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**The milliped family Trichopetalidae,
Part 2: The genera *Trichopetalum*, *Zygonopus* and *Scoterpes*
(Diplopoda: Chordeumatida, Cleidogonoidea)**

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Abstract

The genera *Trichopetalum* Harger, 1872, *Zygonopus* Ryder, 1881 and *Scoterpes* Cope, 1872 are revised. Illustrations are provided for all but one species, and distributions are mapped. The first known authentic chordeumatidan spermatophores are described for *Trichopetalum dux* (Chamberlin), 1940. The production of a sticky secretion from the bases of the segmental setae, possibly defensive in function, is also described. The **new subfamily Mexiterpetinae** is established for the genus *Mexiterpes* Causey, 1963; the remaining genera of Trichopetalidae are grouped in subfamily Trichopetalinae Verhoeff, 1914 (tribe Scoterpetini Causey, 1969, **n. syn.**). *Trichopetalum* consists of seven species, all surface-dwelling or troglomorphic: *lunatum* Harger, 1872, *uncum* Cook & Collins, 1895, *dux* (Chamberlin), 1940, *montis* Chamberlin, 1951, *stannardi* (Causey), 1951, ***dickbrucei* n. sp. and *jerryblatti* n. sp.** *Zygonopus* is resurrected from synonymy with *Trichopetalum*; it contains four troglomorphic species: *whitei* Ryder, 1881 (for which a **neotype** specimen is designated), *krekeri* Causey, 1960, *packardi* Causey, 1960 and *weyeriensis* Causey, 1960. *Scoterpes* likewise is made up entirely of troglomorphic species, including *copei* (Packard), 1881, *austrinus* Loomis, 1943, *nudus* Chamberlin, 1946, *ventus* Shear, 1972, *syntheticus* (Shear), 1972, *sollmani* Lewis, 2000, and the following new species: ***alabama*, *hesperus*, *jackdanieli*, *musicarustica*, *stewartpecki*, *tombbarri*, *tricornis* and *willreevesi***. It is likely that at least *S. copei* and *S. ventus* are “superspecies,” consisting of numerous genetically isolated populations, which await study with molecular and/or morphometric methods.

Key words: troglomorphosis, caves, karst, troglomorphy

Introduction

The milliped family Trichopetalidae, endemic to the eastern United States, eastern Canada, and northeastern Mexico, was redescribed in the first paper in this series (Shear 2003). That paper covered the genera *Trigenotyla* Causey, 1951, *Nannopetalum* Shear, 2003, and *Causeyella* Shear, 2003. The present and final installment treats the remaining genera in the family, *Trichopetalum* Harger, 1872, *Scoterpes* Cope, 1872, and *Zygonopus* Ryder, 1881.

Trichopetalum includes seven species of litter-dwelling millipeds that are sometimes collected in caves as troglomorphs or troglomorphs. The individual species may have surprisingly wide ranges, considering that the animals are small and intolerant of deviations from their apparent preferred physical conditions of 100% humidity and cool temperatures. *Trichopetalum lunatum* Harger ranges farther to the north from its southernmost records in West Virginia and Indiana than any other native milliped in eastern North America, except *Underwoodia iuloides* (Harger), 1972 (Caseyidae), with which it co-occurs, and few millipeds at all are found north of its stations in Newfoundland (Palmén 1952). *Trichopetalum uncum* Cook & Collins, on the other hand, reaches as far south as southern Mississippi, and west to the fringes of the Great Plains. Two new species, evidently with more restricted ranges, are named and described below.

The genus *Zygonopus* is here restored to independent status for reasons stated below. It had been considered (Shear 1972) a synonym of *Trichopetalum*. The four included species are highly adapted troglomorphs occurring in caves in Virginia and West Virginia.

Scoterpes also consists entirely of troglomorphic species; five have previously been described and nine new ones are named below. Species of *Scoterpes* are most common in the interior karst regions of Kentucky, Tennessee, and Alabama. To the north, their range crosses the Ohio River into southern Indiana, and at the southern end of the generic range, some species have made an “end run” around the southernmost ridges of the Appalachian Ridge and Valley Province and are found in Georgia and the Great Smoky Mountains National Park (Tennessee). Distribution of individual species of *Scoterpes* is highly variable. In the interior basins, where flat-lying limestone strata extend over considerable distances, *Scoterpes* species seem to be widespread, while those that have invaded the Ridge and Valley Province, where limestone strata are highly folded, and may be separated from each other by noncavernous rocks, have small ranges. It is possible (even likely) that the widespread species are in fact each complexes of cryptic species, an issue that can only be resolved by

an examination of molecular characters or by detailed morphometric analyses of gonopods, methods not feasible in this first revision of the genus. A complete restudy of *Scoterpes* would be an ideal doctoral thesis, and would present many interesting ecological and evolutionary problems.

Segmental setae

During the course of my earlier study of trichopetalids (Shear 2003) and again in the present work, I noted the extremely long segmental setae in trichopetalids. In some species of *Scoterpes*, these setae are as long or longer than the width of the body (Fig. 55). The six segmental setae, three on each side of each metatergite, are diagnostic for the Order Chordeumatida, but differ considerably in their form from family to family. The longest setae are found in the trichopetalids and the shortest in some species of striariids, where they can indeed be detected only with great difficulty. Setae throughout the order may be aciculate, ensiform, or even with branched, brush-like tips. Microsculpture of the setae is also variable; longer, aciculate setae often spiral tightly like a unicorn's horn. In trichopetalids the elongate, stiff setae are gently curved and probably to some extent movable—this movement would be facilitated by the abrupt narrowing of the seta just as it emerges from the socket. The most usual position of the setae in living animals is curving over the animal's dorsum, forming an interlocking barrier. Under SEM, the microsculpture of the seta is seen to consist of ten to twelve deep, parallel grooves that run nearly the whole length (Fig. 34). The socket of each seta is larger than the base of the seta itself, leaving a space between the seta and the rim of the socket. From this space, a secretion can be produced that is extremely sticky, and in preserved specimens, the coagulated secretion is often found partway up the seta as a blob (Fig. 56). Clearly the parallel grooves on the seta facilitate the movement of the secretion toward the tip of the seta. Preliminary chemistry has not shown any extractable or volatile repugnatorial secretion connected with the setal "glue." I am grateful to Norman Youngsteadt, who drew my attention to the stickiness of the secretion and provided samples for analysis.

Cave localities

The genera *Zygonopus* and *Scoterpes* consist entirely of troglobionts, so all known localities are from caves. This presents difficulties in mapping localities. Label data for cave-collected specimens often do not give the exact location of the cave itself. Older labels may have older names for caves, which names have since been replaced in the literature or in local lore by newer names, or the names may be illegible or misspelled, leading to confusion (for example, are Horseskull and Horseshoe Cave in the same Alabama County the same cave, with the two names due to a misunderstanding or a spelling/transcription error?). Often cave names show little imagination; there are many "Cave Spring Caves" and "Spring Caves" scattered across North America. Many caves do not have local names and have been named by speleologists who have visited them, often only once, and such names may have lost meaning if unpublished. Even if a cave name is current, if only the cave name is given on the label, without any additional data, it may prove impossible to exactly locate the cave. States in the eastern and central US which include extensive karst areas may have publications which list, locate, and describe some known caves; this is true (luckily) for Alabama, Tennessee, and Virginia, though the youngest of these manuals is now over 30 years old, and all are outdated. Unfortunately no such compendium exists for the state of Kentucky. Such as they are, these manuals may be difficult to obtain.

Other considerations arise. In the past few decades, caves, especially those with active streams or which reach the water table, have been recognized as valuable natural resources, and a large proportion of the endangered or threatened animal species in the United States, listed both nationally and state-by-state, are cave-limited animals. Thus there are conservation reasons for not publicly revealing the exact locations of certain caves.

Therefore in the species descriptions which follow, I have not given exact locations for many caves, but have placed the cave in question as accurately as possible on an accompanying small-scale map. The idea

here is to transmit biogeographic data while remaining concerned about the conservation implications of providing exact locations. Of course in numerous cases, caves named on labels could not be located at all and are not on maps. In that case, the cave names are given in the Distribution sections under each species but are not on the maps; it is necessary to examine these sections to understand the full distribution of each species. The only exception is that if an unlocatable cave record is the only one for a county, a symbol has been placed near the center of the county to indicate the species' presence there.

Species synopsis

Some of my taxonomic conclusions have changed since the publication of the first part of the revision in 2003, and the number of species now stands at 42, in two subfamilies and seven genera. In that paper, I provided a list of trichopetalid genera and species as presented by Hoffman (1999). Below is a revised list which reflects taxonomic changes in the 2003 paper as well as the present work. Under each genus, the type species is in bold type.

Family Trichopetalidae Verhoeff, 1914

Subfamily Mexiterpetinae, new

Mexiterpes Causey, 1963: 7 species, all from Mexico

Mexiterpes calenturas Shear, 1982: caves in Tamaulipas

M. egeo (Causey), 1969: Cueva de el Puente, San Luis Potosi

M. fishi (Causey), 1969: caves in San Luis Potosi and Queretaro

M. metallicus, Shear 1972: Pinal de Amoles, Queretaro

M. nogal, Shear 1982: Sotano de Nogal, Queretaro

M. sabinus, Causey 1963: Sotano del Arroyo, San Luis Potosi

M. sangregorio, Shear 1986: Resumidero San Gregorio, Guerrero

Subfamily Trichopetalinae Verhoeff, 1914

Causeyella Shear, 2003

Causeyella causeyae Shear, 2003: Caves in Independence, Stone and IZard Cos., Arkansas

***C. dendropus* (Loomis), 1939**: Caves in SW Missouri, NW Arkansas

C. youngsteadtorum Shear, 2003: Caves in Boone Co., Arkansas

Nannopetalum Shear, 2003

Nannopetalum fontis Shear 2003: Springville Cave, St. Clair Co., Alabama

***N. pattersonorum* Shear, 2003**: Piedmont region of Virginia

N. vespertilio Shear, 2003: Bat Cave, Henderson Co., North Carolina

Scoterpes Cope, 1872 (all species from caves)

Scoterpes alabama, n. sp.: Northern Alabama

S. austrinus Loomis, 1943: NW Georgia, NE Alabama

***S. copei* (Packard), 1881**: Kentucky, Tennessee

S. hesperus, n. sp.: Central Tennessee

S. jackdanieli n. sp.: Central Tennessee

S. musicarustica n. sp.: Nashville Basin of Tennessee

S. nudus Chamberlin, 1946: NW Georgia

S. sollmani Lewis, 2000: southern Indiana

S. stewartpecki n. sp.: Southcentral Tennessee, northern Alabama

S. syntheticum (Shear), 1972: northern Alabama

S. tombarri n. sp.: SW Tennessee

S. tricorner n. sp.: Central Tennessee

S. ventus Shear, 1972: Central Tennessee

S. willreevesi n. sp.: NW Georgia, NE Alabama
Trichopetalum Harger, 1872
T. dux (Chamberlin), 1940
T. dickbrucei n. sp.: Western North Carolina
T. jerryblatti n. sp.: SE West Virginia, western Virginia
***T. lunatum* Harger, 1872**: NE United States, SE Canada
T. montis Chamberlin, 1951: Gatlinburg, Tennessee, or environs
T. stannardi (Causey), 1951: Illinois east to Virginia
T. unicum Cook & Collins, 1895: Southcentral United States
Trigenotyia Causey, 1951
Trigenotyia blacki Shear, 2003: NE Oklahoma
***T. parca* Causey, 1951**: NW Arkansas
T. seminole Shear, 2003: Seminole Co. Oklahoma
T. vaga Causey, 1959: Oklahoma south of Canadian River
Zygonopus Ryder 1881 (all species from caves)
Z. krekeleeri Causey, 1960: NW West Virginia
Z. packardi Causey, 1960: SW West Virginia, adjacent Virginia
Z. weyerienseis Causey, 1960: Westcentral Virginia, adjacent West Virginia
***Z. whitei* Ryder, 1881**: NW West Virginia, adjacent Virginia

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I am grateful to Petra Sierwald for hospitality during visits to Chicago and the Field Museum, and for the use of the scanning electron microscope facility there.

