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SPEODESMUS CAVE MILLIPEDES. FOUR NEW SPECIES FROM CENTRAL TEXAS (DIPLOPODA: POLYDESMIDA: POLYDESMIDAE)

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ABSTRACT

Four new species of troglobitic millipedes are described from central Texas caves: *Speodesmus castellanus* from Fort Hood, Bell and Coryell counties; *S. falcatus* from Camp Bullis, north central Bexar County; *S. reddelli* from Government Canyon State Natural Area, Helotes and other points in northwestern Bexar and northeastern Medina counties; and *S. ivyi* from Camp Bullis and San Antonio, Bexar County, and Comal County. The closest relative of *S. castellanus* is *S. bicornourus*, from caves in Williamson, Travis, and Burnet counties, Texas. *Speodesmus falcatus* and *S. reddelli* are relatives of *S. echinourus*, which is distributed across the Edwards Plateau and parts of the Balcones Escarpment, central Texas. *Speodesmus ivyi* is similar to *Speodesmus* n.sp. 1, Val Verde County. Some characters previously thought to distinguish species groups of *Speodesmus* may be unsuitable for separating groups within the genus.

INTRODUCTION

The genus *Speodesmus* currently contains four described species: *S. echinourus* Loomis, 1939 (Fig. 1); *S. tuganbius* (Chamberlin, 1952), re-described by Shear (1974); *S. bicornourus* Causey, 1959; and *S. aquiliensis* Shear, 1984. All occur only in caves. At least six undescribed species are known from Texas caves; four are described in the current publication.

MATERIALS AND METHODS

During the course of cave studies since 1992 at Fort Hood, Camp Bullis, and other areas, 441 specimens of *Speodesmus* were collected, most of which I examined and identified. Specimens were collected by hand into 80% ethanol, labeled, and curated at the Texas Memorial Museum and in the author's private collection.

I studied specimens with the following procedures on a stereo microscope (up to 120 X) using a fiber-optics illuminator with incident light and a compound light microscope (up to 400X). Specimens were placed in a clear dish in 80% ethanol on a dark background and manipulated with minuten probes. Measurements were

Fig. 1.-*Speodesmus echinourus* Loomis, male about 10 mm long, in Wyatt Cave, Edwards County, Texas, 1974.

made of most specimens with a calibrated ocular micrometer or small scales placed in the dish. The sexes, size range, and number of preanal setae were recorded for each collection in a database. Representative, intact specimens were selected as types, the preferred holotype being male. The male gonopod was removed by hooking it with a minuten and pulling it off or by dissecting segment 7. Gonopods and other parts were temporarily mounted in a depression slide with glycerin for study and digital photography on the compound microscope. Drawings were traced from some prints and others were digitized on a computer. The drawings were further revised while studying specimens microscopically. A "troglomorphy index" was calculated for each species, based on leg length divided by body length; a higher index is more troglomorphic and more cave-adapted, with longer legs relative to body length. Holotypes and allotypes are deposited in the U.S. National Museum of Natural History; some paratypes and most collections are in the Texas Natural History Collections, Texas Memorial Museum, Austin; representative nontype specimens are held in my private collection. Records are listed with the number of adult males, adult females and immatures in that order in the form 1-1-1, followed by the size range of adults.

ACKNOWLEDGMENTS

I am grateful to the many collectors who participated in various projects. Collectors' names are given as initials as follows: Allan Cobb (AC), Andy Grubbs (AG), Alvis Hill (AH), Bruce Johnson (BJ), Carmen Goyette (CG), C. Huebner (CH), Carmen Soileau (CSO), Charley Savvas (CS), Doug Allen (DA), Doug Drysdale (DD), Dan Love (DL), David McKenzie (DM), Dub Bechtol (DB), Gary McDaniel (GM), Gary Poole (GP), George Veni (GV), James Cokendolpher (JC), John Fish (JF), Joe Ivy (JI), James Loftin (JL), James R. Reddell (JRR), Lee J. Graves (LJG), Jean Krecja (JK), Jim Kennedy (JKN), John Porter (JP), Karen Veni (KV), Kemble White (KW), Logan McNatt (LM), Marvin Miller (MM), Marcelino Reyes (MR), Mike Warton (MW), Orion Knox (OK), Peter Sprouse (PS), Peter Strickland (PST), Randy Waters (RW), Suzanne Fowler (SF), Scott Harden (SH), Tannika Engelhard (TE), William H. Russell (WHR) and William R. Elliott (WRE). Joe Ivy was an observant and jovial field companion. George Veni, James R. Reddell and David McKenzie provided invaluable aid and data in these studies. The Missouri Department of Conservation provided access to microscopes for my work, and the Texas Memorial Museum provided specimens. I thank the U.S. Army, Camp Bullis and Fort Hood, and project leaders George Veni and James R. Reddell for their support of this study. This research was funded in part by The Nature Conservancy through cooperative agreement DPW-ENV-02-A-0001 between the Department of the Army and The Nature Conservancy. Information contained in this report does not necessarily reflect the position or the policy of the government and no official endorsement should be inferred.

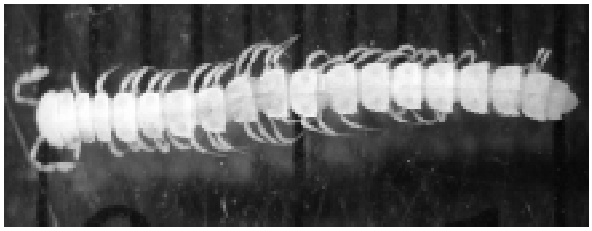


Fig. 2-*Speodesmus castellanus* n. sp., preserved holotype male from Rocket River Cave, Coryell County, Texas

TAXONOMY

Speodesmus castellanus, new species
Figs. 2-7, 8

Types.—I examined 117 specimens from 18 caves, from which I selected representative types, given below. The adult male holotype, female allotype and two male paratypes are from Rocket River Cave, Fort Hood, Coryell County, Texas, collected 16-17 January 1992 by Lee J. Graves, Mike Warton, and Charley Savvas. Deposited in the U.S. National Museum of Natural History and Texas Memorial Museum, Texas Natural History Collections (two male paratypes).

Etymology.—The species epithet, *castellanus*, is a Latin adjective referring to a fortress (Fort Hood). Common name: Fort Hood cave millipede.

Diagnosis.—Twenty segments in adults as in other central Texas *Speodesmus*, a smaller, sister species to *S. bicornourus*, about half as long (8-11 mm), with a similar, fused, nearly straight, telopodite in the gonopod, but the retrorse spine, prominent in *S. bicornourus*, is lacking or it is a vestigial bump in *S. castellanus.*

Description.—Male holotype (Figs. 2-7): A small, but highly troglomorphic form, 10.50 mm long, greatest width 0.95 mm (segment 2), body width/length ratio 9%. Head 0.95 mm wide, subglobular. Antenna 1.4 mm long, joint 5 widest with absent or small sensory organ, four conical tufts of setae on the tip of the antenna. Collum (segment 1) 0.91 mm wide, semicircular, with 30 setae arranged in 3 rows and 4 marginal setae, no teeth. Narrowest segment 19. Ozopore formula 5, 7, 9, 10, 12, 13, 15-18; ozopore on 18 very small. Anterior marginal teeth weak, nonporiferous segments with 3 marginal teeth, poriferous segments with 4 marginal teeth, each with a seta. Setation: Hirsute, with about 725 dorsal setae posterior to the head. Each of segments 2-4 with three rows

