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RE-DESCRIPTION OF *TOGWOTEEUS BICEPS* (ARACHNIDA, OPILIONES, SCLEROSOMATIDAE) WITH NOTES ON ITS MORPHOLOGY, KARYOLOGY AND PHENOLOGY

Robert G. Holmberg[1]: Centre for Natural and Human Science, Athabasca University, Athabasca, Alberta T9S 3A3 Canada

James C. Cokendolpher: 2007 29th Street, Lubbock, Texas 79411 USA

ABSTRACT. The harvestman genus *Togwoteeus* Roewer 1952 is monotypic. Its only species, *T. biceps* (Thorell 1877), is known from throughout western Canada and USA and is newly recorded from California, Nebraska, Nevada, Oregon, South Dakota, and Utah. This species occurs below 500 m and at the highest elevation (4100 m) of any recorded harvestman in North America. It ranges from about 33–54° N and exhibits considerable variation in its morphological measurements. Twenty-seven such measurements are summarized for 80 males and 74 females. Ultrastructural details of the integument, appendages and genital organs are presented. The karyotype is 2n = 22 for both sexes. All chromosomes are metacentric and obvious sex chromosomes were not detected. Immature *T. biceps* overwinter and reach adulthood in late spring or early summer. Adults die by late fall.

Members of the monotypic genus *Togwoteeus* Roewer 1952 are common harvestmen of prairie and mountain habitats in western regions of Canada and USA. For nearly 100 years, the single species currently recognized was known by the name *Homolophus biceps* (Thorell 1877). Cokendolpher (1987) proposed the new combination *Togwoteeus biceps* because true members of the genus *Homolophus* Banks 1894 are known only from Asia. *Togwoteeus* was transferred from the family Phalangiidae to the Sclerosomatidae by Crawford (1992). Examination of museum specimens revealed considerable variation within this species, e.g., specimens from British Columbia and Idaho had exceptionally longer legs. Because this species is found over such a large region of North America and was poorly studied, we sought to determine if the observed morphological variations were due to the existence of unrecognized new species. While doing this study we documented morphological, chromosomal, and phenological information which we herein present.

METHODS

Collections from which samples were examined, other than those of the authors, are listed in the Acknowledgments. Specimens used for measurements are described in Table 1. Those from Edmonton and Writing-on-Stone are retained by RGH. Those from Wyoming and Utah are in the American Museum of Natural History. One count and 27 measurements were made: four of the body, eight of the pedipalp, femora I-IV, tibiae I-IV, three of the genital operculum, four of the ocular tubercle; and the number of metatarsal bands on leg II. Measurements, examination methods, and terminology were as presented by Cokendolpher (1981), except the palpal femur and tibia lengths were measured along their greatest lengths (i.e., in lateral view, longitudinal distance between diagonal lines drawn from basoventral point to proximodistal point, Fig. 36, *fl* and *tl*). The ovipositors were cleared with lactophenol for examination and drawing of the seminal receptacles. Statistics were analyzed with the statistical computer program SPSS®. For morphological measurements two-tailed *t*-tests were used. For the single count, the Kolmogorov-Smirnov two-sample test was used. Alcohol preserved specimens were critical point dried, sputter coated with gold and photographed with scanning electron microscopes (SEM). Photographs

[1]To whom correspondence should be addressed.

Table 1.—Specimens used for body measurements.

Location	Latitude N, Longitude W	Altitude (m)	Collection dates	Males	Females
Edmonton, Alberta	53°46′, 113°25′	580	May–August 1982	20	20
Writing-on-Stone Provincial Park, Alberta	49°05′, 111°38′	915	May–July 1981	20	20
Grand Teton National Park, Wyoming	43°29′, 110°50′	2260–2440	July–August 1962, August 1969	20	14
Timpanogos, Utah County & Mill Creek Canyon, Salt Lake County, Utah	40°26–41′, 111°30–50′	1585–1725	May–June 1931–1941	20	20

were also taken through dissecting microscopes. Methods for the preparation of the karyotypes are reported by Cokendolpher & Brown (1985). The karyotypes were done in July 1983 from gonads of subadult specimens collected at the Logan Canyon summit, Cache County, Utah. The specimens were collected under rocks in the snow and transported alive in an ice-chest to Lubbock, Texas. They were maintained in the refrigerator until dissected.

RESULTS AND DISCUSSION

Togwoteeus Roewer

Mitopus: Thorell 1877:525; Banks 1893:206.

Homolophus: Banks 1894:160, 163, 164 (in part); 1900:123; 1901:674; Cockerell 1911:253; Roewer 1910:259 (in part); 1912:31 (in part); 1923:879–880 (in part); 1929:2 (in part); 1952: 268 (in part); 1957:355 (in part); 1960:24, 30 (in part); Comstock 1912:66, 71; 1940:66, 71; Kästner 1937:392 (in part); Katayama & Post 1974:13–14; Cokendolpher & Cokendolpher 1982:1215; Cokendolpher 1985:371, 399 (in part); 1987:89, 94 (in part).

Togwoteeus Roewer 1952:268; 1957:356; Crawford 1992:45; Cokendolpher & Lee 1993:16.

Type species.—*Togwoteeus granipalpus* Roewer 1952; by monotypy. Junior subjective synonym of *Mitopus biceps* Thorell 1877 and *Homolophus punctatus* Banks 1894.

Diagnosis.—Body with thick, hard, tuberculate-microgranulate cuticle; off-center micropores present on dorsal tubercles; preocular area without mound but with two groups of small denticles near anterior margin edge; supracheliceral lamellae well developed and toothed; pedipalps without apophyses on distal ends of patellae or tibiae in juveniles or adults, without campaniform organ on distal end of femora, claw smooth, not toothed; male pedipalps enlarged, tarsus bulbous at base and with ventral teeth; legs generally short, femur I usually equal to or shorter than body length, no pseudoarticulary nodules in femora; leg coxae without lateral rows of denticles; penis alate, i.e., with wing-like extensions.

Comparisons.—The presence of an alate penis and a smooth palpal claw separate *Togwoteeus* from all sclerosomatid opilions, except *Leuronychus* Banks 1900 and *Cosmobunus* Simon 1879. These genera can be easily distinguished from *Togwoteeus* by their longer legs (femur I always much longer than the body length) and lack of denticles in front of the ocular tubercle.

Subordinate taxa.—The genus is monotypic.

Distribution.—Western North America (Fig. 1).

Togwoteeus biceps (Thorell) (Figs. 1–38)

Mitopus biceps Thorell 1877:525–528; Pavesi 1889:531; Banks 1893:206, 207; Cokendolpher 1987:94; Crawford 1992:45.

Homolophus biceps: Banks 1894:163; 1895:431; 1900:123; 1901:674; 1902:593; 1916:72; Cockerell 1907:620; 1911:253; Roewer 1912:31; 1923:880; 1957:355; Comstock 1912:71; 1940: 71; Levi & Levi 1951:219, 221, fig. 1; 1955:32; 1968:245; Goodnight & Goodnight 1953:175; Holmberg 1970:127–129, figs. 3. 4, 3. 7, A. 1; Schmoller 1970:127–128, 132; 1971a:323, 327; 1971b:346, 348; Bragg & Leech 1972:67; Katayama & Post 1974:8–10, 13, 14, 20, fig. 1; Holmberg et al. 1981:19; Holmberg & Kokko 1983: 49–52, figs. 1–4; Cokendolpher 1985:399; 1987: 94; Poinar 1985:122.

Togwoteeus biceps: Cokendolpher 1987:94; Cokendolpher 1993:129, 132, 138; Cokendolpher & Lee 1993:16, 25–31.

