

## A re-evaluation of the milliped genus *Motyxia* Chamberlin, with a re-diagnosis of the tribe Xystocheirini and remarks on the bioluminescence (Polydesmida: Xystodesmidae)

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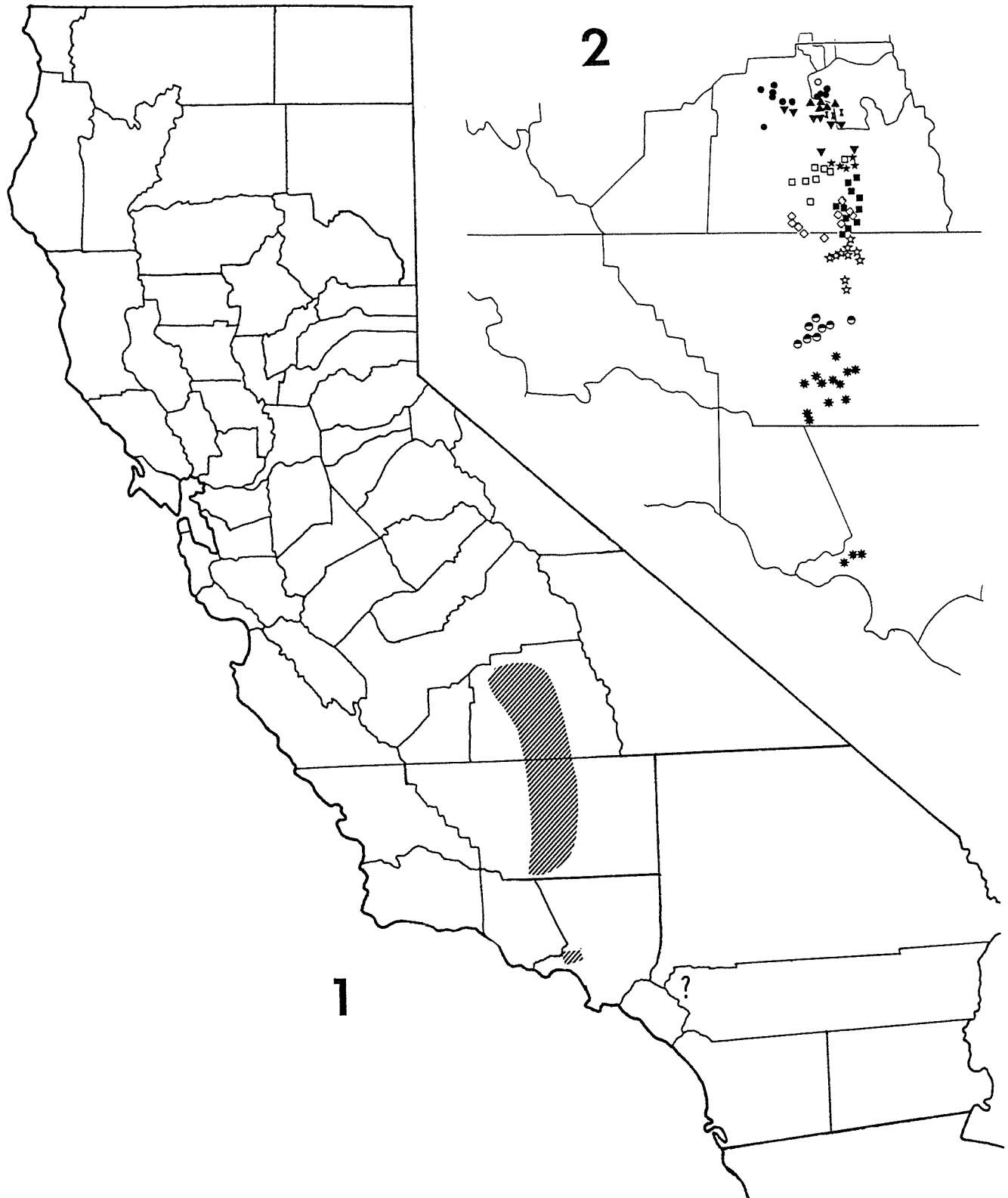
**Abstract:** *Motyxia* Chamberlin is comprised of eight species of bioluminescent xystocheirine millipeds in which the gonopodal solenomere arises at different positions, from basally and subbasally on the acropodite to being fused with the companion acropodal branch and detaching proximad or near midlength. Previous synonymies of *Amplocheir* Chamberlin and *Luminodesmus* Loomis and Davenport under *Motyxia* are confirmed as is its assignment to the tribe Xystocheirini, which is redefined. Component species are *M. kerna* Chamberlin, the type species, *monica* Chamberlin, *sequoiae* (Loomis and Davenport), *tularea* (Chamberlin), *sequoia* (Chamberlin), *pior* Chamberlin, *porrecta* Causey and Tiemann, and *tiemanni* Causey. *Motyxia sequoia* is comprised of two races, the nominate and *sequoia alia* Causey and Tiemann; *sequoia ollae* Causey and Tiemann is properly a subspecies of *tularea*. *Motyxia pior* form *secca* is an invalid name without standing in nomenclature, and *M. tejona* Chamberlin, and *M. expansa* and *exilis*, both by Loomis, are placed in synonymy under *M. monica*, the oldest name for the southernmost species, as *Polydesmus dissectus* Wood is referable to *Xystocheir* Cook. The bioluminescence is a continuous, neon-white glow of the entire dorsal surface including the antennae and legs. Its visibility at night suggests a warning function analogous to aposematic coloration. The phenomenon may observe a circadian rhythm, and controlled photoperiod experimentation may be productive.

### Introduction

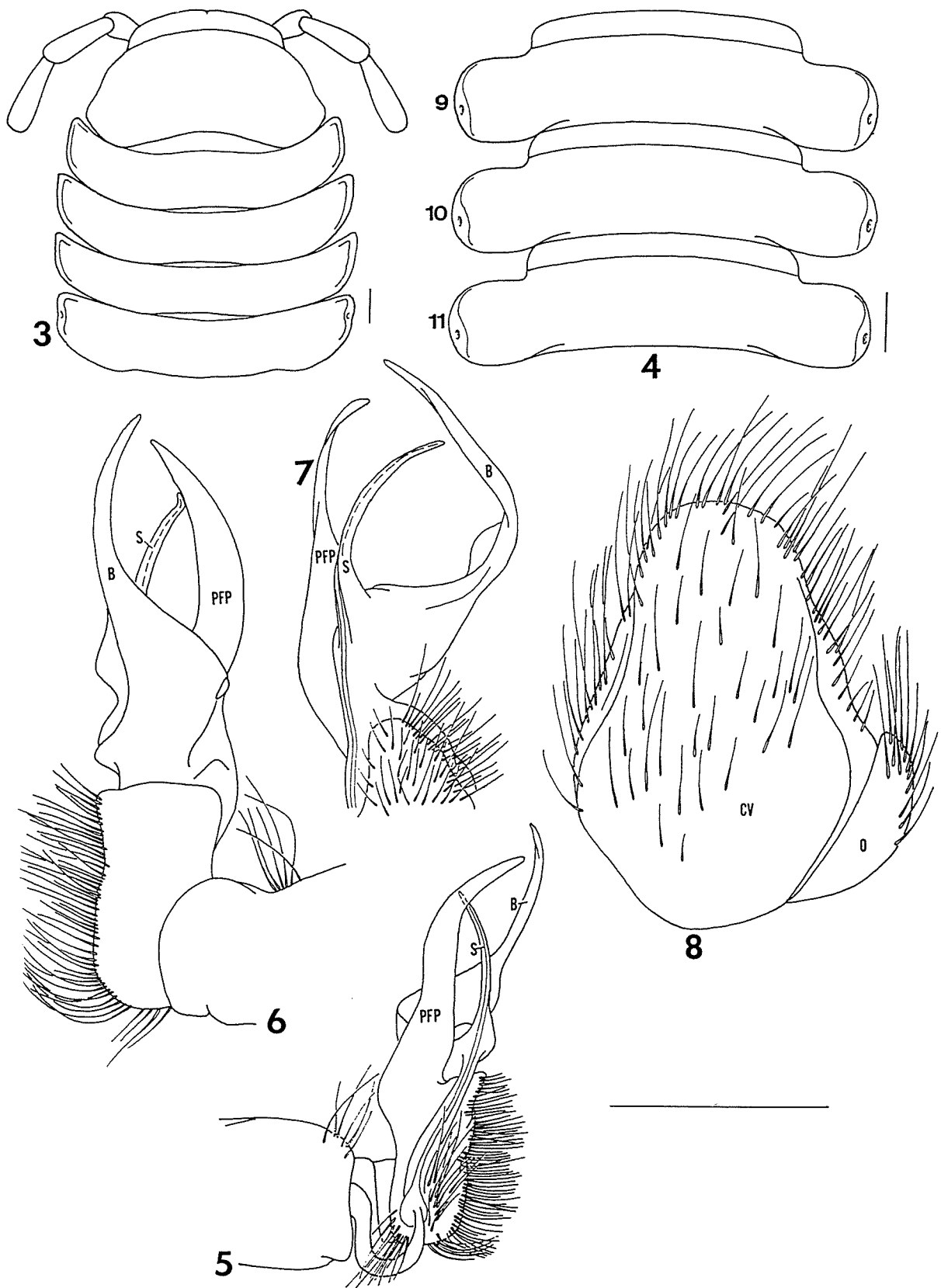
The dominant xystodesmid milliped genus in the southern Sierra Nevada, south of Sequoia National Park, is *Motyxia* Chamberlin. It ranges westward to the Pacific Ocean through the Tehachapi and Santa Monica Mountains and is the southernmost representative of the family in California and western North America (Figs. 1, 2). The only genus of bioluminescent millipeds, *Motyxia*, was revised by Causey and Tiemann (1969), but the cyphopods were not characterized, and two nomenclatural changes are necessary. *Motyxia sequoia ollae* Causey and Tiemann is actually a race of *M. tularea* (Chamberlin), and *M. monica* Chamberlin, the oldest of four synonyms, is the correct name for the southernmost species, as *Polydesmus dissectus* Wood is referable to *Xystocheir* Cook (Shelley 1996).

*Motyxia* comprises a spectrum of forms in which the origin of the solenomere undergoes a complete transition regarding its position relative to the companion acropodal branch. The solenomere originates basally on the acropodite and is widely segregated from the companion branch in *M. kerna* Chamberlin, the type species, *M. monica*, and *M. sequoiae* (Loomis and Davenport); it arises basally and is narrowly segregated from the companion branch in *M. tiemanni* Causey; it arises subbasally and is moderately segregated from the latter in

both subspecies of *M. tularea*; it is fused basally to the companion branch and detaches proximad in *M. sequoia alia* Causey and Tiemann; and it is fused and detaches near midlength in *M. s. sequoia* (Chamberlin), the type species of *Amplocheir* Chamberlin, *M. pior* Chamberlin, and *M. porrecta*. The intermediate positions between the extremes in the type species of *Motyxia* and *Amplocheir* confirm Causey and Tiemann's assignment (1969) of the latter to synonymy, as *Motyxia* is the oldest genus-group name for this assemblage. The third nominal genus, *Luminodesmus* Loomis and Davenport, is an obvious synonym because the gonopods of its type species conform to the pattern in *M. kerna*. *Motyxia* encompasses relatively large-bodied xystodesmids that are distinguished somatically by their orange base color, absence of dorsal papillation, and orientation of the anterior paranota, which angle anteriolaterad on segments 2-5 (Figs. 3-4). Gonopodal similarities between *M. s. sequoia* and *Xystocheir reducta* (Causey) indicate generic affinity and contribal status, so the Xystocheirini must be rediagnosed to accommodate *Motyxia*, whose species lack the lobes on the 3rd coxae of males and the 2nd of females that are present on other tribal components (Hoffman 1980). Because of apparent homologies, I assign the companion acropodal projection in *Motyxia*, lying caudad/laterad to the solenomere, the same label as in *Xystocheir*, "process 'B'" (Shelley 1996).



