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A contribution on the milliped tribe Nannariini (Polydesmida: Xystodesmidae): Revalidation of *Mimuloria* Chamberlin 1928; identities of *Fontaria oblonga* C. L. Koch 1847, and *Nannaria minor* Chamberlin 1918; elucidation of the tribal range; and commentaries on *Nannaria* Chamberlin 1918, and *Oenomaea* Hoffman 1964

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Abstract. *Mimuloria* Chamberlin 1928 is revived from synonymy under *Nannaria* Chamberlin 1918a for Nannariini (Polydesmida: Xystodesmidae) with simple but apically ornamented gonopodal acropodites that arch or lean mediad and cross body midlines and opposing acropodites *in situ*. It encompasses two assemblages based primarily on the nature of the ornamentations, the castanea and dilatata species groups. The former includes three established species [*M. castanea* (McNeill 1887) *M. missouriensis* Chamberlin 1928 and *M. davidcauseyi* (Causey 1950a)], and the latter contains two new ones (***M. dilatata* [*M. d. dilatata*, *M. d. sigmoidea*]**, and ***M. rhysodesmoides***). *Castanaria* Causey 1950b is returned to synonymy under *Mimuloria*, and *C. depalmai* Causey 1950b is placed under *M. castanea*, thereby constituting a **new synonymy.** The first illustrations of the holotype gonopods of *Fontaria oblonga* C. L. Koch 1847 and *N. minor* Chamberlin 1918a unequivocally establish their identities, and the convoluted nomenclatural tangle involving *Oenomaea* Hoffman 1964 and *O. pulchella* (Bollman 1889a) is detailed. Whether in *Oenomaea* or a new genus, separate generic status seems appropriate for Nannariini with subterminal solenomeres; *N. morrisoni* Hoffman 1948 and its potential synonym *N. shenandoa* Hoffman 1949 may also belong here. Initial tribal localities are reported from Alabama, South Carolina, and coastal Virginia and Maryland, and "*O. pulchella*" occurs in northern Alabama north/west of the Tennessee River; *M. castanea* is newly recorded from Missouri and Tennessee. A horizontally subtriangular distribution in the eastern and midwestern states is projected for Nannariini, which even occur on South Bass Island, Ohio, in Lake Erie, and may thus inhabit nearby Pelee Island, Ontario, Canada.

Key words: acropodite, Arkansas, Indiana, Jefferson County, lobe(s), Missouri, Ohio, prefemoral process, *pulchella*, Tennessee

Introduction

When Richard Hoffman, the Grand Master of Diplopodology, died in 2012, he carried with him most of man's knowledge of a host of genera, two of which – *Apheloria* Chamberlin 1921 (tribe Apheloriini) and *Nannaria* Chamberlin 1918a (Nannariini) – are eastern representatives of Xystodesmidae, the dominant Nearctic polydesmidan taxon. Several contributions exist on Apheloriini, but we must begin anew with both genera and Nannariini collectively because few studies address this tribe. It presently comprises two genera, *Oenomaea* Hoffman 1964, monotypic for *O. pulchella* (Bollman 1889a) in Jefferson County (Co.), Tennessee, and *Nannaria*, occurring throughout the tribal range; the other applicable generic names, *Mimuloria* Chamberlin 1928 and *Castanaria* Causey 1950b, are synonyms of *Nannaria* (Chamberlin and Hoffman 1958; Hoffman 1980, 1999; Marek et al. 2014). According to Hoffman (1964, 1999), Nannariini contains numerous additional genera and around 200 species, and our research shows that the gonopods of forms west of the Mississippi River differ fundamentally from those of *Nannaria* and *Oenomaea*, as defined by their type-species. Since this assemblage contains its type, we revive *Mimuloria* to accommodate it and transfer synonymy of *Castanaria* from *Nannaria*.

This study originated as a review of nannariinines in Arkansas and Missouri, their only occurrences west of the Mississippi River, to complement ones on "western" representatives of other "eastern" xystodesmid taxa – *Apheloria* and *Boraria*, both by Chamberlin, *Pleuroloma* Rafinesque, and Pachydesmini (Shelley 1980; Shelley and McAllister 2007a, b; Shelley et al. 2004, 2011). However, to fully address *Mimuloria*, we had to trace it eastward to determine which, and how many, species conform to its characters, and McNeill's (1887, fig. 4) gonopod illustration shows that *Polydesmus castaneus*, in Monroe Co., Indiana, is the oldest applicable name. The project thus morphed into a review of *Mimuloria* in which we examined types of all nannariinines proposed before 1950 except *Fontaria oblonga* C. L. Koch 1847, from an unknown site in Pennsylvania. As the oldest tribal species-group name, it holds priority over all others, but its identity is unknown. The type is housed at the **ZMHB** (acronyms below), and Dr. Hoffman's files contained a gonopodal sketch made during a visit, which we publish crediting him as the source. To further facilitate the needed tribal revision, we provide commentaries on *Oenomaea* and *Nannaria* and illustrate the holotype gonopod of *N. minor* to supplement Hoffman's (1964) drawings of a male 43.2 km (27.0 mi) from the type locality.

Materials

Acronyms are as follows: **AMNH**, American Museum of Natural History, New York, New York; **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania; **FSCA**, Florida State Collection of Arthropods, Gainesville; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh; **NMNH**, National Museum of Natural History, Smithsonian Institution, Washington, DC.; **RLH**, peripheral tribal localities in Dr. Hoffman's files; and **ZMHB**, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Taxonomy

Family Xystodesmidae Cook 1895
Subfamily Xystodesminae Cook 1895
Tribe Nannariini Hoffman 1964

Nannarini (sic.) Hoffman 1964: 26–27; 1980: 159; 1999: 365. Snyder 2008: 27. Marek et al. 2014: 35.
Nannariini: Shelley and Whitehead 1986: 214 (in text). Marek et al. 2014: 35.

Diagnosis (adapted from that of Hoffman [1964]). Small-bodied, parallel-sided Xystodesminae with following characteristics. Male pregonopodal sterna narrow, unmodified except for paramedian lobes between 4th legs. Postgonopodal sterna and all sterna of females flat or only slightly elevated medially; caudal margins of 8th-18th sterna in males convexly recessed in midlines and produced into subtriangular spines subtending posterior coxae, anterior coxae subtended by smaller spines. Pregonopodal tarsal claws of males broad and spatulate, twisted or not, most midbody and all posterior leg claws gently curved and acuminate. Gonopodal aperture proportionately large, extending anteriad beyond stricture into prozonite and laterad beyond lateral margins of coxal condyles. Gonopods *in situ*, extending variably anteriad/ nteriomediad from aperture, either upright for most of length and subparallel to opposite member or curving/leaning variably mediad and overlapping same. Coxae without apophyses, connected by membrane and muscle, without sclerotized sternum or remnant of same. Prefemoral process either short and blunt/acuminate with or without variably long acicular/falcate/laminate projections arising from either corner, or with single long acicular/laminate projection with or without short basal spine. Acropodite with moderately long hairs extending varying distances along stem and tending to cluster distad into "tufts"; stem elongate, slender, or blade-like, with or without variable subterminal solenomere, tip either continuous with stem or bent abruptly caudomediad, with or without small distal lobes or projections on anterior/dorsal/ventral surfaces and additional subtriangular lamina from inner surface carrying prostatic groove to terminal opening.

Components. *Nannaria* Chamberlin 1918a, *Mimuloria* Chamberlin 1928, *Oenomaea* Hoffman 1964. According to Hoffman (1999, pers. comm. to RMS), there are a "lot" of new nannariinine genera, and our examinations of samples throughout the range support his insight. Though not erecting such here, we examined numerous males with complex gonopodal telopodites possessing laminae, cingula, torsion, etc., that we cannot accept as congeneric with *N. minor* (Fig. 25; Hoffman 1964, fig. 11), type-species of *Nannaria*. For example, *N. scutellaria* Causey 1942, from the Great Smoky Mountains National Park, Sevier Co., Tennessee, and *N. ericacea* Hoffman 1949, from Alleghany Co., Virginia (Causey 1942, 1950c; Hoffman 1949), seem improperly assigned.

Distribution (Fig. 1–2). Hoffman's (1999) characterization as the "eastern US" is overly generalized, and Nannariini do not occupy New England, as implied by his including "northeastern states" in the range of *Nannaria*. Based on peripheral records, primarily in Dr. Hoffman's files, we project a horizontally subtriangular range, wider to the east, that encompasses the eastern and central US from westcentral New York and the western shore of Chesapeake Bay (Maryland and Virginia) to southwestern Missouri and adjacent northwestern Arkansas. North/south, the area spreads southward from Lakes Ontario and Erie (New York and Ohio), northeastern Indiana, and central Missouri (just north of the Missouri River) to northern Arkansas and the northern peripheries of Mississippi through South Carolina (Fig. 1–2). Maximal dimensions are approximately 1,520 km (950 mi), east/west, and 1,056 km (660 mi) and 408 km (255 mi), north/south, in the east and west, respectively. Spanning major rivers like the Potomac, New/Kanawha, Ohio, Allegheny, Monongahela, Tennessee, Cumberland, Wabash, Mississippi, and Missouri, the tribe covers parts of 17 states including all of Kentucky, Tennessee, and West Virginia, and all but the northwestern corner of Ohio and the Eastern Shore and the cities of Norfolk and Virginia Beach, Virginia. Nannariini even occur on South Bass Island, Ottawa Co., Ohio, in southern Lake Erie, so while unknown from Canada, they may inhabit Pelee Island, Ontario, only 9.6 km (6.0 mi) to the northeast, and the Niagara River Valley in this province, although RMS sampled there in 1986 and did not find them. The distribution encompasses southern Illinois and the northern periphery of Mississippi that lack vouchers, although Hoffman (1964) cited the latter state in general. Likewise, no localities are known from Alabama and South Carolina, so we report three peripheral ones below. The westernmost sites in Missouri are only around 80 km (50 mi) from the northeastern/southeastern corners of Oklahoma and Kansas, so both Nannariini and *Mimuloria* may be encountered in these states.

