A TAXONOMIC INVESTIGATION OF *CUSCUTA ATTENUATA* (CUSCUTACEAE) AND RELATED TAXA

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ABSTRACT

Examination of the taxonomic relationships of the rare parasitic vine *Cuscuta attenuata* Waterf. to other species of the genus reveals that it should be positioned in subsect. *Indecorae* Yunck. rather than *Lepidanche* Engelm. as previously placed. Analyses of morphological variation, via univariate analysis, UPGMA clustering, principal component analysis, and discriminant analysis, indicate that it is distinct from *C. compacta* Juss. and *C. cuspidata* Engelm. but morphologically similar to *C. indecora* Choisy, especially var. *longisepala* Yunck. Results obtained in a program of interspecific hybridizations reveal that *C. attenuata* is reproductively isolated from the other taxa. These data suggest that *C. attenuata* merits continued recognition as a distinct species.

RESUMEN

El examen de las relaciones taxonómicas de la rara parásita *Cuscuta attenuata* con otras especies del género revela que debe ser colocada en la subsect. *Indecorae* en vez de la subsect. *Lepidanche* como se había hecho previamente. Los análisis de la variación morfológica, mediante análisis univariante, agrupamiento UPGMA, análisis de componentes principales y análisis discriminante, indican que es distinta de *C. compacta* Juss. y de *C. cuspidata* Engelm., aunque morfológicamente semejante a *C. indecora* Choisy, especialmente a la var. *longisepala* Yunck. Los resultados obtenidos en un programa de hibridaciones interespecíficas revela que *C. attenuata* está aislada reproductivamente de los otros taxa. Estos datos sugieren que *C. attenuata* debe continuar reconociéndose como una especie distinta.

INTRODUCTION

Because of its rarity and uncertain taxonomic status, *Cuscuta attenuata* Waterf. has merited much attention (Tyrl et al. 1978; Taylor & Taylor 1980; Prather 1990; Prather & Tyrl 1993). The species was described from plants

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collected from two neighboring populations in the Red River floodplain of extreme southeastern Oklahoma (Waterfall 1971). Prior to 1989 the species was known from only four populations within a few km of one another (Tyrl et al. 1978; Taylor & Taylor 1980). Because of its limited geographical distribution, it was considered to warrant possible designation as an endangered species and was declared a Category 1 species by the U. S. Fish & Wildlife Service's Office of Endangered Species (1980 FR 45:82500; 1985 FR 50:39526). Prather (1990) and Prather and Tyrl (1993) reported four extant and six historical populations in Kansas, Oklahoma, and Texas. As a result, the status of the species was modified to Category 2 (1993 FR 58:51159).

Waterfall (1971) tentatively placed *C. attenuata* in subsect. *Lepidanche* Engelm. on the basis of his interpretation that the calyx was polysepalous. He suggested, however, that formation of a new subsection to accommodate the species might be appropriate because its capsule shape and the distribution of its floral bracts were not consistent with Yuncker's circumscription of subsect. *Lepidanche* (Yuncker 1965). Tyrl et al. (1978) echoed Waterfall's uncertainty about the species' relationships and called for taxonomic investigations of the species and its putative relatives.

Among the species of subsect. *Lepidanche*, Waterfall stated that *C. attenuata* most closely resembled *C. compacta* Juss. but distinguished them on the basis that: (1) *C. attenuata* has a pedicel while *C. compacta* does not, (2) *C. attenuata* has only one floral bract which is at the base of the pedicel while *C. compacta* has 1–10 bracts which are situated along the length of the pedicel, and (3) *C. attenuata* has lanceolate, attenuate sepals while *C. compacta* has ovate, obtuse sepals (Table 1). Waterfall also stated that *C. attenuata* resembled *C. cuspidata* Engelm. in the presence of pedicels, which all other species in the subsect. *Lepidanche* lack. They are different in that *C. cuspidata* has a much more open inflorescence; ovate, cuspidate sepals; and usually one or two bracts along the pedicel (Table 1).

During a preliminary examination of herbarium specimens, including the holotype, it was discovered that the calyx of *C. attenuata* is gamosepalous and not polysepalous as Waterfall stated in his diagnosis. Because of this fusion, *C. attenuata* clearly seems better placed within subsect. *Indecorae* Yunck. rather than in subsect. *Lepidanche*. The two subsections are not thought to be closely related though both are positioned within sect. *Cleistogrammica* Engelm. (Yuncker 1932, 1965). With the exception of its somewhat dense inflorescence, all of the characters of *C. attenuata* are better accomodated in subsect. *Indecorae* (Table 1).

