REVISION AND CLADISTIC ANALYSIS OF THE ERIGONINE SPIDER GENUS *SISICOTTUS* (ARANEAE, LINYPHIIDAE, ERIGONINAE)

Jeremy A. Miller: Department of Biological Sciences, The George Washington University, Washington, D.C., 20052, and Department of Entomology, National Museum of Natural History, NHB-105, Smithsonian Institution, Washington, D.C. 20560 USA

ABSTRACT. The erigonine spider genus *Sisicottus* is revised for the first time. Cladistic analysis of *Sisicottus* suggests the following hypothesis of interspecific relationships: ((*S. montigenus, S. quoylei*) (*S. panopeus* (*S. montanus* (*S. crossoclavis* (*S. cynthiae* (*S. orites* (*S. nesides, S. aenigmaticus*))))))). The monophyly of the genus is unambiguously supported by six putative synapomorphies: a terminal embolic hook, a suprategular membrane projecting apically from the distal suprategular apophysis, copulatory ducts that originate on the ectal side of the spermathecae, imbricated stridulatory striae, the presence of two dorsal macrosetae on tibia III, and the absence of a trichobothrium on metatarsus IV. Evidence for the monophyly of each *Sisicottus* species is discussed. A taxonomic key, diagnoses, descriptions, quantitative character values, illustrations, locality records, natural history information, and distribution maps are presented for the nine recognized species. Five new species are described: **S. quoylei**, **S. panopeus**, **S. crossoclavis**, **S. cynthiae**, and **S. aenigmaticus**. *Typhochrestus uintanus* (NEW COMBINATION) is formally transferred out of *Sisicottus*.

The genus *Sisicottus* Bishop & Crosby 1938 (Linyphiidae) is a lineage of small to medium-size erigonine spiders made up of nine known species. *Sisicottus* species usually live in moss and litter in conifer forests where they presumably build small prey capture webs. The genus is known from North America north of Mexico and from the Kuril Islands between Japan and the Kamchatka Peninsula. It is most diverse in the northwestern United States and southwestern Canada.

By 1995, *Sisicottus* was one of 534 valid linyphiid genera (Platnick 1997). However, it is one of few linyphiid genera defined explicitly by putative synapomorphies. At best, most linyphiid genera seem to be delimited to preserve homogeneity among members. The quality of systematics as an information storage and retrieval system is undermined when genera are circumscribed without due consideration of evidence in support of monophyly. The original diagnosis of *Sisicottus* was inadequate to prevent *Sisicottus* from serving as a polyphyletic wastebasket. Species once placed in *Sisicottus* are currently placed in four different genera. The erroneous placement of some species in *Sisicottus* appears to

have been based on understandable misinterpretations of homology. In other cases, placement in *Sisicottus* seems inexplicable.

Some morphological features in *Sisicottus* exhibit a range of evolutionary plasticity. The distal suprategular apophysis of the male palpus is recognizably different in every *Sisicottus* species. The shape of the male palpal tibia and the dorsal plate of the female epigynum exhibit slightly less interspecific variation. Other characters, such as the form of the male paracymbium, the marginal suprategular apophysis of the palpus, the embolic division, and the path of the female copulatory ducts are nearly invariant within the genus. If one gives primacy to such characters, *Sisicottus* does in fact comprise a homogeneous group of species. But relying on intuition to predict which characters will be stable and which will be homoplastic is unscientific. Shared derived similarity (synapomorphy) is the evidence upon which monophyletic groups are recognized. Synapomorphies are best discovered by incorporating as much comparative data as possible into a cladistic analysis. The task of bringing phylogenetic order to the chaos that is linyphiid systematics is a monumental one,

but its reward will be a hierarchical structure based on repeatable methods and explicit character evidence. Currently, even most professional spider systematists can identify linyphiids only with difficulty or not at all. An active dialog on the comparative morphology of linyphiids and the history of character states will lead to a phylogenetically based and usable taxonomy. An improved taxonomy will facilitate the communication of ideas and findings concerning this diverse and important spider family. Such communication will not be limited to professional spider systematists, but will include ecologists, biogeographers, conservationists, and amateur taxonomists.

TAXONOMIC HISTORY

Bishop & Crosby (1938) established *Sisicottus* to accommodate *Tmeticus montanus* Emerton 1882 and a new species, *Sisicottus montigenus* Bishop & Crosby 1938. They diagnosed the genus based on characteristics of the male palpus. According to the original description, the two founding species shared similar dorsomesal tibial apophyses, a lamella characteristica (misidentified as a radical tailpiece) described as "bulb-like," and an open-coiled embolus making one turn about the distal end of the bulb (Bishop & Crosby 1938: 57).

Bishop & Crosby synonymized *Erigone collina* Marx 1890, *Grammonota orites* Chamberlin 1919, *Oedothorax nesides* Chamberlin 1921, and *Oedothorax pidacitis* Crosby & Bishop 1927 under *S. montanus*. Although Bishop & Crosby recognized that a "larger and usually somewhat paler" (Bishop & Crosby 1938:59) form existed sympatrically in the west with the smaller form of *S. montanus* typical of eastern populations, they were unable to come up with a reliable way of separating the two morphs. The western form alluded to is undoubtedly *S. orites* and/or *S. nesides*. Both of these species are common and widespread in the west and are larger than *S. montanus*. However, the observation that these western species are typically paler than *S. montanus* is erroneous.

Working near the end of the 19th century, Marx objected to the trend begun by his contemporaries Menge, Emerton, and Simon, of splitting *Erigone* Audouin 1826 into the many smaller genera that now comprise the Erigoninae. Instead of transferring previously described species into *Erigone*, Marx's (1890) catalog features several replacement names for valid species. One example of this was *E. collina*, which was meant to replace *T. montanus*.

Chamberlin & Ivie (1933) synonymized *Oedothorax pidacitis* under *Grammonota orites* and transferred the species to *Oedothorax* Bertkau 1883, making it congeneric with the very similar *O. nesides*. Shortly after the establishment of *Sisicottus* as a new genus, Chamberlin & Ivie (1939) rejected the broad definition of *S. montanus* and re-elevated *S. orites* and *S. nesides* to species status. Although they wrote no justification for their decision, they did illustrate the dorsal view of the male palpal tibiae of *S. orites*, *S. nesides*, and *S. montanus*. Chamberlin & Ivie also placed two new species in *Sisicottus*: *S. uintanus* Chamberlin & Ivie 1939 and *S. cornuella* Chamberlin & Ivie 1939.

Holm (1967) suggested that *S. uintanus* be transferred to *Typhochrestus* Simon 1884 based on a comparison with *T. pygmaeus* (Sørensen 1898), which is not the type species of the genus. He commented on the superficial similarity of an embolus coiled around a straight apophysis shared by *S. uintanus*, *S. montanus*, and *T. pygmaeus*, but realized that the apophysis of *S. uintanus* and *T. pygmaeus* arises from the embolic division whereas the apophysis in *Sisicottus* arises from the supra-tegulum or "median apophysis" in Holm's terminology. Although this change has been adopted by some authors (Buckle et al. 1994), Holm's statement was too tentative to meet Platnick's (1989) criteria for formal transfers.

Sisicottus cornuella was transferred to *Walckenaeria* Blackwall 1833 by Millidge (1983) apparently based on characteristics given in his definition of *Walckenaeria* (e.g., sternum longer than wide, distinctly sclerotized pedicel, fourth metatarsal trichobothrium, strongly pectinate tarsal claws) and on the presence of a short horn on the male carapace and details of the male and female genitalia typical of the *minuta* group of *Walckenaeria* species.

Sisicottus atypicus Chamberlin & Ivie 1944 was described from the male only. *Sciastes ogeechee* Chamberlin & Ivie 1944 was described from a single female in the same paper. These two species were later found to be conspecific and were synonymized under *Souessoula parva* (Banks 1899) by Ivie

(1967). This species lacks nearly all of the characteristics that distinguish *Sisicottus* from other erigonines including a coiled embolus.

Sisicottus hibernus Barrows 1945 is a very unusual species that was inexplicably described as a *Sisicottus*. It shares none of the synapomorphies that define *Sisicottus* and was transferred to *Carorita* Duffey & Merrett 1963 by Zujko-Miller (1999) based on the results of a phylogenetic study.

METHODS

Abbreviations for anatomical structures and quantitative characters are listed in Table 1. Abbreviations for specimen collections are found in the acknowledgments. Boundaries for quantitative characters are illustrated in Figs. 1, 2, 5–7, and 22–24. All measurements are in mm.

Light microscopy.—Measurements were performed using a Leitz binocular dissecting scope with greenough objectives and an eyepiece micrometer scale in 20× oculars. Five specimens were remeasured five times for each character during this study. This sampling indicated that the measurements are accurate to one micrometer unit for both powers of magnification used. Carapace length was measured at 80× and one micrometer unit had a value of 0.024 mm. All other measurements were made at 200× and one micrometer unit had a value of 0.0095 mm. Illustrations of external structures were drawn using a 20 × 20 ocular grid at 200×. For observation of internal structures, specimens were cleared in methyl salicylate (Holm 1979) and illustrated using an Olympus BH-2 compound microscope at 400× fitted with a camera lucida. Cleared specimens were positioned for illustration using the method described by Coddington (1983). Male palpus drawings and scanning electron micrographs are from the left appendage unless otherwise indicated. Specimens in which tracheal structures were to be viewed had windows cut in the dorsal integument of the carapace and abdomen. Specimens were digested in dilute sodium hypochlorite (household bleach) at room temperature for several hours until all the nonchitinous parts had dissolved (Millidge 1984a). Chlorazol black was used to stain the tracheae. Illustrations were made using a Wild M-20 compound microscope fitted with a camera lucida.
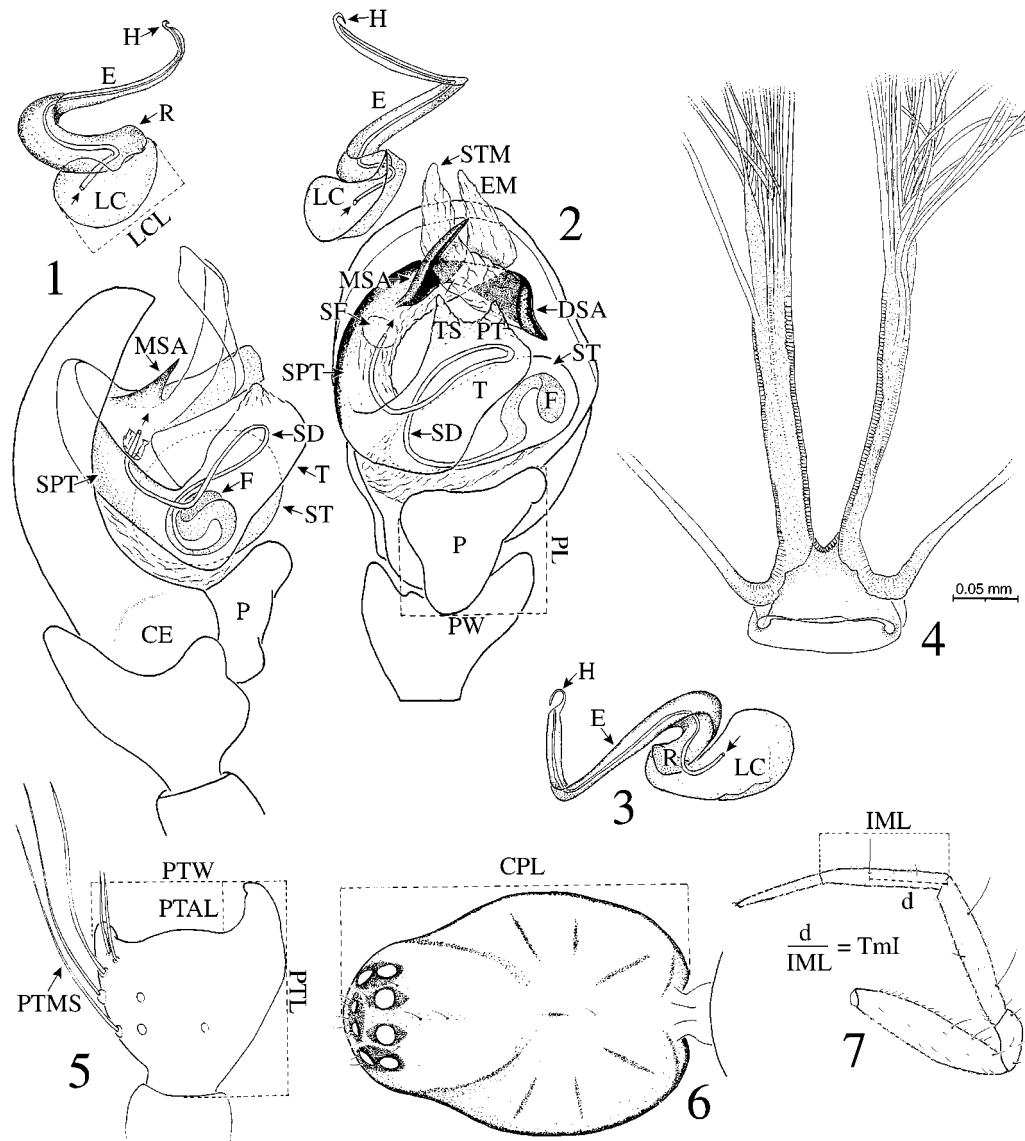
Electron microscopy.—Scanning electron microscopy (SEM) was conducted using a Jeol 35U at Clemson University and an Amray 1810 at the National Museum of Natural History (Smithsonian Institution). Male and female specimens representing most *Sisicottus* species were examined using SEM. I was unable to examine *Sisicottus aenigmaticus* new species or males of *S. quoylei* new species. Male and female specimens of *Typhochrestus uintanus* and *T. digitatus* (O. Pickard-Cambridge 1872) were also examined. This last species was represented by specimens prepared by G. Hormiga according to methods described in Hormiga (in press). I used SEM to observe male and female genitalia and spinneret spigot morphology. Spinneret spigots were identified using Coddington (1989). Abdomens and some genitalia were prepared for SEM by taking them through a rehydration series, placing them in a buffered 2.5% glutaraldehyde solution for 48 hours, then dehydrating to 100% ethanol. Specimens were then ultrasonicated for up to one minute. Ethanol was then removed either by critical point drying in a Seevac CPD-100 or preparation in hexamethyldisilazane for five minutes (Polysciences, Inc., CAT #0629). Some genitalia were simply ultrasonicated, dehydrated in 100% ethanol, placed in hexamethyldisilazane, air dried, and mounted.

Quantitative characters.—Quantitative characters were selected on the basis of their estimated potential utility in distinguishing species and groups of species. Quantitative character values for samples of each species (Tables 2, 3) and for the type specimens alone (Table 4) are an important part of each description.

Descriptions.—Species descriptions draw from as many individuals over as wide a geographic range as possible. This approach was chosen in order to account for as much intraspecific variation as possible. Some illustrations required the examination of multiple specimens to achieve a clear interpretation of the anatomy. Because of the relative difficulty involved in distinguishing some species, the diagnostic section of each species description has been designed to convey all available information that might be relevant to accurate species identification. Descriptions highlight the unique characteristics of each species and

Table 1.—Anatomical and quantitative abbreviations used in text, figures, and tables. For morphometric characters, maximum lengths were recorded unless otherwise specified, # indicates a quantitative character.

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinneret(s)
ARP	anterior radical process (♂)
CD	copulatory duct (♀)
CDC	copulatory duct capsule; sclerotized capsule which covers the copulatory ducts (♀)
CDCW	copulatory duct capsule width, dorsal view (♀, #)
CE	excavation of cymbium on mesal side (♂)
CO	copulatory opening (♀)
CPL	carapace length, dorsal view (#)
CY	cylindrical gland spigot(s)
DF	dorsal fold of dorsal plate (♀)
DP	dorsal plate of epigynum (♀)
DPP	sclerotized posterior face of dorsal plate (♀)
DPPH	dorsal plate, posterior face height (♀, #)
DPPW	dorsal plate, posterior face width (♀, #)
DSA	distal suprategular apophysis (♂)
E	embolus (♂)
EF	epigastric furrow (♀)
EL	length of epigynum from anterior margin of copulatory duct capsule to posterior margin of dorsal plate, dorsal view (♀, #)
EM	embolic membrane (♂)
ETP	ectal tibial process (♂)
F	fundus or reservoir (♂)
FD	fertilization duct (♀)
G	groove in ventral plate (♀)
H	hook on tip of embolus (♂)
IML	metatarsus I length (#)
LC	lamella characteristica (♂)
LCL	length of lamella characteristica (♂, #)
MAP	major ampullate spigot(s)

mAP	minor ampullate spigot(s)
MSA	marginal suprategular apophysis (♂)
NU	nubbin
P	paracymbium (♂)
PI	piriform gland spigot(s)
PL	paracymbium length, ventral view (♂, #)
PLS	posterior lateral spinneret(s)
PME	posterior median eyes
PMS	posterior median spinneret(s)
PT	protegulum (♂)
PTL	palpal tibia length (♂, #)
PTA	palpal tibial apophysis (♂)
PTAL	palpal tibial apophysis length measured from concavity between dorsomesal apophysis and ectal tibial process (♂, #)
PTMS	number of macrosetae in ectal cluster on palpal tibia (♂, #)
PTW	palpal tibia width (♂, #)
PW	paracymbium width, ventral view (♂, #)
R	radix (♂)
S	spermatheca (♀)
SD	sperm duct (♂)
SF	suprategular foramen (♂)
SPT	suprategulum (♂)
ST	subtegulum (♂)
STM	suprategular membrane (♂)
T	tegulum (♂)
TmI	position of trichobothrium on metatarsus I (#)
TP	radical tail piece (♂)
TS	tegular sac (♂)
VP	ventral plate of epigynum (♀)
VPID	ventral plate invagination depth (♀, #)
VPIW	ventral plate invagination width, minimum (♀, #)

Figures 1–7.—Morphology of *Sisicottus* with limits of some quantitative characters. 1, 2, Schematic illustrations of *Sisicottus* palpus. 1, Mesal view with embolic division detached; 2, Ventral view with embolic division detached; 3, Embolic division, ectal view; 4, Tracheal system of female *Sisicottus montanus* from Mt. Mansfield, Vermont, ventral view; 5, Male palpal tibia, dorsal view; 6, Female carapace, dorsal view; 7, Female left leg I, retrolateral view.

the particular expression of characters found across all *Sisicottus* species.

CLADISTIC ANALYSIS

Outgroup selection.—The Linyphiidae represent the largest family of web-building spiders in terms of species diversity (Coddington & Levi 1991). However, phylogenetic relationships among linyphiids are poorly understood, especially among the largest subfamily, the Erigoninae (Hormiga 1993, 1994a, 1994b, in press). This state of almost complete phylogenetic ignorance complicated the problem of identifying close relatives for use as outgroups in the cladistic analysis of *Sisicottus*. *Sisicottus* was appended to a cladistic

analysis of erigonine phylogeny in Hormiga (in press). Outgroup taxa were selected based on the results of this reanalysis.

Hormiga's (in press) cladistic analysis of linyphiid spiders provides the most rigorous hypothesis so far of erigonine relationships. It incorporates 43 terminal taxa, including 31 erigonine genera, representing a wide cross section of the morphological diversity found among these spiders, scored for 73 characters. I reanalyzed Hormiga's data matrix after incorporating *Sisicottus*. All *Sisicottus* species are coded identically when incorporated into Hormiga's data matrix so a single exemplar was used to represent the genus. *Sisicottus* was coded as follows: 0001310101 1011110101 0?01001101   000?000101   0000000000 1000120111 0001100101 1?? (See Hormiga (in press) for character states and descriptions).

Nine exemplar taxa were taken from Hormiga's (in press) analysis to compose the outgroup: *Islandiana princeps* Brændegaard 1932, *Diplocentria bidentata* (Emerton 1882), *Typhochrestus digitatus* (O. Pickard-Cambridge 1872), *Erigone psychrophila* Thorell 1871, *Tmeticus tolli* (Kulczyński 1916), *Walckenaeria directa* (O. Pickard-Cambridge 1874), *Gonatium rubens* (Blackwall 1833), *Gongylidium rufipes* (Sundevall 1829), and *Oedothorax gibbosus* (Blackwall 1841). In addition, *Typhochrestus uintanus* (Chamberlin & Ivie 1939) was included to test Holm's (1967) suggestion that *Sisicottus uintanus* should be transferred to *Typhochrestus*. Character states for these taxa were evaluated using the following material: *I. princeps* [**GREENLAND:** Narssarssuaq, 61°10′N, 45°25′W, 5 July 1983, 1♂, (P. Nielsen, ZMUC); Western Greenland, Disko, Lyngmarksfjeld, 250 m, 13 July 1962, 1♀, (Å. Holm, ZMUC)], *D. bidentata* [**RUSSIA:** N.E. Siberia, Magadan area, Ola, 15–18 July 1992, 2♂16♀, (Y.M. Marusik, USNM). **UNITED STATES:** *New York:* Mount Whiteface, summit, 44°22′N, 73°55′W, 23 October 1936, 4♂10♀, (H. Dietrich, USNM); Mount Whiteface, 23 October 1936, 2♂2♀, (H. Deitrich, USNM). *Utah:* Smith and Morehouse Canyon, 40°47′N, 111°6′W, 7 October 1932, 3♂3♀, (W. Ivie, USNM).], *T. digitatus* [**ENG-LAND:** *Whiteford Burrows:* 1 September 1965, 3♂6♀ (J.A.L. Cook, AMNH); 26 September 1966, 3♂1♀ (J.A.L. Cook, AMNH).], *T. uintanus* [**UNITED STATES:** *Utah:* Fish

Lake, 38°33′N, 111°43′W, 4 September 1929, 4♂4♀ (Chamberlin & Gertsch, AMNH); Mirror Lake, Uintah Mountains, 40°43′N, 111°53′W, 28 July 1936, 3♂1♀ (Ivie, AMNH)], *E. psychrophila* [**UNITED STATES:** *Alaska:* Point Barrow, 71°22′N, 156°30′W, 23 June 1963, 5♂3♀ (R.F. Ashley, AMNH)], *T. tolli* [RUSSIA: NE Siberia, Lankovava River (Ola River basin), 65°45′N, 152°N, 13–19 August 1992, 6♂17♀ (Y.M. Marusik, USNM)], *W. directa* [**CANADA:** *British Colombia:* Terrace, 54°31′N, 128°32′W, March 1933, 3♂1♀ (Hippisley, AMNH)], *Gonatium rubens* [**ENGLAND:** *Surrey:* Yorkshire, 2♂3♀ (Murphy, AMNH)], *Gongylidium rufipes* [**ENGLAND:** *Oxford:* Bampton and/or The Weald, 6 July 1965, 1♂1♀ (J.A.L. Cook, AMNH)], and *O. gibosus* [**ENGLAND:** *Fife:* Tentsmuir Dune, 20 June 1966, 4♂14♀ (J.A.L. Cook, AMNH)]. Further analysis was conducted using *Hylyphantes graminicola* (Sundevall 1829) [**ENGLAND:** Surrey, 1♂2♀ (Murphy, AMNH)].

Characters.—The data matrix used to investigate relationships among *Sisicottus* species contained 41 phylogenetically informative characters. Eighteen concern the male palpus, 16 concern female genitalia, and seven concern somatic morphology. Eighteen characters (1, 6–10, 12, 13, 18, 28, 33, and 35–41) were taken or modified from Hormiga (in press). These are all of the characters in Hormiga's analysis that are phylogenetically informative with respect to relationships among the outgroup taxa and *Sisicottus*. All seven multistate characters (3, 8, 19, 21, 30, 31, and 38) were treated as unordered. Characters with ambiguous optimization were resolved to favor secondary loss over convergence (Farris or ACCTRAN optimization) unless otherwise stated. An expanded treatment of each character used in the analysis follows.

Male palpus: (1). Embolus length: 0 = short; 1 = long (Fig. 3, E). (2). Terminal embolic hook: 0 = absent; 1 = present (Figs. 3, 8, H). All species of *Sisicottus* have a hook on the terminal part of the embolus that curves back over the opening of the sperm duct. (3). Distal suprategular apophysis sclerotization: 0 = membranous; 1 = light; 2 = heavy. The distal suprategular apophysis is an extension of the suprategulum beyond the suprategular foramen, the aperture through which the sperm duct leaves the tegular divi-

sion (Hormiga in press). The distal suprategular apophysis of *Sisicottus montigenus* is generally transparent throughout its length. The distal suprategular apophysis of some other *Sisicottus* species is black and completely opaque. The intermediate state is usually orange in color and opaque to slightly translucent. (4). Distal suprategular apophysis length: 0 = short (Fig. 61, DSA); 1 = long (Fig. 19, DSA). The short distal suprategular apophysis never extends more than about half way down the unexpanded palpal bulb. The long distal suprategular apophysis extends to about the ventral midline of the unexpanded palpal bulb. (5). Suprategular embolic membrane: 0 = absent; 1 = present (Figs. 2, 42, STM). This membrane arises from the distal suprategular apophysis. In *Sisicottus*, this membrane projects anteriorly and is closely associated with the embolic membrane and the tip of the embolus. (6). Marginal suprategular apophysis: 0 = absent; 1 = present (Figs. 2, 42, MSA). The marginal suprategular apophysis is a tooth-like process on the distal part of the suprategulum and is located near the suprategular foramen (Hormiga in press). The marginal suprategular apophysis of *Sisicottus* is straight and quite prominent. (7). Radical tailpiece: 0 = present; 1 = absent. (8). Shape of radical tailpiece: 0 = straight; 1 = spiraled; 2 = curved ectally; 3 = anteriorly directed. The radix is the sclerite of the linyphiid palpus through which the sperm duct passes between the column and the embolus. In addition, the radix may have a process known as the tailpiece that is highly variable in form across taxa. Homology between the araneid radix and the linyphiid radix has been seriously questioned on several occasions (Hormiga 1993, 1994a). Recent phylogenetic analyses of araneoid relationships have concluded that araneids and linyphiids are somewhat distantly related and the presence of a radix can only be optimized as evolving independently in araneids and linyphiids (Hormiga et al. 1995; Scharff & Coddington 1997; Griswold et al. 1998). Close relatives of linyphiids include pimoids, theridiids, theridiosomatids, and tetragnathids, none of which have a sclerite that can be convincingly homologized with the linyphiid radix (Coddington 1990; Hormiga 1994b; Hormiga et al. 1995). The status of the linyphiid radix as a synapomorphy for the Linyphiidae seems well

supported by the data available (Hormiga in press). (9). Lamella characteristica: 0 = absent; 1 = present (Fig. 59, LC). The lamella characteristica arises from the basal part of the radix and does not conduct the sperm duct (Hormiga 1994a). Some erigonines have both a radical tailpiece and a lamella characteristica (e.g., *Gonatium rubens*, fig. 10f, Hormiga in press). (10). Anterior radical process (process of radical part (rpp) *sensu* Merrett 1963): 0 = absent; 1 = present. The anterior radical process arises adjacent to the embolus and projects distally (Hormiga in press). (11). Shape of anterior radical process: 0 = short; 1 = long, spiral (Figs. 111–113, ARP). A long, spiraled anterior radical process is diagnostic for *Typhochrestus*. (12). Protegular papillae: 0 = absent; 1 = present. Protegular papillae are small and scale like in *Sisicottus* (Fig. 46); they are much more conspicuous in some other erigonines. (13). Tegular sac: 0 = absent; 1= present (Fig. 2, TS). The tegular sac is a membranous process arising from the tegulum adjacent to the protegulum (Hormiga in press). (14). Paracymbium in ventral view: 0 = restricted to ectal side of palpus; 1 = a broad, flat plate that extends to the mesal side of the palpus (Fig. 2, P). (15). Cymbial excavation: 0 = small; 1 = conspicuous (Fig. 17, CE). All erigoines examined have a glabrous region on the mesal side of the cymbium near its junction with the palpal tibia. In *Sisicottus* and some other taxa, this region is quite conspicuous. In other taxa, this region is more or less restricted to the cymbial margin and often obscured by the palpal tibia. (16). Length of palpal tibial apophysis: 0 = short, hardly extending away from cymbium (Fig. 20, PTA); 1 = long, extending upward or anteriorly over cymbium (Fig. 94, PTA). (17). Ectal tibial process: 0 = strong (Fig. 94, ETP); 1 = weak or absent (Fig. 41). Many erigonines have a prominent, often ectally curving palpal tibial apophysis originating from the dorsomesal side of the tibia. The ectal tibial process is a smaller structure located on the dorsoectal side of the tibia. (18). Male pedipalpal patella ventral apophysis: 0 = absent; 1 = present.

