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A review of literature and a reevaluation of *Diplocardia verrucosa* Ude, 1895 resulted in the discovery of a new species in southern New Mexico and west Texas, USA

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Abstract

A new earthworm species, *Diplocardia farrishi* **sp. nov.**, was collected from multiple sites within the Chihuahuan Desert of southern New Mexico and West Texas, USA. This new species was only recently recognized as such after a review of the literature on *Diplocardia verrucosa* Ude, 1895. Corrections in the literature of *D. verrucosa*, with additional morphological detail are offered with a detailed description of the species. The description of *D. farrishi* **sp. nov.** is compared with *D. verrucosa* based on the male pore, intestinal origin, genital tumescences, and habitat. *Diplocardia farrishi* differs from similar species with a posteriorly displaced male field in having an intestinal origin in xviii, male field in xix–xxi, and lacking genital tumescences or markings. A key to *Diplocardia* species with posteriorly displaced male field is included.

Key words: *Diplocardia farrishi*, Acanthodrilidae, earthworm, biogeography, Chihuahuan Desert

Resumen

Se colectó una nueva especie, *Diplocardia farrishi* **sp. nov.**, en varios lugares adyacentes al desierto de Chihuahua al sur de Nuevo México y el oeste de Texas, Estados Unidos. Esta especie fue identificada únicamente después de una revisión literaria de *Diplocardia verrucosa* Ude, 1895. Redescribimos *D. verrucosa*, expandimos en datos morfológicos adicionales e incluimos una descripción detallada de la especie. Se compara *D. farrishi* **sp. nov.** con *D. verrucosa* basados en los poros masculinos, origen del intestino, marcas genitales y hábitats. *Diplocardia farrishi* se distingue de las demás especies con el campo masculino posteriormente desplazado en su origen del intestino en xviii, campo masculino en xix–xxi y al no presentar marcas genitales. Se incluye una clave para las especies de *Diplocardia* con campo masculino posteriormente desplazado.

Palabras clave: *Diplocardia farrishi*, Acanthodrilidae, lombriz de tierra, biogeografía, Desierto de Chihuahua

Introduction

The earthworm genus *Diplocardia* is indigenous to North America. Most described species are confined to the eastern half of the US below the Wisconsin glaciation boundary, increasing in number of species from north to south (James 1995), including high numbers of species in east Texas and Oklahoma (Damoff & Reynolds 2009, 2019; Reynolds & Damoff 2010). There are fewer reports of diplocardian species in west Texas, New Mexico, Arizona, and southern California, but this could simply be the result of few researchers investigating sites suitable to diplocardians under favorable weather conditions and appropriate time of year. There are over 50 described species of *Diplocardia* (Misirlioğlu *et al.* 2023), with less than a handful reported from Mexico. There remains large regions

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of the USA and Mexico sparsely surveyed for earthworms and, when rectified, will doubtless extend the range of many described *Diplocardia* as well as uncover additional new species for the genus.

In 2005 the first author collected numerous diplocardian specimens from multiple sites in the northeast region of the Chihuahuan Desert, including a first-time examination of *Diplocardia verrucosa* Ude, 1895, or so he thought. The collection of *D. verrucosa* from this region of the USA seemed confirmed by a description of the species by Gates (1967) from a collection made in SW New Mexico by D.E. Beck in 1966. These *D. verrucosa* specimens along with three other diplocardian species were reported in Reynolds & Damoff (2009).

Every county of Tennessee (TN) was surveyed for earthworms in the late 1960s through the early 1970s that resulted in a collection of over 4400 diplocardian specimens presently curated by the Canadian Museum of Nature (CMN). Over a span of nearly ten years through loans to the first author a total of 25 diplocardian species were reported for the state, 19 for the first time (Damoff & Reynolds 2019), with another reported as a new species (Damoff & Reynolds 2017). Also, in Damoff & Reynolds (2019) several specimens from western Tennessee were provisionally identified as *Diplocardia* **sp. nov.** TN01 and are revisited in this paper. Additional records of diplocardian specimens identified by other researchers were reported in Damoff & Reynolds (2019) including one clitellate specimen identified as *D. verrucosa* from a site in the southern corner of Tennessee, bordering North Carolina.

Concurrent with the years of intermittent microscopic examinations of the CMN TN specimens by the first author, field collections for other research projects were made in Oklahoma (OK) and Texas (TX). These earthworms aligned with the CMN *Diplocardia* **sp. nov.** TN01 specimens collected from western-most counties of TN, all thought to be the same new species to science. The TN collections are separated by nearly 40 years from the OK and TX collections. Over a decade prior to the examinations of the CMN specimens and the more recent collections in TX and OK described above, the diplocardian specimens that were collected by the first author in 2005 in SE NM and W TX were still thought to be *D. verrucosa* based on the key by James (1990). However, once a detailed description was begun for the OK, TN, and TX specimens, a review of the primary source material describing *D. verrucosa* was made for the first time, and only then was it realized that the OK, TN, and TX specimens were *D. verrucosa* and that the 2005 NM specimens were a possible new species to science. Why the confusion and misidentification?

Literature review

Confusion on the morphological identity of *Diplocardia verrucosa* Ude, 1895 can be traced to the earliest publications of the species when Eisen (1899, 1900) questions Ude's location of the spermathecal pores in ix and x. All subsequent publications that detail the morphology of *D. verrucosa* describe the spermathecal pores in viii and ix. However, in the latter half of the 20th century morphological questions for *D. verrucosa* arose associated with three characters: genital tumescences, segment location of the male pores, and segment origination of the intestine. Relevant descriptions and comments from the authors will be included to highlight why this correction is necessary for *D. verrucosa*, which in turn has resulted in the identification of *D. farrishi* **sp. nov.** from specimens collected in southern New Mexico and west Texas, USA.

Ude (1895) published the original description of *Diplocardia verrucosa* in German, based on three specimens curated at the Museum of Nature Hamburg. These specimens were sent to him from Omaha, Nebraska while living in Switzerland. The male (seminal) grooves are simply described as xix─xxi; the male pore is not referenced specifically. The strongly expanded midgut ("stark erweiterte Mitteldarm") or intestine origin begins in xvi. Ude describes the presence of genital tumescences as follows, paired in xix and xxi, before and after the seminal furrows (respectively) and three tumescences in xxii, middle tumescence larger than the two on the sides, which are aligned to the seminal furrows.

Four years later Eisen (1899) describes *D. verrucosa* with two deep grooves from ½ xix─½ xxi, prostate pores on xix and xxi, and the male (spermiducal) pores on xx, with intestinal origin in xvi. Numerous ventral papillae (genital tumescences)—solitary and in pairs—are reported, all postclitellar segments. A year later Eisen (1900) included a similar description of *D. verrucosa* based on his 1899 paper.

Descriptions of *D. verrucosa* remained relatively simple for the first five decades of the 20th century with numerous researchers variously reporting on the three delineating characters. Smith (1915, 1928) reported

specimens collected in 1895 were in abundance in Illinois bottomland forests with male pores in xx, prostate pores in xix, xxi (implying a male groove xix─xxi); there is no mention of genital tumescences or intestinal origin. Gates (1977) makes the single observation that the male pores of *D. verrucosa* are "on segment twenty" in his survey of earthworms of North America and observes there is "…remarkable variation in the position of the male pores…" for the genus *Diplocardia*. Stephenson (1930) does not list *D. verrucosa* among the six species of diplocardians in his encyclopedic work, *The Oligochaeta*. Olson (1933) published the first record of *D. verrucosa* in Ohio with "Prostate pores on 19, 21. Spermiducal pores in somites [*sic*] 20…." based on a single specimen collected on the shore of a lake. There is no mention of genital tumescences or intestinal origin. Harman (1960) states that the male pores of *D. verrucosa* are in xix with no mention of genital tumescences or intestine origin and notes that the species seems confined to north central USA.

Murchie (1962) provides a thorough review *D. verrucosa* and includes Michaelsen's (1900) correction of Ude's interpretation of the openings of the spermathecal pores occurring on segments viii and ix rather than ix and x. Murchie examined many specimens curated at the US National Museum, corresponded with a museum in Germany where type material is housed, as well as specimens he collected from numerous sites in Oklahoma associated with heavy alluvial soils associated with large streams. From his observations he concludes there are two subspecies—with no intergrades—*Diplocardia verrucosa verrucosa* Ude, 1895 and *D. verrucosa recta* Murchie, 1962. This description is based on differences in clitellar margins, position variation in spermathecal pores in viii and ix, and location of glandular tumescences. Both subspecies have male pores on xx and an intestine that expands abruptly in xvi, which for the former, Murchie notes is unique for *Diplocardia*.