Within the subsection, *C. attenuata* is morphologically similar to *C. indecora* var. *longisepala* Yunck., and specimens of *C. attenuata* key to var.

TABLE 1. Comparison of morphological characters of *Cuscuta* species.

	Calyx	Bracts	Inflorescences
Subsection *Lepidanche*			
C. compacta	polysepalous, ovate, obtuse	1–10 along pedicel	compact
C. cuspidata	polysepalous, ovate, cuspidate	1 at base and 1–2 along pedicel	open
Subsection *Indecorae*			
C. attenuata	gamosepalous, lanceolate, attenuate	1 at base of pedicel	somewhat compact
C. indecora			
var. *indecora*	gamosepalous, triangular-ovate, acute-obtuse	1 at base of pedicel	open
var. *longisepala*	gamosepalous, lanceolate, acute	1 at base of pedicel	open

longisepala in Yuncker's 1965 key. Waterfall's description of *C. attenuata* (Waterfall 1971) and Yuncker's description of *C. indecora* var. *longisepala* (Yuncker 1965) are similar for every character state. In 1965, Yuncker examined one of the specimens identified in this study as *C. attenuata* (*C.J. Eskew 1395*, OKL). Recognizing the distinctiveness of the specimen, he made the following annotation: "*C. indecora* Choisy. The long narrow calyx lobes would make it var. *longisepala* Yunck. However, the specimen looks teratological and may not be the variety but only an abnormal form."

Cuscuta indecora is widespread in North and South America and is highly variable throughout its range (Hunziker 1950; Yuncker 1965; Beliz 1986). The infraspecific classification is somewhat controversial and Yuncker (1920, 1932, 1965) accepted different varieties in each of his treatments. *Cuscuta indecora* var. *longisepala* occurs throughout much of the range of *C. indecora*, including South America where the variation is similar to that found in North America (Hunziker 1950). Beliz (1986) does not mention *C. indecora* var. *longisepala* or list it in synonymy. Variability over the range of *C. indecora* is not discussed nor were representative specimens west of Arizona cited.

The few chromosome numbers known for taxa of the two subsections are invariant. *Cuscuta indecora* and *C. glomerata* Choisy (subsect. *Lepidanche*) are both reported as n=15 (Freeman & Brooks 1988; Pinkava et al. 1974) while *C. attenuata* is reported as 2n=30 (Prather & Tyrl 1993).

An investigation of the relationship of *C. attenuata* to other taxa of *Cuscuta* by means of analyses of morphological variation and a program of interspecific hybridization was undertaken in an attempt to clarify the taxonomic position and rank of the species.

MATERIALS AND METHODS

Analyses of morphological variation.—To examine morphological variation within and between taxa, 186 herbarium specimens of *Cuscuta* from DUR, ECSC, LL, NLU, NOSU, NWOSU, OCLA, OKL, OKLA, SMU, TAES, TEX, TULS, UARK, and the herbarium at Cameron University in Lawton, Oklahoma were examined—10 of *C. attenuata*; 50 each of *C. compacta*, *C. cuspidata*, and *C. indecora* var. *indecora*; and 26 of *C. indecora* var. *longisepala* (Prather 1990).

In a preliminary analysis, five flowers each were examined on several specimens of each taxon. It was determined that variation among flowers of the same plant was negligible, therefore one flower was used from each specimen, which was treated as an OTU. One individual per population was examined. The data recorded for each specimen are presented in Prather (1990). Because *Cuscuta* lacks roots and well-developed leaves, and because stem features could not be accurately scored from herbarium specimens, only floral characters were used.

One flower, with its pedicel and bract(s), was removed from each specimen. To minimize variation resulting from flower age, all flowers selected had dehiscing anthers, a stage which lasts only a short time (Prather & Tyrl 1993). Observations were made after softening each flower by boiling in water to facilitate examination of the inner floral parts (Yuncker 1920). Samples were examined with a dissecting microscope at a magnification of 30x to score characters. Measurements were recorded to the nearest 0.1 mm using an ocular micrometer. Many of the measurements were incorporated in the analyses as ratios to minimize the effect of size which may be influenced by environmental factors. Forty-four characters were scored for each sample. The first 27 characters (Table 2) were qualitative and therefore suitable for use in all analyses. Characters 28–44 (Table 3) were qualitative characters and thus could only be used in the multivariate analyses.