Peripheral tribal records indicated by stars in Fig. 2 (clockwise from Ohio [dark green star] to Alabama): Ohio: *Butler Co.*, Oxford (Chamberlin and Hoffman 1958, Hoffman 1999, RLH). *Crawford Co.*, 6.4 km (4.0 mi) SW Bucyrus, Sears Woods (NCSM). *Ottawa Co.*, South Bass I., Put-In-Bay (RLH). **New York:** *Monroe Co.*, southwest metropolitan Rochester (RLH). *Tompkins Co.*, Ithaca (Chamberlin 1949; Chamberlin and Hoffman 1958; Kevan 1983; Shelley 1988, 2002; Hoffman 1999). **Pennsylvania:** *Centre Co.*, Toftress State Game Lands (NCSM). **Maryland:** *Prince George's Co.*, Lanham (RLH). **Virginia:** *York Co.*, Yorktown (RLH). *Suffolk City* (RLH). **North Carolina:** *Johnston Co.*, 17.8 km (11.1 mi) SW Smithfield (Shelley 1975, 1978, 2000). **South Carolina:** *Greenville Co.*, ca. 43.2 km (27.0 mi) N Greenville, Walnut Mtn. (RLH) **New State Record. Georgia:** *Dawson Co.*, Amicalola Falls State Park (RLH). *Gordon Co.*, 2.4 km (1.5 mi) S Oakman (Hoffman 1964, 1999; Marek et al. 2014). **Alabama**: *Jackson Co.*, 12.8 km (8.0 mi) S Stevenson, SW slope of Little Coon Mtn. (FSCA). *Limestone Co.*, Wheeler National Wildlife Refuge, details in *Oenomaea* account (NCSM) **New State Records.**

Remarks. As noted by Shelley and Whitehead (1986), the tribal name derives from dropping the terminal "a" in *Nannaria* to form "Nannari" then adding the tribal suffix, "ini." Thus, "Nannariini" is the correct spelling rather than "Nannarini."

Not only do our examinations reveal a host of new genus- and species-group taxa, but Nannariini may even rival or exceed Apheloriini in overall diversity. During the 1970s-80s, RMS meticulously collected "sigmoid" apheloriinines in the Carolinas, Georgia, Florida, Alabama, and Tennessee, sampling faunal interfaces every 16–32 km (10–20 mi) and gaps between published localities. This field research revealed that *Sigmoria* Chamberlin, the dominant "sigmoid" genus, is a giant mosaic complex comprising eight major components that are not separate and distinct entities but blend together through anatomical intermediates. Basing taxonomic hypotheses on 10 morphological characters, Shelley and Whitehead (1986) recognized the components at the subgeneric level and defined this category as one where anatomically-based diagnoses, which necessarily encompass all an entities' variants while simultaneously excluding all variants of the surrounding entities, were not possible with the available data. In molecularly-based research on this tribe, Marek and Bond (2006: 718) concluded that the entities constitute full genera and, apparently alluding to Shelley and Whitehead's system, the only other one available then or now, stated, "Overturning or ignoring our classification system on the basis of unsupported opinion or deference to authority should be unacceptable to the systematics and diplopod community as a whole." Everyone agrees that "unsupported opinion" (e. g., guesswork) by anyone, authority or novice, is scientifically unacceptable, but **in no way** does Shelley and Whitehead's anatomically-based system even remotely approximate this descriptor or "deference to authority." It derives from, and is copiously supported by, hundreds of published and unpublished anatomical drawings and hundreds if not thousands of preserved apheloriinines in North American and European repositories plus those collected during Shelley's sampling program, all of which are documented in two monographs (Shelley 1981, Shelley and Whitehead 1986) and numerous smaller works cited therein. Somehow, Marek and Bond failed to mention these highly relevant facts. Our observations suggest that Nannariini may also comprise mosaic complexes, but whether one subscribes to the subgeneric (Shelley and Whitehead 1986, Shelley 2000) or generic (Hoffman 1999; Marek and Bond 2006, 2007; Marek et al. 2014) concepts, it is clearly an intricate taxon. Years of targeted sampling in gaps seem necessary to fully grasp its complexities, but as nannariinines are small-bodied, they are difficult to find. Unlike the "sigmoid" apheloriinines that are large-bodied and primarily inhabit wet "cove" environments (Shelley and Whitehead 1986), nannariinines cannot be deliberately sought with any real prospect of success; moreover, only three to four individuals are usually encountered per site. In 1988, the collection at the Coweeta Hydrologic Station, Macon Co., North Carolina, was transferred to the NCSM; most of its millipeds came from pitfall traps in an experiment comparing litter faunas of clearcut versus uncut/control forests. As expected, samples from the latter contained only a few nannariinines each, but ones from the former contained as many as 50–60 individuals. This striking disparity may reflect unfavorable environmental changes; perhaps removal of the canopy, its moisture-retaining shade, and concomitant temperature rise forced nannariinines into atypical movement, whence they fell into the traps. Clearcutting may have altered the environment so drastically that these relatively stationary and scattered xystodesmids were

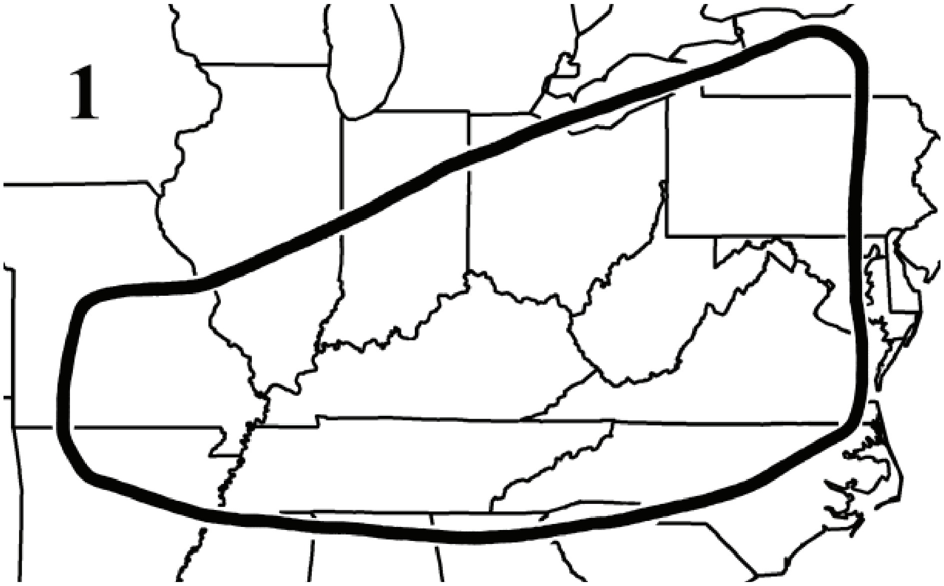


Figure 1. Projected distribution of Nannariini.

compelled to disperse *en masse* and seek favorable conditions. Perhaps pitfall trapping, even without environmental alterations, is a better technique for obtaining nannariinines than hand sampling.

Genus *Mimuloria* Chamberlin 1928, revalidated

Mimuloria Chamberlin 1928: 155. Attems 1940: 490, 530. Causey 1952: 7–8; 1955: 30. Chamberlin and Hoffman 1958: 37. Jeekel 1971: 273.
Castanaria Causey 1950b: 1. Jeekel 1971: 254.

Type-species. Of *Mimuloria*, *M. missouriensis* Chamberlin 1928, by original designation; of *Castanaria*, *C. depalmai* Causey 1950b, by original designation. Causey (1952) placed *Castanaria* in synonymy under *Mimuloria*, which was accepted by Chamberlin and Hoffman (1958).

Diagnosis. Gonopod without solenomere; acropodite arching mediad *in situ*, crossing opposite member distally or near midlength and terminating over opposing coxa; tip ornamented with either variably rounded lobe or short spiniform projection on anterior surface, or narrow lobes on dorsal and ventral margins and caudally directed, subtriangular lamina extending from inner surface and carrying prostatic groove.

Components. We recognize two assemblages that are based primarily on the distal acropodital configuration and named for the dominant species.

Distribution. Northeastern Indiana and east central Tennessee to southwestern Missouri and northwestern Arkansas.

Remarks. Representatives of the dilatata group possess anterior lobes/ornamentations at the same terminal position as the dorsal/ventral ones of the castanea group. We combine these conditions and define *Mimuloria* as having apically lobed or ornamented acropodites.