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Causey Collection

The late Nell B. Causey (1910–1979), with the help of speleobiologists Barr and Peck, John Holsinger, and Harrison Steeves, over many years amassed a very large collection of *Scoterpes* and had sorted them out into morphospecies, many of which were labelled with manuscript species or subspecies names. Causey's intended revision of the genus never appeared; she saw intractable problems in questions of species and subspecies identity in the genus (Causey, pers. comm. to WS, 1972). After her death in 1979, her large personal collection was deposited in the Florida State Collection of Arthropods, located in Gainesville, Florida. Unfortunately, Causey had mounted permanently on microscope slides the gonopods of many of the samples, and the medium (probably Hoyer's) used for these slides has deteriorated so badly as to make them unusable. Further, much of the collection appears at one time or another to have dried out, and the lightly sclerotized trichopetalids have become distorted. With the help of my student Chad Harte, we have at least partially rehabilitated many of these specimens, using trisodium phosphate as a rehydrating agent; air bubbles inside specimens were expelled by heating, then rapid cooling.

I have not always agreed with Causey's taxonomic decisions in this study, but my task of determining species limits in this complex genus was made considerably easier by her previous work. Because Causey had widely disseminated information about her manuscript species names to speleobiologists, I have briefly discussed her use of such names under each of the species she studied. Colleagues have raised the question of inadvertently making available such names by mentioning them in context with other details, but Article 11.6 of the International Code of Zoological Nomenclature clearly indicates that this is not the case, since even if the names were validated by such mention, they would immediately become junior synonyms, and names so mentioned after 1960 are not available.

Order Chordeumatida Koch, 1847

Superfamily Cleidogonoidea, Cook 1896¹

Family Trichopetalidae, Verhoeff 1914

Trichopetalinae Verhoeff, 1914:347.

Trichopetalidae Verhoeff, 1932:485. Hoffman, 1961:262; 1999:233 (list). Shear, 1972:274; 2003:12.

Type genus: Trichopetalum Harger 1872.

Included genera: Trichopetalum Harger 1872, *Scoterpes* Cope 1872, *Zygonopus* Ryder 1881, *Trigenotylo* Causey 1951, *Mexiterpes* Causey 1963, *Causeyella* Shear 2003, *Nannopetalum* Shear 2003.

Diagnosis: A family of Cleidogonoidea distinct in the modification of the ninth legs of males (telopodites reduced to one or a few articles and directed laterally or dorsally), great development of the metatergal setae, and in the (usual) presence of a strong fimbriate branch on the gonopod colpocoxite. Many, but not all, species have distinctive trichomes on the gonopod coxae and angiocoxites. For further details, see Shear (2003).

Distribution: North America, from Newfoundland west to Ontario and Wisconsin and south to Georgia, Alabama, Mississippi, Arkansas and Oklahoma (few records from the coastal plain from Virginia to Georgia or the Gulf Coastal Plain), highlands of northeastern and central Mexico.

1. In the previous part of this series (Shear 2003) I mistakenly attributed this superfamily to Shear, 1972. Of course, Cook's 1896 proposal of the Family Cleidogonidae included the superfamily name. Shear (1972) raised the name to superfamily status.

Discussion: Causey (1969) established a tribe “Scoterpini” (*recte*: Scoterpetini) to include the genera *Scoterpes* and *Trigenotyla*; this was missed by Hoffman in his monumental *Checklist of the Millipeds of North and Middle America* (2000), although Causey’s paper appears in his bibliography. Otherwise no division of the family into subordinate family-level taxa has been made previously.

Mexiterpes clearly stands apart from the rest of the family, so is herein made the type of a new subfamily.

Subfamily Mexiterpetinae, new

Type and only genus: *Mexiterpes* Causey 1963.

Diagnosis: The eighth sternum completely surrounds the bases of the gonopods, which lack a fimbriate branch and incorporate median structures probably derived from the fused bases of the colpocoxites; the ninth legs have two to five articles distal to the coxa instead of having all distal articles fused into one. The pregonopodal legs are only slightly encrassate; legpair 6 not especially so.

Distribution: Seven species are found as troglobionts in caves in the Mexican states of Tamaulipas, San Luis Potosi, Queretaro and Guerrero.

Discussion: *Mexiterpes* is not treated in detail in this paper because each of the included species (listed in Shear 2003) was well-described and illustrated originally. No new material or information on the genus has come to light since the publication of the most recent of these descriptions.

Mexiterpes is included as a trichopetalid largely on the basis of the much-elongated metatergal setae, but the gonopods bear many resemblances to those found in the cleidogonid genus *Pseudotremia* Cope, 1869 (see illustrations in Shear, 1972, of both genera). The ninth legs are more reduced, however, than those in *Pseudotremia* species, and the pattern of reduction suggests a trichopetalid assignment. A study of *Mexiterpes* solidifies the position of the trichopetalids as close to the cleidogonids, and indeed a more conservative taxonomist than this author might consider Trichopetalidae a subfamily under Cleidogonidae, while others, less conservative, might consider the mexiterpetines worthy of full family status.

Subfamily Trichopetalinae Verhoeff 1914

Trichopetalinae Verhoeff, 1914:347.

Scoterpini (*recte*:Scoterpetini) Causey, 1969:44. **New synonymy.**

Type genus: *Trichopetalum* Harger, 1872.

Included genera: *Trichopetalum* Harger, 1872, *Scoterpes* Cope, 1872, *Zygonopus* Ryder, 1881, *Trigenotyla* Causey, 1963, *Nannopetalum* Shear, 2003, *Causeyella* Shear, 2003.

Diagnosis: The gonopods have a fimbriate branch arising from the colpocoxite or the posterior surface of the angiocoxite, the gonopod sternum is posteriorly reduced to a narrow band or absent, anteriorly the sternum may be much enlarged and partially or wholly fused with the gonopod coxae. The anterior surfaces of the gonopod coxae and angiocoxites may or may not bear characteristic trichomes (unsocketed, acutely tapering cuticular extensions). These trichomes are not so obvious in species of *Trigenotyla*, often detectable only with scanning electron microscopy, and appear to be completely absent in species of *Scoterpes*. The ninth legs consist of two segments: the coxa, and a telopod segment resulting from the fusion of all distal segments; frequently signs of vestigial segmentation are visible distally, or indicated by vestigial musculature (Fig. 46), and a claw may be present or absent; in *Causeyella* and *Trigenotyla*, there may actually be 1–3 small, button-like terminal segments. The ninth leg coxae may have small, vestigial, eversible coxal glands, presumably homologous to those found on the tenth and eleventh legpairs. The pregonopodal legs of the males are slightly to distinctly encrassate, with legpair 6 usually the largest; this is very obvious in *Zygonopus*. Prefemur 6 is usually modified: slightly to very swollen, sometimes with a ventral distal projection.

Note: Because *Scoterpes* and *Trichopetalum* belong in the same subfamily, the family-level name Scoterpetini (*nom. corr.* from Scoterpini) has to be treated as a synonym of the older Trichopetalinae.

Distribution: Range of the family, except for Mexico.

Key to genera, based on males

- 1a. Twenty-eight trunk segments in adults..... 2.
1b. Thirty trunk segments in adults..... 3.
- 2a. Gonopod angiocoxites complexly branched, trichomes reduced *Nannopetalum* Shear.
2b. Gonopod angiocoxites simple, trichomes obvious, often hair-like..... *Trichopetalum* Harger.
- 3a. Eyeless, unpigmented species 4.
3b. With eyes, and usually pigmented..... *Trigenotyla* Causey.
- 4a. Sixth legpair of males strongly enlarged and curved *Zygonopus* Ryder.
4b. Sixth legpair of males slightly or not all enlarged compared to adjacent legpairs..... 5.
- 5a. Ninth leg telopodites of males cylindrical, usually with distal, button-shaped, vestigial articles; gonopod trichomes present..... *Causeyella* Shear.
5b. Ninth leg telopodites of males spindle-shaped or clavate, usually without distal vestigial articles (if present they are conical and clawed, never button-shaped); gonopod trichomes absent..... *Scoterpes* Cope.

The genera *Nannopetalum*, *Trigenotyla* and *Causeyella* were treated in the first paper in this series (Shear 2003).

Genus *Trichopetalum* Harger 1872

Trichopetalum Harger, 1872:117. Cook & Collins, 1895:62. Hoffman, 2000:235 (list). Shear, 1972:277, 2003:4 *et seq.*
Tynopus Chamberlin, 1940:57.
Flagellopetalum Causey, 1951:120.

Type species: *Trichopetalum lunatum* Harger 1872, by subsequent designation of Cook & Collins (1895); for *Tynopus*, *T. dux* Chamberlin 1940; for *Flagellopetalum*, *F. stannardi* Causey 1951.

Included species: In addition to the type, *T. jerryblatti* n. sp., *T. dickbrucei* n. sp., *T. dux* (Chamberlin) 1940, *T. montis* Chamberlin 1951, *T. stannardi* (Causey) 1951, *T. unicum* Cook & Collins 1895.

Diagnosis: Differing from members of *Zygonopus* and *Scoterpes* in having 28 trunk segments rather than 30, and in having ocelli. The coxal trichomes, or setulae, are abundant, prominent and often elongated and hairlike (Fig. 5). The single angiocoxite may be entire, divided at the tip, or deeply divided into two branches. There may also be a lateral process. The fimbriate branch arises from the posterior surface of the angiocoxite, or may be a separate articulated element. The colopoxite is well-sclerotized and diagnostic in form for species. Male legpair 2 with a distinct coxal hook (Fig. 27), legpairs 3–7 variably enlarged, either 4 and 5, or 6 the largest, femur 6 sometimes modified.

Distribution: Eastern North America, from Newfoundland, Maine and New Hampshire west to Michigan, Wisconsin and Minnesota, and thence south to Mississippi. From New York the range extends down the Appalachian Mountains and adjoining Piedmont Region to northern Georgia. Shelley (1988) reports female *Trichopetalum* from eastern Canada as *T. lunatum*; this is probably correct but is not based on males. *Trichopetalum lunatum* has evidently re-invaded glaciated territory in the last 12,000 years, and *lunatum* now occurs farther north (in southern Newfoundland) than any other native eastern North American milliped species

except *Underwoodia iuloides*, which gets even farther north in Newfoundland (Palmèn 1952). How these small, delicate, slow-moving milliped species with their evident requirements for high humidity accomplished this feat of distribution is a matter for speculation. Species of *Trichopetalum* have unusually large ranges for small millipeds, and records tend to be scattered. The latter effect may be due to the hygrophilous and psychrophilous nature of the species, which makes them hard to find during the usual collecting season, and to their small size, which makes them easy to overlook.

In 1972, I reported *Trichopetalum lunatum* from British Columbia, but this record has never been confirmed, and the examination of many recent samples of hundreds of chordeumatidan millipeds from the Pacific Northwest, including British Columbia, has revealed no trichopetalids. The original specimens (MCZ) must have been mislabelled. Causey (1963) implied occurrence in Louisiana and Colorado; I have seen no specimens from Louisiana, but there is a remote possibility of *Trigenotyta* being found there. The Colorado specimens (examined, FSCA) are juveniles of the conotyloid *Austrotyla coloradensis* (Chamberlin). The American Museum collection (AMNH) contained a number of samples from the Dakotas labelled "*Trichopetalum* sp." These are all female and juvenile specimens of *Underwoodia iuloides*.

Notes: Shelley (1993) has assigned Harger's (1872) *Trichopetalum glomeratum*, from Oregon, to the conotyloid genus *Taiyutyla*, a reasonable conclusion drawn from study of the female holotype in the Peabody Museum of Natural History at Yale University. *Trichopetalum iuloides* Harger, 1872 is *Underwoodia iuloides* (Caseyidae; Cook & Collins 1895). *Polydesmus ocellatus* Packard 1883 was tentatively placed in *Trichopetalum* by Cook & Collins (1895) but as it was described from Oregon, where *Trichopetalum* does not occur, that is unlikely. Hoffman (2000) speculated that it might be a rhiscosomidid, but the illustrations of the specimen by Cook & Collins show the collum narrower than the head, while in rhiscosomidids the collum is much wider than the head, and other illustrated details do not fit. The illustrations and description are more like a species of *Tingupa*, but in the absence of the only specimen (which in any case was probably immature) we will never know the identity of this name. *Crasedosoma flavidum* Bollman 1888 was also placed by Cook & Collins (1895) in *Trichopetalum*, but they could only find "...a small yellow female specimen with 26 segments purporting to be the type of this species...." in the USNM. That specimen appears no longer to be in the collection, and the descriptions of both Bollman (1888) and Cook & Collins (1895) are not sufficient to place the species, so this name, too, will be forever in doubt and have to be arbitrarily assigned. If the 26-segmented specimen was indeed a mature female, then it is possibly *Branneria carinata* (Bollman), 1893 or *Buotus carolinus* Chamberlin, 1940 (Shear 2009) — unfortunately both younger and much more-used names.

