this analysis are plotted in Fig. 7. The eigenvalue for the first canonical variate was 1.534, the second was 0.710, and the third was 0.204

Table 6. Between groups F-matrix for the four variety a priori groups analysis.

Group	***inuloides***	***leptoglossa***	***rosei***
leptoglossa	6.637		
rosei	1.795	2.411	
viridis	3.909	7.186	3.487

Wilks' lambda = 0.1916 df = 8 3 49
Approx. F= 3.9028 df = 24 122 prob = 0.0000

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four *a priori* groups; *a posteriori* placements to groups in rows.

Group	*inuloides*	*leptoglossa*	*rosei*	*viridis*	% correct
inuloides	16	1	2	3	73
leptoglossa	0	11	0	1	92
rosei	1	2	5	1	56
viridis	2	0	0	8	80
Totals	19	14	7	13	75

Jackknifed classification matrix

Group	*inuloides*	*leptoglossa*	*rosei*	*viridis*	% correct
inuloides	13	2	4	3	59
leptoglossa	0	11	0	1	92
rosei	2	5	1	1	11
viridis	2	1	1	6	60
Totals	17	19	6	11	58

DISCUSSION

The results of the discriminant analysis indicate that there is support for the recognition of four varietal level groups within *Heterotheca inuloides* rather than 4 species following Nesom (2019). Variety *leptoglossa*, var. *viridis*, and var. *inuloides* had very strong to moderate degrees of *a posteriori* placement of specimens to respective varieties using characteristics not used to place specimens into varieties *a priori*. Placement *a posteriori* to var. *leptoglossa* was the highest (92% in both the classification matrix and the jacknifed classificatio), which could be argued is sufficient to warrant species level status. In contrast, placement *a posteriori* to var. *rosei* was only 56%, which is low but the sample size was small. In the Jacknife Classification correct placement of var. *rosei* dropped to only 11%. Recognizing this taxon as *H. rosei* is not supported by the discriminant analysis, which did not include characters used to define the *a priori* groups and did not include characters which correlated highly (i.e. $| r | > 0.7$) and were excluded. Thus, these varieties were discriminated in the analyses based on characters not used to define membership. The assumption is that if truly distinct, i.e. worthy of species level recognition, the four groups would still separate strongly, but some do not. The ranges indicated in Fig. 4 show more overlap in ranges than did the map in Nesom (2019), we agree that the four varieties have ranges that are mostly allopatric, but not exclusively. We found some difficulty in determining levels of phyllary pigmentation. Thus, we agree that it is a useful trait in separating the four taxa but may not be as absolute as Nesom (1919) indicated. Also, anthocyanin concentration may decrease with age of the collection and and as a result of the method used to dry collections in the field.

A main factor which will affect the separation of the groups is the sample size examined. While 22 specimens were identified *a priori* as *Heterotheca inuloides* var. *inuloides*, only 12 as var. *leptoglossa*, 10 as var. *viridis*, and 9 as var. *rosei* were analyzed in the discriminant analysis. With such small sample sizes for some *a priori* groups, variances among the individual plants is high. If the sample sizes were increased to include at least 20-30 individuals of each variety, the variance could decrease dramatically thereby potentially increasing the separation of the groups. All available specimens at the same stage of development were included in this examination. If work on this species is to continue in the future, more loans from herbaria specializing in collections from Mexico would need to be procured.

The geographic locations of specimens with weak a posteriori placement to the *a priori* taxa were checked to see if such specimens came from near the range limits of each taxon where two or more varieties are sympatric. The 4 specimens of var. *rosei* assigned *a posteriori* to other taxa came from within the range of the variety in Jalisco and far western Michoacan States in Mexico which is in the allopatric portion of the variety's range. The 2 specimens var. *viridis* assigned *a posteriori* to var. *inuloides* came from the central and southern portions of Oaxaca state which is in the heart of the allopatric portion of the variety's range. The 6 var. *inuloides* specimens assigned *a posteriori* to other varieties came from the states of Mexico, and northern Puebla. The 1 specimen of var. *leptoglossa* assigned a posteriori to var. *viridis* came from eastern Zacatecas state in the disjunct portion of the range. All but 1 of the misassigned specimens came from the allopatric portions of ranges of the varieties. If these specimens were initially misassigned to the incorrect variety respectively, then the ranges of distribution of the four varieties would be far more sympatric than the *a priori* assignments indicate in Fig. 4 which includes ranges with more areas of sympatry than Nesom (2019) indicated.

Nesom (1919) used perenniality as a secondary key character with his *Heterotheca inuloides* and *H. viridis* being perennial and his *H. leptoglossa* and *H. rosei* being annual to biennial or perennial. Thus perenniality is a sometimes weak or non discriminating character in this group of taxa. The most likely situation is that, due to the latitude of the region, there are only mild winter periods in some years thus allowing plants which might not be able to persist for several years to persist longer under more favorable conditions (Venable and Levin, 1983). Thus, the boundary between annual and perennial is blurred.

Another major distinguishing character between the species *Heterotheca inuloides* and *H. leptoglossa* according to Wagenknecht (1960) was head height with the heads of *H. inuloides* ranging from 1.5-3.0 cm and those of *H. leptoglossa* ranging from 0.5-1.2 cm. As can be seen in Appendix 3, there is no major difference in involucre heights between the four *a priori* groups. Nesom (2019) used phyllary indument traits to distinguish his four species which are more strongly supported traits and are discussed further below.

In his key to the four species of the *Heterotheca inuloides* complex, Nesom (2019) used the absence of or very low number of non-glandular hairs to identify var. *rosei*. In the analysis of the specimens examined, no such plants were identified (Fig. 6 C-E). All of the specimens of var. *rosei* examined except one had some non-glandular hairs present on the distal half of the phyllaries. Wagenknecht (1960) and Semple (1996) both used indument features of the stem and leaves and sparse hairs on the phyllaries to distinguish var. *rosei*. As can be seen in Figs. 6 C-E, there are less hairs on the outer phyllaries of the var. *rosei* specimens, particularly on the distal third of the phyllaries, in comparison with var. *inuloides* and var. *viridis*. While plants of var. *leptoglossa* also have few to no hairs on the phyllaries, they also tend to have few glands on the phyllaries. The other three varieties of *H. inuloides* can be considerably more glandular.