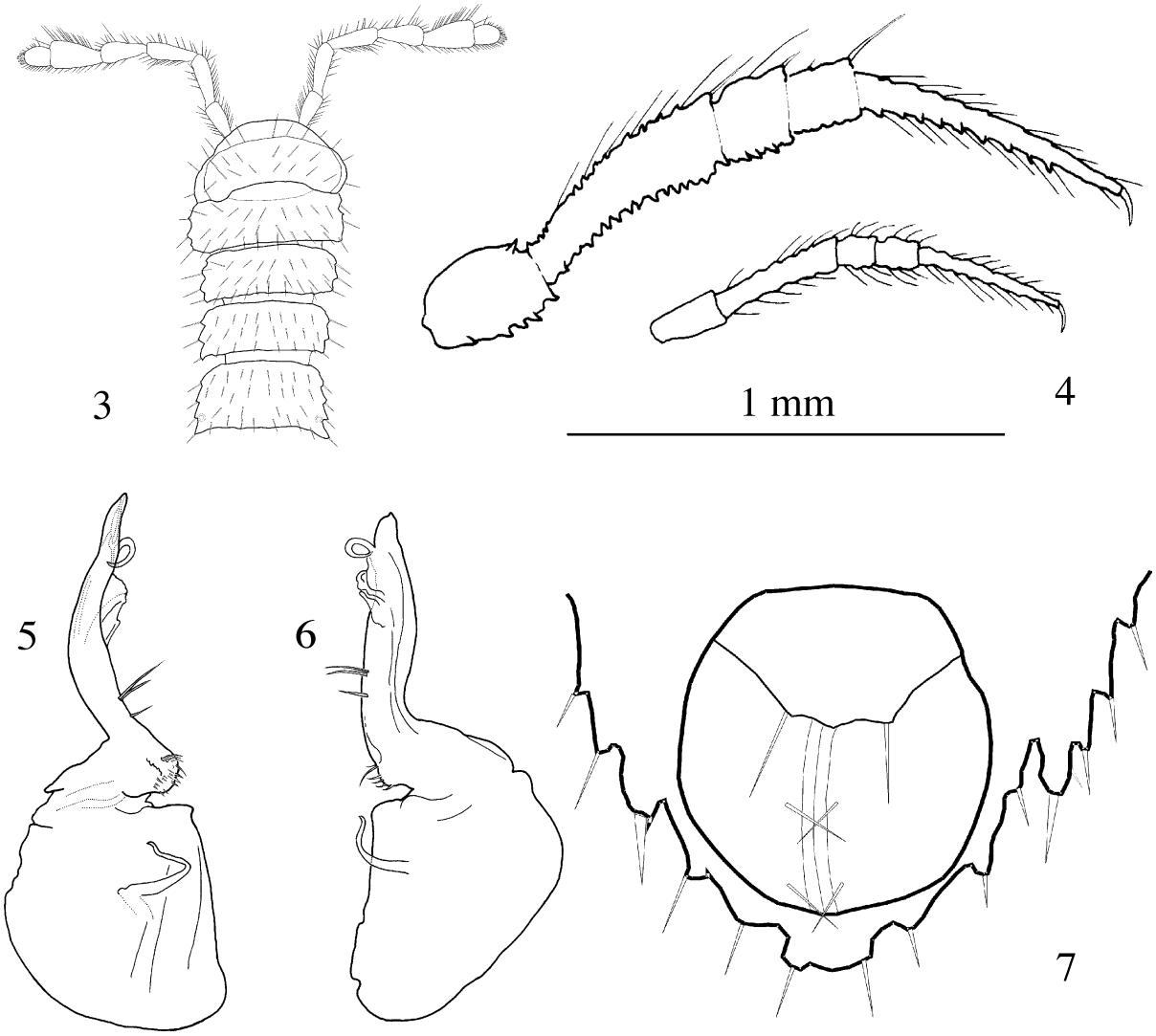
of strong, acicular setae totalling about 30, including 3 setae on each lateral margin. Segments 5-19 with four or five irregular rows of setae, numbering about 32-53, including 4 setae on each lateral margin. Segment width/length ratio decreases toward segment 18, then increases. Preanal scale angular, with three vertices on posterior. Two setae on preanal scale (*bicornourus* condition). Periprocts swollen, with margins. Legs (Fig. 4): typical midbody leg 1.8 mm long (not including coxa), 0.15 mm wide, swollen, and clavate, with coarse granules on most joints. Leg width/length ratio 8%. Troglomorphy index (leg/body length) 17%.

Gonopods (Figs. 5-6): Large coxae closely appressed and flattened on mesal side, long coxal solenite with sharp bend in the middle and small hook at tip; fused telopodite, nearly straight from the mesal view; solenomerite without fimbriate pad at opening of the seminal canal; lateral branch of acropodite with flattened blade-like tip; mesal accessory branch hooked in a circular pattern with small barbs near the tip.

Female allotype: 10.2 mm long, greatest width 0.85 mm (segment 2), width/length ratio 9%. Head 0.92 mm wide, subglobular. Most features as in male except that the legs are shorter, more slender, and without tubercles. Typical midbody leg half as long as in male (0.92 mm), 40% as wide (0.06 mm), leg width/length ratio 7% (Fig. 4).

Two male paratypes: 10.2 and 9.5 mm long. Body width/length ratio 10-11%. Leg width/length ratio 6%. Troglomorphy index 15%.

Variation.—Eight adult males from the type locality ranged from 9.4-10.8 mm long; five adult females ranged from 10.0-11.5 mm long. All had two preanal setae. The largest male is 11.0 mm from Fellers Cave.



Figs. 3-7.-*Speodesmus castellanus* n. sp.. 3, head and five body segments of male holotype; 4. mid-body, male leg with large tubercles above, female leg at same scale below; 5, mesal view of left gonopod; 6, lateral view of left gonopod; 7, ventral view of preanal scale and epiproct.