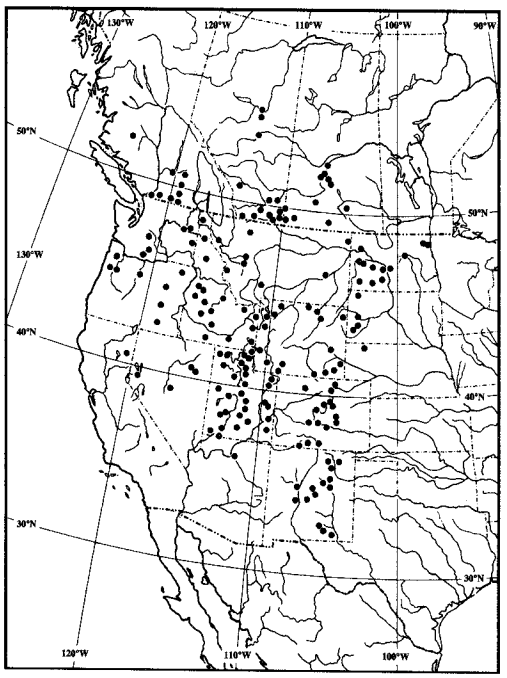


Figure 1.—Distribution of *Togwoteeus biceps* in western North America. Collection sites that had nearly the same location were not mapped.

Togwoteeus (= *Homolophus*) *biceps*: Edgar 1990: 567.

Homolophus punctatus Banks 1894:164; 1901:674; Roewer 1923:880–881; Cokendolpher 1987:94.

Togwoteeus granipalpus Roewer 1952:268, fig. 2; 1957:356; Levi & Levi 1955:32; Cokendolpher 1985:399; 1987:94; Crawford 1992:45.

Globipes sp.: Blake 1945:232 (misidentification).

Types.—The holotype of *Togwoteeus granipalpus* is labeled "Dr. E.C. Zimmerman 18.8.1951 Opiliones. Leptobuninae No. 14 *Togwoteeus granipalpus* Rwr 1M Genotypus n.g. n.sp. Wyoming. Togwotee Pass 2743 m, Teton Co., Zimmerman Leh Rwr det. 1952" and is housed in Senckenberg Natur-Museum (RII/11047/14). JCC examined the specimen and found it to be a female.

The types of *Mitopus biceps* were from USA: Idaho, no specific locality (5 July), and Colorado, [Clear Creek County] Gray's Peak (a little below the summit), (7 July). These were apparently lost by the early part of the 20th century (Roewer 1923). Dr. Arbocco (pers. comm. 1981) checked the collection at Museo Civico di Storia Naturale "Giacoma Doria" twice for the types of this species without success and agreed that the lectotype should be designated from material collected by Thorell at the Naturhistoriska Riksmuseet. Thus, we are designating the male and female from the Naturhistoriska Riksmuseet as the lectotype and paralectotype, respectively. They have both been labeled as such: "det. Cokendolpher 1981". The original data labels in the vial with the types correspond with those published except for the date: "Riksmuseets Entomologiska Afdelnig. Collectio T. Thorell Mitopus biceps Thor. Idaho U.S.A. (Packard) no. 73", "March 2 1891", and "Mitopus biceps Thor. Idaho U.S.A. Packard Md." As the labels are of unknown authorship it is possible they are incorrect. The specimens closely match Thorell's (1877) detailed written description.

The types of *Homolophus punctatus* were from the USA: Olympia, Thurston County, Washington (1♂, Trevor Kincaid) and Bear, Adams County, Idaho (1♀, L.M. Cockerell). These have apparently been lost. They were not examined by Rower (1923).

Distribution.—Three most western provinces of Canada and 14 western states of USA (Fig. 1). The records for California, Nebraska, Nevada, Oregon, South Dakota, and Utah are the first published for these states.

The female (SMF RII/2663/5) reported by Roewer (1957) from Pueblo, México, is either misidentified or mislabeled. The specimen cannot be located at Senckenberg Natur-Museum (Grasshoff pers. comm. 1981), and possibly originated from Pueblo, New Mexico, or the well-known Pueblo, Colorado.

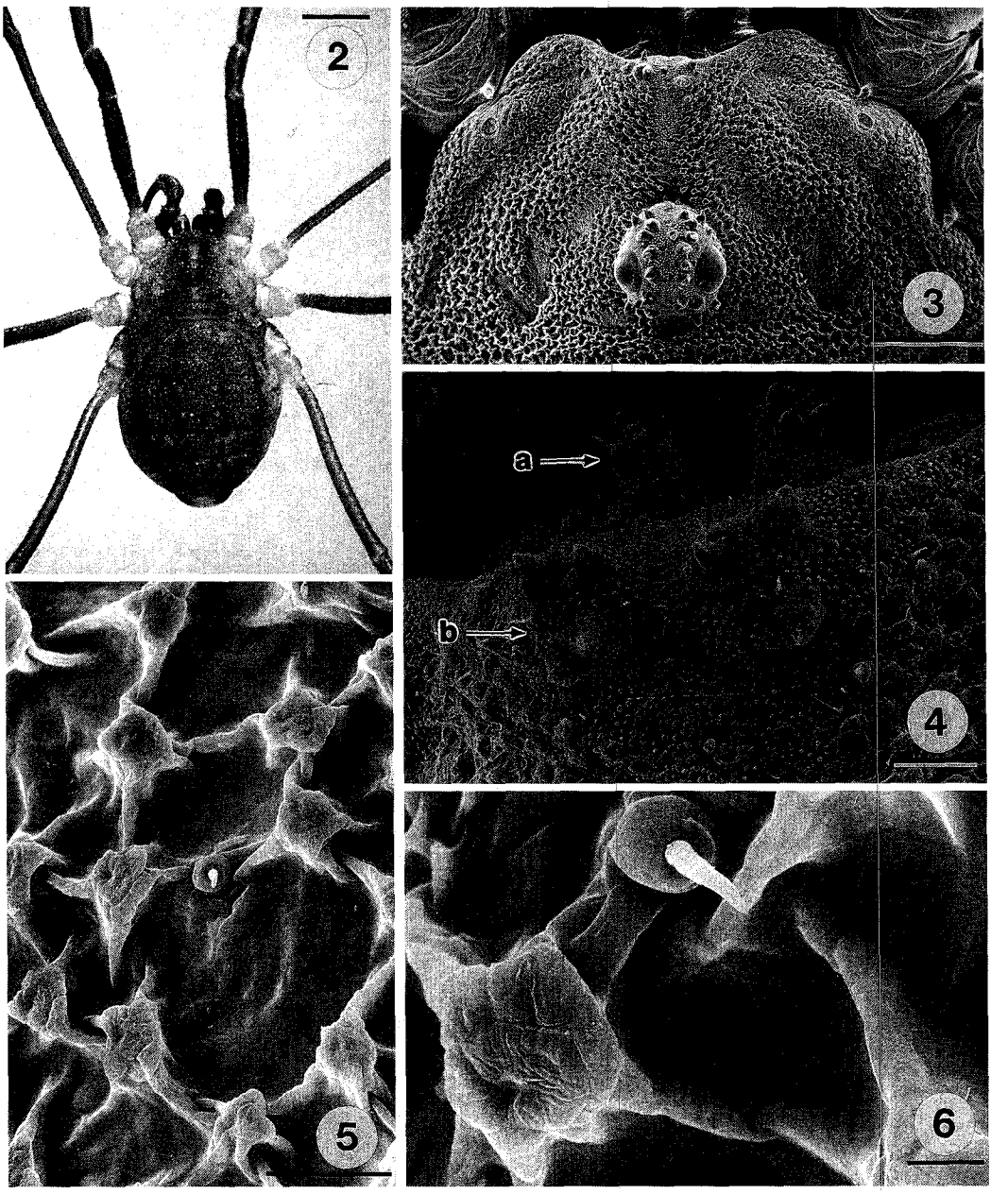
We are unable to locate the specimens reported from near Centennial, Wyoming by Blake (1945) as *Globipes* sp. They are certainly misidentified, as no known *Globipes* sp. occurs in or near Wyoming, the nearest records being from Arizona and New Mexico (JCC pers. obs.). Blake's specimens are probably members of *Togwoteeus*, as this is the only genus of the region which resembles *Globipes*. We have also examined a series of *T. biceps* collected in Medicine Bow Mountains, near Blake's collection site.