For characters 1 and 5–27 an unprotected LSD test was performed. Characters 2–4 were excluded because the values were invariant among individuals of at least one taxon. The multivariate analyses comprised UPGMA clustering, a principal component analysis, and a discriminant analysis. Statistical Analysis System (SAS Institute, Inc. 1985) was employed to perform these analyses except the unprotected LSD tests which were performed using Statview (Abacus Concepts, Inc. 1992). The UNIVARIATE procedure of SAS was used to confirm that the assumption normality of the LSD test was not violated. The UPGMA clustering analysis was performed using the AVERAGE option of the CLUSTER procedure on data that had been standardized by the STD option which changes the mean to zero and the standard deviation to one. The varimax rotation method was used in the principal component analysis. Because the other statistical methods

TABLE 2. Means, standard deviations, minima, maxima, and results of the unprotected LSD test of characters 1–27.

	Mean (S.D.)	Min. - Max.	Significance*
	1. Pedicel Length (mm)		
C. attenuata	1.2 (±0.49)	0.6–2.2	I,L
C. i. longisepala	2.6 (±1.3)	0.5–5.8	A,M,S
C. i. indecora	2.3 (±0.98)	0.8–4.9	A,M,S
C. compacta	1.0 (±0.42)	0.3–1.8	I,L,S
C. cuspidata	1.6 (±1.0)	0.2–4.0	I,L,M
	2. Number of Bracts at Pedicel Base**		
C. attenuata	1.0 (±0.00)	1–1	
C. i. longisepala	1.0 (±0.00)	1–1	
C. i. indecora	0.9 (±0.24)	0–1	
C. compacta	1.1 (±0.35)	1–2	
C. cuspidata	1.0 (±0.14)	0–1	
	3. Number of Bracts Along Pedicel**		
C. attenuata	0.0 (±0.00)	0–0	
C. i. longisepala	0.0 (±0.00)	0–0	
C. i. indecora	0.0 (±0.14)	0–1	
C. compacta	2.8 (±1.3)	1–7	
C. cuspidata	0.7 (±0.88)	0–3	
	4. Number of bracts at Pedicel Apex**		
C. attenuata	0.0 (±0.00)	0–0	
C. i. longisepala	0.0 (±0.00)	0–0	
C. i. indecora	0.0 (±0.00)	0–0	
C. compacta	1.6 (±0.50)	1–2	
C. cuspidata	1.2 (±0.82)	0–3	
	5. Bract Length/Calyx Length		
C. attenuata	0.82 (±0.22)	0.56–1.27	–
C. i. longisepala	0.78 (±0.19)	0.45–1.11	I,M,S
C. i. indecora	0.91 (±0.24)	0.50–1.63	L
C. compacta	0.89 (±0.13)	0.59–1.15	L
C. cuspidata	0.85 (±0.14)	0.44–1.13	L
	6. Bract Length/Bract Width		
C. attenuata	2.2 (±0.53)	1.1–3.3	I,L[1],M,S
C. i. longisepala	1.8 (±0.38)	1.3–2.6	A[1],I,M,S
C. i. indecora	1.4 (±0.30)	1.0–2.3	A,L,M,S
C. compacta	0.72 (±0.12)	0.39–0.99	A,I,L,S
C. cuspidata	1.2 (±0.23)	0.78–1.8	A,I,L,M
	7. Calyx Length (mm)		
C. attenuata	2.6 (±0.52)	1.5–3.2	I,L,M,S
C. i. longisepala	2.1 (±0.44)	1.6–2.9	A,I,S
C. i. indecora	1.4 (±0.27)	0.8–2.0	A,L,M,S
C. compacta	2.1 (±0.25)	1.7–2.6	A,I,S
C. cuspidata	1.7 (±0.17)	1.3–2.1	A,I,L,M
	8. Calyx Tube Length/Total Calyx Length		
C. attenuata	0.22 (±0.06)	0.12–0.32	I,L,S
C. i. longisepala	0.33 (±0.12)	0.13–0.53	A,I,M,S
C. i. indecora	0.50 (±0.11)	0.31–0.73	A,L,M,S
C. compacta	0.20 (±0.09)	0.05–0.53	I,L,S
C. cuspidata	0.13 (±0.04)	0.07–0.20	A,I,L,M