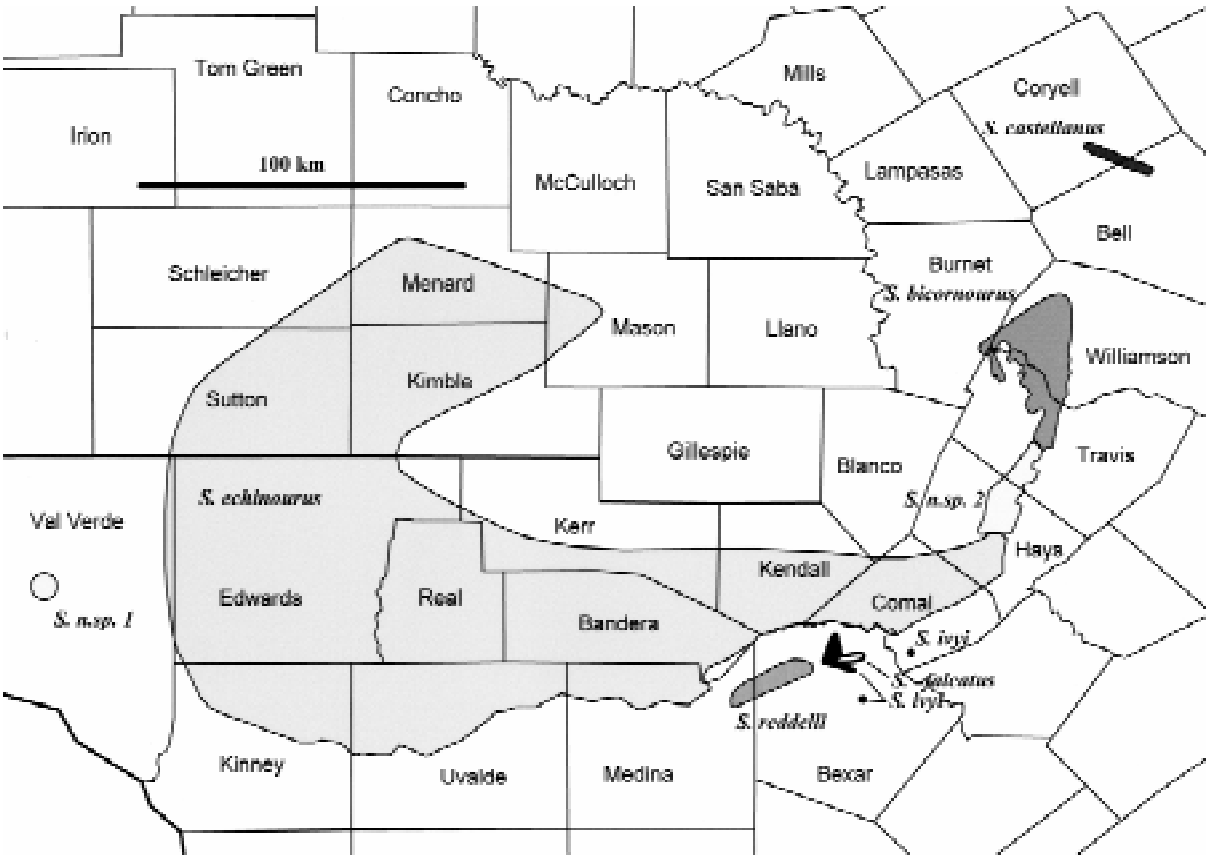


Fig. 8.-Map of central Texas, showing the ranges of eight *Speodesmus* species.

The smallest males are 8.0 mm from Bumelia and Keyhole caves. The series from Keyhole Cave tend to be small (8-9 mm males), while the Rocket River series tend to be large. One female from Triple J Cave is 9 mm and has three preanal setae.

Ecology.—Though highly troglomorphic, with relatively long legs, *S. castellanus* is moderately small and sometimes burrows in soil (James Reddell, pers. comm.). *Speodesmus bicornourus* is a giant in comparison, up to twice as long at 20 mm, and often is found walking on bare flowstone and other moist substrates.

Distribution.—Caves at Fort Hood, Bell and Coryell counties, Texas (Fig. 8). The 117 specimens were taken in 26 collections from nine caves in Bell County and nine caves in Coryell County, between January 1992 and June 2000. Nine collections (seven caves) had adult males, whereas 17 collections (11 caves) lacked adult males. Specimens were taken in all seasons, but there was no apparent seasonality in age or sex ratios in those collections that were large enough to assess these ratios. About 28% of the specimens were adult males, and 35% were adult females.

Records.—Adult males of *S. castellanus* have been identified from seven of 18 caves. The seven caves with males are distributed throughout the range of known caves at Fort Hood, so the 11 other caves probably belong to this species as well, although this is not certain.

Bell County: Bumelia Cave, 28 October 1994 (DA, DL), 1-0-0, 8 mm; Fellers Cave, 6 May 1998 (LJG, JRR, MR), 1-1-0, 10-11 mm; Lucky Rock Cave, 10 September 1997 (LJG, JRR, MR), 1-0-0, 8 mm; Price Pit, 6 May 1999 (JRR, MR), 1-2-0, 8 mm.

Coryell County: B.R.'s Secret Cave, 5 November 1992 (JRR, MR), 2-0-0, 10 mm; Keyhole Cave, 20 February 1999 (JRR, MR), 10-6-0, 8-9 mm; Rocket River Cave, 14 January 1992 (LJG, MW, CS), 2-2-0, 9.4-10 mm; 16 July 1992 (LJG, MW, CS), 21-13-17; 16 July 1993 (JRR, MR), 1-2-0.

Other Collections.— I could not assign the following collections from 15 caves to *S. castellanus* because adult males were lacking, but they probably belong to that species. However, four of the caves (names followed by asterisks) also have adult males from other collecting trips (see above).

Bell County: Buchanan Cave, 7 May 1998 (LJG, JRR, MR), 0-1-0, 14 mm; Fellers Cave*, 4 December 1992 (JRR, MR), 0-0-1; Figure 8 Cave, 9 February 1996 (MW), 0-0-1; 3 November 1998 (JC, MR), 0-1-0, 9 mm, enlarged gonopore; Lucky Rock Cave*, 22 February 1996 (DA, LJG, DL), 0-0-1; Sanford Pit Cave, 23 November

1994 (MW), 0-0-1; 4 November 1998 (JK), bottom of pit, 0-2-1, 8 mm; Streak Cave, 26 October 1997 (LJG, JRR, MR), 0-1-4,10 mm; Triple J Cave, 14 June 2000 (JK, JRR, MR, PS), 0-1-0, 9 mm, 3 preanal setae (extra one on left side).

Coryell County: Big Red Cave, 6 May 1999 (JRR, MR), 0-0-2; Copperhead Cave, 30 April 1998 (JRR, MR), 0-2-1, 8-9 mm; Cornelius Cave, 21 November 1995 (JRR, MR), 1 fragment; Ingram Cave, 7 April 1999 (JRR, MR), 0-2-1, 8 mm; Keyhole Cave*, 6 May 1999 (JRR, MR), 0-0-1; Mixmaster Cave, 9 March 1993 (JRR), 0-0-1; Rocket River Cave*, 27 October 1994 (MW) 2-1-2; Tippit Cave, 8 April 1999 (JRR, MR), 0-0-1.

Speodesmus falcatus, new species
Figs. 8-10, 18

Types.—I examined 85 specimens. Adult male holotype, female allotype and female paratype, collected in Cross the Creek Cave, Camp Bullis, Bexar County, Texas, 21 April 1999 by James R. Reddell and Marcelino Reyes; male paratype collected 10 September 1998 by the same. Deposited in the U.S. National Museum of Natural History (holotype and allotype) and Texas Memorial Museum, Texas Natural History Collections (paratypes).

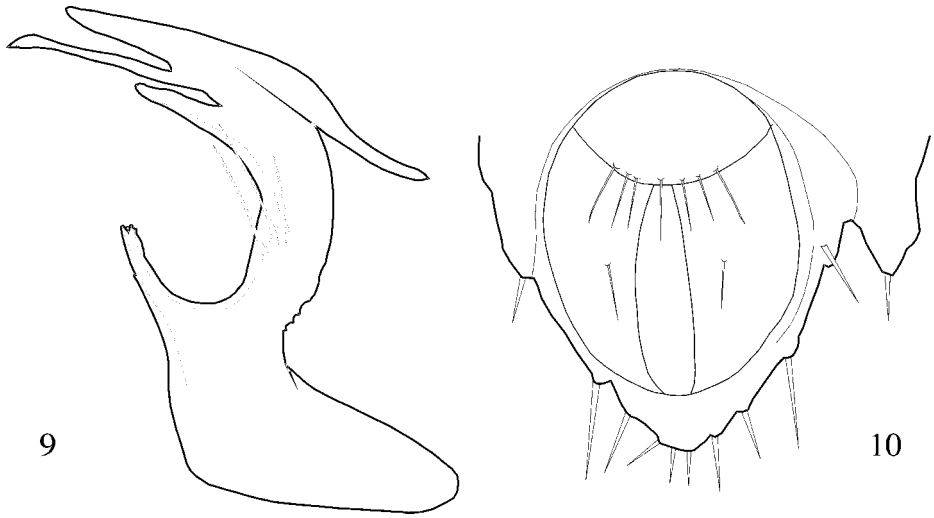
Etymology.—The species epithet¸ *falcatus*, is a Latin adjective referring to the sickle-shaped gonopod. Common name: Sickled cave millipede.

Diagnosis.—*Speodesmus falcatus* is closely related to *S. echinourus*, which occurs north of Cibolo Creek, but it has a prominent, mesal process on the gonopod, lacking in *S. echinourus*, and a longer, lateral retrorse barb. *Speodesmus reddelli* is slightly larger than *S. falcatus* and also has a long retrorse barb, but lacks the mesal process on the gonopod, and it occurs only in western Bexar and eastern Medina counties in a different karst area. At Camp Bullis smaller adults (7 mm) with a bifurcate epiproct probably are *S. ivyi* (described below).