**Fig. 1.** Distribution of *Motyxia*. A smooth curve is drawn around range extremes in all directions, and the question mark denotes the dubious record of *M. monica* from Riverside County. **Fig. 2.** Distributions of species of *Motyxia*. asterisks, *M. monica*; diamonds, *M. kerna*; solid stars, *M. sequoiae*; solid squares, *M. t. tularea*; open squares, *M. tularea ollae*; triangles, *M. s. sequoia*; inverted triangles, *M. sequoia alia*; X's, *M. sequoia* intergrades; dots, *M. pior* (the circle indicates the sight record from Crystal Cave); half-shaded dots, *M. porrecta*; open stars, *M. tiemanni*.



**Figs. 3-8.** *Motyxia monica*. 3, head and tergites 1-4 of a male from Woodford, dorsal view. 4, tergites 9-11 of the same, dorsal view. 5, left gonopod of the same, medial view. 6, the same, lateral view. 7, acropodite of the same, caudal view. 8, left cyphopod of female from the same locality, caudal view. B, process "B"; CV, caudal valve; O, operculum; PFP, prefemoral process; S, solenomere. Scale lines for figs. 3-4 = 1.00 mm; line for other figs. = 1.00 mm for each.

The dominant North American polydesmoid family, occurring in three areas of the continent (Shelley 1987) — east of the Central Plains, along the Pacific Coast from Los Angeles to southern Alaska and inland to western Montana, and from southern Texas and New Mexico to El Salvador — the Xystodesmidae has been the subject of numerous systematic studies since 1940. This contribution completes modern treatments of the west-Nearctic fauna that began with the revision of *Orophe* Chamberlin and the proposal of the subfamily Orophinae (Hoffman 1964). Buckett and Gardner (1968a, b) revised *Harpaphe* Cook (Harpaphini) and *Wamokia* Chamberlin (Xystocheirini), and subsequently proposed the new genera *Anombrocheir* (Xystocheirini) (1969a, b) and *Metaxycheir* (Chonaphini) (1969c). After Causey and Tiemann's (1969) study of *Motyxia*, eleven years elapsed before Hoffman (1980) established the Harpaphini and Xystocheirini, and reduced the Orophinae and Chonaphinae Verhoeff (1941) to tribal status in the subfamily Xystodesminae. Thirteen years later, I (Shelley 1993a, b, c) updated *Orophe*, proposed *Thrinaphe* (Harpaphini), and revised *Isaphe* Cook (= *Hybaphe* Cook) (Harpaphini). These were followed by revisions of the tribes Chonaphini and Sismocheirini (Shelley 1994, 1995a) and the proposal of *Parcipromus* (Xystocheirini) (Shelley 1995b). The companion publication on *Xystocheir* (Shelley 1996) addresses the last unrevised "western" genus, leaving only two unstudied genera in the United States -- the "eastern" taxa *Apheloria* and *Nannaria*, both authored by Chamberlin. Shelley (1989) described *Rhysodesmus chisosi*, from Big Bend National Park, Texas, and (1987, 1992) addressed *Stenodesmus tuobitus* (Chamberlin), in southern Texas and New Mexico, these being representatives of the "Meso-American fauna." This reexamination of *Motyxia* supplements Causey and Tiemann's revision (1969) by providing a historical section, an improved key to species and subspecies, cyphopod illustrations, and standardized gonopod drawings in medial and lateral views that are more readily compared and interpreted than their SEM photos. Species accounts include synonymies, listings of type specimens, diagnoses, statements on variation and distribution, and new localities (the initials DLT identify samples collected by Darwin L. Tiemann). I also supplement previous reports on the bioluminescence (Loomis and Davenport 1951; Davenport et al., 1952; Causey and Tiemann 1969, 1970) by summarizing current knowledge, adding

personal observations, and suggesting a possible avenue for productive research. Acronyms of sources of preserved study material are as follows:

- AMNH - American Museum of Natural History, New York, New York.
- CAS - California Academy of Sciences, San Francisco.
- FSCA - Florida State Collection of Arthropods, Gainesville.
- LACMNH - Los Angeles County Museum of Natural History, Los Angeles, California.
- NCSM - North Carolina State Museum of Natural Sciences, Raleigh.
- NMNH - National Museum of Natural History, Smithsonian Institution, Washington, D. C.
- UCB - Essig Entomological Museum, University of California at Berkeley.
- UCD - Bohart Entomological Museum, University of California at Davis.
- UCR - Entomology Department, University of California at Riverside.

### Literature Review

The history of *Motyxia* began with the paper by Chamberlin (1941), in which he described *Xystocheir sequoia*, from Sequoia National Park, and erected *Motyxia* for *M. kerna*, from Kern, and *M. pior*, from Tulare, counties. Chamberlin (1944, 1947) proposed *M. monica*, from the Santa Monica Mountains, and *M. tejona*, from Fort Tejon, respectively; he (Chamberlin 1949) proposed *X. tularea* for another species from Tulare County and established *Amplocheir* for *X. sequoia*. Loomis and Davenport (1951) proposed *Luminodesmus* for *L. sequoiae*, also from Tulare County, and Davenport et al. (1952) studied its ecology, life history, and bioluminescence, one of the few works on the "biology" of any xystodesmid. Loomis (1953) described *M. exilis*, from the Tehachapi Mountains, and *M. expansa*, from Fort Tejon, the second nominal species to be proposed from this site. Chamberlin and Hoffman (1958) incorporated all of the preceding taxa into the North American Checklist and placed *Luminodesmus* in synonymy under *Xystocheir*.

In recent works, Causey (1960) described *M. tiemanni*, from Kern County, but Buckett (1964) omitted this species from his list of California millipeds. Causey and Tiemann (1969) revised *Motyxia*, placed *Amplocheir* and *Luminodesmus* in synonymy, and transferred *X. dissecta* and *tularea*, *A. sequoia*, and *L. sequoiae* into the genus. They also placed *M. monica*, *tejona*, *expansa*, and *exilis* in synonymy under *dissecta*; proposed *M. porrecta* for another species from Kern County; and divided

*M. sequoia* into three races, the nominate and the new subspecies, *M. s. alia* and *s. ollae*. The same authors (Causey and Tiemann 1970) summarized the distribution, biology, and bioluminescence of the species of *Motyxia*, and Jeekel (1971) included *Motyxia*, *Amplocheir*, and *Luminodesmus* in the Nomenclator. In the final relevant work, Hoffman (1980) assigned *Motyxia*, with the synonym *Luminodesmus*, to the new tribe Xystocheirini and revived *Amplocheir* as a monotypic genus for *X. sequoia*, the type species.

### Tribe Xystocheirini Hoffman

**Diagnosis.** Moderate to large size Xystodesmiinae with smooth and glossy to variably papillate dorsums, pustulate caudad in some species; sides of collum gently curved or folded and uplifted at midlength; caudolateral paranotal corners either broadly rounded and not prolonged or subacuminate and extending slightly or strongly caudad, occasionally curving mediad and appearing uncinata; 3rd male coxae with or without subconical, anteriorly directed lobes; 2nd female coxae with or without long, conical lobes overlying cyphopodal aperture; gonopodal aperture generally ovoid, caudal margin with at most only slight caudal extension; gonosternum strong, oriented along longitudinal, anterior/posterior body axis; coxa flattened, without apophysis, usually with one or two macrosetae, occasionally with field; prefemur generally sublinear and massive, densely or sparsely hirsute, with or without distolateral lobe extending beyond acropodal articulation; prefemoral process usually strong and clearly detached from stem, occasionally vestigial or absent, located either on anteriolateral corner, on medial surface short of latter, or caudolateral corner; acropodite highly variable and clearly demarcated from prefemur, consisting of either an undivided/shallowly divided structure, either upright, curving in sigmoid configuration, or narrow proximad and expanded distad, or from two to four terminal projections of varying configurations; solenomere either a separate branch arising from base to midlength of acropodite or a shorter projection arising proximad to near midlength of caudal acropodal branch (process "B"); cyphopods usually oriented transversely in aperture, valves usually densely hirsute, often with bent hairs, with hirsute operculum and hirsute or glabrous receptacle located on dorsolateral and dorsomedial corners of valves, respectively, with or without moderately sclerotized, glabrous, lateral accessory body.

**Components.** *Xystocheir* Cook, *Wamokia* Chamberlin, *Motyxia* Chamberlin, *Anombrocheir* Buckett and Gardner, *Parcipromus* Shelley.

### Genus *Motyxia* Chamberlin

*Motyxia* Chamberlin, 1941:15. Chamberlin and Hoffman, 1958:38. Buckett, 1964:9. Causey and Tiemann, 1969:14-20. Jeekel, 1971:274. Hoffman, 1980:157.

*Amplocheir* Chamberlin, 1949:97. Chamberlin and Hoffman, 1958:17. Buckett, 1964:7. Jeekel, 1971:247. Hoffman, 1980:157.

*Luminodesmus* Loomis and Davenport, 1951:270-271. Jeekel, 1971:271.

**Type species.** Of *Motyxia*, *M. kerna* Chamberlin, 1941, by original designation; of *Amplocheir*, *Xystocheir sequoia* Chamberlin, 1941, by original designation; of *Luminodesmus*, *L. sequoiae* Loomis and Davenport, 1951, by original designation.

**Diagnosis.** Moderate-size to large, bioluminescent Xystocheirini with orange base color; metatergites smooth and glossy, without papillation; sides of collum not uplifted; caudolateral paranotal corners broadly rounded, not prolonged caudad; 3rd male and 2nd female coxae without lobes; gonopodal prefemur generally upright, usually sparsely hirsute, with or without distolateral lobe; prefemoral process variable but usually long and broad, upright, sinuate, or curving anteriorly or caudad, entire or divided into variably broad medial, and narrower lateral, subbranches, former with or without basal spur; solenomere variably long, arising either basally from acropodite as distinct, acicular projection, curving strongly or gently caudolaterad, widely or narrowly segregated from process "B", or fused basally to latter and detaching proximad or near midlength; process "B" varying in length, breadth, and configuration, broad and sublaminar or narrow and subacicular, upright, sinuate, or curving variably anteromedially; cyphopods oriented transversely in aperture, valves large and moderately hirsute, unequal with anterior valve larger, receptacle varying in size, hirsute or glabrous, absent from one species, operculum small and moderately hirsute.

**Distribution.** Occupying two segregated areas in southern California, a broad one extending in a generally north/south direction from the western side of Sequoia National Park, in northern Tulare County, through the southern periphery of the Sierra Nevada and the Tehachapi Mountains to Fort Tejon, in southern Kern County, and a small, disjunct area near the Pacific Coast in the Santa

Monica Mountains, Los Angeles County (Fig. 1). Species distributions are mutually exclusive except for overlap between *M. kerna*, *tularea*, and *sequoiae* in central and southern Tulare County (Fig. 2). The species with undivided prefemoral processes (three total telopodal projections) occur on the peripheries -- *M. pior* on the north, and *M. tiemanni*, *porrecta*, and *monica* on the south -- while those with divided processes (four total branches) occur centrally. This pattern implies that loss of the second prefemoral subbranch has occurred twice and that the three-branched condition in *M. pior* is convergent with those in the other species.

**Species.** Eight, two divided into two geographic races each. The occupied area in California has been thoroughly sampled (Tiemann 1963, 1964), and all species have probably been discovered. However, future sampling may disclose interconnecting forms among the species with divided prefemoral processes. *Motyxia sequoia* is definitely composed of two races, as the nominate subspecies and *M. s. alia* are linked by anatomically and geographically intermediate forms in the vicinity of Clough Cave in the southwestern corner of Sequoia National Park. I also recognize two races of *M. tularea* because of their narrow separation and the close similarity of their gonopods; while none are available, intergrades are presumed to occur in the lacuna. *Motyxia kerna* and *M. sequoiae* are also very close anatomically, the chief difference being the apical configuration of the medial prefemoral subbranch; however, the intervening area has been reasonably well sampled without the discovery of intergrades, so I interpret this difference as evidence of reproductive isolation. Beyond these examples, I think that meticulous sampling in uncollected areas in central Tulare County may reveal anatomically intermediate forms that join all the four-branched species, because their gonopodal differences are so small as to be easily bridged. For example, *M. sequoia* is diagnosed primarily by the basal spur on the medial prefemoral subbranch, but this structure varies in size, and a vestigial spur, coupled with a more proximal detachment of the solenomere from process "B", would blur the distinction between *M. s. alia* and *M. tularea ollae*, and imply that *M. sequoia* and *tularea* are conspecific. Thus, while the present material indicates eight species, the actual number may be only four or five.