The species originally described in *Zygonopus* Ryder, 1881, were transferred to *Trichopetalum* by me in 1972, an action I now think was in error, and *Zygonopus* is reinstated below as a valid genus (in 2003, in the first paper in this series, I suggested subgeneric status under *Trichopetalum*). There can be no doubt, however, that the two genera are closely related. The following new synonymies and combinations are proposed: *Trichopetalum appropinquo* (Causey, 1969) and *T. quadratum* (Loomis, 1966) are both synonyms of *T. stannardi* (Causey, 1951), *T. cornutum* Cook and Collins, 1895, is a synonym of *T. lunatum* Cook and Collins, 1895, *T. subterraneum* Causey, 1967 is a synonym of *T. dux* (Chamberlin, 1940), and *T. syntheticum* Shear, 1972 is a species of *Scoterpes*.

Key to Species, based on males

- 1a. Femur of leg 6 with mesodistal knob or hook (Fig. 21)..... *stannardi*.
- 1b. Femur of leg 6 without such a knob or hook 2.
- 2a. Angiocoxite of gonopod deeply divided (Fig. 30)..... *jerryblatti*.
- 2b. Angiocoxite not deeply divided, sometimes apically cleft 3.

- 3a. Angiocoxite with strong lateral branch (Fig. 11) *uncum*.
 3b. Angiocoxite without a branch, or only a short branch 4.
- 4a. Angiocoxite tip cleft (Figs. 23, 25, 26) 5.
 4b. Angiocoxite tip entire or emarginate (Figs. 7, 13) 6.
- 5a. Colpocoxite apex acute; angiocoxite tips subequal in width. *dickbrucei*.
 5b. Colpocoxite apex quadrate; ventral angiocoxite tip much wider than dorsal *montis*.
- 6a. Angiocoxite short, with small lateral branch; colpocoxite distinctly lamellate *dux*.
 6b. Angiocoxite long, curved, lacking lateral branch; colpocoxite acute *lunatum*.

***Trichopetalum lunatum* (Harger)**

Figs. 1–10, Map 1

T. lunatum Harger, 1872:118. Cook & Collins, 1895:63, figs. 52–54. Palmén, 1952:8, figs. 10–19. Shear, 1972:277, figs. 497–499.

Trichopetalum album Cook & Collins, 1895:64, figs. 22–29. Synonymized by Causey 1969:119.

Trichopetalum cornutum Cook & Collins, 1895:66, figs. 46–49. **NEW SYNONYMY.** Not Shear, 1972:288, figs. 511–518.

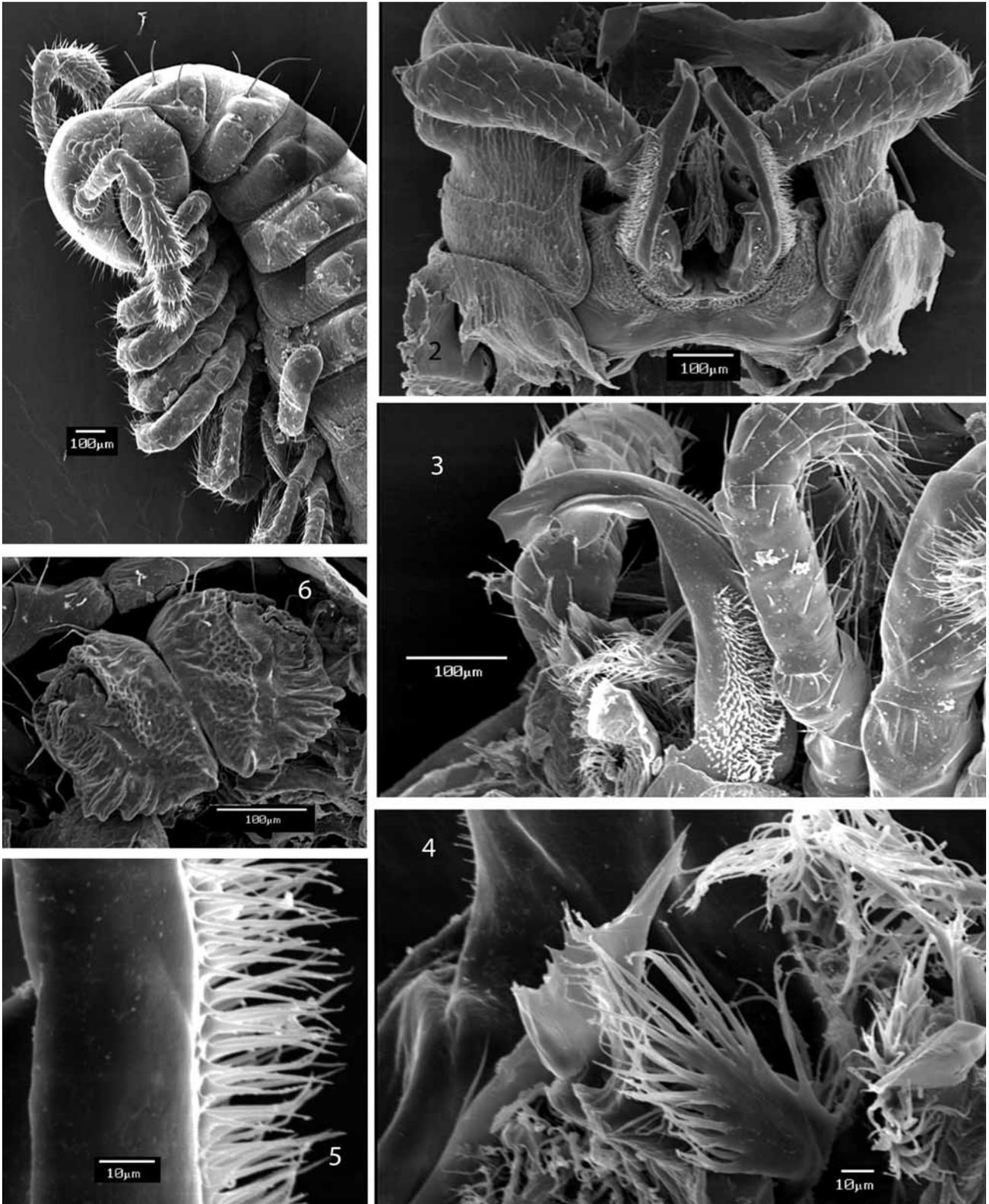
Types: Holotype from New Haven, Connecticut, in Peabody Museum of Natural History at Yale University, New Haven (Shelley 1993); Types of *T. album* from Syracuse, New York, probably in USNM but not located in 2000. There are several samples of *T. lunatum* from New York in the USNM general collection that are labelled with collecting dates in the 1890s, but which have no further locality data. The handwriting on these labels is identical to that on handwritten labels by O. F. Cook. Types of *T. cornutum* from Bloomington, Indiana, are probably in USNM, but were not located in 2000, though the specimens had been seen by Lewis and Hoffman (1997).

Note on synonymy: *Trichopetalum cornutum* has been consistently regarded as a distinct species, but even Cook & Collins (1895) were able to demonstrate little difference between it and *album*. My studies of all available specimens place the original illustrations within the variation found in *lunatum*, of which *album* is a clear synonym. Seeing only New York material and comparing it with Indiana specimens, Cook & Collins were not able to recognize the range of variation. The Michigan, Indiana and Illinois specimens so reported by Causey (1951, 1967) are, to the extent that I could track them down, based on males of *lunatum* or on samples of females only. Snider (1991) reported only *lunatum* from Michigan, and strongly doubted Causey’s record of *cornutum*. Causey (1967) also reported *cornutum* from Kentucky and Tennessee; I was unable to trace these specimens. In 1972, I illustrated what I thought was *cornutum* from Highlands, North Carolina, but those specimens and others from the same region are described below as *Trichopetalum dickbrucei*, new species.

Diagnosis: Distinct from *T. uncum* in lacking a large lateral branch of the angiocoxite (Fig. 11), from *T. dickbrucei* in the blunter, much less incised tip of the angiocoxite (Fig. 26), and from *T. montis*, which has a much expanded angiocoxite tip (Fig. 23).

Etymology: the species name means “like a crescent moon,” and refers to the shape of the eyepatch (Cook & Collins 1895).

Male from Bethany, Connecticut: Length, 6.5 mm, width 0.85 mm. Color pale tan (after long preservation; fresh specimens almost white), faintly mottled darker purplish tan on head, collum, and anterior segments. Ten ocelli in lunate patch. Pregonopodal legs strongly crassate (Fig. 1), legpair 6 not distinctly the largest, legpair 7 only slightly larger than postgonopodal legs. Legpairs 10, 11 with coxal glands, otherwise unmodified.



FIGURES 1–6. *Trichopetalum lunatum*, Scanning Electron Micrographs. 1. Anterior end of male, lateral view. 2. Gonopods and ninth leg pair of male, ventral view. 3. Gonopods, seventh and sixth legs of male, lateral view. 4. Gonopod colpocoxite, lateral view. 5. Setulae or fimbriae on gonopod angiocoxite, lateral view. 6. Cyphopods of female, ventral view.

Gonopods (Figs. 2–5, 7, 8) with large sternum bulging anteriorly on each side, poorly sclerotized and incomplete posteriorly. Coxae fused in midline; angiocoxites tapering, curved, tip with one or two shallow indentations, unbranched. Colpocoxite well-sclerotized, with characteristic branches and teeth; large fimbri-

ate branch arises basally near juncture of colpocoxite with coxal body. Ninth legpair strongly reduced (Fig. 9).