Description.—Male holotype (Figs. 9-10): A large species, 20 segments in adults as in other *Speodesmus*, 16.0 mm long, ivory to white color, widest at segment 9 (1.2 mm), body width/length ratio 8%. Head 1.2 mm wide, ovoid. Antenna 2.3 mm, joint 6 widest with sensory organ. Collum (segment 1) 3.2 mm wide, arc-shaped, with 24 setae arranged in three rows and one marginal tooth on each side. Narrowest segment 19. Ozopore formula. 5, 7, 9, 10, 12, 13, 15-19. Anterior marginal teeth weak, nonporiferous segments with 3 marginal teeth, poriferous segments with 4 marginal teeth, each with a seta. Setation: About 520 dorsal setae posterior to the head. Each of segments 2-4 with three rows of strong, acicular setae totalling about 24, including 3 setae on each lateral margin. Segments 5-19 with three or four rows of setae, numbering about 24-28, including 3 setae on each lateral margin. Preanal scale rounded, with seven setae (*echinourus* condition). Legs: Typical midbody leg 2.2 mm long (not including coxa), 0.15 mm wide, with slight tubercles at the base of femoral setae. Leg width/length ratio 7%. Troglomorphy index 14%.

Gonopods (Fig. 9): Gonopod 510 µm long, curved, similar to *S. echinourus*, but a flattened, blade-like mesal process that gives the entire gonopod the appearance of a sickle from the ventral aspect. Mesal process tipped with small teeth. Much longer, lateral retrorse barb, which is small or lacking in some *echinourus* populations.

Female allotype: 16.0 mm, widest at segments 7 and 12 (1.2 mm), body width/length ratio 8%. Midbody leg 2.3 mm long, 1.3 mm wide, no tubercles, width/length ratio 6%. Troglomorphy index 14%. Preanal scale rounded triangle with 8 setae.



Figs. 9-10. *Speodesmus falcatus* n. sp. 9, ventral view of left gonopod; 10, prenal scale and epiproct.

Paratypes: Male 15.5 mm long, 7 preanal setae. Female 16.0 mm long, 8 preanal setae.

Variation.—Immatures have fewer preanal setae. Cross the Creek Cave: adults 13-16 mm, 4-6 preanal setae. Dos Viboras Cave: 14-16 mm, 4-13 preanal setae. Hold Me Back Cave: 15-17 mm, 5-9 preanal setae on males, 10 on a female, tooth near mesal base of mesal process of gonopod. MARS Pit: 5-7 preanal setae. MARS Shaft: 15-16 mm, 3-4 preanal setae, female with large everted cyphopods. Root Toupee Cave: 14-15 mm. Elmore Cave: 16 mm, 3-4 preanal setae.

Ecology.—*Speodesmus falcatus* is highly troglomorphic, and usually is found on moist surfaces. In vertical caves it has been found in all levels in the dark zone.

Distribution.—Known only from the Stone Oak Karst Fauna Region, north of San Antonio, Bexar County, Texas; seven caves in the southeastern portion of Camp Bullis, and one cave east of Camp Bullis. The range is about 2 by 8 km (Figs. 8 and 19). To date *S. falcatus* is the most common and abundant *Speodesmus* at Camp Bullis, but it is not found in all caves (see *S. ivyi* below).

Records.—*Bexar County*: Camp Bullis: Cross the Creek Cave, 31 March 1995 (JRR, MR), 1-1-2; 6 October 1995 (JRR, MR), 0-1-2; 10 September 1998, (JRR, MR), 1-1-1; 21 April 1999 (JRR, MR), 1-7-0; Dos Viboras Cave, 14 December 1994 (GM), Zone 3, dark, 71-72° F, 0-1-5; 9 January 1995 (JRR, MR), 2-0-4; 6 October 1995 (JRR, MR), 4-1-1; Hold Me Back Cave, 3 March 1994 (WRE), Zone 4, 1-0-0; 3 March 1994 (WRE, LM), Zone 3, 1-0-0; 9 November 2000 (JK, PS), 7-5-3, 3 females with everted cyphopods (genitalia) and triangular projections on posterior of coxae of segment 3 at edge of gonopore; 25 October 2001 (JK, PS), 0-1-1, female with everted cyphopods; 25 October 2001 (JK, PS), 5-4-8; MARS Pit, 29 October 2001 (JK, PS), 1-2-0; MARS Shaft, 4 March 1994 (JI), Zone 3, 1-0-0; 4 March 1994 (WRE), Zone 3, 0-3-3, 1 female with everted cyphopods (Fig. 11); 4 March 1994 (WRE), Zone 2, 0-5-1, three females with everted cyphopods; 20 September 1994 (WRE, JI), Zone 3, 70° F, 1-1-2; 20 September 1994 (WRE, JI), Zone 4, 69° F, 0-0-4; Root Toupee Cave, 17 November 1998 (PS, GV), 1-3-0; 20 April 1999 (MR), lower level, 3-1-0; Stone Oak Area: Elmore Cave, 14 July 1993 (JRR, MR), 1-1-1.

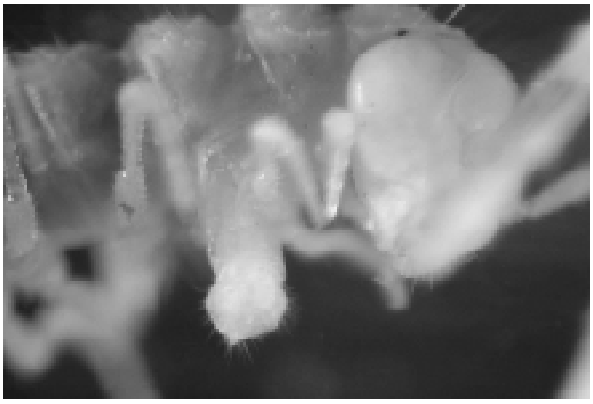


Fig. 11.-Preserved female *Speodesmus falcatus* n. sp. with everted cyphopods, from MARS Shaft, Bexar County, Texas.

Speodesmus ivyi, new species
Figs. 8, 12, 13, 15, 16, 18

Types.—Up to 63 specimens from eight caves may belong to this species. Adult male holotype, female allotype and female paratype collected in Platypus Pit, from soil in Zone 2 just below the climbdown off the bottom of the entrance pit, Camp Bullis, Bexar County, Texas, 21 October 1997 by William R. Elliott and Joe Ivy. Deposited in the U.S. National Museum of Natural History and Texas Memorial Museum, Natural History Collections (paratype).

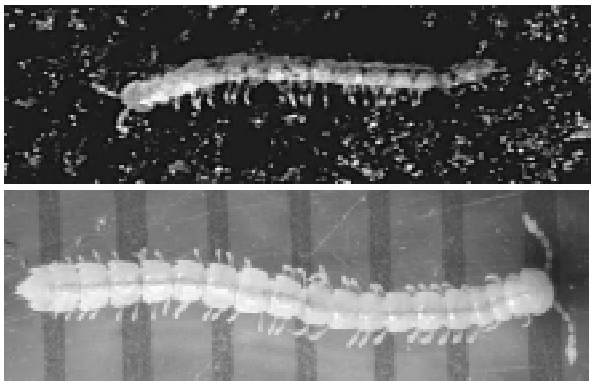
Etymology.—Named *ivyi* in memory of Joe Ivy, valiant cave explorer and surveyor, who died tragically on September 30, 2000, while exploring O-9 Well, Crockett County, Texas. Joe and I found this unusual species in Platypus Pit. Common name: Ivy's cave millipede.

Diagnosis.—This species is half the size of *S. reddelli* and *S. falcatus*, has very different gonopods, two preanal setae, and a bifurcate epiproct.