**Remarks.** Aside from bioluminescence, *Motyxia* is characterized by a loss of hairs on both the gonopods and cyphopods. Except for *M. monica*, the

gonopod prefemora are sparsely hirsute with only scattered hairs on the stem and a light cluster or no hairs basally around the pit of the prostatic groove. The cyphopod receptacle is absent from this species, glabrous in *M. tularea*, *porrecta*, and *tiemanni*, and hirsute in the remaining species; however, the setation is notably sparse in *M. kerna*, *sequoiae*, and *pior*. The glabrous receptacles distinguish these species from all other western xystodesmids, and *M. monica* is the only Pacific representative lacking the structure.

Many specimens of *Motyxia* were collected in the 1960's by Darwin L. Tiemann (Shelley 1995a, 1996); some were coated with shellac or another substance and placed on insect pins at the LACM-NH, and most of the others were deposited in Dr. Causey's private collection, which was transferred to the FSCA after her death in 1979. The pinned specimens are unusable except for external, *in situ* examinations and measurements, and I present tabulated data for all taxa in the variation sections, with localities listed in general north to south sequences.

#### Key to species and subspecies of *Motyxia*

1. Prefemoral process divided into medial and lateral subbranches, telopodite with 4 terminal projections (Figs. 9-11, 13-15, 17-19, 21-26, 28-31) .. 2
  - Prefemoral process not divided, telopodite with 3 terminal projections (Figs. 5-7, 32-36-38, 40-41) ..... 7
2. Medial subbranch of prefemoral process with variable basal spur; solenomere fused basally to process "B" (Figs. 25-26, 28-31) *sequoia* (Chamberlin)3
  - Medial subbranch of prefemoral process without basal spur; solenomere arising basally or subbasally from acropodite (Figs. 9-11, 13-15, 17-19, 21-24) ..... 4
3. Detached part of solenomere relatively long, subequal in length to distal part of process "B"; latter and medial subbranch of prefemoral process relatively narrow for entire lengths, sides tapering smoothly and continuously to subacuminate tips (Figs. 25-26); vicinity of Hammond, Tulare County ..... *s. sequoia* (Chamberlin)
  - Detached part of solenomere relatively short, less than half as long as distal part of process "B"; latter and medial subbranch of prefemoral process relatively broad to subspatulate for at least part of length, sides expanding either proximad or distad, apically broad or rounded (Figs. 28-29); Three Rivers to Balch Mountain Park,

- Tulare County .....  
 ..... *s. alia* Causey and Tiemann
4. Solenomere arising basally on acropodite, curving strongly caudolaterad, overlapping margin of process "B"; latter extending caudolaterad basally then curving anteromedial and extending ventrad (Figs. 11-15) ..... 5  
 — Solenomere arising subbasally on acropodite, either upright and extending directly ventrad or curving only apically and at most only slightly caudolaterad; process "B" generally upright (Figs. 17-19, 21-24) *tularea* (Chamberlin) ..... 6
5. Medial branch of prefemoral process apically expanded and upright (Figs. 9-10); Cold Springs Saddle and White River vicinity, Tulare County, to northern fringe of Kern County .....  
 ..... *kerna* Chamberlin  
 — Medial branch of prefemoral process apically sigmoid, curving caudolaterad (Figs. 13-14); Camp Wishon to Coy Flat, Tulare County .....  
 ..... *sequoiae* (Loomis and Davenport)
6. Medial branch of prefemoral process with caudal margin indented apically, tip acuminate (Figs. 17-19); Quaker Meadows, Tulare County, to northern fringe of Kern County .....  
 ..... *tularea tulareae* (Chamberlin)  
 — Medial branch of prefemoral process apically expanded and rounded (Figs. 21-22, 24); Camp Wishon to Deer Creek Road south of Tule River Indian Reservation .....  
 ..... *tularea ollae* Causey and Tiemann
7. Solenomere arising basally on acropodite (Figs. 5, 7, 40) ..... 8  
 — Solenomere fused basally to process "B", detaching proximad to near midlength (Figs. 33-34, 37-38) ..... 9
8. Solenomere widely segregated basally from process "B"; latter extending sublateral basally then curving broadly anteromedial and extending ventrad; cyphopod without receptacle (Figs. 7-8); vicinity of Breckenridge, Kern County, to Santa Monica Mountains, Los Angeles County .....  
 ..... *monica* Chamberlin  
 — Solenomere narrowly segregated basally from process "B"; latter upright, extending directly ventrad; cyphopod with receptacle (Figs. 40, 42); Greenhorn Mountains from Tulare County Line to Evans Flat, Kern County .....  
 ..... *tiemanni* Causey
9. Process "B" broad and semilunar; detached part of solenomere minute and blunt, barely projecting beyond margin of process "B" (Figs. 32-24); Woodlake Valley east to Crystal Cave and Hos-

- pital Rock, Sequoia National Park, Tulare County .....  
 ..... *pior* Chamberlin  
 — Process "B" subspatulate, extending ventrad in sinuate configuration; detached part of solenomere short but distinct, clearly projecting from margin of process "B" (Figs. 36-39); Kern River Valley, Kern County .....  
 ..... *porrecta* Causey and Tiemann

***Motyxia monica* Chamberlin**

Figs. 3-8

- Motyxia monica* Chamberlin, 1944:57, figs. 1-3. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9.  
*Motyxia tejona* Chamberlin, 1947:25, figs. 4, 4a. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9. **New synonymy.**  
*Motyxia expansa* Loomis, 1953:422, fig. 19. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9. **New synonymy.**  
*Motyxia exilis* Loomis, 1953:422, fig. 20. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9. **New synonymy.**  
*Motyxia dissecta* (Nec Wood) Causey and Tiemann, 1969:21-22, figs. 2-3, 8, 10-12.

**Type specimen.** Male holotype (NMNH) collected by R C. Stebbins, 4 March 1944, at "Madelia Canyon," Sherman Oaks, Santa Monica Mountains, Los Angeles County. The vial label and original description state, "Meadow Canyon," which is believed to be a *lapsus* for Madelia Canyon. Madelia Avenue is a short street off Valley Vista Boulevard west of Beverly Glen Boulevard on the north slope of the Santa Monica Mountains in Sherman Oaks, between Mulholland Drive and the Ventura Freeway.

**Diagnosis.** Prefemoral process entire, broad basally, narrowing smoothly and continuously to narrowly rounded tip, curving broadly laterad; solenomere arising basally from acropodite, curving broadly caudolaterad, directed toward midlength of, but not overlapping, process "B"; latter widely segregated basally from solenomere, extending sublateral basally then curving broadly anteromedial and extending curvilinearly ventrad, sides expanding basally then narrowing smoothly and continuously to subacuminate tip; cyphopod without receptacle (Figs. 5-8).

**Variation.** The gonopods of *M. monica* are quite uniform, the only observable variation being slightly less or greater curvatures of the projections than illustrated in figs. 5-7. Measurements of pinned adults are summarized in table 1; sexes are subequal in size, and on the average, individuals be-

come shorter and narrower to the south in the range.

**Distribution.** Occurring south of the Kern River in two apparently disjunct areas of unequal size, the larger extending from Breckenridge Mountain through the Tehachapi Mountains to Fort Tejon, Kern County, and the smaller being near the Pacific Ocean, some 50 mi (80 km) to the south, in the Santa Monica Mountains, Los Angeles County. Known elevations range from around 700 to 7,000 ft. The intervening area of eastern Ventura County, in the Los Padres National Forest around Pyramid and Pinu Lakes, is plausible for *M. monica*.

A new locality is available from the Santa Monica Mountains, but metropolitan Los Angeles now covers much of this range, and south-facing canyons like Beverley Glen are virtually completely urbanized. I drove the length of Beverley Glen Boulevard in 1989, but with continuous houses and private property on both sides, could not find anyplace to search. Western facing Topanga Canyon, in the Santa Monica Mountains National Recreation Area, is a more plausible site, but I could not find any specimens in three visits. Searches to the east, in the San Gabriel Mountains of Los Angeles and San Bernardino counties, have not revealed the milliped, but a dubious sample is available from Riverside, Riverside County, some 80 mi (128 km) east southeast of the Santa Monicas. This city is inconsistent with the known, coherent ranges of both the genus and species; specimens have not been collected there again; and the precise location in Riverside is unknown. The desert habitat at Riverside is wrong for *M. monica*, whose known environments are more moist with an abundance of trees, so the locality almost surely is wrong. Specimens were examined from the following new localities: **Los Angeles Co.**, Santa Monica Mts., Topanga Cyn. at Greenleaf Cyn., 10M, 5F, 8 December 1966, DLT (LACMNH), and Beverly Glen Cyn., 2M, F, March 1953, collector unknown (NMNH).

**Dubious Record.** **Riverside Co.**, Riverside, 3M, Fall 1953, L. D. Anderson (UCR).

**Remarks.** Shelley (1996) showed that Wood's name, *dissecta*, is correctly referable to *Xystocheir* Cook and that the purported locality, Fort Tejon, is wrong. Consequently, *M. monica*, the oldest of the four available species-group names, is the correct name for this species.

#### *Motyxia kerna* Chamberlin

Figs. 9-12

*Motyxia kerna* Chamberlin, 1941:15, pl. 3, fig. 29. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9. Causey and Tiemann, 1969:25, figs. 4, 19-20.

**Type specimen.** Male holotype (NMNH) collected by S. and D. Mulaik, 19 March 1942, 7 mi (11.2 km) N Glenville, Kern County.

**Diagnosis.** Prefemoral process divided basally into narrow, linear lateral, and broad, expanded medial subbranches, former 3/4 as long as latter, not bowed anteriorly, latter entirely upright, apically expanded and broadly rounded; solenomere arising basally from acropodite, curving strongly caudolaterad, overlapping and extending slightly beyond margin of process "B"; latter widely segregated basally from solenomere, extending directly laterad basally then curving strongly anteromedial and extending sublinearly ventrad, sides expanding slightly distal to curve then narrowing to narrowly rounded tip; cyphopod with hirsute receptacle (Figs. 9-12).

**Variation.** The apical expansion of the medial prefemoral subbranch is greater in scattered males, and the solenomere curls dorsad apically in a few males from the vicinity of White River. Measurements of pinned adults are summarized in table 2; the few available females are larger in both dimensions than average males from the same sites, but no geographic trends are evident.

**Distribution.** Southern Tulare County from the vicinity of Cold Springs Saddle to the adjacent northern fringe of Kern County, extending westward to the vicinity of White River along Arrastre Creek Road, distances of around 10.8 mi (17.3 km), north/south, and 12.8 mi (20.5 km), east/west. Specimens were examined from the following new localities: **Tulare Co.**, 7.3 mi (11.7 km) NE White River, 68M, 15F, 21 February 1965, DLT (FSCA, LACMNH); 1 mi (1.6 km) "below" Sugarloaf Mtn. Park, 18M, 8F, DLT (FSCA); and 7 mi (11.2 km) Greenhorn Mtn. Peak, along CA hwy. 15, M, F, 1 June 1984, T. Schackman (NCSM).