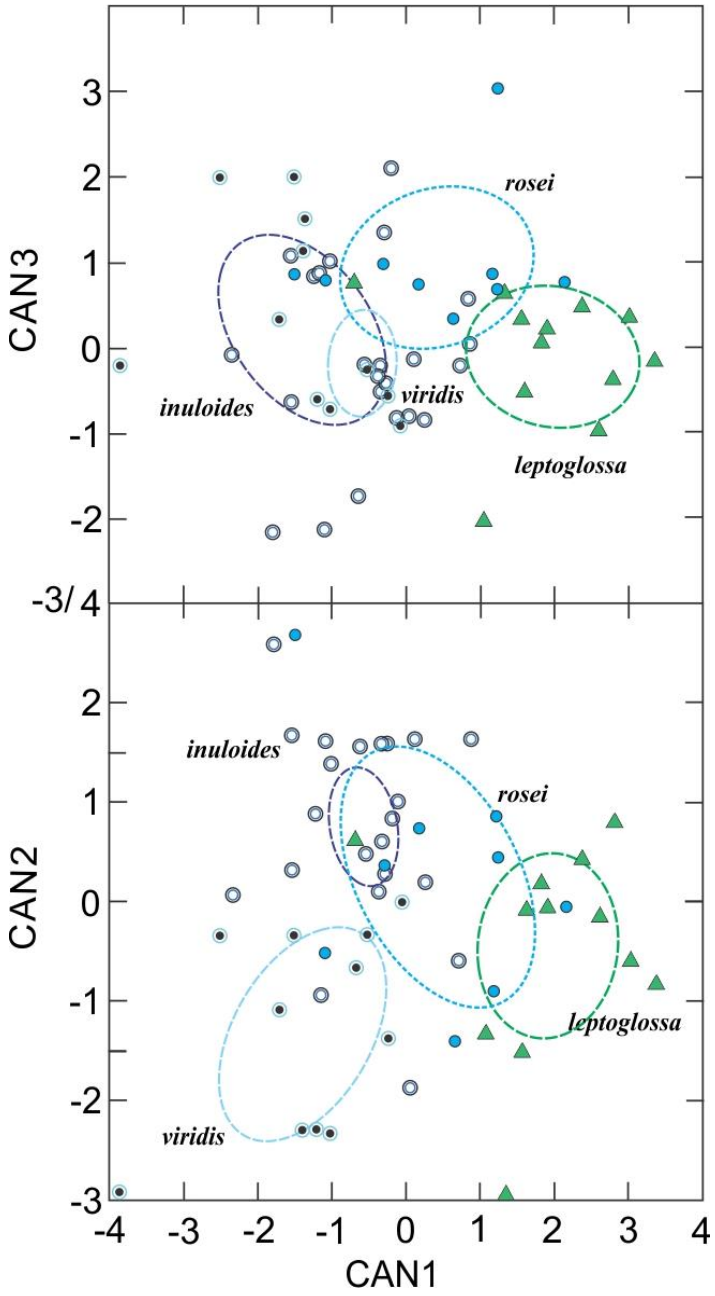

Figure 7. Plot of canonical scores (CAN1 vs CAN2 and CAN1 vs CAN3) generated by a COMPLETE discriminant analysis using 8 traits of 53 specimens of *Heterotheca inuloides*: var. *inuloides* (white dots, black outline, blue inner outline), var. *leptoglossa* (green triangles), var. *rosei* (bright blue dots with black outlines), and var. *viridis* (dark blue dots with outer light blue circles). Symbols are the same as used on the range map (Fig. 4).

In his protologue for var. *viridis*, Nesom (1990) described the phyllaries as completely lacking purple colouration and as having thin based non-glandular trichomes. Semple (1996) used stem, leaf, and phyllary indument traits to identify this variety. Several of the specimens examined, which were determined *a posteriori* to belong to the var. *viridis*, showed a slight purple colouration on the apices of the outer phyllaries (average purple colouration of 0.2 on a scale of 0-1 with a range of 0.0-0.7). The trait of purple colouration was used to determine the *a priori* groups, and hence was

excluded from the discriminant analysis. Thus, these plants were determined *a posteriori* to belong to the var. *viridis* even though they had a slight purple colouration of the phyllaries. This indicates that the absence of purple colouration on the apices of the phyllaries is not a fully diagnostic trait for separating var. *viridis* from the other varieties. Anthocyanin, which is responsible for the purple colouration, breaks down over time and is environmentally plastic. Thus, the extent of purple colouration of the apices of the phyllaries can be a weak character for use in distinguishing between varieties.

Figure 7 shows plots of the canonical variant scores on the first and second and first and third canonical axes (CAN 1 vs. CAN 2, and CAN1 vs. CAN3). The four *a priori* groups are partially separated from one another. If *Heterotheca inuloides* and *H. leptoglossa* were distinct species, it would be expected that the specimens of *H. leptoglossa* would separate strongly from those of the varieties of *H. inuloides*. This is not the case in Fig. 7 as the 95% confidence limits of var. *leptoglossa* overlaps with var. *rosei* in both the CAN1 vs CAN2 and CAN1 vs CAN3 plots in Fig. 7. Also, the between group Mahalanobis distances (Table 4), while supporting the presence of four groups, do not show strong support for retaining *H. leptoglossa* as a separate species.

The var. *viridis* and var. *rosei* of *Heterotheca inuloides* are difficult to distinguish from one another based on the diagnostic traits in the previously published keys. A new key to the *Heterotheca inuloides* var. *inuloide*s, var *viridis*, var. *rosei* and var. *leptoglossa* is presented below and is based on the existing keys and on the characteristics analyzed in this investigation.