Records.—(Based only on specimens examined; including adults and some immatures.) **CANADA.** *Alberta:* Athabasca; 30 km N of Athabasca; Big Hill Springs Provincial Park, near Cochrane; Etzikomi; Lodgepole Pine Campground area, Cypress Hills Provincial Park; Edmonton; Elkwater; Hwy. 48, N Elkwater Provincial Park; Etzikom; Leth-

bridge; 16 km S Magrath; Medicine Hat; Seven Persons; Canadian Forces Base, Suffield; Waterton Lakes; Chief Mountain Road, Waterton Lakes National Park; Lewis Overthrust, Waterton Lakes National Park; Lookout Butte, Waterton Lakes National Park; Writing-on-Stone Provincial Park. *British Columbia*: Anarchist Mountain; Apex Mountain, near Keremeos; near Inkaneep Park along Okanogan River; Kamloops; Kleena Kleene; Manning Provincial Park; Beaver Pond Trail, Manning Provincial Park; isolated small park 6.4 km N Oliver; Meyers Flats, Oliver; Vaseaux Lake, Oliver; Ecological Reserve, Osoyoos; Kruger Springs, Osoyoos; Osoyoos Lake; Salmon Arm; Summerland; Rattlesnake Point, Vernon; White Lake, 10 km S of Penticton. *Saskatchewan*: Buffalo Pound Provincial Park; Central Block and West Block, Cypress Hills Provincial Park; 17.7 km S Cypress Hills Provincial Park; Cypress Lake; 9.7 km WSW Dundurn; Fort Walsh; Killdeer badlands; Saskatoon; Beaver Creek Park, 12.9 km SSW Saskatoon; 4.8 km NE Saskatoon; 8 km S Saskatoon; 20.9 km N Saskatoon; 22.5 km SSW Saskatoon; Saskatchewan Landing; Saskatchewan Landing Provincial Park. **USA.** *Arizona:* Coconino County: Kaibab National Forest, Grand Canyon. *California*: Lassan County: Blue Lake. *Colorado*: County?: Mummy Range (3353 m); Pingree Park. Archuleta County: Pagosa Springs. Boulder County: Arapaho Pass; Boulder Cañon (2246 m); Longs Peak Valley, Rocky Mountain National Park (2774 m); Longs Peak, Rocky Mountain National Park (3400 and 4100 m). Chaffee County: Upper Spring Creek, near Monarch Pass. Clear Creek County: Loveland Pass; Mt. Evans; Summit Lake, Mt. Evans (3900 m). Conejos County: at top of Cumbres Pass; Trujillo Meadow Camp, 4.8 km N Cumbres (3048 m). Custer County: West Cliff (= Westcliffe). El Paso County: on mountain side above Hwy 70, Pikes Peak; Pikes Peak (3048, 3658, 4115m); Canyon, Pikes Peak; Printing Office, Pikes Peak (3048 m). Freemont County: Wet Mountains, Stations 40, 47, 50 and 52 (2316, 2164, 2072, and 2127 m). Gilpin County: Gilpin. Grand County: Arapaho Peak (3962 m); Milner Pass. Gunnison County: Meyers Gulch. La Plata County: Cascade; Eldora (2438 m); Electra Lake (2560 m); Ward (2743 m). Larimer County: Glen Haven; near Long's Park campground south of Estes Park Village; 16.1 km W Estes Park, Rocky Mountain National Park; Big Thompson Canyon, 11.3 km S Estes Park; Rustic. Pitkin County: Aspen (3292 m). Rio Blanco County: small run beside route 13 *ca.* 9.7 km S Axial. Saguache County: Cochetopa Pass; Rist Cañon, Fort Collins. Summit County: Hoosier Pass, south of Brekenridge. Teller County: near Florissant. *Idaho*: Adams County: Summit, 11.3 km NE Council; canyon east of Meadows; north end of Payette Lake. Bear Lake County: Brentwood Lodge, Fish Haven; Georgetown; Montpelier. Boise County: 12.9 km S Galena (=Gardena?) Summit, junction Cherry and Coyote Creeks; Boise River, near entrance of north fork; Boundary Creek, Boise National Forest. Bonner County: Hana Flats, 8 km SW Nordman. Bonneville County: 16.1 km S Swan Valley. Cassia County: Rock Creek Canyon, 24 km S of Rock Creek; Sublett Reservoir. Clark County: Spencer. Custer County: Salmon River Gorge, above Challis. Fremont County: St. Anthony. Kootenai County: Coeur d'Alene. Lincoln County: Little Wood River, Pagari. Nez Perce County: 8 km NW Culdesac. Twin Falls County: no specific location. Washington County: 11.3 km NE Cambridge. *Montana*: Carbon County: E Rosebud (1890 m); Medicine Lake. Gallatin County: 9.7 km W Belgrade, W Gallstin River. Glacier County: 7 km W Browning. Granite County: Clark Fork near Bearmouth; Nimrod. Ravalli County: Gird's Creek, Hamilton. Sanders County: Thompson Falls. *Nebraska*: Dawes County: Belmont. *Nevada*: Elko County: Thomas Canyon Camp, 14.5 km SSE Lamoille Ruby Mountains (2286 m); Ruby Valley. Lander County: Kingston Camp, 48.3 km S Austin, Toiyabe Range. Washoe County: Reno. *New Mexico*: Bernialillo County: Sandia Mountains; near Crest, Sandia Mountains. Los Alamos County: Camp May (2900 m). Otero County: Bluff Springs, 14.5 km S Cloudcroft; Camp Deerhead, 1.6 km S Cloudcroft; Lincoln National Forest, Fir Forest Campground. San Miguel County: Gallinas Canyon, NW of Las Vegas; just W Cowles; Lake Kathrine Trail, Cowles; Penitente Park, Cowles; Spirit Lake Trail, Cowles. Sandoval County: Jemez Mountains; Sandia Mountains. Santa Fe County: Lake Peak NE of Santa Fe; near ski area NE Santa Fe. Taos County: 4.8 km E Questa; Frazier Mt., Twining; Williams Lake Trail, Twining; Gold Hill near Red River; just E of Rio Puebla; Red River Pass; trail from Red River to Wheeler Peak. Valencia County: Grants, Mt. Taylor Summit (3353 m); Mount Taylor. *North Dakota*: Benson County: no specific location. Billings County: T.R. National Memorial Park. Dunn County: T146-R97-S25-P400; Killdeer Mountains. McKenzie County: N unit T.R. Park; T146-R98-S16-P110. Mclean County: Washburn Park; 6.4 km S Washburn Rest Area. Mercer County: Hazen. Monton County: no specific location. Pembina County: no specific location. Slope County: Chalky Buttes; T136-R102-S14-P200; Burning Coal Vein. Williams County: no specific location. *Oregon*: Benton County: Corvallis Entomological Research Farm; Marys Peak Parker Creek, near Marys Peak Campground. Grant County: Malheur National Forest, Blue Mountain Hot Springs. Harney County: 24 km S Burns; Steen Mountains. Jefferson County: head of Metolius River, Riverside Forest Camp. Union County: Insler, Harris Mountains. Yamhill County: McMinnville. *South Dakota*:

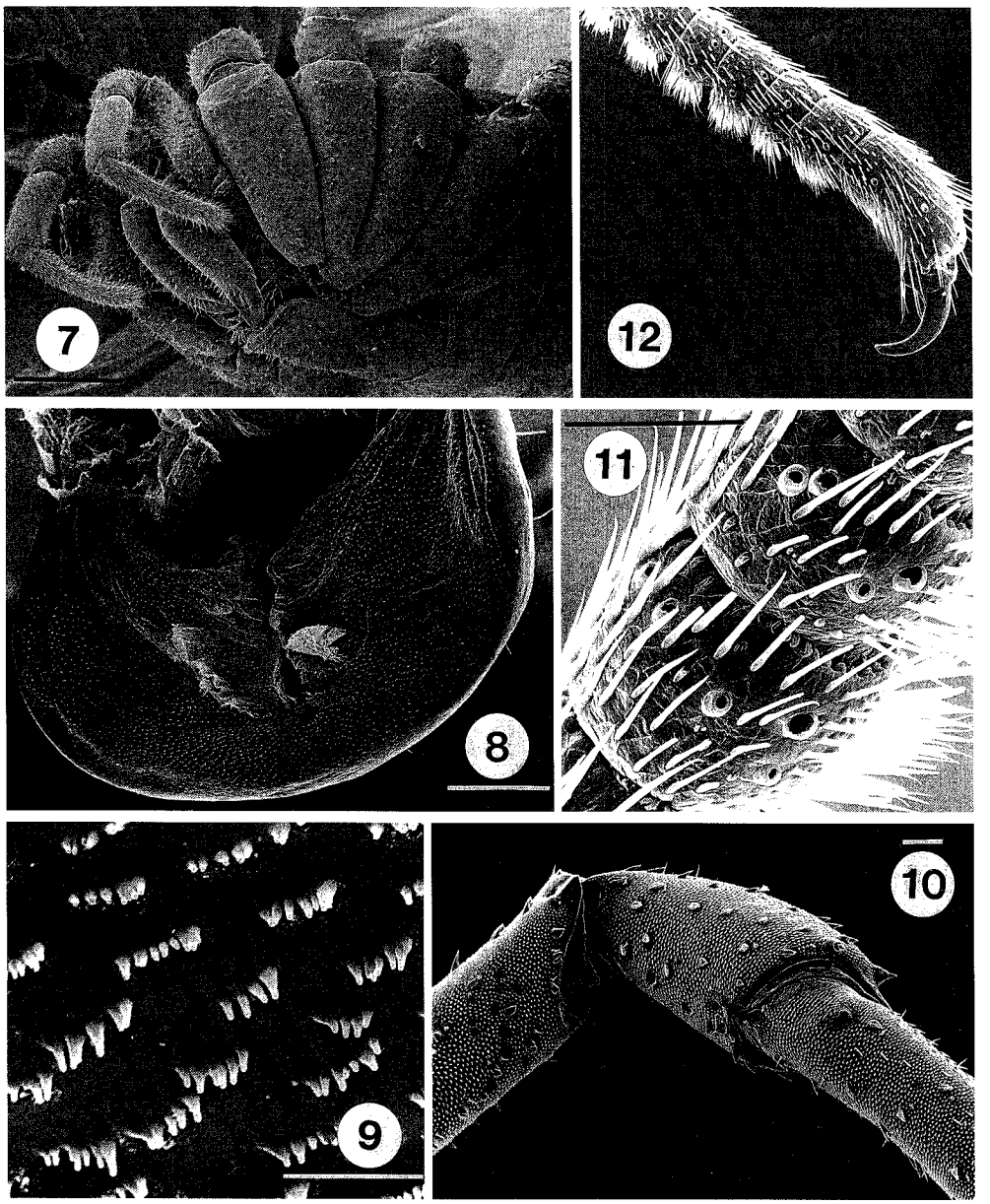
Custer County: Custer State Park. Lawrence County: Custer Park; 5.5 km S Deadwood on Highway 85A; Spring Creek Camp, 17.7 km NE Hill City. Pennington County: Mount Rushmore. *Utah*: County?: Blacksmith Fork Canyon; Butterfield Canyon, Oquirrh Mountains; Othess Mantes Canyon; Puffer Lake. Beaver County: Beaver Canyon, 16 km (direction?) from Beaver City; Kents Lake Camp, 25.8 km E Beaver City. Box Elder County: Bear River City; Clear Creek, Raft River Mountains; Dove Creek, Raft River Mountains; Rabbit Springs, 9.7 km N Lucin; Raft River Mountains, 12.9 km S Lynn. Cache County: Beaver Mountain, Wasatch Range; Logan Canyon; Logan River; Red Banks, Logan Canyon (1829 m). Dagget County: Hideout Canyon; Junction Deep and Carter Creek. Emery County: Ferron Reservoir; Huntington Canyon. Garfield or Wayne County: Horse Valley, Henry Mountains. Garfield County: Aquarius Plateau, Steep Creek; Blue Spruce Camp, 29 km N Escalante (2438 m); Wild Cat Ranger Station, 24.2 km N Boulder. Grand County: La Sal Mountains; Mirror Lake, Uintah Mountains; Warner Ranger Station, 45.1 km ESE Moar (2804 m). Iron County: Cedar Breaks. Juab County: Trout Creek. Morgan County: Bells Canyon. Millard County: Oak Creek Camp, 14 km E Oak City. Rich County: Bear Lake (east side). Salt Lake County: 6.4 km up City Creek Canyon, Salt Lake City; City Creek, Salt Lake City; Emigration Canyon; Mill Creek Canyon; Mill Creek, Salt Lake City; Salt Lake City. San Juan County: Buckboard Flat Camp, 11.3 km W Monticello (2682 m); Dalton Springs Camp, 8 km W Monticello (2591 m); La Sal Mountains. Sanpete County: Moroni. Sevier County: Fish Lake. Summit County: Beaver Canyon; Hoop Lake, Uintah Mountains. Tooele County: Loop Camp, 20.9 km SW Grantsville (2256 m); South Willow Canyon. Uintah County: Iron Springs Camp, 40.3 km N Vernal (2652 m); Kaler Hollow Camp, 35.4 km NNW Vernal (2713 m). Utah County: American Fork Canyon, Timponogos; Aspen Grove; Timpanogos. Wasatch County: Provo River at North Fork. Washington County: Pine Valley Mountains; Zion National Park. *Washington*: Kittitas County: Ellensberg. Klickitat County: near Maryhill, 11.3 km E Daller Ferry; Trout Lake County Park. Stevens County: 4.8 km N, 12.8 km NE and 40 km N Wellpinit. Whitman County: Elberton. *Wyoming*: County?: Freemouth. Albany County: Medicine Bow Peak, near Centennial; Woods Landing. Big Horn County: Porcupine Camp, 53.7 km E Lovell. Carbon County: Bottle Creek Camp, 11.3 km SW of Encampment; 12.9 km SW of Encampment (2621 m). Converse County: Medicine Bow Mountains; Summit Laramire Mountains near Pole Mountains. Crook County: Reuter Canyon Camp, 8 km NW Sundance (1737 m); 8 km N Sundance. Johnson County: Bighorn National Forest, Circle Park Rec. Area. Laramie County: Cheyenne. Lincoln County: Cokeville. Park County: Lake Creek Camp, 20.9 km SE Cooke; Lost Creek Camp; Mount Washburn Summit, Yellowstone National Park. Sheridan County: Ranger Creek Camp, 30.6 km SW Big Horn (2377 m). Sublette County: Lower Green River Lake, Wind River Range (2438 m). Sweetwater County: Green River. Teton County: Grand Teton National Park; near Moran; Moran Junction; Owl Creek Headquarters, 48 km N Jackson; Stewart River Station; spring runs crossing Route 287 in Togwotee Pass; Teton Pass; Wilson; Old Faithful, Yellowstone National Park; near Yellowstone Lake, Yellowstone National Park.

