APPARENT INTERGRADATION IN TEXAS BETWEEN THE SUBSPECIES OF THE TEXAS BLIND SNAKE (*LEPTOTYPHLOPS DULCIS*)

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Further evidence derived from 135 specimens from Texas and adjacent parts of Colorado and Oklahoma support Klauber's conclusion that *L. d. dulcis* and *L. dulcis dissectus* are conspecific, but the area of intergradation is much broader in Texas and Oklahoma, based on dorsal scale count as well as on division of the anterior supralabial, than he and subsequent workers have thought.

The list of taxa (Collins, 1991) that merit reexamination of their species-group nomenclatural rank (Dowling, 1993) might well have included *Leptotyphlops d. dulcis* (Baird and Girard) and *L. dulcis dissectus* (Cope), which Klauber (1940: map) depicted with broadly overlapping ranges and (ibid: 116) suggested might be allospecific (in which case *dissectus* would be a subspecies of *L. myopicus* (Garman)). Smith (1944: 136) concluded that the broad overlap depicted in Klauber's work is better interpreted as indicative of allospecificity of *L. dulcis* and *L. myopicus*. That conclusion was reiterated in Smith and Taylor (1945: 21, 23) and in Smith and Sanders (1952: 215-217). However, faith in the sound authority of Klauber's conclusion of conspecificity has since then prevailed.

Klauber (1940) assigned his material of this complex to their respective taxa on the basis of presence of one (*L. dulcis*) or two (*L. dulcis dissectus*) anterior supralabials (as here expressed, merely for convenience; Klauber correctly, we think, regarded the anterior supralabial simply as divided or not); specimens with two on one side and one on the other were regarded as intergrades. His map thus depicted a considerable overlap of the ranges of the two subspecies, with intergrades scattered throughout much of the overlap area. Several other general distinctions between the two taxa were noted in detail (number of dorsal scales, division of the occipital, width of the 5th dorsal) in his very thorough survey of variation, but ultimate taxonomic assignment was individually typological (based strictly on the anterior supralabial), not populational.

It was on populational grounds that Smith and Sanders (1952) argued for allospecificity, admittedly by conjecture, since adequate

comparative material was not available to them, although the conclusion of conspecificity was at that time, and earlier, equally conjectural.

Inasmuch as the rank of these two taxa has not been addressed seriously since 1952, we here report pertinent data on 135 specimens, mostly from critical areas of range overlap or intergradation. Seven previously reported by Smith and Sanders (1952) from Baylor and Montague Cos., Texas, are included among those 135 because of their critical import; none of the other 128 have been reported in the present context. Those 128 are in the collections of Midwestern State University of Wichita Falls, Texas (MWSU, 36) Texas Technological University (TTU, 24), West Texas State University (WTSU 63) and the University of Colorado Museum (UCM, 5). The material reported by Smith and Sanders (1952) is in the University of Illinois Museum of Natural History (UIMNH, 7).

Results

Allocations. The results of our study are best discussed in terms of our final taxonomic assignments (Fig. 1; Appendix). Specimens assigned to *L. dulcis dissectus* (19) are from Baca Co., Colorado, and Hemphill, Hutchinson, Lubbock, Potter and Randall Cos., Texas, all in or near the Texas Panhandle. *L. d. dulcis* is represented by specimens (32) from Murray Co., Oklahoma, and Bandera, Coleman, Gonzales, Guadalupe, Hays, Kimble, Mills and Travis Cos., Texas. The remaining 84 are all regarded as intergrades between the preceding two taxa, and are from Jefferson Co., Oklahoma, and Archer, Baylor, Childress, Clay, Crosby, Dickens, Garza, King, Llano, Montague, Motley, Terrell and Young Cos., Texas (localities within counties are given in the Appendix).

Anterior supraoculars. All 19 specimens assigned to *L. dulcis dissectus* have 2-2 anterior supraoculars, except for the one from Lubbock Co., with 1-2. The latter specimen was taken very near intergrade territory in adjacent Crosby and Garza Cos., and perhaps should also be considered an intergrade; its dorsal scale count of 234, however, combined with its 1-2 anterior supralabials and fringe position between the ranges of the two subspecies, leads us to assign it to *L. dulcis dissectus.*

All 32 *L. d. dulcis* have 1-1 anterior supralabials, and only three (of 15 from Mills Co., close to the area of intergradation, with 233, 235, and 238 dorsals) have more than 231 dorsals.