At this point in the timeline of descriptions for *D. verrucosa* something unusual occurs. Gates (1967) reviews one specimen from Wisconsin and ten from the southwest corner of New Mexico where all have male pores in xx. However, only the Wisconsin specimen has "abundant" genital tumescences, consistent with the Murchie (1962) description, but the New Mexico specimens are devoid of this character. Regarding the intestinal origin, Gates wrestles, "Intestinal origin, doubtfully in xvi (Wisconsin and 2, New Mexico), in xviii (8, New Mexico). Such variation seemed unusual." Ten years later Gates (1977) again reviews *D. verrucosa* (along with three dozen other diplocardian species) examining 14 specimens (ten adults) from Missouri, Texas, Tennessee, and Illinois. He continues to mull the apparent variableness of the intestinal origin for *D. verrucosa* even noting that McKey-Fender (*in lit)* was "not clear" on this character after examining specimens from three aforementioned states as well as Maryland. However, at the end of this paper Gates introduces a key for the genus where he apparently had settled in his mind that the location of the intestinal origin for *D. verrucosa* is xviii. Also, though without explicit mention of Murchie's 1962 publication that designates two subspecies for *D. verrucosa*, Gates seemingly dismisses these by observing, "Genital markings and/or tumescences, with regard to presence or absence, number, regional position, intrasegmental location or across intersegmental furrows, show greater variation than has yet been recorded in other diplocardias [*sic*]." Other than the citation of Murchie (1962), Gates (1967) makes no mention of subspecies for *D. verrucosa*.

James (1983,1988, 1989, 1991) includes *D. verrucosa* in a series of field studies on the response of native and nonnative earthworm species to fire in tallgrass prairie soils of Kansas. The scope of the projects does not require morphological descriptions of the species. In James (1990) an updated key for the genus *Diplocardia* designates the intestinal origin in xviii for *D. verrucosa* and makes no mention of the two subspecies delineated by Murchie. Since the *D. verrucosa* specimens in these studies were collected in prairie soils not associated with lotic systems and, if the male groove was in xix–xxi, then it may be possible that these specimens are *D. farrishi* **sp. nov.**, or perhaps *D. patuxentis* Csuzdi & Szlávecz, 2002.

Csuzdi & Szlávecz (2002) note the similarities of *D. patuxentis* to *D. verrucosa* with male pores in xx and an intestinal origin at xviii/xix, though differing from it with an annular clitellum, the shape and position of genital markings, and the presence of copulatory setae. In addition, they observe that *D. patuxentis* might be identical to *Diplocardia* sp. V. partially described by Gates (1977). This specimen was not conclusively described by Gates due to its poorly preserved condition, yet he lists it in association with *D. verrucosa* because it has male pores in xx. Gates suspects it is a different species because the last hearts are in xiii, *not* because the intestinal origin is in xviii.

For 17 years no further significant reports of *D. verrucosa* appear in publications until Damoff & Reynolds (2019) catalog a large collection of diplocardians from Tennessee, that includes one clitellate specimen of *Diplocardia verrucosa* collected in 1963 (but not previously published) from a site in the southern corner of Tennessee that borders North Carolina. No other *D. verrucosa* specimens were reported for the entire state at that time.

Methods

Collection site locations (Figure 1) and descriptions for the *D. verrucosa* and *D. farrishi* **sp. nov.** specimens are presented in Tables 1 and 2. Coordinates for the Tennessee sites are approximated using Google Earth® based on 1971 field collection notes of cities/towns, highways, and other landmarks. For New Mexico, Oklahoma, and Texas, a Magellan GPS Mapping Receiver was used to record coordinates. For the NM, OK, and TX collections, earthworms were collected by digging with a shovel and handsorting. Specimens were placed in soil bags along with some of the soil from which they were collected and stored in a cool place out of direct sunlight. No attempts were made to quantify earthworms per area or volume of soil. Within 24 h the earthworms were processed in a manner that is conducive for identification of the species under a microscope: specimens were rinsed in water, relaxed in gradual increases of ethanol concentrations until no longer responsive to touch, fixed in 5% formalin for 48 hours, then triple rinsed and stored in 70% ethanol. DNA samples were taken from several of the OK and TX specimens. The TN specimens were collected, fixed, and preserved by John Reynolds in 1971 and curated at the Canadian Museum of Nature (Damoff & Reynolds 2019). The NM specimens collected by Beck (Gates 1967) have no record of collection or preservation methods. Specimen colorations are described using the color notations in Munsell® Soil Color Charts (Munsell Color 2000).

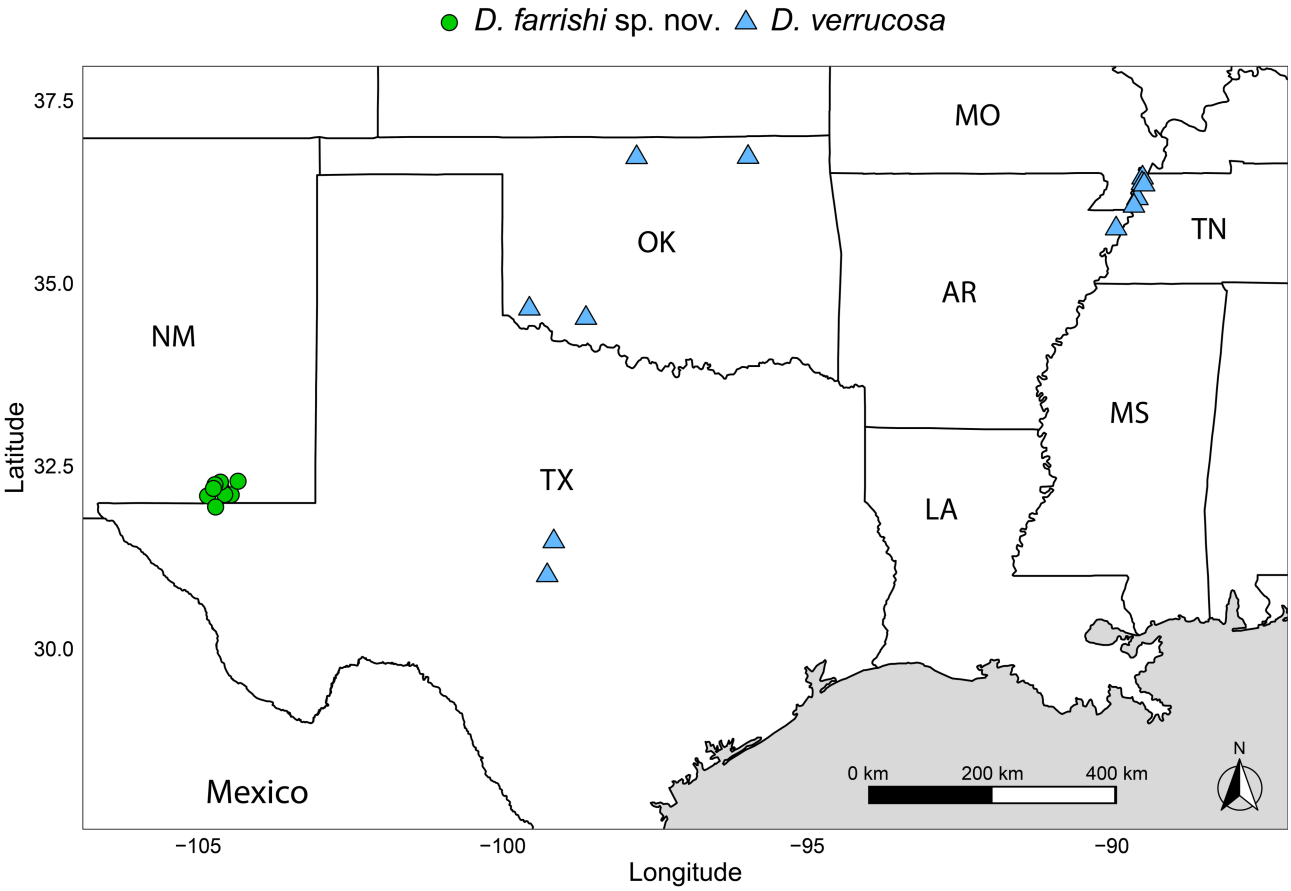

FIGURE 1. Map showing locations of specimen collection described in Tables 1 and 2. State abbreviations: AR, Arkansas; LA, Louisiana; MO, Missouri; MS, Mississippi; NM, New Mexico; OK, Oklahoma; TN, Tennessee; and TX, Texas.