#### *Motyxia sequoiae* (Loomis and Davenport)

Figs. 13-16

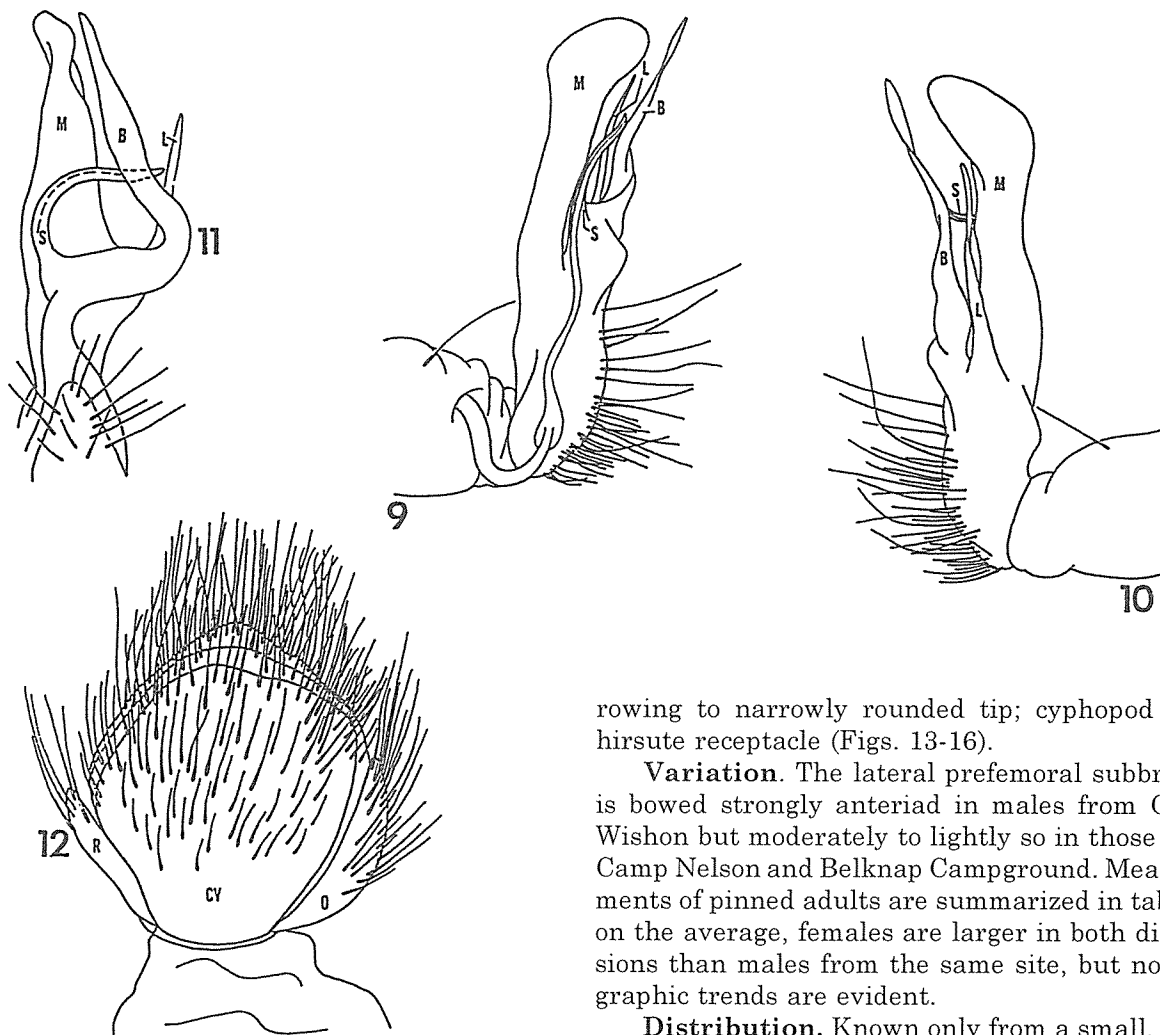
*Luminodesmus sequoiae* Loomis and Davenport, 1951:271-272, fig. 1.

*Xystocheir sequoiae*: Chamberlin and Hoffman, 1958:54-55. Buckett, 1964:10.

*Motyxia sequoiae* Causey and Tiemann, 1969:31, figs. 17-18.

**Type specimens.** Male holotype and female paratype (NMNH) collected by D. L. Tiemann, 12-14 May 1950, above Camp Nelson, Sequoia National Forest, Tulare County.





Figs. 9-12. *Motyxia kerna*. 9, left gonopod of a male from 3.3 mi (5.3 km) SE White River, medial view. 10, the same, lateral view. 11, acropodite of the same, caudal view. 12, left cyphopod of a female from the same locality, caudal view. L, lateral subbranch of prefemoral process; M, medial subbranch of prefemoral process; R, receptacle; other abbreviations as in figs. 3-8. Scale line = 1.00 mm for all figs.

**Diagnosis.** Prefemoral process divided basally into relatively narrow, linear lateral and moderately broad, expanded medial subbranches, former 3/4 as long as latter, not bowed anteriorly, latter generally upright but curving caudolaterad distally in sigmoid configuration, sides narrowing proximal to curve, expanding greatly distad then narrowing to blunt tip; solenomere arising basally from acropodite, curving strongly caudolaterad, overlapping but not extending beyond process "B"; latter widely segregated basally from solenomere, angling sublateral basally then curving broadly anteromedially and extending curvilinearly ventrad, sides expanding strongly distal to curve then nar-

rowing to narrowly rounded tip; cyphopod with hirsute receptacle (Figs. 13-16).

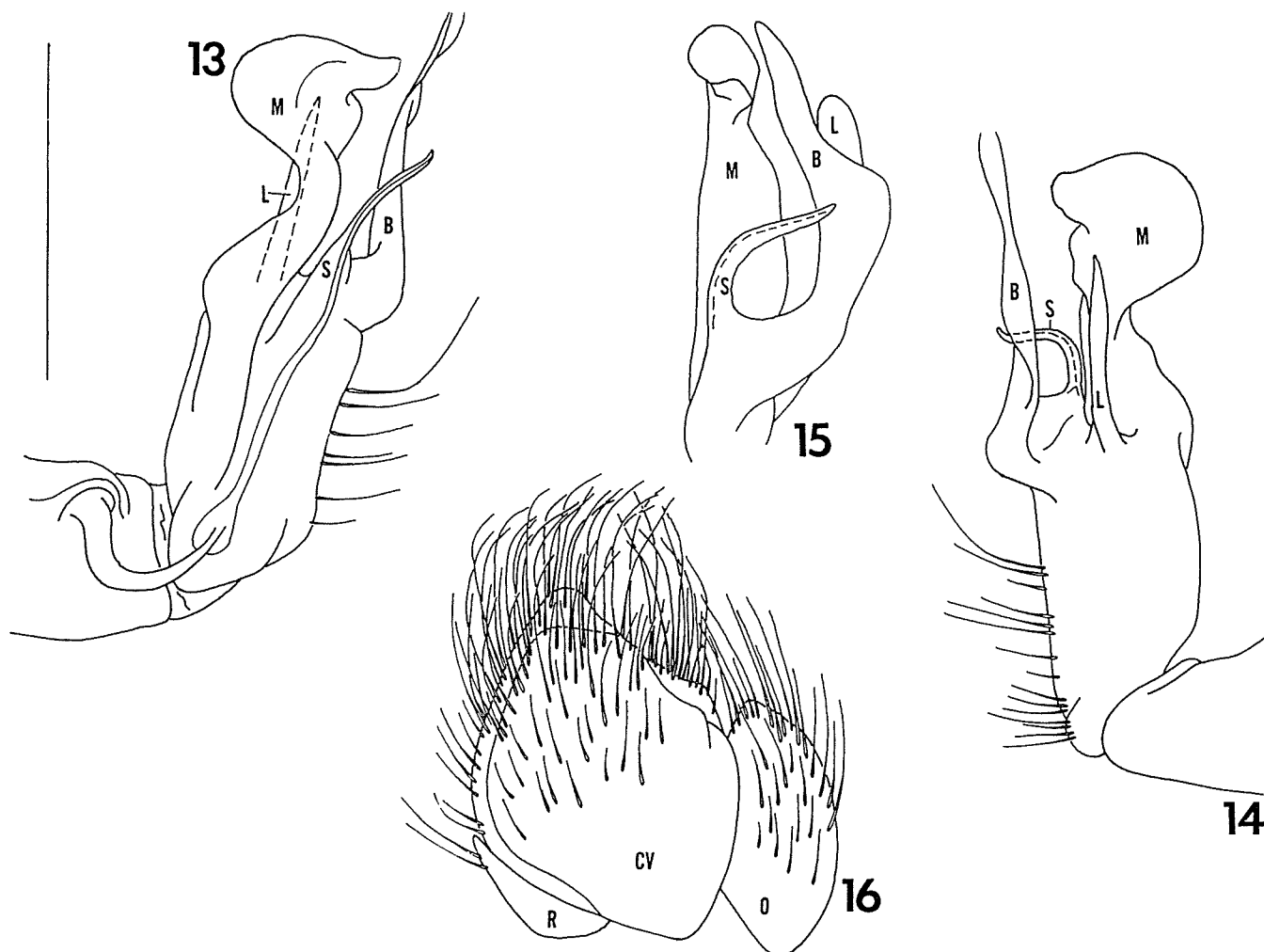
**Variation.** The lateral prefemoral subbranch is bowed strongly anteriorly in males from Camp Wishon but moderately to lightly so in those from Camp Nelson and Belknap Campground. Measurements of pinned adults are summarized in table 3; on the average, females are larger in both dimensions than males from the same site, but no geographic trends are evident.

**Distribution.** Known only from a small, symmetrical area, 4.4 mi (7.0 km) in both dimensions, in the headwaters of the Middle Fork of the Tule River. It extends, north/south, from Camp Wishon to Coy Flat and, east/west, from Cedar Slope to the crossing of Moorehouse Creek by highway 190. No new localities are known.

#### *Motyxia tularea* (Chamberlin)

**Diagnosis.** Prefemoral process divided basally into narrow, linear lateral and broad, expanded, subspatulate medial subbranches, former 1/2-3/4 as long as latter, bowed slightly anteriorly, latter upright, apically broad or narrow; solenomere arising subbasally from acropodite, generally upright, at most curving only slightly caudolaterad, barely overlapping process "B"; latter generally upright, sides expanding proximally, narrowing distad to narrowly rounded tip; cyphopod with glabrous receptacle.

**Remarks.** Intergrades are not available, but two closely similar and narrowly segregated forms,



**Figs. 13-16.** *Motyxia sequoiae*. 13, left gonopod of a male from Belknap Campground, medial view. 14, the same, lateral view. 15, acropodite of the same, caudal view. 16, left cyphopod of a female from the same locality, caudal view. Abbreviations as in figs. 3-8, 9-12. Scale line = 1.00 mm for all figs.

differing primarily in the apical configurations of the medial prefemoral subbranch and process "B", are interpreted as representing races of this species.

***Motyxia tularea tularea* (Chamberlin), new status**

Figs. 17-20

*Xystocheir tularea* Chamberlin, 1949:101, fig. 27. Chamberlin and Hoffman, 1958:55. Buckett, 1964:11.

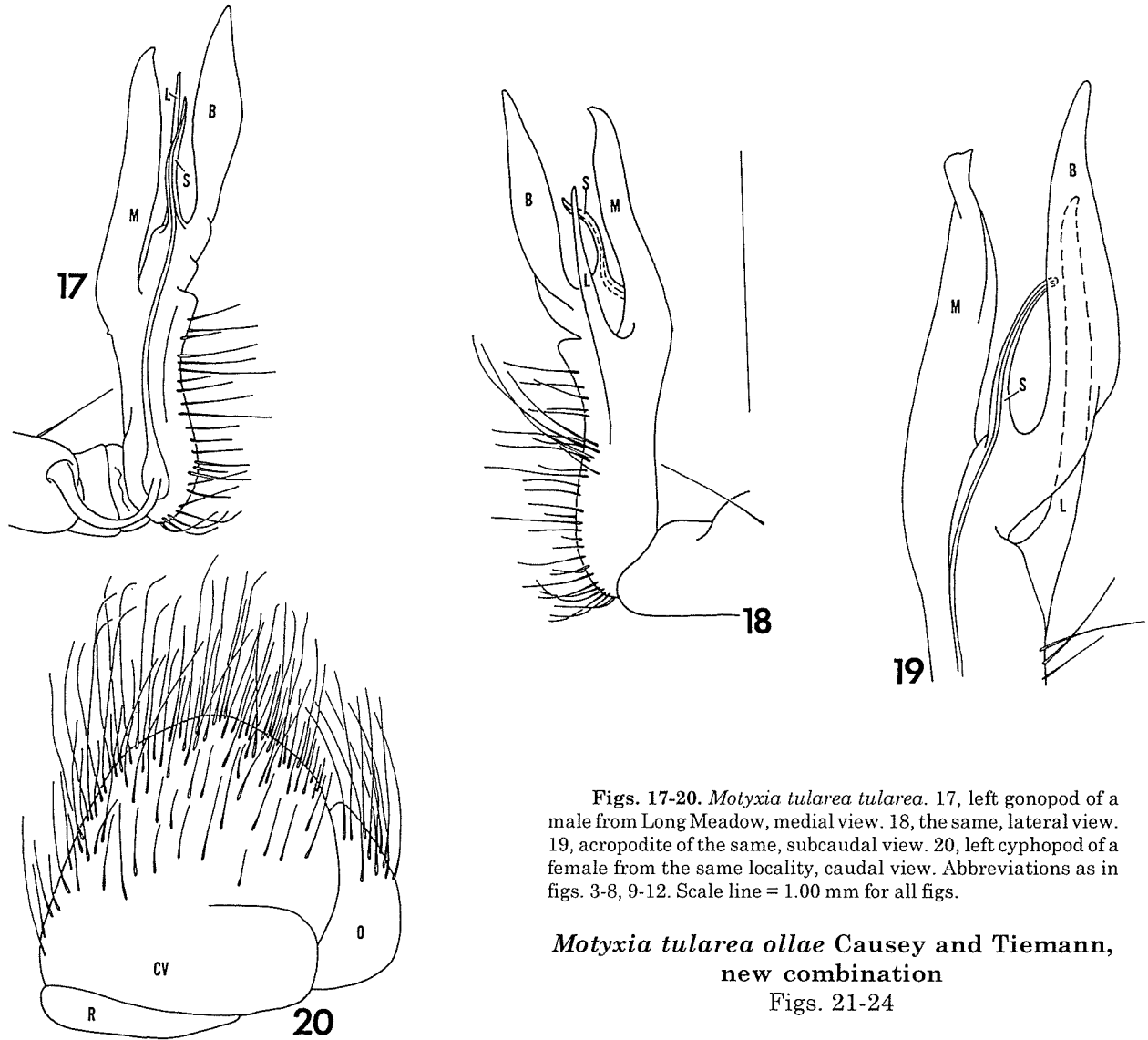
*Motyxia tularea* Causey and Tiemann, 1969:32, figs. 25-26.