TAXONOMIC TREATMENT

Heterotheca inuloides Cass., Dict. Sci. Nat.51: 460. 1827. **TYPE**: **MEXICO**. without other data. (Probable holotype: FI-Herb. Webbianum ex Herb. Desf., GH photo!, annotated in Cassini's hand as "Heterotheca inuloides, H. Cass.").

Nesom (1990) noted that according to Cassini the plant came from Desfontaines and originated in México. It was sent by de Candolle from Geneva to the Jardin du Roi (presumably Paris). A second specimen (G-DC!; "J. de Paris 1828) is a possible duplicate).

Biennial to perennial from woody taproots, STEMS one to several, ascending to erect standing, (4.9)-22.4-**40.2**-58.0-(83.0) cm tall. LOWER STEM LEAVES spatulate to lanceolate, (1.7)-2.6-**3.8**-4.9-(7.6) cm long, (0.4)-0.7-**1.1**-1.4-(2.1) cm wide, sessile, sparsely to moderately hispid to hispid-strigose (3)-8-**15**-22-(35) hairs/mm^2, sparsely to moderately glandular (1)-2-**7**-12-(27) glands/mm^2, margins with (0)-1-**3**-5-(7) dentations. UPPER STEM LEAVES narrowly lanceolate to lanceolate, sessile, (1.1)-1.3-**1.9**-2.5-(4.1) cm long, (0.2)-0.3-**0.4**-0.6-(1.0) cm wide, bases rounded, sparsely to densely hispid (2)-8-**17**-27-(51) hairs/mm^2, sparsely to moderately glandular (1)-2-**9**-17-(35) glands/mm^2, margins entire to slightly dentate. CAPITULESCENCE solitary or paniculiform, branches ascending. INVOLUCRES cylindrical or campanulate when fresh, campanulate upon drying, (0.7)-0.8-**0.9**-1.0-(1.4) cm high, (1.3)-1.5-**1.7**-1.9-(2.3) cm wide; phyllaries in 4-6 imbricate series, outer 1/4-1/3 length of inner, distal 1/3 of outer phyllaries sparsely to moderately glandular (1)-7-**13**-19-(28) glands/mm^2, sparsely to moderately hispid-strigose (0.0)-1-**9**-16-(36) hairs/mm ^{2}; medial 1/3 of outer phyllaries sparsely to densely glandular (4)-7-**19**-30-(48) glands/mm^2, sparsely to densely hispid-strigose (1)-5-**17**-29-(50) hairs/mm^2; proximal 1/3 of outer phyllaries sparsely to densely glandular (0)-0-**11**-22-(68) glands/mm^2, sparsely to moderately hispid (0)-1-**7**-13-(28) hairs/mm^2; purple colouration of the phyllary apices (0)-0.1-**0.5**-1.0-(1.0) on a scale of 0-1. RAY FLORETS (20)-23-**30**-36-(46), strap yellow, (4.5)-7.1-**9.5**-12.0-(15.1) mm long, (0.7)-0.9-**1.4**-1.8-(2.8) mm wide; corolla (2.8)-3.6-**4.2**-4.9-(7.0) mm long; achenes (0.6)-1.1-**1.7**-2.2-(3.2) mm long, sparsely to densely pubescent (0.0)-0.0-**1.0**-2.0-(5.0) on a scale of 0-5. DISC FLORETS (33)-64-**84**-105-(151), yellow, corolla (4.5)-5.0-**5.6**-6.2-(6.8) mm long; achenes (0.6)-1.2-**1.8**-2.5-(4.0) mm long, moderately to densely pubescent (2.6)-3.5-**4.3**-5.0-(5.0) on a scale of 0-5; pappus (4.4)-5.1-**5.8**-6.5-

(7.8) mm long. Chromosome number 2*n*=18.

Distribution. Much of south central Mexico (Fig. 4); 300-3000m elevation. Details of the distribution are discussed below under each variety.

Discussion. *Heterotheca inuloides* is distinguished from the other members of sect. *Heterotheca* by its large head size (involucre height of 7.0-14.0 mm). It is also the only species of the section native to south central inland Mexico. The species is divided into four varieties differentiated on the basis of leaf and phyllary indument traits and, to a lesser extent, geographical distribution.

Key to the varieties of *Heterotheca inuloides* Cass.
(based on Wagenknecht 1960, Nesom 1990, and Semple 1996, with modifications)

1. Outer phyllaries moderately to densely hispid-strigose with hairs along the length of the phyllary.

   2. Phyllaries with distinct purple coloration at the apices, with large, non-glandular trichomes and sparse glands; Michoacan, E to western Veracruz and S to Puebla in Mexico, 300-3000 m ..... **H. inuloides** var. **inuloides**

   2. Outer phyllaries with weak to no purple coloration at the apices with relatively thin based, non-glandular trichomes, densely glandular along the entire length of the phyllary; NE Michoacan, E to Hidalgo and S to Oaxaca in Mexico, 1000-3400 m ..... **H. inuloides** var. **viridis**

1. Outer phyllaries with sparse hairs, if present concentrated on the distal 1/3 of the phyllary.

   3. Outer phyllaries moderately glandular on the distal half sometimes with moderate purple color along the edges and apices; habit erect; S Jalisco and western Michoacan; 1000-2800 m ..... **H. inuloides** var. **rosei**

   3. Outer phyllaries sparsely glandular and hairy with strong purple coloration isolated at the apices; habit strongly erect; Aguascalientes SE to Guanajuato and Querétaro and disjunct in exteme SE Durango and adjacent Zacatecas states; 1900-2800 m ..... **H. inuloides** var. **leptoglossa**