The pregonopodal tarsal claws in *Mimuloria* are the second type that Hoffman (1964) characterized in Note 1 at the conclusion of his work. They are broad and somewhat flattened/ spatulate but not

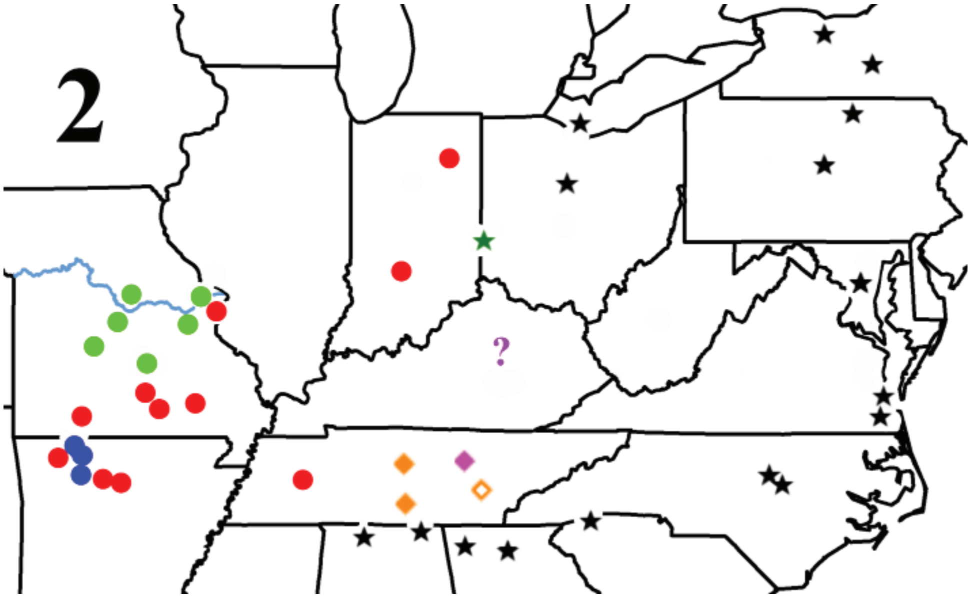


Figure 2. Distribution of *Mimuloria* (colored symbols) with peripheral tribal records (black and green stars). Dots, castanea group. Red, *M. castanea*; green, *M. missouriensis*; blue, *M. davidcauseyi*. Diamonds, dilatata group. Solid orange, *M. d. dilatata*; open orange, *M. dilatata sigmoidea*; pink, *M. rhysodesmoides*; violet question mark, *Mimuloria* sp. The course of the Missouri River across Missouri is shown in light blue.

twisted; they also narrow apically and are subacuminate rather than truncate (Fig. 7). Gonapophyses are broad basally and relatively long for such relatively small-bodied millipeds (Fig. 5).

The Castanea Group. Acropodites of the castanea group angle or arch variably mediad *in situ*, thereby crossing midlines of the bodies and the opposite members, terminating at the level of the latter's coxa. The apical acropodital lobes are short, narrow, and inconspicuous in ventral view; one must reorient the structure or focus down on the terminus to see them. Instead of terminating at this position, a short, subtriangular, caudally-directed lamina arises from the inner acropodital surface that carries the prostatic groove to its opening (Fig. 9, 11–13, 15–17). Prefemoral processes vary from short to nubbin-like, and variable projections may or may not arise from its corners. That from the inner corner (relative to the acropodital arc) is longer and more prominent, being blade-like and extending for 1/3 of the acropodital length in *M. davidcauseyi* and short, narrow, and acuminate in *M. castanea.*

Components. *M. castanea* (McNeill 1887), *M. missouriensis* Chamberlin 1928, and *M. davidcauseyi* (Causey 1950a).

Distribution. The castanea group is the exclusive inhabitant of the western 1/3 of the tribal distribution, extending from northeastern Indiana and western Tennessee to northwestern Arkansas and southwestern Missouri.

Mimuloria castanea **(McNeill 1887)**
Fig. 3, 9–14.

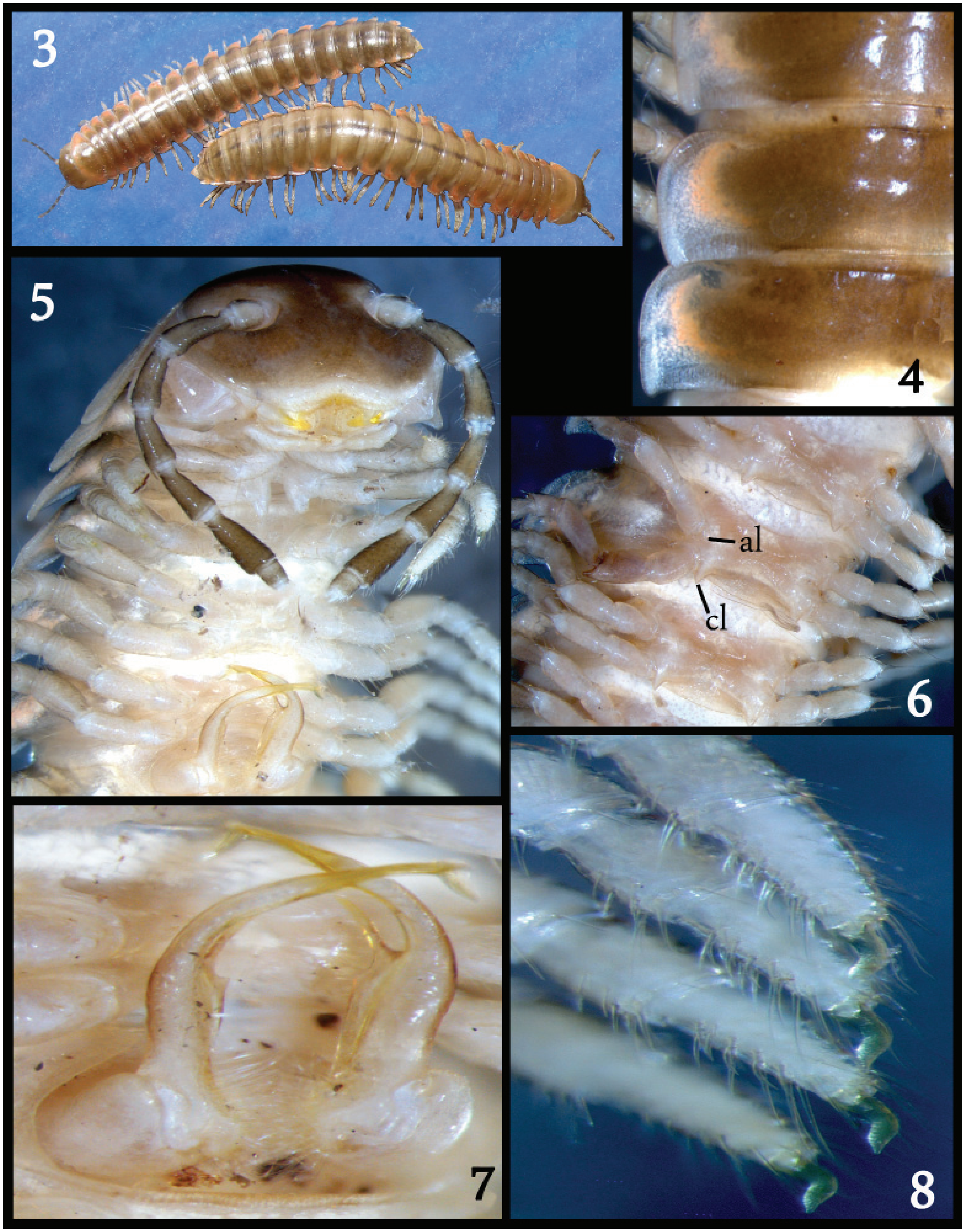
Polydesmus castaneus McNeill 1887: 329, fig. 8.
Fontaria castanea (not Williams and Hefner 1928: 106, fig. 9b): Bollman 1893: 123.
Mimuloria castanea: Chamberlin 1928: 153. Causey 1952: 8, fig. 6c; 1955: 30. Chamberlin and Hoffman 1958: 37.
Nannaria castanea: Chamberlin 1928: 153; 1949: 4. Hoffman 1999: 365–366. Marek et al. 2014: 36.
Castanaria castanea: Causey 1950b: 1.
Castanaria depalmai Causey 1950b: 1–3, fig. 1. **New synonymy.**
Mimuloria depalmai: Causey 1952: 9. Chamberlin and Hoffman 1958: 37–38.
Nannaria depalmai: Hoffman 1999: 366. Marek et al. 2014: 36.

Type specimens. Male holotype and one female paratype (NMNH) collected on an unknown date prior to 1887 in Bloomington, Monroe Co., Indiana, probably by Jerome McNeill.

Diagnosis. Acropodite arching strongly and broadly mediad; inner projection from prefemoral process relatively short, acuminate, and variably falcate, extending for 1/8 of acropodital length.

Color in life. According to Causey (1950b, 1952), individuals from Barry Co., Missouri, had reddish-orange paranota and a "black-brown" dorsum. Recently molted females that DAH collected in Carroll Co., Arkansas, evidenced by the black middorsal haemolymph vessels' being partly visible through the tegument, displayed light pinkish-orange paranota with broad, concolorous bands along the anterior margins of the collums against light olive-green base colors that were darker along the anterior halves of the metaterga than on the caudal halves (Fig. 3).