TABLE 1. Collecting sites of *Diplocardia verrucosa* Ude, 1895 specimens from three USA states (ST): Oklahoma (OK), Tennessee (TN), and Texas (TX); from eight counties (Cty); site time stamp; date of collection (YYYYMMDD), latitude and longitude, nearest lotic system (LO) (stream, creek, river); distance to nearest LO; soil texture and color; and site characteristics.

ST	Cty*	Site	Date	Lat/Lon	Stream‡	Distance	Soil characteristics	Topographic features & notes
OK	CM	1015	20170520	34˚31’26”N 98˚37’57”W	PO	30 m	clay loam, dusky red	N of creek; roadway shoulder in wood chips and grasses
	GT	1510	20170406	36˚43’22”N 97˚48’02”W	PD	< 1 m	silty clay loam, dusky red	E of creek; saturated soils of stream bank
	GT	1330	20170502	36˚43’22”N 97˚48’02”W	PD	< 1 m	silty clay loam, dark reddish brown	E of creek; saturated soils of stream bank
	JK	1230	20181020	34˚39’03”N 99˚33’40”W	TU	6 m	silty clay loam, dark reddish brown	N of creek; steep slope under canopy of ash trees
	WT	0730	20170524	36˚43’35”N 95˚58’15”W	CA	0.5 km	silty clay, very dark gray	SW of river; closed canopy of hardwoods in flood plain, coarse woody debris, herbaceous plants
TN	DY	08	19711130	36˚09’40”N 89˚34’44”W	MS	0.7 km	silty clay loam, brown	WSW of river; under log
	DY	14	19711130	36˚03’30”N 89˚38’09”W	MS	4 km	silty clay loam, brown	W of river; under logs
	LK	03	19710323	36˚26’38”N 89˚29’39”W	MS	3 km	silt loam, grayish brown	WNW of river; ditch
	LK	09	19711129	36˚22’01”N 89˚30’09”W	MS	150 m	silty clay loam, very dark gray	E of river; ditch
	LK	12	19711130	36˚20’57”N 89˚28’07”W	MS	4 km	silty clay loam, very dark gray	W of river; under logs
	LD	08	19711110	35˚44’52”N 89˚55’42”W	MS	5 m	silt loam, grayish brown	Shoreline of river; Pink’s Boat Dock - picking
TX	MC	1125	20151215	31˚28’04”N 99˚09’38”W	CO	3 m	sandy clay loam, dark brown	S of river; ledge 5 m above water
	MC	0740	20160321	31˚28’04”N 99˚09’38”W	CO	3 m	silty clay, brown	S of river; ledge 5 m above water
	MC	0950	20160321	31˚00’14”N 99˚16’07”W	SS	6 m	clay loam, black	S of river; open canopy of small trees & coarse woody debris

*** Counties** (Cty): Comanche = CM; Grant = GT; Jackson = JK; Washington = WT; Dyer = DY; Lake = LK; Lauderdale = LD; McCulloch = MC.

‡ **Nearest stream**: PO = Little Post Oak Creek; PD = Pond Creek; TU = Turkey Creek; CA = Caney River ; MS = Mississippi River; CO = Colorado River; SS = San Saba River.

TABLE 2. Collection sites of *Diplocardia farrishi* **sp. nov.** specimens collected in two USA states (ST): New Mexico (NM) and Texas (TX); from three counties (Cty): Eddy (ED), Otero (OT), and Culberson (CU); site time stamp; date of collection (YYYYMMDD); latitude and longitude; nearest lotic system (LO) (stream, spring); distance to nearest LO; soil texture and color; and site characteristics.

ST	Cty*	Site	Date	Lat/Lon	LO‡	Distance	Soil texture, color	Site characteristics
NM	ED	1000	20050317	32˚06’24”N 104˚27’25”W	BR	~30 m above	loam, very dark gray	among willow grove & grasses; deep A horizon; not hydric soil
	ED	1400	20050317	32˚17’30”N 104˚20’40”W	un	~3 m above	sandy loam, dark reddish brown	near cactus & juniper; 80% open field, 20% herbs; washout into arroyo meters above dry stream channel
	ED	1600	20050317	32˚12’08”N 104˚37’29”W	none	-	loam, dark reddish brown	under old juniper, deep ravine parallel CR 410; 100% mineral soil; not hydric soil
	OT	1400	20050318	32˚05’29”N 104˚50’41”W	none	-	sandy loam, dark reddish brown	10% mineral, 90% herbs; 2 m above dry wash filled with cobble
	ED	1600	20050321	32˚06’37”N 104˚33’45”W	YD	in draw	loam, dark reddish brown	open canopy; 10% mineral, 90% herbs, under hdwd litter; coppice of sugarberry & other woody veg.
	ED	1205	20050322	32˚16’46”N 104˚38’00”W	un	~3 m above	loam, dark reddish brown	N facing rock ledge; grasses under oaks, A horizon 15 cm, over cobble; creek bed dry, few pools, 5 m wide
	ED	1700	20050322	32˚14’40”N 104˚43’23”W	WOS	5 m above	silt loam, black	closed canopy; 100% leaf litter over mineral soil
	ED	1700	20050322	32˚14’40”N 104˚43’23”W	WOS	3 km	silt loam, black	in channel, rich OM, silt loam, leaf particles somewhat discernable
	ED	1700	20050322	32˚14’40”N 104˚43’23”W	WOS	~3 m above	silt loam, black	North end of ravine under big tooth maple *Acer grandidentatum* Nutt.
	ED	1030	20050323	32˚11’35”N 104˚44’55”W	none	-	silt loam, dark reddish brown	open canopy; 50% min., 50% herbs, cedar & lg sprawling oak; grasses in clumps; not hydric soil
TX	CU	1300	20050321	31˚56’23”N 104˚42’45”W	un	0.5 m above	sandy loam, dark reddish brown	0.5 m above stream channel; nearly closed canopy of cedars; 60 % hdwd, 40% conifer leaf litter over mineral

*** Counties** (Cty): Eddy = ED; Otero = OT; Culberson = CU

‡ **Nearest stream**: BR = Black River; YD = Yucca Draw; WOS = White Oak Spring; un = unnamed arroyo/draw/creek/stream.

Soil texture was determined using the texture-by-feel method (USDA-NRCS 2018). Soil and earthworm color was determined using Munsell Soil Color Charts (2000). Soil pH was determined with a Lovibond® Soil pH Test Kit. For the OK and TX soils from which *D. verrucosa* was collected, all parameters were determined in the lab within 48 hours of the collecting event; for the soils of the TN counties, pH and soil texture were determined from online soil series publications (USDA-NRCS 2024).

The last five or so segments from a few *D. verrucosa* specimens were extracted and preserved in ethanol 95% for DNA extraction. In March 2022 we attempted to collect living *D. farrishi* specimens but were unsuccessful because of low soil moisture. Consequently, we attempted to extract DNA from six specimens from the 2005 formalin fix collections, following protocols in James *et al*. (2010). DNA was extracted using the Qiagen™ DNeasy® Blood &

Tissue DNA extraction kit and DNA concentrations were quantified using the QuantiFlour® ONE dsDNA System (Promega) and a Quantus™ Fluorometer (Promega), following manufacture instructions. Samples were then amplified for the mitochondrial Cytochrome c Oxidase subunit I (COI) barcode gene using the primers LCO1490 [5` - GGT CAA CAA ATC ATA AAG ATA TTG G - 3`; Folmer *et al.* (1994)] and COI2198E [5′-TAW ACT TCW GGG TGW CCR AAR AAT CA-3′, Ikeda *et al.* (2018)]. PCR protocols, cleanup, and sequencing followed those described in Carrera-Martínez *et al*. (2021; 2025). Since all formalin-fixed tissues failed to amplify using this set of primers, we designed six pairs of primers using Geneious Prime (https://www.geneious.com/) that would amplify overlaying 130–240 bp of COI fragments within the products of LCO1490 and COI2198E primers described above. Since no sequence of the species described below is available, we used a consensus sequences generated from the *D. verrucosa* samples as the reference sequence. The primers sequences are available in Appendix 1.