Of the 84 intergrades, all have 1-1 anterior supralabials except for two with 2-2 (MWSU 28, Clay Co.; MWSU 1447, Archer Co.) and one with 1-

2 (UIMNH 24578, Montague Co.). The Clay Co. specimen has a horizontal instead of a vertical division of the anterior supraocular on one side. Klauber (1940: 115) reported four intergrades (i.e., specimens with 1-2 anterior supraoculars) from three localities in central and southwestern Oklahoma, north of which, in northern Oklahoma and southwestern Kansas, all specimens had 2-2 anterior supralabials and were therefore regarded as *L. dulcis dissectus*. One with 2-2 anterior supralabials, from southwestern Oklahoma, Klauber assigned to *L. dulcis dissectus* in spite of being surrounded by localities from which *L. d. dulcis* came and having fewer than 224 dorsals.

On the basis of this character, the two taxa may be judged as constituting two sympatric species, with occasional hybridization (as Klauber was tempted to conclude, and indirectly so argued), or as subspecies having an erratic occurrence of one or two anterior supralabials throughout an area of intergradation. The evidence is inconclusive, except that the former conclusion presupposes that variation in other respects, especially in the dorsal scale count, is meaningless.

Dorsals. We counted these scales by Klauber's method, beginning with the first scale posterior to the rostral, and not including the terminal spine. All counts are shown in Table 2. As Klauber was well aware, the two taxa differ markedly in number of dorsals, the more western subspecies having more (230 or more, with the one exception previously mentioned, with 224), the eastern one fewer ("in the area of intergradation, usually...less than 220"). However, Klauber's concept of the area of intergradation was limited to central and southwestern Oklahoma, the only area where he knew the condition of 1-2 anterior supraoculars occurred. Such specimens are now known from northern Texas, and presumably occur in other areas we interpret as zones of intergradation, depending perhaps upon sample size, which was small in Klauber's study.

However, the total range of variation in dorsal scale count in *L. d. dulcis*, as assigned by Klauber (1940: 109, 113), is 206-255, overlapping completely his range of *L. dulcis dissectus* (224-246, all but one of which we would regard as intergrades, 230 or more). The great range in the former taxon was suggestive to Klauber (1940: 111) of the possibility that *L. d. dulcis* "may really be a composite." On the contrary, much of that variation is due to a strong N-S cline, as Klauber pointed out (1940: 111), with a shift of means from 219 in Comanche Co., southwestern Oklahoma, to 227 in central Texas, and to 237 is southern Texas. Equally strong, in our opinion, is the influence of intergradation between the two subspecies in the areas of Texas noted in Fig. 1.

In those areas, of particular note is the total range of variation (214-245) in the intergrade material from northern central and central Texas,

Garza Co. (233-245) and Terrell Co. (221, 240). On the contrary, the counts in southern central Texas (of *L. d. dulcis*) are consistently low (217-231, with three exceptions, to 238), and those of *L. dulcis dissectus* in Colorado and the Texas Panhandle vicinity are consistently high (230-242). With our small samples of non-intergrade populations these figures would be suspect statistically, but their validity, in general, is fully supported by Klauber's (1940) data.

The over-all picture derived from the dorsal scale counts is highly suggestive of a broad area of intergradation between the two taxa, as shown in Fig. 1; there is no hiatus indicative of allospecificity as suggested might occur by Smith and Sanders (1952). Analysis of variance reveals a significant variation among the means (Fig. 2) for *L. d. dulcis*, *L. dulcis dissectus* and the proposed intergrades ($F = 20.33$, $df = 2132$, $P<0.01$). Non-orthogonal contrasts (Dunn, 1961) showed that the means for *L. d. dulcis* and the intergrades do not differ but that both of these are significantly lower than the mean for *L. dulcis dissectus*. Neither the divided anterior supralabial nor the high dorsal scale count characteristic of *L. dulcis dissectus* exhibits much penetrance into the genome of *L. d. dulcis*, although the latter character is less completely overwhelmed than the former.