1. ***Heterotheca inuloides*** Cass. var. ***inuloides***

Biennial to perennial from woody taproots, STEMS one to several, erect standing (4.9)-15.5-**34.9**-54.3-(83.0) cm tall. LOWER STEM LEAVES spatulate to lanceolate, (2.4)-2.5-**3.8**-5.0-(7.6) cm long, (0.5)-0.8-**1.1**-1.5-(1.7) cm wide, sessile, sparsely to moderately hispid (4)-7-**12**-18-(27) hairs/mm^2, sparsely glandular (1)-3-**6**-9-(15) glands/mm^2, margins with (0)-1-**3**-4-(5) dentations. UPPER STEM LEAVES narrowly lanceolate to lanceolate, sessile, (1.2)-1.5-**2.1**-2.7-(3.4) cm long, (0.2)-0.3-**0.5**-0.8-(1.0) cm wide, bases rounded, sparsely to moderately hispid (6)-8-**12**-16-(19) hairs/mm^2, sparsely to slightly glandular (2)-2-**8**-13-(17) glands/mm^2, margins entire to slightly dentate. CAPITULESCENCE solitary or paniculiform, branches ascending. INVOLUCRES cylindrical or campanulate when fresh, campanulate upon drying, (0.8)-0.9-**1.0**-1.1-(1.1) cm high, (1.3)-1.4-**1.6**-1.8-(1.9) cm wide; phyllaries in 4-6 imbricate series, outer 1/4-1/3 length of inner, distal 1/3 of outer phyllaries sparsely to moderately glandular (2)-9-**14**-18-(23) glands/mm^2, sparsely to moderately hispid-strigose (1)-5-**10**-16-(25) hairs/mm ^{2}; medial 1/3 of outer phyllaries sparsely to moderately glandular (7)-7-**13**-20-(29) glands/mm^2, sparsely to densely hispid-strigose (6)-11-**20**-29-(43) hairs/mm^2; proximal 1/3 of outer phyllaries sparsely glandular (1)-2-**7**-11-(18) glands/mm^2, sparsely to moderately hispid (1)-4-**10**-16-(21) hairs/mm^2; strong purple colouration of the phyllary apices (0)-0.3-**0.7**-1.0-(1.0) on a scale of 0-1. RAY FLORETS (21)-23-**28**-32-(36), strap yellow, (5.6)-6.5-**8.7**-10.9-(13.8) mm long, (0.7)-1.0-**1.3**-1.7-(2.1) mm wide; corolla (2.8)-3.6-**4.2**-4.8-(5.0) mm long; achenes (1.0)-1.2-**1.6**-1.9-(2.4) mm long, sparsely to moderately pubescent (0.0)-0.6-**1.3**-2.1-(2.4) on a scale of 0-5. DISC FLORETS (33)-54-**78**-102-(151), yellow, corolla (4.7)-5.1-**5.5**-6.0-

(6.7) mm long; achenes (1.1)-1.3-**1.7**-2.2-(3.1) mm long, moderately to densely pubescent (2.6)-3.1-**4.0**-4.9-(5.0) on a scale of 0-5; pappus (4.9)-5.3-**5.6**-6.0-(6.2) mm long. Chromosome number 2n=18.

Distribution. Northern Michoacan, Mexico, Hidalgo, Federales, Tlaxcala, northern Puebla and adjacent Veracruz states in central Mexico (Figure 4); 300-3000m elevation.

Discussion. Var. *inuloides* is distinguished from the other varieties of *Heterotheca inuloides* by its outer phyllary indument traits. The outer phyllaries are moderately to strongly hispid along the entire length of the phyllary with sparse glands and strong purple colouration at the apices (Figure. 3A). Its lower leaves have few serrations.

2. ***Heterotheca inuloides*** Cass. var. ***viridis*** Nesom, Phytologia 69: 286. 1990. **TYPE**: **MEXICO**. **Oaxaca**. Dist. del Centro, Monte Alban, 1850 m, 14 Oct 1932, *C. Conzatti 4794* (holotype: LL; isotype: MEXU, digital image!).

Biennial to perennial from woody taproots, STEMS one to several, erect standing (17.7)-29.1-**44.6**-60.2-(64.0) cm tall. LOWER STEM LEAVES spatulate to lanceolate, (3.2)-3.1-**4.1**-5.1-(6.2) cm long, (0.6)-0.7-**1.0**-1.3-(1.9) cm wide, sessile, sparsely to moderately hispid-strigose (6)-9-**13**-17-(20) hairs/mm^2, sparsely to moderately glandular (2)-3-**10**-17-(27) glands/mm^2, margins with (0)-1-**2**-3-(4) dentations. UPPER STEM LEAVES narrowly lanceolate to lanceolate, sessile, (1.3)-1.5-**2.1**-2.6-(3.1) cm long, (0.2)-0.3-**0.5**-0.6-(0.8) cm wide, bases rounded, sparsely to moderately hispid (4)-10-**16**-22-(31) hairs/mm^2, sparsely to strongly glandular (2)-7-**16**-24-(35) glands/mm^2, margins entire. CAPITULESCENCE solitary or paniculiform, branches ascending. INVOLUCRES cylindrical or campanulate when fresh, campanulate upon drying, (0.8)-0.8-**1.0**-1.1-(1.4) cm high, (1.4)-1.5-**1.8**-2.1-(2.3) cm wide; phyllaries in 4-6 imbricate series, outer 1/4-1/3 length of inner, distal 1/3 of outer phyllaries sparsely to moderately glandular (9)-10-**13**-17-(20) glands/mm^2, sparsely to moderately hispid-strigose (3)-4-**14**-24-(36) hairs/mm ^{2}; medial 1/3 of outer phyllaries moderately to strongly glandular (8)-14-**26**-39-(46) glands/mm^2, strongly hispid-strigose (10)-17-**28**-39-(50) hairs/mm^2; proximal 1/3 of outer phyllaries moderately to strongly glandular (1)-5-**20**-36-(68) glands/mm^2, sparsely hispid (4)-5-**9**-13-(19) hairs/mm^2; weak purple colouration of the phyllary apices (0)-0-**0.2**-0.4-(0.7) on a scale of 0-1. RAY FLORETS (20)-22-**27**-32-(38), strap yellow, (4.5)-6.5-**8.9**-11.3-(12.3) mm long, (0.8)-0.9-**1.2**-1.5-(1.6) mm wide; corolla (3.4)-3.8-**4.7**-5.5-(7.0) mm long; achenes (1.0)-1.2-**1.9**-2.6-(3.2) mm long, sparsely pubescent (0.0)-0.0-**0.4**-0.9-(1.2) on a scale of 0-5. DISC FLORETS (45)-60-**79**-97-(103), yellow, corolla (4.8)-5.1-**5.8**-6.4-(6.7) mm long; achenes (0.6)-1.1-**2.1**-3.1-(4.0) mm long, densely pubescent (3.4)-3.8-**4.4**-5.0-(5.0) on a scale of 0-5; pappus (4.9)-5.5-**6.5**-7.4-(7.8) mm long. Chromosome number 2n=18.