TABLE 2. *(Continued)*

	Mean (S.D.)	Min. - Max.	Significance*
	9. Calyx Length/Calyx Width		
C. attenuata	2.7 (±0.45)	2.2–3.8	I,L[1],M,S
C. i. longisepala	2.2 (±0.65)	1.1–4.0	A[1],I,M,S
C. i. indecora	1.4 (±0.30)	0.96–2.3	A,L,M,S[1]
C. compacta	1.1 (±0.19)	0.20–1.6	A,I,L,S
C. cuspidata	1.3 (±0.16)	0.95–1.7	A,I[1],L,M
	10. Corolla Length/Calyx Length		
C. attenuata	1.2 (±0.16)	1.0–1.4	I,L,M,S
C. i. longisepala	1.6 (±0.33)	1.0–2.3	A,I,M,S
C. i. indecora	2.2 (±0.37)	1.5–3.3	A,L,M
C. compacta	1.8 (±0.23)	1.4–2.4	A,L,I,S
C. cuspidata	2.2 (±0.33)	1.4–3.2	A,L,M
	11. Corolla Tube Length/Total Corolla Length		
C. attenuata	0.58 (±0.04)	0.53–0.64	L[1],M
C. i. longisepala	0.54 (±0.05)	0.46–0.63	A[1],I[1],M,S
C. i. indecora	0.57 (±0.04)	0.46–0.67	L[1],M,S[1]
C. compacta	0.72 (±0.06)	0.59–0.86	A,I,L,S
C. cuspidata	0.61 (±0.12)	0.46–1.4	I[1],L,M
	12. Corolla Lobe Length/Corolla Lobe Width		
C. attenuata	3.3 (±0.42)	2.8–4.3	I,M,S[1]
C. i. longisepala	3.1 (±0.36)	2.4–3.8	I[1],M,S
C. i. indecora	3.O (±0.29)	2.4–3.6	A,L[1],M,S
C. compacta	3.7 (±0.45)	2.9–5.0	A,I,L
C. cuspidata	3.8 (±0.57)	2.0–4.8	A[1],I,L
	13. Corolla Length (mm)		
C. attenuata	3.4 (±0.42)	2.8–4.3	I,M[1],S[1]
C. i. longisepala	3.1 (±0.34)	2.4–3.8	M,S
C. i. indecora	3.0 (±0.30)	2.4–3.6	A,M,S
C. compacta	3.7 (±0.45)	2.9–5.0	A[1],I,L
C. cuspidata	3.8 (±0.57)	2.0–4.8	A[1],I,L
	14. Number of Fringes Per Corolla Appendage		
C. attenuata	26.8 (±3.3)	24–35	M
C. i. longisepala	24.7 (±6.6)	6–36	M
C. i. indecora	26.6 (±5.8)	17–46	M
C. compacta	13.2 (±2.1)	7–18	A,I,L,S
C. cuspidata	26.4 (±4.8)	16–36	M
	15. Length of Corolla Appendage (mm)		
C. attenuata	1.8 (±0.43)	1.0–2.6	I[1],M
C. i. longisepala	1.9 (±0.63)	1.2–4.6	I[1],M
C. i. indecora	1.6 (±0.27)	1.1–2.2	A[1],L[1],M,S
C. compacta	2.3 (±0.30)	1.5–3.4	A,I,L,S
C. cuspidata	2.1 (±0.44)	1.0–2.8	I,M
	16. Appendage Length/Length of Corolla Tube		
C. attenuata	0.92 (±0.16)	0.56–1.1	–
C. i. longisepala	1.1 (±0.40)	0.83–2.9	I,M,S
C. i. indecora	0.94 (±0.12)	0.68–1.3	L,M
C. compacta	0.86 (±0.09)	0.74–1.1	I,L,S[1]
C. cuspidata	0.91 (±0.13)	0.37–1.5	L,M[1]