Female genitalia: (19). Ventral plate: 0 = posterior margin overhangs epigastric furrow (fig. 156, Millidge 1984b); 1 = slightly invaginated (Fig. 43, VP); 2 = ventral plate deeply invaginated (Fig. 96, VP). (20). Me-

dian part of posterior margin of ventral plate in ventral view: 0 = distinctly convex (Fig. 110, VP); 1 = nearly flat to concave (Fig. 22, VP). (21). Posterior face of dorsal plate: 0 = subrectangular (Fig. 23, DPP); 1 = triangular with ventral apex (Fig. 63, DPP); 2 = triangular with dorsal apex; 3 = trapezoidal (Fig. 107, DPP). (22). Sides of posterior face of dorsal plate: 0 = nearly straight to convex (Fig. 23, DPP); 1 = distinctly concave (Fig. 107, DPP). (23). Ventral margin of posterior face of dorsal plate: 0 = distinctly concave (fig. 149, Millidge 1984b); 1 = nearly straight to convex (Figs. 23, 64, DPP). (24). Dorsal fold of dorsal plate: 0 = membranous (Fig. 24, DF); 1 = sclerotized (Fig. 71, DF). In dorsal view, a fold on the posterior margin of the dorsal plate forms a surface that may be membranous or sclerotized. (25). Copulatory openings: 0 = small; 1 = large and conspicuous (Fig. 110, CO). (26). Copulatory duct origin: 0 = ectal (Fig. 24, CD); 1 = mesal (fig. 603, Wiehle 1960). Copulatory ducts may originate from either the ectal or mesal side of the spermathecae. (27). Copulatory duct path: 0 = without distinct anterior projection (fig. 160, Millidge 1984b); 1 = with distinct anterior projection (Fig. 24, CD). (28). Copulatory duct encapsulation (Millidge 1984a): 0 = absent; 1 = present (Fig. 65, CDC). (29). Copulatory duct capsule: 0 = partial (fig. 21f, Hormiga in press); 1 = complete (Fig. 65). The copulatory duct capsule arises from the spermathecae and partially covers the copulatory ducts. In some cases, the capsules from each spermatheca meet in the center and may fuse together. This is a complete capsule. When not joined centrally, the capsule is partial. (30). Lateral lobes at anterior margin of complete capsule: 0 = concave (Wiehle 1960, fig. 603); 1 = straight (Fig. 38, CDC); 2 = convex (Fig. 65, CDC). In dorsal view, the epigynal capsule of *Sisicottus* species is roughly m-shaped with the two arches of the ''m'' oriented anteriorly. The lateral lobes at the anterior margin of the capsule are analogous to the humps on either side of the top of the ''m.'' In all *Sisicottus* species, this region is straight or with a pair of convex lobes. (31). Lateral margin of complete capsule: 0 = simple curve to sinuous (Fig. 65, CDC); 1 = strongly bowed (Fig. 98, CDC). In some species, the legs of the ''m'' on the right and left side form strongly bowed convex lateral mar-

gins. All species with this character state have the left and right feet of the ''m'' oriented mesally toward each other. (32). Orientation of posterior part of complete capsule: 0 = posterior (Fig. 65, CDC); 1= mesal (Fig. 78, CDC). The left and right feet of the ''m'' may be oriented mesally toward each other even if the capsule is not strongly bowed. (33). Fertilization duct orientation on exit from spermathecae: 0 = posterior (Millidge 1984b, fig. 160); 1 = mesal (Fig. 33, FD). (34). Fertilization duct shape: 0 = straight to sinuous (Fig. 24, FD); 1 = spiral (Fig. 98, FD).

Somatic morphology: (35). Male cephalic region: 0 = not raised; 1 = raised. (36). Male post-PME lobe: 0 = absent; 1 = present. (37). Male cephalic cuticular pores: 0 = absent; 1 = present. (38). Cheliceral stridulatory striae: 0 = ridged; 1 = scaly; 2 = imbricated (Fig. 10). (39). Dorsal spur on male chelicera: 0 = absent; 1 = present. (40). Dorsal macrosetae on tibia III: 0 = two; 1 = one. (41). Trichobothrium on metatarsus IV: 0 = absent; 1 = present. All characters of the somatic morphology considered in this analysis are constant within *Sisicottus*. See Hormiga (in press) for further discussion of these characters.

Analysis.—I used Hennig86 version 1.5 (Farris 1988), PAUP version 3.1.1 (Swofford 1993), and NONA version 1.6 (Goloboff 1993a) to analyze Hormiga's (in press) data matrix with *Sisicottus* appended (44 taxa, 73 characters). I then used these same programs and search strategies to analyze the data matrix in Table 5 for the most parsimonious phylogenetic hypothesis of *Sisicottus* species. Further analysis of *Sisicottus* species relationships was conducted using Pee-Wee version 2.6 (Goloboff 1993b) to calculate the fittest tree (Goloboff 1993c) and PHAST version 1.1 (Goloboff 1995) to calculate the Bremer support index (Bremer 1988).

In Hennig86, I used the ''mh∗,bb∗'' search strategy. In PAUP, I ran a heuristic search with 100 replicates of random taxon addition subjected to tree bisection-reconnection branch swapping. In NONA, I ran a search with the ''mult∗'' random taxon addition algorithm for 100 replicates followed by the ''max∗'' branch-swapping algorithm. This strategy was repeated under both the ''amb='' (modified rule 3) and ''amb-'' (rule 1) settings. Hennig86 and PAUP use only rule 3. Under rule 1, branches are collapsed if the minimum pos-

sible branch length is zero, i.e., if all characters with potential support for a node can be placed on other branches. Under rule 3, branches are collapsed only if the maximum possible branch length is zero, i.e., if there is no character that can be optimized to support a node. Under the "amb=" setting, nodes are also collapsed if the ancestral and descendant state sets are identical. This version of rule 3 is slightly different from that implemented in Hennig86 and PAUP (see also Coddington & Scharff 1994).

Successive character weighting (Farris 1969; Carpenter 1988) by the maximum value of the rescaled consistency index was performed in PAUP with the base weight set to 1000. Trees found by Hennig86, PAUP and NONA (under the "amb=" setting) were imported into PAUP. NONA trees were saved using the ksv∗ command. PAUP will arbitrarily resolve polytomies in trees saved using NONA's sv command. The solution set from all three programs (Hennig86, PAUP, and NONA) was combined. Duplicate trees were eliminated. The remaining unique trees were then filtered to exclude polytomous trees when more highly resolved compatible trees were found (Coddington & Scharff 1996). This set of trees was reweighted and the data reanalyzed in PAUP.

For the analysis of *Sisicottus* species, I calculated the fittest tree in Pee-Wee using the "mult∗100" command followed by the "max∗" algorithm under the "amb=" setting. I used the entire range of values for the concave function allowed by Pee-Wee ("conc1" through "conc6"). This setting determines the shape of the concave function of homoplasy used to calculate fit. Lower values of the concave function deviate more extremely from the linear function of homoplasy that is equivalent to standard parsimony (Goloboff 1993b, 1993c). I calculated the Bremer support index (Bremer 1988) using PHAST with the following commands: "h∗", "amb-", "sub5", "find∗", "bs". I used MacClade version 3.0 (Maddison & Maddison 1992) to analyze character optimization.

RESULTS

Phylogenetic context.—The cladistic analysis of Hormiga's (in press) data matrix plus *Sisicottus* yielded multiple most parsimonious rule 3 trees. Hennig86 found 12 trees while PAUP and NONA each found 18 trees. NONA also found two rule 1 trees. Both of the rule 1 trees are less resolved than any of the trees found under rule 3. After the exclusion of six uninformative characters, all 20 trees had a length of 225 steps, a consistency index of 0.378 and a retention index of 0.680. One of the rule 3 trees is identical to Hormiga's (in press) preferred topology with *Sisicottus* placed sister to *Oedothorax*. A strict consensus of all rule 3 trees, all rule 1 trees, or all trees from both sets is identical. The consensus tree places *Sisicottus* in a polytomy with *Oedothorax*, *Hylyphantes* Simon 1884, and *Gongylidium* Menge 1868. Among the alternative most parsimonious trees, *Sisicottus* is either placed sister to *Oedothorax* or to a clade consisiting of *Oedothorax*, *Hylyphantes* and *Gongylidium*. In the consensus tree, the four taxon clade containing *Sisicottus* is part of another polytomy consisting of *Walckenaeria*, *Gonatium*, and a resolved clade made up of *Grammonota* and six other genera. *Tmeticus* and *Erigone* have a pectinate arrangement out from this polytomy. Sister to all other "distal erigonines" is a clade composed basally of *Islandiana* and *Diplocentria*. Five other genera are also included in this clade including *Typhochrestus*. There are two additional areas of conflict: relationships among *Drepanotylus*, *Sciastes*, and the "distal erigoinines" clade, and also relationships among the linyphiines, the micronetines, and all other linyphiids. Both of these areas of conflict were present in Hormiga's (in press) original analysis.

Among the rule 3 trees found by Hennig86, PAUP and NONA, only six were both unique and more resolved than otherwise compatible trees. Successive character weighting of these six trees results stabilizes on a different set of six trees. This result is stable to subsequent iterations of reweighting. The strict consensus of the six reweighted trees is consistent with Hormiga's (in press) preferred topology. Relationships among the "distal erigoinies" are identical and fully resolved in all six trees. The "distal erigonines" are topologically identical to Hormiga's (in press) preferred tree with *Sisicottus* placed sister to *Oedothorax*.

Phylogeny of *Sisicottus*.—The analysis of the data matrix in Table 5 yielded three most parsimonious trees. Results were identical under both rule 1 and rule 3 analyses. Each tree

had a length of 101 steps, a consistency index of 0.485, and a retention index of 0.681. Relationships among *Sisicottus* species were identical in all three trees. In the outgroup, the three possible resolutions of *Gonatium*, *Gongylidium*, and the *Oedothorax* plus *Sisicottus* clade make up the three most parsimonious trees. Otherwise, outgroup relationships are identical to the topology in Hormiga (in press). All most parsimonious trees support the monophyly of *Typhochrestus*.

Successive character weighting of the three most parsimonious trees stabilizes on a single tree (Fig. 115). This tree is identical to one of the most parsimonious tree under equal weights. Outgroup relationships are identical to those preferred by Hormiga (in press). Pee-Wee's implied weights algorithm found the topology in Fig. 115 when the concavity function was set between 4 and 6. For lower values of the concavity function, outgroup relationships were rearranged. These topologies found *Gongylidium* to be the sister taxon to *Sisicottus* and added one or two extra steps under equal weights. In all Pee-Wee trees, relationships among *Sisicottus* species were identical.

Although Hormiga's (in press) hypothesis of erigonine relationships is a great step forward in linyphiid systematics, several nodes are somewhat weakly supported by the available data. This is evidenced by the sensitivity of the topology to taxon sampling. According to the modified version of Hormiga's analysis, *Hylyphantes* is sister to the *Gongylidium-Oedothorax-Sisicottus* clade. However, inclusion of *Hylyphantes graminicola* (Sundevall 1829) in the analysis of *Sisicottus* resulted in six trees, none of which are consistent with Hormiga's (in press) topology. Nevertheless, relationships among *Sisicottus* species were the same in all trees and identical to those shown in Fig. 115. All trees support the monophyly of *Typhochrestus*. *Hylyphantes* can be added to Table 5 as follows: 0010001–10 –101110121 001000110– –010000111 1.

Optimization and support.—Six unambiguous synapomorphies support the monophyly of *Sisicottus* (node 8): a terminal embolic hook (character 2), a suprategular membrane projecting apically from the distal suprategular apophysis (character 5), copulatory ducts that originate on the ectal side of the spermathecae (character 26), imbricated stridulatory striae (character 38), the presence of two dorsal macrosetae on tibia III (character 40), and the absence of a trichobothrium on metatarsus IV (character 41). The loss of the ectal tibial process (character 17) and the absence of a dorsal spur on the male chelicera (character 39) are also optimized to support this node under Farris optimization. The Bremer support index (Bremer 1988) gives node 8 five steps of support making it the best supported node in the analysis. Additional character optimizations and Bremer support values are illustrated in Fig. 115.

Exceptions to Farris optimization were made for characters 12 (protegular papillae), 30 (shape of lateral lobes at anterior margin of complete capsule), and 37 (male cephalic cuticular pores). Character 12 must be optimized either at node 9 or 10. Farris optimization would place a change in character 12 at node 9. However, since *Gongylidium rufipes* lacks a protegulum, it was coded as not applicable for character 12. Optimizing character 12 at node 9 implies a hypothesis of synapomorphy where data are available for only one of the sister clades. Only at node 10 is there evidence of synapomorphy. The case with character 30 is very similar to that of character 12 with a step required at either node 12 or 13 for a character that is not applicable for *Tmeticus tolli*. Character 37 was optimized as an autapomorphy of *Typhochrestus digitatus* rather than a synapomorphy of clade 15. The character state of *T. uintanus* was not determined for character 37. This optimization maintains a conservative estimate of the character support for a monophyletic *Typhochrestus* recircumscribed to include *T. uintanus*. The monophyly of *Typhochrestus* (node 15) is unambiguously supported by 5 characters.

Character 28 (copulatory duct encapsulation) equivocally satisfies Farris optimization criteria under both possible resolutions. Hormiga's (in press) analysis indicates that the primitive condition for node 18 in Fig. 115 is the presence of copulatory duct encapsulation. Character 28 has been optimized to reflect this hypothesis.

The presence of a paracymbium that is wide in ventral view (character 14) is a rare character state among erigonines that is useful in diagnosing *Sisicottus*. However, a similar character state is exhibited by *Gongylidium*

rufipes. While optimization of this character is ambiguous, Farris optimization suggests that the wide paracymbium character state had a common origin in *Gongylidium* and *Sisicottus* (node 10) and was subsequently lost in *Oedothorax*.

Independence.—Since characters come from a small number of character systems and characters within character systems might be linked, non-independence of characters was a concern. However, no two characters had identical distributions across taxa. Since linked characters would be expected to have identical or nearly identical distributions, character non-independence is considered a negligible factor in this analysis.

DISCUSSION

Conflict in erigonine topologies.—The object of appending *Sisicottus* to Hormiga's (in press) analysis was to discover a suitable set of outgroup taxa with which to root the phylogeny of *Sisicottus* species. Despite some instability within the outgroup, relationships among *Sisicottus* species appear to be robustly supported under a wide variety of analytical permutations. My analysis of *Sisicottus* species and their outgroups is not intended to be a test of Hormiga's (in press) phylogenetic hypothesis of erigonine relationships. Although recovery of Hormiga's topology in the outgroup of the *Sisicottus* phylogeny was found to be sensitive to taxon sampling, Hormiga's (in press) topology remains for now the most rigorous hypothesis of erigonine relationships. Nevertheless, it seems clear that systematists should work toward a more robust phylogeny of erigonine relationships by discovering new characters and adding more taxa.

Monophyletic species.—The phylogenetic species concept (Donoghue 1985) has aroused considerable debate (Nelson 1989; de Queiroz & Donoghue 1990; Nixon & Wheeler 1990; Wheeler & Nixon 1990). This concept proposes that the notion of monophyly is applicable to all taxa regardless of rank and that species should therefore be circumscribed on the basis of shared derived similarity. However, cladistic methods are not applicable to resolving tokogenetic relationships. Factors such as polymorphism and unexpressed alleles make this problem intractable. This limitation was discussed by Hennig (1966) and has been leveled as a criticism against the phylogenetic

species concept (Nixon & Wheeler 1990; Wheeler & Nixon 1990). Nevertheless, once a novel character state becomes fixed throughout a population, the resulting autapomorphy constitutes evidence of monophyly in that a character state change occurred in a single common ancestor and subsequently came to exist in all its descendants (Nelson 1989; de Queiroz & Donoghue 1990).

All *Sisicottus* species for which males are known can be diagnosed based on the distal suprategular apophysis alone. The male palpal tibia and the posterior face of the dorsal plate in females are almost as useful taxonomically. Although these characters can be optimized on the tree as autapomorphies, not all *Sisicottus* species have unambiguous character support for monophyly. In a character as rapidly evolving as the distal suprategular apophysis, a unique character state can be assigned to each applicable species. Given the phylogeny of *Sisicottus* in Fig. 115, such a character can be equivocally optimized with between two and all of the states as autapomorphies (no less than one for each sister species pair). Several *Sisicottus* species are supported as monophyletic by unambiguous autapomorphies. These are *S. montigenus* (membranous distal suprategular apophysis, character 3), *S. montanus* (groove in ventral plate, Fig. 64), *S. cynthiae* (large ectal tibial process, Fig. 75; level of ventral margin of dorsal plate, Fig. 77), and *S. aenigmaticus* (posterior face of dorsal plate trapezoidal, character 21; wide ventral plate invagination, Fig. 106; small, widely-spaced spermathecae with narrow margin and narrow copulatory ducts, Fig. 108). Like all *Sisicottus* species for which males are known, *S. quoylei*, *S. panopeus*, *S. crossoclavis*, and *S. orites* have unique distal suprategular apophyses which might represent autapomorphic conditions. However, if each *Sisicottus* species is assigned a unique character state for the form of its distal suprategular apophysis, many character optimizations are possible including the possibility that none of these four species are defined by autapomorphy.

Sisicottus nesides is a special problem, in part because of our ignorance of males of its sister species, *S. aenigmaticus*. Females of *S. nesides* exhibit no autapomorphies. Females of *S. nesides* are almost identical to females *S. orites*. Females of *Sisicottus nesides* and *S. orites* are distinguished only on the basis of

the synapomorphy shared by *S. nesides* and *S. aenigmaticus* (posterior face of dorsal plate with concave sides, character 22). (Although certain quantitative characters are taxonomically useful for separating females of *S. orites* from those of *S. nesides* and *S. aenigmaticus* (Fig. 100), these characters exhibit considerable overlap and cannot be considered as discrete cladistic characters.) *Sisicottus nesides* and *S. aenigmaticus* differ in character states that are unambiguous autapomorphies of *S. aenigmaticus*. Thus, a hypothesis of *S. nesides* as a paraphyletic species cannot be falsified based on females alone. The only character that distinguishes males of *S. nesides* from *S. orites* without overlap is the form of the distal suprategular apophysis. If males of *S. aenigmaticus* are found to have a distal suprategular apophysis like that of *S. orites*, and the discovery of males of *S. aenigmaticus* does not result in a new phylogeny of *Sisicottus*, then *S. nesides* will have an unambiguous autapomorphy supporting its monophyly. If males of *S. aenigmaticus* are found to have a unique distal suprategular apophysis, then *S. nesides* will have ambiguous support for monophyly, just as *S. quoylei*, *S. panopeus*, *S. crossoclavis*, and *S. orites* do. If males of *S. aenigmaticus* are found to share a distal suprategular apophysis form with *S. nesides*, then *S. nesides* will be diagnosed based on plesiomorphic characters and the hypothesis that *S. nesides* is paraphyletic will remain unfalsified.

TAXONOMY

Sisicottus Bishop & Crosby 1938

Sisicottus Bishop & Crosby 1938: 57–61. Type species by original designation *Tmeticus montanus* Emerton 1882. Chamberlin & Ivie 1939: 65–66. Roewer 1942: 650. Lowrie & Gertsch 1955: 6. Bonnet 1958: 4065–4066. Holm 1960: 124; 1967: 61. Bragg & Leech 1972: 69. Kaston 1981: 208-209. Brignoli 1983: 356. West et al. 1984: 87. Koponen 1987: 281–283, 285. Crawford 1988: 15. Crawford & Edwards 1988: 437. Jennings et al. 1988: 61, 63. Platnick 1989: 282; 1993: 351; 1997: 427. Aitchison-Benell & Dondale 1990: 224. Dondale et al. 1997: 89.

Etymology.—Bishop & Crosby (1938) did not explain the etymology of *Sisicottus* or any of the other new taxonomic names established therein. It is therefore left to latter-day scholars of nomenclature and classical languages to investigate the meaning of these names. According to H.D. Cameron, the obscure Greek masculine noun *sisys*, known from ancient lexicons and commentaries, is translated as, "any coarse or cheap garment." This word appears to be the root of three generic names which were erected in Bishop & Crosby 1938. The genus *Sisis* Bishop & Crosby 1938, though not a literal transliteration, is a Latinized derivation of *sisys*. Both *Sisicus* Bishop & Crosby 1938 and *Sisicottus* embellish the same root. Bishop & Crosby do not indicate that the nomenclatural similarity shared by these three genera was meant to imply a hypothesis of phylogenetic affinity. By the rules of zoological nomenclature, *Sisicottus* should be considered an arbitrary combination of letters with has the form of a masculine Latin word (Art. 11b.iii, International Commission on Zoological Nomenclature 1985).

Diagnosis.—*Sisicottus* males differ from other erigonine genera with a long, single turn spiral embolus by the presence of a paracymbium in the form of a wide plate in ventral view (Fig. 60, character 14), a hook recurved over the aperture at the tip of the embolus (Fig. 8, character 2), an anteriorly projecting suprategular membrane (Fig. 42, character 6), a straight, tapered marginal suprategular apophysis (Figs. 95, character 6), a conspicuous distal suprategular apophysis that lies across part of the tegulum in ectal view (Figs. 61, 93, character 4), a glabrous excavation on the mesal side of the cymbium near the palpal tibia (Fig. 59, character 15), a lamella characteristica in the shape of a comma (Fig. 59, character 9), the absence of a radical tailpiece (character 7), a palpal tibial apophysis originating from the mesal side (Fig. 62), and by the presence of a protegulum with scale like papillae and a tegular sac arising from the tegulum (Figs. 46, 60, characters 12, 13). Females can be distinguished from other erigonine genera with complete encapsulation of the copulatory ducts (character 28) by the small copulatory duct openings (Fig. 65, character 25), the origin of the copulatory ducts from the ectal side of the spermathecae (Fig. 65, character 26), and the path of the copulatory ducts which initially project anteriorly from the spermathecae then turn to pass between the spermathecae and terminate at copulatory openings near the epigastric furrow (Fig. 65, character 27).

Description.—Small to medium-sized eri-
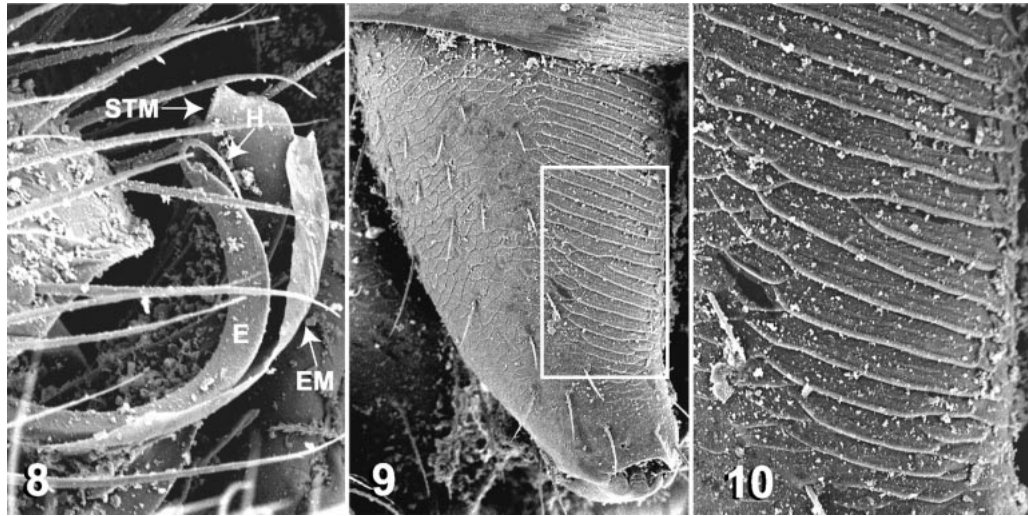
Figures 8–10.—Scanning electron micrographs of *Sisicottus panopeus* from Lake Louise, Alberta. 8, Ectal view of right palpus showing embolic hook; 9, 10, Left chelicera of male.

gonine spiders (carapace length = 0.67–1.24 mm). Carapace usually orange with dusky highlights, darker in ocular region; glabrous except for several rigid setae in line between thoracic groove (itself little more than a narrow line of darker pigment) and ocular area (which is clothed in fine setae) (Fig. 6). Sternum and labium darker than carapace; legs and palpi often slightly lighter. Chelicerae of both sexes with imbricated stridulatory files (Figs. 9, 10; Hormiga in press); small plectra visible near base of palpal femora. Fang furrow armed with usually five large anterior teeth and 4–5 minute posterior teeth. Palpal tibiae of both sexes with one prolateral and two retrolateral trichobothria. Tibiae of legs I-III with two dorsal macrosetae; fourth tibia with only proximal macroseta. Metatarsal trichobothria present on legs I-III; absent from leg IV. TmI usually ranges between 0.44–0.65 (range of mean plus or minus one standard deviation values; Fig. 7; Tables 2, 3); variation appears constant across sexes, species, and individuals. Main tarsal claws with several teeth; auxiliary claw with single preterminal tooth (Fig. 109).