**Type specimens.** Male holotype, female allotype, and two male and one female paratypes (NMNH) collected by K. Denner on an unknown

date in 1930 on Sugarloaf Mountain, Tulare County.

**Diagnosis.** Medial subbranch of prefemoral process apically narrow and acuminate, indented on caudal margin and curving caudad; process "B" entirely upright, sides narrowing gradually distal to midlength (Figs. 17-20).

**Variation.** The medial prefemoral subbranch is curved more strongly caudad and has two tiny apical teeth in males from Tyler and Quaker Meadows; those from along Capinero Creek have the teeth but are curved as in the drawings. Measurements of pinned adults are summarized in table 4; on the average, females are larger than males from the same sites, and there is a general trend toward shorter and narrower individuals to the south in the range.



Figs. 17-20. *Motyxia tularea tularea*. 17, left gonopod of a male from Long Meadow, medial view. 18, the same, lateral view. 19, acropodite of the same, subcaudal view. 20, left cyphopod of a female from the same locality, caudal view. Abbreviations as in figs. 3-8, 9-12. Scale line = 1.00 mm for all figs.

*Motyxia tularea ollae* Causey and Tiemann,  
new combination

Figs. 21-24

*Motyxia sequoia ollae* Causey and Tiemann, 1969:29-30,  
figs. 6, 27-28.

**Distribution.** A sublinear area extending from Quaker Meadows in Tulare County to the adjacent northern fringe of Kern County in the Greenhorn Mountains, a distance of some 21.3 mi (34.1 km). The race occurs sympatrically with *M. kerna* in the Sugarloaf Mountain area in southern Tulare County. Specimens were examined from the following new localities: **Tulare Co.**, Long Mdw. W of Johnsondale, 19M, 2F, 28 May and 16 June 1961, DLT (FSCA, LACMNH); Tyler Mdw., 5M, 6F, 10 June 1962, DLT (LACMNH); 0.9 mi (1.4 km) N Kern Co. Line, Greenhorn Mts., 30M, 4F, 15 May 1965, DLT, L. W. Nichols (LACMNH); and Kern/Tulare Co. Line, 5M, F, 15 May 1965, DLT, L. W. Nichols (LACMNH). **Kern Co.**, 0.2 mi (0.3 km) S Tulare Co. Line, 28M, 4F, DLT, L. W. Nichols (LACMNH).

**Type specimens.** Male holotype, female allotype, and 15 male and 9 female paratypes (FSCA) collected by D. L. Tiemann, 28 February 1965, 5.4 mi (8.6 km) W of the Tule River Indian Reservation, Tulare County. For data on other paratype samples, see Causey and Tiemann (1969).

**Diagnosis.** Medial subbranch of prefemoral process apically broad and expanded; process "B" curving slightly caudad, sides narrowing rapidly distal to midlength (Figs. 21-24).

**Variation.** The medial prefemoral subbranch curves more strongly caudad in males from below Camp Wishon, Deer Creek Road at Pothole Creek, and 4.1 mi (6.6 km) east of the entrance to the Tule River Indian Reservation (Fig. 24). These individ-

uals vaguely resemble *M. kerna* but are distinguished by the upright solenomere. Measurements of pinned adults are summarized in table 5; except for the one from Pothole Creek, females are larger in both dimensions than males from the same sites, and there is a general trend toward larger individuals to the south in the range.

**Distribution.** From just below Camp Wishon, on the North Fork of the Middle Fork of the Tule River, southward to Deer Creek Road at Pothole Creek, south of the Tule River Indian Reservation, westward to 5.4 mi (8.6 km) west of the entrance to the latter. Dimensions are approximately 16.8 mi (26.9 km), north/south, and 11.1 mi (17.8 km), east/west. Specimens were examined from the following new localities: **Tulare Co.**, along Dunn R. Fire Tr., 2.5 mi (4.0 km) "below" Camp Wishon, 12M, 28 December 1963, DLT (FSCA); and entrance to Tule R. Indian Res., 4M, 12F, 28 February 1965, DLT (FSCA).

**Remarks.** After restudying all of Causey and Tiemann's material, now at the FSCA, I agree with their conclusion as to the existence of the species-group taxon that they named *ollae*. However, it is a race of *M. tularea* instead of *M. sequoia*, both of which possess two prefemoral and two acropodal projections. The lateral prefemoral subbranch is not bowed anteriad as strongly as in *M. sequoia*, and the medial one lacks the basal spur, the key diagnostic feature of the latter. Likewise, the distal configurations of the medial prefemoral subbranch and process "B" conform to the general shape of the structures in *M. tularea* and differ from those in any form of *M. sequoia*. Finally, the solenomere arises subbasally from the acropodite as in *M. tularea*, instead of on process "B" as in *M. sequoia*.

#### *Motyxia sequoia* (Chamberlin)

**Diagnosis.** Prefemoral process divided basally into relatively narrow lateral and variably broad medial subbranches, former bowed strongly or gently anteriad, apically relatively narrow, subequal in length to, or moderately shorter than, medial subbranch, latter often closely appressed to acropodite, with variable basal spur, breadth variable, leaning or curving apically, tip broad to acumi-

nate; solenomere fused basally to process "B", arising proximad to near midlength of latter, detached part varying in length and breadth, subequal to, or much shorter than, distal part of process "B", extending subparallel to latter or diverging slightly, apically acuminate; distal part of process "B" long and variably broad, narrow to subspatulate, generally upright, either reflexed caudad apically or curving or leaning gently to broadly anteriad, apically broad or acuminate; cyphopod with hirsute receptacle.

**Remarks.** *Motyxia sequoia* is comprised of peripheral races connected by geographically and anatomically intermediate forms. Chamberlin's original assignment (1941) to *Xystocheir* was reasonable, because its two-branched acropodite demonstrates the pattern of this genus, particularly that of *X. reducta* (Causey), and the complex prefemoral process is reminiscent of that in *X. stolonifera* Shelley (Shelley 1996). However, without dorsal papillation and lobes on the 3rd male and 2nd female coxae, *sequoia* was misplaced in *Xystocheir*, which may be why Chamberlin (1949) established *Amplocheir* to accommodate it. As explained previously, *Amplocheir* is a synonym of *Motyxia*, and because of the gonopodal similarity between *M. sequoia* and *X. reducta*, *Motyxia* is clearly contribal with *Xystocheir*.

#### *Motyxia sequoia sequoia* (Chamberlin)

Figs. 25-27

*Xystocheir sequoia* Chamberlin, 1941:15, pl. 3, fig. 28.

*Amplocheir sequoia* Chamberlin, 1949:97, figs. 12-13.

Chamberlin and Hoffman, 1958:17. Buckett, 1964:7.

*Motyxia sequoia* Causey and Tiemann, 1969:29.

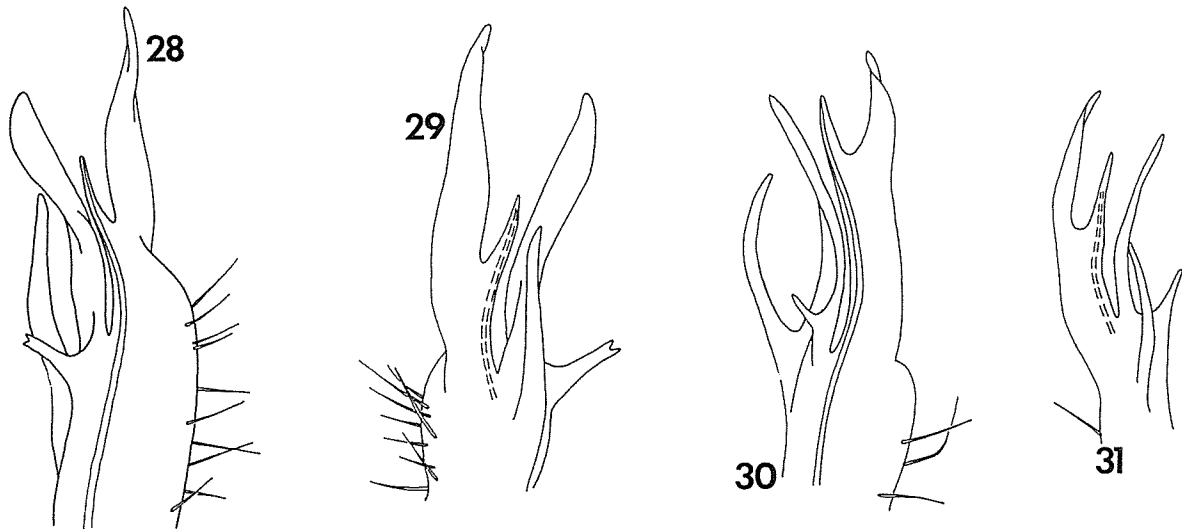
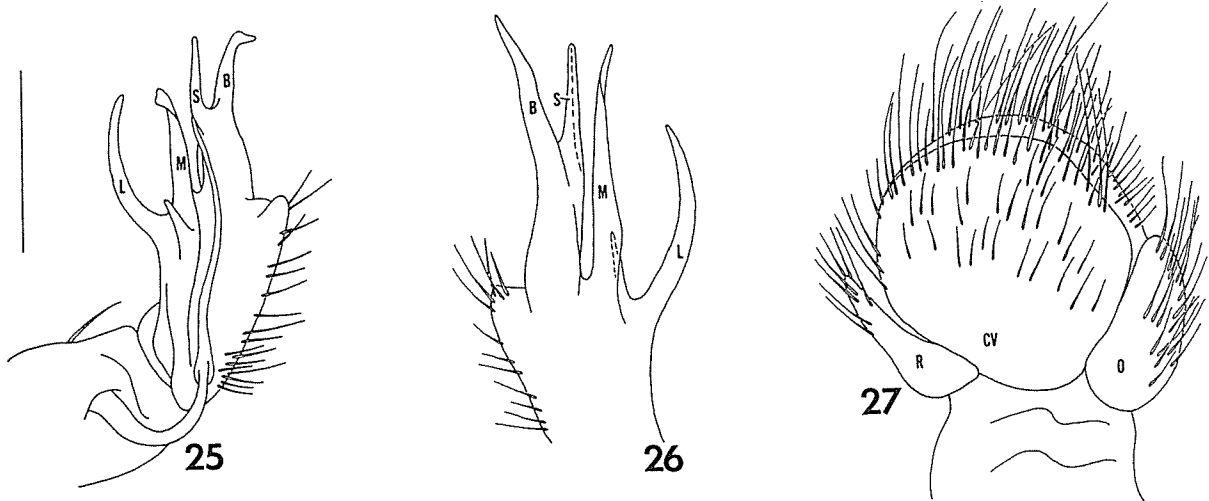
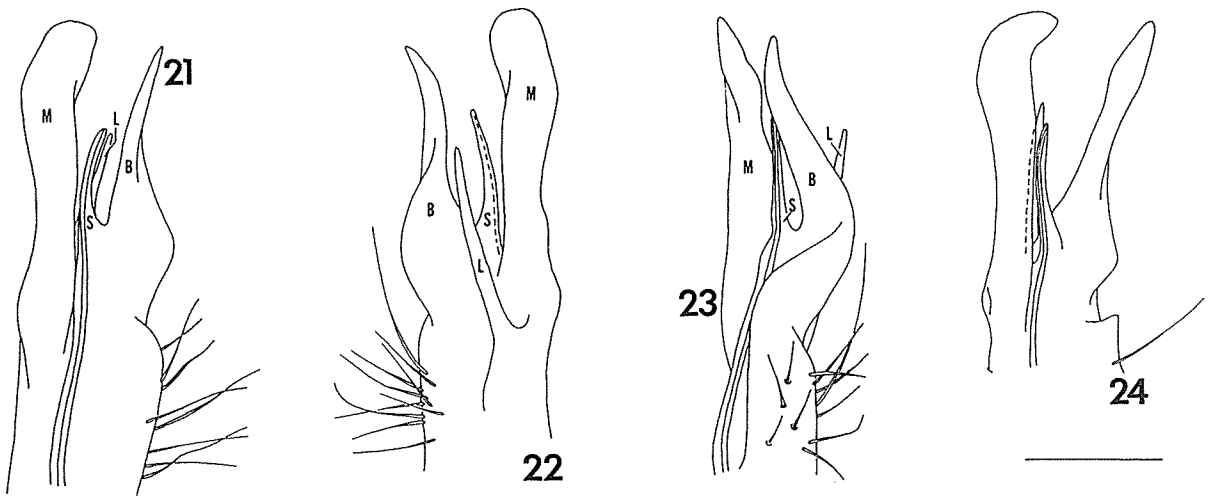
*Motyxia sequoia sequoia* Causey and Tiemann, 1969:330-31, figs. 31-32.