Occipitals. As pointed out by Klauber (1940: 116), the occipitals are frequently split into two scales in *L. dulcis dissectus*, seldom in *L. d. dulcis* (one in 53 from Texas and Oklahoma). Ten of our 19 of the former subspecies have the occipital split on one or both sides (the exceptions are from every county except Hemphill); it is split on one side only in one of our 32 *L. d. dulcis*. In only two of our 84 intergrades is the occipital split, and in both on one side only (King and Llano Cos., Texas). The character is of little value in establishing rank of the two taxa; although the split condition occurs in a strong, statistically significant proportion of *L. dulcis dissectus*, it is not an acceptable taxonomically diagnostic proportion (about half).

Fifth dorsal. Klauber (1940: 116) noted that the first postcranial dorsal scale is wider than the following scales in the western subspecies, seldom in the eastern. In our 19 *L. dulcis dissectus*, only 12 have that scale widened, and in five of the 32 *L. d. dulcis* it is also widened. Among the 84 intergrades, the scale is widened in 13. The character is of minimal diagnostic value.

Other differentiae. Smith and Sanders (1952) suggested two other features that, with larger series, might prove to differentiate the two taxa: pigmented infralabials, and more numerous (9-11) pigmented posterior dorsal scale rows in *L. dulcis dissectus* than in *L. d. dulcis* (with no pigmented infralabials and seven pigmented posterior dorsal scale rows). We found four

specimens (3 *L. d. dulcis*, 1 intergrade) in the present series of 135 with pigmented infralabials, and the number of pigmented posterior dorsal scale rows varied 5-9 without taxonomic correlation. Many of the specimens were, however, either too faded or too discolored for evaluation of either character.

Aberrations. Several anomalous variations were noted, as follows. The supraoculars are in contact medially in TTU 2442b from Terrell Co., and the right one is divided in MWSU 1441 from Clay Co. The frontal is split into two scales, and the interoccipital into three, in MWSU 1440, also from Clay Co. The right parietal is divided in MWSU 6 from Archer Co. The 5th dorsal is divided in UCM 55596 from Baca Co., much reduced in size, to that of the preceding dorsals, in WTSU 10882 from Coleman Co., and is preceded by medial contact of the anterior paravertebral scales in WTSU 13823 from Guadalupe Co.

It may be of interest to note that the smallest individual examined measured 71 mm in total length.

Discussion

Apparently *L. d. dulcis* and *L. dulcis dissectus* are externally distinguishable from each other only on the bases of two characters: number of anterior supralabials, and number of dorsals. Those two characters exhibit intermediacy or breakdown in partly disparate regions. The anterior supralabials are 1-2 only in specimens recorded from northern Texas (Archer, Clay, Lubbock and Montague Cos.) and (as reported by Klauber, 1940) in central and southwestern Oklahoma. There is in addition an anomalous (?) specimen with 1-1 supralabials (not seen by us but assigned by Klauber to *L. d. dulcis* on the basis of its single anterior supralabial; its dorsal scale count was not given, but probably conforms with other *L. dulcis dissectus* if it is correctly thought to be from Cimarron Co., Oklahoma, in the middle of the range of the latter subspecies; that locality may be in error, but the museum was not cited and therefore we could not check the specimen).

The dorsal scale counts, however, range widely where we indicate (Fig. 1) the area of intergradation, spanning our count extremes for both *L. d. dulcis* and *L. dulcis dissectus*, and that area overlaps the area of intermediate supralabial counts and extends through most of central western Texas.

Since the area of broad overlap in dorsal scale count includes the area of anterior supralabial intermediacy, we conclude that not only are the two taxa conspecific (although allosubspecific), but their area of intergradation

should be conceived as coincident with the approximate area of dorsal scale count overlap, as shown in Fig. 1, not the very restricted area from which intermediate anterior supralabial counts are now known.

The erratic distribution of variation in the intergrade area, rather than a smooth transition from one range of variation to the other, suggests that Klauber (1940: 116) correctly surmised that the two subspecies are of secondary origin, having remerged after a period of separation. Subsequent introgression through interbreeding apparently has been too extensive to warrant recognition of the two taxa, as they now stand, as separate species.