Abdomen usually uniform dark to light grey and clothed in fine setae. Anterior lateral spinnerets with 9–13 piriform spigots, a single major ampullate spigot, and a nubbin in both sexes (Figs. 13, 14); posterior lateral spinnerets with 4–7 aciniform spigots, two aggregate

spigots, and one flagelliform spigot plus two cylindrical spigots in females only (Figs. 15, 16); posterior median spinnerets with one minor ampullate spigot, two aciniform spigots, and, in females, one cylindrical spigot (Figs. 11, 12). Tracheae desmitracheate (Millidge 1984a); median trunks with many tracheoles that pass through the pedicel; lateral trunks unbranched and confined to abdomen; tracheoles of uniform diameter and without taenidia (*sensu* Blest 1976); spiracle a single slit-like opening, somewhat rounded laterally (Fig. 4).

Males: Embolus sclerotized and rigid, describing single spiral turn; arises from radix on mesal side of bulb, passes under alveolus, and associates distally with an embolic membrane and a suprategular membrane (Fig. 42), and terminates in a hook (Figs. 3, 8). Radix closely joined to lamella characteristica by membrane (Figs. 1, 3). Radical tailpiece absent. Distal suprategular apophysis ribbon-like, membranous to heavily sclerotized, lying across tegulum in ectal view (Fig. 61). Straight, tapered marginal suprategular apophysis varies little in shape, orientation, or relative length (Fig. 42). Paracymbium with three macrosetae (occasionally four) arising near cymbial margin (Fig. 61); formed into wide plate in ventral view with single macroseta (occasionally two) arising centrally (Fig. 60). Protegulum semitransparent to opaque with ectal apex; tegular sac arises from mesal
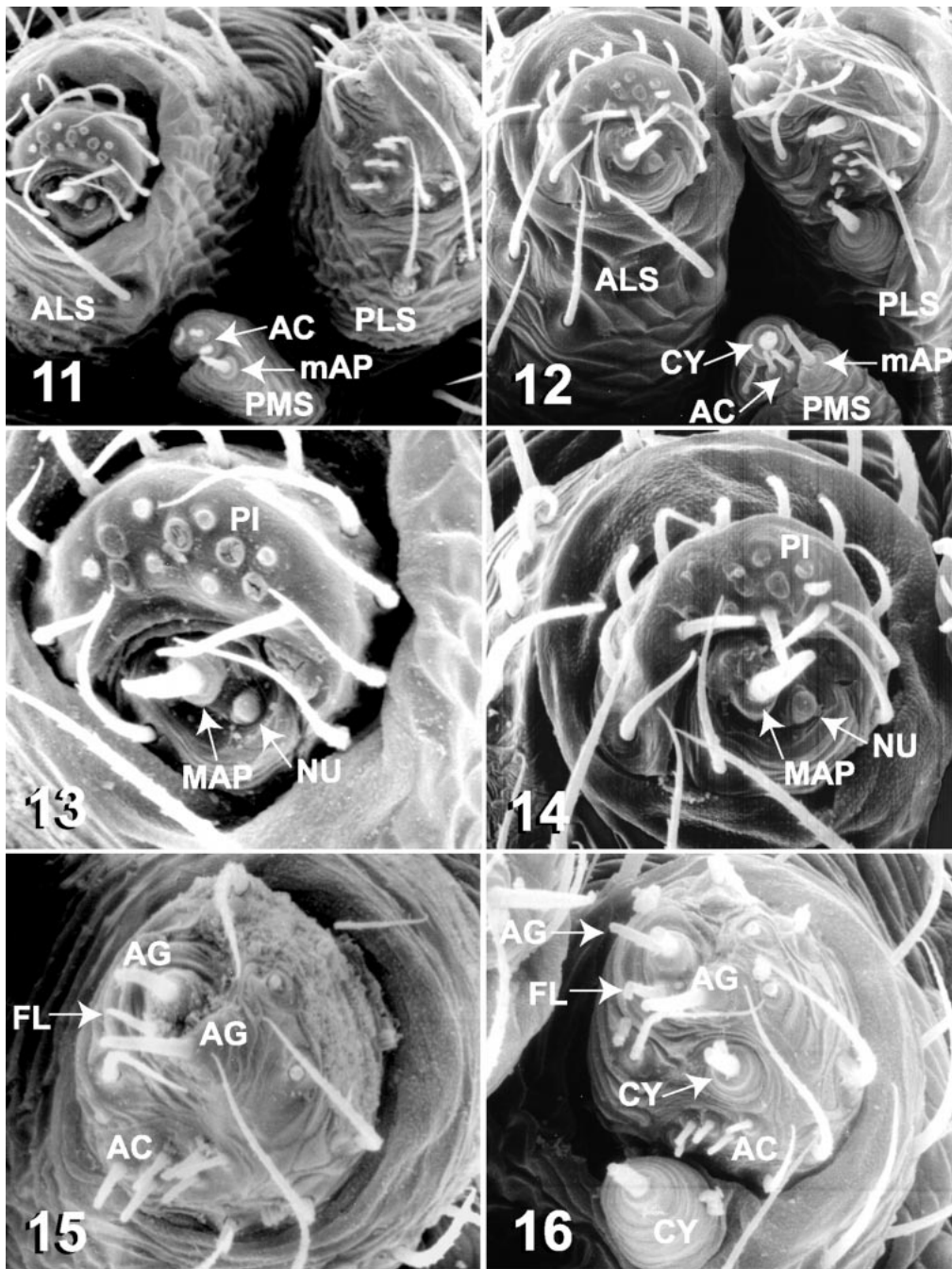
Figures 11–16.—Scanning electron micrographs showing spinneret spigot morphology, left side. 11, 13, 15, Male *Sisicottus nesides* from Primrose Camp, Alaska. 12, 14, Female *S. montanus* from Mt. Mainsfield, Vermont. 16, Female *S. crossoclavis* from Deemer Creek, Washington; 11, 12, Spinnerets; 13, 14, Anterior lateral spinnerets; 15, 16, Posterior lateral spinnerets.

side (Fig. 46); scale-like papillae cover much of protegulum. Glabrous area near base of cymbium on mesal side set apart by fine sclerotized ridge (Fig. 59). Palpal tibia with mesal apophysis that is often curved ectally (Fig. 62), although it is very short and not distinctly curved in some species (Fig. 20). Clusters of macrosetae occur on ectoventral quarter of palpal tibia (Fig. 5) and distal part of cymbium.

Females: Epigynum a ventral plate and dorsal plate. In ventral view, ventral plate often with median invagination at posterior margin revealing dorsal plate below (Figs. 28, 87). Dorsal plate folded posteriorly at right angle to ventral plate where it forms a surface (the DPP) that can be of diagnostic value at the species level. Single pair of spermathecae situated near posterior margin of epigynum (Fig. 65). Copulatory ducts usually thick proximally, narrow distally, and encapsulated; they arise from ectal half of spermathecae, travel mesally across spermathecae, run anteriorly, then double back to terminate as copulatory openings near posterior margin of epigynum between spermathecae (Fig. 65). Fertilization ducts lightly sclerotized, sinuous or looped, and arising from the mesal region of spermathecae (Figs. 65, 98). Fertilization ducts terminate at dorsal margin of epigynum near anterior extension of dorsal fold of dorsal plate.

Natural history.—Most of what is known about the natural history of these spiders comes from brief remarks in papers on spider ecology and distribution (Koponen 1987; Crawford 1988; Crawford & Edwards 1988; Jennings et al. 1988; Aitchison-Benell & Dondale 1990) and in the form of notes written by collectors on data labels. Data labels indicate that these spiders are usually associated with wet moss, leaf litter, or other ground microhabitats in boreal forests and bogs. Occa-

sionally, they are beaten off arboreal, woody, or herbaceous vegetation or swept from meadow vegetation. The data label for a series of *S. crossoclavis* new species from Washington reports finding one adult female in a web. The capture of two male *S. nesides* from British Columbia in a flight intercept trap suggests that adult male *Sisicottus* may disperse by ballooning. The extraction of a female *S. cynthiae* new species from the stomach of a newt offers a hint as to one role these spiders play in the trophic structure of their communities.

Distribution.—In North America: Canada, Alaska, eastern United States south to North Carolina and Tennessee, and western United States south to California, Arizona, and New Mexico. In Asia, currently known only from the Kuril Islands.

Composition.—Nine species: *Sisicottus montigenus* Bishop & Crosby 1938, **S. quoylei** new species, *S. montanus* (Emerton 1882), **S. panopeus** new species, **S. crossoclavis** new species, **S. cynthiae** new species, *S. orites* (Chamberlin 1919), *S. nesides* (Chamberlin 1921) and **S. aenigmaticus** new species.

Misplaced species.—Examination of the type specimens of *Sisicottus uintanus*, *S. cornuella*, *S. atypicus* Chamberlin & Ivie (1944) (all in AMNH), and *S. hibernus* (OSU) confirms that none of these species belong to *Sisicottus*. *Sisicottus uintanus* is formally transferred to *Typhochrestus* (NEW COMBINATION). See also taxonomic history section above.

Sisicottus uintanus Chamberlin & Ivie 1939: 65, figs. 31–34 [♂,♀] = *Typhochrestus uintanus*. NEW COMBINATION.

Sisicottus cornuella Chamberlin & Ivie 1939: 65–66, figs. 35–37 [♂] = *Walckenaeria cornuella*. Transfer by Millidge 1983.

Sisicottus atypicus Chamberlin & Ivie 1944: 76–77, figs. 139, 140 [♂] = *Souessoula parva* (Banks). Synonymy by Ivie 1967.

Sisicottus hibernus Barrows 1945:74, figs. 1, 2 [♂] = *Carorita hiberna*. Transfer by Zujko-Miller (1999).

KEY TO SPECIES OF THE GENUS *SISICOTTUS*

Males
(*note:* male of *S. aenigmaticus* is unknown)

1. Distal suprategular apophysis heavily sclerotized (Fig. 93, DSA). Western North America 2
   Distal suprategular apophysis membranous to lightly sclerotized (Fig. 61, DSA). Asia, eastern or western North America 5
2 (1). Terminus of distal suprategular apophysis widened with serrated margin (Fig. 67, DSA). Ectal tibial process absent (Fig. 68) . . . . ***crossoclavis*** new species

Terminus of distal suprategular apophysis flat to wavy or bifid with two pointed apices; not more than slightly widened distally. Ectal tibial process prominent (Fig. 94) 3

3 (2). Terminus of distal suprategular apophysis bifid with two pointed apices, the inner more pronounced than the outer (Figs. 84, 102, DSA) . . . . *nesides* (Chamberlin 1921)
Terminus of distal suprategular apophysis flat to wavy; never with pointed apices 4

4 (3). Terminus of distal suprategular apophysis with wavy margin (Figs. 73, 80, DSA). Palpal tibia with large ectal tibial process and short palpal tibial apophysis (palpal tibial apophysis length $<$ 0.09 mm; Fig. 75, ETP, PTA) . . . . ***cynthiae*** new species
Terminus of distal suprategular apophysis flat or with two rounded lobes (Fig. 92, DSA). Palpal tibia with short ectal tibial process and long palpal tibial apophysis (palpal tibial apophysis length $>$ 0.12 mm; Fig. 94, ETP, PTA) . . . . *orites* (Chamberlin 1919)

5 (1). Distal suprategular apophysis extends to ventral midline of palpal bulb (Fig. 19). Palpal tibial apophysis very short (palpal tibial apophysis length $<$ 0.04 mm; Fig. 20, PTA). Eastern North America 6
Distal suprategular apophysis extends about half way down palpal bulb (Fig. 61). Palpal tibial apophysis longer (palpal tibial apophysis length $>$ 0.04 mm; Fig. 62, PTA). Asia, eastern or western North America 7

6 (5). Distal suprategular apophysis membranous; inner margin strongly convex; terminal margin serrated (Figs. 19, 26). North Carolina and Tennessee . . . . *montigenus* Bishop & Crosby 1938
Distal suprategular apophysis moderately sclerotized; inner margin sinuous; terminus a sharp apex (Fig. 34). Northeastern United States, southeastern Canada . . . . ***quoylei*** new species

7 (5). Palpal tibial apophysis short (palpal tibial apophysis length $<$ 0.08 mm); ectal tibial process present (Fig. 62, ETP). Distal suprategular apophysis extends ventrally beyond level of suprategular membrane (Figs. 47, 61, DSA). Less than 6 macrosetae in cluster on ectal side of palpal tibia. Widespread in North America . . . . *montanus* (Emerton 1882)
Palpal tibial apophysis long (palpal tibial apophysis length $>$ 0.08 mm); ectal tibial process absent (Fig. 41). Distal suprategular apophysis does not extend ventrally beyond level of suprategular membrane (Figs. 40, 45, DSA). More than 7 macrosetae in cluster on ectal side of palpal tibia. Western North America and Asia . . . . ***panopeus*** new species

Females

1.   Ventral plate of epigynum with deep invagination (ventral plate invagination depth $<$ 0.04 mm; Fig. 96, VP) 2
Ventral plate of epigynum with invagination shallow or absent (ventral plate invagination depth $<$ 0.04 mm; Figs. 63, 76, VP) 6

2 (1). Posterior face of dorsal plate narrow (width of posterior face of dorsal plate $<$ 0.12 mm), subrectangular with convex lateral margins (Fig. 37, DPP). Dorsal fold of dorsal plate membranous. Lateral margin of epigynal capsule straight (Fig. 38, CDC). Carapace small (carapace length $<$ 0.80 mm). Eastern North America 3
Posterior face of dorsal plate wide (width of posterior face of dorsal plate $>$ 0.12 mm), triangular or trapezoidal with straight to concave lateral margins (Fig. 97, DPP). Dorsal fold of dorsal plate sclerotized, trapezoidal, widest posteriorly. Lateral margin of epigynal capsule strongly bowed (Fig. 98, CDC). Carapace large (carapace length $>$ 0.86 mm). Western North America 4

3 (2). Ventral plate invagination wide and very deep (ventral plate invagination width $>$ 0.06 mm; ventral plate invagination depth $>$ 0.09 mm; Fig. 22, VPIW, VPID) . . . .
. . . . *montigenus* Bishop & Crosby 1938
Ventral plate invagination narrow and only moderately deep (ventral plate invagination width $<$ 0.05 mm, ventral plate invagination depth $<$ 0.09 mm; Fig. 36) . . . . ***quoylei*** new species

4 (2). Ventral plate invagination wide (ventral plate invagination width ca. 0.06 mm). Posterior face of dorsal plate trapezoidal (Fig. 107, DPP) . . . . ***aenigmaticus*** new species
Ventral plate invagination narrow (ventral plate invagination width $<$ 0.05 mm). Posterior face of dorsal plate triangular (Figs. 97, 105, DPP) 5

5 (4). Posterior face of dorsal plate with lateral margins never more than slightly concave (Fig. 97,

DPP). Epignynum long (epignynum length = 0.152–0.209 mm). Copulatory duct capsule wide (copulatory duct capsule width = 0.143–0.238 mm) . . . . *orites* (Chamberlin 1919)

Posterior face of dorsal plate with concave lateral margins (Fig. 105, DPP). Epignynum short (epignynum length = 0.133–0.181 mm). Copulatory duct capsule narrow (copulatory duct capsule width = 0.100–0.176 mm) . . . . *nesides* (Chamberlin 1921)

6 (1). Dorsal fold of dorsal plate membranous (Fig. 65, DF) 7

Dorsal fold of dorsal plate sclerotized, trapezoidal, widest posteriorly (Fig. 71, DF) 8

7 (6). Ventral plate enfolded forming broad groove (Figs. 53, 54, G). Posterior face of dorsal plate triangular with sharply pointed ventral margin (Fig. 64, DPP). Eastern or western North America . . . . *montanus* (Emerton 1882)

Ventral plate without groove (Figs. 51, 52). Posterior face of dorsal plate subrectangular with flat ventral margin (Fig. 44, DPP). Western North America and Asia . . . . . **panopeus** new species

8 (6). Ventral margin of posterior face of dorsal plate dorsal to ventral extent of spermathecae (Fig. 77, DPP). Posterior margin of copulatory duct capsule oriented anteriorly (Fig. 78, CDC). Oregon . . . . **cynthiae** new species

Ventral margin of posterior face of dorsal plate about level with ventral extent of spermathecae (Fig. 70, DPP). Posterior margin of copulatory duct capsule oriented posteriorly (Fig. 71, CDC). Western North America . . . . **crossoclavis** new species

Sisicottus montigenus Bishop & Crosby 1938
Figs. 17–28, 31, 32

Sisicottus montigenus, in part: Bishop & Crosby 1938: 60–61, figs. 10–11 [♂,♀]. Roewer 1942: 650. Bonnet 1958: 4066. 3♂4♀ syntypes from UNITED STATES: North Carolina, Yancey County, Mt. Mitchell, 12 October 1923, in AMNH, examined.

Diagnosis.—Males of *S. montigenus* are distinguished from those of all other *Sisicottus* species except its sister species, *S. quoylei,* by the form of the palpal tibial apophysis, which is quite short with a flat distal margin and no ectal tibial process (Fig. 20, characters 16, 17). The form of the distal suprategular apophysis is unique among *Sisicottus,* being membranous and quite transparent, extending to near the ventral midline of the palpal bulb with variable amounts of serration along the margin, especially in the near terminus (Figs. 25–27, characters 3, 4). This characteristic is the most reliable way to distinguish this species from all other *Sisicottus* species including *S. quoylei.*

Females of *S. montigenus* have a ventral plate invagination that is almost always deeper than any other *Sisicottus* species (Fig. 22). They can be distinguished from other species with a deep ventral plate invagination, except *S. quoylei*, by the posterior face of the dorsal plate, which is subrectangular (Fig. 23, character 21) and the membranous dorsal fold of the dorsal plate (Fig. 24, character 24). The

ventral plate invagination is wider than any species except *S. aenigmaticus* (Table 3). *Sisicottus montigenus* can be distinguished from all species except *S. quoylei* by the form of the anterior margin of the capsule which is nearly flat rather then formed into two convex lateral lobes (Fig. 24, character 30). Depth and width of the ventral plate invagination reliably separate *S. montigenus* from its sister species, *S. quoylei* (Fig. 31).

Description.—Small (carapace length = 0.67–0.80 mm); coloration much darker than in other *Sisicottus* species. Distal suprategular apophysis of male palpus membranous, long, extends to near ventral midline of palpal bulb; with serrated outside and terminal margins (Figs. 25–27). Palpal tibia short; palpal tibial apophysis short with flat distal margin and no ectal tibial process (Fig. 20); sparse cluster of macrosetae (3–7) on ectal side of palpal tibia. Females with deep and wide invagination of ventral plate of epignynum (Figs. 22, 31). Posterior face of dorsal plate generally rectangular, usually slightly taller than wide with a flat or slightly convex ventral margin (Fig. 23). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule nearly flat; fertilization ducts sinuous (Fig. 24). See Tables 2–4.

Natural history.—*Sisicottus montigenus* has been collected exclusively in high elevation spruce and Fraser fir forests of the southern Appalachian mountains. Over the last decade, much of this habitat has been severely
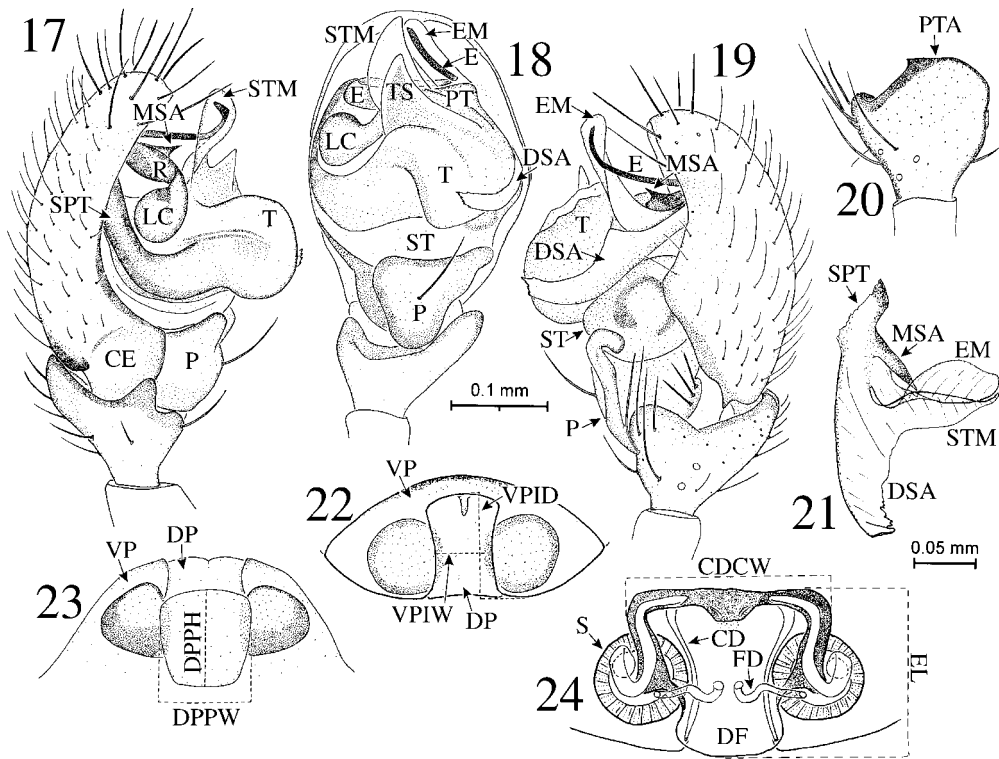
Figures 17–24.—*Sisicottus montigenus* with limits of some quantitative characters. 17–20, Palpus of male from Mt. Mitchell, North Carolina. 17, Mesal view; 18, Ventral view; 19, Ectal view; 20, Palpal tibia, dorsal view; 21, Suprategulum separated from palpus of male from Clingman's Dome, North Carolina, ectal view; 22, 23, Epigynum of female from Mt. Mitchell, North Carolina. 22, Ventral view; 23, Posterior view. 24, Cleared epigynum from Clingman's Dome, North Carolina, dorsal view. *Scales:* Figs. 21, 24 = 0.05 mm; other figures = 0.1 mm.

altered. The extensive damage to these forests has been blamed principally on the balsam wooly adelgid, *Adelges piceae* Ratzeburg (Homoptera: Adelgidae), an introduced European pest of firs. *Sisicottus montigenus* is usually associated with ground microhabitats, particularly mosses, but has also been taken on beating sheets. In one collection from Clingman's Dome, North Carolina in 1977, *S. montigenus* was the most abundant spider species. However, my repeated collecting efforts at this now much altered locality (Wheeler & McHugh 1994; F. Coyle pers. comm.) have failed to produce additional specimens. This apparent rapid change in population size in response to environmental degradation suggests that this species may be worthy of consideration for federal protection as a threatened or endangered species.

Distribution.—North Carolina and Tennessee; restricted to high elevation spruce-fir for-

ests (Fig. 32). A record from Michigan is almost certainly erroneous (Drew 1967), although this site is not very far outside the currently recognized range of *S. quoylei*. Any *Sisicottus* that Drew may have collected appear to be lost; no *Sisicottus* specimens can be found in the Michigan State University Entomology Museum (R.J. Snider pers. comm.).

Material examined.—UNITED STATES: *North Carolina:* Mitchell County., Roan High Bluff, 6200 feet, in moss from rocks in spruce-fir forest, 17 November 1978, 1♂5♀ (F. Coyle & D. Pittillo, FAC); Swain County, Clingman's Dome, 6600 feet, in moss from spruce-fir forest floor, 6 November 1977, 9♂26♀ (F. Coyle, FAC); Mt. Mitchell, 6600 feet, in moss from spruce-fir forest floor, 20 October 1977, 3♂12♀ (F. Coyle, FAC), Mt. Mitchell, 6600 feet, in moss from rock ledges in spruce-fir forest, 20 October 1977, 7♀ (F. Coyle, FAC). *Tennessee:* Sevier County, GSMNP, Mt. LeConte, 100 m below spring along Trillium Gap
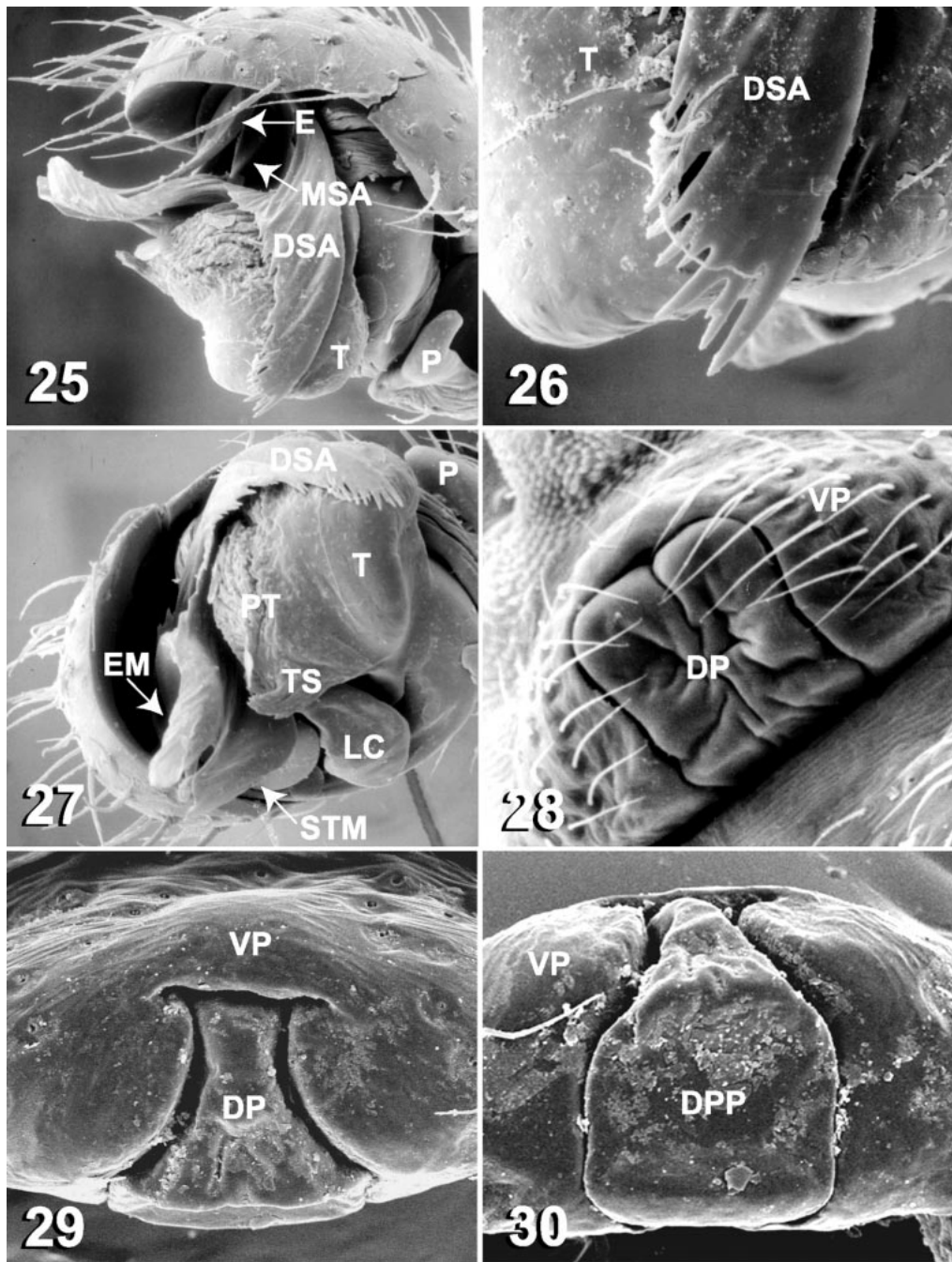
Figures 25–30.—Scanning electron micrographs of *Sisicottus montigenus* and *S. quoylei*. 25–28, *S. montigenus* from Mt. Mitchell, North Carolina. 25, Palpus, ectal view; 26, Terminus of distal suprategular apophysis; 27, Palpus, ventral view; 28, Epigynum, ventral view. 29, 30, Epigynum of female *S. quoylei* from Mt. MacIntyre, New York. 29, Ventral; 30, Posterior.