Results

A total of 110 adult and subadult *Diplocardia verrucosa* Ude 1895 specimens were examined with 38 from OK, 55 from TN, and 17 from TX. Key characteristics consistently observed are a male groove in xix─xxi, a high number of genital tumescences (GT) in pre-, intra- and post-clitellar segments, the intestinal origin in xvi, and relatively low number of segments (Table 3).

TABLE 3. Comparison of specimen morphological characters for *Diplocardia verrucosa* Ude, 1895 (*Dv*) from Oklahoma (OK), Tennessee (TN), and Texas (TX), USA and *Diplocardia farrishi* **sp. nov.** from New Mexico (NM) and TX, USA. Length (L), diameter (D), and number of segments (S) stacked as mean, range, and number (*n*)*. Tongue type (T), genital tumescence (GT), male groove (MG), intestinal origin (IO), and first dorsal pore (FDP).

ST/species	L (mm)	D (mm)	S	T	GT‡	MGᵠ	IOᐞ	FDP (range, outliers)
D verrucosa	87	2.1	129	epilobous	ix–xxiv	1/4xix–	xvi	5/6–15/16,
OK	71–123	1.3–2.6	91–146		*n* = 22	1/2xxi	taper absent	26/27
	n = 22	*n* = 29	*n* = 29				*n* = 29	*n* = 36
D verrucosa	107	2.0	117	epilobous	vii–xxii	1/4xix–	xvi	6/7–13/14
TN	70–142	1.9–2.7	80–149		*n* = 14	1/2xxi	20 taper	*n* = 51
	n = 14	*n* = 14	*n* = 49				*n* = 49	
D verrucosa	91	2.1	124	epilobous	ix–xxii	1/4xix–	xvi	8/9–12/13,
TX	65–130	1.8–2.4	94–143		*n* = 11	1/2xxi	11 taper	19/20
	n = 11	*n* = 11	*n* = 17				*n* = 15	*n* = 16
D farrishi	90	2.6	142	epilobous (65)	none	1/2xix–	xviii	6/7–10/11
TX/NM	65–140	2.0–3.7	95–176	tanylobous (1)	*n* = 56	1/2xxi	1/2xviii (3)	*n* = 18
	n = 32	*n* = 51	*n* = 35	*n* = 66		*n* = 56	*n* = 66	

**n* = based on number of specimens that display character. Variance of *n* within a row is the result of exclusion of specimens that were cut during collection, an amputee, or an unusable life stage.

‡ GT with various arrangements pre-, intra- and postclitellar; single, paired, tetrads, or asymmetrical within segments or across intersegmental grooves.

ᵠMG segmental extent for *D. verrucosa* varies within a range of 1/4–2/3 in xix to 1/3–1/2xxi.

ᐞ IO, unless otherwise noted, full diameter in entire segment. Taper = gradual expansion from esophagus to full diameter within segment of origination.

A total of 66 adult and subadult *Diplocardia farrishi* **sp. nov.** specimens were examined by the authors from collections made in 2005 in SE NM and W TX—59 from nine sites in Eddy County, NM; one from Otero County, NM; and six from one site in Culberson County, TX (Table 2.) Key characteristics consistently observed are the male groove in xix─xxi, absence of genital tumescences (GT), and the intestinal origin in xviii, and relatively high number of segments (Table 3).

Additional collections concurrent with the above included three native species: *Diplocardia eiseni* (Michaelsen, 1895); *Diplocardia smithii* Macnab and McKey-Fender, 1955; and *Diplocardia texensis* (Smith, 1924) and three nonnative species: *Aporrectodea trapezoides* (Dugès, 1828); *Aporrectodea rosea* (Savigny, 1826); and *Microscolex phosphoreus* (Dugès, 1837). Notably, no nonnative earthworm species were collected in the remote White Oak Spring site.

While a limited amount of genomic DNA seems to have been extracted from one specimen of formalin-fixed *D. farrishi* (a concentration of 1.56 ng/μL), attempts to sequence COI (either as a single sequence or six overlaying fragments) failed. COI sequences of two *D. verrucosa* specimens, one from McCulloch Co., Texas, and the second from Grant Co., Oklahoma, are freely available on GenBank (accession numbers PP844713 and PP844714, respectively).

Taxonomy

Family Acanthodrilidae Claus, 1880

Genus *Diplocardia* Garman, 1888

Type species: *Diplocardia communis* Garman, 1888.

Diplocardia verrucosa Ude, 1895

(Figure 2 A–C)

Material examined. Representative specimen: Clitellate, USNM 1742101, within the city limits of Bartlesville, Washington County, Oklahoma, USA (36˚43’35”N, 95˚58’15”W). Collector George A. Damoff on 24 May 2017, elevation 194 m, 0.5 km southwest of Caney River in a closed canopy of bottomland hardwoods in deep silty clay. Additional specimens: 21 clitellates and and subadults also collected at numerous sites in Oklahoma and Texas, USNM 1742102–1742105. Additionally, 55 specimens are curated at the Canadian Museum of Nature, although recently reported as *Diplocardia* **sp. nov.** TN01 in Damoff and Reynolds (2019) for reasons explained above.

Diagnosis. Small-sized, quadrithecal earthworm, 123 mm length X 2.5 mm diameter (xxx). Segment count 141. Epilobous tongue 1/2 width of segment, open, with minimal slight crisscrossed rugosities that contrast with smooth surface of ii. Saddled-shaped clitellum with ventral margin slightly dorsad to *b*. Genital tumescences range from spherical to irregular margins present in pre-, intra- and post-clitellar segments. Male groove narrow and shallow in 1/2xix─1/3xxi, nearly straight with secondary indentations associated with segmentation. Single dorsal blood vessel throughout. Last hearts xii. Intestinal origin xvi. Calciferous lamellae absent. Acryptate spermathecae with oblong diverticulum attached by a short stalk near base of ovoid ampulla.

Description

EXTERNAL.—Small-sized earthworm. For all three states (OK, TN, and TX), mean length of intact adult specimens 94 mm (range 64–142; $n = 47$); mean segment count of intact subadult and adult specimens 125 (range 71–149; $n = 95$); mean clitellate width 2.1 mm (range 1.3–2.7).

Body shape cylindrical throughout. Triannulation begins at vi and strongly evident in clitellar and postclitellar segments, except last five. Other specimens from OK, TN, and TX most often display triannulation over majority of length, a few specimens do not.