Distribution. Northeastern Michoacan, east to Hidalgo and south to Oaxaca, Mexico (Fig. 4); 1000-3400 m elevation. The type comes from Oaxaca state although we have been unable to locate it.

Discussion. Var. *viridis* is distinguished based on the absent to weak purple colouration of the apices of its phyllaries and its densely glandular outer phyllaries. Plants in the southern part of the range in Oaxaca tend to have long hispid to hispid-strigose hairs on the phyllaries and leaves. Although plants of var. *inuloides* and var. *viridis* have similar numbers of hairs/mm^2, the hairs on the leaves of the plants of var. *viridis* are more visible due to their length. The purple colouration of the apices of the phyllaries of the plants from this portion of the range is absent to very weak. Plants from the northern edge of the range appear less hispid and have weak to moderate purple colouration of the apices of the phyllaries. These plants were still strongly supported statistically as belonging to var. *viridis*.

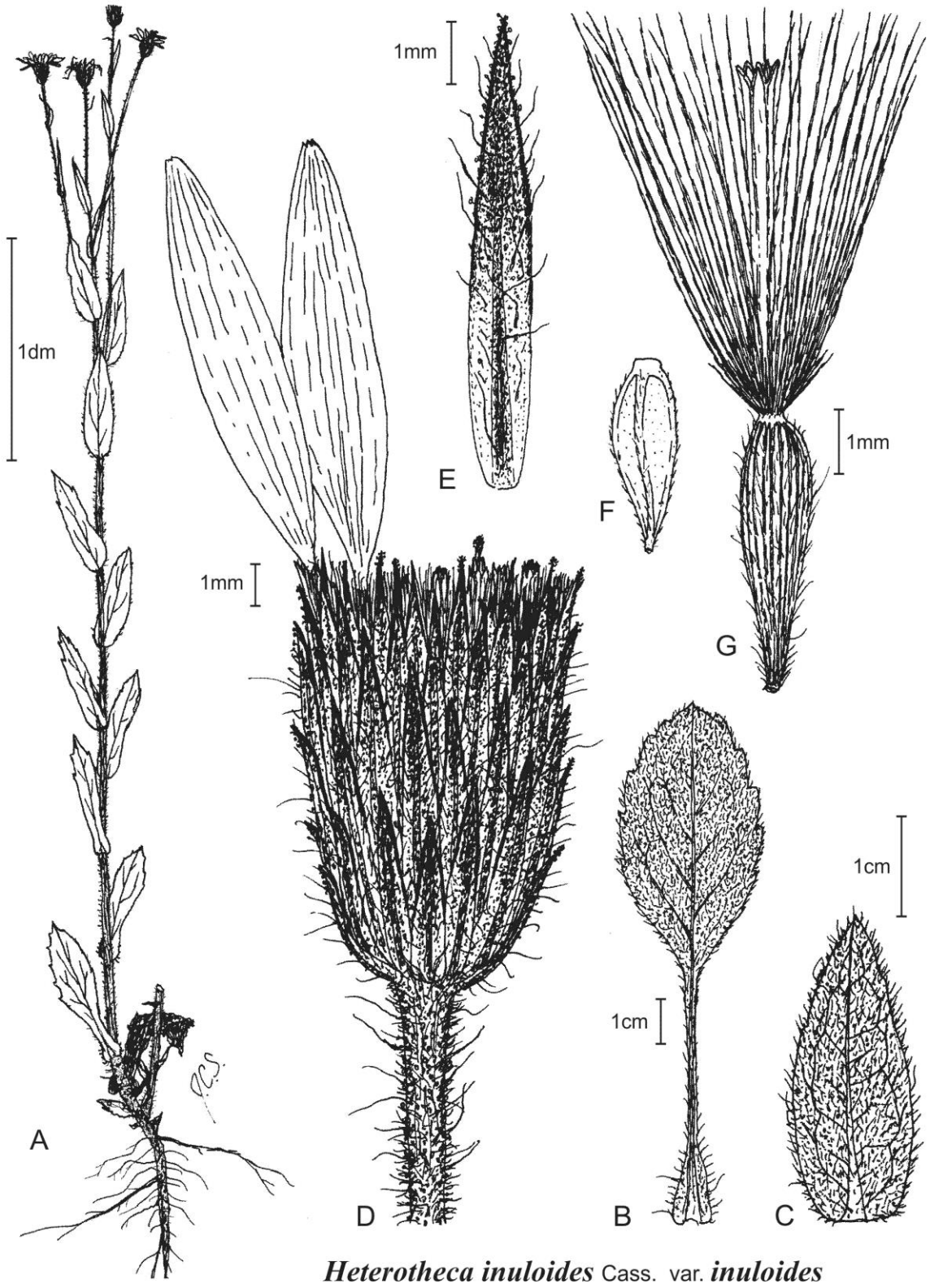

Figure 4. Morphology of *Heterotheca inuloides* var. *inuloides*. **A.** Habit. **B.** basal rosette leaf.. **C.** Ovate mid stem leaf. **D.** Head with only some ray florets illustrated. **E.** Mid series phyllary. **F.** Ray floret cypsela. **G.** Disc floret cypsela.

3. ***Heterotheca inuloides*** Cass. var. ***rosei*** Wagenknecht, Rhodora 62: 69. 1960. **TYPE**: **MEXICO**. **Jalisco**. 30 mi E of Guadalajara, sandy soil, grassland and roadsides, 25 Jul 1956, *Wagnknecht 2846* (holotype: KANU!; isotype: F! MIN!, NY!).