Tr., UTM: N394833 E27913, 6300 feet, beating 14: 20–15:20 in 25 yr-old fir forest, 19 July 1995, 1♂3♀ (Coyle, Williams & Carbiener, GSMNP); Mt. LeConte, 35°37′N, 83°27′W, 5♂10♀ (AMNH).

Sisicottus quoylei new species
Figs. 29–38

Sisicottus montigenus, in part: Bishop & Crosby 1938: 60–61, fig. 9 [♂]. Roewer 1942: 650. Bonnet 1958: 4066.

Types.—Male holotype with one female paratype from CANADA: Newfoundland, King's Point, beating black spruce, 19 August 1984, L. Hollett, deposited in CNC.

Etymology.—Named for the protagonist in E. Annie Proulx's Pulitzer Prize winning novel, *The Shipping News*, which is set within the range of this species. The name is also a homonym of the patronymic that would result from a species named for Dr. Frederick A. Coyle, my master's thesis advisor.

Diagnosis.—Males of *S. quoylei* are distinguished from those of all other *Sisicottus* species except its sister species, *S. montigenus,* by the form of the palpal tibial apophysis, which is quite short with a flat distal margin and no ectal tibial process (Fig. 35, characters 16, 17). It is separated from *S. montigenus* males by a moderately sclerotized distal suprategular apophysis (membranous in *S. montigenus*) which tapers to a single sharp terminal apex on its inside margin (Fig. 34, character 3).

Females of *S. quoylei* are distinguished from all other *Sisicottus* species except *S. montigenus* by the form of the anterior margin of the capsule which is nearly flat rather than formed into two convex lateral lobes (Fig. 38, character 30). They are separated from *S. montigenus* by the form of the ventral plate invagination which is wider and deeper in *S. montigenus* (Figs. 31, 38). Females of *S. quoylei* have a ventral plate invagination that is deeper than that of *S. montanus*, *S. panopeus*, *S. crossoclavis*, or *S. cynthiae* (character 19). They can be distinguished from other species with a deep ventral plate invagination, except *S. montigenus*, by having a dorsal plate with a subrectangular rather then triangular or trapezoidal posterior face (Fig. 37, character 21), and by the dorsal fold of the dorsal plate, which is membranous rather then sclerotized (Fig. 38, characer 24).
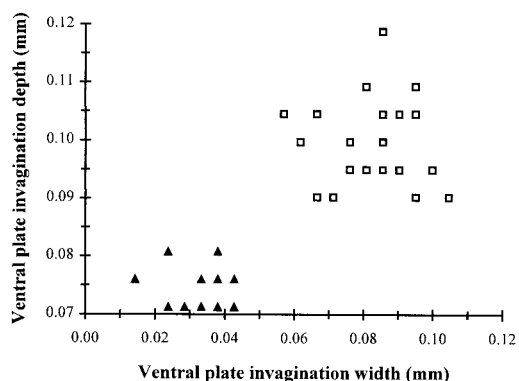
Figure 31.—Scattergram of ventral plate invagination depth plotted against ventral plate invagination width for females of *Sisicottus montigenus* (●) and *S. quoylei* (▲).

Description.—Small (carapace length 0.71–0.82 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus moderately sclerotized, long, extends to near ventral midline of palpal bulb; terminus pointed (Fig. 34). Palpal tibia short; palpal tibial apophysis short with flat distal margin without ectal tibial process (Fig. 35); sparse cluster of macrosetae (3–6) on ectal side of palpal tibia. Females with deep and narrow invagination of ventral plate of epigynum (Fig. 36). Posterior face of dorsal plate generally rectangular, usually slightly taller than wide with convex ventral margin (Fig. 37). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule nearly flat; fertilization ducts sinuous (Fig. 38). See Tables 2–4.

Natural history.—Locality labels indicate that this species is associated with conifer forests, especially balsam fir. It is sympatric with *S. montanus* over at least part of its range.

Distribution.—New Brunswick, Newfoundland, Nova Scotia, and New York (Fig. 32).

Material examined.—CANADA: *New Brunswick:* Green River, 30 mi N. Edmundston, balsam fir, 6 June 1959, 1♂1♀ (T.R. Renoult, CNC), balsam fir, 30 June 1965, 1♂ (T.R. Renoult, CNC); Kedgwick River, balsam fir, 27 June 1966, 1♀ (T.R. Renoult, CNC). *Newfoundland:* Bottom Brook, beating balsam fir, 15 August 1984, 1♂ (L. Hollett, CNC); Gallants, fir foliage, 23 June 1982, 1♂ (K.P. Lim, CNC); Hampden, beating balsam fir, 14 June
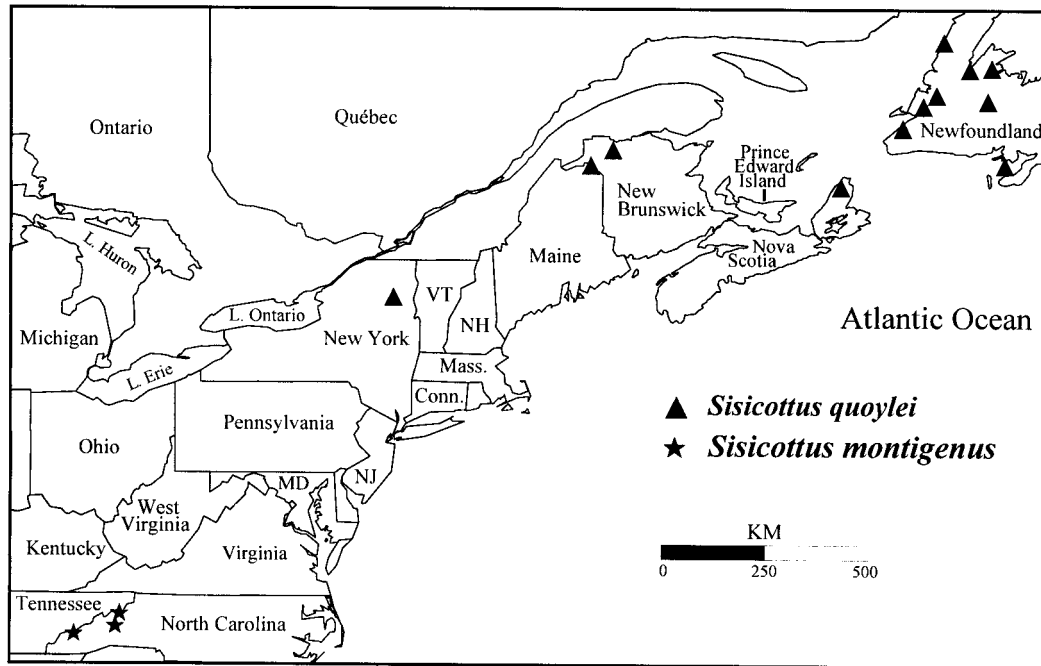
Figure 32.—Eastern United States and southeastern Canada, showing distribution of *Sisicottus montigenus* (★) and *S. quoylei* (▲).

1977, 1♀ (CNC); Noel Pauls Brook, *ex Abies balsamea*, 26 June 1977, 1♀ (L. Hollett, CNC), *ex Abies balsamea*, 8 August 1977, 1♂ (L. Hollett, CNC), *Abies balsamea,* July 1984, 1♀ (L. Hollett, CNC); Paddys Brook, 10 mi. W St. Johns, November 1982-April 1983, 1♀ (D.W. Langer, CNC); Portland Creek, June 1974, 1♀ (Heinrich, CNC); Steady Brook, 48°57′N, 57°50′W, beating balsam fir, 17 August 1984, 1♀ (L. Hollett, CNC); St. Fintans, 30 June 1942, 1♀ (E.J. Gillan, CNC). *Nova Scotia:*
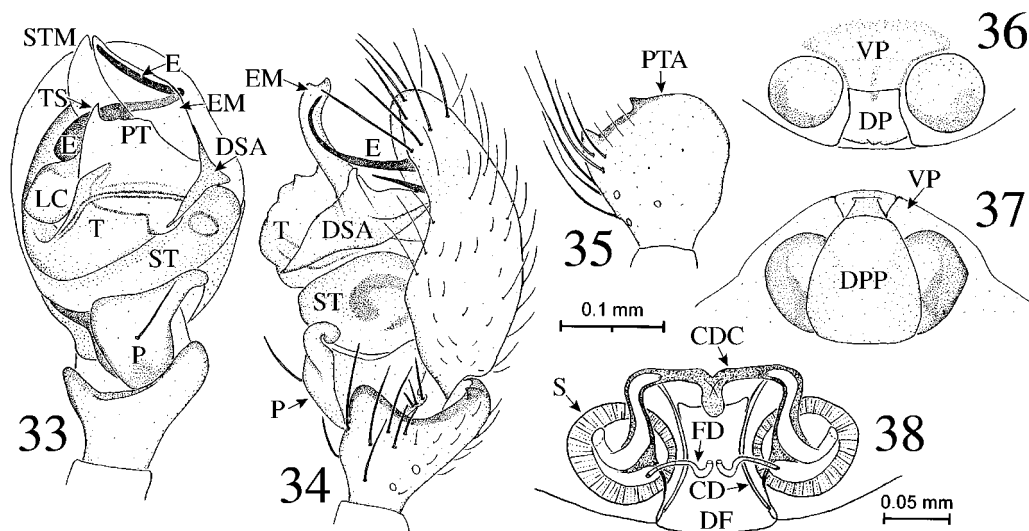
Figures 33–38.—*Sisicottus quoylei* from King's Point, Newfoundland. 33, Palpus, ventral view; 34, Palpus, ectal view; 35, Palpal tibia, dorsal view; 36, Epigynum, ventral view; 37, Epigynum, posterior view; 38, Cleared epigynum, dorsal view. *Scales:* Fig. 38 = 0.05 mm; all others = 0.1 mm.
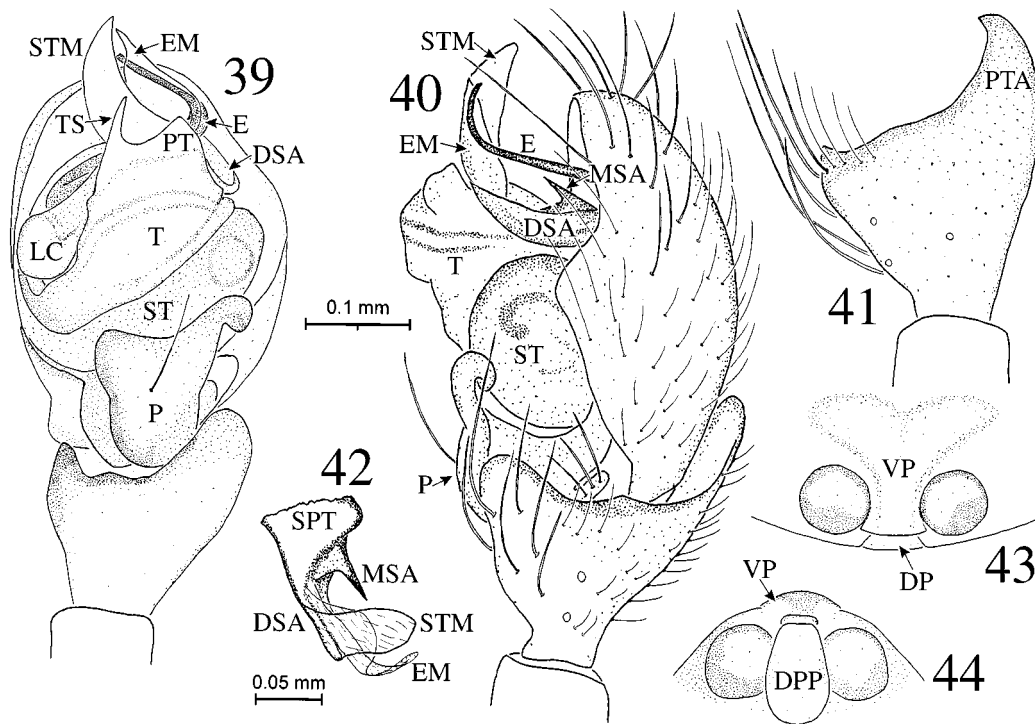
Figures 39–44.—*Sisicottus panopeus* from Mt. Rainier, Washington. 39–42, Male palpus. 39, Ventral view; 40, Ectal view; 41, Palpal tibia, dorsal view; 42, Suprategulum separated from palpus, ectal view. 43, 44, Epigynum. 43, Ventral view; 44, Posterior view. *Scales:* Fig. 42 = 0.05 mm; all others = 0.1 mm.

Cape Breton Highlands National Park, North Mountain, 46°48′N, 60°41′W , *ex* fen-pans, 8 June 1983, 1♀ (H. Goulet, CNC). **UNITED STATES:** *New York:* Lake Tear, Mt. Marcy, 4 September 1922, 1♂ (Bishop, AMNH); Mt. MacIntyre, 1 July 1923, 1♂1♀ (Crosby, AMNH).

Sisicottus panopeus new species
Figs. 39–46, 51, 52, 57, 58

Sisicottus montanus: Lowrie & Gertsch 1955: 6 (misidentification). Holm 1960: 124 (misidentification). Bragg & Leech 1972: 69 (misidentification). Crawford 1988: 15 (in part). Crawford & Edwards 1988: 437, figs. 21–22 [♀] (misidentification). Platnick 1993: 351.

Types.—Male holotype from UNITED STATES: Washington, Mt. Rainier National Park, Paradise, 46°48′N, 121°44′W, 12 September 1965, J. & W. Ivie, deposited in AMNH.

Etymology.—Derived from the monotypic mollusc genus *Panope; P. generosa*, the geoduck clam, is the mascot of my alma mater, The Evergreen State College.

Diagnosis.—Males of *S. panopeus* share with *S. montanus* and *S. crossoclavis* a distal suprategular apophysis that extends about half way down the ectal side of the palpal bulb (Fig. 40, character 4); in all other *Sisicottus* species, the distal suprategular apophysis extends to near the ventral midline of the papal bulb. They are distinguished from *S. montanus* by their longer palpal tibia and palpal tibial apophysis (Figs. 41, 57), by the lack of an ectal tibial process (Fig. 41, character 17), by the presence of more macrosetae in their ectal tibial cluster (7–11 in *S. panopeus*, 2–6 in *S. montanus*), and by the form of the distal suprategular apophysis which projects ventrally past the level of the suprategular membrane in *S. montanus* (Figs. 47, 61) but stops near the level of the suprategular membrane in *S. panopeus* (Figs. 40, 45). *Sisicottus crossoclavis* can be distinguished from both of these species by its heavily sclerotized distal suprategular apophysis with a serrated terminal margin (Fig. 67, character 3); *S. panopeus* and *S. montanus* have a moderately sclerotized distal suprategular apophysis with a rounded terminal margin (Fig. 40).
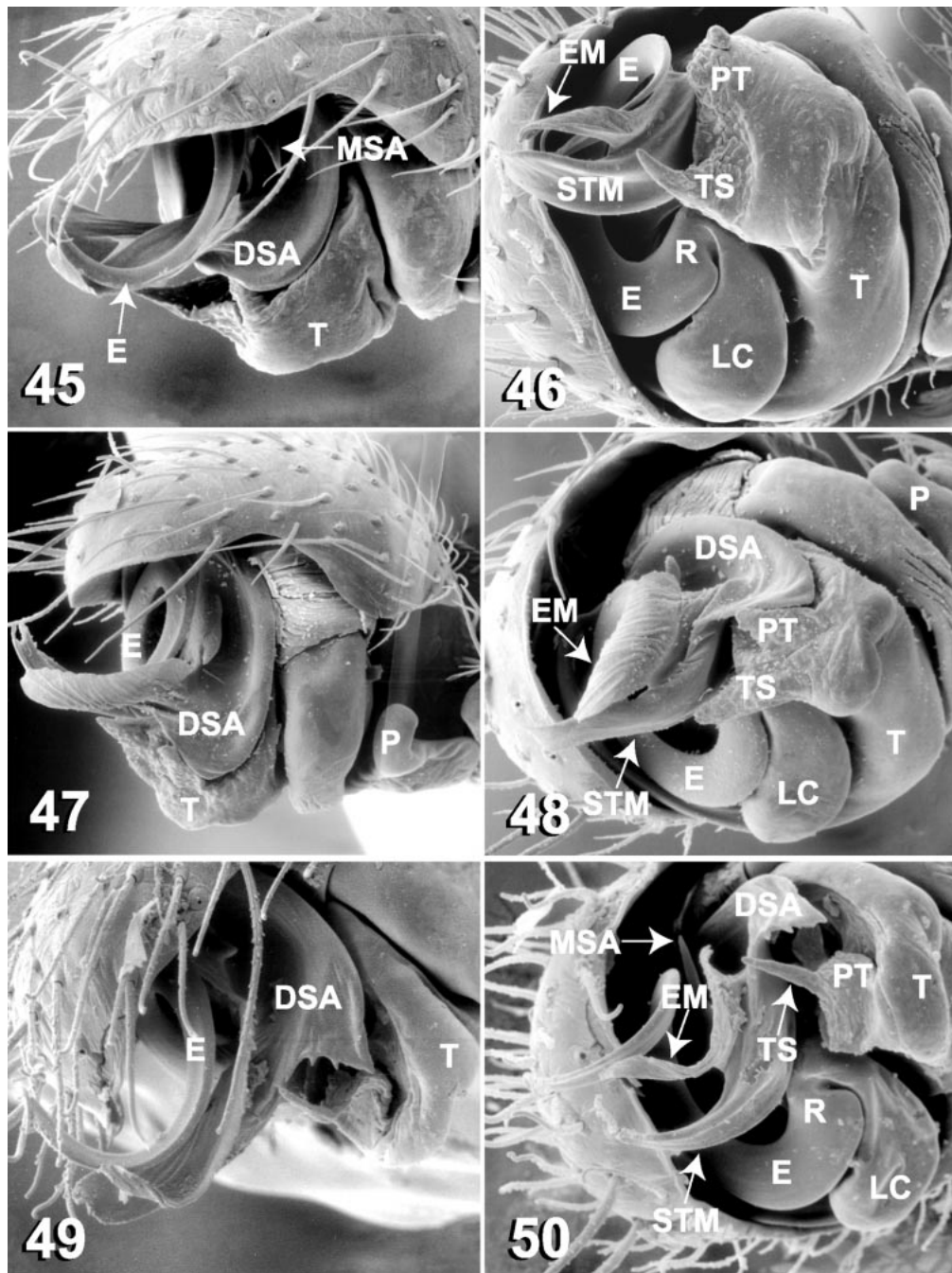
Figures 45–50.—Scanning electron micrographs of *Sisicottus* palpi. 45, 46, *S. panopeus* from Mt. Rainier, Washington. 45, Ectal view; 46, Ventral view. 47, 48, *S. montanus* from Mt. Mansfield, Vermont. 47, Ectal view; 48, Ventral view. 49, 50, *S. crossoclavis* from Rabbit Creek, Washington. 49, Ectal view detailing distal suprategular apophysis; 50, Ventral view.
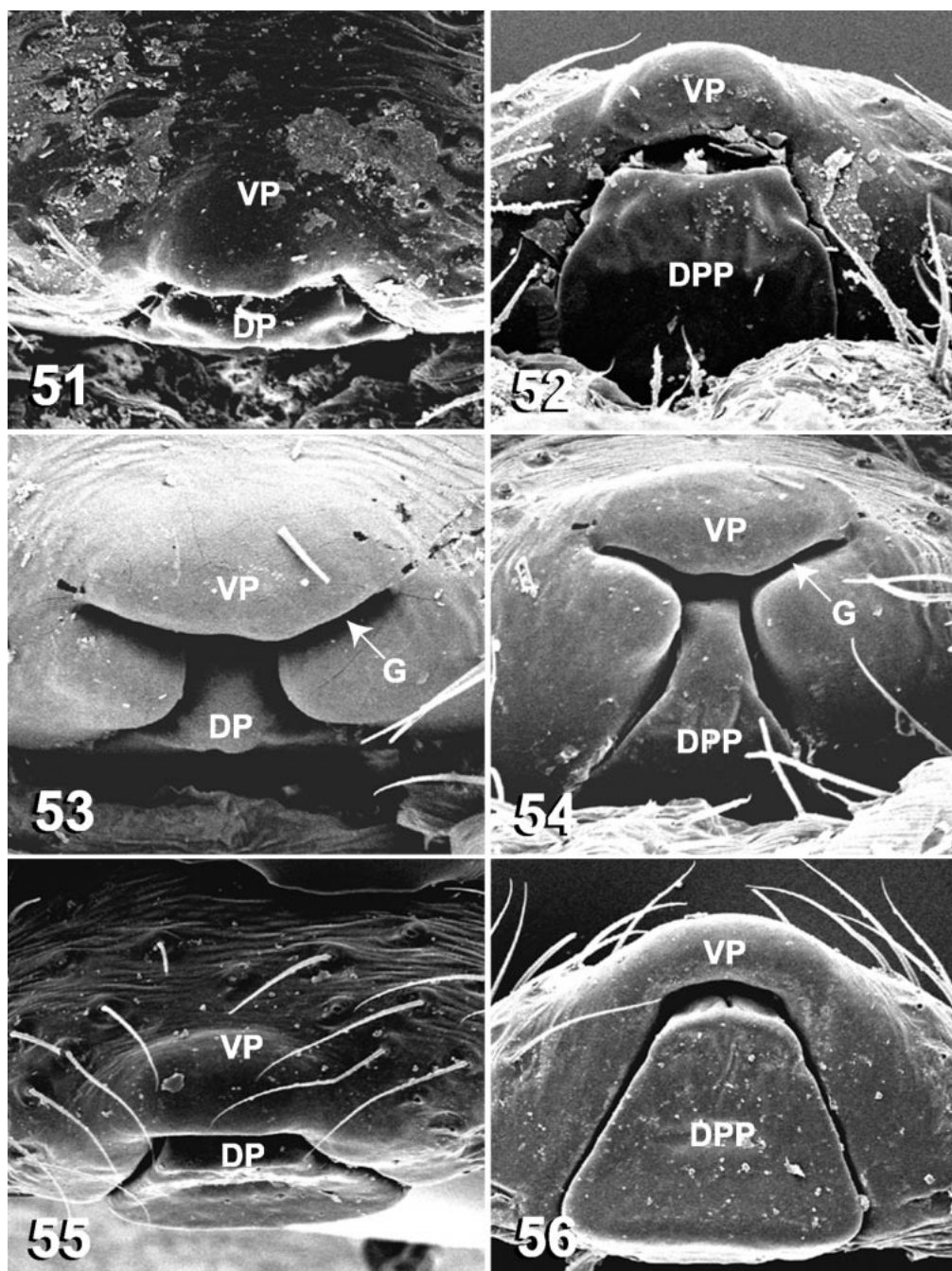
Figures 51–56.—Scanning electron micrographs of *Sisicottus* epigyna. 51, 52, *S. panopeus* from Lake Louise, Alberta. 51, Ventral view; 52, Posterior view. 53, 54, *S. montanus* from Piscataquis County, Maine. 53, Ventral view; 54, Posterior view. 55, 56, *S. crossoclavis* from Deemer Creek, Washington. 55, Ventral view; 56, Posterior view.
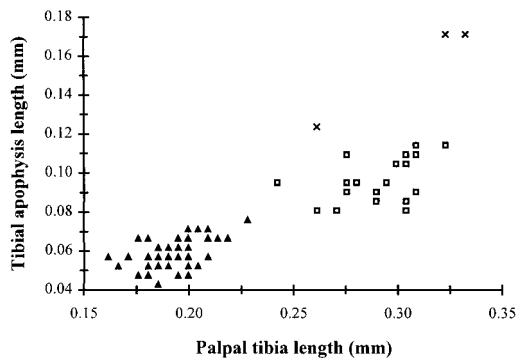
Figure 57.—Scattergram of palpal tibial apophysis length plotted against palpal tibia length for males of *Sisicottus panopeus* (●), *S. montanus* (▲), and *S. crossoclavis* (×).

Females of *S. panopeus*, like those of *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, have a shallow ventral plate invagination (Fig. 43, character 19); this separates them from females of *S. montigenus, S. quoylei, S. orites*, *S. nesides*, and *S. aenigmaticus*. *Sisicottus panopeus* is unique among species with a shallow ventral plate invagination in having a dorsal plate with a posterior face that is subrectangular with a flat ventral margin (Fig. 44, character 21). *Sisicottus panopeus* can also be distinguished from *S. crossoclavis*, *S. cynthiae*, *S. orites*, *S. nesides*, and *S. aenigmaticus* by the form of the dorsal fold of the dorsal plate which is membranous in *S. panopeus* (*cf.* Fig. 65, character 24) instead of sclerotized (Fig. 71).

Description.—Medium-sized (carapace length = 0.67–0.96 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus moderately sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; rounded on inside margin; terminal margin about level with suprategular membrane (Figs. 40, 45). Palpal tibia moderately long with a long apophysis; ectal tibial process absent (Fig. 41); dense cluster of macrosetae (7–11) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 43, 51). Posterior face of dorsal plate subrectangular with flat ventral margin (Figs. 44, 52). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts sinuous (*cf.* Fig. 65). Internal structure of epigynum virtually identical to that of *S. montanus* (Fig. 65). See Tables 2–4.