Description (derived from the fragmented holotype and intact topotypes [FSCA]). Holotype length ~23 mm; segmental widths as follows: collum ~3.7 mm, segment 2 ~4.0 mm, 5 ~4.1 mm, 12 ~4.2 mm (maximal width); W/L ratio 18.3%. Facial setae lost in some individuals but sockets visible: epicranial 0–0, interantennal 1–1, frontal 1–1, genal 0–0, clypeal 2–2, labral 14–14. Antennae reaching back to middle of 4th tergite, ~4.3 mm long; 1st antennomere slightly ovoid, 2–6 clavate, 7 truncated and cy-



Figures 3–8. The castanea group, somatic and *in situ* features. **3)** *M. castanea*, dorsal views of two recently molted females from Carroll Co., Arkansas. **4–8)** *M. davidcauseyi* male from Newton Co., Arkansas. **4)** Left side of three midbody tergites, dorsal view. **5)** Head, antennae, and segments 1–7, anterior and subventral views, respectively. **6)** Midbody sterna and basal podomeres, ventral view. **7)** Gonopods *in situ*, ventral view. al, anterior sternal lobe; cl, caudal sternal lobe. **8)** Pregonopodal tarsal claws, ventral view.

lindrical, with four terminal sensory cones within setose rim; antennomeres 2–5 sparsely setose, 6–7 denser; relative lengths of antennomeres 6>3>2=4=5>1>7.

Dorsum smooth, polished (Fig. 3). Collum ~1.1 mm long, sides slightly elevated, corners rounded. Caudal paranotal margins slanting upwards or dorsad, overlapping anterior margins of succeeding paranota, caudolateral corners becoming progressively more extended and triangular from 15th paranota caudad. Ozopores opening laterad, positioned centrally in midbody peritremata and more caudally in posterior ones. Epiproct subtriangular, slanting downward or ventrad, with two submarginal setae on each side and six apical ones arising from spinnerets. Paraprocts smooth, margins rimmed. Hypoproct semilunar, with one submarginal seta per side.

Sides of metaterga with noticeable grooves dorsad and shallow ones ventrad. Strictures narrow. Spiracles ovoid, oriented along lengthwise body axis, margins not elevated, clearly separated from coxae, anterior segmental spiracles larger than posterior ones. Postgonopodal sterna smooth and glabrous except for two small tubercles between 9th legs (caudal legs on segment 7). Legs generally long and slender, present on segments 2–18; 1st legs short, 2nd legs slightly crassate with long, subcylindrical gonapophyses extending caudad from coxae, vasa deferentia opening apically. Prefemoral spines long, acuminate, overhanging femora and extending for 1/3 of postfemoral lengths, relative lengths of podomeres 3>6>2>5=1=4. Coxae hirsute proximal to midlengths, setae of succeeding podomeres becoming progressively denser distad. Tarsal claws on legs 2–9 (on segments 3–7) spatulate but not twisted.

Gonopodal aperture ovoid, sides and caudal margin elevated. Gonopods *in situ* with acropodites arching broadly mediad, extending well beyond segmental midwidth, overlapping opposite member near midlength, arch projecting over caudal half of 6th sternum. Gonopod structure as follows (Fig. 9–13): Prefemoral process short or nubbin-like with short, slender, falcate projection arising from inner corner. Acropodite tapering for most of length, expanding apically with short, narrow, lobes opposing each other on dorsal/ventral surfaces and caudally directed, triangular, and apically rounded lamina arising between them on inner surface. Prostatic groove arising in pit in prefemur, extending along acropodital stem onto terminal triangular lamina.

Cyphopodal aperture oblong, narrow. Cyphopod (Fig. 14) small, positioned just inside aperture; valves located lateral to receptacle, caudal valve slightly larger, surfaces without noticeable hairs; receptacle proportionally large, subtriangular, subequal in size to both valves combined, with three long hairs arising anteriolaterad; operculum not evident.

Variation. Causey (1955) surmised that the prefemoral process "may be expected to show some variation when the species is better known," and indeed this is true. The basal structure may be triangular or subrhomboid and vary in size from short, inconspicuous, and nubbin-like to larger and distinct. Additionally, the length and degree of curvature of the inner projection vary from short and strongly falcate to longer and gently curved (Fig. 9, 10). Though sclerotized, they are so thin, fine, and even acicular, particularly when falcate, as to resemble macrosetae on initial viewing; they are fragile and would seem to be easily broken, which would leave an unadorned structure like that in *M. missouriensis*. The acropodital lobes in the males from Tennessee are narrower and less distinct, and the terminal lamina is less clearly demarcated from the stem.

Ecology. The species inhabits oak-hickory woodlands in Arkansas and Missouri (Causey 1950a).

Distribution (Fig. 2). Northeastern Indiana and western Tennessee to southwestern Missouri and northwestern Arkansas, a distance of approximately 792 km (495 mi). Grant Co., Indiana, is the northern- and easternmost record; Henderson Co., Tennessee, is the southernmost; and Carroll Co., Arkansas, and Barry Co., Missouri, are the westernmost.

Published records. **General range statement.** Ozark region (Chamberlin and Hoffman 1958).

Arkansas: Arkansas in general (Causey 1955). Carroll Co., Lake Leatherwood and 0.3 km (0.2 mi) S of it (Causey 1950b, Chamberlin and Hoffman 1958, Hoffman 1999, Marek et al. 2014).

Indiana: Indiana in general (Chamberlin and Hoffman 1958). Southern Indiana in general (Chamberlin and Hoffman 1958). Grant Co., erroneously assigned to *N. terricola* by Causey (1952) and

Chamberlin and Hoffman (1958). Monroe Co. (Causey 1950b), Bloomington (McNeill 1887; Causey 1952, 1955; Chamberlin and Hoffman 1958; Hoffman 1999; Marek et al. 2014).

Missouri: Barry Co., Mark Twain National Forest (Causey 1952). St. Louis Co. (Causey 1955). Wayne Co., Patterson, Holmes Cave, erroneously assigned to *M. missouriensis* by Causey (1952).

New samples (in all accounts, samples based solely on females are assigned geographically)**.**

Arkansas: Searcy Co., 8 km (5 mi) S Mull (in Marion Co.), M, 22 March 2011, M. B. Connior (NCSM). Stone Co., Blanchard Springs, 2F, 18 May 1973, D. H. Kavanaugh, H. Goulet (NMNH). **Indiana**: Monroe Co., Bloomington, MM, FF, juvs., C. H. Bollman (NMNH), and M, F, R. W. Siegel (FSCA). **Missouri**: Dent Co., along Dry Fork Cr., F, 28 August 1964, H, Exline (FSCA). Jefferson Co., 3.2 km (2 mi) SE Pacific, M, 3 November 1935, and M, 3 November 1936, L. Hubricht (NMNH) **New State Record.** Wright Co., Norwood, F, 22 May 1966, W. E. LaBerge (NMNH). **Tennessee**: Henderson Co., Natchez Trace State Park, Fern Nature Trail, 3M, 4F, 26 May 1980, R. M. Shelley (NCSM) **New State Record.**

Remarks. Causey (1952) and Chamberlin and Hoffman (1958) erroneously assigned the Grant Co., Indiana, record to *N. terricola* Williams and Hefner 1928, then in *Mimuloria*. We examined this sample, and it actually is *M. castanea*; likewise, we examined the sample from Wayne Co., Missouri, and found it to be *M. castanea*, not *M. missouriensis* as Causey (1952) reported.

We emphasize that *Mimuloria castanea* is not the same species as, and should not be confused with, *Fontaria castanea* Williams and Hefner 1928, for which Loomis and Hoffman (1948) proposed *Nannaria ohionis*. Loomis and Hoffman (1948), Chamberlin and Hoffman (1958), and Hoffman (1999) have cited *castanea* from both Ohio in general and southern Ohio, but neither it nor *Mimuloria* as we define the taxon is presently known from this state.

***Mimuloria missouriensis* Chamberlin 1928**

Fig. 15.

Mimuloria missouriensis Chamberlin 1928: 155. Attems 1940: 490. Causey 1952: 106, fig. 6a. Chamberlin and Hoffman 1958: 38.

Nannaria missouriensis: Hoffman 1999: 367. Marek et al. 2014: 37.

Type specimens. Male holotype and two male and three female paratypes (NMNH) collected by M. J. Brown on an unspecified date in 1926 in St. Charles, St. Charles Co., Missouri; one male, one female, and three juvenile paratypes (NMNH) taken by the same collector at the same locality on an unknown date in 1927.

Diagnosis. Acropodite bending or arching strongly mediad; prefemoral process subrhomboid or triangular, without projections.

Holotype. Highly fragmented, length unmeasurable; maximum width ~4.5 mm. Somatic features agreeing closely with those of *M. castanea* with following exceptions. Facial setae not detected. Antennae reaching back to midlength of 3rd tergite; relative lengths of antennomeres 3>6>2>4=5>1>7. Margins of collum slightly raised laterad. Anterior corners of 2nd – 4th paranota rounded; caudolateral corners of 5th–19th slightly extended. Relative lengths of postgonopodal podomeres 3>2>1>6>4>5. Coxae with one long, distoventral macroseta; prefemora, femora, and postfemora sparsely hirsute; tibiae and tarsi more densely so. Prefemoral spines short, only slightly overhanging femora. Tarsal claws spatulate on legs 1–9. Gonopods *in situ* and gonopod structure as in *M. castanea* except prefemoral process entirely triangular or subrhomboid and nubbin-like, without projections (Fig. 15).

Paratypes. The male paratypes agree with the holotype in all particulars.

Variation. The short, unadorned prefemoral process can be either triangular or subrhomboid, and these different configurations can also result from slight differences in orientation, as shown in our illustrations of the holotype of *M. davidcauseyi* (Fig. 16–17); the basal prefemoral spur is apically blunt in the former and triangular in the latter. Some triangular prefemoral processes of *M. missouriensis* are substantially larger than mere nubbins.