**Type specimens.** Male holotype and one male and one female paratypes (NMNH) collected by S. and D. Mulaik, 20 March 1941, 10 mi (16 km) E Hammond, Tulare County.

**Diagnosis.** Medial branch of prefemoral process narrow and sublinear, apically acuminate; solenomere relatively long, subequal in length to distal part of process "B"; latter narrow, sublinear

**Figs. 21-24 (facing page).** *Motyxia tularea ollae*. 21, acropodite of left gonopod of holotype, medial view. 22, the same, lateral view. 23, the same, subcaudal view. 24, acropodite of left gonopod of a male from Deer Creek Road at Pothole Creek, medial view. Abbreviations as in figs. 3-8, 9-12. Scale line = 0.50 mm for all figs.

**Figs. 25-31 (facing page).** *Motyxia sequoia*. 25-27, *M. s. sequoia*. 25, left gonopod of a male from 8 mi (12.8 km) "above" Hammond, medial view. 26, acropodite of the same, lateral view. 27, left cyphopod of female from the same locality, caudal view. 28-29, *M. s. alia*. 28, acropodite of left gonopod of holotype, medial view. 29, the same, lateral view. 30-31, *M. sequoia* intergrades. 30, acropodite of left gonopod of a male from 4.1 mi (6.6 km) N Clough Cave, medial view. 31, the same, lateral view. Abbreviations as in figs. 3-8, 9-12. Scale line = 1.00 mm for all figs.



for most of length, curved gently mediad or reflexed caudad distally, apically subacuminate (Figs. 25-27).

**Variation.** On the prefemoral process, the relative lengths of the subbranches vary, although the lateral is generally shorter than the medial, which tends to be slightly wider and curve broadly mediad in southern males. The most dramatic changes, however, involve the basal spur, which becomes proportionally longer 8-12 mi (12.8-19.2 km) south and east of Hammond such that the process appears three-branched. On the acropodite, the length of the solenomere relative to the distal part of process "B" varies, although the former is always at least 2/3 to 3/4 as long. Process "B" may also be reflexed caudad distad or curved gently mediad.

Measurements of pinned adults are summarized in table 6; no generalizations are possible from these data.

**Distribution.** The vicinity of Hammond on the East Fork of the Kaweah River along California highway 198, extending into the adjacent fringe of Sequoia National Park. Specimens were examined from the following new locality, buried in debris in a concrete sluice high on the mountainside: **Tulare Co.**, 2.8 mi (4.5 km) E Hammond, Kaweah Powerhouse #3, M, 4F, juv., 1 April 1989, N. J. Smith, R. D. Haines (NCSM) and MM, FF, 22 April 1991, N. J. Smith, R. D. Haines, R. M. Shelley (NCSM).

***Motyxia sequoia alia* Causey and Tiemann**  
Figs. 28-29

*Motyxia sequoia alia* Causey and Tiemann, 1969:29, figs. 5, 29-30.

**Type specimens.** Male holotype, female allotype, and 5 male and 6 female paratypes (FSCA) collected by D. L. Tiemann and D. D. Linsdale, 6 March 1964, along California highway 198 at Horsehoe Creek, SE Lake Kaweah, Tulare County.

**Diagnosis.** Medial branch of prefemoral process variably broad to subspatulate, apically rounded; solenomere short, less than half as long as distal part of process "B"; latter broad to subspatulate, curvilinear (Figs. 28-29).

**Variation.** The breadths of the medial prefemoral subbranch and process "B" vary, and the latter may be suberect or curve slightly caudad. The most variable structure is the prefemoral spur; it is long in the types, short, broad, and trifurcate in males near Terminal Reservoir, very short in ones from

Yakohl Valley, and absent from males near Balch Mountain Park. The chief diagnostic feature, however, the length of the solenomere, less than half the length of the distal part of process "B", does not vary, nor does the position of its detachment from the latter.

Measurements of pinned adults are summarized in table 7; no generalizations are possible from these data.

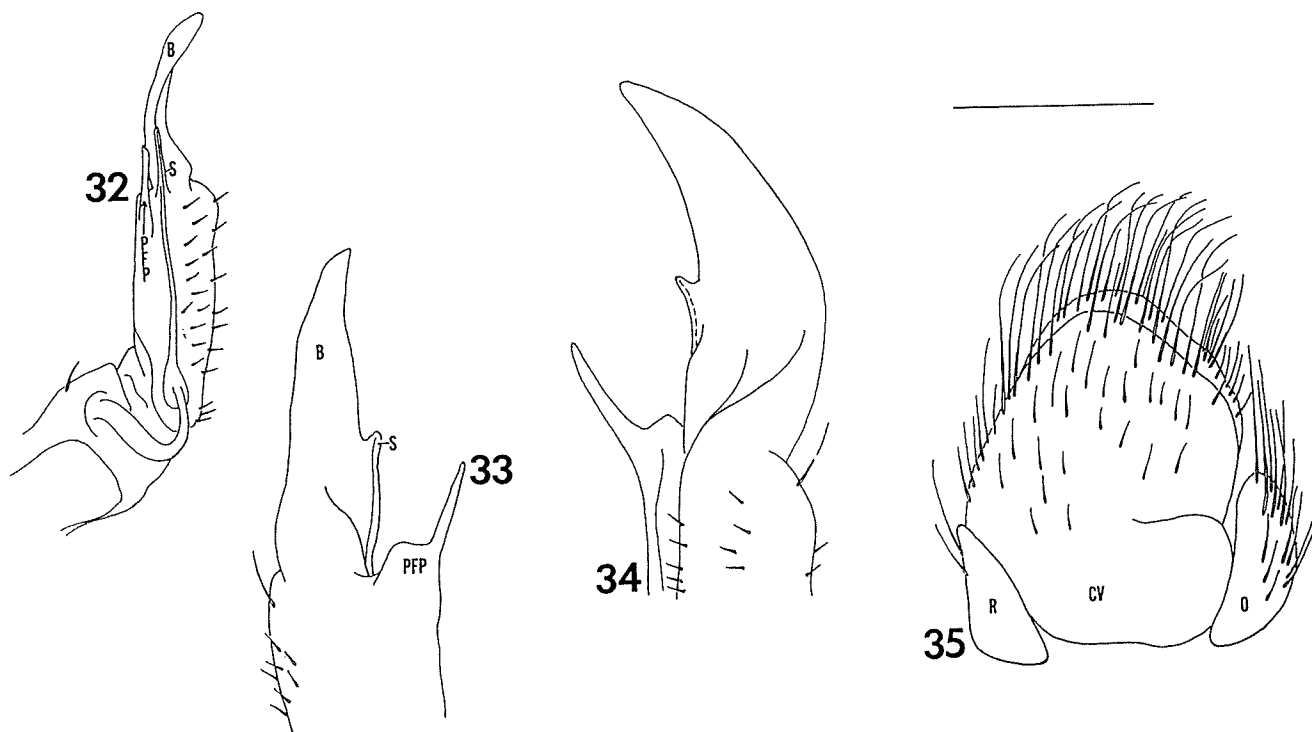
**Distribution.** From the vicinity of Three Rivers, on highway 198, to Clough Cave, in the southwestern corner of Sequoia National Park, to Balch Mountain Park. Dimensions are 16 mi (25.6 km), north/south, and 11.1 mi (17.8 km), east/west. Specimens were examined from the following new localities: **Tulare Co.**, 10 mi (16 km) SE Three Rivers, along S Fork Kaweah R., 5M, 3 May 1979, J. T. Doyen (UCB); and 13 mi (20.8 km) SE Three Rivers, South Fork Camp, 3M, 3 May 1979, M. F. Burgler (UCB).

***Motyxia sequoia intergrades***  
Figs. 30-31

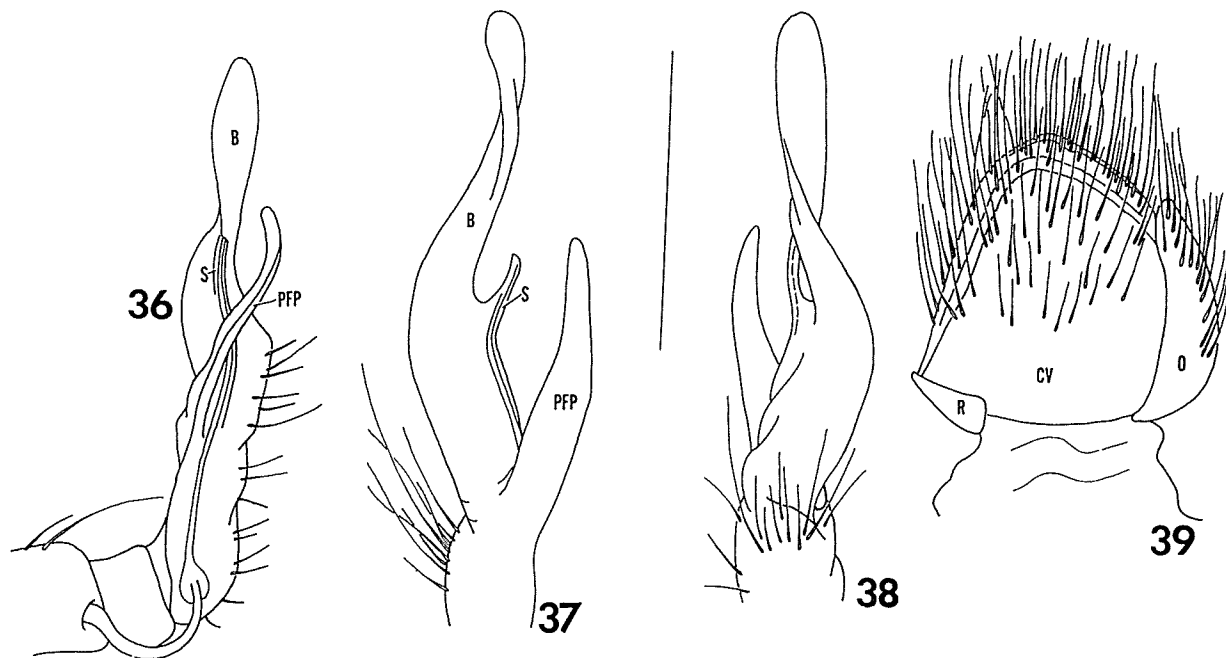
Geographically intermediate specimens west and northwest of Clough Cave are also anatomically intermediate in the conditions of the medial branch of the prefemoral process, the solenomere, and process "B". The first and last are broader than in the nominate subspecies but narrower than in *M. s. alia*, and the solenomere is more than half as long as the distal part of process "B" but never equal to the latter and hence shorter than in the nominate race. Measurements of pinned adults are summarized in table 8; on the average, females are larger than males in both dimensions.