Natural history.—*Sisicottus panopeus* and *S. nesides* were found in the same vial or identically labeled vials several times during this study. Crawford & Edwards (1988) observed that in Washington these two species occupy distinct ecological niches, with *S. panopeus* apparently restricted to alpine and subalpine habitats and *S. nesides* more common at lower elevations. These two species are syntopic, however, where their ecological ranges overlap at or just below the tree line. *Sisicottus panopeus* has also been collected syntopically
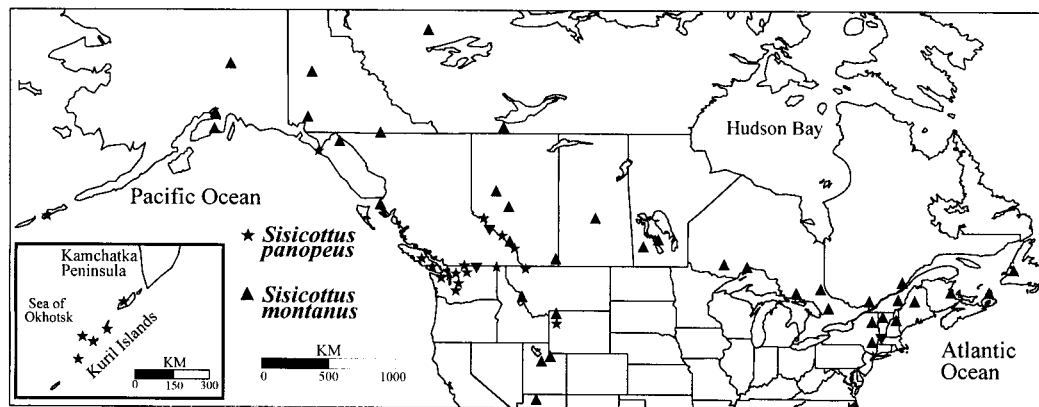

Figure 58.—North America with inset of the Kuril Islands, showing distribution of *Sisicottus panopeus* (★) and *S. montanus* (▲).

with *S. montanus*, *S. crossoclavis,* and *S. or-
ites*. Collection labels indicate that this species
may be found in moss, bogs, meadows, and
forests, especially those with a conifer com-
ponent. However, *Sisicottus panopeus* from
the Kuril Islands occur in an ecological niche
that is unusual for *Sisicottus* since many of the
records come from islands that are completely
unforested and occasionally devoid of even
shrub vegetation (R. Crawford pers. comm.).

Distribution.—Wyoming, Montana, Wash-
ington, Alberta, British Columbia and Alaska.
Recent collections of this species from the
Kuril Islands (between Japan and the Kam-
chatka Peninsula) make it the only *Sisicottus*
species known from Asia (Fig. 58). Further
collections in Asia may well yield additional
records of *S. panopeus*.

Material examined.—CANADA: *Alberta:* Bow
Lake, Banff Nat'l Park, elev. 6400 feet, moss and
willow litter nr lake, 9 August 1973, 1♀ (E.E. Lind-
quist, CNC); Bow Pass, 64 mi. NW Banff, Berlese
spruce duff, 12 October 1953, 1♂2♀ (O. Peck,
CNC); Cathedral Prov. Park, Pyramid L. Trail, 5–9
July 1986, 1♂1♀ (S.G. Cannings, CNC); Mt. Edith,
Cavill Lodge, 52°41′N, 118°09′W, 24 August 1965,
1♀ (J. & W. Ivie, AMNH); Highwood Pass, 35 mi.
S Kananaskis, *ex* spruce-larch litter, 28 July 1970,
1♀ (E.E. Lindquist, CNC); Kananaskis P.P., Mt. In-
defatigable, lichens on stones in lodgepole pine for-
est at base of mountain, 20 July 1983, 2♂1♀ (V.
Behan, CNC); Lake Louise, 4 August 1927, 3♂
(Crosby, AMNH); Marmot Cr., 13 mi. SW Kan-
anaskis F.E.S., 6000 feet, *ex* damp moss cover on
forest floor, 20 August 1970, 1♂1♀ (E.E. Lindquist,
CNC); Cameron Lake, Waterton Lakes Nat'l Park,
interception trap, 4–17 July 1980, 2♂4♀ (H.J. Tes-
key, CNC), Crandell L. trail, mossy area on N.
slope in mixed woods, 13 June 1980, 3♀ (I.M.
Smith, CNC), Rowe Lake Trail, 6300 feet, sifting
moss, edge of stream, 7 June 1980, 5♀ (J.M. Camp-
bell, CNC). *British Columbia:* Manning Prov. Pk.,
Skyline Trail, 1768 m, *Phyllodose*, *Kalmia*, moss,
lichen, 12 July 1986, 3♀ (V. Behan, CNC); Nitinat,
Heather Mtn., V.I., *ca.* 3600 feet, moss on seepage
slope, 14 July 1979, 3♀ (I.M. Smith, CNC), moss
at cold seepage area, 27 July 1979, 4♀ (I.M. Smith,
CNC); Strathcona Park, Vancouver Is., Cream
Lake, 1260 m, moss litter, 18 August 1988, 2♀ (C.
Guppy, CNC); Yoho Glacier, 5 August 1914, 1♂1♀
(Emerton, AMNH); Yoho Glacier Camp, 5 August
1914, 6♂7♀ (Emerton, MCZ). **RUSSIA:** *Kuril Is-
lands:* Ekarma Island, E side Cape Shpileroi, 4 m,
48.958°N, 153.920°E, in grass litter of beach mead-
ow, 10 August 1996, 1♂6♀ (T.W. Pietsch,
UWBM); Kharimotan Island, Inland from Svergi-
na Bay, 15 m, 49.159°N, 154.478°E, *ex* sphagnum

and other mosses around dry interdune wetlands, 8
August 1996, 5♀ (R. Crawford, UWBM); Matua
Island, army base, east end of island, 25 m,
48.068°N, 153.257°E, *ex* alder and grass litter in
thickets of *Alnus maximowiczii*, 14 August 1996,
1♂5♀ (R. Crawford, UWBM); Ohirinkotan Island,
E side Cape Ptichy, NW corner of island, 15 m,
48.986°N, 153.472°E, litter of tall grass meadow on
steep slope -treeless, 10 August 1996, 5♀ (T.W.
Pietsch, UWBM); Onekotan Island, slope above
Trundi River, 90 m, 49.280°N, 154.749°E, *ex* alder
thicket litter in coastal slope meadow, 9 August
1996, 2♂2♀ (R.L. Crawford, T. Pearce, UWBM);
Onekotan Island, 2 km S of Cape Subbotyna -river
valley, 49.396°N, 154.646°E, *ex* herbaceous litter in
river valley, 5 August 1996, 2♀, (T. Pearce,
UWBM); Paramushir Island, SW shore, Sholikhoua
Bay, 50°22′N, 155°37′E, 13–25 August 1996, 1♂
(Y. Marusik, UWBM); Shiashkotan Island, Zakat-
naya Bay, 20 m, 48.778°N, 54.036°E, ravine in
coastal slope meadow *ex* litter *Alnus maximowiczii*,
Sorbus samburifolia, 11 August 1996, 5♂17♀ (R.
Crawford, UWBM); Ushishir Island, Kraternaya
Bay (central peninsula), 5–20 m, 47.510°N,
152.815°E, *ex* litter of Petasites patch in north ex-
posed steep grass meadow, 20 August 1995, 2♂3♀
(Y. Marusik, UWBM). **UNITED STATES:** *Alaska:*
Aleutian Isl., Umnak, Fox Islands, July 1958,
4♂5♀ (C. Lindroth, MCZ); Lituya Bay, Glacier
Bay National Monument, Mt. Blunt, subalpine,
58.630°N, 137.493°W, 2100 feet, sifted from moss
in shrubland, 9 August 1979, 1♂1♀ (D.H. Mann,
UWBM). *Montana:* Glacier National Park, Swift-
current Mountain, 7500 feet, 19 August 1953, 1♀
(Levi, MCZ); *Washington:* Clallam County, Olym-
pic National Park, Waterhole Camp, 4975 feet,
47.944°N, 123.425°W, pitfalls in spring meadow, 30
July-8 August 1986, 11♂3♀ (R. Crawford,
UWBM); Olympic Nat'l Park, Obstruction Peak,
5900–6000 feet, 3 August 1973, 3♂4♀ (A. Sme-
tana, AMNH); King County, Source Lake 3760–
3840 feet, 47.455°N, 121.451°W, under rock up
slope from lake adjacent to snowfield, 2 August
1986, 1♂ (R. Crawford, UWBM); Okanogan Coun-
ty, Cold Spr Camp, 1850 m, 48.938°N, 119.789°W,
ex rotten log, 3 August 1985, 1♂1♀ (R. Crawford,
UWBM); Pend Oreille County, Deemer Creek,
4600 feet, 48.931°N, 117.089°W, sifted from willow
litter in bog, 13 June 1986, 1♀ (R. Crawford,
UWBM); Pierce County, Mt. Rainier National Park,
Golden Gate 6400 feet, 46.799°N, 121.722°W, 2 pit-
falls -heather and sedge meadow, 25 August-6 Sep-
tember 1975, 1♀ (D.H. Mann, UWBM); Paradise
Camp, Mt. Rainier, 19 August 1927, 2♂6♀ (Cros-
by, 1927); Paradise, Mt. Rainier National Park,
46°48′N, 121°44′W, 12 September 1965, 10♂13♀
(J. & W. Ivie, AMNH); Pierce County, Bearhead
Mtn., 6000–6089 feet, 47.023°N, 121.814°W, *ex*
heather and under rock, 15 August 1982, 5♀ (R.
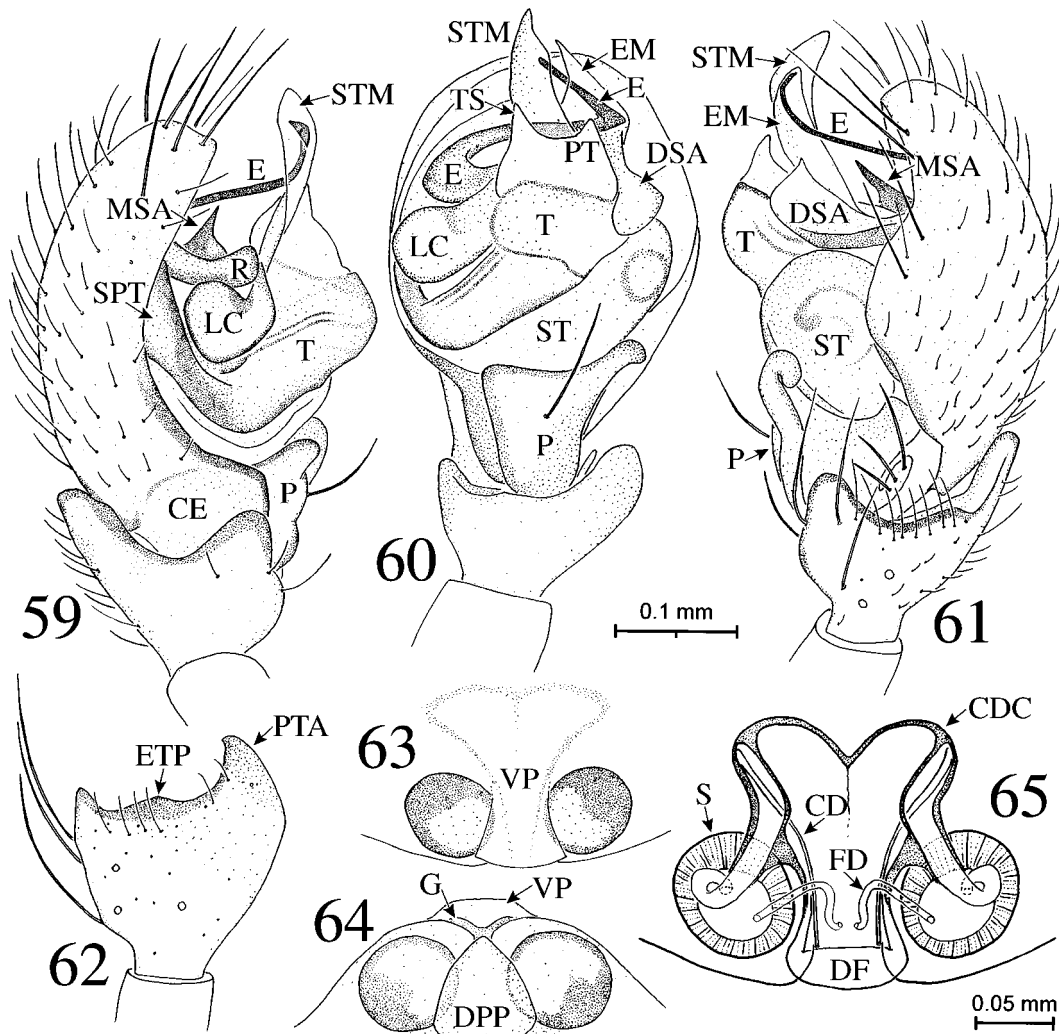
Figures 59–65.—*Sisicottus montanus*. 59–62, Palpus of male from Mt. Washington, New Hampshire. 59, Mesal view; 60, Ventral view; 61, Ectal view; 62, Palpal tibia, dorsal view. 63, 64, Epigynum of female from Mt. Washington, New Hampshire. 63, Ventral view; 64, Posterior view. 65, Cleared epigynum of female from near Soubunge Mountain, Pascataquis County, Maine, dorsal view. *Scales:* Fig. 65 =.05 mm; other figures = 0.1 mm.

Crawford, UWBM); Skagit County, Coney Pass, 3400 feet, 48.329–331°N, 121.736°W, swept -subalpine meadow, 27 July 1980, 1♂, (R. Crawford, UWBM); Skagit County, Dock Butte, 5000 feet, 48.640°N, 122.803°W, under rocks and wood, 13 September 1986, 6♂11♀ (R. Crawford, UWBM); Snohomish County, Box Mtn. Lake, 5050 feet, 48.223°N, 121.121-3°W, under wood on sand/mud shore, 5 August 1989, 2♀ (R. Crawford, UWBM). *Wyoming:* Grand Canyon, Yellowstone Park, 30 August 1927, 2♂ (Crosby, AMNH); Teton Park, Holly Lake, 9400 feet, 43°N, 110°W, 10 August 1950, 1♂5♀ (D.C. Lowrie, AMNH); Togwatee

Pass, 10,000 feet, 43°N, 110°W, 8 August 1950, 1♀ (D.C. Lowrie, AMNH).

Sisicottus montanus (Emerton 1882)
Figs. 47, 48, 53, 54, 57–65

Tmeticus montanus Emerton 1882: 55, fig. pl. xvi, fig. 3 [♂,♀]. Male lectotype from UNITED STATES: New Hampshire, Mt. Washington, 13 June 1877, J.H. Emerton, in MCZ, examined.
Erigone collina Marx 1890: 533, 538, 593 (*nomen novum*). Synonymy by Bishop & Crosby 1938.

Oedothorax montanus: Crosby 1905: 312; Petrunk-evitch 1911: 264.

Gongylidium montanus: Emerton 1920: 315.

Sisicottus montanus: Bishop & Crosby 1938: 57–60, figs. 6–8 [♂♀]. Chamberlin & Ivie 1939, fig. 40 [♂]. Roewer 1942: 650. Bonnet 1958: 4065. Holm 1967: 61. Kaston 1981: 208–209, figs. 653–657 [♂,♀]. West et al. 1984: 87. Koponen 1987: 281–283, 285. Crawford 1988: 15 (in part). Jennings et al. 1988: 61, 63. Aitchison-Benell & Dondale 1990: 224. Dondale et al. 1997: 89. Plat-nick 1993: 351 (after Crawford & Edwards 1988, misidentification); 1997: 427.

Diagnosis.—Males of *S. montanus* are distinguished from those of all other *Sisicottus* species by the form of the palpal tibia; the palpal tibial apophysis is tapered, ectally curved, and longer than that of *S. montigenus* and *S. quoylei* and the palpal tibia is shorter than that of *S. panopeus, S. crossoclavis, S. cynthiae, S. orites* and *S. nesides* (Figs. 57, 62, character 16). *Sisicottus montanus* males share with *S. panopeus* and *S. crossoclavis* a distal suprategular apophysis that extends about half way down the ectal side of the palpal bulb (Fig. 61, character 4); all other *Sisicottus* species have a distal suprategular apophysis that extends to near the ventral midline of the palpal bulb. *Sisicottus montanus* is distinguished from *S. panopeus* and *S. crossoclavis* by the presence of an ectal tibial process in *S. montanus* (Fig. 62, character 17). Also, the form of the distal suprategular apophysis is very different in these species. *Sisicottus crossoclavis* has a heavily sclerotized distal suprategular apophysis with a serrated terminal margin (Fig. 67, character 3). *Sisicottus montanus* and *S. panopeus* both have a moderately sclerotized distal suprategular apophysis (character 3) but in *S. montanus*, the distal suprategular apophysis projects ventrally past the level of the suprategular membrane (Fig. 61) while in *S. panopeus*, the distal suprategular apophysis projects at most only slightly beyond the level of the suprategular membrane (Fig. 40). *Sisicottus panopeus* and *S. crossoclavis* also have more macrosetae in their ectal tibial cluster (7–11 in *S. panopeus*; 7–9 in *S. crossoclavis*) than does *S. montanus* (2–6).

Females of *S. montanus*, like those of *S. panopeus, S. crossoclavis*, and *S. cynthiae*, have a shallow ventral plate invagination (Fig. 63, character 19); this separates them from fe-males of *S. montigenus, S. quoylei, S. aenigmaticus, S. orites*, and *S. nesides*. *Sisicottus montanus* is unique among species with a shallow ventral plate invagination in having a groove formed by the enfolding of the ventral plate (Figs. 53, 54). *Sisicottus montanus* can also be distinguished from *S. panopeus* by the form of the posterior face of the dorsal plate which is pointed ventrally in *S. montanus* (Fig. 64, character 21) and is flat ventrally in *S. panopeus* (Fig. 44). *Sisicottus montanus* can also be distinguished from *S. crossoclavis, S. cynthiae, S. orites, S. nesides* and *S. aenigmaticus* by the form of the dorsal fold of the dorsal plate, which is membranous in *S. montanus* (Fig. 65, character 24) instead of sclerotized (Fig. 71).

Description.—Medium-sized (carapace length = 0.67–0.96 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus moderately sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; rounded on inside margin; terminal margin ventral to level of suprategular membrane (Figs. 47, 61). Palpal tibia short with moderately short palpal tibial apophysis (Fig. 62); small ectal tibial process present; sparse cluster of macrosetae (2–6) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 53, 63). Posterior face of dorsal plate triangular, widest near its dorsal margin with sharply rounded or pointed ventral apex (Fig. 64). Ventral plate enfolded forming a groove (Figs. 53, 54). Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts sinuous (Fig. 65). See Tables 2–4.

Natural history.—Aitchison-Benell & Dondale (1990) have reported that *S. montanus* in Manitoba may be found in boreal forest, bogs, ditches, mixed woods, leaf litter, moss and grass. Jennings et al. (1988) found that *S. montanus* in Maine preferred uncut spruce-fir forest habitats over clearcut strips. In a study of spiders living in ground habitats across an ecological/elevational gradient in Quebec, Koponen (1987) found *S. montanus* to be the dominant species in his collections from balsam fir forest at 850 m elevation. In this study, *S. montanus* was more rarely found in three other habitats: a mixed deciduous forest site

at 580 m elevation, a windy high elevation (920 m) scrub forest habitat near the tree line, and a somewhat sheltered summit below the tree line (870 m) with short birch and spruce trees. Collection labels record *S. montanus* from elevations of sea level to above tree line. This species is often associated with moss, bogs, and forest litter, especially from forests with a conifer component. It has been collected syntopically with *S. panopeus*, *S. orites,* and *S. nesides* and is also sympatric with *S. quoylei.*

Distribution.—Canada, New England, Alaska, Washington, and the Rocky Mountains region south to Arizona (Fig. 58).

Material examined.—CANADA: *Alberta:* Lake Louise, 4 August 1927, 3♂16♀ (Crosby, AMNH); Sulfur Mt., Banff, 2 August 1927, 1♂ (Crosby, AMNH); Lodgepole Pine Cpgd area, 1 mi. S Elkwater, Cypress Hills Prov. Pk., *ex* moist herbal mate substrate by seepage, 20–27 July 1978, 1♀, (E.E. Lindquist, CNC); House R. at Little Smoky River, 55°27′N, 117°10′W, 6 September 1968, 1♂3♀, (W. Ivie, AMNH); Jasper, 18 August 1914, 1♂ (Emerton, MCZ); White Court, 54°08′N, 115°41′W, 6 September 1968, 3♂7♀ (W. Ivie, AMNH). *British Columbia:* Metlakatla, 1♂1♀ (Emerton, AMNH); Summit Lake, pitfall in moss above tree line, 1 June-8 July 1981, 2♂1♀ (Dondale, CNC). *Manitoba:* R.M.N. Pk., Clear Lake, pan trap, beaver meadow, 8 June 1979, 1♂1♀ (S.J. Miller, CNC); Lake Audy, Riding Mtn. Nat'l Park, sifting grass and moss, 28 August 1979, 8♂17♀ (J. & M. Redner, CNC); nr. Wasagaming Riding Mtn. Nat'l P., in boggy area, 23 August 1979, 1♀ (J. & M. Redner, CNC). *New Brunswick:* Kouchibouguac N.P., forest edge on beach, 8 June 1977, 1♂ (S.J. Miller, CNC). *Newfoundland:* Corner Brook Lake, sifted from moss, 13 July 1984, 2♂1♀ (L. Hollett, CNC). *Northwest Territories:* Mackenzie, Alexandra Falls, Hay River, 60°30′N, 166°17′W, 16 August 1965, 1♀, (J. & W. Ivie, AMNH); Lac Maunoir, pitfall trap, 19–27 July 1969, 2♂4♀ (G.E. Shewell, CNC). *Nova Scotia:* Cape Breton Highlands National Park, MacKenzie Mtn., 300 m, *ex* malaise trough, 28 June-7 July 1983, 2♂1♀ (J.R. Vockeroth, CNC); Cape Breton Highlands National Park, 46°48′N, 60°41′W, 400 m, *ex* fen-pans, 8 June 1983, 1♂ (H. Goulet, CNC). *Ontario:* Bondi Village, Kuskoka District, moss in fir woods, 28 August 1975, 1♂2♀ (D. Maddison, CNC); English River (settlement), 49°13′N, 90°58′W, 24 July 1965, 2♀ (J. & W. Ivie, AMNH); Goward, 47°03′N, 79°55′W, 20 August 1952, 1♀ (C. Goodnight, AMNH); Nipigon, 48°N, 88°W, 12 August 1948, 1♀ (Gertsch & Kurata, AMNH). *Quebec:* Lac Cornu, Cté de Terrebonne, 3–4 September 1989, 1♀ (R. Hutchinson, CNC);

Parc des Grandes Jardins, Mont du Lac des Cygnes, 2 June-14 September 1985, 70♂45♀ (S. Koponen, UTZM); St. Méthode, nr. Lac St. Jean, litter, river bank, 13 July 1982, 1♂ (C. Dondale & J. Redner, CNC); Sherbrooke, sifting litter under trees, 20 September 1972, 2♂2♀ (Dondale & Redner, CNC). *Saskatchewan:* Prince Albert, 24 August 1914, 1♂ (Emerton, MCZ). *Yukon:* Alaska Hiway, Milepost 700, 60°05′N, 130°25′W, 2 September 1968, 1♂ (W. Ivie, AMNH); Dempster Hwy., km 220N, Tamarack Bog, *ex Alnus crispa*, *Picea mariana* litter, 26 June 1987, 1♀ (V. Behan, CNC); Kluane Lake, Kluane Nat'l Park, litter, 6 July 1981, 2♂2♀ (C.D. Dondale, CNC); North Fork Pass, 64°33′N, 138°15′W, sifting litter, 20 June 1981, 5♀ (C.D. Dondale, CNC). **UNITED STATES:** *Alaska:* Chatanika River Roadside Park, 65°08′N, 147°30′W, 17 August 1968, 1♂3♀ (W. Ivie, CNC); Trail to Denver Glacier, Skagway, 25 June 1936, 1♂ (Crosby, AMNH); Matanuska, 61°32′N, 149°12′W, September 1944, 1♀ (Chamberlin, AMNH), October 1943, 1♂ (J.C. Chamberlin, AMNH); Primrose Camp, 18 mi. N. of Seward, 60°20′N, 149°20′W, 24 August 1968, 15♂23♀ (W. Ivie, AMNH). *Arizona:* Kaibab For., 36°30′N, 112°30′W, 4 September 1931, 4♂4♀ (R.V. Chamberlin, AMNH). *Maine:* Pascataquis County: near Soubunge Mtn., pitfall coll., dense and stripcut spruce-fir forest, May, June, and July, 1977 and 1978, specimens in many vials, (D.T. Jennings, M.W. Houseweart, AMNH, CAS, CNC, USNM); Van Buren, 15 July 1914, 1♂ (Emerton, MCZ). *Massachusetts:* Berkshire County, Mt. Greylock, 3400 feet, decid. litter, 15 October 1990, 2♂1♀ (R.L. Edwards, USNM). *Montana:* Gird Creek, Ravalli County, 26 August 1934, 1♀ (W.L. Jellison, AMNH). *New Hampshire:* Coos County, Mt. Washington toll road, 0.3 mi. below halfway hse., 1100 m, Berl. litter, spruce-fir-birch forest, 15 October 1978, 1♂ (A. Newton, M. Thayer, MCZ); Mt. Washington, 13 June 1877, 3♀ paralectotypes, (J.H. Emerton, MCZ). *New York:* Catskill Mtn. Pk., North Mtn. Trail, *ex* litter under balsam fir, 1 August 1985, 1♀ (V. Behan, CNC); Mt. MacIntyre, Essex County, 1 July 1923, 1♀ (AMNH). *Utah:* Mirror Lake, Uintah Mountains, 40°43′N, 110°53′W, 28 July 1936, 4♂4♀ (W. Ivie, AMNH); west side Utah Lake, heron rookery, 27 May 1934, 4♀ (Ivie, AMNH). *Vermont:* Camels Hump, 7 September 1908, 2♂ (Emerton, MCZ); Mt. Mansfield, pitfall B fir forest, 26 May-15 June 1982, 85♂30♀ (C. Dondale, J. Redner, CNC); Stratton Mtn., 3000 feet, 4 July 1913, 1♂ (Emerton, MCZ). *Washington:* Okanogan County, Cold Spring Camp, 1850 m, *ex* rotten log, 48.938°N, 119.789°W, 3 August 1985, 1♂ (R. Crawford, UWBM). *Wyoming:* Bay Bridge, Yellowstone Lake, 11 August 1940, 8♂9♀ (W. Ivie, AMNH); Grand Canyon, Yellowstone Park, 30 August 1927, 1♂ (Crosby, AMNH).
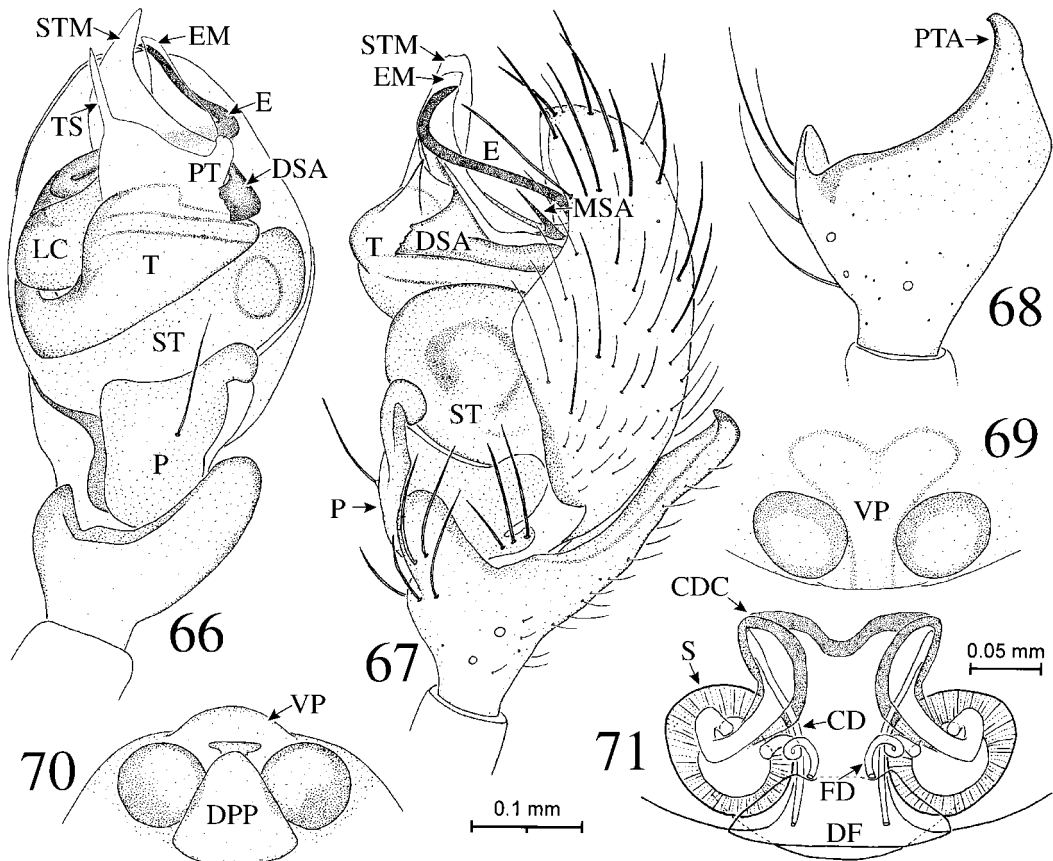
Figures 66–71.—*Sisicottus crossoclavis.* 66–68, Palpus of holotype from Hayden Lake, Idaho. 66, Ventral view; 67, Ectal view; 68, Palpal tibia, dorsal view. 69, 70, Epigynum of female from Deemer Creek, Washington. 69, Ventral view; 70, Posterior view. 71, Cleared epigynum of female from Rabbit Creek, Washington, dorsal view. *Scales:* Fig. 71 = 0.05 mm; other figures = 0.1 mm.