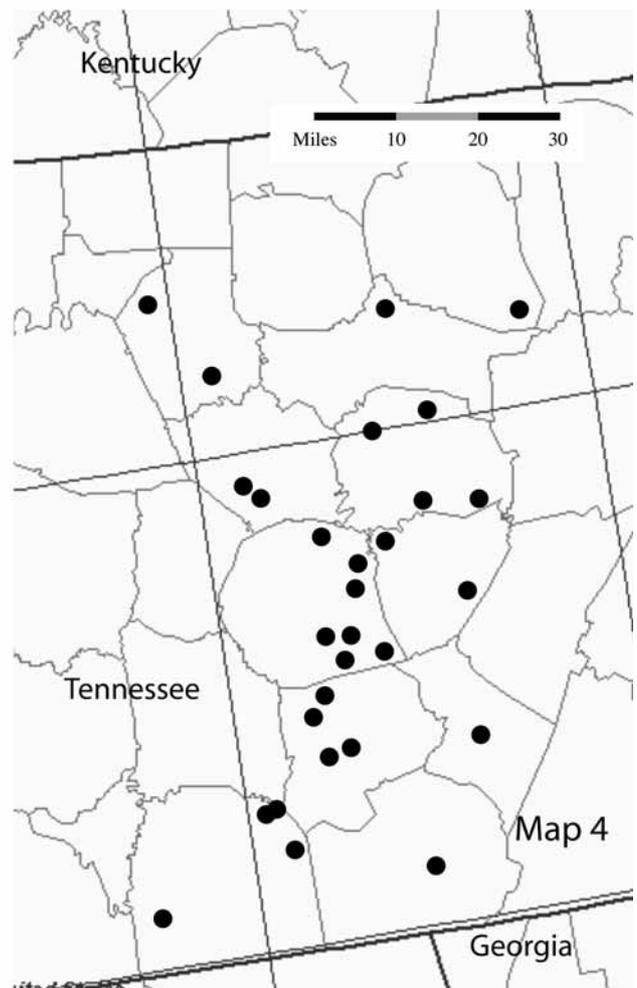
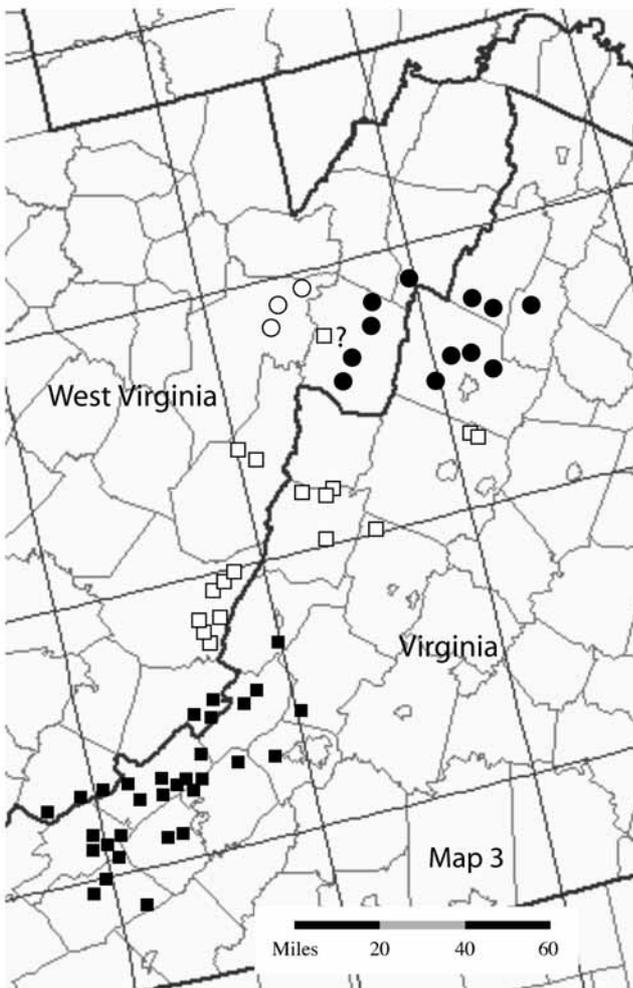
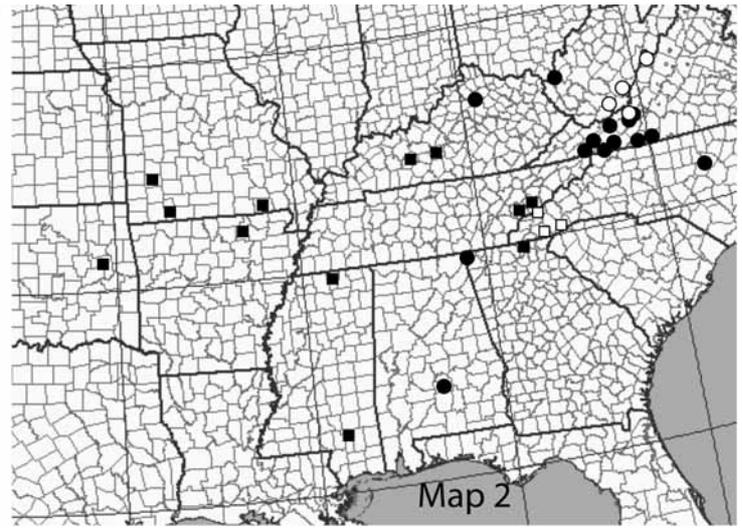
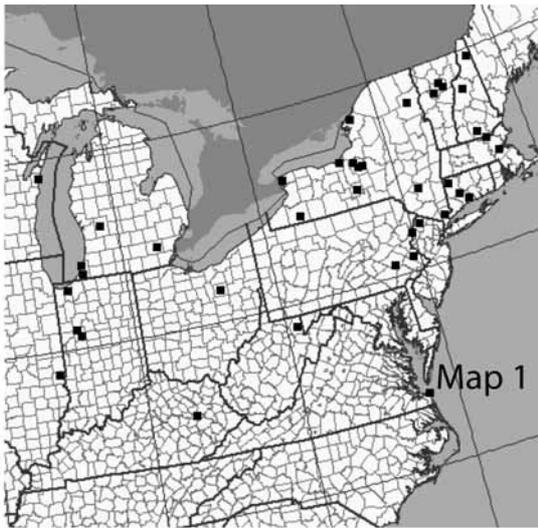
Female from Bethany, Connecticut: Length, 6.7 mm, width 0.90 mm. Similar in nonsexual characters to male. Cyphopods as in Fig. 6.



FIGURES 7–10. *Trichopetalum lunatum* male. 7. Gonopods, anterior view. 8. Left gonopod, lateral view. 9. Colpocoxite of right gonopod, lateral view. 10. Right leg 9, anterior view.

Distribution: See Map 1 for selected records. Material examined: CONNECTICUT: *Litchfield Co.*: Kettletown State Park, 14 May 1964, J. and W. Ivie, male, female (AMNH). *New Haven Co.*: Bog 2 mi N of Bethany, 29 May 1965, J. and W. Ivie, male, female (AMNH); Yale Bird Preserve, New Haven, 3 April 1960, C. Remington, female (VMNH). ILLINOIS: *Clark Co.*: Rocky Branch, Dolson, 13 April 1949, E. Ross et al, (INHS). INDIANA: *Clark Co.*: Rocky Branch, Dolson, 13 April 1949, E. Ross, males (INHS). *Porter Co.*: Dune Acres, 28 March 1943, H. Dybas, male, females (FMNH); Dune Acres, Cowle's Bog, 16 April 1960, W. Suter, male, females (FSCA). *Tippecanoe Co.*: Wabash Township, south Section 22, 8, 15 May 1971, H. Lawson, males (FSCA). KENTUCKY: *Wolfe Co.*: 6.3 mi NW Pine Ridge, 12 March 1966, B. Branson (FSCA). MASSACHUSETTS: *Middlesex Co.*: Pepperell, May 1961, H. W. Levi, female (MCZ). *Norfolk Co.*: Wellesley, 18 May 1913, collector unknown, female (USNM). MICHIGAN: *Berrien Co.*: Bridgeman, 4 May 1962, males, W. Suter (FSCA); Lakeside, Warren Woods, 14 January 1960, W. Suter, (FSCA). *Kent Co.*: Rogue River State Game Area, near Kent City, 4 October 1968, B. Armstrong (FSCA). *Washtenaw Co.*: Ann Arbor, 2 April 1930, S. L. Mines, male, female (USNM). NEW HAMPSHIRE: *Coos Co.*: near Second Lake, October 1969, P. J. Darlington, male, females (VMNH). *Grafton Co.*: Zealand Road, 6 mi SSE of Twin Mtn., 600 m asl, A. Newton and M. Thayer, male, female (MCZ); West Thornton, Hubbard Brook, 24 September 1982, R. Reeves, males, females (WAS). *Hillsboro Co.*: Mt. Monadnock, 14 June 1970, S. B. Peck, females (MCZ). NEW JERSEY: *Essex Co.*: Short Hills, 13 June 1908, collector unknown, female (AMNH). *Warren Co.*: Delaware Water Gap, 12 November 1962, D. Whitehead, male (USNM). NEW YORK: *Cattaraugus Co.*: Allegany State Park, 17 June 1968, S. B. Peck, males, females (VMNH), 27 June 1971, W. Muchmore, male, females (VMNH). *Essex Co.*: Big Moose, 13 August 1904, "FCP," females (USNM). *Jefferson Co.*: Clayton, May 1891, O. F. Cook and G. Collins, males, females (USNM). *Niagara Co.*: Niagara Falls, 27 June 1908, F. Silvestri, male, female (AMNH). *Onondaga Co.*: Marcellus, June 1890, collector unknown, males, females (USNM); Skaneateles, 25 June 1908, F. Silvestri, males, females (AMNH). *Tompkins Co.*: Ithaca, F. Silvestri, juveniles (AMNH). *Wayne Co.*: Wolcott, May 1893, collector unknown (USNM). *Westchester Co.*: Fort Lee, 16 June 1908, F. Silvestri, males, females (AMNH). OHIO: *Wayne Co.*: Funk's Hollow, Wooster, September, 1959, 10 May 1962, 7 September 1966, A. Weaver, males, females (NCSM). PENNSYLVANIA: *Berks Co.*: Morgantown, 27 March 1971, W. B. Muchmore, female (VMNH). *Bucks Co.*: Jamison, Horseshoe Bend, Neshaminy Creek, 4 April, 10 October 1954, W. Ivie, males, females (AMNH). *Montgomery Co.*: Telford, 1 October 1947, T. Stannard, male, female (FMNH, INHS, FSCA). VERMONT: *Caledonia Co.*: Grant's Mill, July 1913, R. V. Chamberlin, male, females (MCZ); Lake Groton, same data; St. Johnsbury, same data (MCZ). *Windham Co.*: Jamaica, 11 July 1913, R. V. Chamberlin (?), males, females (USNM). VIRGINIA: *City of Virginia Beach*: Seashore State Park, 31 March 1987, K. A. Buhlmann, males (VMNH). WEST VIRGINIA: *Preston Co.*: Cooper's Rock State Forest, 25 June 1971, W. A. Shear, males, females (VMNH). *Randolph Co.*: Cheat Bridge, TNC Preserve, 3850' asl, N38.61667°, W79.97083°, 8 October 2000, W. Arnold and M. Hight, males (WAS); Bear Haven Recreation Area, Monongahela National Forest, 3423' asl, N38.9°, N82.1°, 20 February 1998, W. Arnold, female (WAS). WISCONSIN: *Kewaunee Co.*: Kewaunee, 1 May 1955, A. Ziemer, males, females (FMNH).

Literature records: localities in southern NEWFOUNDLAND, Canada (Palmén 1952: excellent illustrations of gonopods). Localities in ONTARIO, QUEBEC, and NOVA SCOTIA (Shelley, 1988). MICHIGAN: *Alcona, Cheboygan, Chippewa, Crawford, Gratiot, Hillsdale, Kalkaska, Livingston, Montmorency, Muskegon, Ogemaw, Oscoda* and *Washtenaw Counties* (Snider, 1991). It is likely the species is general in Michigan. Williams & Hefner (1928) recorded the species from OHIO, but without specific localities: "southern half of the state." The *Wayne Co.* records given here are from northern Ohio; *lunatum* is probably general throughout the state. The single Virginia record given above is anomalous, since only *T. stannardi* Causey has been reported (see below) from the Atlantic coastal plain south of New York. Perhaps this represents an introduction.



Maps 1–4. Map 1. Eastern United States, showing selected records of *Trichopetalum lunatum* (filled squares). Map 2. Central eastern United States, showing selected records of *T. uncum* (filled squares), *T. dux* (filled circles), *T. jerryblatti* (open circles), *T. dickbrucei* (filled squares). Map 3. Parts of Virginia and West Virginia, showing selected records of *Zygonopus* species. *Z. whitei*, filled circles; *Z. krekeleri*, open circles; *Z. weyerienses*, open squares; *Z. packardi*, filled squares. Map 4. Central Tennessee, showing selected records of *Scoterpes ventus* (filled circles)

Causey (1967) reported this species (as *cornutum*) from *Wolfe Co.*, KENTUCKY, but those specimens could not be found and it is likely that the Ohio River is a barrier to *lunatum*, which must have entered glaciated territory in Ohio from the northeast. Also reporting the species as *cornutum*, Causey (1951) recorded it from *Clark Co.* and “Donaldson”, ILLINOIS, “Donaldson” could not be located, nor could the specimens, but the Clark Co. specimens are *T. unicum*; see the discussion of that species below. Causey (1967) listed *cornutum* from Cade’s Cove, *Blount Co.*, TENNESSEE, but I have only seen *T. unicum* from that place. I do not think that *T. lunatum* occurs in Illinois, Kentucky or Tennessee.

Though not recorded from MAINE, it undoubtedly exists there, having been collected just over the border at Second Lake in northern New Hampshire, and the West Virginia records also make occurrence in western MARYLAND almost certain. Shelley (1988) argues convincingly for occurrence in PRINCE EDWARD ISLAND and NEW BRUNSWICK, Canada. My 1972 report of *lunatum* from British Columbia was based on a mislabelled specimen.

Notes: Some midwestern specimens (Indiana) previously assigned to *T. cornutum* have a slightly different angiocoxite tip (Fig. 8), but specimens from Michigan and Ohio are intermediate between these and the New England-New York material.