Description.—Body with thick, hard, tuberculate-microgranulate cuticle on dorsal surface (Figs. 2, 3); off-center micropores present on dorsal tubercles (Figs. 5, 6); base coloration varies from amber to black, with dorsal specks or patterns of lighter color sometimes present; dorsum sometimes with faint central figure; males tend to be more sclerotized and have more denticles and therefore appear darker than females; preocular area without mound but with two groups of small denticles near anterior margin edge (Fig. 4, arrow b); supracheliceral lamellae well developed and toothed (Fig. 4, arrow a); ocular tubercle low, rounded, covered by many prominent spines (Fig. 3); darker ring often encircling each eye; light area extends between the eyes and from the ocular tubercle to the anterior edge of the prosoma and usually forms a distinct bifid stripe (Fig. 2). Abdomen with faint indication of segmentation dorsally. Genital operculum without noticeable crest ventrally; with many microscopic spicules dorsally (Figs. 7–9). Chelicerae not enlarged, without apophyses on jaws, ventral spur on basal segment large and covered with many spicules; with 4–6 slit sensilla on second segment (Figs. 18, 21). Pedipalps without apophyses on distal ends of patellae or tibiae in juveniles or adults, distal end of femora without campaniform organ (slit-sensillum present), claw smooth, not toothed (Figs. 13, 14, 17); pedipalps sexually dimorphic; male pedipalps modified, enlarged, tarsus bulbous at base and with two rows of ventral denticles; midventral area of tibia slightly compressed (most noticeable on mesal side) (Figs. 14–16, 36, 37). Legs generally short and wide; femur I as wide or wider than ocular tubercle, femora I usually equal to or shorter than body length, no pseudoarticulary nodules in femora,



Figures 2–6.—Body and integument of *Togwoteeus biceps*. 2, Dorsal view of adult male (non-SEM); 3, Ocular tubercle and anterior portion of cephalothorax of male; 4, Supracheliceral lamella (arrow a) and anterior portion of cephalothorax of female with tubercles (arrow b); 5, Cuticle of prosoma of male; 6, Detail of cuticle. Scales = 0.5 mm in Figs. 2, 3; 0.1 mm in Fig. 4; 0.05 mm in Fig. 5; 10 μm in Fig. 6.

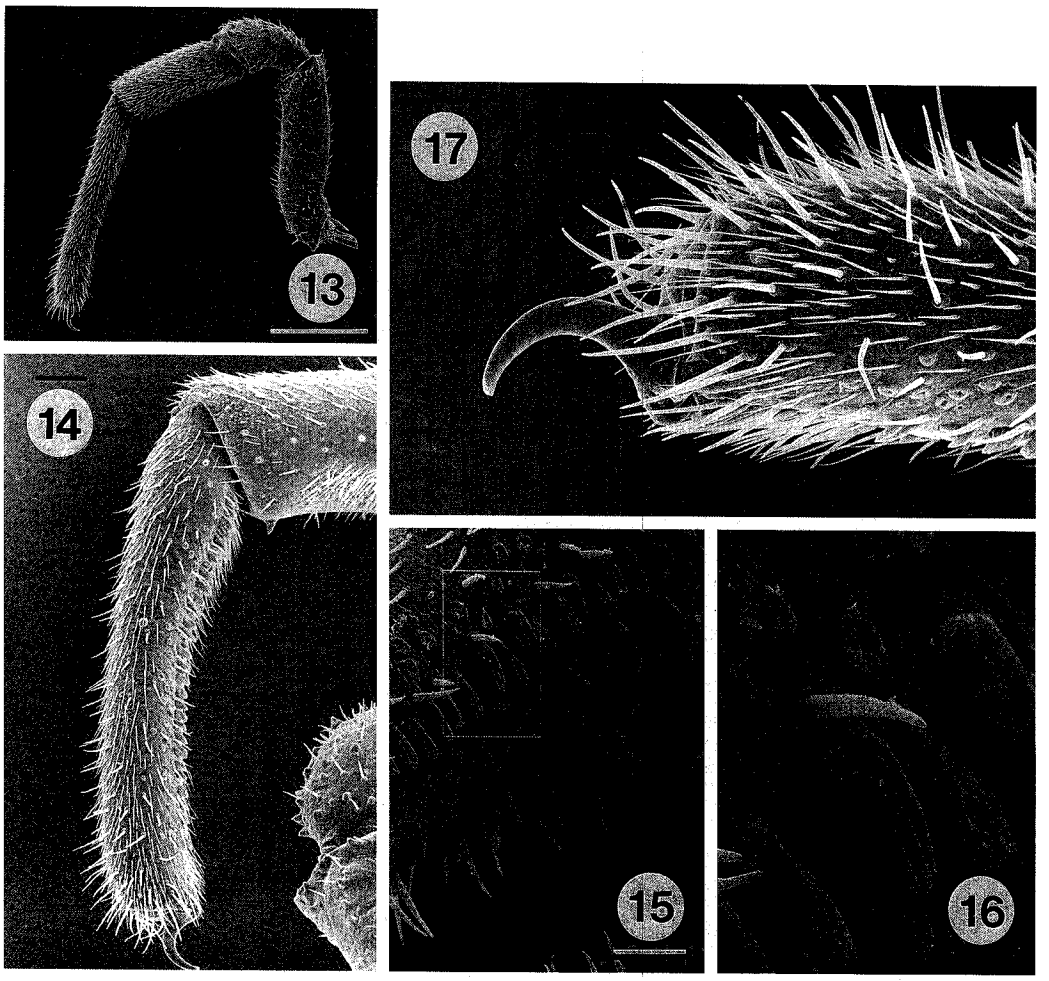
tibiae II with (longer legged specimens) or without (lectotype and shorter legged specimens) pseudosegments; tibiae I, III, IV without pseudosegments; femora, patellae, tibiae with randomly spaced (without rows) pointed tubercles (Fig. 10); patellae and distal tips of leg femora and tibiae often darkly shaded; each leg coxa with center spine dorsally, with at most a weakly developed lateral row of denticles (Fig. 7). Penis alate (Figs. 22–25, 31–33); *ca.* 5 μm longitudinal slit near the tip of the stylus of the penis glans (Fig. 24). Ovi-



Figures 7–12.—Morphology and anatomy of *Togwoteeus biceps*. 7, Anteroventral view of anterior portion of male; 8, Spicules on inner lining of the anterior edge of male genital operculum; 9, Detail of operculum spicules; 10, Lateral view of leg I of female; 11, Detail of tarsal leg pores of female; 12, Tip of leg tarsus with smooth claw of male. Scales = 1 mm in Fig. 7; 0.1 mm in Figs. 8, 10, 12; 0.5 mm in Fig. 11; 10 μm in Fig. 9.

positor relatively long, 34 segmented in paralectotype; with four slit-sensilla (two dorsal, two ventral) per lateral half; 3 segmented furca (Figs. 26, 27, 35). Ovipositor enclosed in two sheaths, details as in Figs. 28–30. Seminal receptacles as in Fig. 34, located in segments 3–4 of ovipositor (Fig. 35).