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Table 1. Dorsal Scale Count Distribution in Present Samples of *Leptotyphlops dulcis**

1	2	3	4	5
213	1	0	0	1
214	1	1	0	0
215	5	2	0	3
216	1	1	0	0
217	3	1	0	2
218	4	3	0	1
219	6	6	0	0
220	4	3	0	1
221	12	8	0	4
222	8	5	0	3
223	10	7	0	3
224	8	7	0	1
225	3	3	0	0
226	6	2	0	4
227	4	3	0	1
228	3	3	0	0
229	3	1	0	2
230	1	0	1	0
231	6	3	0	3
232	4	4	0	0
233	6	1	4	1
234	6	2	4	0
235	7	5	1	1
236	4	3	1	0
237	5	3	2	0
238	5	2	2	1
239	2	1	1	0
240	2	1	1	0
241	1	0	1	0
242	2	1	1	0
243	1	1	0	0
244	0	0	0	0
245	1	1	0	0
Total	135	84	19	32

*Columns: 1, no. of dorsals, total range; 2, distribution in all specimens examined; 3, distribution only of "intergrade" material (see Fig. 1 and Appendix); 4, distribution in *L. dulcis dissectus* only; 5, distribution in *L. d. dulcis* only, outside of the area of assumed intergradation.

Table 2. Raw Dorsal Scale Counts in *Leptotyphlops dulcis*

County	Dorsal Scale Counts
Archer	- 223, 224, 225, 226 (2), 228, 235, 238
Baca	- 234, 235, 236
Bandera	- 220, 224, 226, 231 (2)
Baylor	- 221, 223
Childress	- 225
Clay	- 215, 218, 219 (3), 220, 221 (2), 222 (2), 223 (3), 224 (3), 228, 229, 231, 232 (2), 234, 235, 237, 242
Coleman	- 217, 221
Crosby	- 221
Dickens	- 228, 231
Garza	- 233, 236, 243, 245
Gonzales	- 229
Guadalupe	- 218, 223, 226
Hays	- 217
Hemphill	- 233 (2)
Hutchinson	- 233, 234, 237, 239, 240, 241
Jefferson	- 219, 223, 235
Kimble	- 213
King	- 227, 234
Llano	- 214, 217, 218 (2), 219 (2), 220 (2), 221 (3), 222 (2), 223, 224 (2), 227 (2), 231, 232 (2), 235, 236 (2), 237, 238, 239
Lubbock	- 234
Mills	- 215 (2), 221 (3), 222 (2), 223 (2), 227, 229, 231, 233, 235, 238
Montague	- 215, 216, 222, 224, 235
Motley	- 225
Murray	- 215
Potter	- 230, 234, 238 (2), 242
Randall	- 233, 237
Terrell	- 221, 240
Travis	- 222, 226 (2)
Young	- 237