TABLE 2. *(Continued)*

	17. Proportion of Appendage Fused to Corolla		
C. attenuata	0.45 (±0.07)	0.33–0.55	S
C. i. longisepala	0.42 (±0.09)	0.27–0.71	S
C. i. indecora	0.44 (±0.07)	0.31–0.65	S
C. compacta	0.46 (±0.09)	0.29–0.78	S
C. cuspidata	0.61 (±0.06)	0.49–0.77	A,I,L,M
	18. Appendage Length/Appendage Width		
C. attenuata	1.6 (±0.28)	1.3–2.2	I[1],M,S
C. i. longisepala	1.8 (±0.32)	1.4–3.0	M,S
C. i. indecora	1.8 (±0.26)	1.2–2.4	A[1],M,S
C. compacta	4.2 (±0.65)	2.3–5.6	A,I,L,S
C. cuspidata	3.8 (±0.61)	2.7–5.6	A,I,L,M
	19. Filament Length (mm)		
C. attenuata	0.8 (±0.2)	0.5–1.0	I,L[1],M,S[1]
C. i. longisepala	0.7 (±0.1)	0.4–0.9	A[1],I[1],M
C. i. indecora	0.6 (±0.2)	0.3–0.9	A,L[1],M,S[1]
C. compacta	0.2 (±0.1)	0.1–0.4	A,I,L,S
C. cuspidata	0.7 (±0.2)	0.4–1.0	A[1],I[1],M
	20. Anther Length (mm)		
C. attenuata	0.8 (±0.1)	0.7–1.0	M,S
C. i. longisepala	0.7 (±0.2)	0.4–1.1	M
C. i. indecora	0.7 (±0.1)	0.5–1.0	M
C. compacta	0.4 (±0.1)	0.1–0.6	A,I,L,S
C. cuspidata	0.7 (±0.1)	0.4–0.9	A,M
	21. Filament Length/Anther Length		
C. attenuata	0.99 (±0.17)	0.71–1.3	I[1],M
C. i. longisepala	0.96 (±0.24)	0.50–1.4	I[1],M
C. i. indecora	0.80 (±0.27)	0.38–1.8	A[1],L[1],M,S
C. compacta	0.54 (±0.28)	0.20–2.0	A,I,L,S
C. cuspidata	0.96 (±0.24)	0.50–1.5	I,M
	22. Anther Length/Anther Width		
C. attenuata	1.3 (±0.18)	1.1–1.6	S
C. i. longisepala	1.3 (±0.19)	0.91–1.6	S
C. i. indecora	1.4 (±0.21)	0.92–1.8	M,S
C. compacta	1.2 (±0.26)	0.74–1.7	I,S
C. cuspidata	1.9 (±0.34)	1.1–2.7	A,I,L,M
	23. Longer Style Length (mm)		
C. attenuata	1.4 (±0.45)	0.8–2.0	I,S
C. i. longisepala	1.1 (±0.38)	0.5–1.8	S
C. i. indecora	1.1 (±0.30)	0.6–2.1	A,M,S
C. compacta	1.3 (±0.30)	0.6–2.0	I,S
C. cuspidata	2.3 (±0.63)	1.3–3.9	A,I,L,M
	24. Longer Style Length/Shorter Style Length		
C. attenuata	1.1 (±0.06)	1.0–1.2	M,S
C. i. longisepala	1.1 (±0.07)	1.0–1.3	M,S
C. i. indecora	1.1 (±0.10)	1.0–1.4	M,S
C. compacta	1.3 (±0.19)	1.0–2.1	A,I,L
C. cuspidata	1.3 (±0.16)	1.0–1.8	A,I,L

TABLE 2. *(Continued)*

	25. Stigma Length/Stigma Width		
C. attenuata	0.73 (±0.08)	0.61–0.85	–
C. i. longisepala	0.75 (±0.08)	0.57–0.91	S[1]
C. i. indecora	0.75 (±0.08)	0.55–0.86	S
C. compacta	0.75 (±0.08)	0.56–0.94	S
C. cuspidata	0.70 (±0.09)	0.46–0.89	I,L[1],M
	26. Ovary Length (mm)		
C. attenuata	1.4 (±0.25)	1.0–1.7	I,L[1],S
C. i. longisepala	1.2 (±0.21)	0.8–1.6	A[1],M,S
C. i. indecora	1.2 (±0.20)	0.8–1.6	A,M,S
C. compacta	1.4 (±0.17)	1.0–1.8	I,L,S
C. cuspidata	0.8 (±0.18)	0.5–1.2	A,I,L,M
	27. Ovary Length/Ovary Width		
C. attenuata	1.0 (±0.13)	0.80–1.2	I,M[1],S
C. i. longisepala	0.97 (±0.15)	0.74–1.4	I,M,S
C. i. indecora	0.84 (±0.12)	0.54–1.1	A,L,M
C. compacta	1.1 (±0.10)	0.80–1.2	A[1],I,L,S
C. cuspidata	0.81 (±0.13)	0.60–1.3	A,L,M

*No significant difference between taxa except those listed under significance and the taxa labelling the row; p<0.01 unless otherwise indicated. A = *C. attenuata*, I = *C. indecora* var. *indecora*, L = *C. indecora* var. *longisepala*, M = *C. compacta*, and S = *C. cuspidata*.