Biennial to perennial from woody taproots, STEMS one to several, erect standing (26.4)-29.2-**46.9**-64.6-(80.0) cm tall. LOWER STEM LEAVES spatulate to lanceolate, (2.2)-2.4-**3.7**-4.9-(6.7) cm long, (0.6)-0.7-**1.1**-1.6-(2.1) cm wide, sessile, sparsely to moderately hispid to hispid-strigose (3)-8-**16**-24-(35) hairs/mm^2, sparsely glandular (0)-4-**8**-11-(16) glands/mm^2, margins with (2)-3-**5**-6-(7) dentations. UPPER STEM LEAVES narrowly lanceolate to lanceolate, sessile, (1.1)-1.2-**1.9**-2.5-(4.1) cm long, (0.3)-0.3-**0.4**-0.6-(0.8) cm wide, bases rounded, sparsely to moderately hispid (2)-7-**16**-25-(41) hairs/mm^2, sparsely to slightly glandular (3)-4-**9**-14-(23) glands/mm^2, margins entire to slightly dentate. CAPITULESCENCE solitary or paniculiform, branches ascending. INVOLUCRES cylindrical or campanulate when fresh, campanulate upon drying, (0.7)-0.8-**0.9**-1.0-(1.1) cm high, (1.5)-1.6-**1.7**-1.9-(2.1) cm wide; phyllaries in 4-6 imbricate series, outer 1/4-1/3 length of inner, distal 1/3 of outer phyllaries sparsely to moderately glandular (6)-11-**16**-21-(28) glands/mm^2, sparsely hispid (0)-0-**5**-10-(23) hairs/mm ^{2}; medial 1/3 of outer phyllaries sparsely to moderately glandular (9)-12-**23**-34-(48) glands/mm^2, sparsely hispid (1)-**10**-21-(39) hairs/mm^2; proximal 1/3 of outer phyllaries sparsely glandular (1)-2-**11**-19-(31) glands/mm^2, sparsely hispid (0)-0-**5**-11-(28) hairs/mm^2; moderate purple colouration of the phyllary apices (0)-0.1-**0.5**-0.9-(1.0) on a scale of 0-1. RAY FLORETS (21)-24-**31**-39-(42), strap yellow, (6.0)-7.7-**10.4**-13.2-(15.1) mm long, (0.7)-1.1-**1.7**-2.2-(2.8) mm wide; corolla (3.2)-3.7-**4.1**-4.6-(5.0) mm long; achenes (0.6)-1.1-**1.5**-2.0-(2.5) mm long, sparsely to moderately pubescent (0.0)-0.1-**1.5**-2.8-(5.0) on a scale of 0-5. DISC FLORETS (62)-73-**92**-111-(123), yellow, corolla (4.5)-4.9-**5.4**-5.9-(6.5) mm long; achenes (0.9)-1.1-**1.7**-2.3-(3.1) mm long, densely pubescent (3.2)-4.1-**4.6**-5.0-(5.0) on a scale of 0-5; pappus (4.4)-4.9-**5.5**-6.2-(6.5) mm long. Chromosome number 2n=18.

Distribution. Central and southern Zacatecas and adjacent Durango, Nayarit, Jalisco, and Michoacan states in Mexico (Figure 4); 1000-2800m elevation. Plants of var. *rosei* can be found throughout most of the range of the species with the exception of the state of Oaxaca. Two plants were collected outside of the identified range in the states of Sonora and Sinaloa. These plants were likely escaped cultivars.

Discussion. Var. *rosei* is distinguished by its outer phyllary indument traits. Its outer phyllaries have sparse hairs which are mostly concentrated on the distal half. The phyllaries are moderately glandular with 2-3 times as many glands as hairs. The phyllaries also can have moderate purple coloration of the apices.

4. ***Heterotheca inuloides*** Cass. var. ***leptoglossa*** (DC.) R.E. Cook and Semple, in Semple, Botany (Ottawa) 86(8): 892. 2008. *Heterotheca leptoglossa* DC., Prodr. 5: 317. 1836. **TYPE**: **MEXICO**. **Guanajuato**. León to Guanajuato, 1827, *Mendez s.n.* (lectotype designated in Semple 2008: G-DC!; isolectotypes: G-DC!, GH!)

Biennial to perennial from woody taproots, STEMS one to several, erect standing (23.8)-24.3-**28.7**-33.2-(32.4) cm tall. LOWER STEM LEAVES spatulate to lanceolate, (1.7)-2.4-**3.4**-4.3-(4.8) cm long, (0.4)-0.6-**0.9**-1.1-(1.3) cm wide, sessile, moderately hispid-strigose (11)-14-**22**-30-(34) hairs/mm^2, sparsely glandular (1)-1-**3**-6-(9) glands/mm^2, margins with (0)-2-**3**-5-(6) dentations. UPPER STEM LEAVES narrowly lanceolate to lanceolate, sessile, (1.2)-1.3-**1.5**-1.7-(1.8) cm long, (0.2)-0.2-**0.3**-0.3-(0.3) cm wide, bases rounded, strongly hispid-strigose (21)-25-**33**-42-(51) hairs/mm^2, sparsely glandular (1)-1-**3**-7-(9) glands/mm^2, margins entire to slightly dentate. CAPITULESCENCE solitary or paniculiform, branches ascending. INVOLUCRES cylindrical or campanulate when fresh, campanulate upon drying, (0.8)-0.8-**0.9**-1.0-(1.0) cm high, (1.5)-1.6-**1.7**-1.9-(1.9) cm wide; phyllaries in 4-6 imbricate series, outer 1/4-1/3 length of inner, distal 1/3 of outer phyllaries sparsely glandular (2)-**5**-12-(22) glands/mm^2, sparsely hispid (2)-2-**4**-6-(7) hairs/mm ^{2};