Sisicottus crossoclavis new species
Figs. 49, 50, 55–57, 66–72

Sisicottus sp. #1: Crawford 1988: 15.

Types.—Male holotype with female para-
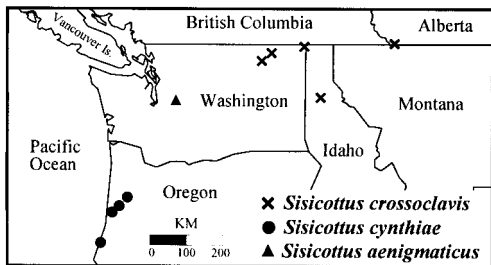
Figure 72.—Northwestern United States and southwestern Canada, showing distribution of *Sisicottus crossoclavis* (×), *S. cynthiae* (●), and *S. aenigmaticus* (▲).

type from UNITED STATES: Idaho, Harrison Cr., E side Hayden Lake, 47°N, 116°W, 25 July 1959, F.C. Raney, deposited in AMNH.

Etymology.—Formed form the Greek word *krossos,* meaning tasseled, and *clavis,* a synonym for the suprategulum used by F.O. Pickard-Cambridge (H.D. Cameron pers. comm.).

Diagnosis.—The distal suprategular apophysis in males of *S. crossoclavis* is widened distally with a serrated terminal margin and is unique among *Sisicottus* (Fig. 67). Males of *S. crossoclavis* share with *S. cynthiae*, *S. orites*, and *S. nesides* a heavily sclerotized distal suprategular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They share with *S. panopeus* and *S. montanus* a distal suprategular apophysis that extends about half way down the ectal

side of the palpal bulb (Fig. 67, character 4); all other *Sisicottus* species have a distal suprategular apophysis that extends to near the ventral margin. They are distinguished from all other *Sisicottus* species except *S. panopeus* by the lack of an ectal tibial process (Fig. 68, character 17).

Females of *S. crossoclavis*, like those of *S. panopeus*, *S. montanus*, and *S. cynthiae*, have a shallow ventral plate invagination (Figs. 69, character 19); this separates them from females of *S. montigenus, S. quoylei, S. orites*, *S. nesides*, and *S. aenigmaticus*. *Sisicottus crossoclavis* is distinguished from *S. panopeus*, *S. montanus*, *S. montigenus*, and *S. quoylei* by the form of the dorsal fold of the dorsal plate which is sclerotized rather then membranous (character 24). *Sisicottus crossoclavis* is distinguished from *S. cynthiae* by the unusual form of the dorsal plate in *S. cynthiae*. In *S. cynthiae*, the posterior face of the dorsal plate has a ventral margin that is dorsal to the ventral extent of the spermathecae (Fig. 77); in all other *Sisicottus* species, including *S. crossoclavis*, the ventral margin of the posterior face of the dorsal plate is at about the level of the ventral extent of the spermathecae (Fig. 70).

Description.—Medium-sized (carapace length = 0.81–0.97 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of palpus heavily sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; widened distally with serrated terminal margin (Fig. 67). Palpal tibia long with long, gradually curving palpal tibial apophysis; ectal tibial process absent (Fig. 75); dense cluster of macrosetae (7–9) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 55, 69). Posterior face of dorsal plate triangular with broadly rounded ventral margin (Figs. 56, 70). Dorsal fold of dorsal plate sclerotized (Fig. 71). Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts spiral (Fig. 71). See Tables 2–4.

Variation.—Of three known male specimens, two have a very long palpal tibial apophysis and palpal tibia, but a third specimen from Rabbit Creek, Washington has a palpal tibial apophysis and palpal tibia of more moderate length (Fig. 57). Despite the difference in size, the tibias are similar in shape. Furthermore, all three specimens share virtually identical palpal bulbs and were found associated with indistinguishable females. I have concluded that both tibial morphotypes belong to a single species. The short tibia in the Rabbit Creek specimen may have been due unfavorable conditions during development or to some genetic condition.

Natural history.—*Sisicottus crossoclavis* has been collected from moss, rotting logs, and forest litter. Collection labels suggest that this species may have an affinity for relatively wet microhabitats.

Distribution.—Alberta, Idaho, and Washington (Fig. 72).

Material examined.—CANADA: *Alberta:* Waterton Lakes N.P., moss and litter on damp seepage rock face, 26 June 1980, 1♀ (I.M. Smith, CNC); **UNITED STATES:** *Washington:* Ferry County, S Fk. Boulder Cr., 2560 feet, 48.756°N, 118.249°W, *ex* cottonwood-cedar litter, 15 July 1989, 1♀ (R. Crawford, UWBM). Ferry County, Rabbit Creek, 3500 feet, 48.539°N, 118.605°W, *ex* alder litter; *ex* moss, logs, and ground in forest, 18 July 1989, 1♂5♀ (R. Crawford, UWBM). Pend Oreille County, Deemer Creek, 4600 feet, 48.931°N, 117.089°W, under rocks and logs; from pitfalls; in soggy moss at stream edge; web in soil depression; rotting log, 11–14 July 1986, 1♂6♀ (R. Crawford, UWBM); Spokane County, Mt. Spokane, 5000 feet, *ex* moss, herbs, nr. edge seepage area, 28 August 1985, 1♀ (C.C. Lindquist, CNC).
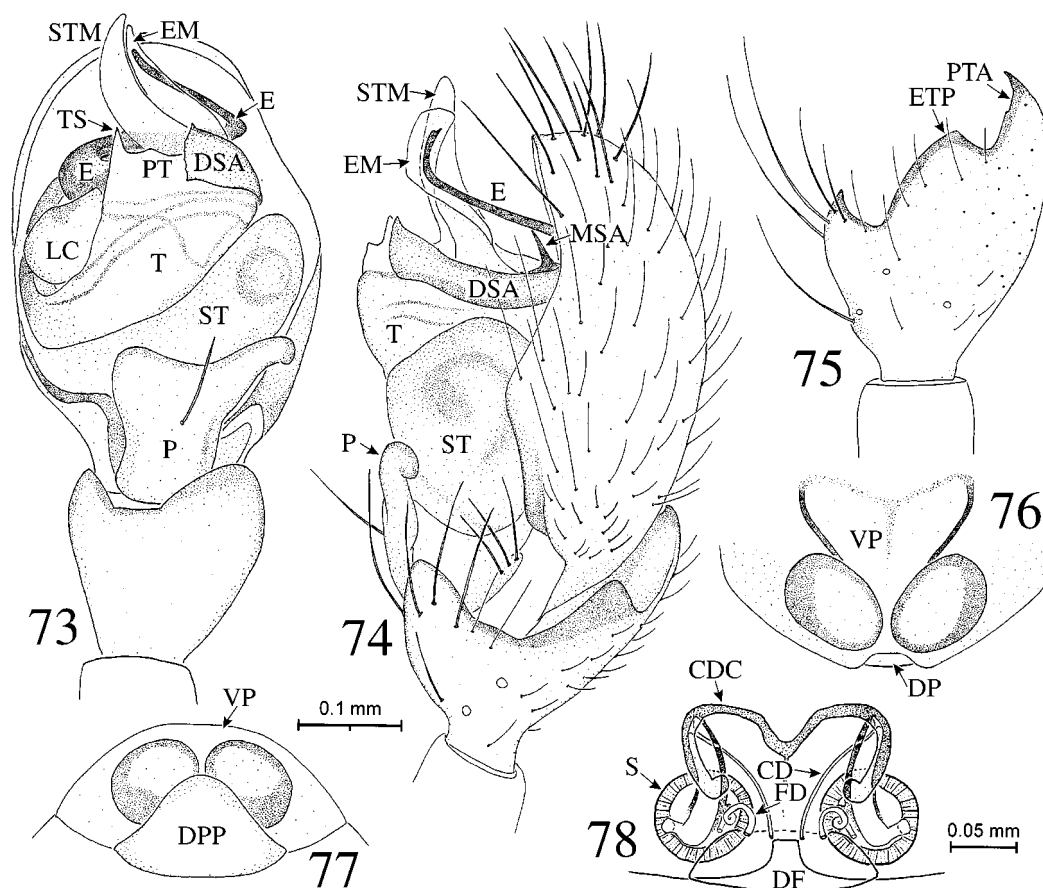
Sisicottus cynthiae new species
Figs. 72–80, 85, 86

Types.—Male holotype from UNITED STATES: Oregon, Benton County, Mary's Peak, 44°N, 123°W, 29 September 1960, J.D. Lattin, deposited in AMNH.

Etymology.—Named for my friend, Cynthia Zujko-Miller, whose support during the course of this project contributed substantially to its completion.

Diagnosis.—Males of *S. cynthiae* share with *S. crossoclavis*, *S. orites*, and *S. nesides* a heavily sclerotized distal suprategular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They are distinguished from *S. crossoclavis* and *S. orites* by their much shorter palpal tibial apophysis (Fig. 75) and from *S. nesides* by

Figures 73–78.—*Sisicottus cynthiae*. 73–75, Palpus of holotype from Mary's Peak, Oregon. 73, Ventral view; 74, Ectal view; 75, Palpal tibia, dorsal view. 76, 77, Epigynum of female from Mary's Peak, Oregon. 76, Ventral view; 77, Posterior view. 78, Cleared epigynum of female from Grass Mountain, Oregon, dorsal view. *Scales:* Fig. 78 = 0.05 mm; other figures = 0.1 mm.

the terminus of the distal suprategular apophysis which has a broad, rippled ventral margin in *S. cynthiae* (Fig. 73). The corresponding region in *S. nesides* terminates in two apical points and is not widened distally (Fig. 102). The form of the ectal tibial process is unique in *S. cynthiae* being generally larger and more ectally placed than in other *Sisicottus* species (Fig. 75, character 17).

Females of *S. cynthiae* are distinguished from those of all other *Sisicottus* species by the form of the posterior face of the dorsal plate. In *S. cynthiae*, the posterior face of the dorsal plate has a ventral margin that is dorsal to the ventral extent of the spermathecae (Fig. 77); in all other *Sisicottus* species, the ventral margin of the posterior face of the dorsal plate is at about the level of the ventral extent of

the spermathecae (Fig. 70). *Sisicottus cynthiae*, like *S. panopeus*, *S. montanus*, and *S. crossoclavis*, have a shallow ventral plate invagination (Figs. 76, character 19); this separates them from females of *S. montigenus, S. quoylei, S. orites, S. nesides*, and *S. aenigmaticus*. *Sisicottus cynthiae* is distinguished from *S. panopeus*, *S. montanus*, and *S. crossoclavis* by the orientation of the posterior part of the copulatory duct capsule (character 32). In *S. cynthiae*, the posterior tips of the capsule are oriented mesally (Fig. 78). In *S. panopeus*, *S. montanus*, and *S. crossoclavis*, the posterior tips of the capsule are oriented posteriorly (Fig. 65). *Sisicottus cynthiae* is distinguished from *S. panopeus*, *S. montanus*, *S. montigenus*, and *S. quoylei* by the form of the dorsal fold of the dorsal plate which is sclerotized
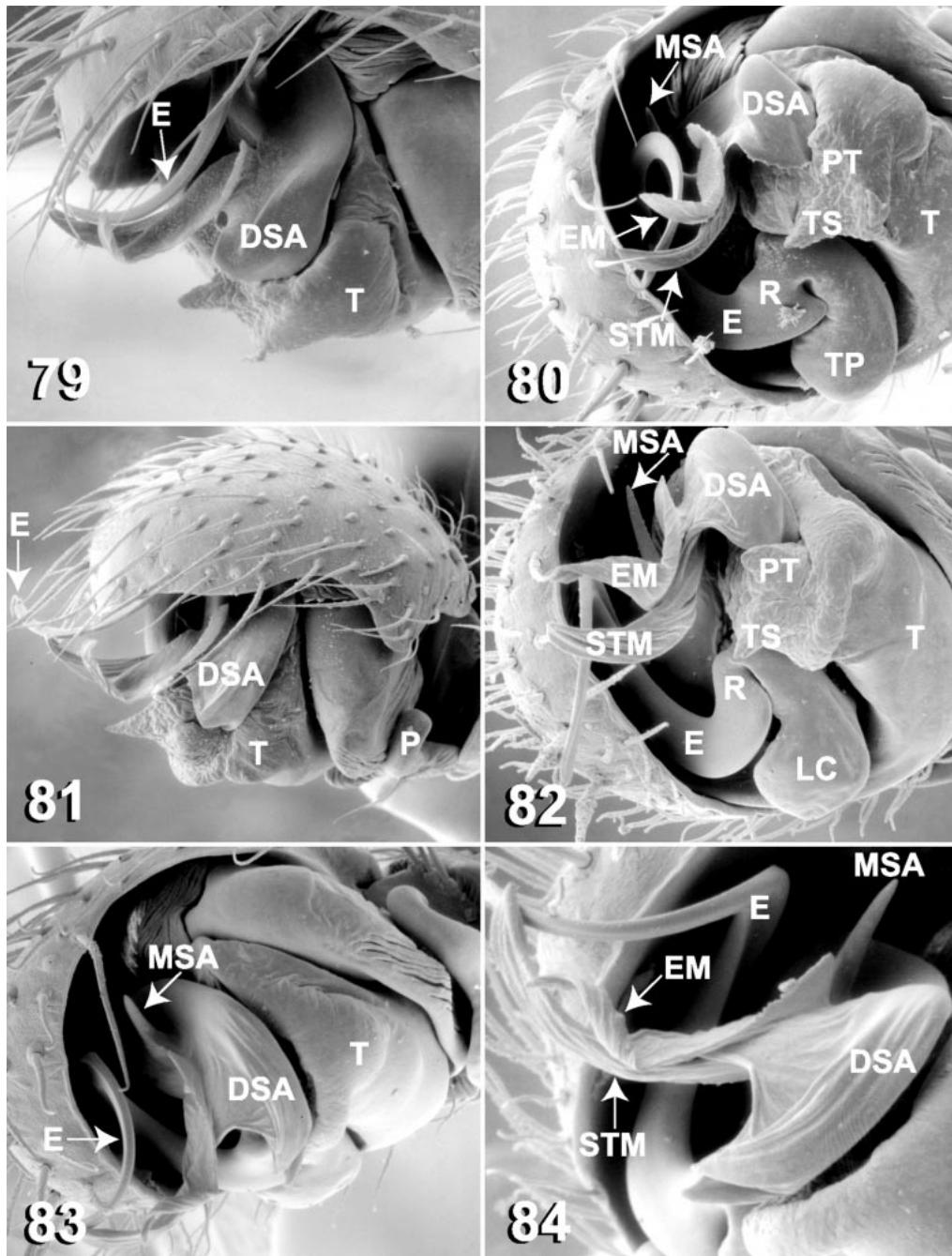
Figures 79–84.—Scanning electron micrographs of *Sisicottus* palpi. 79, 80, *S. cynthiae* from Mary's Peak, Oregon. 79, Ectal view; 80, Ventral view. 81, 82, *S. orites* from Mirror Lake, Utah. 81, Ectal view; 82, Ventral view. 83, 84, *S. nesides* from Primrose Camp, Alaska. 83, Ectoventral view; 84, Ventral view detailing distal suprategular apophysis.
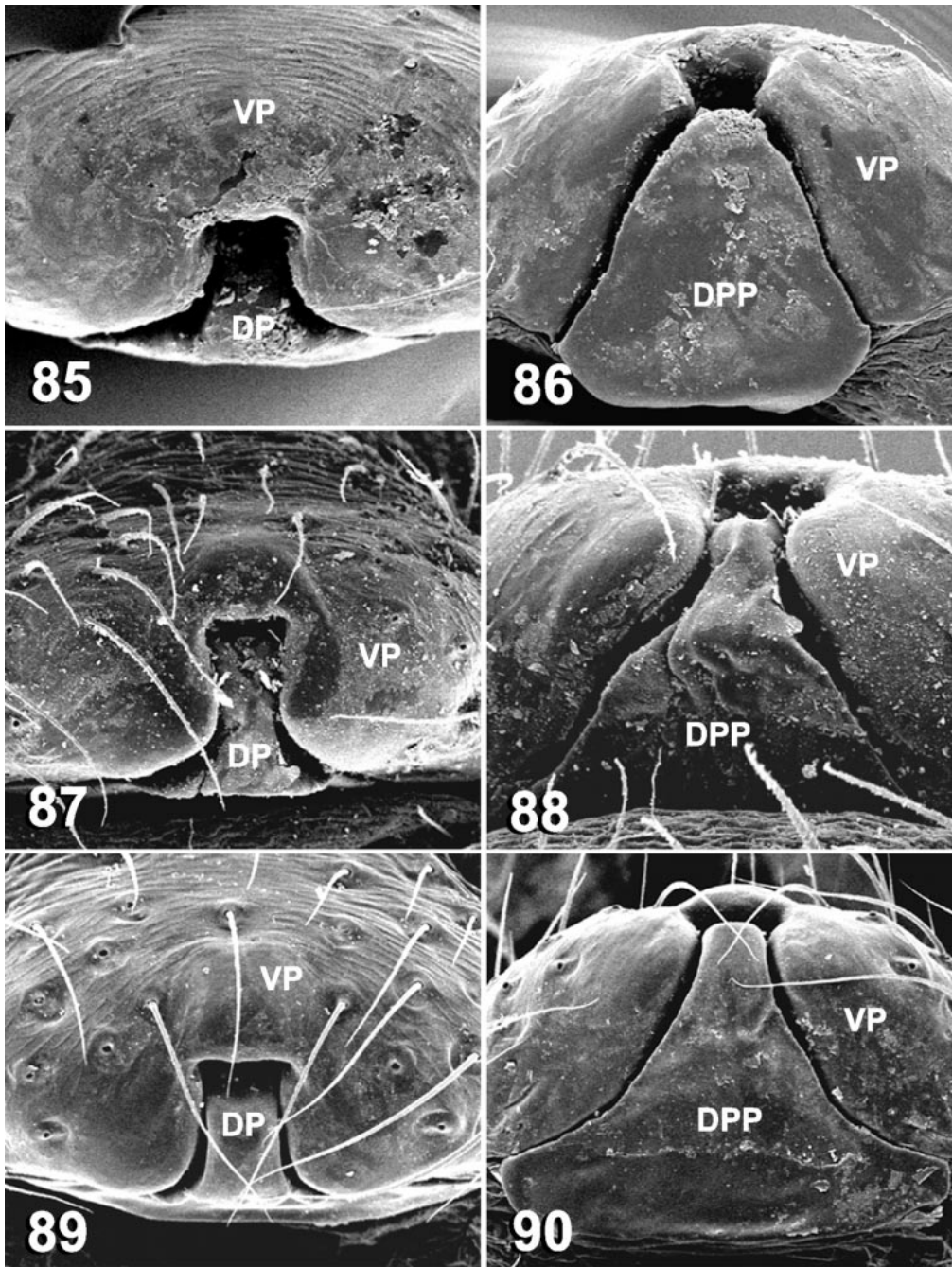
Figures 85–90.—Scanning electron micrographs of *Sisicottus* epigyna. 85, 86, *S. cynthiae* from Charleston, Oregon. 85, Ventral view; 86, Posterior view. 87, 88, *S. orites* from Smith and Morehouse Canyon, Utah. 87, Ventral view; 88, Posterior view. 89, 90, *S. nesides* from Change Creek, King County, Washington. 89, Ventral view; 90, Posterior view.

rather then membranous (Fig. 78, character 24).

Description.—Large (carapace length = 0.88–1.10 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus heavily sclerotized, long, extends to near ventral midline of palpal bulb; slightly widened near terminal margin, which has rippled appearance (Figs. 73, 80). Palpal tibia long with medium sized apophysis; ectal tibial process pronounced (Fig. 75); moderately dense cluster of macrosetae (6–8) on ectal side of palpal tibia. Female with shallow ventral plate invagination (Figs. 76, 85). Posterior face of dorsal plate triangular with broadly rounded ventral margin located dorsal to ventral extent of spermathecae (Fig. 77). Lateral margins of copulatory duct capsule in dorsal view sinuous with tips of capsule oriented mesally toward each other; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 78). See Tables 2–4.

Natural history.—One collection label states that *S. cynthiae* has been collected from moss and another indicates that a female specimen was found in the stomach of a salamander. *Sisicottus cynthiae* is syntopic with *S. nesides*.

Distribution.—Oregon (Fig. 72).

Material examined.—UNITED STATES: *Oregon:* Benton County, Mary's Peak, 44°N, 123°W, 29 September 1960, 4♂1♀ (J.D. Lattin, AMNH); Benton County, Grass Mountain, 44°N, 123°W, 30 October 1960, 4♂4♀ (J.D. Lattin, AMNH); Benton County, McGlynn Dr. ravine, moss on road bank, 23 January 1977, 1♂ (L. Russell, CNC); Charleston, 43°20′N, 124°20′W, 7 August 1947, 1♂5♀ (I.M. Newell, AMNH), July 1947, 1♂2♀ (I.M. Newell, AMNH); Lane County, Klickitat Mtn., N side, 23 January 1977, 2♀ (L. Russell, CNC); 10 mi. N of Philomath (*ex newt*), 44°40′N, 123°22′W, about 1950, 1♀ (R. Freiburg, AMNH).

Sisicottus orites (Chamberlin 1919)
Figs. 81, 82, 87, 88, 91–101

Grammonota orites Chamberlin 1919: 249 [♂,♀]. Male holotype from UNITED STATES: Utah, Chalk Creek, Chamberlin, in MCZ, examined.
Oedothorax pidacitis Crosby & Bishop 1927: 151 [♂]. Male holotype from UNITED STATES: Colorado, Larimer County, Pingree Park, Stormy Peaks, 10,000 feet, 20 August 1924, Crosby, in

AMNH, examined. Synonymy by Chamberlin & Ivie 1933.
*Oedothorax orites*: Chamberlin & Ivie 1933: 22 [♀].
Sisicottus montanus, in part: Bishop & Crosby 1938: 57–60, fig. 5 [♂].
Sisicottus orites: Chamberlin & Ivie 1939: fig. 38 [♂]. Platnick 1993: 351.

Diagnosis.—Males of *S. orites* share with *S. crossoclavis*, *S. cynthiae*, and *S. nesides* a heavily sclerotized distal suprategular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They are distinguished from *S. cynthiae* by their longer palpal tibial apophysis (Fig. 94). They are distinguished from *S. crossoclavis* by the presence of an ectal tibial process (Fig. 94, character 17), a long distal suprategular apophysis that extends to near the ventral midline of the palpal bulb, and a smooth terminal margin of the distal suprategular apophysis (Fig. 92, character 4). They are distinguished from *S. nesides* by the terminus of the distal suprategular apophysis which is rounded, often with a shallow central concavity (Fig. 92); in *S. nesides*, the terminus is bifurcated with the inside lobe coming to a sharp apex on or outside of the median line of the distal suprategular apophysis and the outside lobe coming to its apex on the outer margin (Fig. 102). Dimensions of the palpal tibia (Fig. 99) and the number of macrosetae in the ectal tibial cluster (8–13 in *S. orites*; 7–10 in *S. nesides*) may also be useful for distinguishing *S. orites* from *S. nesides*.