Distribution. East- and southcentral Missouri from St. Charles to Morgan cos. and traversing the Missouri River, an east/west distance of about 192 km (120 mi). North/south, the range extends around 96 km (60 mi), from the latitudes of St. Charles to Phelps cos.

Published records. Missouri: St. Charles Co.. St. Charles (Chamberlin 1928, Chamberlin and Hoffman 1958, Hoffman 1999, Marek et al. 2014).

New samples and records. Missouri: Callaway Co., no further data, FF, 7 May 1969, W. W. Dowdy (FSCA). Cole Co., Jefferson City, M, F, October 1964, W. W. Dowdy (NCSM) and LePage Rd., F, 15 April 1965, W. W. Dowdy (NMNH). Morgan Co., Versailles, M, April 1959, J. N. Brooks (NCSM). Phelps Co., 9.6 km (6.0 mi) S Rolla, M, 11 October 1966, J. and W. Ivie (AMNH). St. Charles Co., St. Charles, 4 juvs., 1926 (NMNH).

Remarks. We retain *M. missouriensis* as a valid species because the gonopodal prefemoral processes lack projections. As previously mentioned, if the inner prefemoral projection of *M. castanea* were completely broken, the resultant configuration would be that of *M. missouriensis*. Consequently, we carefully examined all prefemoral processes for evidence of breakage and finding none, conclude that the unadorned structures in this species are genetically-based rather than reflecting dissection errors. Samples of *M. missouriensis* also cluster (Fig. 2) and its range is parapatric with that of *M. castanea* to the south; one would expect random occurrences of unadorned processes throughout *M. castanea*'s range if the projections had been broken.

Attems (1938) reported *M. missouriensis* but completely missed *F. castanea* nor did he mention the latter in the Strongylosomidae volume (Attems 1937).

Mimuloria davidcauseyi **(Causey 1950a), revived combination**

Fig. 4–8, 16–17.

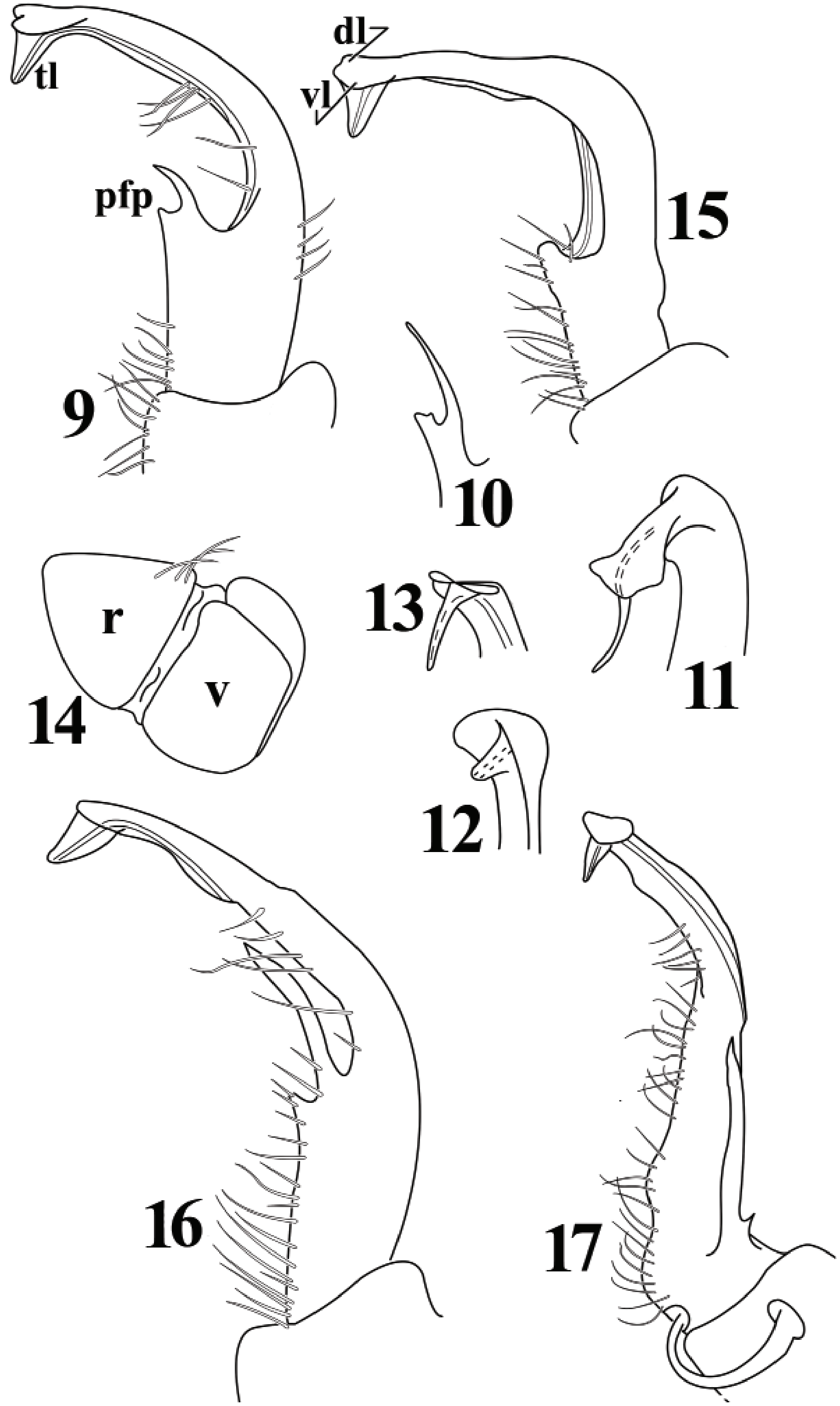
Nannaria davidcauseyi Causey 1950a: 194, fig. 3–4. Hoffman 1999: 366. Marek et al. 2014: 36.
Castanaria davidcauseyi: Causey 1950b: 1.
Mimuloria davidcauseyi: Causey 1955: 30. Chamberlin and Hoffman 1958: 37.

Type specimens. Male holotype (ANSP) and one male, one female, and one juvenile paratypes (FSCA) collected by David Causey, 25 August 1950, at Jasper, Newton Co., Arkansas.

Diagnosis. Acropodite sublinear, angling or leaning mediad rather than curving or arching; inner projection of prefemoral process long and blade-like, extending for 1/3 or more of acropodital length.

Color in life. Males from Newton Co., Arkansas, were more fully tanned than the *M. castanea* females, but displayed similar colors and patterns. Paranotal margins and peritremata were clear, translucent, and colorless with irregular, light pinkish-orange spots internally (Fig. 4) and broad, concolorous bands along the anterior margins of the collums. The background color was a moderately dark olive-green that was the same darkness on both the anterior and caudal halves of the metaterga. The head color was an even darker olive green on the epicranium that became slightly but progressively lighter anteriorly. Antennomeres 2–6 were moderately dark and articles 1 and 6 were white and slightly tinted, respectively (Fig. 5).

Holotype. Fragmented into four pieces; length 21.8 mm, maximum width 4.0 mm (Causey 1950a), W/L ratio 18.3%. Somatic features agreeing closely with those of *M. castanea* with following exceptions. Width across genal apices 2.5 mm, segmental widths: collum 3.3 mm, 2nd – 16th segments 4.0



Figures 9–17. The castanea group, genitalic features**.** **9–14**) *M. castanea.* **9**) Telopodite of left gonopod of holotype, ventral view. **10**) Prefemoral process of variant with long inner branch, ventral view. **11–13**) Distal extremities of acropodital variants in medial, dorsomedial, and dorsal views, respectively. **14**) Left cyphopod of female paratype, subventral view. **15**) *M. missouriensis* holotype, telopodite of left gonopod, ventral view. **16–17**) *M. davidcauseyi* holotype. **16**) Telopodite of left gonopod, ventral view. **17**) The same submedial view. dl, dorsal apical lobe; pfp, prefemoral process; r, receptacle; tl, terminal triangular lamina; v, valve; vl, ventral apical lobe.

mm, 17 ~3.5 mm. Facial setae as follows: epicranial 0–0, interantennal 2–2, subantennal 1–1, frontal 1–1, genal 0–0, clypeal 1–1, labral 12–12. Antennae 2.5 mm long, reaching back to midlength of 3rd tergite; relative lengths of antennomeres 6=3>4=5=2>1>7 (Fig. 5). Collum 1.6 mm long. Terga with faint wrinkling. Anterior corners of 2nd – 4th paranota rounded, caudolateral corners slightly extended, becoming more so and triangular on 12th paranota. Caudal sternal spines strong and robust, anterior ones smaller and broader (Fig. 6). Relative lengths of postgonopodal podomeres 3>6>2>4=5=1. Coxae sparsely hirsute, prefemora with hairs distal to midlengths, becoming progressively denser on distal podomeres (Fig. 7), those on tarsi exceeding lengths of claws; prefemoral spines moderately long (Fig. 6). Tarsal claws broadened, flattened, and somewhat spatulate but not twisted on legs 1–14 (segment 2 through anterior legs on segment 10), apically subacuminate (Fig. 7).

Gonopods *in situ* (Fig. 5, 8) overhanging caudal extremity of 5th sternum. Gonopod structure (Fig. 8, 16–17) as follows: Prefemoral process long and blade-like, extending for nearly half of acropodital length. Latter sublinear, angling mediad; otherwise as described for *M. castanea*.