Collection records show this species being most commonly collected in the spring and autumn, with a few winter records (December-February). Late June and July records are mostly from higher elevations in the south, or from the most northerly localities. This suggests a pattern of winter activity. Palmén (1952) remarked that when held in the hand or exposed to sunlight for only a few minutes, specimens of *T. lunatum* curled up and died. Sparse ecological notes on collecting labels associate the species most often with deciduous leaf litter, but at least in some places with spruce or hemlock litter, and once with sphagnum moss. In Indiana it was collected in leaf mould from a tamarack swamp between sand dunes. I collected *lunatum* in Preston Co., West Virginia, sorting chestnut oak litter under a cliff, an unusually dry habitat for the species, which was also collected in Massachusetts in “dry woods.” As well as hand-sorting, specimens were taken in Berlese samples and in pitfall traps.

Causey (1951) identified the specimens (see above records) from Telford, Pennsylvania, as *T. lunatum*, but curiously, specimens from this locality retained in her own collection (now FSCA) are labelled as types of a never-published new species, “*Trichopetalum orientalis*.” Confusingly, a type series under this unpublished, and hence unavailable, name is also in INHS.

***Trichopetalum unicum* Cook & Collins**

Figs. 11–13, Map 2

Trichopetalum unicum Cook & Collins, 1895:66, fig. 51. Shear, 1972:277, figs. 500, 501.

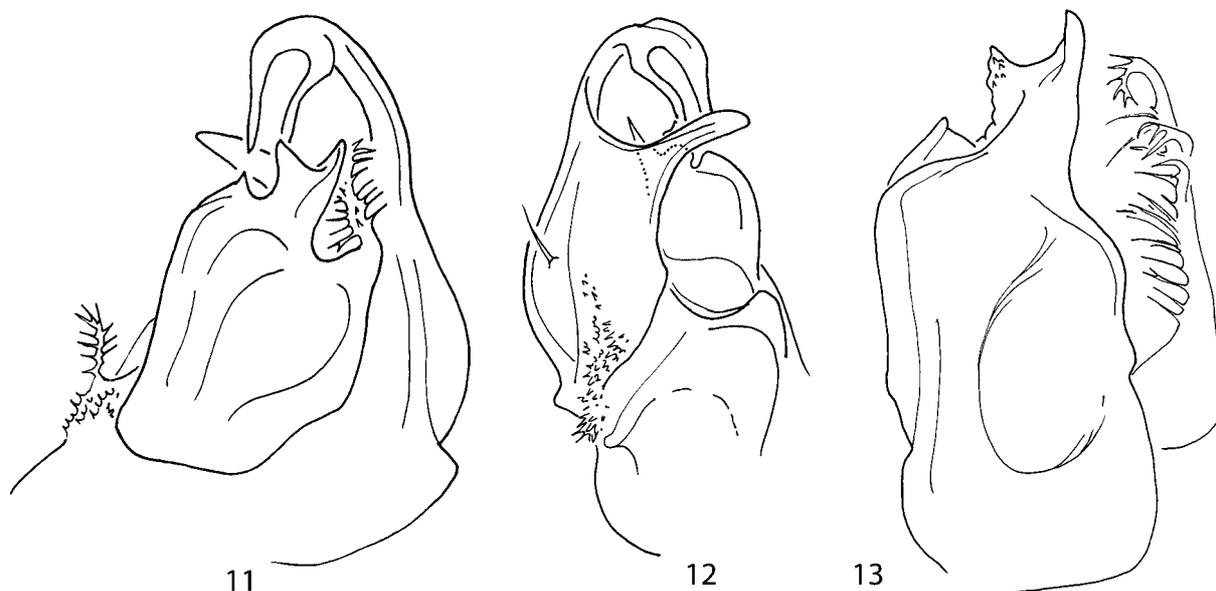
Types: Male holotype from Bloomington, Indiana, said to be in USNM, but not located in 2000. According to Cook & Collins, the single male known to them was found in the same vial as Bollman’s type material of *T. cornutum*. The presently known distribution of *unicum*, with a single exception (*Clarke Co.*, Illinois, see below), is well south of central Indiana.

Diagnosis: Easily distinguished from all other *Trichopetalum* species by the large lateral branch of the gonopod angiocoxite (Figs. 11, 12).

Etymology: The species name, *unicum*, is a Latin adjective meaning “hooked, barbed,” and refers to the form of the gonopod angiocoxite.

Male from Marvel Cave, Stone Co., Missouri: Length, 7.2 mm, width, 0.75 mm. Color pale yellowish tan. Ocelli 3 in single row. Legpairs 3–7 enlarged, pairs 4, 5 the largest, pair 7 significantly larger than postgonopodal legs. Gonopods (Figs. 11–13) robust, angiocoxite strongly bent posteriorly, broad in lateral view, with

strong lateral branch; apex of coxite deeply divided. Colpocoxite (Fig. 13) differing in form from that in *T. lunatum*, broader, without acute apical branch, fimbriate branch large, prominent. Ninth legs as in *T. lunatum*. Tenth and eleventh legpairs with coxal glands.



FIGURES 11–13. *Trichopetalum uncum* male. 11. Right gonopod, mesal view. 12. Same, lateral view. 13. Right gonopod colpocoxite, mesal view.

Female from Marvel Cave, Stone Co., Missouri: Length, 7.7 mm, width 0.80 mm. Similar to male in non-sexual characters.

Distribution: See Map 2 for selected records. Material examined: ARKANSAS: *Sharp Co.:* Center Cave, 2 mi E, 1 mi S of Center, 9 November 1974, V. McDaniel, male (FSCA). GEORGIA: *Union Co.:* Brasstown Bald, 4700' asl, 27 May 1978, F. A. Coyle, male, female (VMNH). ILLINOIS: *Clark Co.:* Rocky Branch, 13 May 1949, H. Ross, male (INHS). KENTUCKY: *Butler Co.:* Ravine below Granny's Rockhouse, 2.5 mi SE of Welch's Creek, 23 February 1957, L. Hubricht, male (VMNH). MISSISSIPPI: *Benton Co.:* 1 mi W of Canaan, 27 February 1962, L. Hubricht, male, female (VMNH); *Forrest Co.:* 3.8 mi SE of McCallum, 1 November 1962, L. Hubricht, male, females (VMNH). MISSOURI: *Dade Co.:* Carrico Cave, 31 March 1965, B. Prasman, male (FSCA); *Ripley Co.:* Panther Cave, 16 mi NW of Doniphan, 11 September 1978, male (NCSM); *Stone Co.:* Marvel Cave, 2 April 1959, T. Barr, males, female (FSCA); *Washington Co.:* 1 mi W of Bliss, 14 November 1942, L. Hubricht, males, females (FSCA). OKLAHOMA: *Muskogee Co.:* Dresser Cove, 5 mi N of Ft. Gibson, no date, no collector, male (FSCA). SOUTH CAROLINA: *Pickens Co.* Sassafras Mtn., N35°06', W82°77', 30 December 2005, W. Reeves (WAS). TENNESSEE: *Blount Co.:* along Big Poplar Trail, Cades Cove, Great Smoky Mountains National Park, 23 May 1962, L. Hubricht, males (VMNH); *Franklin Co.:* Buck Creek Cove, 3 mi W of Anderson, 20 May 1963, L. Hubricht, male (VMNH); *Knox Co.:* 4 mi NW of Hall's Crossroads, 20 May 1961, L. Hubricht, male (VMNH).

Literature Records: "several places in *Washington* and *Logan Cos.*" ARKANSAS (Causey, 1951); Mammoth Cave National Park, *Edmonson Co.*, KENTUCKY (Causey, 1967). Lewis and Hoffman (1997) report the species from caves in *Jennings* and *Monroe Cos.*, INDIANA.

The northern boundaries of the distribution remain to be defined. Lewis and Hoffman (1997) suggest the type locality could be further narrowed to Coon's Cave, near Bloomington, since that was the label data in USNM collection #42, where the single specimen was found in company with *T. lunatum* (as *T. cornutum*; Cook & Collins 1895). Clark Co., Illinois, is about on the latitude of Bloomington and on the border of Illi-

nois with Indiana. This is the only find of *uncum* in the extensive collection of the Illinois Natural History Survey. There are no specimens of *uncum* in the Illinois collections of the Field Museum, Chicago, Illinois. The Clark Co. locality is also the type locality for *T. stannardi* (see below).

Trichopetalum unicum should be expected in northern ALABAMA, since it occurs nearby in Tennessee and is found in Georgia and Mississippi. Likewise it may occur in northern LOUISIANA. The single Oklahoma record indicates a slight chance of occurrence in northeastern TEXAS. On the North Carolina side of the Blue Ridge, this species seems to be replaced by *T. dickbrucei*, new species, and in the North Carolina piedmont by *T. dux*, but the single, recent record from South Carolina indicates that *T. unicum* could co-occur with either of the other species in SOUTH CAROLINA.

Notes: Ecological notes on labels are sparse, but collecting dates are obviously biased toward cooler times of the year. Again, deciduous leaf litter seems the preferred habitat on the surface. It appears that this species replaces *T. lunatum* in the south, but based on the Indiana records, the two may at some places be sympatric. In Marvel Cave, Missouri, *unicum* is sympatric with another trichopetalid, *Causeyella dendropus* (Loomis, 1939). The latter is a highly evolved trogllobiont. While *unicum* shows a greater predilection for troglomorphy than other *Trichopetalum*, signs of modification for an underground life are few and limited to a reduction in the number of ocelli (to 3 or fewer on each side; the usual number for epigeal specimens is 6–8). However, the association with caves is not as strong as suggested by Lewis and Hoffman (1997); based on the records above, *unicum* is frequently found in surface habitats. For much of the species' range, collecting has been much more thorough in caves than in appropriate surface habitats.

***Trichopetalum dux* (Chamberlin)**

Figs. 14–18, Map 2

Tynopus dux Chamberlin, 1940:57.

Trichopetalum dux, Shear, 1972:288, figs. 511–513.

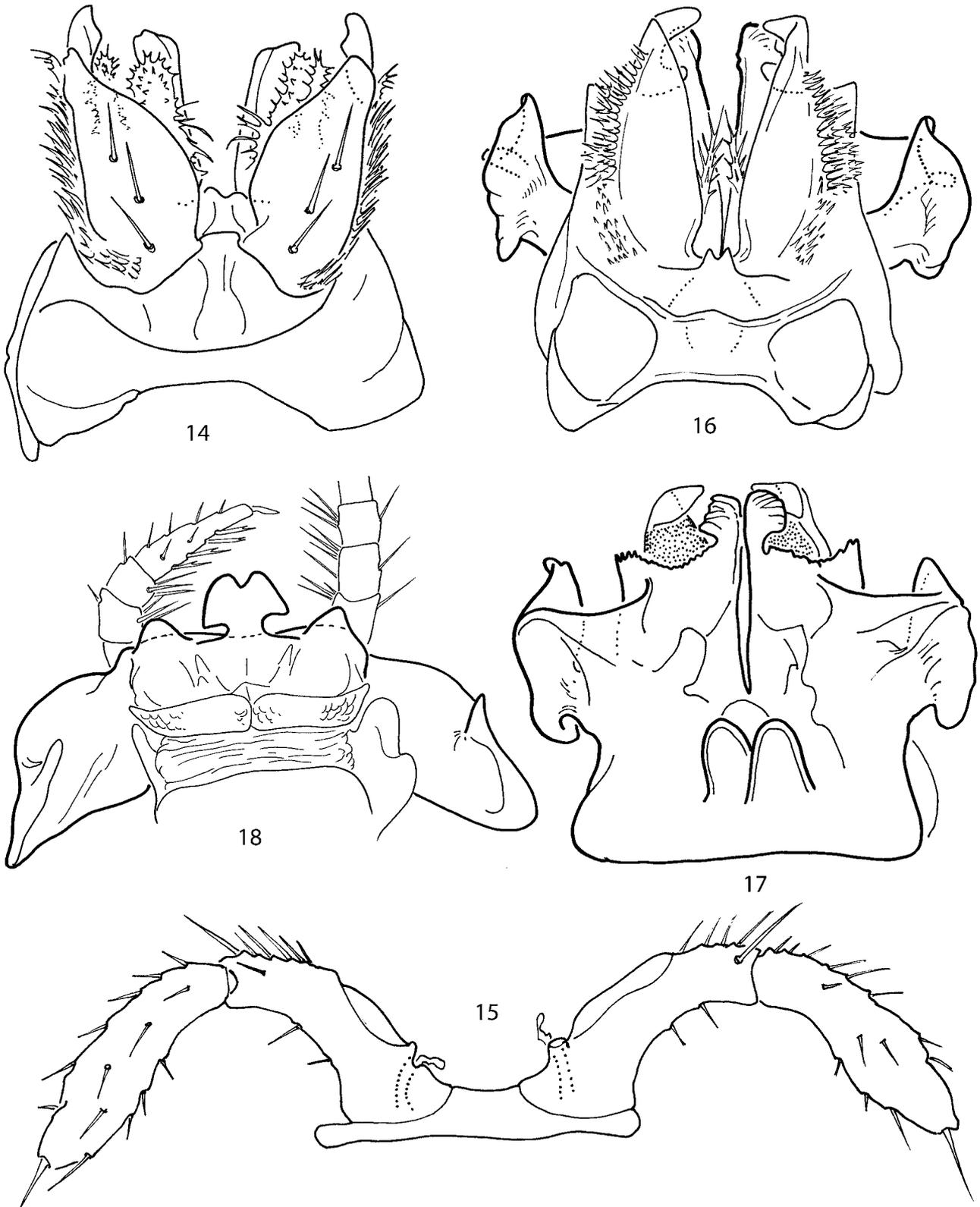
Trichopetalum subterraneum Causey, 1967:129, figs. 2–5. **NEW SYNONYMY.**

Types: Male holotype from Duke Forest, Durham Co., North Carolina, in USNM (examined in 1971). Male holotype and male and female paratypes of *T. subterraneum* from Slacks (=Bryants) Cave, Scott Co., Kentucky, in USNM and FSCA, examined.