Description.—Male holotype: (Figs. 12, 13, 15, 16) A tiny species with 20 segments in adults and relatively short legs. Color ivory, length 7 mm, greatest width 0.6 mm at segment 18, narrowest 19, body width/length ratio 9%. Head ovoid, 0.6 mm wide. Antenna 0.8 mm long, widest at joint 6, with sensory organ. Collum with rounded anterior, straight posterior, 24 setae and rounded margins (no teeth). Marginal teeth of paranota indistinct on most segments, 4 on segment 8. Dorsal setation relatively reduced, with about 530 setae posterior to the head. Ozopore formula 5, 7, 9, 10, 12, 13, 15-18. Mid-body (segment 10) leg 0.71 mm, leg width 0.07 mm, leg width/length ratio 10%. Male legs lack tubercles and are not noticeably thickened. Preanal scale a truncated triangle with 2 setae. The epiproct (posterior tip of last segment) is unusual in being bifurcate, with two small processes each provided with a small seta (Fig. 15). Troglomorphy index 10%, less than other *Speodesmus* in this study.

Gonopods: Unusual among *Speodesmus*, curved, somewhat like *S. echinourus*, but with a thin, transparent, outer shelf from the tip to the lateral side. The retrose barb is modified into a curled, thickened rib at the lateroproximal margin (Fig. 16).

Female allotype: Ivory color, 7.0 mm long, greatest width 0.6 mm at segments 8 and 9, antenna 0.9 mm,



Figs. 12-13.-*Speodesmus ivyi*, n. sp. 12 (top), about 7 mm, burrowing in soil in Lewis Cave, Comal County, Texas, 1975; 13 (bottom), preserved male holotype, 7 mm, from Platypus Pit, Bexar County, Texas.

midbody leg 0.6 mm, ozopores 5, 7, 9, 10, 12, 13, 15-18. Two preanal setae, troglomorphy index 8%.

Female paratype: Ivory color, 6.8 mm long, 2 preanal setae.

Variation.—The author collected a series from Lewis Cave in July, 1974, and drew the gonopod for his dissertation. The male specimens dried out later and were not useable. I recently re-examined a Lewis Cave female, which was similar to the Platypus Pit specimens, with the same bifurcate epiproct, 7.5 mm long with 20 segments, body width/length ratio of 8%, 24 collum setae, weak marginal teeth on most paranota, same ozopore formula as holotype except a possible small ozopore on segment 19. In 1980 I studied specimens from Robber Baron Cave and found them to be similar to the Lewis Cave form. During the current study I re-examined the Robber Baron specimens, and I found the unique, bifurcate epiproct and gonopods like those in the Platypus Pit collection. Other localities in the Stone Oak and Alamo Heights Karst Fauna Regions that lack males are tentatively identified as *S. ivyi* on the basis of the unique, bifurcate epiproct, two preanal setae and small size. Adults are 6.5-7.5 mm long.

Ecology.—*S. ivyi* is the least troglomorphic of the central Texas species I have studied, with a troglomorphy index of 8-10%, compared to 14-17% in other species in this study. Its small size and short legs enable it to burrow between soil grains. In 1975 I photographed it burrowing in top soil, under ranch trash, in Lewis Cave, Comal County (Fig. 12). I saw it on soil in Platypus Pit in 1995, but I thought it was immature and did not collect it. From 1995 through 1998 Joe Ivy and I made regular ecological monitoring trips into Headquarters Cave, Eagles Nest Cave, Platypus Pit and MARS Pit. In numerous trips we never observed a *Speodesmus* in the first two caves, and we collected it but once in Playtpus Pit; MARS Pit contained *S. falcatus*. *Speodesmus ivyi* was collected but once in each of five Camp Bullis caves, but it may have been overlooked at other times because of its burrowing habits and small size.

Distribution.—Known from eight caves, five in Camp Bullis, two in San Antonio and one in Comal County.

Records.—*Bexar County*: Camp Bullis: Headquarters Cave, 8 September 1998 (JC, JRR, MR), 0-1-1; Hector Hole, 15 April 2002 (JRR, MR, GV), 0-1-1; Isocow Cave, 12 December 2001 (JK, TE), 0-0-1; Well Done Cave, 15 April 2002 (JRR, MR, GV), 3-3-0; Hollywood Park Area: Cueva Cave, 10 October 1983 (GV, CG), 0-1-0; San Antonio: Robber Baron Cave, spring 1977 (no collector recorded), 5-3-2; 11 December 1982 (RW), 1-0-0; 6 April 1983 (RW), 1-0-0; 31 March 1985 (DD, RW), 0-0-2.

Comal County: Bat Cave Area: Lewis Cave, 8 March 1968 (JRR, JF, SF), 15-8-11; 8 July 1975 (WRE, CSO, PST), 0-1-0.

Speodesmus reddelli, new species
Figs. 8, 14, 17-19

Types.—I examined 108 specimens from 15 caves. Male holotype and female allotype collected in Surprise Sink, Government Canyon State Natural Area, Bexar County, Texas, 21 April 1996 by George Veni, Karen Veni and Jim Kennedy. Male paratype collected 24 May 1998 by James R. Reddell and Marcelino Reyes. Holotype and allotype deposited in the U.S. National Museum of Natural History; paratype deposited in the Texas Memorial Museum, Texas Natural History Collections.

Etymology.—Named in honor of James R. Reddell, the leading student of cave life in Texas and Mexico for many years, who collected many of the examples of this new species. Common name: Reddell's cave millipede.

Diagnosis.—*Speodesmus reddelli* can be distinguished from *S. echinourus* by its larger size, gonopods more blade-like dorso-ventrad, longer retrorse barb, and fewer preanal setae (two to seven). *Speodesmus falcatus* is a similar size, but has sickle-like gonopods and seven preanal setae. *Speodesmus ivyi* is half the size of *S. reddelli* and *S. falcatus*, has very different gonopods and a bifurcate epiproct.

Description.—Male holotype (Figs. 14, 17, 18): A large, slender, highly troglomorphic species, 20 segments