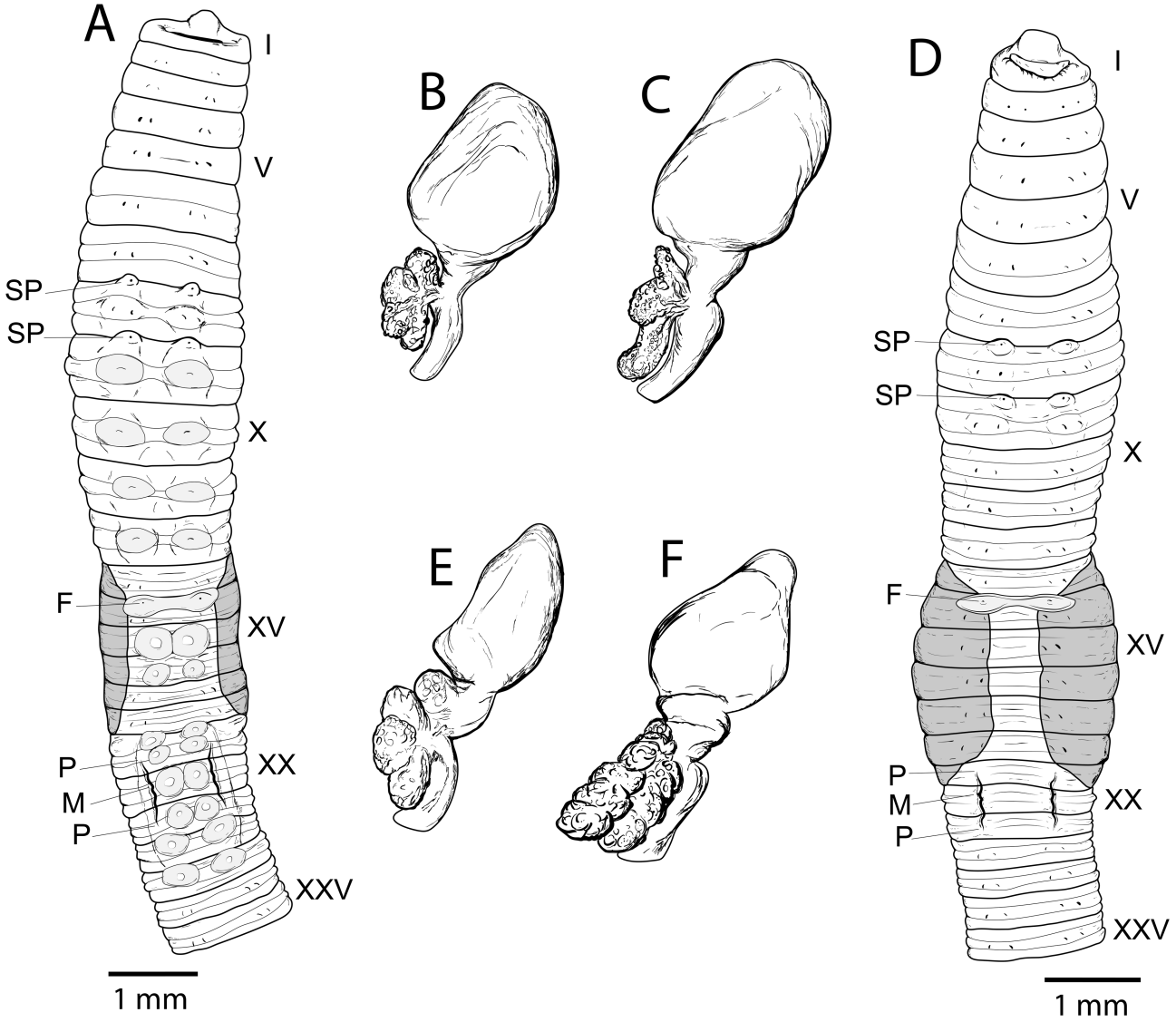

FIGURE 2. *Diplocardia verrucosa*: (A) ventral view, spermathecae from (B) viii, and (C) ix; *Diplocardia farrishi* sp. nov.: (D) ventral view, spermathecae from (E) viii, and (F) ix. SP, spermathecae pores; F, female pores; P, prostatic pores; and M, male pores.

No pigmentation. Body color of formalin-fixed, ethanol-stored specimens uniform throughout: pinkish white (7.5YR 8/2) clitellum pink (7.5YR 7/4). TN specimens color dark reddish brown (2.5 YR 5/4) from 50 years of storage in ethanol; distinctly different color from OK and TX specimens.

Epilobous tongue about 1/2 width of segment, open though some have crease at base that gives closed appearance. Slight crisscrossed rugosities that contrast with smooth surface of ii.

First dorsal pore varied widely for populations within and between OK, TN, and TX with a range of 5/6–26/27. Nephridiopores not obvious.

Saddle-shaped clitellum xiii─xviii. Specifically, dorsal extent variable where anteriorly all or a fraction of xiii then most often extending posteriorly through all of xviii, though a few all or part of xix. Ventral extent slightly less than anterior segments and margin varies from slightly lateral to *b* or to *a*. Setal pairs visible in all clitellar segments. If first dorsal pore anterior to 13/14 then dorsal pores visible in clitellum.

Setae begin ii, closely paired below mL line. Ambulatory setae conspicuous, somewhat dark, observed in most segments before periproct. Setal arrangement at x: *aa*:*ab*:*bc*:*cd*:*dd* = 5:1:2.7:1.3:16.3 and at xxx: 4.3:1:2.3:1:13.3. Presence of copulatory setae variable, absent to present; if present, two in viii and two in ix. Penial setae also variable regardless of lifestage, either absent or present. If present, internally observed in xix and xxi; infrequently

visible externally at one to all tips of male grooves. The penial setae of the TN specimens easily seen (red) in xix and xxi, length 0.5 mm, width about 0.05 mm. Setae *a* and *b* less conspicuous in viii and ix than in vii and x. Setae *a* and *b* missing in xix, xx, and xxi.

Spermathecal pores near anterior margin of viii, ix, all 0.1 mm in diameter, slightly raised (about 0.1 mm) on conical papillae (about 0.2 mm diameter). Pores of viii 0.3 mm from anterior margin, 0.25 mm from setae, and <0.05 mm lateral to *a;* pores of ix 0.5 mm from anterior margin, 0.3 mm from setae and <0.05 mm lateral to *a*.

Ovipores in xiv, presetal, slightly mesad or in line with *a*, less than 0.1 mm diameter. Commonly observed pinkish white papillae ("halo") surrounding the single pair of ovipores, oval to slight dumbbell-shaped boundary that extends slightly lateral to *b*─*b*. Strong brown color of papillae in TN specimens same as clitellum.

Male groove, in line with *a*, extends from 1/2xix–1/3xxi, nearly straight to slightly sigmoid with secondary indentations associated with intersegmental grooves and secondary annulations. Shallow, narrow (greatest width about 0.1 mm), and flush with surrounding adjacent ventral surface. Prostatic pores inconspicuous in tips of male groove. Male pore xx, at anterior-most margin of 19/20 within male groove, occasionally conspicuous. Associated with numerous genital tumescences (GT).

GT are frequently in ix to xxiv, in intersegmental furrows frequently in 12/13 to 16/17, 18/19; these segments can have up to 7 GTs, some are occasionally unpaired mV. All are slightly raised above the external body wall. Paired GT vary in width apart, from slightly merged within *a*─*a*, to widely separated each between *a*─*b*. GT not spanning an intersegmental groove are postsetal. As with dorsal pores, GT distribution varied for populations within and between states. OK and TX specimens typically had a similar range of segments with GT, x to xxiv, and number of GT per segment, 1, 2, 4, and less frequent, 3. These differed from the TN specimens with range of GT segments, vii to xxii, and number of GT per segment, 1, 2, 4, 6 and less frequent, 3, 5, or 7. Most GT are circular though some have irregular margins that vary in diameter 0.2─0.9 mm. Color of GT for OK and TX specimens are a near white inner area contrasted by a narrow border of light brown; TN specimens are shades of reddish brown. Contrast with surrounding tissue is not sharp.

Spermatophores. None observed adhering to the exterior body wall.

INTERNAL.—Septa thickened 6/7─12/13 and slight musculature evident in 6/7─10/11, with greatest thickness 7/8─9/10. All septa posterior to 12/13 same thickness. All preclitellar septa drape anteriorly covering all internal organs in the adjacent anterior segment where septa attach to the body wall. Intersegmental bands extend posteriorly from the surface of the pharynx (ii–iv) and gizzards (v–vi). Transeptal muscles numerous in ii–xii, with greatest abundance associated with the pharynx, penetrate muscled septa at oblique angles. Most transeptal muscle bands confined to two adjacent segments, yet at least one penetrates through 6/7─8/9 septa. Anterior end attached to an organ of the alimentary canal and the posterior end attached to the body wall. Integument and body musculature (longitudinal and transverse muscle layers) each about 0.1 mm thick.

Coagulum (preserved coelomic fluids), abundant throughout, denser in segments anterior to intestine, especially in ix─xi. Same opaque white as seminal vesicle making it difficult to parse the two.

Alimentary canal. Pharynx in ii–iv covered in transeptal muscle bands, whitish in color, 0.1–0.2 mm width, in numerous distinct layers over dorsal and lateral surfaces of the pharynx, extending posteriorly, anchored in body wall. Two gizzards in v–vi without distinct demarcation also with numerous transeptal muscle bands extending posteriorly for one or two segments. Esophagus vii–xv, uniform in diameter from xiii–xv. Calciferous glands or lamellae absent. Intestinal origin xvi, fully expanded at junction with esophagus at septum 15/16. The intestine of a few specimens expands (tapers) gradually to full diameter in xvi, while a few others display an abrupt expansion somewhere well within xvi; only one of the 110 specimens had the intestinal origin in xvii and this may have been a result of obvious external trauma to the body wall during development. Simple lamelliform typhlosole most often begins in xviii, occasionally in xix, and extends about 0.5 mm into lumen or 1/4 to 1/3 of the inside lumen diameter. Remainder of gut lining generally smooth with few ridges.

Nephridia. Holoic, in iii to terminal segments near periproct. Tubules about 0.03 mm diameter, centered on *d*. Exoic duct exits coelom 0.2─0.3 mm anterior to *d*. Avesiculate.

Vascular system. Dorsal vessel single throughout; blood engorgement often observed but span of segments highly variable between specimens. Ventral vessel most easily observed in xvi; dorsal to and immediately adjacent to the ventral nerve cord; greatest diameter 0.4 mm. Paired latero-esophageal vessels (hearts) x–xii often engorged with blood. Extra-esophageal vessels vii–ix, about 1/4 less diameter than hearts and occupy same position in each segment as the hearts.