Note on synonymy: The types of *Trichopetalum subterraneum* are nearly identical in all respects to Virginia and North Carolina specimens of *T. dux*. Chamberlin (1940) did not illustrate *T. dux* and described it in a different genus (*Tynopus*), which he compared to *Conotyia* rather than *Trichopetalum*. Perhaps for this reason, Causey (1967) did not mention *dux* in describing *subterraneum*, and while reviewing the known species of *Trichopetalum*. The only available checklist in 1967 was Chamberlin and Hoffman (1958), which listed *Tynopus dux* as a conotyloid. The types were in the personal collection of R. V. Chamberlin, unavailable in 1967, and were from a locality far from central Kentucky. Thus, Causey's description of *subterraneum* as a distinct species was quite understandable. Ironically, the type specimen of *dux* was collected by Causey herself (and sent to Chamberlin for identification) in 1939, at the outset of her scientific career. Thirty-eight years later, she unknowingly redescribed the same species under a new name, but from a far-distant locality.

Diagnosis: Distinct in the colpocoxite of the gonopod, which instead of being dentate as in the preceding two species, is in the form of a broad, transverse lamella; the angiocoxite is significantly shorter and straighter than in other *Trichopetalum* species.

Etymology: There is a Latin word *dux*, meaning “conductor,” or “guide,” but I suspect that Chamberlin wanted the name pronounced “dukes” to commemorate the type locality in the Duke Forest. In either case, a noun in apposition.



FIGURES 14–18. *Trichopetalum dux*. 14. Gonopods, anterior view. 15. Legpair 9, anterior view. 16. Gonopods with spermatophore, anterior view. 17. Same, posterior view. 18. Cyphopods of female with spermatophore, posterior view.

Male from near Blacksburg, Virginia: Length, 5.5 mm, width, 0.75 mm. Color white to pale yellowish tan. Ocelli 8, dorsal row of 6, ventral row of 2; ocelli poorly pigmented. Pregonopodal legs: pairs 3–5 somewhat enlarged compared to postgonopodal legs, pairs 6–7 of normal size. Legpairs 10, 11 with coxal glands; legpair 10 with prefemora and femora smaller, thinner than those of legpair 11. Gonopods (Fig. 14) with the

usual anteriorly swollen sternum and fused coxae, 3 coxal setae on each side in vertical row, coxal trichomes long, prominent. Angiocoxites short, slightly curved posteriorly, tip vaguely emarginate to squared-off; small, lateral, quadrate branch occurs close to base of coxite (ectal coxite of Causey 1967). Fimbriate branch well-defined, somewhat lamellate. Colpocoxite robust, subglobular basally, distally with pointed, transverse lamina. Ninth legpair (Fig. 15) as usual for genus. Coxae 10 and 11 with glands.

Female from near Blacksburg, Virginia: Length, 6.2 mm, width, 0.80 mm. Nonsexual characters as in male, but ocelli 10, well-pigmented, anterior segments with faint brownish reticulations laterally.

Distribution: For selected records, see Map 2. Material examined (unless noted otherwise, all specimens VMNH): ALABAMA: *Lowndes Co.:* Wooded hillside 4 mi E of Braggs, 23 April 1960, L. Hubricht, male, females. GEORGIA: *Dade Co.:* Sutton's Gulf, 6 April 1999, W. Reeves, male. NORTH CAROLINA: *Wake Co.:* 4.3 mi S of Cary, hemlock bluffs, no date, no collector, male, females (NCSM). VIRGINIA: *Bland Co.:* west side of Big Walker Mtn., 6 km E Sharon Springs, 3600' asl, 9 May 1981, R. L. Hoffman, male, female. *Grayson Co.:* Comer's Rock, Iron Mountains, 4000' asl, 12 December 1965, R. L. Hoffman, male, female; Whitetop Mtn., south slope on SR600, 5000' asl, 23 December 1984, R. L. Hoffman, males, females. *Henry Co.:* along creek near Leatherwood, 2 May 1959, R. L. Hoffman, females. *Montgomery Co.:* Price's Fork Hollow, 5 mi W of Blacksburg, 1900' asl, 20 April 1976, W. A. Shear, male, female; Toms Creek, 3 mi N of Blacksburg, 27 February 1951, R. L. Hoffman, males, females. *Patrick Co.:* Kibler Park, below Pinnacles Powerhouse, 8 April 1961, L. Hubricht, male, female. *Smyth Co.:* North side of Whitetop Mtn. on SR600, 3500' asl, 4 May 1964, R. L. Hoffman, male, female. *Washington Co.:* junction of SR614 and 612, 3 mi NE of Mendota, 3 December 1997, R. L. Hoffman, males, females. WEST VIRGINIA: *Cabell Co.:* Kilgore Creek, 2mi N, 2.7 mi E of Milton, 650' asl, N38.45°, W82.1°, 20 February 1998, W. Arnold, male, female (WAS).

Literature records: Shelley (1978) reports *T. dux* from *Chatham Co.*, and Filka and Shelley (1980) have it from *Gaston Co.*, NORTH CAROLINA, but both these records are based on females or juveniles.

Trichopetalum dux may be expected to occur in the piedmont regions of GEORGIA and SOUTH CAROLINA, based on existing Alabama, Georgia and North Carolina records. Further collecting should reveal the species general through WEST VIRGINIA (the Bland Co., Virginia, record is very close to the West Virginia border) and at least eastern and central KENTUCKY. Sympatry with *T. uncum* could occur in central Kentucky or piedmont South Carolina, with *T. lunatum* in northern West Virginia, with *T. jerryblatti* in southern West Virginia, and with *T. dickbrucei* near the Blue Ridge front in North Carolina. The concentration of localities of *T. dux* in Virginia is a result of collecting bias: R. L. Hoffman has thoroughly collected in the state at all seasons, including winter and early spring. Similar efforts should fill in the implied gaps in the species' distribution between the outliers in West Virginia, Kentucky ("subterranean") and Alabama.

Notes: Given the fact that Hoffman has collected in Virginia most intensively in the spring and summer, the winter records of mature specimens of *dux* make a good case for cold-weather maturity and activity of the species. Many of the Virginia localities are from high elevations to 5000' (1524 m), but the species is also found in the piedmont at elevations less than 1000' (305 m). Ecological notes on labels are very few; two collections were made using Berlese funnels, and one was from a pile of sawdust.

I have illustrated (Figs.16, 17) spermatophores on both the gonopods of males and the cyphopods of females (Fig. 18) from the Washington Co., Virginia, population, taken in December. A single female from Montgomery Co., collected in February, was also carrying a spermatophore. These are the first spermatophores recorded from either anatomical site for any North American chordeumatidan milliped, though putative spermatophores have been found previously, associated with the coxal glands of the tenth legpair. The spermatophores are orange in color and contrast strongly with the white animals; at first I thought them to be the bizarre, heavily sclerotized gonopods of a unique new species. However, closer examination showed their true nature. The spermatophores are much too large to have been formed in the coxal glands of the tenth legs, which are too small to hold them by at least an order of magnitude. The shape and appearance of these sper-

matophores casts doubt on the nature of previously reported spermatophores emerging from the tenth legpair coxal glands, which tend to show up as small, coiled, coagulated and rather unformed masses. How the *dux* spermatophores are formed and how they function can only be a subject for speculation. While only three males were available carrying the spermatophores, the form was constant from specimen to specimen and on the single female. It is possible that one function of the gonopods is to mold or shape this spermatophore, which is then transferred to the female. In both scorpions and pseudoscorpions, which mate by spermatophore transfer, an internal mold in the male genitalia forms the species-specific shape of the spermatophore. A function for the fimbriate branch of the gonopod could be to hold the spermatophore firmly attached to the gonopods until it is transferred, perhaps softened by a secretion. The real answer will not be known until mating can be studied under controlled conditions, not a likely event given the obvious practical difficulties.

***Trichopetalum stannardi* (Causey)**

Figs. 19–22

Flagellopetalum stannardi Causey 1951:120, figs. 9–12.

Trichopetalum stannardi, Shear, 1972: 277.

Flagellopetalum quadratum Loomis 1966:229, figs. 17–19. **NEW SYNONYMY.**

Flagellopetalum appropinquo Causey 1969:44, figs. 1–4. **NEW SYNONYMY.**

Types: Male holotype of *F. stannardi* from Rocky Branch, Clark Co., Illinois, deposited in INHS, examined. Male holotype of *F. quadratum* from Glendale, Prince Georges Co. Maryland, to have been deposited in USNM, but was not to be found there. Male holotype of *F. appropinquo* from Rohresville Caves, Washington Co., Maryland, deposited in MCZ, examined (in 1970).

Notes on synonymy: In 1972, I synonymized *Flagellopetalum* with *Trichopetalum*, bringing the three included species into the genus. That synonymy was not based on specimens, only the illustrations that had been provided by Loomis (1966) and Causey (1951, 1969). After that paper had been written, the type of *F. appropinquo* arrived at the MCZ, and examination of it confirmed my conclusions, which were further strengthened by the more recent collection of the species from Nansemond Co., Virginia. For this study I found the holotype (INHS) of *stannardi*, which Hoffman (1999) had reported as “location unknown.” Unfortunately, the specimen, a fragment, provides little information. The label says “gonopods on slide” but no slide was located. Causey’s illustrations of this specimen, however, are exemplary and inspire confidence in the generic and specific synonymies.

Diagnosis: The angiocoxite is deeply divided into two thin, acutely tapering, sinuous branches unlike that of any other species of *Trichopetalum*, the colpocoxite is very large and lobular, and the fimbriate branch is suppressed. The femora of the sixth legpair of the males have a distinct distal, inner process (Fig. 22), this is absent in all other *Trichopetalum*.

Etymology: The species name honors the collector, L. J. Stannard, an entomologist and prolific collector at INHS, who supplied Nell Causey with a steady stream of interesting specimens from the midwest. The synonymous name “*appropinquo*” is a nomenclatural anomaly, the only species epithet I know that is a verb (Latin) meaning “to approach closely.”