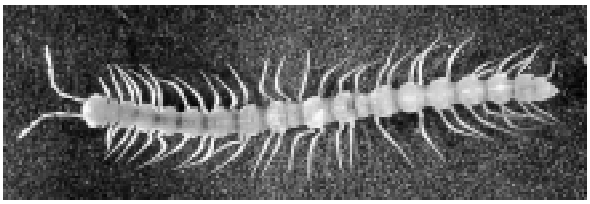


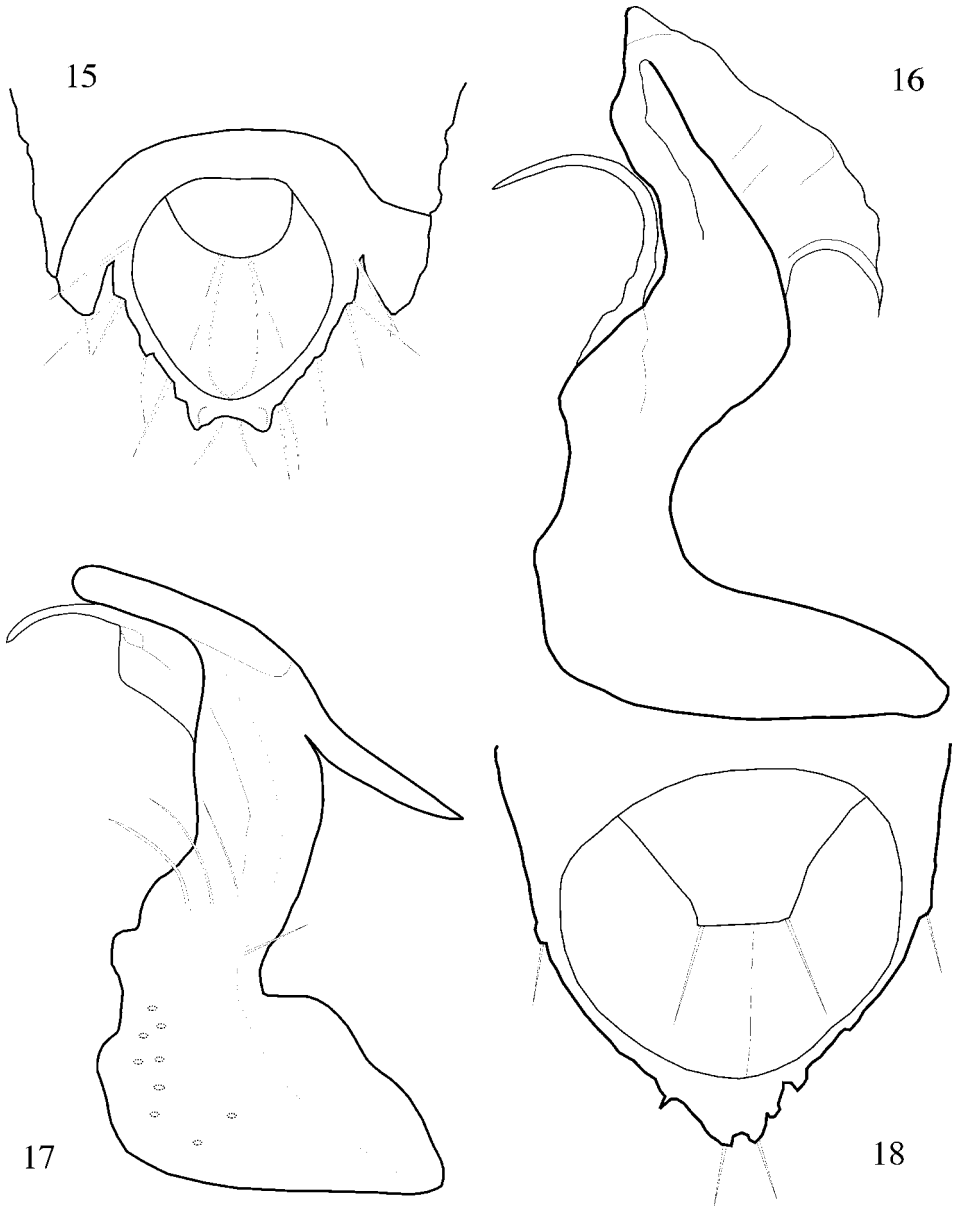
Fig. 14.-*Speodesmus reddelli*, n. sp., preserved male holotype, 16 mm, from Surprise Sink, Bexar County, Texas.

in adults, 16.0 mm long, translucent pale pinkish white, widest at segment 18 (1.07 mm), body width/length ratio 6%. Head 1.2 mm wide, ovoid. Antenna 3.0 mm, joint 6 widest with sensory organ. Collum 0.9 mm wide, arc-shaped, with 30 setae arranged in three rows and two marginal teeth on each side. Narrowest segment 19. Ozopore formula 5, 7, 9, 10, 12, 13, 15-18. Marginal teeth 4 on most, 5 on segment 8. Setation: Relatively hirsute, about 630 dorsal setae posterior to the head on the male (female has about 588). Segments 2-4 with three rows of setae totalling 28-30 each. Segments 5-19 with four rows of setae, numbering 29-36 per segment. Preanal scale a truncated triangle with two setae (Fig. 18); other localities have more setae. Legs: Typical midbody leg 2.6 mm long, 0.20 mm wide, no tubercles. Leg width/length ratio 8%. Troglomorphy index 16%.

Gonopods (Fig. 17): Curved, similar to *S. echinourus*, but blunter and with a more blade-like dorso-ventral aspect versus cylindrical, and a much longer, lateral retrorse barb, which is small or lacking in some *S. echinourus* populations.

Female allotype: 16.5 mm, widest at segment 9 (1.4 mm), body width/length ratio 9%. Antenna length 0.25 mm. Collum setae 29, with two teeth each side. Fewer dorsal setae (about 588) than male (about 630). Preanal scale and setae as in male.

Male and female paratypes: Male 16.0 mm, female 16.5 mm.



Figs. 15-18.- *Speodesmus* males. 15-16, *S. ivyi*, n. sp. 15, preanal scale and epiproct with bifurcate processes; 16, ventral view of left gonopod. 17-18, *S. reddelli*, 17, ventral view of left gonopod; 18, holotype preanal scale, with two setae, and epiproct, with single caudal process.

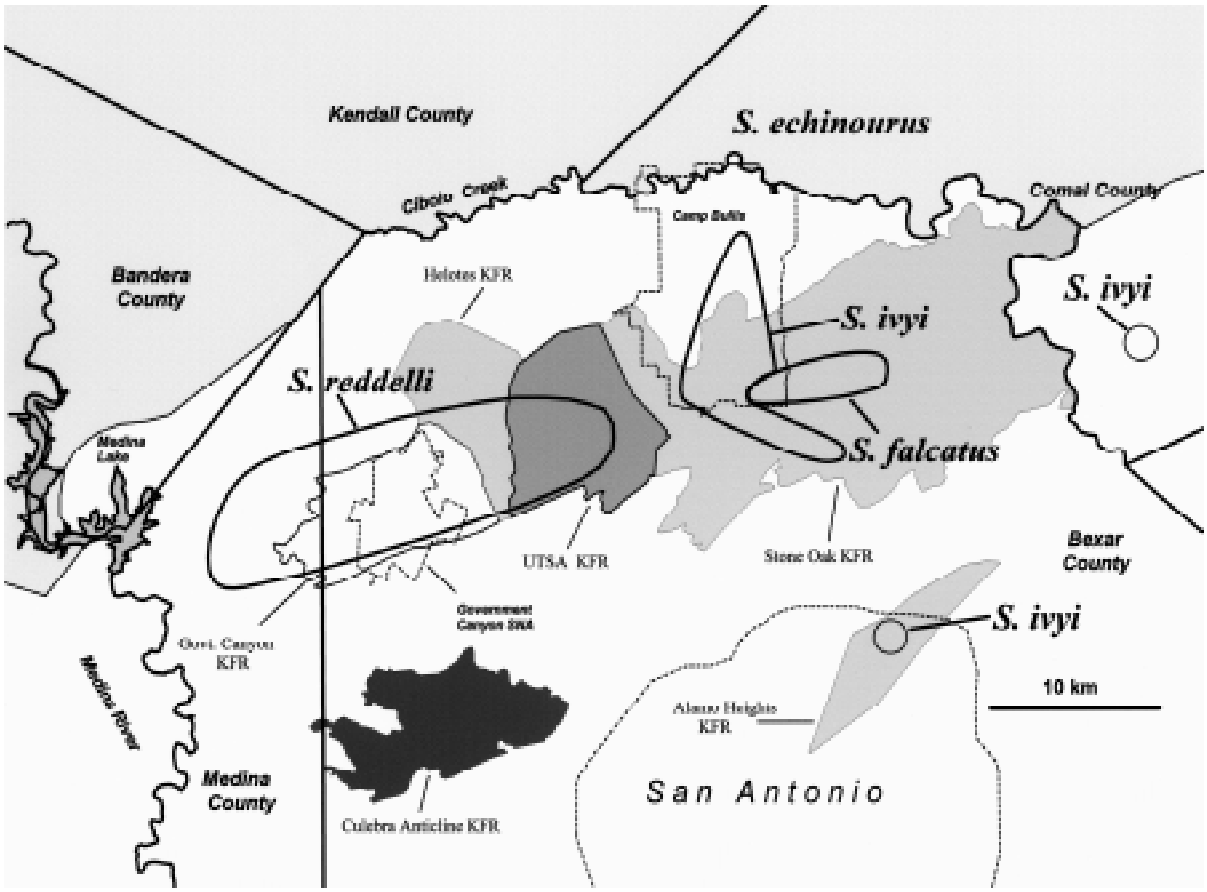


Fig. 19.-Map of the San Antonio area showing the ranges of five *Speodesmus* species, streams, karst faunal regions, counties, Camp Bullis and Government Canyon State Natural Area. All caves that were sampled contained just one *Speodesmus* species.