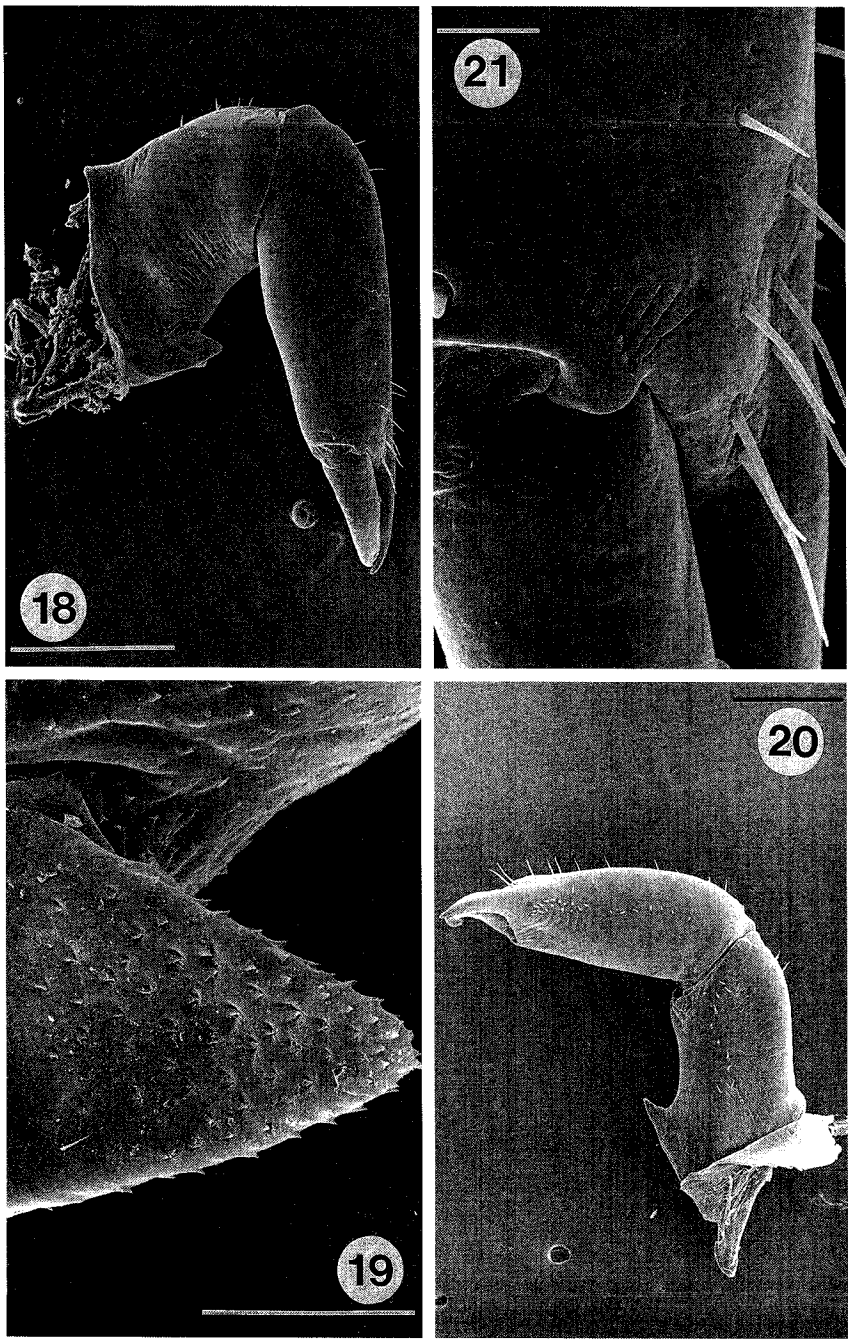
Body measurements.—The results of measuring 80 males and 74 females are given in Table 2. No simple measurement cline was observed between the four areas (Table 1) and the data were pooled. Female body measurements are larger than those of males. Male pedipalps measurements are larger than fe-



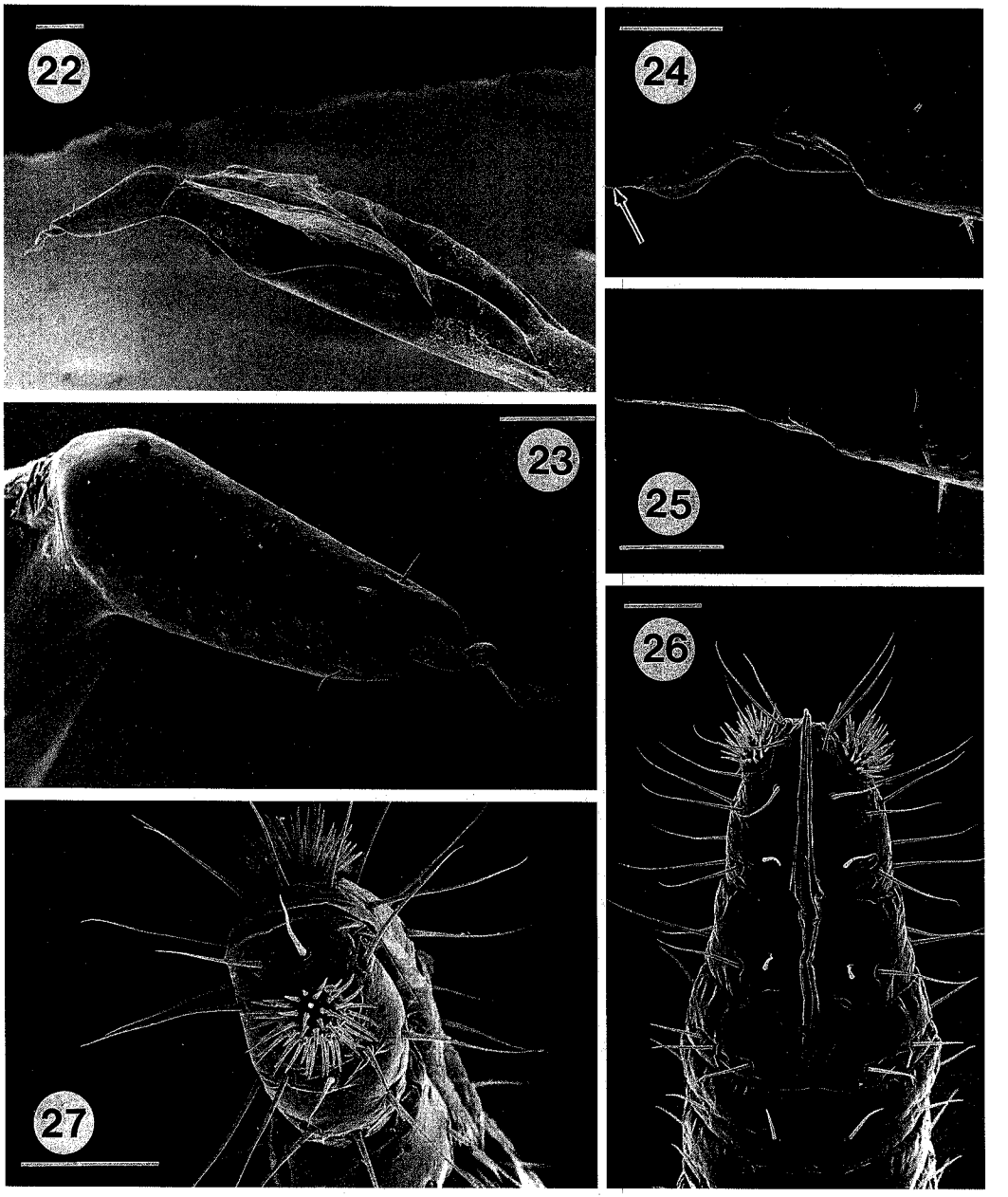
Figures 13–17.—Right pedipalp of *Togwoteeus biceps*. 13, Lateral view of female; 14, Detail of male tarsus; 15, Denticles and pores on tarsus of male; 16, Detail (3.4× enlargement) from insert in Fig. 15; 17, Smooth claw of male. Scales = 0.5 mm in Fig. 13; 0.1 mm in Fig. 14; 0.05 mm in Figure 17; 50 μm in Fig. 15.

males, except for palpal tarsus length (which is longer in females) and width (which is the same for both sexes). Male leg measurements were generally longer except for femur II and IV. The length of the genital operculum is longer in males but wider at the base in females. The neck width is the same. Male and female measurements for the ocular tubercle are the same except that the female's is slightly closer to the anterior margin. The mode numbers of metatarsal bands for both sexes are four; the range varies between 2–10.

Ultrastructure.—The pedipalp sense organs of *Togwoteeus* appear similar to those observed by Spicer (1987) in other harvestmen, i.e., *Leiobunum* C. Koch 1839 and *Eumesosoma* Cokendolpher 1980. Like Spicer, we found sensilla trichodea and chaetica on the pedipalps of *T. biceps* (Figs. 11, 12, 14, 17). The "tarsal organs" of Spicer were also observed on the ventral surface of the pedipalp tarsus (Figs. 15, 16). The prosomal dorsum revealed a tuberculate-microgranulate morphology (Figs. 3–4). The prominent tubercles have asymmetrical arms, with the central regions containing off-center micropores. The abdominal setae arise from tubercles elevated from the surface of the integument. These tubercles appear to be constricted at their bases. The dorsal morphology of *T. biceps* is unlike any other harvestman thus far examined (*cf.* Murphree 1988). The off-center