Male from Nansemond Co., Virginia: Length, 4.6 mm, width, 0.47 mm. Color medium brown, anterior segments mottled darker in reticulate pattern (specimens may have been stained in preservation). Ocelli 8, upper row of 6 gently curved, lower row of 2 at midpoint of upper row. Legpairs 3–7 encrassate, pairs 4–6 largest, pair 7 slightly smaller than pair 2; femora of legs 5 with mesal triangular projection (Fig. 21); femora of legs 6 with distal hooked process (Fig. 22). Gonopods in anterior view (Fig. 14) with reduced trichomes, single seta posterio-basal on coxa. Angiocoxite deeply divided, possibly with 2 branches, both thin, sinuously curved; group of 5 setae on each angiocoxite. Fimbriate branch strongly reduced but present, not seen unless

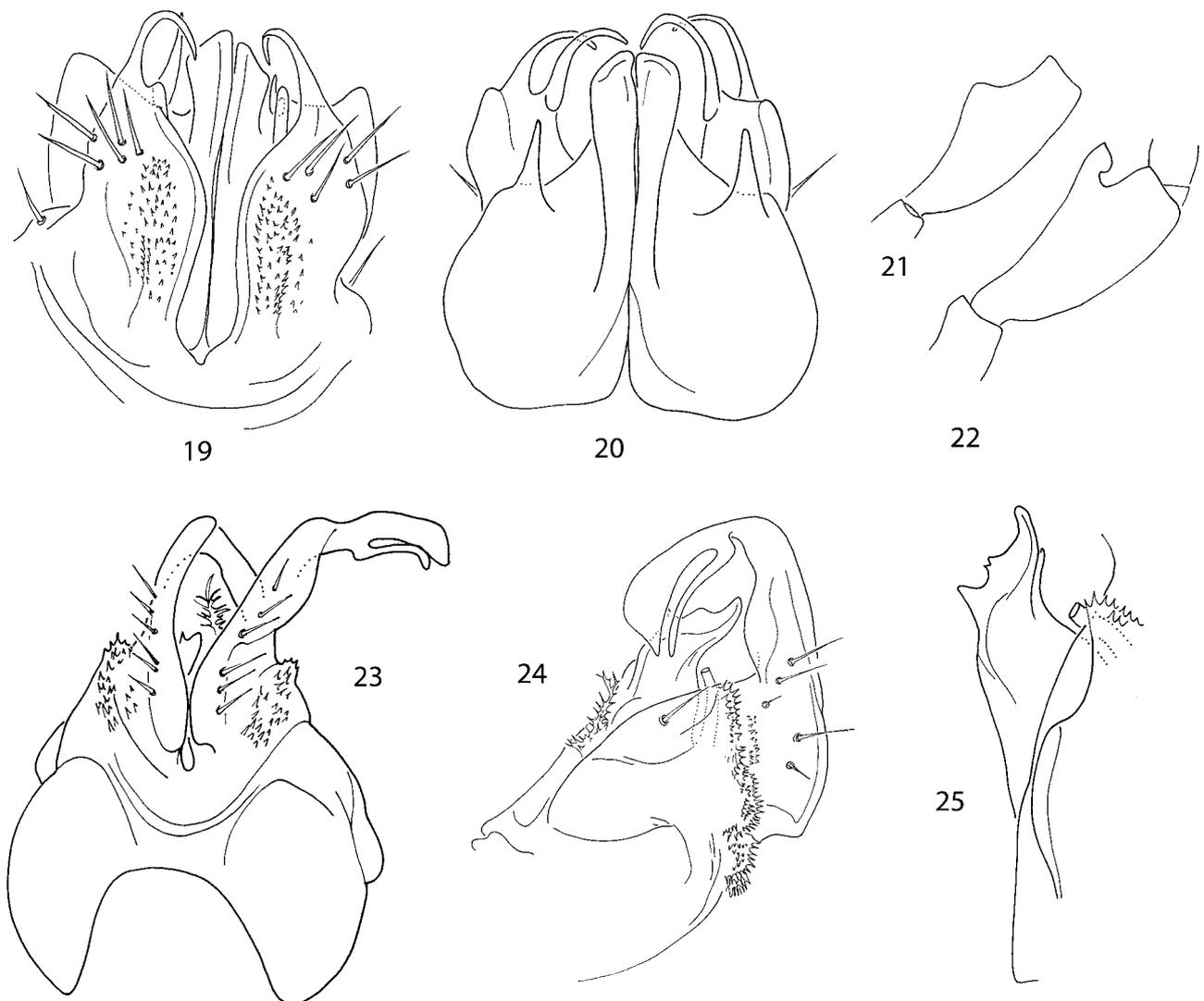
gonopod is broken into components. Colpocoxite very large, well sclerotized, angular, with appressed mesal knobs, acute posterior process (Fig. 20). Legpair 9 reduced to 2 segments as usual. Legpairs 10, 11 with coxal glands; pair 10 with slightly reduced telopodites.

Female from Nansemond Co., Virginia: Length, 6.1 mm, width, 0.52 mm. Nonsexual characters as in male.

Distribution: Material examined: VIRGINIA: *Nansemond Co.:* near Suffolk, 20 March 1983, D. Waller, males, females (WAS).

Literature records: Only the type localities listed above.

The scattered localities for this species suggest that it is far less frequent in occurrence than any other in the genus, save *Trichopetalum montis*. The species should occur in WEST VIRGINIA in the “panhandle” adjacent to Maryland, and should be looked for in localities in OHIO, INDIANA and KENTUCKY between the stations in Maryland and Illinois. It is possible it might be found in southern PENNSYLVANIA. *Trichopetalum stannardi* is narrowly sympatric (even syntopic) with *T. uncum* at the only known Illinois locality for either species; sympatry with *lunatum* might be expected in northern West Virginia, and *stannardi* and *lunatum* again occur close together in the Hampton Roads region of coastal Virginia, but there *lunatum* may be introduced.



FIGURES 19–25. *Trichopetalum* spp. 19–22, *T. stannardi* male. 19. Gonopods, anterior view. 20. Same, posterior view. 21. Femur of right leg 5, posterior view. 22. Femur of right leg 6, posterior view. 23–25, *T. montis* male. 23. Gonopods, anterior view. 24. Left gonopod, lateral view. 25. Left gonopod colpocoxite, lateral view.

Notes: Curiously, Causey (1969) described *appropinquo* as new even though it was very similar to both Loomis' (1966) description and illustrations of *quadratum*, which went unmentioned in her paper, and to her own species, *stannardi*. The type localities of *quadratum* and *appropinquo* are about 200 miles apart and in different physiographic regions; Washington Co. is in the Ridge and Valley Province of the Appalachian Mountains, and Prince Georges Co. is on the Coastal Plain. This presaged the collection of *stannardi* on the Coastal Plain in Virginia. The Illinois record (the type locality) is the same place as the outlying northern record of *uncum* from Illinois, but the type of *stannardi* was collected two years earlier. *Trichopetalum stannardi* has gonopods with a deeply divided angiocoxite, and so superficially resembles species of *Zygonopus*; a further similarity is seen in the strongly modified femora of the sixth legs. However, *Zygonopus* species have 30 segments as adults, and *stannardi* has the 28 segments typical of *Trichopetalum*. See further discussion under the description of *T. jerryblatti*, new species, and the generic description of *Zygonopus*.

***Trichopetalum montis* Chamberlin**

Figs. 23–25

Trichopetalum montis Chamberlin 1951:214, figs. 13–15.

Types: Male holotype and male paratype from Gatlinburg, Tennessee, in USNM, examined. The USNM collection contains other specimens of *montis* labelled as from Gatlinburg and collected at the same time, but not labelled as types. The types were taken from a “grassy area” and a “spruce-fir area,” but not separately labelled as such. Assuming that Chamberlin was referring to a naturally occurring spruce-fir community (and perhaps to a grassy Appalachian “bald”), the nearest possible locality to the town of Gatlinburg would be about 10 road miles to the southeast, in the Great Smoky Mountains National Park, and at an altitude at least 3500' (1067m) higher.

Diagnosis: The gonopod angiocoxite is distally expanded, deeply cleft, and bent dorsally, resembling *T. uncum*, but there is no lateral branch; the colpocoxite resembles that of *uncum* but differs in detail.

Etymology: The species epithet, *montis*, Latin, “of the mountains,” refers to the Great Smoky Mountains.

Male from “Gatlinburg,” Tennessee: Length, 4.5 mm, width, 0.40 mm. Color pale yellowish white. Ocelli 8, upper row of 6 strongly curved, lower row of 2 at midpoint of upper row. Legpairs 3–7 encrassate, pairs 4, 5 the largest. Gonopods (Figs. 23–25) large for size of animal, with usual inflated sternum; coxae with scattered setulae not hairlike, culminating in distal coxal shoulder; single coxal seta shifted to lateral surface; angiocoxite large, broad, with group of 6 setae, sharply elbowed midlength, tip expanded, deeply cleft, ventral division 5 times broader in lateral view than dorsal. Fimbriate branch large, robust (truncated in drawings). Colpocoxite similar to that of *T. uncum* but with additional small teeth. Legpairs 10 and 11 with glands, telopodite of pair 10 slightly reduced.

Female from “Gatlinburg,” Tennessee: Length, 4.8 mm, width, 0.45 mm. Nonsexual characters as in male.

Distribution: Material examined: TENNESSEE: *Sevier Co.:* Gatlinburg, spruce-fir, 11 July 1947, H. Hanson, males, female (USNM).

Notes: Doubts about the actual type locality were expressed in the *Types* section above. The collection in July of mature specimens would further suggest that the real type locality is at a much higher altitude than the town of Gatlinburg. Hence I suggest Newfound Gap, easily accessible by highway from Gatlinburg.

Chamberlin's figure of the gonopod (1951, his fig. 14) looks nothing like the gonopods of the specimens, and nothing like a *Trichopetalum* gonopod.

Four males were included in the collection I examined. Lengths given in the description are approximate because all specimens are fragmentary. Two of the males had large, orange structures attached to the gonopods and tenth legs; these are likely spermatophores, as discussed under *T. dux*, above, but were seemingly

much more amorphous in form. The specimens had lost many legs and segmental setae, however, so it is possible rough handling has broken or damaged the supposed spermatophores.

Despite a significant collecting effort on spruce-fir peaks in the Great Smoky Mountains National Park and elsewhere in North Carolina and Tennessee by F. A. Coyle, myself, and others, *Trichopetalum montis* has never been recollected. Just to the southeast in North Carolina, the new species *T. dickbrucei*, quite different in appearance from *montis*, is the only trichopetalid that has been found. *Trichopetalum dickbrucei* has been taken at Newfound Gap, which place is suspected as the real type locality of *T. montis*. The new species, described below, is variable in the form of the tip of the angiocoxite, but the Newfound Gap specimens of *dickbrucei* do not look at all like *montis*, and *montis* gonopods are significantly outside the known range of variation of *dickbrucei*. Taken all in all, one has to wonder if the true provenance of the types of *montis* may be somewhere far distant from Gatlinburg, Tennessee, and if they were grossly mislabelled. On the other hand, aside from the lack of a lateral branch, the gonopods look a good deal like those of *uncum*, which occurs at lower elevations in eastern Tennessee.

***Trichopetalum dickbrucei*, new species**

Figs. 26–29, Map 2

Types: All specimens VMNH. Male holotype and male and female paratypes from Highlands, *Macon Co.*, North Carolina, collected 16 November 1961 by R. L. Hoffman. The following specimens may be considered paratypes: NORTH CAROLINA: *Macon Co.*: Between Cashiers and Highlands on US64, 25 October 1969, W. A. Shear, males, females. *Transylvania Co.*: 1.5 mi N of Looking Glass Rock, 25 May 1958, L. Hubricht, male; Whitewater Falls, Pisgah National Forest, 13 March 1971, W. A. Shear, males. TENNESSEE: *Sevier Co.*: Newfound Gap, 5000' asl, 25 May 1962, L. Hubricht, male.

Diagnosis: Most similar to *T. lunatum*, but differing in the deeply cleft apex of the angiocoxite; distinct from *T. unicum* in lacking a lateral branch of the angiocoxite, and from *T. dux* in the form of the colopocoxite. In *T. montis* the ventral tip of the angiocoxite is much wider than the dorsal; in *dickbrucei* they are subequal.

Etymology: The species epithet honors Richard Bruce, former Director of the Highlands Biological Station, Highlands, North Carolina, in recognition of my long and pleasant association with the Station, his many kindnesses during that period, and his continued friendship.