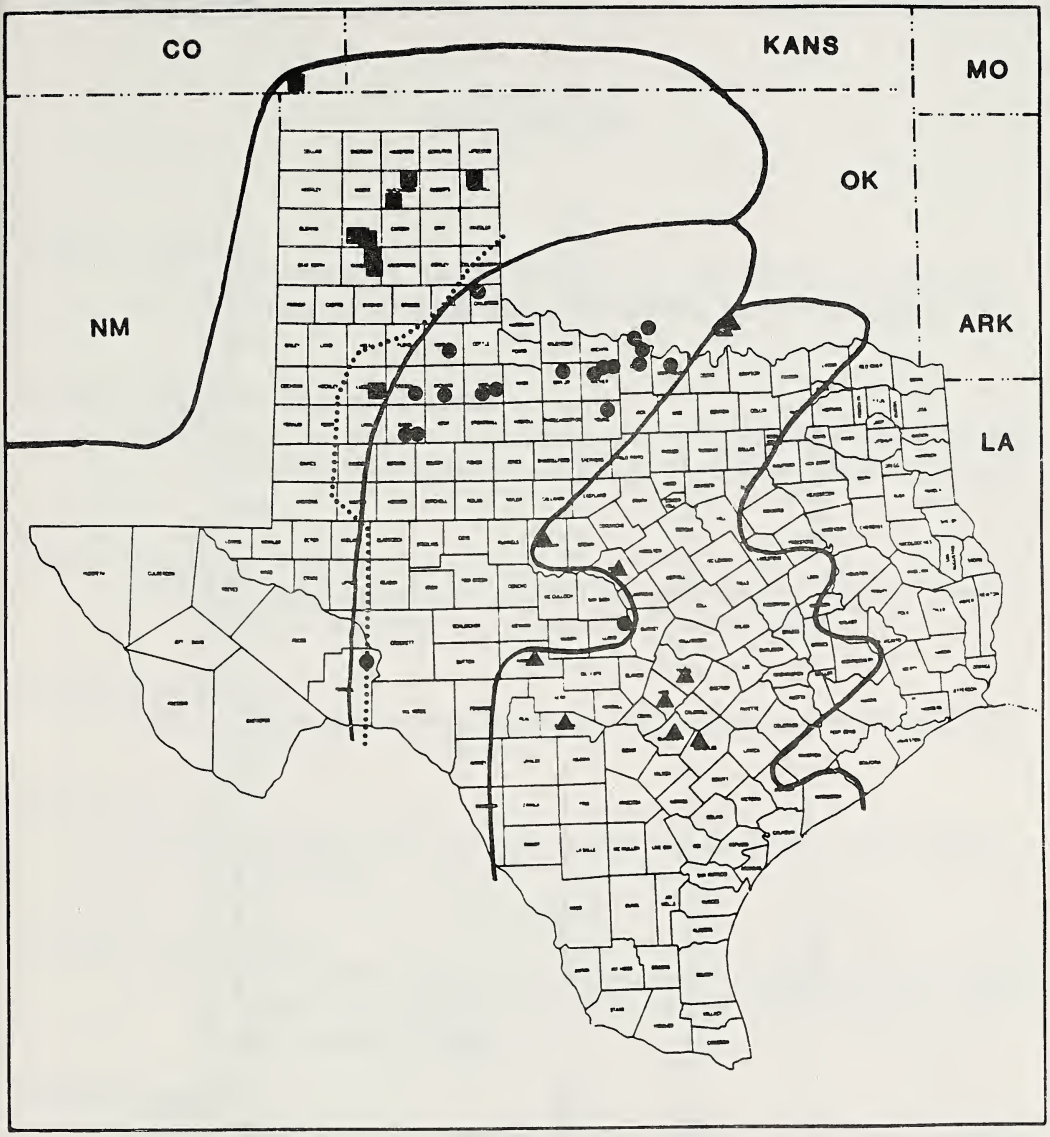

Fig. 1. Distribution of *Leptotyphlops dulcis* in Texas and adjacent areas to the north (base map adapted from Dixon (1987: 135), with symbols indicating localities represented by material examined (squares, *L. d. dissectus*; dots, *L. dulcis dissectus* x *L. d. dulcis*; triangles, *L. d. dulcis*). The dot north of Clay Co., Texas, represents Waurika, Jefferson Co., Oklahoma; north of Cooke Co., 15 mi N Ardmore, Murray Co., Oklahoma; and north of Dallam Co., Sand Canyon, Baca Co., Colorado. Dotted line, boundary between the ranges of the two subspecies as depicted by Davis (1987: 234). Areas outlined by continuous lines represent the approximate range limits of the taxa indicated by enclosed symbols (adapted from present data; Conant and Collins, 1991: map 138; Dixon, 1987: 234; and Klauber, 1940: 158).