Nervous system. Dorsal bi-lobed cerebral ganglion on dorsal surface of pharynx in iii united with ventral nerve cord by circumpharyngeal connectives that pass over the lateral surface of the pharynx. Ventral nerve cord easily observed, sandwiched between the ventral blood vessel and body wall; opaque and about the same diameter as the ventral blood vessel.

Male sexual system. Testes holandric in x and xi, attached near mV posterior surface of septa 9/10 and 10/11, respectively. Series of strings branching from a single trunk attached to septum has a similar appearance, though smaller size, as ovaries of some diplocardians. Periesophageal testis sac not detected. Male funnels, conspicuous (about 0.5 mm diameter), attached to anterior surfaces of septa 10/11 and 11/12, near *a–b*. Iridescence observed on both testes and male funnels. Racemose seminal vesicles in ix typically smaller than those in xii which often fills the entire coelomic cavity; often absent in ix for the OK specimens, especially for those collected in Jackson County. Prostates paired in xix and xxi, in line with *a*. Sharp transition in diameter from duct to gland. Curved prostatic duct short (*ca.* 2 mm long) and narrow (<0.1 mm diameter). Gland with smooth margin and sharp folds—sometimes more than six 90° and 180° loops—with asymmetrical distribution of R/L, anterior/posterior prostates that span three or more pre- and post-segments adjacent to segment of duct; overall length can exceed 3 cm. Penisetal bundles about 0.5 mm in length and 0.05 mm diameter, in xix and xxi, penetrating body wall with prostatic duct. Transverse muscle bands observed only in TN specimens.

Female sexual system. Ovaries in xiii, conspicuous conical cluster (not distinct strings) attached to ventrad posterior surface of septum 12/13. Ovarian funnels conspicuous, attached to ventrad anterior surface of septum 13/14, irregular wavy rim about 0.3 mm diameter. Oviducts pass through 13/14 septum, short duct in xiv about 0.2 mm diameter, penetrates body wall adjacent to ventral nerve cord, near *a*.

Spermathecae. Quadrithecal, in viii and ix. Duct emerges near *a*, length about 1─2 mm long by <1 mm diameter. Acryptate. Diverticulum sessile or on a short stalk attached near ectal end (near ampulla); oblong single chamber; length at least double the width; with iridescence on some specimens. Ampulla ovoid, relatively large compared to overall size of clitellate specimens, 1─2 mm long by 1─2 mm wide, sometimes width slightly greater than length; iridescence not observed (Fig. 2).

Remarks

Ude's 1895 original description of *Diplocardia verrucosa* is based on three specimens that are supposed to be the type series. There are only two specimens presently curated in the Museum of Nature Hamburg, Germany that are designated syntypes (accession number: ZMH-ANN-OL-V382). While at the current time we are unable to study the specimens in person (due to the fragility of the material, shipping for examination was not an option), digital photographs provided by the museum curator of one of the two specimens shows that it has its male field in xix-xxi, consistent to *D. verrucosa*, but completely lacks the genital tumescence described by Ude and recognized as a major diagnostic feature for this species by multiple authorities (*e.g.*, Murchie 1962, Gates 1967, 1977). Furthermore, this specimen lacks a clitellum, while Ude describes the presence of it. The second specimen in this lot lacks its anterior portion and therefore its identification is not possible. Given this and that Ude used three specimens, and that one of the specimens do not seem to fit Ude's description, it is possible that these specimens might not be those used by Ude to describe *D. verrucosa* and were mislabeled at some point. Another possibility is that these specimens have been worn due to their age and these diagnostic characters have been damaged or lost. In any case, careful in person examination of the one full specimen should be carried out to confirm if it fits the original description by Ude (1895). If this specimen is indeed an inadequate representation of the species, a neotype could be proposed from its type locality at Omaha, Nebraska following the International Commission on Zoological Nomenclature Code (1999) Article 75. Such determination should be carried out in a future study.

The Tennessee specimens differ from the other specimens in numbers per segment and segment range of GT; other than slight variation in overall size (likely due to site quality), this single character is the only notable difference for all 110 specimens from all three states.

Gut content mostly fine sand (0.05 mm dia.) with low amount (<10%) of short dark fibers and scattered pieces of woody material (up to 1 X 2 mm); TX specimens had slightly larger sand grains.

Based on collection records that span over a century from multiple sites in more than a dozen states in the USA *D. verrucosa* clearly prefers hydric soils.

***Diplocardia farrishi* Damoff & Carrera-Martínez sp. nov.**
urn:lsid:zoobank.org:act:12A34A02-93E9-4D4A-9D68-B74A6C29C3BB
Figure 2 D–F

Synonyms. *Diplocardia verrucosa* Gates, 1967, 1977 (in part).

Material examined. Holotype: Clitellate, USNM 1742106. White Oak Springs, Lincoln National Forest, Eddy County, New Mexico, USA (32˚14'40"N, 104˚43'23"W; elevation 1562 m). Collectors George A. Damoff and Michael A. Damoff on 22 March 2005. Site accessed by approximately 0.5 km hike from north terminus of side road off of Forest Service Road 525. Closed canopy of mixed hardwoods in deep narrow ravine with deep silt loam among boulders in the Chihuahuan Desert. Paratypes: 12 .USNM 1742107–1742118.

Etymology. Named in honor of Ken Farrish, the dissertation director of the first author, whose engaging manner during soil lectures was the providential means first used to direct his attention to the great need of earthworm ecology research. In the many years that have followed, Ken has continued to give much enthusiastic guidance, support, and encouragement. There is a slight regret that the specimens named in his honor lack semblance of colors to the Farrish tartan, but this deficiency may be overlooked if the species proves to enhance the flavor of the family haggis recipe.

Diagnosis. Small-sized, quadrithecal earthworm, 140 mm length X 3.4 mm diameter (xxx). Segment count 134. Epilobous tongue 1/2 width of segment, open, with minimal slight rugosities parallel to long axis of organism. Saddled-shaped clitellum, dorsal and ventral extent all of xiii–xix, with ventral margin slightly ventrad to *a*. No genital tumescences. Male groove narrow and shallow in 1/2xix─1/2xxi, nearly straight without secondary indentations associated with segmentation. Single dorsal blood vessel throughout. Last hearts xii. Intestinal origin xviii. Calciferous lamellae absent. Acryptate spermathecae with sessile quadruple-lobed diverticulum near base of ovoid ampulla.

Description

EXTERNAL.—Small-sized earthworm. Mean length, width, segment count and other character traits are in figure 2 and table 3.

Body shape generally cylindrical throughout. Widest at vi–ix, postclitellum diameter uniform nearly to last dozen segments where body on some specimens somewhat flattens. Biannulation begins around iv and transitions to triannulate around viii through xii, little or no annulation in clitellar segments xiii–xix, triannulation resumes at xx and continues through remaining segments, with the last half dozen or more absent of any annulation.

Pigmentation absent. Body color of formalin-fixed, ethanol-stored specimens (nearly 20 years) uniform throughout: brown (7.5YR 5/4), clitellum strong brown (7.5YR 5/8).

Epilobous tongue *ca.* 1/2 width of segment, with some isolated populations at divergent sites with a closed epilobous tongue and others open. One specimen tanylobous. Rugosae on peristomium slight and mostly parallel with the long axis.

First dorsal pore 6/7 or 7/8, no dorsal pores evident in clitellar segments, with dorsal pores evident in all postclitellar segments except last few. Nephridiopores inconspicuous at *d*.

Saddle-shaped clitellum xiii─xix filling all segments both dorsally and ventrally, though less thick in xiii and xix. Ventral margin of clitellum distinct, 0.1 mm within *a–a*, resulting in a distinct ventral 0.3 mm region absent of clitellar material extending all of xiii–xix. All setal pairs visible in all clitellar segments.

Setae begin ii, closely paired below mL line. Ambulatory setae, both pairs, conspicuous in all segments before periproct including viii, ix, xiv, xix, and xxi; only *a* and *b* of xx not observed. Holotype setal arrangement the same at x and xxx: *aa*:*ab*:*bc*:*cd*:*dd* = 4.4:1:3.2:1.2:17.6. Copulatory and penial setae are unmodified or absent.

Spermathecal pores in line with *a*, on anterior margins of viii, ix, both the same size (less than 0.1 mm in diameter), slightly raised (about 0.1 mm) on conical papillae (about 0.2 mm diameter) that extends anteriad about 0.1 mm over intersegmental furrow.