Male paratype. The male paratype agrees closely with the holotype.

Variation. We examined six males of this species and found no variation.

Distribution. Known only from a two county area in northwestern Arkansas. *Mimuloria davidcauseyi* seems to have "carved out" a small enclave in northwestern Arkansas just inside the peripheries of the generic/tribal ranges and that of *M. castanea*.

Published records. **Arkansas:** *Newton* *Co*. (Causey 1950b), Jasper and 4.8 km (3.0 mi) NW Jasper (Causey 1950a 1955; Chamberlin and Hoffman 1958; Hoffman 1999; Marek et al. 2014). **Kentucky:** *Fayette* *Co*., Lexington (Causey 1955).

Deletion. Kentucky in general and *Fayette* *Co*., Lexington (Causey 1955).

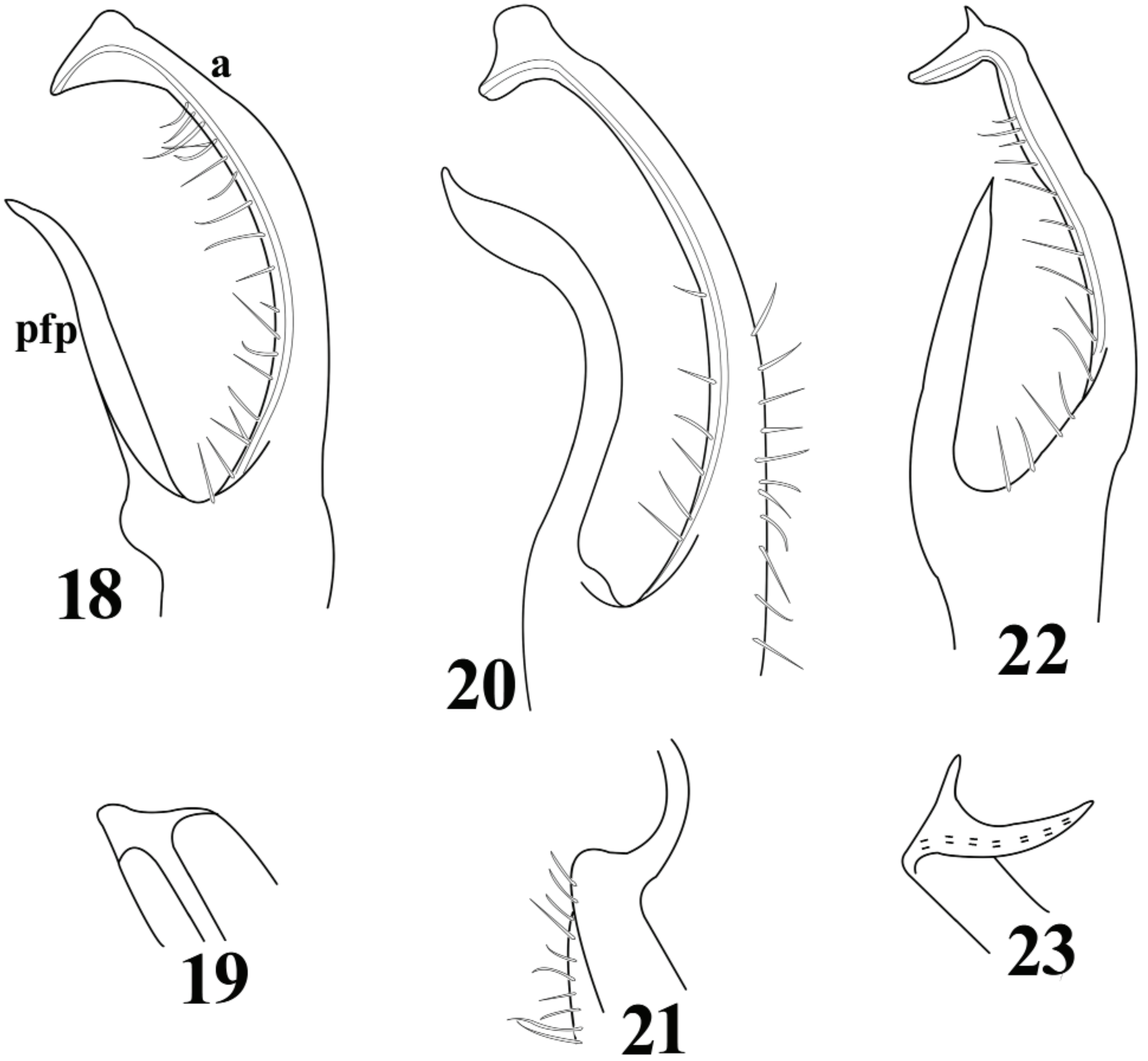
New records. Arkansas: *Johnson* *Co*., Haw Creek Falls Recreation area near Ft. Douglas, Ozark National Forest, M, 4 June 1969, D. M. Johnson (NCSM). *Newton* *Co*., Steel Cr., Buffalo National River, 36°2'16.86" N, 93°20'24.96" W, pitfall trap, 2M, 7 November 2013, M. J. Skvarla (NCSM); and Dismal Hollow, F, 2 November 2013, M. J. Skvarla (NCSM).

Remarks. With a spur on the outer corner of the prefemoral process, *M. davidcauseyi* could be regarded as a localized variant of *M. castanea*, particularly because it occupies an enclave within the latter's range. The acropodite, however, leans mediad rather than arching (compare fig. 9 and 16), and coupled with the prefemoral differences, we believe full specific status is warranted. An analogous situation exists in the Californian xystodesmid genus *Xystocheir* Cook (Xystocheirini), where *X. prolixorama* Shelley 1996 occupies an even smaller area near the peripheries of the generic/tribal ranges and that of the widespread *X. dissecta* (Wood 1867) (Shelley 1996). Figures 16–17, with the basal prefemoral spur blunt in the former and acuminate in the latter, illustrate the effect of orientation differences on structural configurations.

The Dilatata Group. Representatives of the dilatata group exhibit subupright acropodites that curve or lean gently mediad *in situ*. Subapical ornamentations, on the anterior rather than dorsal/ventral margins, vary from a low, indistinct swelling to a distinct rounded lobe to a short, acuminate spur. Termini angle ventromediad in lobed forms and submediad in that with a spur. Prefemoral processes lack basal spurs, replaced by lobes or swellings in one species, and resemble the long projection of *M. davidcauseyi* in being broad, blade-like, and extending for at least ½ of the acropodital lengths. When RMS first viewed the *in situ* gonopods of *M. d. dilatata*, they looked like those of *M. davidcauseyi* because of the long prefemoral processes. Dissection proved otherwise, but the analogy seems significant because Causey (1955) reported a male of this species from Lexington, Fayette Co., Kentucky, some 816 km (510 mi) east-northeast of its area in Arkansas. We could not locate this sample but suspect a representative of the dilatata group with the characteristic prefemoral processes (Fig. 18, 20, 22). Lexington is ca. 80 km (50 mi) north-northeast of the group's area in Tennessee, so we cite it provisionally as *Mimuloria* sp.

Components. *M. dilatata*, new species (*M. d. dilatata*; *M. dilatata sigmoidea*, new subspecies), and *M. rhysodesmoides*, new species.

Distribution. The dilatata group occupies central/eastcentral Tennessee, spreading westward from the Tennessee River Valley and east of the River itself to the Nashville Basin and the western Cumberland Plateau. With potential occurrence in Fayette Co., the area may extend northward to central Kentucky.



Figures 18–23. The dilatata group. **18–19**) *M. d. dilatata* holotype. **18**) Telopodite of left gonopod, ventral view. **19**) Distal extremity of acropodite, medial view. **20–21**) *M. d. sigmoidea* holotype. **20**) Telopodite of left gonopod, ventral view. **21**) Basal flange/shoulder of prefemoral process, medial view. **22–23**) *M. rhysodesmoides* holotype. **22**) Telopodite of left gonopod, ventral view. **23**) Distal extremity of acropodite, submedial view. a, acropodite; pfp, prefemoral process.

Mimuloria dilatata, new species

Diagnosis. Acropodite curving gently mediad, ornamentation a variably rounded lobe or swelling; prefemoral process extending for 3/4 or more of acropodital length, terminating outside of arc and directed away from stem, with variable basal lobe.

Etymology. The specific name references the apical dilation on the outer/anterior acropodital surface.

Distribution. Occurring in Tennessee from the western Cumberland Plateau to the Ridge and Valley Province and spanning the Tennessee River.

Mimuloria dilatata dilatata, new status

Fig. 18–19.

?*Fontaria tennesseensis* (not Bollman, 1889b): Chamberlin 1918b: 28.

Type specimens. Male holotype (FSCA) and one male and two female paratypes (FSCA, NCSM), collected by R. M. Shelley, 9 May 1979, in the campground of Henry Horton State Park, Marshall Co., Tennessee.

Diagnosis. Acropodital lobe an indistinct, poorly defined swelling; prefemoral process sublinear or curving gently mediad distally, terminating well below level of acropodital tip, basal lobe small, rounded.

Holotype. Length unmeasurable, maximum width ~4.1 mm.