**Not tested because the values for some taxa were invariant.

[1]Significant only at p<0.05

had established that *C. compacta* and *C. cuspidata* were easily distinguished from *C. attenuata*, only *C. attenuata* and the two varieties of *C. indecora* were examined in the discriminant analysis. Prior probability of the discriminant analysis was set proportional to the number of specimens of each taxon used in the analysis.

Interspecific hybridizations.—Parasitized host plants of all taxa were transported to the plant growth facility at OSU and maintained as described previously (Prather & Tyrl 1993). Attempts to maintain *C. compacta* in the laboratory were unsuccessful because transplanting its woody hosts was not possible and cuttings did not survive under laboratory conditions. Pollen of *C. compacta*, therefore, was collected from five individuals in the field and used immediately in crosses in the laboratory. Vouchers of all populations used were deposited in OKLA.

Individual flowers of *C. attenuata* were emasculated before anther dehiscence and mature pollen from individuals of another taxon was manually transferred to the stigmas (Radford et al. 1974). Reciprocal crosses with all taxa, except *C. compacta*, were performed in the same manner. Twenty crosses were performed between *C. attenuata* and *C. compacta*, 9 between *C. attenuata* and *C. cuspidata*, 16 between *C. attenuata* and *C. indecora* var. *indecora*, and 25 between *C. attenuata* and *C. indecora* var. *longisepala*.

TABLE 3. Qualitative morphological characters (28–44) of *Cuscuta* which were used in the multivariate analyses.

No.	Character	No.	Character
28.	Bract orientation	37.	Presence of calyx papillations
29.	Calyx orientation	38.	Presence of calyx laticifers
30.	Corolla orientation	39.	Shape of corolla margin
31.	Shape of bract margin	40.	Shape of corolla apex
32	Shape of bract apex	41.	Presence of corolla papillations
33.	Presence of bract laticifers	42.	Inflexing of corolla lobe tips
34.	Overlap of calyx lobes	43.	Orientatin of styles
35.	Shape of calyx margin	44.	Presence of stylopodium
36.	Shape of calyx apex		

RESULTS AND DISCUSSION

On the basis of univariate and multivariate analyses, *C. attenuata* is a morphologically distinctive taxon albeit similar to *C. indecora*, particularly var. *longisepala*. Means, standard deviations, and minimum and maximum values for all characters are given in Table 2, as well as LSD test results between all taxa for those characters tested. As revealed by the univariate analysis, the means of four characters are significantly different ($p<0.01$) between *C. attenuata* and each of the other taxa (Table 2, Fig. 1). The mean of *C. attenuata* differs significantly ($p<0.05$) from that of *C. compacta*, *C. cuspidata*, and *C. indecora* var. *indecora*, for over half of the characters (15, 16, and 15, respectively); and from *C. indecora* var. *longisepala* for one-third of the characters.

Multivariate analyses revealed that *C. attenuata* is distinct from *C. compacta* and *C. cuspidata* but morphologically similar to *C. indecora*. In the UPGMA analysis, *C. compacta* and *C. cuspidata* each formed distinct groupings. However, *C. attenuata*, *C. indecora* var. *indecora* and *C. indecora* var. *longisepala* did not form distinct groupings, but rather one large cluster.

In the principal component analysis, the first three components explained 56.4% of the variation (Fig. 2). The remaining variation was accounted for by the other factors in 1–4% increments. The first principal component, which accounted for 31.1% of the variation, was weighted for characters 28, 29, 34, and 41. The second principal component, which accounted for 18.2% of the variation, was weighted for characters 14, 21, 31, 32, 39, and 40. The third principal component, which accounted for 7.1% of the variation, was weighted for characters 5, 7, 9, 10, and 37. As in the UPGMA analysis, *C. compacta* and *C. cuspidata* formed distinct clusters and the three remaining taxa did not. The third principal component was weighted for characters which dealt with variation in the calyces. For those characters, *C. indecora* var. *longisepala* was always intermediate between *C. indecora* var. *indecora* and *C. attenuata*.