Ovipores in xiv, slightly within *a–a* (less than 0.1 mm) and midway between anterior margin and *a*. The pair of pores slightly raised on a single ovoid papilla ("halo") that extends slightly lateral to *a–a*; similar strong brown color as clitellum.

Male groove, in line with *a*, extends from 1/2xix–1/2xxi, nearly straight to slightly crescentic without secondary indentations associated with intersegmental grooves or secondary annulations. Short (slightly greater than 1 mm length), shallow (less than 0.1 mm), narrow (greatest width less than 0.1 mm). Slight ridge entire circumference (about 0.1 mm height). Prostatic pores inconspicuous in tips of male groove. Male pore at anterior-most margin of xx within male groove.

Genital tumescences (GT) absent on all specimens examined.

Spermatophores. None observed adhering to the exterior body wall.

INTERNAL.—Septa thickened yet translucent 6/7─9/10, musculature not evident. All septa posterior to 12/13 same thickness. Many preclitellar septa drape anteriad covering internal organs in the adjacent anterior segment where septa attach to the body wall. Intersegmental bands extend posteriorly from the surface of the pharynx (ii–iv) and gizzards (v–vi). Slender transeptal muscle bundles (less than 0.1 mm diameter) extend posteriorly, with greatest abundance associated with the pharynx, penetrate septa at oblique angles. Anterior end attached to an organ of the alimentary canal and the posterior end attached to the body wall.

Coagulum (preserved coelomic fluids), not overly abundant in segments anterior to intestine. Body musculature gracile throughout though slightly thicker in vi–xx.

Alimentary canal. Pharynx in ii–iv covered in slender transeptal muscle bands, whitish in color, in numerous distinct layers over dorsal and lateral surfaces of the pharynx, extending posteriorly, anchored in body wall. Two gizzards in v–vi without distinct demarcation also with numerous transeptal muscle bands extending posteriorly for one or two segments. Esophagus vii–xvii, generally uniform in diameter (about 0.7 mm) from xiii–xv. Calciferous glands or lamellae absent. Intestinal origin xviii fully expanded (1.8 mm diameter) at junction with esophagus at septum xvii/xviii with few exceptions where intestine tapers to full diameter in xviii. Simple lamelliform typhlosole begins in or near xxi and extends over half of intestinal length, protrudes about 0.5 mm into lumen or 1/4 to 1/3 of the inside lumen diameter. Gut lining smooth with few ridges.

Nephridia. Holoic, in iii to terminal segments near periproct. Tubules 2–3 loops, overall length 3–4 mm, diameter uniform less than 0.1 mm. Exoic duct exits coelom anterior to *d*. Avesiculate.

Vascular system. Dorsal vessel single throughout. Ventral vessel most easily observed in xv–xvii dorsad and in contact with the ventral nerve cord. Paired latero-esophageal vessels (hearts) x, xi, and xii often engorged with blood. Extra-esophageal vessels vii–ix, less diameter than hearts and occupy same position in each segment as the hearts.

Nervous system. Dorsal bi-lobed cerebral ganglion on dorsal surface of pharynx in iii united with ventral nerve cord by circumpharyngeal connectives that pass over the lateral surface of the pharynx. Ventral nerve cord 0.2 mm diameter easily observed in xv–xvii, sandwiched between the ventral blood vessel and body wall.

Male sexual system. Testes holandric, inconspicuous, lack iridescence, in x and xi. Male funnels, iridescent and conspicuous (*ca.* 0.8 mm dia.), attached to anterior surfaces of septa 10/11 and 11/12. Racemose seminal vesicles in ix half the size of those in xii. Prostates paired in xix and xxi. Sharp transition in diameter from duct to gland. Prostatic duct straight and short (0.2 mm long) and narrow (<0.1 mm dia.). Gland (*ca.* 0.4 mm dia.) with smooth margin and sharp folds with asymmetrical distribution of R/L anterior/posterior prostates that span three or more pre-segments and five or more post-segments. Penisetal bundles and transverse muscle bands absent in xix and xxi.

Female sexual system. Ovaries in xiii, conspicuous cluster, no distinct strings, attached to ventrad posterior surface of septum 12/13. Ovarian funnels conspicuous, attached to ventrad anterior surface of septum 13/14, irregular wavy rim *ca.* 0.3 mm diameter. Oviducts pass through 13/14 septum, short duct in xiv *ca.* 0.2 mm diameter, penetrates body wall adjacent to ventral nerve cord, mesiad to *a*.

Spermathecae. Quadrithecal, in viii and ix. Duct emerges near *a*, length about 1─2 mm long by <1 mm diameter. Acryptate. Diverticulum (length twice as long as width) sessile or short stalk (<0.1 mm) attached near base of ampulla; oblong quadruple seminal chamber; iridescence on most specimens. Ampulla ovoid, relatively large compared to overall size of clitellate specimens, 2.4 mm long by 1.8 mm wide (Fig. 2).

Remarks

Gut ingesta varies according to soils at diverse sites. Most specimens with an abundance of fine sand, with a few sand grains larger than diameter of esophagus (range <0.01–1.0 mm dia.). Light brown fine-grained organic

material suspended in coagulated mucus. Large (*ca.* 0.5 mm dia.) opaque white spheres with a globular surface, perhaps calcium aggregates, randomly distributed in the ingesta, similar in distribution and scarcity as the large sand grains.

Ingesta of the White Oak Spring (WOS) specimens limited to relatively low amount of very fine sand and an abundance of dark brown (Munsell 7.5 YR 3/3) hemic organic matter. The spring is in a deep narrow ravine with a nearly closed canopy of white oak (*Quercus* sp.), bigtooth maple (*Acer grandidentatum*), Texas madrone (*Arbutus xalapensis*), very little understory vegetation, and a deep layer of leaf litter over deep silt loam soil. Even here, though, earthworms were in soils well above the spring pool. The specimens from the north end of WOS appeared post reproductive as evidenced by slight rings of brown pigment in the preclitellar intersegmental furrows, a lack of iridescence on diverticula and male funnels, less prominent spermathecal pores than most other adult specimens collected at the other sites, and spermathecae that appeared collapsed.

Five *D. eiseni* specimens, along with *Aporrectodea rosea*, were collected in a black loam hydric soil of the Black River in Eddy County; *D. farrishi* was not collected at this site. Elsewhere in the USA, it is our observation that *D. eiseni* is often found in hydric soils. In the numerous papers referenced above where James collects purported *D. verrucosa* he also reports *D. smithii*. Our single collection of *D. smithii* (along with numerous *Ap. rosea*) is from one site on a ledge 3 m above a small stream. *D. texensis*, with a male groove that spans xx—xxii, was collected at three sites associated with hydric soils and never collected with *D. farrishi*. The only earthworm species collected at the White Oak Spring site was *D. farrishi*, the site from which the holotype was selected.

Because of the unique region from which *D. farrishi* was collected, we propose as a common name the Chihuahuan Desert earthworm.

Discussion

Diplocardia verrucosa first entered the scientific literature in 1895 and in less than five years discrepancies in morphological traits appeared in subsequent publications on the species. As noted above, some corrections have been made, yet additional incongruities have entered and remain in the literature. *Diplocardia farrishi* **sp. nov.** first appeared in the scientific literature when Gates (1967) struggled to describe poorly preserved specimens from SW New Mexico and misidentified the specimens as *D. verrucosa*. Then again, ten years later, Gates (1977) continues to wrestle with a precise description of the intestinal origin of *D. verrucosa*, where he references Murchie (1962) and McKey-Fender (*in lit*), without a firm conclusion. In both these publications by Gates the stark difference of genital tumescences combined with differences in the intestinal origin do not factor into his conclusions. Therefore, contrary to publications by Gates (1967) and after revising specimens from Reynolds and Damoff (2009), *D. verrucosa* is likely not present in New Mexico. The one exception may be a single adult specimen collected by Reynolds and Brody in 1998 where they report collecting it from a riverbank (Reynolds & Damoff 2009), habitat that resembles the preponderance of reports for *D. verrucosa* specimens collected from multiple other states in the USA since 1895.