**Distribution.** The area west and northwest of Clough Cave, in the southwestern corner of Sequoia National Park and the adjoining part of the Sequoia National Forest. As Causey and Tiemann (1969) confusingly record intergrades in the subspecies accounts, I record below all samples that I examined: **Tulare Co.**, Sequoia Nat. Pk., 1 mi (1.6 km) W Clough Cv. Ranger Sta., 3M, 14F, 25 March 1967, DLT (FSCA); 4.1 mi (6.6 km) N Clough Cv., 2M, 25 March 1967, DLT (FSCA); 4.1 mi (6.6 km) NW Clough Cv., 2820', 4M, 2F, 25 March 1967, DLT (LACMNH); and 8.7 mi (13.9 km) NW Clough Cv., 9M, 12F, 25 March 1967, DLT (FSCA, LACMNH).

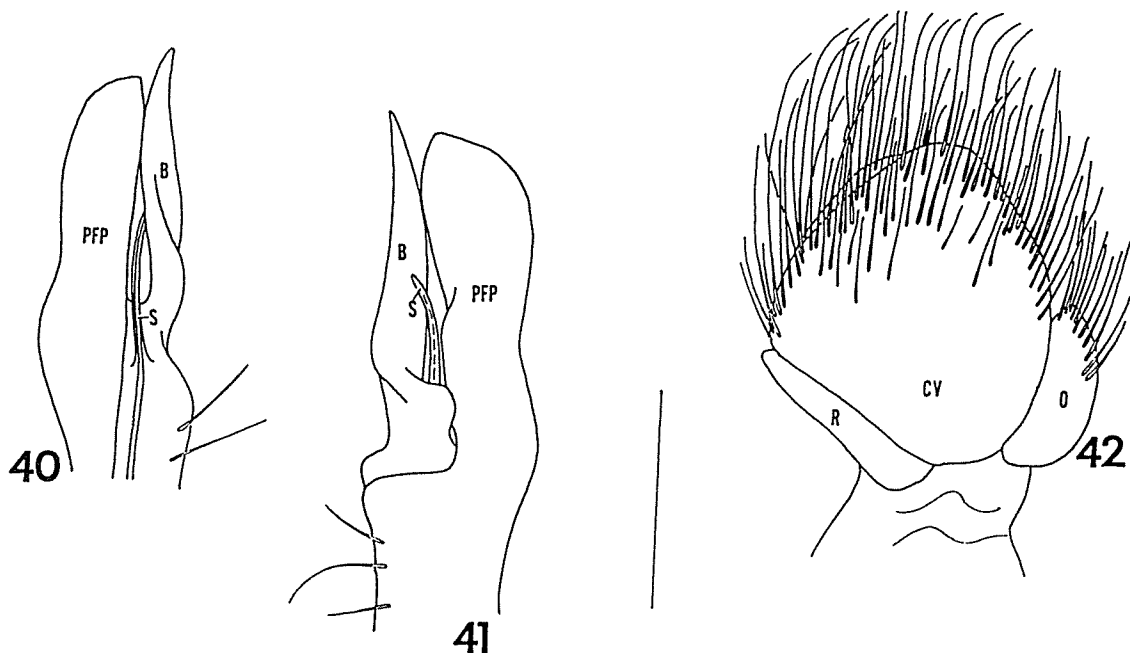
**Remarks.** A male from the last site has a gonopod on the right, at the anterior position on segment 7, and a normal walking leg on the left, a classical example of hysterotely (Shelley 1977).



**Figs. 32-35.** *Motyxia pior*. 32, left gonopod of a male from 6.8 mi (10.9 km) S Badger, medial view. 33, acropodite of the same, lateral view. 34, the same, caudal view. 35, left cyphopod of a female from the same locality, caudal view. Abbreviations as in figs. 3-8, 9-12. Scale line = 1.00 mm for all figs.



**Figs. 36-39.** *Motyxia porrecta*. 36, left gonopod of lectotype, medial view. 37, acropodite of the same, lateral view. 38, the same, caudal view. 39, left cyphopod of female paralectotype, caudal view. Abbreviations as in figs. 3-8, 9-12. Scale line = 1.00 mm for all figs.



Figs. 40-42. *Motyxia tiemanni*. 40, acropodite of left gonopod of holotype, medial view. 41, the same, lateral view. 42, left cyphopod of female allotype, caudal view. Abbreviations as in figs. 3-8. 9-12. Scale line = 1.00 mm for all figs.

### *Motyxia pior* Chamberlin

Figs. 32-35

*Motyxia pior* Chamberlin, 1941:16. Chamberlin and Hoffman, 1958:39. Buckett, 1964:9. Causey and Tiemann, 1969:25-27, figs. 13-16.

*Motyxia pior* form *secca* Causey and Tiemann, 1969:27, figs. 15-16. (Invalidly proposed for a minor variant of *pior* and without standing in nomenclature.)

**Type specimens.** Female holotype (NMNH) collected by S. and D. Mulaik, 21 March 1941, 12 mi (19.2 km) NE Hammond, Tulare County.

**Diagnosis.** Prefemoral process upright and entire, a short, spiniform projection extending to near level of distal extremity of solenomere; latter fused basally to process "B", detaching near midlength, detached part minute, blunt, and indistinct, much shorter than distal part of process "B"; latter broad and irregularly semilunar, suberect, medial margin curvilinear, lateral margin subcontinuous, curving generally mediad, apically subacuminate; cyphopod with hirsute receptacle (Figs. 32-35).

**Variation.** The prefemoral process may or may not have a short basal tooth on either or both sides; the detached part of the solenomere may be slightly longer than shown in figs. 32-34 and

subacuminate; and process "B" may be broader than shown and lean slightly anterior or caudad. Additionally, there may be a single, moderately long macroseta distad on the prefemur; it may or may not arise from a minute papilla, and the latter can also exist without the seta. This seta is particularly prominent in males collected along Dry Creek, south of Badger, and SEM photos make it look even larger. Causey and Tiemann (1969) therefore thought it was a sclerotized structure representing a second prefemoral branch, concluded that *M. pior* is polymorphic, and named this variant "*secca*" because of its prevalence along Dry Creek. However, the International Code of Zoological Nomenclature has no provision for naming variants, and the authors did not officially propose a subspecies, so the name, "*secca*," has no standing in nomenclature.

Measurements of pinned adults are summarized in table 9; on the average females are larger in both dimensions than males at the two sites with both sexes, and individuals tend to be longer and broader to the west in the range.

**Distribution.** According to a guide, bioluminescent millipeds have been seen inside Crystal Caverns, Sequoia National Park. None has ever been collected there, but the site record is plausible



and conforms to the known distribution of *M. pior*. This is the northernmost known locality for bioluminescent millipeds, and the species' range extends, east/west, from Woodlake Valley north of Elderwood to the vicinity of Hospital Rock in Sequoia National Park, a distance of some 16 mi (25.6 km). Specimens were examined from the following new localities: **Tulare Co.**, 6.8 mi (10.9 km) S Badger, along Dry Cr. Rd., 17M, 22F, 2 juvs., 1 April 1964, DLT (FSCA, LACMNH); 9.3 mi (14.9 km) S Badger, along Dry Cr. Rd., 4M, 6F, juv., 31 March 1964, DLT (FSCA); and 2 mi (3.2 km) "above" Three Rivers, 3M, 3F, DLT, D. D. Linsdale (FSCA).

***Motyxia porrecta* Causey and Tiemann**

Figs. 36-39

*Motyxia porrecta* Causey and Tiemann, 1969:27, 29, figs. 7, 21-22.

**Type specimens.** Male holotype, female allotype, and 6 male and one female paratypes (FSCA) collected by D. L. Tiemann, 27 January 1965, at Stork Creek county picnic site, Kern River Canyon, Kern County. Twenty-six male paratypes (FSCA) and 5 male paratypes (LACMNH) taken by same collector on same date, 1.3 mi (2.1 km) "below" Miracle Hot Springs, Kern River Canyon, Kern County.

**Diagnosis.** Prefemoral process entire, moderately long and gently sinuate, apically rounded, extending to near level of distal extremity of solenomere; latter fused basally to process "B", detaching proximal to midlength, detached part short but distinct, clearly extending from process "B", apically blunt; process "B" long and subspatulate, distal part curving in gently sinuate configuration but extending nearly directly ventrad, sides tapering gradually distad to rounded tip; cyphopod with glabrous receptacle (Figs. 36-39).

**Variation.** The only gonopodal variation involves slight differences in the length and curvature of the telopodal branches. Measurements of pinned adults are summarized in table 10; females are slightly larger in both dimensions than males at two of the three sites with both sexes, but no geographic trends are evident.

**Distribution.** The Kern River Valley from below the entrance to the Sequoia National Forest to near Miracle Hot Springs, and north to Oak Flat on the Western Divide (Rancheria) Road. Approximate dimensions are 20.8 mi (33.3 km), east/west,

and 10.2 mi (16.3 km), north/south. Specimens were examined from the following new localities: **Kern Co.**, Greenhorn Mts., exact locality not specified, M, 24 July 1955, A. R. Hardy (LACMNH); along Western Divide Rd. at Rattlesnake Cr., 35M, 2F, 21 February 1966, D. L. & D. A. Tiemann (LACMNH); along Western Divide Rd. at Oak Flat, 3M, 6F, 21 February 1966, D. L. & D. A. Tiemann (LACMNH); Democrat Hot Spgs. turnoff, Kern R. Cyn., 23M, F, 27 January 1965, D. L. & P. M. Tiemann (LACMNH); and 7 mi (11.2 km) SW Democrat Hot Spgs., Upper Richbar Cpgd., 34M, 29F, 22 December 1967, J. S. Buckett, M. R. Gardner (UCD).

***Motyxia tiemanni* Causey**

Figs. 40-42

*Motyxia tiemanni* Causey, 1960:132-135, figs. 1-2. Causey and Tiemann, 1969:31-32, figs. 9, 23-24.

**Type specimens.** Male holotype and female allotype (AMNH), two male and two female paratypes (NMNH), and one male and one female paratypes (FSCA) collected by D. L. Tiemann, 11 May 1959, at Shirley Meadows, ca. 6 mi (9.6 km) W north arm of Lake Isabella, Sequoia National Forest, Kern County. Three male paratypes (FSCA) taken by same collector in May 1959.

**Diagnosis.** Prefemoral process upright and entire, very broad basally, narrowing slightly at midlength then expanding again to broad tip, slightly shorter than, or subequal in length to, process "B"; solenomere arising basally from acropodite, upright for most of length, curving slightly caudolaterad apically and overlapping process "B"; latter long and upright, narrowly segregated basally from solenomere, expanded basally, narrowing gradually distad to subacuminate tip; cyphopod with glabrous receptacle (Figs. 40-42).

**Variation.** The general configurations of the branches are constant, but their relative lengths vary. The prefemoral process may be subequal in length to process "B", and the solenomere varies from 1/2 to 2/3 as long as the latter. Measurements of pinned adults are summarized in table 11; females at Shirley Meadows are larger in both dimensions than males, and individuals from east of Glenville tend to be longer than those to the north-east from Shirley Meadows.

**Distribution.** The Greenhorn Mountains of northern Kern County, from just below the Tulare County Line to Evans Flat Campground, some 9.6 mi (15.4 km) to the south. Specimens were exam-

ined from the following new localities: Kern Co., E of Glenville, M, 18 March 1941, S. and D. Mulaik (NMNH); and Alder Cr. Cpgd., ca. 2.5 mi (6.3 km) NW Shirley Mdws., 2M, 24 March 1970, H. B. Leech (CAS).