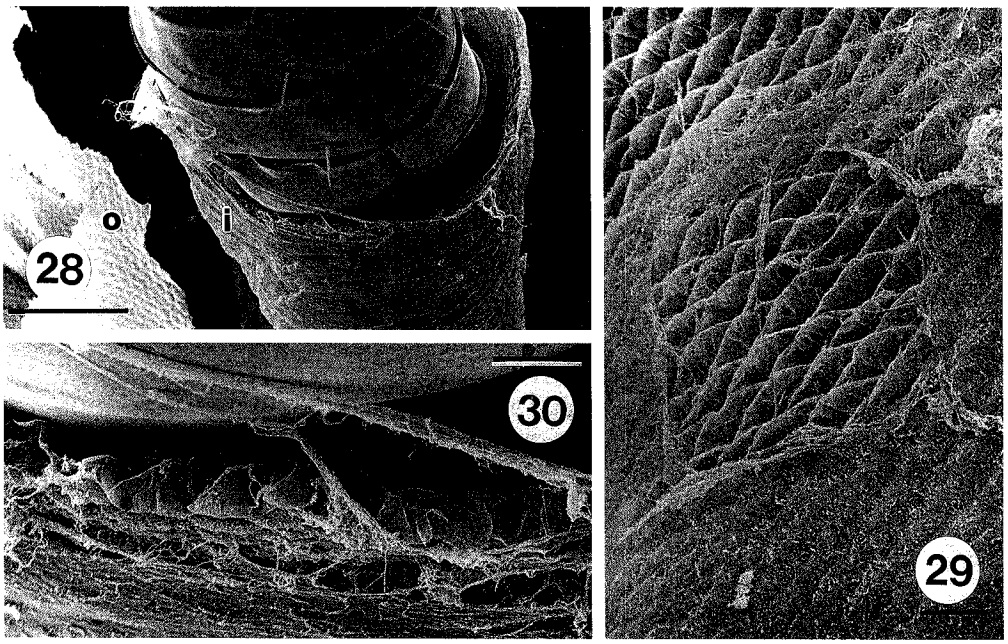
Figures 18–21.—Chelicerae of female *Togwoteeus biceps*. 18, Lateral view; 19, Lateral view of basal tooth with numerous spicules (close-up of Fig. 18); 20, Mesal view; 21, Detail of slit sense organ at base of movable cheliceral jaw (close-up of Fig. 18). Scales = 0.5 mm in Figs. 18, 20; 0.05 mm in Figs. 19, 21.



Figures 22–27.—Genital structures of *Togwoteeus biceps*. 22, Ventrolateral view of distal end of penis; 23, Lateral view of glans of penis; 24, Lateral view of stylus of penis – arrow indicates location of a 5 μm slit; 25, Dorsal view of stylus of penis; 26, Distal end of ovipositor with 3-segmented furca; 27, Distolateral view of sensillae on ovipositor. Scales = 0.1 mm in Figs. 22, 26, 27; 0.05 mm in Figs. 23–25.

placement of micropores is unlike the central placement of members of *Leiobunum* and *Hadrobunus* Banks 1900. *Eumesosoma* apparently does not have micropores atop of dorsal tubercles (Murphree 1988: Fig. 18). The ultrastructure of the ovipositor sheaths are herein illustrated for the first time as are some details of the penis and ovipositor.

Variation.—We occasionally found specimens that had leg lengths nearly double the

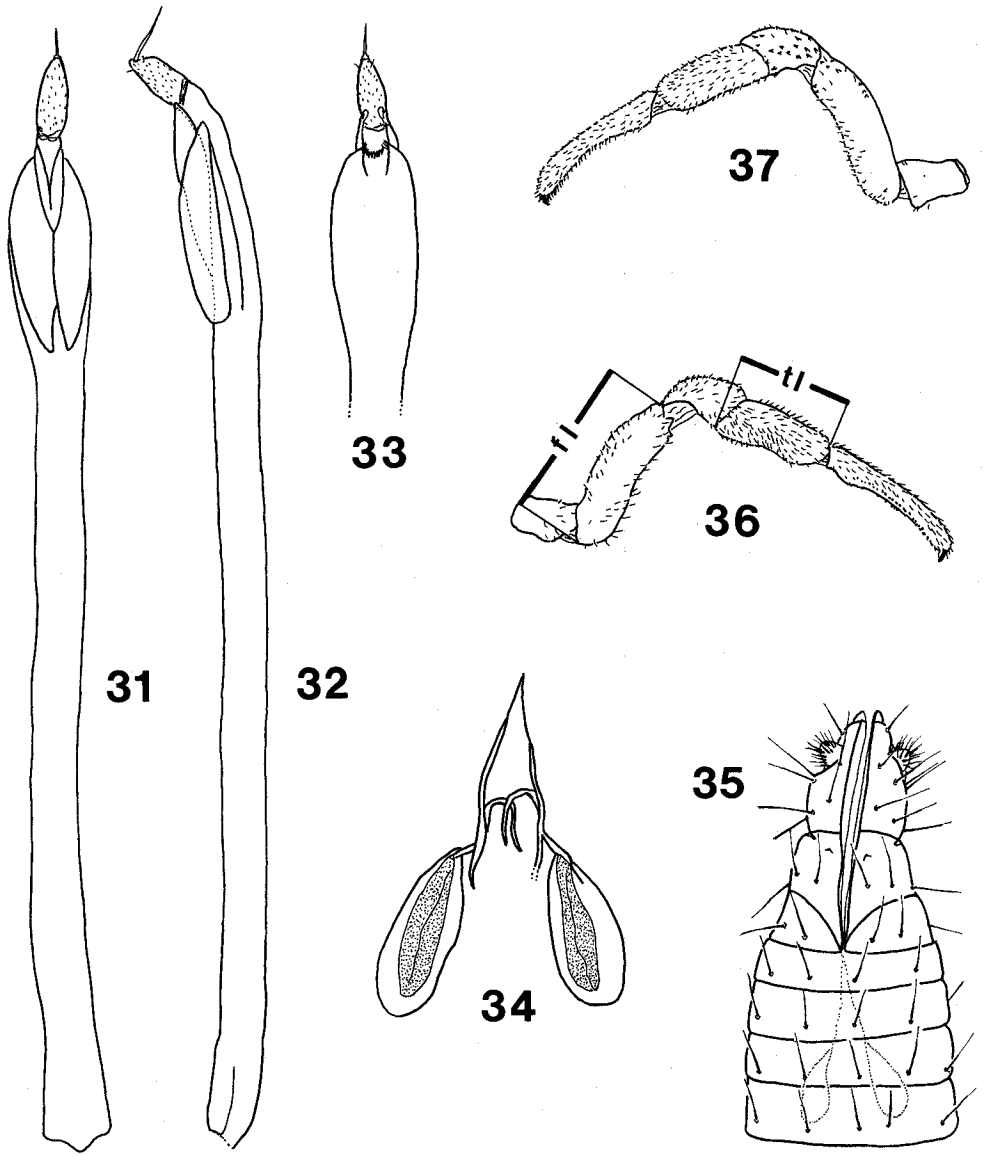


Figures 28–30.—Ovipositor of *Togwoteeus biceps*. 28, Mid-section of ovipositor and broken sheaths, o = outer and i = inner sheaths; 29, Expanded view of inner sheath of ovipositor; 30, Expanded view of cross-section of inner sheath. Scales = 0.1 mm in Fig. 28, 10 μm in Figs. 29, 30.

normal. For example, a female specimen from near Osyoos, British Columbia had a femur II length of 9.60 mm (*cf.* mean of 5.35 mm, Table 2). However after examining other characteristics and measuring many individuals, we concluded that these were exceptional individuals and not another species. Goodnight & Goodnight (1953) stated that a north-south cline in coloration could be demonstrated for this species. The lighter colored individuals were in the north and the darker colored individuals were in the south. While this may be partially true, it is not as simple as that. It appears age and sex of the animal may play a significant role in the color of the animal. Examination of series collected through time revealed older animals and males are darker. The role of elevation and moisture have not been investigated, but as evidenced in other arthropods they may play a role in the determination of pigmentation. There was no obvious cline in the morphological measurements of the specimens examined in this study.

Anomalies.—Holmberg & Kokko (1983) reported on an eye-less *T. biceps*. It had no ocular tubercle and only degenerate optic nerve masses. This anomaly was found in only one specimen. During this study some abnormalities were noticed in the formation of the denticles near the anterior edge of the cephalothorax and the supracheliceral lamellae. Usually one such structure was smaller than normal and with fewer and smaller denticles.