Females of *S. orites*, *S. nesides*, and *S. aenigmaticus* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (Fig. 98, character 31); in all other *Sisicottus* species, the lateral margins are sinuous to moderately bowed. Unlike *S. panopeus*, *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, these species have a deep ventral plate invagination (Fig. 96, character 19). *Sisicottus orites* is distinguished from *S. aenigmaticus* by the width of the ventral plate invagination and by the form of the posterior face of the dorsal plate which is trapezoidal with concave sides in *S. aenigmaticus* (Fig. 107) and triangular with nearly straight sides in *S. orites* (Fig. 97, characters 21, 22). Females of *S. orites* are difficult to
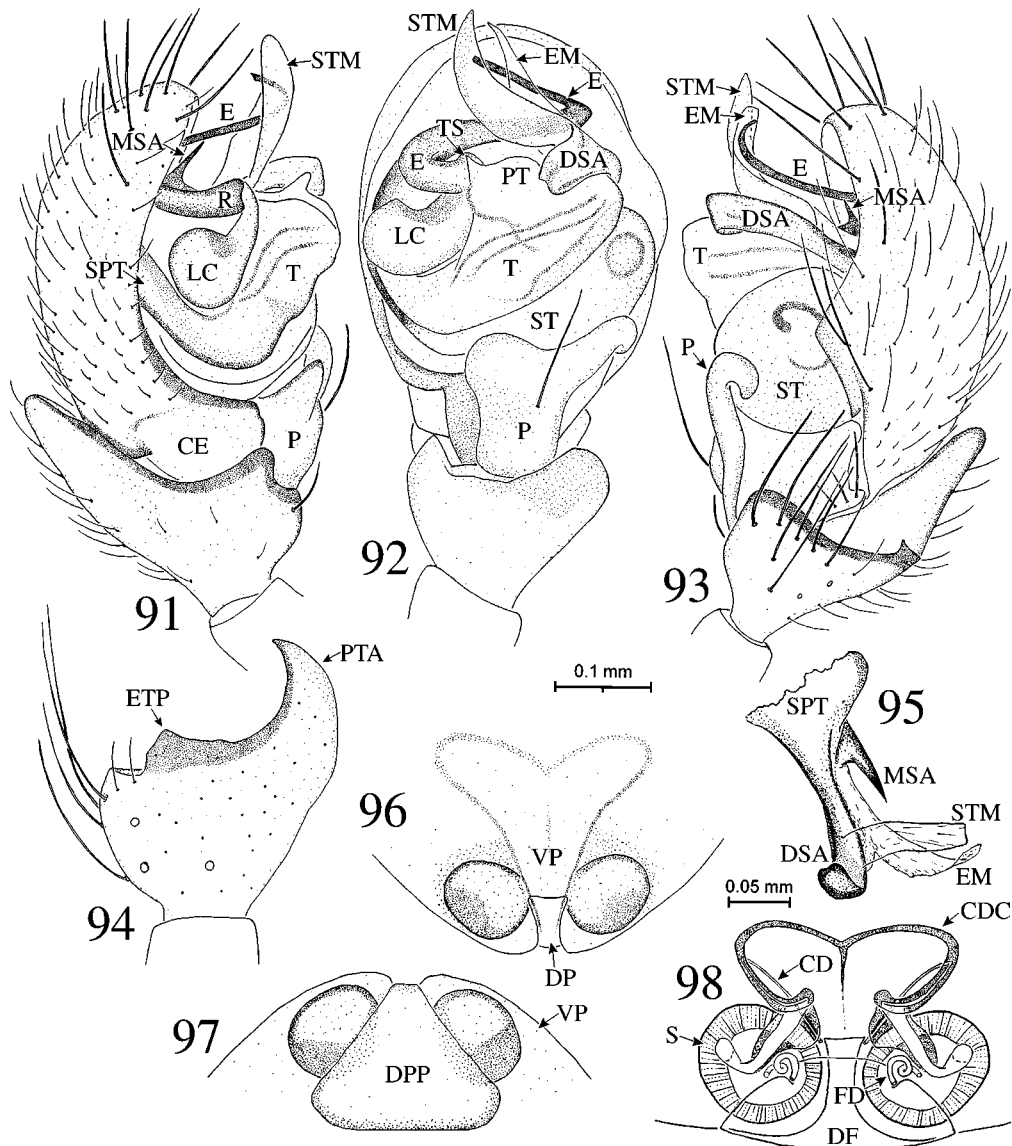
Figures 91–98.—*Sisicottus orites*. 91–94, Palpus of male from Mirror Lake, Utah. 91, Mesal view; 92, Ventral view; 93, Ectal view; 94, Palpal tibia, dorsal view. 95, Suprategulum separated from palpus of male from Smith and Morehouse Canyon, Utah, ectal view. 96, 97, Epigynum of female from Mirror Lake, Utah. 96, Ventral view; 97, Posterior view. 98, Cleared epigynum of female from Smith and Morehouse Canyon, Utah, dorsal view. *Scales:* Figs. 95, 98 = 0.05 mm; other figures = 0.1 mm.

distinguish from those of *S. nesides*. *Sisicottus nesides*, like *S. aenigmaticus*, have a dorsal plate with concave sides on its posterior face (character 22). Also, epigynum length and copulatory duct capsule width are both usually larger in *S. orites* than in either *S. nesides* or *S. aenigmaticus* (Fig. 100).

Description.—Large (carapace length =

0.88–0.20 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus heavily sclerotized, long, extends to near ventral midline of palpal bulb; terminal margin rounded or with shallow concave invagination (Figs. 82, 92). Palpal tibia long with long apophysis; ectal tibial process present (Fig. 94); very
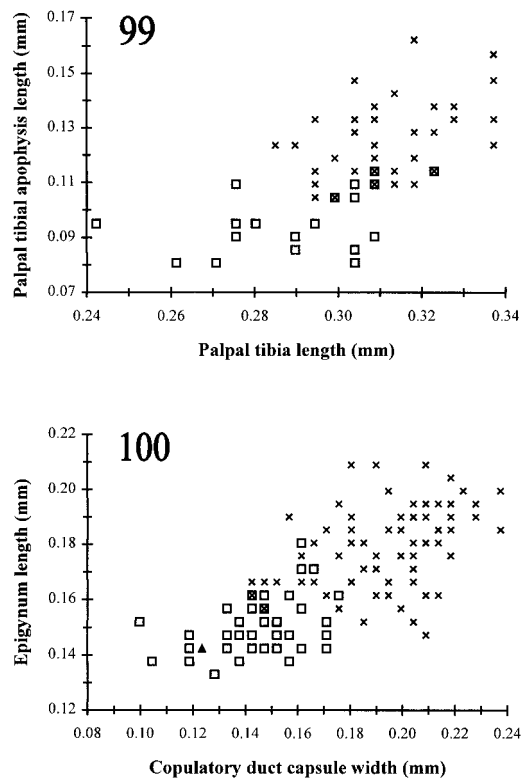
Figures 99–100.—Scattergrams of morphometric characters for males and females of *Sisicottus orites* (×) and *S. nesides* (□) and female of *S. aenigmaticus* (▲). 99, Palpal tibial apophysis length plotted against palpal tibia length in males; 100, Epigynum length plotted against copulatory duct capsule width in females.

dense cluster of macrosetae (8–13) on ectal side of palpal tibia. Females with deep ventral plate invagination (Figs. 87, 96). Posterior face of dorsal plate triangular with nearly straight sides (Figs. 88, 97). Dorsal fold of dorsal plate sclerotized (Fig. 98). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with tips of capsule oriented mesally toward each other; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 98). See Table 2–4.

Natural history.—Collection labels indicate that this species is associated with wet moss and similar microhabitats. It has been collected syntopically with *S. montanus*, *S. panopeus*, and *S. nesides*.

Distribution.—From California, Utah, and

New Mexico north to Washington and Alberta (Fig. 101).

Material examined.—CANADA: *Alberta:* Waterton Lakes Nat'l Park, Cameron Lake, 5300–5500 feet, 9–19 June 1980, 8♂2♀ (J.M. Campbell, CNC), Lower Bertha Falls, sifted moss, 10 June 1980, 1♀ (J.M. Campbell, CNC); Lake Louise, 4 August 1927, 1♂4♀ (Crosby, AMNH); Mt. Edith, Cavill Lodge, 52°41′N, 118°09′W, 24 August 1965, 10♀ (J. & W. Ivie, AMNH); Whitemud Creek, Edmonton, soil sample, 8 May 1959, 3♀ (L.K. Smith, CNC). UNITED STATES: *California:* Laguna Lake, Laguna Canyon, 33°36′N, 117°45′W, 6 July 1934, 1♀ (Ivie & Rasmussen, AMNH). *Colorado:* Berthoud Pass, 39°58′N, 105°48′W, 24 August 1935, 1♂4♀ (Ivie, AMNH); Cameron Pass, 11,000 feet, 40°31′N, 105°52′W, 3 August 1946, 1♀ (C.C. Hoff, AMNH); Miguel County, Trout Lk., NE of Lizard Head Pass, San Juan Mtns., 3100 m, mud flats, moist sedges, 20 July 1959, 1♀ (H.W. Levi, MCZ); Pikes Peak, 11,600 feet, 38°52′N, 105°5′W, 22 July 1940, 3♀ (Ivie, AMNH). *Idaho:* 2 miles south of Tamarack, 44°56′N, 116°23′W, 17 October 1944, 2♂2♀ (Ivie, AMNH); Targhee Pass, 44°38′N, 111°18′W, 30 June 1962, 2♀ (Ivie, AMNH); Willow Flat camp, Franklin County, 42°N, 111°W, 5 July 1952, 3♀ (B. Malkin, AMNH). *Nevada:* Ruby Valley, 40°15′N, 115°25′W, September 1937, 2♂5♀ (Chamberlin, AMNH); White Pine County, Schell Mtns., Timber Cr. Cpgd. area, 30 mi. NE Ely, 8700 feet, from wet moss and substrate, 27 June 1989, 1♀ (E.E. Lindquist, CNC); White Pine County, Schell Mtns., 15 mi SE Ely, 7500 feet, wet moss-stream edge, 26 June 1989, 1♀ (E.E. Lindquist, CNC). *New Mexico:* Panchuela Cpgd, 18 mi. N Pecos, 8400 feet, *ex* liverwort carpet on moist rock wall, 28 August 1973, 1♂ (E.E. Lindquist, CNC). *Oregon:* Douglas County, Diamond Lake, 43°10′N, 122°08′W, 7 September 1949, 1♀ (V. Roth, AMNH); Grant County, Strawberry Creek Falls, 6800 feet, *ex* moss on rocks in falls spray zone, 23 July 1985, 1♀ (E.E. Lindquist, CNC); Grant County, Strawberry Lake area, 6400 feet, *ex* moss, herbs, rotting wood in seepage, 23 August 1985, 1♂ (E.E. Lindquist, CNC); Langdon Lake, Blue Mts, 13 September 1949, 4♀ (V. Roth, AMNH). *Utah:* nr Alta, Little Cottonwood Canyon, under stones in creek, 25 June 1985, 2♀ (C. Dondale & J. Redner, CNC); City Creek Can., Rotary Park, 46°48′N, 111°46′W, 11 September 1942, 8♂8♀ (Ivie, AMNH), 16 September 1942, 4♂4♀ (Ivie, AMNH); Logan Canyon, 4♀ (Chamberlin, MCZ); Mirror Lake, Uintah Mountains, 40°43′N, 110°53′W, 22 September 1932, 4♂4♀ (Ivie, AMNH), 28 July 1936, 4♂4♀ (Ivie, AMNH), 18 August 1942, 4♂4♀ (Ivie, AMNH); Smith and Morehouse Canyon, 40°47′N, 110°6′W, 7 October 1932, 4♂4♀ (W. Ivie, USNM); So. Fork Raft Riv., 8 mi. So. Lynn, 41°53′N,
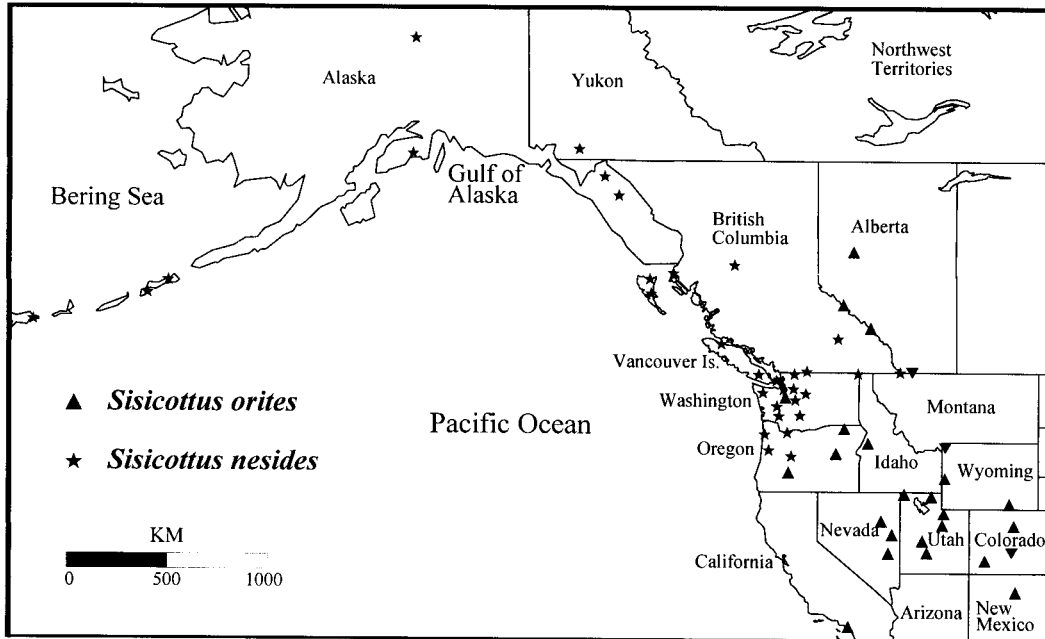
Figure 101.—Western North America, showing distribution of *Sisicottus orites* (▲) and *S. nesides* (★).

113°45′W, 6 September 1932, 5♂10♀ (Chamberlin & Ivie, AMNH); Vicinity of Salt Lake City, quad 40°N, 111°W, misc. 1928–1936, 4♂12♀ (AMNH). *Washington:* Seattle, 47°35′N, 122°20′W, May 1952, 1♂1♀ (Borys Malkin, AMNH). *Wyoming:* Canyon east of Bedford, 42°50′N, 110°50′W, 27 June 1962, 2♀ (Ivie, AMNH); Centennial, Wyoming University, 9500 feet, under log, 17 August 1936, 1♂ (AMNH).

Sisicottus nesides (Chamberlin 1921)
Figs. 83, 84, 89, 90, 99–105

Oedothorax nesides Chamberlin 1921: 36, plate III, figs. 1–2 [♂]. Male holotype from UNITED STATES: Alaska, St. Paul Island, 1910, H. Heath, in MCZ, examined.

Sisicottus montanus: Bishop & Crosby 1938: 57–60, fig. 4 [♂] (in part). Bragg & Leech 1972: 69 (misidentification).

Sisicottus nesides: Chamberlin & Ivie 1939: fig. 39 [♂]. Crawford & Edwards 1988: 437; figs. 23–24 [♀]. Platnick 1993: 351. Dondale et al. 1997: 89.

Sisicottus montanus nesides: Holm 1960: 124. Elevated by Crawford & Edwards 1988.

Sisicottus orites: West et al. 1984: 87 (misidentification).

Diagnosis.—Males of *S. nesides* share with *S. crossoclavis*, *S. cynthiae*, and *S. orites* a heavily sclerotized distal suprategular apoph-

ysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They are distinguished from *S. crossoclavis* by the presence of an ectal tibial process (Fig. 103, character 17) and a long distal suprategular apophysis that extends to near the ventral midline of the palpal bulb and lacks a serrated terminal margin (Fig. 102, character 4); the distal suprategular apophysis in *S. crossoclavis* extends only about half way down the ectal face of the palpal bulb and has a serrated terminal margin (Fig. 67). *Sisicottus nesides* can be distinguished from other *Sisicottus* species with a long, heavily sclerotized distal suprategular apophysis by the terminus of the distal suprategular apophysis which is bifurcated with the inside apex coming to a sharp point on or outside of the median line and the outside apex coming to a point on the outer margin; this condition is unique among *Sisicottus* (Figs. 84, 102). The distal suprategular apophysis in *S. cynthiae* has a rippled terminal margin (Fig. 73); the distal suprategular apophysis in *S. orites* has a rounded terminal margin, often with a shallow central concavity (Fig. 92). Dimensions of the palpal tibia (Fig. 99) and the number of macrosetae in the ectal tib-

ial cluster (7–10 in *S. nesides*; 8–13 in *S. orites*) may also be useful for distinguishing *S. nesides* from *S. orites*.

Females of *S. nesides*, *S. orites*, and *S. aenigmaticus* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (*cf.* Fig. 98, character 31); in all other species, the lateral margins are sinuous to moderately bowed. Unlike *S. panopeus*, *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, these species have a deep ventral plate invagination (Fig. 104, character 19). *Sisicottus nesides* is distinguished from *S. aenigmaticus* by the width of the ventral plate invagination and by the form of the posterior face of the dorsal plate which is trapezoidal in *S. aenigmaticus* (Fig. 107, character 21) and triangular in *S. nesides* (Fig. 105). Females of *S. nesides* are difficult to distinguish from those of *S. orites*. *Sisicottus nesides* have a dorsal plate with concave sides on the posterior face (Fig. 105, character 22) while the dorsal plate of *S. orites* has nearly straight sides on the posterior face (Fig. 97). Also, epigynum length and copulatory duct capsule width are both usually greater in *S. orites* than in either *S. nesides* or *S. aenigmaticus* (Fig. 100).

Description.—Large (carapace length = 0.88–1.20 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis heavily sclerotized, long, extends to near ventral midline; terminus bifurcated with longer inside apex coming to sharp point on or outside median line and the shorter outside apex coming to point on the outside margin (Figs. 84, 102). Palpal tibia moderately long with moderately long palpal tibial apophysis; ectal tibial process present (Fig. 103, character 17); dense cluster of macrosetae (7–9) on ectal side of palpal tibia. Females with deep ventral plate invagination (Figs. 89, 104). Posterior face of dorsal plate triangular with concave sides (Figs. 90, 105). Dorsal fold of dorsal plate sclerotized (*cf.* Fig. 98). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with tips of capsule oriented mesally toward each other; fertilization ducts looped (*cf.* Fig. 98). Aside from some quantitative differences (Fig. 100), internal structure of epigynum virtually identical to that of *S. orites* (Fig. 98). See Tables 2–4.

Natural history.—This species has often been collected in moss and litter microhabitats in forests. In Washington, this species is partially separated from *S. panopeus* by ecological/elevational constraints (Crawford & Edwards 1988; also see the Natural History section in *S. panopeus*). *Sisicottus nesides* occurs syntopically with *S. montanus*, *S. cynthiae, S. aenigmaticus, S. crossoclavis,* and *S. orites*.

Distribution.—From Alaska, Alberta, British Columbia, Oregon, Washington, and the Yukon (Fig. 101). A published record from Nebraska is almost certainly erroneous (Rapp 1980 pers. comm.). A male and a female specimen from Lincoln in the UNSRC identified by M.H. Muma as *S. nesides* are in fact a species of *Walckenaeria* (possibly *W. maesta* Millidge 1983) and an unidentified heterospecific female.

Material examined.—CANADA: *Alberta:* Cameron Lake, Waterton Lakes Nat'l Park, 5300 feet, interception trap, 9–28 June 1980, 1♂ (J.M. Campbell, CNC). *British Columbia:* Albert Bay, 50°34′N, 126°58′W, 21 June 1936, 1♀ (Crosby & Bishop, AMNH); Lake Cowichan, moss on log, 8 July 1976, 1♂2♀ (I.M. Smith, CNC); Grahm Island, Masset, 1944, 1♂ (M.C. Clark, MCZ); Johnson Bay, Babine Lake, leaf litter, 4 July 1987, 2♂10♀ (R. West, CNC); Malahat, Goldstream Prov. Park, V.I., moss on rock at spring run, 11 July 1979, 3♂13♀ (I. Smith, CNC); Manning Prov. Park, Pitfall in rhododendron flat, 20 June-3 July 1979, 1♀ (Dondale, CNC); Metlakatla, 1♂2♀ (Emerton, AMNH); Prince Rupert, 54°09′N, 130°20′W, 22 June 1936, 1♀ (C.R. Crosby, AMNH); Queen Charlotte Is., Louise Is., Skedans, wet moss at seepage spots on old rd, 8 August 1983, 1♂ (J.M. Campbell, CNC); 7.0 km NW Q.C. City, 4–15 August 1983, flight intercept trap, 2♂ (J.M. Campbell, CNC); Wap Lake, Revelstoke, pitfall -rocky bank, July 1985, 1♀ (M.E. Martin, CNC); Wellington, V.I., 5 October 1949, 4♂10♀ (R. Guppy, AMNH). *Yukon:* Kathleen Lake, Kulane Nat'l Park, litter and stones, 12–15 June 1981, 2♀ (C.D. Dondale, CNC). UNITED STATES: *Alaska:* Aleutian Isl., Adak Isl., Andreanof Isl., 26–29 July 1958, 1♀ (C.H. Lindroth, MCZ); Umnak, Fox Islands, July 1958, 1♀ (C. Lindroth, MCZ); Unalaska, Fox Islands, Mt. Makushin, 11–14 July 1958, 1♂4♀ (C. Lindroth, MCZ); Trail to Denver Glacier, Skagway, 25 June 1936, 1♂8♀ (Crosby, AMNH); Haines, Quad. 59°N, 135°W, 20–25 August 1945, 1♀ (Chamberlin, AMNH); Juneau, litter and stones, 8–10 June 1981, 2♀ (C.D. Dondale, CNC), 58°N, 134°W, 28–29 April 1945, 1♀ (Chamberlin,

Table 2.—Quantitative character values for adult males of *Sisicottus* species. Range, mean, standard deviation, and sample size are given for all measurements (in mm). For number of macrosetae in tibial cluster, mode is given in parenthesis.

	S. montigenus	*S. quoylei*	*S. panopeus*
Carapace (length)	0.70–0.80	0.75–0.82	0.67–0.96
	0.74 ± 0.03	0.78 ± 0.03	0.87 ± 0.06
	n = 20	*n* = 6	*n* = 20
Metatarsus I (length)	0.40–0.49	0.39–0.47	0.50–0.58
	0.44 ± 0.03	0.43 ± 0.03	0.54 ± 0.02
	n = 19	*n* = 6	*n* = 19
TmI	0.47–0.62	0.41–0.60	0.45–0.54
	0.56 ± 0.04	0.54 ± 0.07	0.50–0.02
	n = 19	*n* = 6	*n* = 19
Palpal tibial apophysis (length)	0.014–0.034	0.019–0.038	0.081–0.124
	0.023 ± 0.007	0.031 ± 0.008	0.102 ± 0.013
	n = 22	*n* = 6	*n* = 20
Palpal tibia (length)	0.138–0.176	0.147–0.171	0.238-0.295
	0.157 ± 0.011	0.163 ± 0.008	0.265 ± 0.016
	n = 22	*n* = 6	*n* = 20
Palpal tibia (width)	0.128–0.166	0.138–0.162	0.181–0.223
	0.150 ± 0.009	0.151 ± 0.008	0.202 ± 0.014
	n = 22	*n* = 6	*n* = 20
Paracymbium (length)	0.095–0.162	0.109–0.119	0.133–0.170
	0.116 ± 0.016	0.115 ± 0.004	0.150 ± 0.008
	n = 20	*n* = 6	*n* = 20
Paracymbium (width)	0.109–0.133	0.119–0.133	0.138–0.162
	0.120 ± 0.006	0.124 ± 0.006	0.152 ± 0.007
	n = 20	*n* = 6	*n* = 20
Lamella characteristica (length)	0.090–0.124	0.109–0.119	0.124–0.156
	0.107 ± 0.010	0.112 ± 0.004	0.138 ± 0.008
	n = 20	*n* = 6	*n* = 20
Number of macrosetae in tibial cluster	3–7 (6)	3–6 (5)	7–11 (8)
	5.35 ± 1.14	4.67 ± 1.03	8.55 ± 0.94
	n = 20	*n* = 6	*n* = 20

AMNH); Primrose Camp, 18 mi. N. of Seward, 60°20′N, 149°20′W, 24 August 1968, 13♂22♀ (W. Ivie, AMNH); 5 mi. S rapids on Richardson Hiway, 26 June 1945, 1♂ (J.C. Chamberlin, AMNH); Skagway, 59°28′N, 135°15′W, 24 June 1939, 2♀ (Crosby, AMNH). *Oregon:* Benton County, Mary's Peak, sod in alder clearing, 28 November 1976, 1♀ (L. Russell, CNC); Latourell Falls, 45°N, 122°W, 4 August 1929, 1♂4♀ (Chamberlin, AMNH); Proxy Falls, Hwy 242, 28 mi. SW Sisters, 3000 feet, *ex* wet moss and debris, depression by waterfall, 19 August 1985, 1♀ (E.E. Lindquist, CNC); Tillamook County, moss near stream, 19 December 1976, 2♀ (L. Russell, CNC). *Washington:* Chelan County, Nason Creek, 47.783°N, 120.874°W, 2280 feet, under rocks by stream, 6 June 1992, 1♂ (Rick Sugg, UWBM); Clallam County, Pillar Pt (W side), 48.220°N, 124.125–130°W, 0–100 feet, *ex* moss on forest floor, 22 May 1987, 2♂ (R. Crawford, UWBM); Emmons Trail, Tainier Park, 46°54′N, 121°39′W, 6 July 1938, 2♀ (Ivie, AMNH); Friday

Harbor, 1924, 1♀ (AMNH); Thurston County, The Evergreen State College, wetland south of Evergreen Parkway, 47°4′10″N, 122°57′39″W, elev. 50 m, *ex* moss on downed *Salix* tree, 16 July 1993, 1♀ (J. Miller, author's personal collection), Woodland SE of Corner of Overhulse Place and Driftwood Road, 47.026°N, 122.962°W, elev. 50 m, 26 October 1992, 1♀ (J. Miller, author's personal collection); Jefferson County, Olympic National Park, Hoh Riv., 510 feet, 47.846°N, 123.960°W, *ex* moss in *Acer macrophyllum*, 29 January 1983, 1♀ (J. Longino, UWBM); Lewis County, Lewis & Clark S.P., 46.519°N, 122.815°W, 380 feet, *ex* leaf litter, 29 October 1988, 1♂1♀ (R. Crawford, UWBM); King County, E. of Change Creek, 1250 feet, 47°44′N, 121°66′W, wet moss and litter in and near seepage, 7 July 1996, 3♂4♀ (J. & C. Zujko-Miller, J. & H. Miller, author's personal collection); King County, W of Change Cr., 1280 feet, 47.439°N, 121.633°W, 9 April 1989, 2♂6♀ (R. Crawford, UWBM); King County, Happy Valley bog, 47.640°N, 122.017°W,

Table 2.—Extended.