medial 1/3 of outer phyllaries sparsely glandular (4)-**9**-15-(26) glands/mm^2, sparsely hispid (5)-6-**10**-14-(19) hairs/mm^2; proximal 1/3 of outer phyllaries sparsely glandular (0)-0-**5**-12-(21) glands/mm^2, sparsely hispid (0)-0-**2**-5-(7) hairs/mm^2; strong purple colouration of the phyllary apices (0.6)-0.8-**0.9**-1.1-(1.0) on a scale of 0-1. RAY FLORETS (25)-28-**35**-42-(46), strap yellow, (9.1)-9.3-**10.6**-11.9-(12.4) mm long, (0.7)-0.8-**1.3**-1.7-(2.1) mm wide; corolla (3.2)-3.5-**3.9**-4.4-(4.6) mm long; achenes (1.1)-1.5-**1.8**-2.1-(2.2) mm long, sparsely pubescent (0.0)-0.0-**0.3**-0.8-(1.2) on a scale of 0-5. DISC FLORETS (65)-75-**89**-102-(108), yellow, corolla (5.4)-5.3-**5.9**-6.5-(6.8) mm long; achenes (1.4)-1.6-**1.9**-2.2-(2.3) mm long, moderately to densely pubescent (2.6)-3.2-**3.8**-4.4-(4.8) on a scale of 0-5; pappus (5.0)-5.0-**5.6**-6.1-(6.4) mm long. Chromosome number 2n=18.

Distribution. Aquascalientes, northeastern Jalisco, Guanajuato, Querétaro, southwestern San Luis Potosí, and disjunct in northwestern Zacatecas and adjacent southeastern Durango states in Mexico; 1900-2800m elevation.

Discussion. Variety *leptoglossa* can be distinguished from the other varieties of *Heterotheca inuloides* based on its strongly erect habit, elongate peduncles and its indument traits. The outer phyllaries are weakly hispid and sparsely glandular. The phyllaries are strongly purple coloured and the colouration is restricted to the tips of the apices. The upper leaves and subtending bracts are strongly hispid-strigose, but weakly glandular. There is no statistical difference between the head size of the plants of var. *leptoglossa* and those of the other varieties of *Heterotheca inuloides*.

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LITERATURE CITED

McVaugh, R. 1984. *Heterotheca.* Flora Nova-Galicia, Vol. 12, Compositae. Univ. Michigan Press, Ann Arbor.

Nesom, G.L. 1990. Taxonomy of *Heterotheca* section *Heterotheca* (Asteraceae: Astereae) in Mexico, with comments on the taxa in the United States. Phytologia 69: 282-294.

Nesom, G.L. 2019. Taxonomic summary of *Heterotheca* (Asteraceae: Astereae): Part 1, sects. *Heterotheca* and *Ammodia*. Phytoneuron 2019-64: 1–44.

Semple, J.C. 1996. A revision of *Heterotheca* sect. *Phyllotheca* (Nutt.) Harms (Compositae: Astereae): the prairie and montane goldenasters of North America. Univ. Waterloo Biol. Series No. 37: 1–164.

Semple, J.C. 2008. Cytotaxonomy and cytogeography of the goldenaster genus *Heterotheca* (Asteraceae: Astereae). Botany 86: 886–900.

SYSTAT version 10 for Windows. 2000. SPSS Inc., Chicago. Illinois.

Thiers, B. M. Updated continuously. Index Herbariorum. <https://sweetgum.nybg.org/science/ih/>

Wagenknecht, B.L. 1960. Revision of *Heterotheca* sect. *Heterotheca* (Compositae). Rhodora 62: 61–76, 97–107.

Appendix 1. Traits characterized and measured for the four varieties of *Heterotheca inuloides*: var. *inuloides*, var. *viridis*, var *rosei* and var. *leptoglossa*. Traits marked with an * were not included in the canonical analyses as they correlated strongly with another trait or traits, they were used in assigning specimens to their *a priori* groups, or there were not enough measurements to be considered representative.

BLLENG	Basal Leaf Length (cm)
BLWID	Basal Leaf Width (cm)
*BLWtoE	Basal Leaf measured from widest point to the end (tip) (cm)
*BLPUBH	Basal Leaf Pubescence - number of hairs measured on 1 mm^2
*BLPUBG	Basal Leaf Pubescence - number of glands measured on 1 mm^2
BLDENT	Basal Leaf Dentation - number of serrations on leaf margin
*ULLENG	Upper Leaf Length (cm)
ULWID	Upper Leaf Width (cm)
*ULWtoE	Upper Leaf measured from widest point to the end (tip) (cm)
*ULPUBH	Upper Leaf Pubescence - number of hairs measured on 1 mm^2
*ULPUBG	Upper Leaf Pubescence - number of glands measured on 1 mm^2
ULDENT	Upper Leaf Dentation - number of serrations on leaf margin
INVOLHT	Height of the Involucre (cm)
HEADWD	Head Width (cm)
OPHLENG	Outer Phyllary Length (mm)
*PPUBGU	Number of glands on the upper third of the phyllary
*PPUBHU	Number of hairs on the upper third of the phyllary
*PPUBGM	Number of glands on the middle third of the phyllary
*PPUBHM	Number of hairs on the middle third of the phyllary
*PPUBGL	Number of glands on the lower third of the phyllary
*PPUBHL	Number of hairs on the lower third of the phyllary
*PHPURP	Purple colouration at phyllary apices - (0-1)
IPHLENG	Inner Phyllary Length (mm)
*RFLOR#	Number of ray florets
RSTPL	Ray Strap Length (mm)
*RSTPW	Ray Strap Width (mm)
*RCORL	Ray Corolla Length - measured from base to beginning of strap (mm)
RACHL	Ray Achene Length (mm)
*RACPUB	Ray Achene Pubescence (0-5)
DFLOR#	Number of disc florets
DCORL	Disk Corolla Length (mm)
DACHL	Disk Achene Length (mm)
DPAPL	Disk Pappus Length (mm)
*DACPUB	Disk Achene Pubescence (0-5)

Appendix 2. Mean +/- standard deviation with ranges shown in parenthesis for the characters used in assigning specimens to *a priori* groups for the varieties of *Heterotheca inuloides*.