#### Remarks and observations on the bioluminescence

A quarter-century has elapsed since the last publication on *Motyxia*, and a summary of current knowledge of the bioluminescence is in order because of the phenomenon's significance to the Diplopoda as a whole; I supplement this with personal observations on live *M. s. sequoia* and *M. pior*, which I have collected and received from California entomologists. Loomis and Davenport (1950), Davenport et al. (1952), and Causey (1960) describe the luminescence as a "greenish-white" glow, but the color that I observed was neon white without a greenish tint, resembling the glow from a "light stick." The luminescence is continuous and not under voluntary control; it seems inexhaustible, and captured individuals of *M. s. sequoia* glowed brightly for many hours on 4-5 consecutive evenings, until they either died or were preserved. The entire dorsum, legs, and antennae glow evenly; I have not checked the ventral surface, but according to Causey and Tiemann (1970), the sterna and gonopods do not emit light. The reaction requires oxygen and takes place in "deeper layers of the integument"; Davenport et al. (1952) did not observe light from egg masses of *M. sequoiae* or first instars individually, but masses of the latter glowed faintly. Older instars apparently did illuminate, because the authors noted a decrease in intensity at the time of molting, which corresponds with a reduced metabolic rate.

Causey and Tiemann (1969, 1970) repeatedly stated that individuals within populations differ as to the intensity of the light and that some are dark and do not luminesce. Similarly, I have had individuals that glowed brightly immediately upon exposure to darkness and others that required handling for 15-20 minutes before they began emitting a faint light. Causey and Tiemann do not indicate the times of their observations, but mine came at different hours of the day, the former at night and the latter during daylight, and suggest a circadian rhythm. Controlled experimentation on photoperiod may therefore be profitable because the reaction may observe a periodicity, taking place immediately in normal hours of darkness, but being slow or

inoperative when an individual is placed in darkness during normal daylight hours.

No author has suggested a function for the luminescence. Davenport et al. (1952) discount recognition, because polydesmoids are blind, and correctly state that the "warning luminescence" hypothesis can only be proved by controlled field experiments. However, this is still a valid hypothesis, and few others seem plausible. Luminescence could conceivably function as a nighttime equivalent of aposematic coloration, as exhibited by east-Nearctic xystodesmids and by Sierran representatives of *Sigmocheir* (Whitehead and Shelley 1992, Shelley 1995a), because the glowing millipeds are quite conspicuous. Causey and Tiemann (1969, 1970) report that they sometimes "resemble the starry sky on a dark night," and while I have not viewed this situation, I have seen several glowing *Motyxias* walking in a dish. The luminescence is a spectacular phenomenon and without question would "warn" predators of the millipeds' presence.

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Tables 1-11.

Table 1. Measurement data of pinned adults of *M. montica*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Kern Co., Keene					
Males n = 84			Females n = 4		
30.17	5.59	21.11	29.07	5.67	19.53
range 20.92-33.78	4.37-6.34	17.93-23.89	range 27.73-30.24	5.40-5.85	18.90-20.48
Kern Co., Fort Tejon					
Males n = 28			Females n = 9		
24.47	4.65	19.01	24.70	4.78	19.35
range 21.24-28.85	4.03-5.49	16.33-22.73	range 18.39-28.05	3.64-5.44	18.89-20.49
Los Angeles Co., Topanga Canyon Rd. at Greenleaf Canyon					
Males n = 10			Females n = 5		
23.42	4.42	18.96	23.74	4.72	19.91
range 18.14-25.79	4.02-4.60	17.33-22.16	range 22.46-24.77	4.53-4.90	18.96-21.32

Table 2. Measurement data of pinned adults of *M. kema*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., Laevis Flat Campground					
Males n = 10			Females		
28.26	5.59	19.78	31.45	6.50	20.67
range 26.60-30.14	5.03-6.20	18.13-21.23			
Tulare Co., Deer Creek Rd.,					
Males n = 10			Females n = 3		
27.90	5.51	19.74	30.86	6.18	20.07
range 25.95-29.80	4.86-5.79	16.31-21.70	range 29.60-33.09	5.98-6.36	18.71-21.29
Tulare Co., 2 mi (3.2 km) S Pine Flat, Caplnero Cr.					
Males n = 23			Females		
31.16	6.27	20.13			
range 26.53-34.84	5.47-6.96	17.28-22.65			
Tulare Co., 3.3 mi (5.3 km) SE White River					
Males n = 17			Females		
26.53	5.36	20.22			
range 21.80-31.00	4.84-5.88	17.55-22.17			
Tulare Co., 7.3 mi (11.7 km) NE White River					
Males n = 35			Females		
26.17	5.32	20.33			
range 22.88-32.29	4.69-6.05	17.66-21.81			

Table 3. Measurement data of pinned adults of *M. sequoiae*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., Coy Flat nr. Camp Nelson					
Males n = 36			Females n = 2		
33.00	6.75	20.47	35.32	7.73	21.87
range 25.05-38.75	5.50-7.25	18.33-22.40	range 34.94-35.65	7.70-7.75	21.60-22.15
Tulare Co., Camp Belknap					
Males n = 170			Females n = 62		
34.81	7.04	20.29	38.12	7.60	19.95
range 28.76-39.60	6.19-7.92	17.15-23.19	range 32.95-43.83	6.66-8.44	17.02-22.59
Tulare Co., along CA Hwy. 190 at Moorehouse Cr.					
Males n = 20			Females n = 3		
32.46	6.58	20.28	37.83	7.67	20.27
range 28.33-37.01	5.60-7.42	18.62-24.19	range 36.70-39.79	7.32-7.91	19.53-21.38

Table 4. Measurement data of pinned adults of *M. tulareae*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., Panorama Campground					
Males n = 2			Females		
32.46	6.06	18.65			
range 32.31-32.60	5.94-6.17	18.38-18.93			
Tulare Co., Greenhorn Mts., 0.9 mi (1.4 km) N Kern Co. line					
Males n = 30			Females n = 4		
25.13	4.84	19.25	31.50	5.93	18.81
range 21.29-29.98	4.17-5.98	16.88-20.95	range 25.60-38.04	5.02-6.76	17.61-19.61
Kern/Tulare, Greenhorn Mts.					
Males n = 5			Female		
25.55	4.55	17.79	26.29	4.88	18.56
range 24.17-26.44	4.28-4.85	16.48-19.86			
Kern Co., 0.2 mi (0.3 km) S Tulare Co. line					
Males n = 28			Females n = 4		
24.22	4.72	19.47	26.23	5.15	19.66
range 22.47-31.90	4.28-6.44	17.60-22.34	range 24.56-29.05	4.90-5.50	18.93-20.60

Table 5. Measurements data of pinned adults of *M. dilarens dilarens*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., Entrance to Tule Indian Res.					
Males n = 4	25.78	5.20	20.18	27.16	5.40
range	23.10-27.22	4.81-5.40	19.21-20.82		19.88
Tulare Co., 4.1 mi (6.6 km) E entrance Tule R. Indian Res.					
Males	29.88	5.61	18.78		
Tulare Co., Deer Cr. Rd. at Pothole Cr.					
Males n = 9	28.48	5.10	17.91	22.73	4.32
range	24.15-34.17	4.50-5.66	14.78-20.60		19.01
Tulare Co., Coffee Campground					
Males n = 112	28.91	5.56	19.24	31.57	6.30
range	23.34-34.83	4.49-6.56	16.53-22.68	range	23.40-38.57 4.66-7.45 18.08-22.65

Table 6. Measurement data of pinned adults of *M. sequoia sequoia*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co. 8.5 mi (13.6) E Hammond					
Males n = 19	32.44	6.10	18.83	35.02	6.90
range	27.08-36.69	4.54-6.73	16.77-20.17	range	32.99-37.39 6.35-7.26 19.13-20.67
Tulare Co., 5.8 mi (9.3 km) E Hammond					
Males n = 2	36.57	5.89	16.10		
range	35.69-37.45	5.70-6.08	15.97-16.23		
Tulare Co., 3.1 mi (5.0 km) S Hammond					
Males n = 32	32.47	6.28	19.42	32.26	6.44
range	27.26-38.42	5.40-7.19	17.37-22.38	range	25.68-37.54 5.15-7.40 17.88-21.93

Table 7. Measurement data of pinned adults of *M. sequoia atla*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., 2 mi (3.2 km) SW Three Rivers					
Males n = 6	26.01	5.35	20.57	29.59	5.73
range	24.00-27.21	5.11-5.84	19.64-22.00	range	25.21-32.69 4.80-6.26 19.04-19.83
Tulare Co., Milo					
Males n = 2	32.71	4.90	15.16		
range	28.69-36.73	4.76-5.04	13.72-16.59		
Tulare Co., opposite Terminal Reservoir					
Males n = 2	30.96	4.79	15.51		
range	26.70-35.31	4.30-5.27	14.92-16.10		
Tulare Co., 1 mi (1.6 km) NW Clough Cave, Sequoia Nat. PK.					
Males n = 127	31.54	6.13	19.43	31.80	5.99
range	25.78-38.72	5.16-7.11	16.19-22.67	range	29.70-34.23 5.52-6.35 16.77-19.87

Table 8. Measurement data of pinned adults of *M. sequoia* Intergrades, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., 4.1 mi (6.6 km) NW Clough Cave					
Males n = 4	27.48	5.36	19.50	28.44	5.79
range	26.11-28.94	4.92-5.71	18.55-19.70	range	27.37-29.50 5.70-5.88 19.32-21.48
Tulare Co., 8.7 mi (13.9 km) NW Clough Cave					
Males n = 10	29.58	5.55	18.78	34.99	6.54
range	27.35-32.22	4.84-6.11	17.38-20.19	range	31.69-39.02 5.83-6.86 17.40-20.74

Table 9. Measurement data of pinned adults of *M. pioi*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Tulare Co., Sequoia Nat. PK., Potwisha Trailer Camp					
Males n = 5	28.33	5.36	19.02		
range	25.26-31.75	5.11-5.70	17.32-20.74		
Tulare Co., Sequoia Nat. PK., Hospital Rock Picnic Area					
Males n = 18	30.57	5.60	18.33	33.65	6.42
range	26.05-33.96	5.17-6.13	16.82-20.00	range	30.30-36.55 6.00-6.77 17.78-20.27
Tulare Co., 0.2 mi (0.3 km) E Three Rivers					
Males n = 2	32.00	5.20	16.26		
range	31.24-32.75	5.08-5.31	15.51-17.00		
Tulare Co., Dry Creek					
Males n = 55	30.39	5.88	19.34	33.84	6.63
range	25.88-35.23	5.18-6.41	17.00-22.30	range	31.52-36.31 6.06-7.34 17.98-20.68

Table 10. Measurement data of pinned adults of *M. porrecta*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Kern Co., Democrat Hot Springs					
Males n = 23	27.96	5.13	18.33	27.69	5.68
range	22.80-31.56	4.55-5.47	17.21-20.22		20.51
Kern Co., 1.3 mi (2.1 km) W Miracle Hot Springs					
Males n = 5	26.27	6.01	22.87		
range	25.13-27.83	5.19-6.75	20.23-25.43		
Kern Co., Western Divide Rd., Rattlesnake Cr.					
Males n = 34	26.03	5.24	20.14	28.87	5.63
range	23.18-28.52	4.33-5.99	17.62-22.14	range	27.86-30.20 5.49-5.75 18.68-20.13
Kern Co., Western Divide Rd., Oak Flat					
Males n = 3	29.99	5.80	19.37	30.40	6.08
range	27.55-31.33	5.50-6.06	18.82-19.96	range	28.63-31.99 5.44-6.44 17.01-21.75
Kern Co., Kern R. Canyon, Stork Cr. Campground					
Males n = 5	29.79	5.63	19.15		
range	26.62-36.16	5.54-5.74	15.43-21.41		

Table 11. Measurement data of pinned adults of *M. hemanni*, summaries of individual measurements.

L (mm)	max W (mm)	W/L ratio	L (mm)	max W (mm)	W/L ratio
Kern Co., Greenhorn Mts., Shirley Meadows					
Males n = 103	28.94	5.87	20.33	30.76	6.26
range	24.15-32.90	5.09-6.81	18.24-23.73	range	27.36-35.90 5.48-7.65 18.55-23.25
Kern Co., 8.3 mi (13.3 km) E Glenville					
Males n = 18	30.81	5.36	17.39		
range	23.83-39.87	4.86-5.78	13.92-21.63		