S. montanus	S. crossoclavis	S. cynthiae	S. orites	S. nesides
0.71–0.93	0.83–0.97	1.00–1.10	0.93–1.20	0.99–1.24
0.86 ± 0.04	0.88 ± 0.08	1.04 ± 0.04	1.07 ± 0.07	1.10 ± 0.08
n = 56	n = 3	n = 9	n = 37	n = 22
0.45–0.58	0.51–0.66	0.67–0.74	0.66–0.81	0.71–0.83
0.52 ± 0.03	0.58 ± 0.07	0.71 ± 0.02	0.73 ± 0.05	0.77 ± 0.03
n = 53	n = 3	n = 9	n = 37	n = 19
0.45–0.65	0.49–0.56	0.49–0.58	0.42–0.56	0.47–0.60
0.58 ± 0.04	0.52 ± 0.04	0.54 ± 0.03	0.50 ± 0.03	0.54 ± 0.04
n = 53	n = 3	n = 9	n = 37	n = 19
0.043–0.076	0.124–0.171	0.067–0.090	0.105–0.162	0.081–0.114
0.058 ± 0.007	0.155 ± 0.027	0.079 ± 0.009	0.126 ± 0.014	0.096 ± 0.011
n = 57	n = 3	n = 9	n = 39	n = 21
0.162–0.228	0.261–0.333	0.257–0.318	0.266–0.337	0.242–0.323
0.193 ± 0.012	0.306 ± 0.039	0.295 ± 0.023	0.306 ± 0.020	0.289 ± 0.021
n = 57	n = 3	n = 9	n = 37	n = 22
0.152–0.185	0.209–0.228	0.176–0.219	0.185–0.261	0.162–0.233
0.172 ± 0.009	0.217 ± 0.010	0.200 ± 0.015	0.229 ± 0.019	0.120 ± 0.016
n = 57	n = 3	n = 9	n = 37	n = 22
0.105–0.152	0.143–0.166	0.124–0.171	0.152–0.195	0.157–0.195
0.130 ± 0.009	0.157 ± 0.013	0.155 ± 0.015	0.175 ± 0.011	0.174 ± 0.010
n = 57	n = 3	n = 9	n = 37	n = 22
0.119–0.152	0.143–0.147	0.152–0.176	0.133–0.190	0.143–0.181
0.136 ± 0.006	0.146 ± 0.003	0.165 ± 0.009	0.178 ± 0.011	0.166 ± 0.008
n = 57	n = 3	n = 9	n = 37	n = 22
0.100–0.133	0.128–0.162	0.133–0.143	0.143–0.176	0.124–0.157
0.121 ± 0.007	0.143 ± 0.017	0.138 ± 0.004	0.159 ± 0.009	0.145 ± 0.009
n = 57	n = 3	n = 9	n = 37	n = 22
2–6 (4)	7–9 (9)	6–8 (7)	8–13 (9)	7–10 (7)
4.16 ± 0.80	8.33 ± 1.16	7.22 ± 0.67	9.38 ± 1.11	7.68 ± 0.72
n = 57	n = 3	n = 9	n = 37	n = 22

125 feet, sifted in deciduous litter, 11 October 1980, 1♂ (R. Crawford, UWBM); Snohomish County, Lake Twentytwo Research Natural Area, trail head, old growth forest, sifted from moss on log, 25 June 1993, 4♀ (J. Miller, author's personal collection); Mt. Rainier Nat. Park, Nisqually River, 3900 feet, 8 August 1973, 1♂11♀ (A. Smetana, CNC); Mt. Rainier Nat. Park, North Puyallup River, 3700 feet, 10 August 1973, 7♀ (A. Smetana, CNC); Paradise, Rainier Nat'l Park, 46°48′N, 121°44′W, 12 September 1965, 3♂10♀ (J. & W. Ivie, AMNH); Pend Oreille County, Deemer Creek, 48.931°N 117.089°W, 4600 feet, sifted from soggy moss at stream edge, 13 June 1986, 1♂ (R. Crawford, UWBM); 4 mi. N Silver Fir Cmpg., Mt Baker, 4000 feet, 16 August 1975, 1♀ (J.M. Campbell, CNC); Skagit County, E of Swede Cr., 48.562–65°N, 122.216°W, 350 feet, *ex* mixed leaf litter, 19 March 1988, 1♀ (R. Crawford, UWBM); 10 miles north of Vancouver, 45°45′N, 122°38′W, 10 September 1935, 1♀ (Chamberlin & Ivie, AMNH); Whatcom

County, Blue Lake Trail, 48.652°N, 121.786°W, 5000 feet, *ex* rotten log, 13 September 1986, 1♀ (R. Crawford, UWBM); Yakima County, Bear Creek Mtn Trail, 46.552°N, 121.315°W, 6160 feet, ♂ *-ex* wet moss by stream, ♀ *-ex* rotten log, 4 September 1986, 1♂1♀ (R. Crawford, UWBM).

Sisicottus aenigmaticus new species
Figs. 72, 100, 106–108

Sisicottus orites: Crawford 1988: 15 (misidentification). Crawford & Edwards 1988: 437; figs. 25–26 [♀] (misidentification).

Types.—Female holotype from UNITED STATES: Washington, King County, W. of Change Cr. 1280 feet, 47.439°N, 121.663°W, *ex* moss in & nr spring, 22 August 1981, R.E. Nelson, deposited in UWBM.

Etymology.—The specific name is a Latin adjective meaning enigmatic.

Table 3.—Quantitative character values for adult females of *Sisicottus* species. *Sisicottus aenigmaticus* is the female holotype alone. For all other species, range, mean, standard deviation, and sample size are given (in mm). Ventral plate invagination width is poorly defined in *S. panopeus, S. montanus,* and *S. crossoclavis* and was not recorded for these species.

	S. montigenus	S. quoylei	S. panopeus	S. montanus
Carapace (length)	0.67–0.80	0.71–0.80	0.82–0.95	0.72–0.88
	0.74 ± 0.03	0.76 ± 0.02	0.88 ± 0.04	0.81 ± 0.04
	n = 33	*n* = 12	*n* = 21	*n* = 57
Metatarsus I (length)	0.31–0.46	0.35–0.42	0.45–0.56	0.39–0.52
	0.42 ± 0.03	0.39 ± 0.02	0.50 ± 0.03	0.45 ± 0.03
	n = 33	*n* = 10	*n* = 21	*n* = 57
TmI	0.48–0.77	0.52–0.63	0.45–0.73	0.50–0.75
	0.60 ± 0.05	0.58 ± 0.04	0.52 ± 0.06	0.59 ± 0.04
	n = 33	*n* = 10	*n* = 21	*n* = 57
Epigynum (length)	0.124–0.176	0.109–0.128	0.114–0.162	0.095–0.166
	0.149 ± 0.012	0.130 ± 0.010	0.139 ± 0.012	0.148 ± 0.012
	n = 33	*n* = 12	*n* = 22	*n* = 59
Copulatory duct capsule (width)	0.124–0.176	0.114–0.152	0.105–0.162	0.109–0.176
	0.149 ± 0.012	0.130 ± 0.010	0.133 ± 0.014	0.138 ± 0.015
	n = 33	*n* = 12	*n* = 22	*n* = 59
Dorsal plate posterior face (width)	0.081–0.119	0.076–0.105	0.076–0.100	0.067–0.114
	0.099 ± 0.010	0.089 ± 0.008	0.085 ± 0.008	0.087 ± 0.011
	n = 33	*n* = 12	*n* = 22	*n* = 59
Dorsal plate posterior face (height)	0.105–0.138	0.081–0.124	0.081–0.109	0.071–0.114
	0.118 ± 0.009	0.112 ± 0.011	0.096 ± 0.009	0.088 ± 0.008
	n = 33	*n* = 12	*n* = 22	*n* = 59
Ventral plate invagination (depth)	0.090–0.119	0.071–0.081	0–0.024	0.005–0.033
	0.095 ± 0.008	0.075 ± 0.004	0.010 ± 0.005	0.019 ± 0.006
	n = 29	*n* = 12	*n* = 22	*n* = 59
Ventral plate invagination (width)	0.062–0.109	0.014–0.043		
	0.080 ± 0.012	0.032 ± 0.009		
	n = 33	*n* = 12		

Diagnosis.—Males are unknown, but are probably similar to *S. orites* and *S. nesides*. Females of *S. aenigmaticus*, *S. orites*, and *S. nesides* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (Fig. 108, character 31); in all other species, the lateral margins are sinuous to moderately bowed. They are distinguished from all other *Sisicottus* species except *S. montigenus* by their very wide ventral plate invagination (Fig. 106). The dorsal plate with a trapezoidal posterior face is unique in *Sisicottus* (Fig. 107, character 21). They also differ from all other *Sisicottus* species in having smaller, more widely spaced spermathecae with very narrow margins and copulatory ducts with a relatively narrow proximal part (Fig. 108).

Description.—Large (carapace length = 0.91 mm); single known specimen lighter than nor-mal (see remarks below). Ventral plate invagination deep and wide (Fig. 106). Posterior face of dorsal plate trapezoidal, flat ventrally, widest dorsally with concave sides (Fig. 107). Dorsal fold of dorsal plate sclerotized (Fig. 108). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with the tips of the capsule oriented mesally toward each other; spermathecae relatively small with very narrow margins; copulatory ducts relatively narrow and sinuous; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 108). See Table 3.

Remarks.—This species is known from a single female specimen. It is lightly sclerotized in a way that is characteristic of specimens that have only recently molted to the adult instar. This specimen may be a mutant individual of *S. nesides*, which has also been collected at the Change Creek site, but I think it more likely that it is a member of a distinct

Table 3.—Extended.

S. crossoclavis	S. cynthiae	S. orites	S. nesides	S. aenigmaticus
0.81–0.90	0.88–1.06	0.88–1.13	0.86–1.12	0.91
0.85 ± 0.04	0.98 ± 0.05	1.00 ± 0.06	0.97 ± 0.07	
n = 13	*n* = 15	*n* = 72	*n* = 45	
0.43–0.53	0.60–0.74	0.55–0.78	0.58–0.71	0.63
0.5 ± 0.03	0.67 ± 0.04	0.65 ± 0.05	0.65 ± 0.04	
n = 13	*n* = 14	*n* = 71	*n* = 39	
0.44–0.54	0.45–0.60	0.34–0.62	0.48–0.63	0.55
0.50 ± 0.03	0.56 ± 0.05	0.51 ± 0.04	0.54 ± 0.03	
n = 12	*n* = 14	*n* = 71	*n* = 39	
0.138–0.166	0.128–0.162	0.152–0.209	0.133–0.181	0.14
0.156 ± 0.009	0.144 ± 0.010	0.179 ± 0.013	0.150 ± 0.010	
n = 13	*n* = 15	*n* = 73	*n* = 50	
0.105–0.147	0.128–0.162	0.143–0.238	0.100–0.176	0.12
0.130 ± 0.013	0.144 ± 0.010	0.187 ± 0.023	0.145 ± 0.016	
n = 13	*n* = 15	*n* = 73	*n* = 50	
0.105–0.143	0.109–0.152	0.124–0.204	0.143–0.228	0.21
0.126 ± 0.014	0.135 ± 0.012	0.165 ± 0.018	0.181 ± 0.019	
n = 13	*n* = 15	*n* = 73	*n* = 50	
0.100–0.124	0.086–0.133	0.109–0.181	0.105–0.171	0.152
0.112 ± 0.007	0.108 ± 0.014	0.152 ± 0.016	0.147 ± 0.014	
n = 13	*n* = 15	*n* = 73	*n* = 50	
0–0.019	0.014–0.038	0.052–0.090	0.043–0.086	0.062
0.011 ± 0.005	0.023 ± 0.007	0.074 ± 0.009	0.058 ± 0.009	
n = 13	*n* = 15	*n* = 60	*n* = 49	
	0.014–0.043	0.005–0.043	0.005–0.043	0.067
	0.023 ± 0.007	0.022 ± 0.009	0.020 ± 0.008	
	n = 15	*n* = 73	*n* = 49	

species. Since syntopy is common for *Sisicottus* species, I do not regard the fact that *S. nesides* have been collected at the type locality of *S. aenigmaticus* as evidence that the later is an aberrant form of the former. Of course, the collection of more specimens will be needed in order to test this hypothesis. The Change Creek collection site has yielded a number of other rare and unique spiders including undescribed species of the linyphiid genera *Hal-*

Table 4.—Quantitative character values for male holotype specimens of *Sisicottus* species. Data for the female holotype of *S. aenigmaticus* are given in Table 3. All measurements in mm.

	S. montigenus	S. quoylei	S. panopeus	S. montanus	S. crossoclavis	S. cynthiae	S. orites	S. nesides
Carapace length	0.75	0.75	0.88	0.89	0.97	1.00	0.97	1.00
Metatarsus I length		0.39	0.52	0.48	0.66	0.68	0.68	
TmI		0.41	0.45	0.64	0.56	0.54	0.54	
Palpal tibial apophysis length	0.02	0.04	0.09	0.06	0.17	0.08	0.12	0.09
Palpal tibia length	0.16	0.15	0.23	0.17	0.32	0.3	0.29	0.28
Palpal tibia width	0.15	0.15	0.2	0.19	0.23	0.2	0.19	0.16
Paracymbium length	0.11	0.11	0.16	0.13	0.17	0.17	0.18	0.17
Paracymbium width	0.12	0.12	0.15	0.13	0.15	0.16	0.15	0.14
Lamella length	0.14	0.11	0.14	0.12	0.16	0.14	0.14	0.13
Macrosetae in tibial cluster	3	6	7	4	7	7	10	7
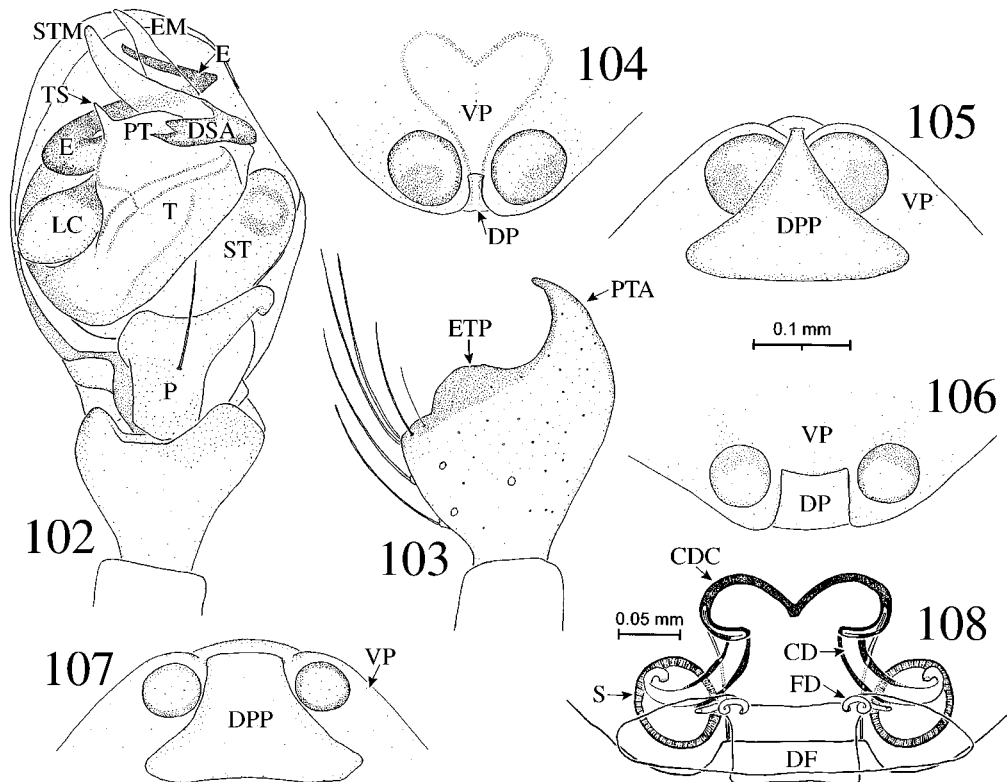
Figures 102–108.—*Sisicottus nesides* and *S. aenigmaticus*. 102–105, *S. nesides* from Primrose Camp, Alaska. 102, Palpus, ventral view; 103, Palpal tibia, dorsal view; 104, Epigynum, ventral view; 105, Epigynum, posterior view. 106–108, Epigynum of *S. aenigmaticus* holotype from Change Creek, Washington. 106, Ventral view; 107, Posterior view; 108, Cleared, dorsal view. *Scales:* Fig. 108 = 0.05 mm; other figures = 0.1 mm.

orates Hull 1911 and *Eulaira* Chamberlin & Ivie 1933, and something that may belong to the dictynid genus *Saltonia* Chamberlin & Ivie 1942 (R. Crawford pers. comm.).

Natural history.—The single specimen was collected from moss in and near a spring.

Distribution.—Known only from the type locality (Fig. 72).

ACKNOWLEDGMENTS

Figures 109–114.—Scanning electron micrographs of *Sisicottus* and *Typhochrestus*. 109, Tarsal claw of female *Sisicottus panopeus* from Mt. Rainier, Washington. 110–112, *Typhochrestus uintanus* from Mirror Lake, Utah. 110, Epigynum, ventral view; 111, Palpus, apical view; 112, Palpus, ectal view. 113, 114, *Typhochrestus digitatus* from Whiteford Burrows, England. 113, Palpus, ventral view; 114, Palpus, ectal view.

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Table 5.—Data matrix, characters and states. Number of steps (St), consistency index (CI), retention index (RI), and rescaled consistency index (RC) are from the preferred most parsimonious tree. "?" = unknown; "—" = not applicable.

Characters and states	Islandiana princeps	Diplocentria bidentata	Typhochrestus digitatus	Typhochrestus uintanus	Erigone psychrophila	Tmeticus tolli	Walckenaeria directa	Gonatium rubens
Male palpus								
1. embolus: short; long	0	0	1	1	0	0	1	1
2. terminal embolic hook: abs; pres	0	0	0	0	0	0	0	0
3. DSA sclerotization: mem; light; heavy	1	1	0	1	2	1	1	1
4. DSA: short; long	0	0	0	0	1	0	0	0
5. STM: absent; present	0	0	0	0	0	0	0	1
6. MSA: absent; present	0	1	1	1	0	0	0	0
7. TP: present; absent	0	0	0	0	0	0	0	0
8. TP shape: straight; spiral; ectal; anterior	2	0	1	1	3	0	1	0
9. LC: absent; present	0	0	0	0	0	0	0	1
10. ARP: absent; present	1	1	1	1	1	1	0	0
11. ARP shape: short; long and spiral	0	0	1	1	0	0	—	—
12. PT papillae: absent; present	1	1	1	1	0	0	0	—
13. TS: absent; present	0	0	0	0	0	1	0	1
14. P, ventral view: narrow; wide	0	0	0	0	0	0	0	0
15. CE: small; large	1	0	0	0	1	0	0	1
16. TA length: short; long	0	1	0	0	1	1	0	0
17. ETP: strong; weak or absent	1	0	0	1	0	0	0	0
18. patella apophysis: absent; present	0	0	0	0	1	1	0	0
Female genitalia								
19. VP: beyond EF; shallow inv; deep inv	0	0	2	2	0	2	2	2
20. median VP: convex; concave	0	0	0	0	1	0	1	1
21. DPP: rect; invert tri; tri; trapezoid	1	0	0	0	1	0	0	2
22. sides DPP: convex; concave	0	0	0	0	0	0	0	0
23. vent mar DPP: concave; convex	1	0	0	0	1	1	1	1
24. DF sclerotization: light; heavy	0	0	0	0	0	0	0	0
25. CO: small; large	1	0	0	1	0	0	1	1
26. CD origin: ectal; mesal	1	0	1	1	1	1	1	1
27. CD anterior proj: absent; present	0	0	1	1	1	0	0	1
28. CD encapsulation: absent; present	0	0	1	0	1	1	1	0
29. CDC: partial; complete	—	—	1	—	1	0	1	—
30. ant lat CDC: concave; straight; convex	—	—	0	—	0	—	1	—
31. lat mar CDC: curved; bowed	—	—	0	—	0	—	0	—
32. post CDC orientation: post; mesal	—	—	0	—	0	0	0	—
33. FD origin: posterior; mesal	1	0	1	1	1	1	1	1
34. FD shape: sinuous; spiral	0	1	0	0	0	0	0	1
Somatic morphology								
35. cephalic region: not raised; raised	0	0	0	0	1	0	0	1
36. post PME lobe: absent; present	0	0	1	0	0	0	0	0
37. cuticular pores: absent; present	0	0	1	?	0	0	1	0
38. cheliceral file: ridged; scaly; imb	2	2	2	?	2	1	0	1
39. dorsal spur: absent; present	0	0	0	0	0	1	0	0
40. tibia III m-setae: two; one	0	1	0	0	0	1	1	1
41. Tm IV: absent; present	0	0	0	0	1	1	1	1

Table 5.—Extended.

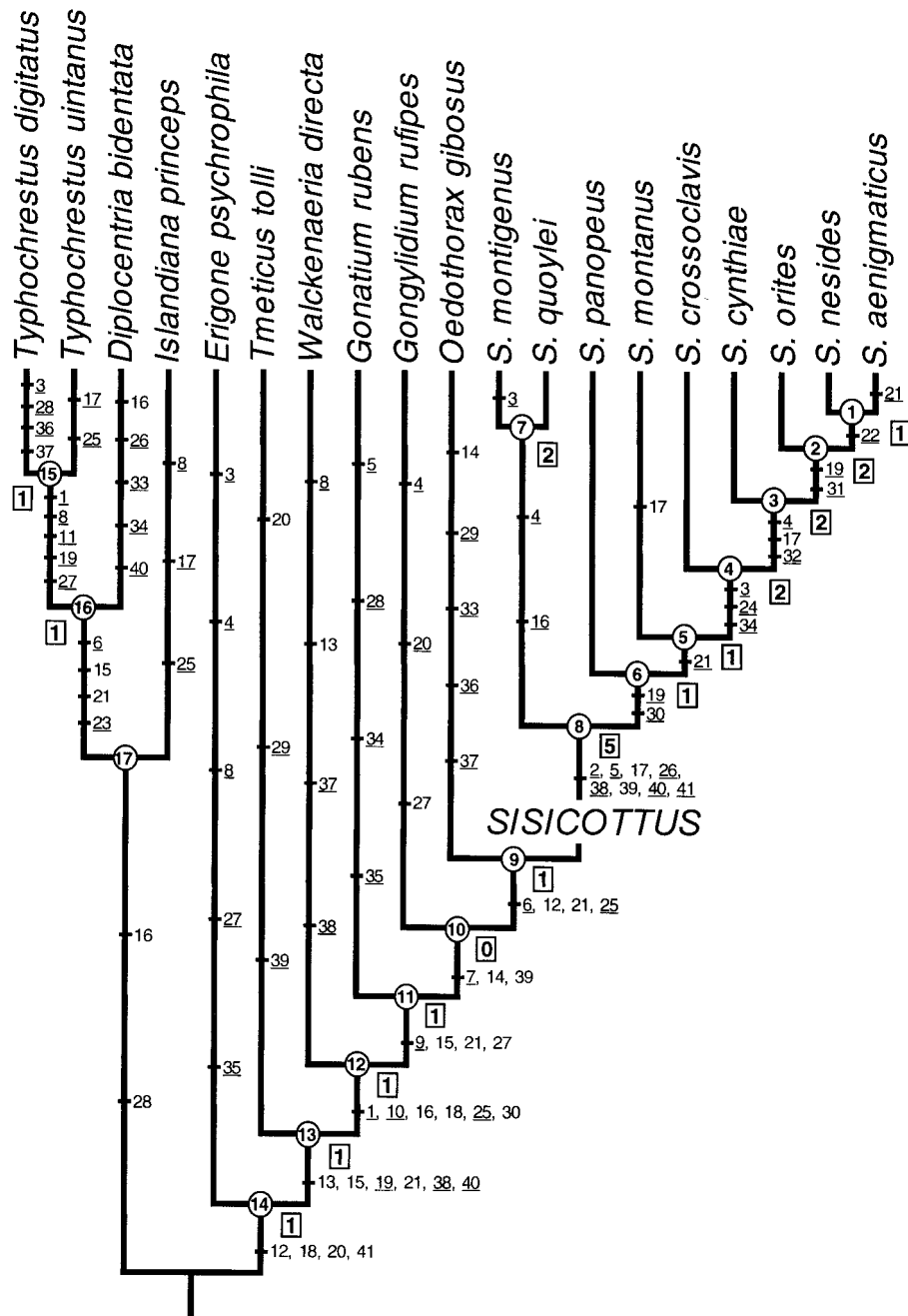| Gongylidium rufipes	Oedothorax gibbosus	Sisicottus montigenus	Sisicottus quoylei	Sisicottus panopeus	Sisicottus montanus	Sisicottus crossoclavis	Sisicottus cynthiae	Sisicottus orites	Sisicottus nesides	Sisicottus aenigmaticus	St	CI	RI	RC
1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.67	0.33
0	0	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
1	1	0	1	1	1	2	2	2	2	?	4	0.50	0.60	0.30
1	0	1	1	0	0	0	1	1	1	?	4	0.25	0.50	0.13
0	0	1	1	1	1	1	1	1	1	?	2	0.50	0.88	0.44
0	1	1	1	1	1	1	1	1	1	?	2	0.50	0.80	0.40
1	1	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	?	4	0.75	0.50	0.38
1	1	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
0	0	0	0	0	0	0	0	0	0	?	1	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	?	1	1.00	1.00	1.00
1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.50	0.25
1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.80	0.40
1	0	1	1	1	1	1	1	1	1	?	2	0.50	0.88	0.44
1	1	1	1	1	1	1	1	1	1	?	3	0.33	0.50	0.17
0	0	1	1	0	0	0	0	0	0	?	4	0.25	0.25	0.06
0	0	1	1	1	0	1	0	0	0	?	5	0.20	0.20	0.04
0	0	0	0	0	0	0	0	0	0	?	2	0.50	0	0
2	2	2	2	1	1	1	1	2	2	2	4	0.50	0.60	0.30
0	1	1	1	1	1	1	1	1	1	1	3	0.33	0.60	0.20
2	0	0	0	0	1	1	1	1	1	3	6	0.50	0.57	0.29
0	0	0	0	0	0	0	0	0	1	1	1	1.00	1.00	1.00
1	1	1	1	1	1	1	1	1	1	1	1	1.00	1.00	1.00
0	0	0	0	0	0	1	1	1	1	1	1	1.00	1.00	1.00
1	0	0	0	0	0	0	0	0	0	0	4	0.25	0.25	0.06
1	1	0	0	0	0	0	0	0	0	0	2	0.50	0.88	0.44
0	1	1	1	1	1	1	1	1	1	1	4	0.25	0.25	0.06
1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.33	0.11
1	0	1	1	1	1	1	1	1	1	1	2	0.50	0	0
1	—	1	1	2	2	2	2	2	2	2	2	1.00	1.00	1.00
0	—	0	0	0	0	0	0	1	1	1	1	1.00	1.00	1.00
0	0	0	0	0	0	0	1	1	1	1	1	1.00	1.00	1.00
1	0	1	1	1	1	1	1	1	1	1	2	0.50	0	0
0	0	0	0	0	0	1	1	1	1	1	3	0.33	0.67	0.22
0	0	0	0	0	0	0	0	0	0	?	2	0.50	0	0
0	1	0	0	0	0	0	0	0	0	?	2	0.50	0	0
0	1	0	0	0	0	0	0	0	0	?	3	0.33	0	0
1	1	2	2	2	2	2	2	2	2	2	3	0.67	0.67	0.44
1	1	0	0	0	0	0	0	0	0	?	3	0.33	0	0
1	1	0	0	0	0	0	0	0	0	0	3	0.33	0.60	0.20
1	1	0	0	0	0	0	0	0	0	0	2	0.50	0.80	0.40

Figure 115.—Preferred most parsimonious cladogram of *Sisicottus* species based on successive character weighting and implied weights. Underlined numbers indicate unambiguous character change optimizations; the remaining characters were optimized to favor reversal over parallel evolution (Farris optimization) unless explicitly justified in the text. Bremer support values appear as boxed numbers to the right of each applicable internode. The circled numbers at each node identify clades discussed in the text.

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Note added in proof: Dondale (1990) included two illustrations labeled "*Sisicottus* sp." in his key to litter-inhabiting spiders in North America. Although there is no documentation of what specimens the illustrations were based on, his figure 17.142 is probably the palpal tibia of *S. quoylei*; his figure 17.157 is probably the epigynum of *S. montanus*.