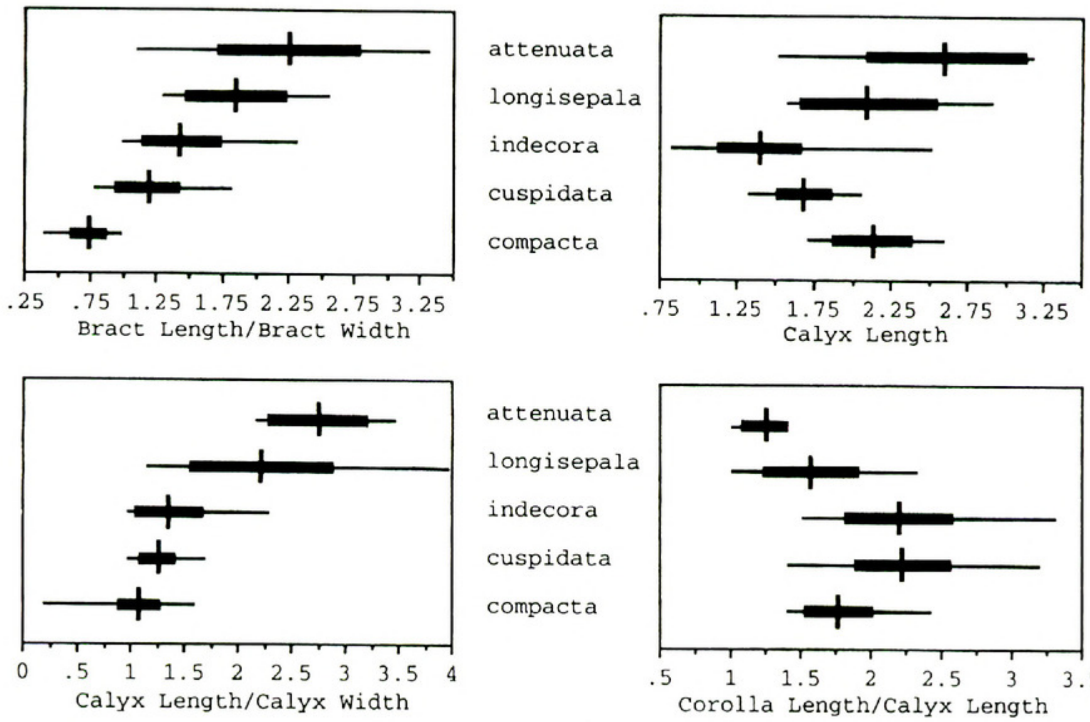

FIG. 1. Univariate analysis of morphological characters in *Cuscuta* taxa. Means (vertical lines), standard deviations (broad horizontal lines), and minima and maxima (narrow horizontal lines) of the four characters for which the means of *C. attenuata* differ significantly ($p<0.01$) from each of the other taxa. Names in the center are epithets except indecora (=*C. indecora* var. *indecora*) and longisepala (=*C. indecora* var. *longisepala*), and apply to the figures on each side.

The discriminant analysis yielded probabilities of >.93 that each specimen was appropriately designated, and thus demonstrated that *C. attenuata* and the two varieties of *C. indecora*, can be distinguished.

Interspecific hybridizations.—None of the crosses between *C. attenuata* and any of the other taxa, including both varieties of *C. indecora*, produced fruits or seeds. In a related study, populations of *C. attenuata* were shown to be interfertile using these same methods (Prather & Tyrl 1993), and in some cases even the same individuals. These intraspecific crosses produced 81–92% fruit set and 38–45% seed set. The lack of fruit and seed set from all interspecific crosses, but high rate of success of intraspecific crosses, suggests that *C. attenuata* is reproductively isolated from the other taxa.

Taxonomic implications.—Although once thought to be related to *C. compacta* and *C. cuspidata*, *C. attenuata* is definitely distinct from these species and should be positioned in subsect. *Indecorae* on the basis of its fused sepals rather than in subsect. *Lepidanche* as proposed by Waterfall (1971). On the basis of the systematic data generated in this study, it is concluded that *C. attenuata* is a distinct species albeit morphologically similar to *C. indecora*. In the absence of reproductive isolation we might treat *C. attenuata* as a variety of *C. indecora*.