Somatic features agreeing closely with those of *M. castanea* with following exceptions. Width across genal apices 3.2 mm. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal 0–0, clypeal about 5–5, labral about 12–12, merging with clypeal series and continuing for short distances along genal borders. Antennae reaching back to caudal margin of 3rd tergite; relative lengths of antennomeres 3>4=5>2=6>1>7. Anterior and caudolateral corners of 2nd – 4th paranota rounded, caudolateral corners of 5th paranota slightly extended, becoming progressively more so on caudal paranota. Sternal spines present on segments 8–18. Relative lengths of postgonopodal podomeres 3>6>4>2>5>1. Coxae through tibiae sparsely hirsute, tarsi with slightly denser hairs; prefemoral spines short, overhanging at most 1/4 – 1/3 of femoral lengths. Tarsal claws spatulate on legs 4–7, broad on legs 9–12.

Gonopod structure (Fig. 18–19) as follows: Prefemoral process extending for approximately ¾ of acropodital length, angling away from stem and tapering smoothly and continuously to subacuminate tip, curving gently mediad distally and terminating well below level of acropodital tip, basal lobe small and rounded, located mediad. Acropodite bowing gently mediad, not overhanging tip of prefemoral process, tapering smoothly and continuously distad but expanding into subapical swelling on outer/anterior margin then angling ventromediad and tapering to narrowly rounded tip; inner margin with narrow, linear lamina opposite swelling.

Male paratype. The male paratype agrees closely with the holotype.

Variation. The basal lobe on the prefemoral process is smaller in the Davidson Co. male, and the distal curve is fainter, though the structure still angles away from the acropodital arc. The subapical acropodital swelling is also smaller.

Distribution. Known from central and southcentral Tennessee along the highway I-65 corridor south of I-440 in Nashville, in the Nashville Basin and western Cumberland Plateau physiographic provinces.

Published record. Tennessee: Davidson Co., "Glendale Hills" (generally south of Nashville but precise location unknown) (Chamberlin 1918b).

Additional record. Tennessee: Davidson Co., Nashville, "Glendale Hills," 2M, June 1917, H. Cummins (NMNH).

Remarks. Two adults and two immatures of "*Fontaria tennesseensis*" Bollman 1889b, now in *Nannaria* (Chamberlin and Hoffman 1958, Hoffman 1999, Marek et al. 2014), were taken at "Glendale Hills" on 21 April 1917 by Harold Cummins (Chamberlin 1918b), but its type and only authentic locality is Jefferson City (formerly Mossy Creek), Jefferson Co., in the Ridge and Valley province ca. 291.2 km (182.0 mi) to the east. Sexes are not provided and the sample is lost, but the adults were surely unidentifiable females that Chamberlin assigned to *F. tennesseensis* because it was the most proximate species at the time. We now assign this record to *M. d. dilatata*, and the fact that Chamberlin did not propose a new species is evidence that the adults were indeed females. With his proclivity for naming and describing ostensible new species, Chamberlin was unlikely to pass up the opportunity to do so with this sample if it had included a mature male. Of course, he also based many names on unidentifiable females, but for some reason did not do so with this sample.

Besides *F. tennesseensis*, Chamberlin (1918b) reported seven additional millipeds from both "Glendale Hills" and "beyond Glendale" and even described two species from the former. All were collected between 14 October 1916 and 6 May 1917 by Mr. Cummins, an anatomy instructor at Vanderbilt University who later earned a Ph. D. from Tulane and became an anatomy professor in its medical school (Holt 1976). As the above males were taken a month later, Cummins probably sent them to Chamberlin even later because, again, he would have described a new species if he had had them earlier. Perhaps Chamberlin asked Cummins to revisit the site and search for a male because he did return and found two. Cummins must have sent them to Chamberlin because the sample is at the NMNH, which contains his former holdings, and it is hard to envision it being there otherwise. Whatever the reason, Chamberlin never described this new species, so we do so now,

***Mimuloria dilatata sigmoidea,* new subspecies**

Fig. 20–21.

Type specimen. Male holotype (NCSM) collected by R. M. Shelley and W. B. Jones, 14 October 1978, ca. 7.2 km (11.5 mi) S Decatur, along county road 4274, 0.8 km (0.5 mi) from junction of Tennessee highway 58, Meigs Co., Tennessee.

Diagnosis. Acropodital lobe broad, well defined, and distinct; prefemoral process with basal shoulder/flange on dorsal surface, configuration broadly sigmoidal, curving strongly inward into acropodital arc and then outward, terminating near level of latter's tip (Fig. 20–21).

Etymology. The subspecific name denotes the overall sigmoidal curvature of the prefemoral process, which also passes through numerous vertical planes.

Distribution. Known only from the type locality, in the Tennessee River Valley on the east side of the river itself.

***Mimuloria rhysodesmoides*, new species**

Fig. 22–23.

Type specimens. Male holotype and five fragmented male paratypes (FSCA) collected by H. E. Evans, 12 April 1958, in Cookeville, Putnam Co., Tennessee. One male paratype retained at NCSM.

Diagnosis. Acropodite subupright, anterior surface with subapical and subacuminate spur; prefemoral process extending for 1/2 – 2/3 of acropodital length, narrowing strongly apically, angling inward into acropodital arc and directed toward latter's stem.

Holotype. Length ca. 18.4 mm, maximum width ca. 4.4 mm, W/L ratio 23.9%. Somatic features agreeing closely with those of *M. castanea* with following exceptions. Width across genal apices 1.4 mm. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal 0–0, clypeal about 6–6, labral about 8–8, merging with clypeal series and continuing for short distances along genal borders. Antennae reaching back to midlength of 4th metatergite; relative lengths of antennomeres 6>2=3>4=5>1>7. Caudolateral corners of 2nd – 4th paranota rounded; those of 5th paranota slightly extended and becoming more so on caudal paranota. Sternal spines present on segments 8–19. Relative lengths of postgonopodal podomeres 3>2>4>6>5>1. Coxae through tibiae only sparsely hirsute; prefemoral spines long, overhanging ½ or more of lengths of femora. Tarsal claws spatulate on legs 2–18 (anterior legs of 10th segment).

Gonopods *in situ* crossing around midlengths, extending anteriad to or beyond midlength of 5th sternum. Gonopod structure (Fig. 22–23) as follows: Prefemoral process long, broad for most of length, narrowing distad, directed inward toward 2/3 length of acropodite, without trace of secondary process, spur, or lobe. Acropodite leaning mediad for most of length, bending more so distad and overhanging tip of prefemoral process; blade-like and subequal in width for most of length, narrowing at distal bend and more so apically, with subapical spur on outer margin distal to bend.

Etymology. The specific name references the apical similarity to the Mexican xystodesmid genus *Rhysodesmus* Cook, 1895 (Rhysodesmini) in possessing the spur on the outer acropodital surface (Hoffman 1966, 1970). *Rhysodesmus* also includes two Appalachian species, *R. restans* Hoffman 1998, from Washington Co., Virginia, and *R. agrestis* Shelley, 1999, from Knox Co., Tennessee (Hoffman 1998, Shelley 1999).

Distribution. Known only from the type locality.

Remarks. Though depigmented after 56 years in preservative, the types show an unequivocal banded color pattern. Broad, light bands extend along caudal metatergal margins connecting equally light paranota; the base color appears to be dark olive.

***Mimuloria* sp.**

The sample seems to be lost, but the record of *M. davidcauseyi* from Lexington, Fayette Co., Kentucky (Causey 1955), indicated by the question mark in fig. 2, is some 848 km (530 mi) east-northeast of this species' enclave in northwestern Arkansas and is unlikely to represent it. Causey's identification equates with RMS' initial conclusion upon viewing *M. dilatata*, suggesting that it constitutes another and an undescribed species of the dilatata group; alternatively, it could also represent a new genus. The locality is too far removed from authentic Arkansas localities to plausibly be *M. davidcauseyi*, so we tentatively assign the Fayette Co., Kentucky, form to the dilatata group.

Genus *Nannaria* Chamberlin 1918a

Nannaria Chamberlin 1918a: 124. Loomis and Hoffman 1948: 53. Hoffman 1949: 381; 1964: 33; 1980: 159; 1999: 365. Chamberlin and Hoffman 1958: 39–40. Jeekel 1971: 274. Kevan 1983: 2968. Shelley 2000: 196. Marek et al. 2014: 36.

Type-species. *Nannaria minor* Chamberlin 1918a, by original designation.

Remarks. *Nannaria* occurs from westcentral New York and southeastern Virginia to western Ohio and perhaps eastcentral Kentucky/Tennessee and northern Alabama/Georgia, and presently comprises 17 species. However, *N. ericacea* and *N. scutellaria*, for example, do not seem congeneric with *N. minor* and appear to require new genera, and numerous new and undiscovered species and genera undoubtedly await discovery in both the field and preserved holdings. A revision is needed but can only derive as part of a comprehensive tribal review, which is well beyond our scope. We note, however, that the holotypes of the two most important components – *N. minor*, the type-species, and *N. oblonga*, the oldest name and thus holding priority over all others – have never been illustrated, and knowledge of their gonopods is essential for generic and tribal revisions to advance. We therefore publish such (Fig. 24–25) to eliminate this void and facilitate future research.

Nannaria oblonga **(C. L. Koch 1847)**

Fig. 24.

Fontaria oblonga C. L. Koch 1847: 175; 1863: 73–74, pl. 32, fig. 64a, b. Attems 1899: 11, 151; 1938: 167. Chamberlin and Hoffman 1958: 55.

Nannaria oblonga: Hoffman 1999: 367. Marek et al. 2014: 37.

Type specimen. Male holotype (ZMHB) taken by unknown collector on an unknown date prior to 1847 at an unknown location in Pennsylvania.