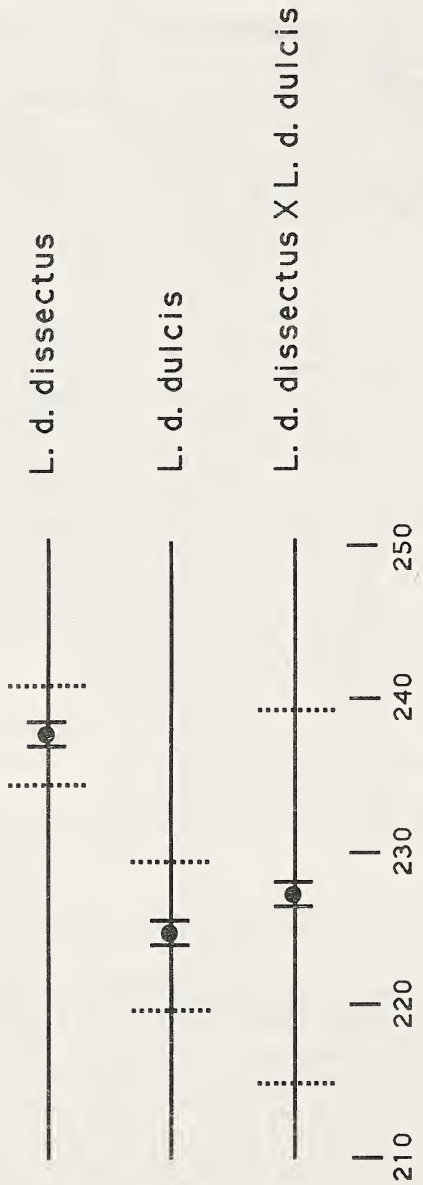

Fig. 2. Mean, standard error of the mean (between solid vertical lines) and standard deviation (between dotted vertical lines) for number of dorsal scales in *L. dulcis dissectus*, *L. d. dulcis* and the proposed intergrades.

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Appendix

The 135 specimens here dealt with are from the following localities, and in the indicated collections.

L. d. dulcis (32)

OKLAHOMA. *Murray Co.*: Hy 77 15 mi N Ardmore (WTSU 10636).

TEXAS. *Bandera Co.*: 10 mi W Medina (TTU 217a-e). *Coleman Co.*: Hords Creek Reservoir (WTSU 10757, 10882). *Gonzales Co.*: Palmetto State Park (WTSU 9912). *Guadalupe Co.*: railroad by McQueeney Dam (WTSU 13823-4); Jct Hy 464 and 1620, 2 km W Seguin (WTSU 14016). *Hays Co.*: 2 mi W Wimberley (UCM 7970). *Kimble Co.*: Robinson Ranch nr Junction (WTSU 9990). *Mills Co.*: Caraway Ranch, 3.4 mi E jct Hy 16 and 3023 (WTSU 3003, 3240, 3280, 3335-8, 3407-11, 3524-6). *Travis Co.*: Austin (WTSU 3276, 8735; UCM 24239).

L. dulcis dissectus (19)

COLORADO. *Baca Co.*: Sand Canyon, 25 mi S Pritchett (UCM 55594-6).

TEXAS. *Hemphill Co.*: 6 mi E Canadian (TTU 1554, 2196). *Hutchinson Co.*: 18 mi N Phillips (NE outskirts of Borger) on Plemons Rd (WTSU 1907-11); 35 mi E Stinnett (TTU 935). *Lubbock Co.*: Buffalo Lakes (TTU 21). *Potter Co.*: Hy 61 34 km NW Hy 66 in Amarillo (WTSU 923); Tascosa Rd, Amarillo (WTSU 1912-5). *Randall Co.*: Palo Duro Canyon (WTSU 3210); Palo Duro State Park (TTU 1818).

L. d. dulcis x *L. dulcis dissectus* (85)

OKLAHOMA. *Jefferson Co.*: Waurika (MWSU 20, 28, 1438, 1440-5, 18358-9).

TEXAS. *Archer Co.* (all MWSU): Lake Kickapoo (1650); 2 mi E Lake Kickapoo (1651); 10 mi N Scotland (1652); 5 mi W (1447), 8 mi S (27), 9 mi S (26, 28), 20 mi SW (6) Wichita Falls. *Baylor Co.*: 15 mi N Seymour (UIMNH 4490-1). *Childress Co.*: 14.5 mi E Memphis (TTU 255). *Clay Co.* (all MWSU): no locality (27); 3 mi SE (1432-7), 4 mi SE (1448-52), 8 mi SE (1431, 1446) Byers; Henrietta (12); 1 mi E Henrietta (1648-9). *Crosby Co.*: 13.5 mi S Crosbyton (TTU 2579). *Dickens Co.*: Spur ranch (TTU 1104a-b). *Garza Co.*: 6 mi E Justiceburg (TTU 521a-b); 10 mi SE Post (TTU 507a-b). *King Co.*: 13 mi W Benjamin (TTU 895); 7.2 mi S Guthrie (TTU 2771). *Llano Co.*: Lake

6712, 6726, 6734, 6774-6, 8398, 8619, 3 uncataloged). *Montague Co.*: 1 mi S St. Jo (UIMNH 14578-82). *Motley Co.*: 2.6 mi SW Matador (TTU 2046). *Terrell Co.*: 22 mi S Sheffield (TTU 2442a-b). *Young Co.*: 5.6 mi NW Loving (TTU 1005).

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