Chromosomes.—Karyotypes from two subadult males and one subadult female revealed 2n = 22, all being metacentric chromosomes (Fig 38). Sex chromosomes were not detected in the male karyotypes. The chromosomes in the two karyotypes from the female were not condensed and sex chromosomes could not be distinguished. Studies detailing chromosomes of harvestmen are few. The known counts/karyotypes were presented or reviewed by Tsurusaki & Cokendolpher (1990) and Cokendolpher & Jones (1991). Including the present study, karyotypes of 40 species of the superfamily Phalangioidea are known. The diploid chromosome numbers thus far known for the superfamily range between 10 and 36, with 22 being recorded in several unrelated genera of the Protolophidae (*Protolophus* Banks 1893)



Figures 31–37.—Anatomy of *Togwoteeus biceps* (male lectotype, female paralectotype). 31, Ventral view of penis; 32, Lateral view of penis; 33, Dorsal view of distal end of penis; 34, Seminal receptacles; 35, Distal end of ovipositor with seminal receptacles (dotted lines); 36, Mesal view of male pedipalp; 37, Lateral view of male pedipalp. *fl* = femur length, *tl* = tibia length.

and Sclerosomatidae (*Dalquestia* Cokendolpher 1984, *Eumesosoma*, *Gagrellula* Roewer 1911, *Leiobunum*).

Habitat.—This species is found in many habitats. In the mountains specimens are often found in densely wooded areas as well as on windswept mountain-tops above the tree line. They also occur in many dry habitats, but often near water bodies, especially in northern prairies. In the southern part of their range, they are restricted to higher elevations. They have been found under rocks, logs, and other ground debris. A few individuals were also obtained in deserted buildings. Only rarely have they been obtained by sweeping vegetation. They do not appear to aggregate in protected sites like many other sclerosomatids.

Phenology.—Although the collection data

Table 2.—Morphological measurements (mm) and counts of *Togwoteeus biceps*. Data pooled from specimens described in Table 1. SE = Standard error. ns = not significant, probability > 0.05. Statistically significant larger values in bold.

	Males			Females			
Body part	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	*P*
Body							
Prosoma width	2.68 (0.031)	2.08–3.12	80	**2.87** (0.035)	2.04–3.40	74	<0.001
Body length	4.84 (0.053)	3.60–5.76	80	**6.16** (0.084)	3.72–7.48	74	<0.001
Abdomen width	2.89 (0.036)	1.88–3.08	80	**3.58** (0.049)	2.28–4.92	74	<0.001
Abdomen height	2.51 (0.029)	1.88–3.08	80	**3.40** (0.061)	1.88–4.68	74	<0.001
Pedipalps							
Femur length	**1.15** (0.015)	0.90–1.36	80	0.99 (0.013)	0.72–1.20	74	<0.001
Femur width	**0.33** (0.005)	0.24–0.44	80	0.25 (0.003)	0.16–0.30	74	<0.001
Patella length	**0.58** (0.006)	0.44–0.66	80	0.48 (0.006)	0.36–0.58	74	<0.001
Patella width	**0.35** (0.004)	0.26–0.40	80	0.30 (0.003)	0.22–0.36	74	<0.001
Tibia length	**0.81** (0.010)	0.62–1.00	80	0.70 (0.009)	0.48–0.88	74	<0.001
Tibia width	**0.34** (0.004)	0.24–0.44	80	0.26 (0.003)	0.20–0.34	74	<0.001
Tarsus length	1.06 (0.013)	0.82–1.28	80	**1.12** (0.014)	0.82–1.38	74	0.002
Tarsus width	0.17 (0.004)	0.12–0.24	80	0.17 (0.003)	0.10–0.22	74	0.23 ns
Legs							
Femur I length	**3.22** (0.087)	2.08–4.92	79	2.90 (0.072)	1.76–4.56	74	<0.006
Tibia I length	**2.59** (0.066)	1.60–3.84	78	2.28 (0.051)	1.52–3.40	73	<0.001
Femur II length	5.76 (0.174)	3.64–9.44	80	5.35 (0.156)	3.36–8.52	74	>0.08 ns
Tibia II length	**5.08** (0.156)	3.08–8.16	80	4.16 (0.130)	2.88–7.32	74	0.02
Femur III length	**3.45** (0.089)	2.24–5.20	80	3.13 (0.072)	2.04–4.56	74	0.006
Tibia III length	**2.71** (0.068)	1.72–3.80	80	2.42 (0.053)	1.60–3.56	74	0.001
Femur IV length	5.11 (0.137)	3.40–7.76	79	4.86 (0.116)	3.20–7.60	74	>0.16 ns
Tibia IV length	**3.80** (0.095)	2.52–5.60	77	3.49 (0.080)	2.32–5.40	74	0.015
Genital operculum							
Length	**3.13** (0.037)	2.48–3.80	80	2.92 (0.036)	2.16–3.48	74	<0.01
Neck width	1.28 (0.013)	0.99–1.52	80	1.29 (0.015)	0.96–1.52	74	0.56 ns
Base width	2.25 (0.026)	1.72–2.88	80	**2.39** (0.026)	1.76–2.92	74	<0.001
Ocular tubercle							
To anterior margin	**0.52** (0.007)	0.38–0.64	80	0.49 (0.007)	0.36–0.64	74	<0.004
Length	0.45 (0.004)	0.38–0.54	80	0.45 (0.006)	0.36–0.56	74	0.66 ns
Width	0.43 (0.003)	0.38–0.50	80	0.43 (0.004)	0.34–0.50	74	0.36 ns
Height	0.26 (0.005)	0.16–0.32	80	0.26 (0.004)	0.20–0.32	74	0.62 ns
Metatarsal II bands	4.82 (0.146)	2–8		4.53 (0.183)	2–10	73	0.35 ns

(Table 3) are biased (i.e., most collection dates in the summer, most specimens collected were larger — usually adults, most collection sites between 40–50°N latitude), it appears that *T. biceps* overwinters as immatures which become adults in May or June and then die by fall. It is likely that the majority of the individuals have a one year life cycle, but it is possible that late maturing adults may produce offspring that take two summers to reach maturity. There is no evidence that this phenology pattern changes over the latitudinal range of the species.

Parasites.—Poinar (1985) reported an un-

Figure 38.—Karyotype (2n = 22) of subadult male *Togwoteeus biceps* from near Logan, Utah.

Table 3.—Latitude versus time of year for collections of *Togwoteeus biceps*. I = immatures, A = adults. Note that 98% of the July records for the latitude 30–34° grouping came from pit traps from one locality. The label date is 3 July but probably most of the collections were from June.

	Spring			Summer			Fall			Winter		
Latitude	Mar. I, A	Apr. I, A	May I, A	June I, A	July I, A	Aug. I, A	Sep. I, A	Oct. I, A	Nov. I, A	Dec. I, A	Jan. I, A	Feb. I, A
50–55°		4, 0	21, 21	10, 17	7, 28	0, 1	1, 2	1, 1				
45–49°	35, 0	47, 0	39, 69	93, 497	11, 493	2, 73	2, 1	14, 4	23, 2	1, 0	5, 0	19, 0
40–44°		3, 0	38, 4	31, 40	25, 63	15, 77	11, 30	0, 1				
35–39°			12, 0	25, 23	6, 89	1, 22	6, 20	0, 2				
30–34°					277, 181	0, 1						
% adults	0	0	46	78	72	91	73	35	9	0	0	0

identified juvenile mermithid nematod (*Agamomermis* sp.) parasite from this harvestman. Cokendolpher (1993) recorded unidentified *Leptus* sp. mites from *T. biceps*.

CONCLUSIONS

It appears that *Togwoteeus biceps* is monotypic. The range of the species extends through much of the western prairie and mountain areas of Canada and USA. The latitudinal range is about 33–54°N, longitudinal about 98–124°W. This species has the greatest elevational range (<500 to 4100 m) and occurs at the highest elevation of any recorded harvestman in North America.

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