Remarks. As with those that Shelley (2014) published of the rhinocricid spirobolidan, *Spirobolus monilicornis* Porat 1876, fig. 24 is an unpublished sketch of the holotype gonopod that Dr. Hoffman made while visiting the ZMHB decades ago. The prefemoral process is substantially shorter than the acropodite and leans toward it, and a basal spur is not apparent in this view. We have not encountered this form in either the field or preserved holdings and cannot suggest a region of Pennsylvania where it may occur. All males from this state and New York that we have seen or have been illustrated possess substantially longer prefemoral processes relative to their acropodites. The proportional disparity seems significant, so we hesitate to assign samples to *N. oblonga* or propose new synonymies, and publish Dr. Hoffman's sketch to benefit future workers.

Nannaria minor **Chamberlin 1918a**

Fig. 25.

Nannaria minor Chamberlin 1918a: 124. Chamberlin and Hoffman 1958: 41. Hoffman 1964: 33, figs. 5–7, 11; 1999: 367. Marek et al. 2014: 37.

Type specimen. Male holotype (MCZ) collected by R. Thaxter in July of an unknown year prior to 1918, at Burbank, Carter Co., Tennessee, in the Cherokee National Forest.

Remarks. Hoffman (1964) observed that *N. minor* had never been illustrated, which constituted an obstacle to advancing knowledge of the genus and tribe. He thus presented three somatic and an *in situ* gonopod drawings of an ostensibly conspecific male taken 43.2 km (27.0 mi) southwest of Burbank, not the holotype itself. We concur that this male is conspecific but believe that a dissected holotype gonopod should be drawn and provide such in fig. 25. The proximal divergence of the acropodite and prefemoral process, as opposed to their converging or being subparallel, seems significant as divergence of these structures in nannariinines is primarily distal. Furthermore, the short prefemoral branch is rounded and digitiform instead of spur-like and (sub)acuminate, as in Dr. Hoffman's (1964, fig. 11) *in situ* drawing. As the holotype is the only type specimen, we cannot determine whether it truly represents the local population or is atypical in these regards. Securing a series of male topotypes, to address this matter and understand the local population, seems a priority for generic and tribal revisions, but fig. 25 depicts attributes of the holotype nearly a century after the genus and species were established (Chamberlin 1918a).

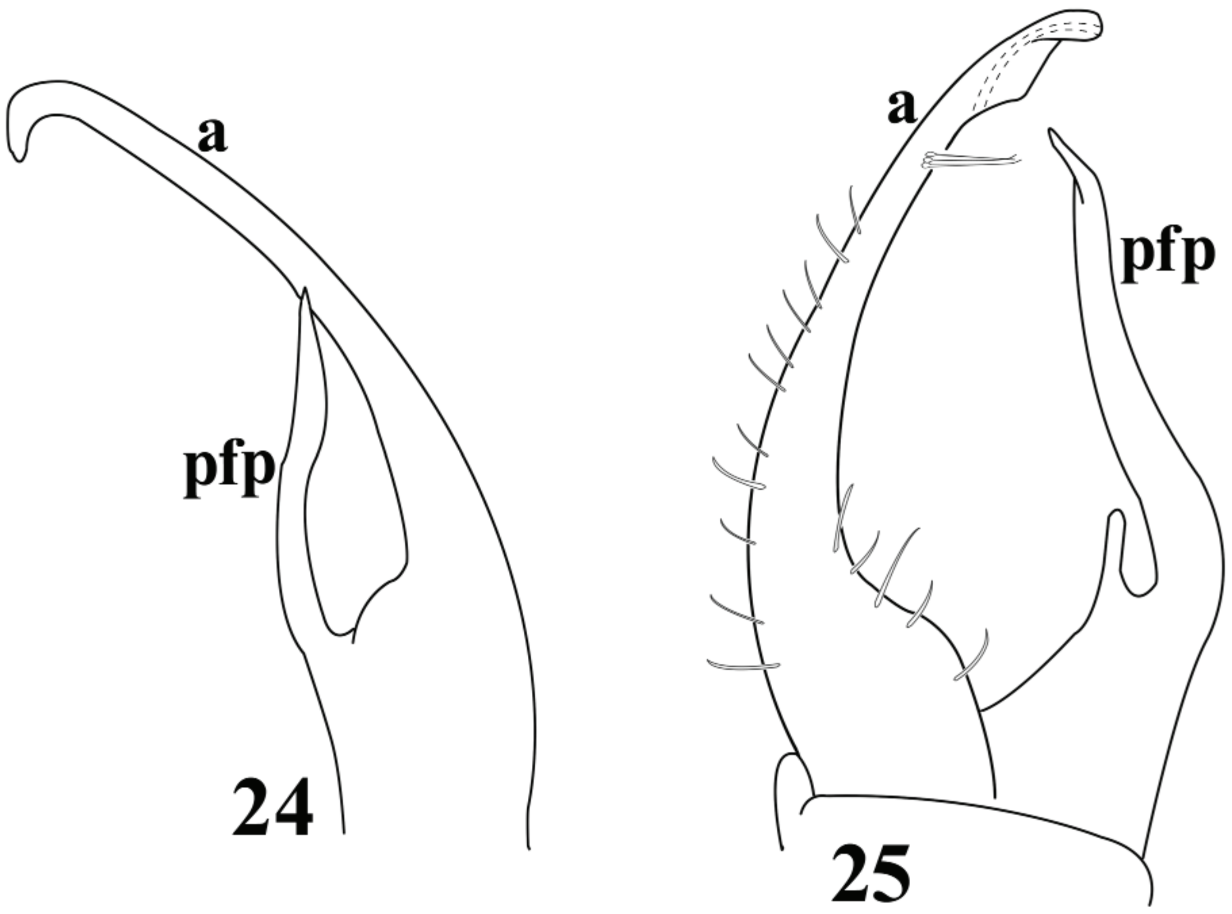
Oenomaea **Hoffman 1964**

Oenomaea Hoffman 1964: 27–29; 1980: 159; 1999, 368. Shelley et al. 2000:115. Marek et al. 2014: 38.

Type- and only component species. *Fontaria pulchella* Bollman 1889a, by original designation. The type locality is Strawberry Plains, an unincorporated community on the bank of the Holston River that straddles the boundary between Jefferson, Knox, and Sevier cos., Tennessee.

Diagnosis. Acropodite with variably broad, medially directed solenomere around 2/3–3/4 length.

Remarks. Hoffman (1964) proposed *Oenomaea* for a male from Gordon Co., Georgia, with a spatulate, subterminal solenomere and, because of somatic concordance, inexplicably concluded that it was conspecific with *Fontaria pulchella* some 240 km (150 mi) to the north-northeast. Bollman (1889a) proposed this name for two female nannariinines, now the syntypes, that are **unidentifiable beyond tribe!** We document a lengthy distribution for *M. castanea* (Fig. 2, red dots), but relatively complete ranges have not been reported for other Nannariini. Indeed, the little known about specific distributions in the tribe suggests that they are primarily restricted. Consequently, no plausible basis exists to assume conspecificity between nannariinine females and a somatically similar, geographically distant male! Hoffman (1964) even acknowledged as much, "…concordance in external features does not necessarily imply specific identity between millipeds, particularly of different sexes…" but then claimed that considering them such caused "no great harm," "there can be no doubt" that they are congeneric, and that if emendation is ever required "…it will merely be necessary to provide a new specific name" for the Georgia male! Later, he (Hoffman 1999) retreated, noting that *O. pulchella* had been reported, "perhaps dubiously," from Georgia. Hoffman (1964) correctly noted that *pulchella* must always refer to the form represented by the Tennessee females, but since he specifically designated it type-species



Figures. 24–25. **24**) *Fontaria oblonga* holotype, sketch of telopodite of left gonopod by R. L. Hoffman, subventral view, hairs and prostatic groove omitted. **25**) *Nannaria minor* holotype, telopodite of right gonopod, ventral view. a, acropodite; pfp, prefemoral process.

of *Oenomaea*, the genus will also refer to the Tennessee form if the Georgia male is **not** congeneric; it will then require **both** a new generic **and** a new specific names. Superficially similar body forms among species that are not congeneric are widespread in Xystodesmidae, so this "worst case scenario" seems likely for what is now *O. pulchella*. Resolving this convoluted tangle requires topotypical males of *F. pulchella* as close to Strawberry Plains as possible, and suitable ones probably already exist in preserved collections. Adding to the probability that the "worst case scenario" will result is the fact that most nannariinine males in that region of Tennessee lack solenomeres and are readily accommodated by *Nannaria*. Consequently, if this is true for topotypical males of *F. pulchella*, not only will the Georgia male require two new names but the melodious Greek name *Oenomaea* will fall in synonymy under *Nannaria* and vanish from nomenclature! We think that separate generic status is appropriate for nannariinines with subterminal solenomeres and note that the potential synonyms, *N. morrisoni* Hoffman 1948 and *N. shenandoa* Hoffman 1949, fit in such a taxon, but it would be imprudent to propose one before the "*Oenomaea* tangle" is fully resolved. One can only assume continued existence of present concepts, so we report the following locality for "*O. pulchella*" based on an Alabama male that nearly exactly matches Hoffman's gonopodal drawings of that from Georgia. It constitutes a new state for the species and extends the generic and specific ranges across the Tennessee River.

Alabama: *Limestone Co*., Wheeler National Wildlife Refuge, Rockhouse Cave, M, 2 April 1968, A. W. Dobson, Jr. (NCSM) **New State Record for both the genus and species.**

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