Murchie's 1962 redescription of *D. verrucosa* (originally described by Ude, 1895) proposes two subspecies based on the extent of ventral development of the clitellum, location of spermathecal pores, and patterns of genital tumescences (GT). In our estimation the first two characters can also be understood as variations within populations collected from disparate sites. The GT of the Tennessee populations reported in this paper generally align with the pattern described for Murchie's *D. verrucosa verrucosa* and the GT patterns of the Oklahoma and Texas specimens reported here with *D. verrucosa recta.* Murchie's redescription is based on a relatively limited number of specimens in comparison to what is now available from twelve US states (Iowa, Illinois, Indiana, Kansas, Maryland, Missouri, Nebraska, Ohio, Oklahoma, Tennessee, Texas, and Wisconsin). While these patterns seem to be consistent with Murchie's (1962) description of both subspecies, we avoid treating both subspecies in this paper until molecular data and more populations between collections sites and respective type localities are available. Curiously, Murchie notes, "Intestine expands abruptly in XVI", yet apparently, he does not regard this trait as noteworthy in the description of the species, an oversight that later influences both Gates (1977) and James (1990) in the development of their keys for the genus.

James first worked with specimens he identified as *D. verrucosa* in 1983 and continued to do so even after making his 1990 key (James, 1991, 1992). It is possible when James externally observed the male groove in xix–

xxi—the only diplocardian at the time in the literature to have that segment range—and then internally observed the last pair of hearts in xii and the intestinal origin in xviii, plus being recently influenced by Gates' key (1977), there was no reason to question otherwise that he was observing *D. verrucosa*. However, the tallgrass prairie habitat of *D. verrucosa* (and other diplocardian species) that James describes aligns more closely with the habitat described for *D. farrishi* (Table 2). Thus in 2005, when the first author encountered for the first time diplocardian specimens with the male groove in xix–xxi, followed by the internal characters that aligned with those highlighted by Gates (1977) and James (1990), *D. verrucosa* was a reasonable conclusion. A reasonable conclusion until years later when the first author observed numerous diplocardian specimens with a male groove in xix–xxi, an intestine that originates in xvi (for most, abruptly), an abundance of genital tumescences, and all taken from hydric soils, most often with a silty soil texture (Table 1).

As noted above, it is a combination of four distinct characters that set *D. farrishi* apart from all other diplocardians. The first trait, male groove in xix–xxi, *D. farrishi* shares with only two other diplocardian species, *D. verrucosa* and *D. patuxentis*. The two morphologic traits, as noted above, that delimit *D. verrucosa* and *D. farrishi* are genital tumescences and the intestinal origin. The fourth characteristic, habitat preference, is contrasted in tables 1 and 2. Most *D. farrishi* specimens collected in 2005 were dug out of semi-arid to xeric soils of the Chihuahuan Desert, well-removed from hydric soils, associated with arroyos (dry washes/gullies), on ledges high above stream channels, and in open grassland areas. The few sites near stream channels did not have saturated soils. The March 2005 Chihuahuan Desert excursion was intentionally made at this time because the region had relatively high soil moisture due to numerous measurable precipitation events spread out over the previous year, including several months prior this trip. The White Oak Spring (WOS) specimens seem an exception to all others collected during the 2005 excursion, yet maybe this somewhat greater soil moisture location is a relic of more typical habitat in the region centuries prior. A fifth more subtle characteristic that somewhat delineates the two species is segment count. Though the range of segment counts for both species overlap considerably, with the low end similar, the upper end appears much higher for *D. farrishi* (Table 3).

While *D. farrishi* seems to be more closely related to *D. verrucosa* and *D. patuxentis*, other *Diplocardia* species (*D. texensis*, *D. woodi* James, 1994, *D. montana* James, 1994, and *D. californica* James, 1994) resembles *D. farrishi* in having a posterior displacement of the male field, two pairs of spermathecae, and lacking GT. *Diplocardia woodi*, *D. montana* and *D. californica* all have their male field in xxi–xxiii, and a longer clitellum in xii–xxi, xxii (James 1994). Similarly, *D. texensis* has a slightly longer clitellum (xiii–xx) and more posteriorly displaced male field (xx–xxii) (Smith 1924, Csuzdi & Szlávecz 2002). *Diplocardia farrishi* differs from *D. patuxentis* in having a saddle-shaped clitellum, and lacking GT, penial, and copulatory setae (Csuzdi & Szlávecz 2002). An additional species, *D. keyesi* Eisen, 1896, shares many similarities with this group as well, with a male field in xx–xxii, lacking GT, and having four spermathecae. However, this species differs from all mentioned before in having its intestinal origin reportedly in xv and without a typhlosole (Eisen 1896). Nonetheless, *D. keyesi* has not been collected ever since its original description, which is based on one posteriorly amputated, and poorly preserved specimen. Damoff & Reynolds (2019) discuss in more details the systematics of *D. keyesi*. Since most of these species were described after James' (1990) key to *Diplocardia* species, we have included a key for species with the male field starting in or after xix.

Most of the species with this combination of characters are found in the Southwestern states of the USA and Northern region of Mexico. While the evolutionary history of this group is still unknown, it is likely that the development of harsh biogeographical boundaries has promoted diversification in isolated places that function as 'refugia,' as suggested by Gates (1967). Furthermore, it appears that some of these species might have specialized to dryer habitats that would normally be considered harsh for earthworms (James 1994; Wood & James 1993). On the other hand, *D. verrucosa* and *D. patuxentis* might have specialized in hydric or more semiaquatic habitats (Csuzdi & Szlávecz 2002), allowing them to perhaps disperse further east. With the discovery of *D. farrishi* and limited sampling on drier regions on the Southwest and West USA, more 'xerophilic' species might be awaiting description. However, before any conclusions can be drawn, further sampling and molecular data are needed in similar habitats of the region (particularly in southern California) to understand the evolutionary history of the *Diplocardia* in this region. Unfortunately, we were unable to obtain barcodes from the *D. farrishi* formalin-fixed specimens. These specimens likely had their DNA broken down to small fragments and other techniques, or preferably fresh material would be needed to obtain reliable molecular data.

Key to species of *Diplocardia* with posteriorly displaced male field

1. Male field in xxi–xxiii; clitellum in xii–xxi, xxii **2**
- Male field in xix–xxi or xx–xxii; clitellum ending at or before xx **4**

2. Testes in xi only; prostomium prolobous . . . . . ***D. montana***
- Testes in x and xi; prostomium epilobous **3**

3. Penial setae present, straighten, 25–30 μm long; typhlosole small, < 1/10 of the intestinal lumen . . . . . ***D. californica***
- Penial setae absent or not modified; typhlosole medium, about 1/5 of the intestinal lumen . . . . . ***D. woodi***

4. Male field in xx–xxii **5**
- Male field in xix–xxi **6**

5. Intestinal origin in xv; typhlosole absent (at least in the anterior 40 segments) . . . . . ***D. keyesi***
- Intestinal origin in xix; typhlosole present . . . . . ***D. texensis***

6. Genital tumesces absent; penial setae absent or not modified . . . . . ***D. farrishi* sp. nov.**
- Genital tumesces present in several segments between vii–xxiv; penial setae present or sometimes absent or not modified **7**

7. Clitellum annular; intestinal origin in xviii . . . . . ***D. patuxentis***
- Clitellum saddle-shaped; intestines starting in xvi, either abrupt or gradual . . . . . ***D. verrucosa***

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APPENDIX 1. Primers of overlapping COI fragments for formalin-fixed *Diplocardia* earthworms.

Fragment	Primer Name	Direction	Seq. L (bp)	Primer Sequence	Reference
1	LCO1490	Forward	234	GGTCAACAAATCATAAAG ATATTGG	Folmer *et al.* (1994)
	DiploVCOI_1R	Reverse		GGTGCACCAAGTATTAGGGGT	This study
2	DiploVCOI_2F	Forward	242	CAACCTGGAGCATTCCTAGG	This study
	DiploVCOI_2R	Reverse		TCCTGCACCTTTTTCAACGG	This study
3	DiploVCOI_3F	Forward	153	AGCATTCCCCCGACTAAACA	This study
	DiploVCOI_3R	Reverse		TACTGATGGACCTGCGTGAG	This study
4	DiploVCOI_4F	Forward	202	TTATTAGTCAGGTCCGCGGC	This study
	DiploVCOI_4R	Reverse		AGTCGTAATCCGGATCATCGT	This study
5	DiploVCOI_5F	Forward	211	AACATAGCTCACGCAGGTCC	This study
	DiploVCOI_5R	Reverse		GCACCTGCTAGTACTGGTAGTG	This study
6	DiploVCOI_6F	Forward	134	CGAGTTCCACTATTTGTGTGAGC	This study
	COI2198E	Reverse		TAWACTTCWGGGTGWCCRAARAATCA	Ikeda *et al.* (2018)