Variation.—Some populations are up to 20 mm long. Most central populations have two preanal setae, but those in John Wagner Ranch Cave No. 3, on the east, have two to four, while those from Goat Cave, Medina County, on the west, have seven. Some males from Logan's Cave have massive legs, an exaggerated sexually dimorphic character. Government Canyon Bat Cave: long legs without bumps. Lucky Hat Cave: male >17 mm, long legs. Porcupine Cave 15-16 mm. John Wagner Ranch Cave No. 3: 17-19 mm, 2-4 preanals; females with everted cyphopods. Kamikazi Cricket Cave: 16-19 mm, 2-3 preanals. Logan's Cave: some males with massive legs from August collection, 18-19 mm, 2-3 preanals. Madla's Drop Cave: 15-16 mm. 2 preanal setae. Crownridge Canyon Cave: no bumps. Robber's Cave: 18 mm, 2 preanal setae. Three-Fingers Cave: 16-17 mm, 2 preanal setae. "Surprise" Cave: 17.5 mm 7 preanals.

Ecology.—The size and troglomorphy of this species hint that it must be highly troglobitic, and by analogy it probably would be found on moist surfaces. However, often it is found in caves that are somewhat dry with only a few wet areas. For example, Surprise Sink is a 3-m-pit into two rooms with thick soil deposits and some flowstone, which are moderately dry. In Porcupine Cave, specimens were collected from wet flowstone in the dark zone. In John Wagner Ranch Cave No. 3 specimens were taken in breakdown crawls that were dry with little sediment, but with some wet areas. In Lithic Ridge Cave, it was collected from moist to wet soil, breakdown and flowstone (George Veni, pers. comm.). I have collected this species in Government Canyon Bat Cave on damp soil and weathered guano of *Myotis velifer.*

Distribution.—The range of *S. reddelli* is about 25 by 7 km, from northwestern Bexar County near Helotes to near Medina Lake, northeastern Medina County (Fig. 19). Known from 15 caves in the Government Canyon, Helotes and UTSA Karst Fauna Regions. Probably occurs in three other caves where no males were collected, within the known range.

Records.—*Bexar County*: Government Canyon Karst Fauna Region and State Natural Area: Government Canyon Bat Cave, 11 August 1965 (JRR, JF), 0-11-0; 24 May 1998 (JRR, MR), 1-1-0; Lithic Ridge Cave, 12 September 2001 (GV), 1-2-3; Lucky Hat Cave, 28 April 200 (MM), 1-0-1; Porcupine Cave, 12 September 2001 (GV), 2-2-2; Surprise Sink, 24 April 1996 (GV,

KV, JKN), 2-0-0; Helotes Karst Fauna Region: Helotes Hilltop Cave, 30 August 1964 (OK), 1-8-0; John Wagner Ranch Cave No. 3 (= Adam Wilson's Cave, Jr.), 23 December 1962 (OK), 0-1-0; 6 October 1963 (JRR, JP), 1-0-0; 15 June 1993 (JL, JRR, MR, GV), 5-4-4; Kamikazi Cricket Cave, 19 January 1986 (AC), 1-0-0; Logan's Cave, 6 August 1993 (JL, JRR, MR, GV), 6-3-1; Madla's Drop Cave, 6 August 1993 (JL, JRR, MR, GV), 2-1-2; UTSA Karst Fauna Region: Crownridge Canyon Cave, 19 November 2002 (JRR, MR), 1-0-0; Robber's Cave, 22 June 1993 (JL, JRR, MR), 1-5-0; Three-Fingers Cave, 22 June 1993 (JL, JRR, MR), 3-4-0.

Medina County: Medina Lake Area: Goat Cave, 10 July 1966 (JRR), 2-0-0; "Surprise" Cave, 15 February 1964 (WHR, DM), 1-0-0; 15 February 1964 (JRR, DM), 0-1-0.

Speodesmus echinourus Loomis
Spiny cave millipede
Figs. 1, 19

Comments.—Besides the two new species described above, Camp Bullis contains *S. echinourus* in Camp Bullis Bad Air Cave, north of Cibolo Creek, within the known range of this species. The gonopod has a short retrorse barb, characteristic of this species. Less troglomorphic than *S. reddelli* and *S. falcatus*.

Records.—*Comal County*: Camp Bullis, Camp Bullis Bad Air Cave, 4 November 1996 (GV, PS), 1-1-1, 10 mm male, 11 mm female; 22 November 1996 (BJ, JRR, MR), Zone 2, 8-1-0.

Speodesmus sp., undetermined sp.

Comments.—Owing to a lack of adult males, the following collections could not be assigned to a species with certainty, although body size, number of preanal setae, and epiproct can provide a probable designation. Cave names followed by asterisks also have adult males from other collecting trips, which have been referred to *S. reddelli* or to *S. falcatus.*

Records.—*Bexar County* (from southwest to northeast): Culebra Anticline Karst Fauna Region: Stevens Ranch Trash Hole Cave, 12 June 1993 (JL), 0-1-0, 8.5 mm, 2 preanal setae, one process on epiproct. Not *S. ivyi*, although small.

Government Canyon Karst Fauna Region and State Natural Area (probably *S. reddelli*): Bone Pile Cave, 29 September 1996 (GV), 0-2-0, 16 mm, 2-3 preanal setae; 24 May 1998 (JRR, MR), 0-2-0, 18-19 mm; 12 September 2001 (GV), 2-2-0, 16-17 mm, 2 preanal setae, 2 females with everted cyphopods; Surprise Sink*, 5 February 1995 (AG), 0-3-0, 16-17 mm, 2 preanal setae; 7 October 1995 (GV, AH), 0-3-0, 16 mm, 2 preanal setae.

Helotes Karst Fauna Region (probably *S. reddelli*): Cave site #305, west of Helotes: 2000 (no exact date) (DB, KW), 0-1-0, 15 mm, 2 preanal setae; Christmas Cave, 25 December 1982 (RW, JI), 0-0-2, not *S. ivyi*, 2 preanal setae; John Wagner Ranch Cave No. 3*: 23 December 1962 (OK, CH), 0-2-0; 25 January 1985 (SH), 0-2-0, 17 mm, 2 preanal setae; 14 July 1993 (JRR, MR), 0-0-2, not *S. ivyi*; Kamikazi Cricket Cave*, 3 October 1984 (JI, GV), 0-0-5, 2 preanal setae; Logan's Cave*, 10 May1992 (GV), 0-3-0, 20 mm, 2 preanal setae.

UTSA Karst Fauna Region (probably *S. reddelli*): Hills and Dales Pit, 9 June 1989 (GV), 0-0-1; 1 November 2000 (KW), 0-0-1; Scorpion Cave, 1 June 1993 (JL, JRR, MR, GV), 0-2-0, 16-17 mm, 2 preanal setae; Young Cave No. 1, 6 September 1993 (JRR, MR), 1-1-0, 2 preanal setae.

Stone Oak Karst Fauna Region (probably *S. falcatus*): Camp Bullis: F-150 Cave, 11 April 2002 (JRR, MR), 0-0-1, immature male, 19 segments, 6.5 mm, one process on epiproct, 2 preanal setae, not *S. ivyi*; Hold Me Back Cave*, 1 December 1993, 14 March 1994?, 0-1-0; 21 September 1994, C Zone 5. 72-74° F, 0-0-1; 21 September 1994 (WRE, JI), Zone 2. 70° F, 0-0-1; 11 October 2000 (JK, PS), 0-1-0; MARS Pit*, 9 October 1995 (MR), Lower level, 0-0-1; East of Camp Bullis, Elmore Cave*, 24 October 1982 (RW), 0-2-2, 15 mm, 4-5 preanal setae; Hairy Tooth Cave, 28 June 1987 (AC), 0-1-0, 17 mm, 11 preanal setae.