Character	var. *inuloides* (N=19)	var. *rosei* (N=16)	var. *viridis* (N=20)	var. *leptoglossa* (N=8)
BLPUBH	14.8 ± 6.9 (4.4-27.0)	14.6 ± 7.6 (2.8-35.0)	13.0 ± 4.6 (5.6-24.2)	21.5 ± 8.3 (10.6-33.6)
BLPUBG	6.5 ± 3.0 (1.8-14.5)	7.8 ± 3.9 (0.4-16.0)	8.7 ± 6.4 (1.2-27.4)	2.6 ± 1.0 (1.2-4.2)
ULPUBH	14.0 ± 5.8 (6.2-28.4)	13.5 ± 6.6 (2.0-26.6)	16.7 ± 8.6 (4.2-40.6)	33.8 ± 8.6 (21.4-51.2)
ULPUBG	7.4 ± 5.3 (1.6-17.2)	10.0 ± 4.9 (3.0-23.0)	13.7 ± 8.2 (1.8-34.8)	2.7 ± 2.4 (0.6-7.2)
PPUBGU	14.2 ± 4.8 (1.6-23.2)	17.4 ± 4.8 (11.0-28.4)	12.4 ± 3.8 (5.8-20.2)	3.2 ± 1.2 (2.0-5.2)
PPUBHU	10.3 ± 5.6 (0.0-24.8)	6.0 ± 5.3 (1.2-23.0)	11.4 ± 9.6 (1.2-36.0)	4.0 ± 2.0 (1.6-7.0)
PPUBGM	13.9 ± 6.4 (6.8-29.8)	24.2 ± 11.3 (9.2-47.6)	23.4 ± 12.6 (6.8-46.2)	6.6 ± 1.5 (4.4-8.6)
PPUBHM	20.4 ± 10.0 (0.0-43.2)	10.6 ± 11.4 (0.7-39.2)	22.9 ± 13.0 (3.4-50.2)	9.5 ± 4.4 (4.8-19.2)
PPUBGL	6.9 ± 4.8 (1.0-17.8)	11.7 ± 9.1 (1.4-30.6)	16.9 ± 14.7 (0.4-68.0)	3.3 ± 1.6 (0.2-4.8)
PPUBHL	10.5 ± 6.1 (0.2-21.4)	5.5 ± 6.6 (0.2-28.4)	7.9 ± 4.6 (1.0-18.8)	2.5 ± 2.3 (0.4-6.8)
PHPURP	0.8 ± 0.2 (0.1-1.0)	0.5 ± 0.4 (0.0-1.0)	0.2 ± 0.2 (0.0-0.7)	0.9 ± 0.1 (0.6-1.0)

Appendix 3. Mean +/- standard deviation with ranges shown in parenthesis for the characters used in the discriminant analysis. (in order of decreasing F-values)

Character	var. *inuloides* (N=19)	var. *rosei* (N=16)	var. *viridis* (N=20)	var. *leptoglossa* (N=8)
Selected by Step-wise discriminant analysis				
ULWID	0.3 ± 0.2 cm (0.3-1)	0.44 ± 0.15 cm (0.28-0.8)	0.44 ± 0.2 cm (0.2-0.44)	0.3 ± 0.1 cm (0.2.0.5)
ULLENG	2.1 ± 0.4 cm (1.2-3.4)	1.75 ± 0.34 cm (1.5-2.4)	2.1 ± 0.6 cm (1.2-3.4)	1.7 ± 0.7 cm (1.1-4.1)
DPAPL	5.6 ± 0.4 mm (4.9-6.2)	5.5 ± 0.6 mm (4.4-6.5)	6.5 ± 0.9 mm (4.9-7.8)	5.6 ± 0.5 mm (5.0-6.4)
HEADHT at anthesis	1.0 ± 0.1 cm (0.8-1.1)	0.9 ± 0.1 cm (0.7-1.1)	1.0 ± 0.1 cm (0.8-1.4)	0.9 ± 0.1 cm (0.8-1.0)
DFLOR	79 ± 23.6 (33-151)	95 ± 18 (68-123)	77 ± 18 (45-103)	90 ± 17 (62-123)
DCORL	5.5 ± 0.5 mm (4.7-6.7)	5.4 ± 0.5 mm (4.5-6.5)	5.8 ± 0.7 mm (4.8-6.7)	5.9 ± 0.6 mm (5.4-6.8)
RSTPL	11.26 ± 12 mm (5.6-13.8)	11.1 ± 2.4 mm (7.9-15.1)	8.8 ± 2.2 mm (4.5-12.3)	10.9 ± 1.8 mm (7.2-13.4)
Not Selected by Step-wise discriminant analysis				
BLLENG	3.8 ± 1.2 (2.4-7.6)	3.7 ± 1.3 (2.2-6.7)	4.1 ± 1.0 (3.2-6.2)	3.4 ± 1.0 (1.7-4.8)
BLDENT	2.7 ± 1.3 (0.3-5.0)	4.8 ± 1.4 (2.3-7.0)	1.8 ± 1.3 (0.0-4.0)	3.4 ± 1.9 (0.3-6.4)
ULDENT	0.5 ± 0.6 (0.0-1.6)	0.3 ± 0.6 (0.0-2.2)	0.0 ± 0.0 (0.0-0.0)	0.0 ± 0.1 (0.0-0.2)
HEADWD	1.6 ± 0.2 (1.3-1.9)	1.7 ± 0.1 (1.5-2.1)	1.8 ± 0.3 (1.4-2.3)	1.7 ± 0.1 (1.5-1.9)
OPHLENG	4.5 ± 0.5 mm (3.3-5.9)	4.4 ± 0.8 mm (3.5-6.1)	4.9 ± 0.5 mm (4.2-5.7)	3.9 ± 0.3 mm (3.5-4.2)
RACHL	1.7 ± 0.4 mm (1-2.5)	1.5 ± 0.46 mm (0.6-2.3)	1.8 ± 0.7 mm (1-3.2)	1.7 ± 0.3 mm (1.1-2.2)