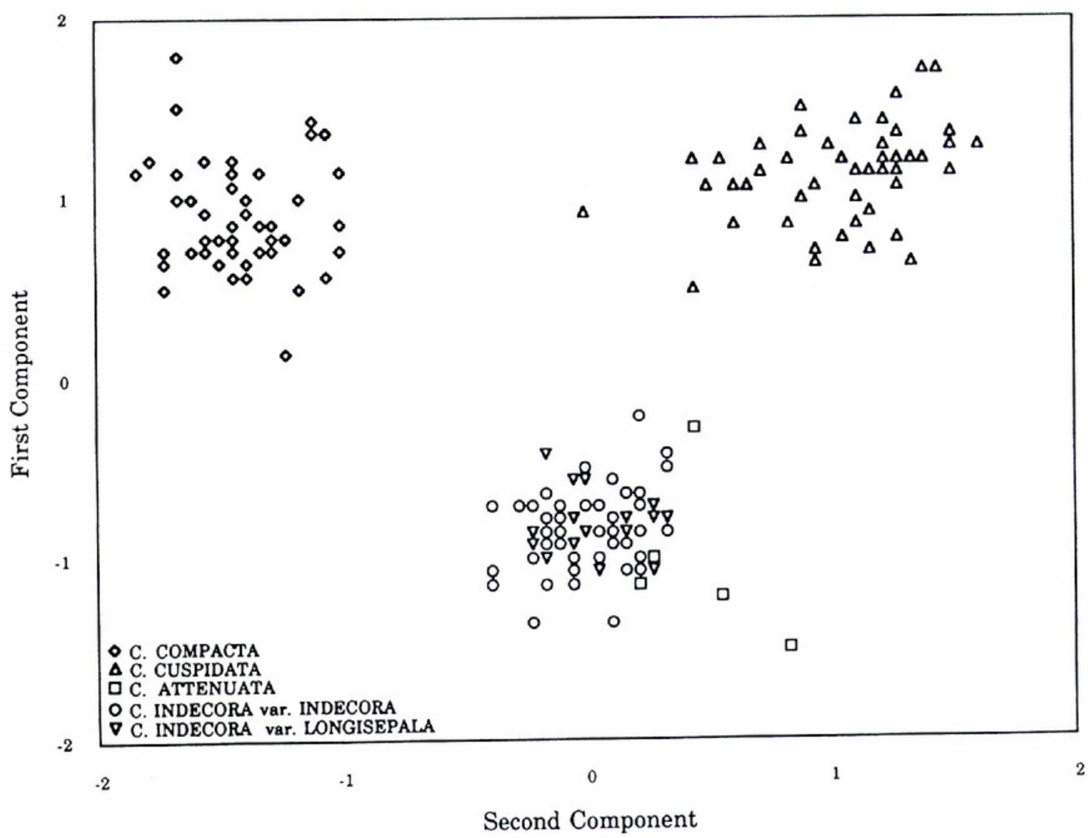

FIG. 2. Principal components analysis of morphological characters in *Cuscuta* taxa. First component plotted against the second component.

The addition of *C. attenuata* to subsect. *Indecorae* brings its total number of species to five: *C. attenuata* parasitizing *Iva annua* in Kansas, Oklahoma, and Texas; *C. coryli* Engelm. parasitizing a wide variety of hosts in the central and eastern U.S.; *C. stenolepis* Engelm. parasitizing unknown hosts in Ecuador; *C. warneri* Yunck. parasitizing *Phyla cuneifolia* in Utah and Arizona; and *C. indecora* with two recognized varieties: var. *indecora* occurring on a wide variety of herbaceous hosts and widespread in North and South America and the West Indies, and var. *longisepala* parasitizing a wide variety of herbaceous hosts in the southwestern U.S., Mexico, and South America (Yuncker 1965). Interestingly, *C. warneri* is also listed as a Category 2 species and is thought to be extinct (1993 FR 58:51159).

ACKNOWLEDGMENTS

The authors thank P. Buck, the late J.K. McPherson, and two anonymous reviewers for their helpful comments. Appreciation is also extened to the curators who kindly loaned specimens of *Cuscuta* for study. This research was supported by the U.S. Fish & Wildlife Service (Project Number 201811-89-00420).

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