Medina County: Quihi Area: Sixty Minute Cave: 17 October 1984, (JRR, DM), 0-1-0, 11 preanal setae.

DISCUSSION

Until now just two described species of *Speodesmus* were known from central Texas. *Speodesmus echinourus* Loomis was distributed in caves across the Edwards Plateau and in some caves along the Balcones Escarpment in Hays and Travis counties. *Speodesmus bicornourus* Causey is found primarily in northern Travis County and Williamson County, with a small morph in some outlying caves in Burnet and Lampasas counties (Fig. 8).

Shear (1973) described *Speodesmus pecki*, a 19-segmented species from a cave in Tamaulipas, Mexico, but he later removed it to the new genus *Sumidero* (Shear, 1982). Shear transferred *Speorthus tuganbius* Chamberlin, 1952, to *Speodesmus*. Shear (1984) described *Speodesmus aquiliensis* from a cave in Colorado; it appears to be close to *S. tuganbius* from New Mexico and West Texas in its deeply divided gonopod branches, but it bears five setae on the preanal scale, reminiscent of *S. echinourus*.

In my doctoral dissertation (Elliott, 1976), I studied *Speodesmus* specimens from 110 central Texas caves.

All populations seemed to have either two (*bicornourus*) or multiple (*echinourus*) setae on the preanal scale, except for a few individuals with three setae from populations that typically had two preanal setae. I had studied 726 specimens from 89 caves morphometrically, and I did univariate and multivariate analyses on three data sets: females, males, and male gonopods. Inter-populational variation was analyzed on the basis of geologic and physiographic variables with the purpose of relating their evolution to geologic history. I postulated two species groups which contained four undescribed species. The *echinourus* group had more than two preanal setae, but also curved gonopods. The *bicornourus* group had two preanal setae and straighter gonopods. The four new species were not formally published, but two of them are described herein as *S. ivyi* and *S. reddelli*. In a future paper I intend to describe two more species, one from Val Verde County (designated here as n.sp. 1) and another from Travis and Hays counties (n.sp. 2, Fig. 8).

In my dissertation the *echinourus* species group was considered a relative late-comer to Texas caves and had not speciated as much as the older *bicornourus* species group, nor had its two species diverged as much. I thought that the wider distribution of the *echinourus* species group probably was related to its having been isolated in caves at a later date than the *bicornourus* species group, at a time when more caves were available for colonization. A study of temporal variation in a few populations revealed some statistically significant changes in a decade's time. Secondary sexual dimorphism was quite similar in the two species groups, but minor intra-specific differences may indicate physical barriers to gene flow.

Since my dissertation many more specimens and several new species were collected, which now give us a better picture of variation and speciation patterns. For example, possessing two preanal setae may be a neotenic and plesiomorphic condition in the order Polydesmida; it is found in all immature *Speodesmus*, but it is also a plastic character in *Speodesmus*. I had observed variation in the number of preanal setae within *S. echinourus* before. Now we see within *S. reddelli* both *bicornourus* and *echinourus*-like populations. I have observed three preanal setae in some specimens of *S. bicornourus* and *S. castellanus*. The general shape of the gonopod may be a better guide to proposing species groups in *Speodesmus*, along with fundamentally different somatic characters, like the bifurcate epiproct in *S. ivyi*, also found in *S.* n.sp. 1 from Val Verde County.

It seems that *S. echinourus* could have evolved in Texas from an ancestor with two preanal setae. *Speodesmus reddelli* may represent an intermediate form on this path. Forms like *S. falcatus* speciated from an *echinourus*-like ancestor in isolated karst blocks along the Balcones Escarpment. Judging from the speciation patterns that we see in *Speodesmus* and other Texas troglobites, there probably are other *Speodesmus* species to be found in island-like karst blocks along the Balcones Escarpment. Camp Bullis has three species of *Speodesmus*, sometimes within 800 meters of each other, but never sympatric!

The small size and soil-burrowing behavior of *S. ivyi* (Fig. 12) may be a primitive condition derived from an edaphic ancestor. *Speodesmus castellanus* still burrows, although it is larger. Gigantism may evolve in some troglobitic millipedes as a result of humid conditions in the caves, which permit them to wander more freely without risking dessication. Increased setation is another adaptation to life in caves. *Speodesmus bicornourus*, *S. falcatus*, and *S. reddelli* have all evolved into such giant forms. *Speodesmus ivyi* is not limited to one karst block, but is from three different ones. It may have been isolated in caves only recently, or it may still be a part-time soil and crack-dweller, especially during moist conditions.

Fort Hood is an isolated karst area. The nearest known occurrence of *S. bicornourus* is in northern Williamson County, about 30 km to the south. A relatively caveless area lies between these two areas. I have identified outlying, small-bodied populations of *S. bicornourus* from caves in Burnet and Lampasas counties, which are isolated geologically and hydrologically from the central population in Travis and Williamson counties. The Fort Hood population lost the retrorse barb of the gonopod, but remained small. Within the central population of *S. bicornourus* there are notable size differences, with the largest body sizes found in northern Travis-southern Williamson counties, from Austin to Georgetown.

It seems likely that a small, soil-dwelling ancestor or ancestors inhabited central Texas in the past, but became isolated in caves because of a drying climate since the Pleistocene. Some populations remained small, soil-burrowing forms while others evolved gigantism where moist, extensive cave habitats were available.

Portions of Bexar, Burnet, Travis and Williamson counties have been divided into karst fauna regions by Veni (1992, 1994, 2002). These are hydrogeologically and biologically defined regions where discontinuities or physical narrowing of cavernous limestone areas pose barriers or restrictions to troglobite gene flow and thus promote speciation between isolated or nearly isolated faunas. Most barriers occur where cavernous limestone is removed by erosion. Restrictions to gene flow usually occur where regions are connected by relatively narrow sections of cavernous limestone, through strata of poorly cavernous limestone, along faults that might develop poorly permeable zones, and/or along faults that juxta-

pose cavernous strata against noncavernous or poorly cavernous strata. The karst fauna regions were delimited for terrestrial troglobites, such as *Rhadine* beetles, spiders, and others. Broad sections of cavernous limestone might be barriers or restrictions to gene flow if little or no portion of those rocks occurs above the water table.

Speodesmus reddelli and *S. falcatus* conform to Veni's karst fauna regions rather well (Fig. 19), but *S. ivyi* does not. I can find no obvious physiographic, lithologic or hydrologic barrier between *S. falcatus* and *S. ivyi*, which are in caves only 800 m apart within Camp Bullis. Relative elevations of the caves overlap, but there is a series of hills and shallow, dry creek bottoms between the two species.

The effect of the karst fauna regions on troglobite distribution is more pronounced with moderately advanced troglobites and species, like some spiders, which do not move far from their origin, as opposed to roving species. Highly advanced troglobitic species from different regions may appear to be the same because of convergence of troglomorphic features, but DNA studies may prove them to be distinct species (see Cokendolpher's discussion of *Chinquipellobunus madlae*, this volume). Species like *S. ivyi*, which may be part-time soil and crack dwellers, may not conform to any karst geology that we can map. This problem is reminiscent of the puzzling, wide ranges of some stygobites (aquatic troglobites), which sometimes are found in nonkarst areas. Some are more strict troglobites, while others are phreatobites, which can exist in nonkarst groundwater (Holsinger, 1994; Culver et al., 2003).

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