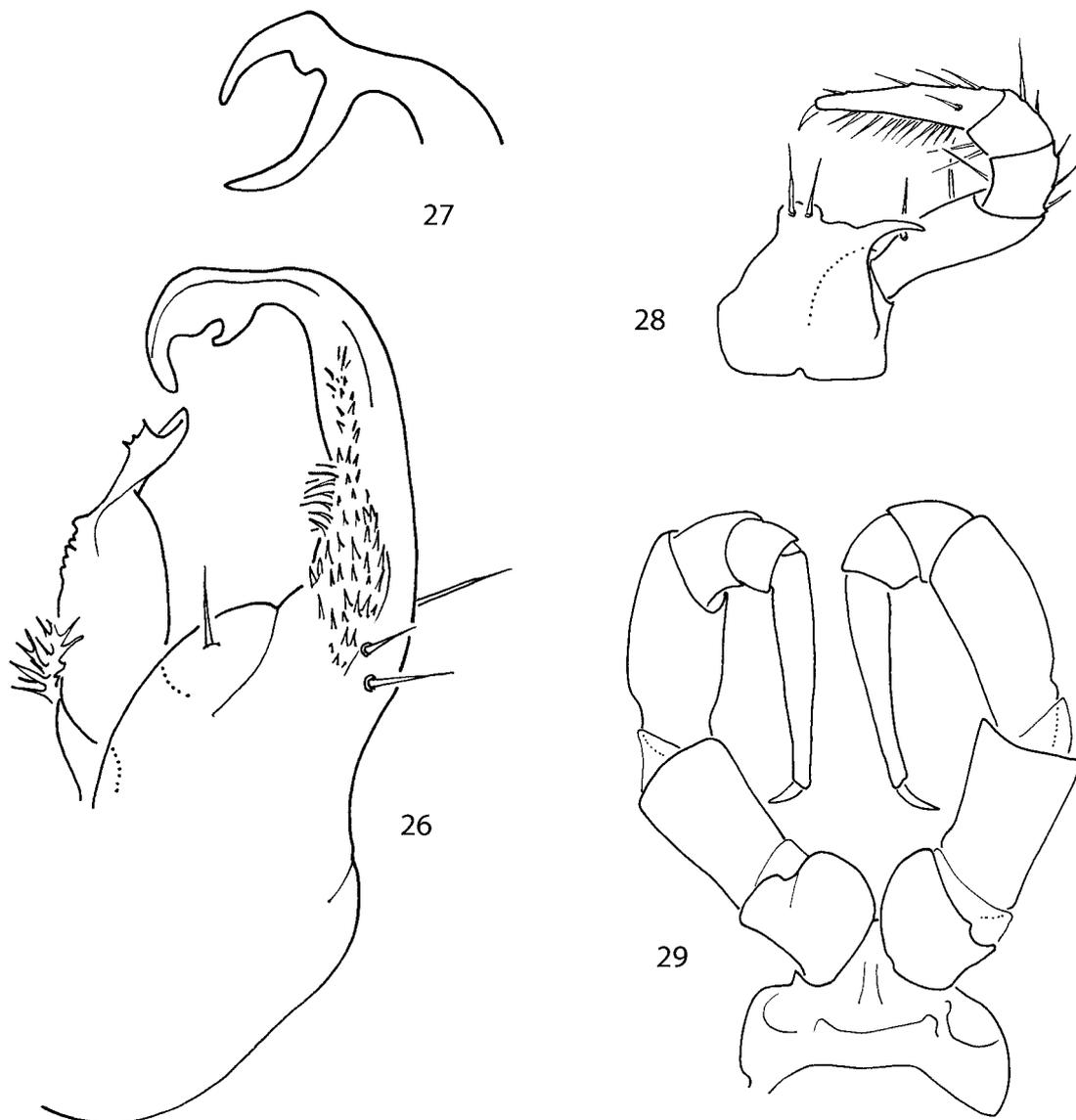
Male from Highlands, North Carolina: Length, 5.5 mm, width, 0.48 mm. Color white. 7 poorly pigmented, irregularly arranged ocelli on each side of head. Pregonopodal legpairs 3–7 enlarged, pair 6 the largest (Fig. 29), pair 7 only slightly larger than typical postgonopodal legs. Gonopods (Figs. 26, 27) with typical sternum and coxae, angiocoxites lack lateral branches, trichomes distinct, hairlike, angiocoxite tip shallowly or deeply cleft into two variably unequal parts. Colpocoxite closely similar to that of *T. lunatum*. Legpairs 10, 11 with coxal glands; telopodite of legpair 10 smaller than that of 11.

Female from Highlands, North Carolina: Length, 5.7 mm, width, 0.52 mm. Nonsexual characters as in male.

Disribution: See list of types, above, and Map 2. This species may be expected in the regions of GEORGIA and SOUTH CAROLINA immediately adjacent to the Highlands Plateau, and future collecting may possibly trace it farther north in North Carolina along the high peaks of the southern Blue Ridge. If, as speculated under that species, the true type locality of *T. montis* is Newfound Gap, *montis* and *dickbrucei* may be syntopic there. *Trichopetalum unicum* has been found in Pickens Co., South Carolina, not far from Highlands, North Carolina, and there may be some chance of sympatry between that species and *dickbrucei*.

Notes: While the tip of the angiocoxite is quite variable in *T. dickbrucei* (cf. Figs. 26, 27) it nowhere approaches the form seen in *montis*. The close correspondence in the form of the sclerotized colpocoxite between *dickbrucei* and *lunatum* is interesting and points to a close relationship between the two species; perhaps *dickbrucei* evolved from an isolated population of a common ancestor of the two, left behind at high altitudes when the Pleistocene glaciers retreated.

Interestingly, in the same vial as the *dickbrucei* holotype were two female specimens obviously belonging to the brannerioid milliped family Tingupidae, and consistent with membership in the genus *Tingupa*. The species of *Tingupa* nearest to the Southern Appalachians is *Tingupa pallida* Loomis, a troglobiont of caves in Illinois and Missouri. The presence of these specimens may be due to a curatorial error.



FIGURES 26–29. *Trichopetalum dickbrucei* male. 26. Left gonopod, lateral view. 27. Angiocoxite tip of another specimen, lateral view. 28. Right leg 2, anterior view. 29. Legpair 6, anterior view.

***Trichopetalum jerryblatti*, new species**

Figs. 30–33, Map 2

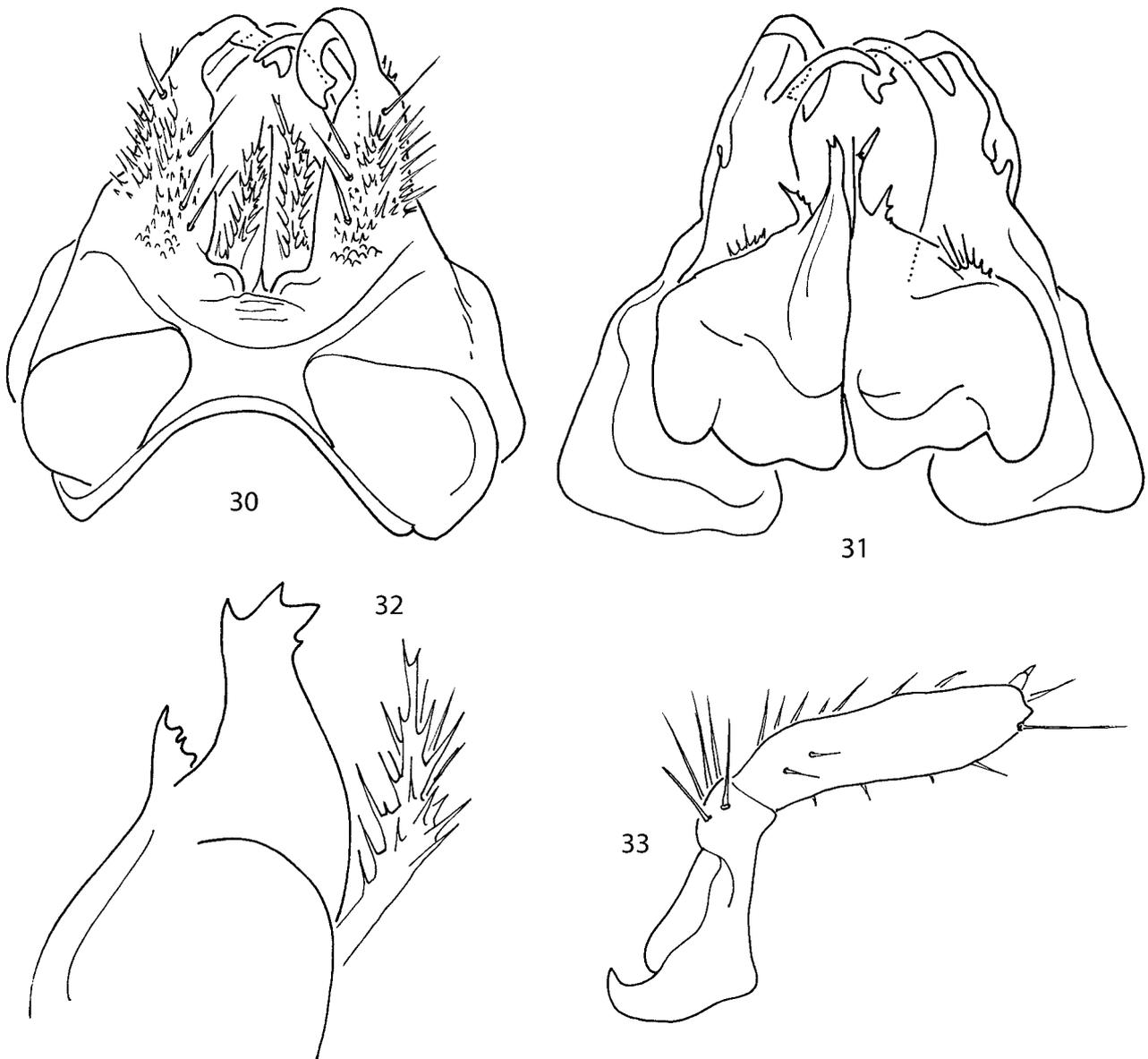
Types: All specimens VMNH. Male holotype and male and female paratypes from Locust Springs Recreation Area, 8 mi NNW of Hightown, *Highland Co.*, Virginia, collected 7 April 1975 by R. L. Hoffman. The following specimens may be considered paratypes: VIRGINIA: *Highland Co.*: Type locality, 23 June 1973, male; type locality, 28 August 1972, male. *Alleghany Co.*: 3 mi N of Clifton Forge, 4 January 1950, R. L. Hoffman, male, female. WEST VIRGINIA: *Greenbrier Co.*: Virgin forest tract on North Anthony Creek, 5 mi NNE of Neola, 1 October 1972, W. Shear & W. Ash, male, female. *Mercer Co.*: Camp Creek State Forest, 4 April 1971, W. Shear, male.

Diagnosis: *Trichopetalum jerryblatti* has deeply divided gonopod angiocoxites, as in *T. stannardi*, but lacks the strongly modified sixth legpair of that species, and the angiocoxite is of a distinctly different form. Both species superficially resemble species of *Zygonopus* in gonopod form, but *Zygonopus* species have 30 trunk segments, and *Trichopetalum* species, 28.

Etymology: This species is dedicated to the late Jeremiah L. Blatt, friend and mentor of the author early in his scientific career at Concord College, Athens, West Virginia.

Male from Locust Springs Recreation Area, Virginia: Length, 5.0 mm, width, 0.44 mm. Color white, very faint brownish reticulations visible with magnification. Ocelli 10 in two moderately curved rows. Legpairs 3–7 encrassate, pairs 4, 5 the largest; pair 7 only slightly larger than postgonopodal legs. Gonopods (Figs. 30–32) with sternum and coxae as usual; coxal setulae long, almost hairlike; angiocoxites deeply divided, lateral division apically slightly enlarged, emarginate, median division thinner, shorter, acuminate. Fimbriate branch large, prominent. Colpocoxite similar to that of *lunatum*, toothed and acute. Ninth legpair (Fig. 33) typical. Tenth and eleventh coxae with glands, tenth legpair telopodite somewhat reduced.

Female from Locust Springs Recreation Area, Virginia: Length, 5.4 mm, width, 0.5 mm. Ocelli 11, 12, single ocellus beneath two rows. Nonsexual characters as in male.



FIGURES 30–33. *Trichopetalum jerryblatti* male. 30. Gonopods, anterior view. 31. Same, posterior view. 32. Right gonopod colpocoxite, lateral view. 33. Right leg 9, anterior view.

Distribution: See list of types, above, and Map 2. This species may be expected in other counties along the Virginia-West Virginia border. Close sympatry with *Trichopetalum dux* is possible, as that species is recorded from the nearby Virginia counties of Montgomery and Bland, and both species from Alleghany Co.

Notes: *Trichopetalum jerryblatti* strongly resembles species of *Zygonopus* in gonopod anatomy, especially *Z. weyeriensis*. Two *Zygonopus* species, *weyeriensis* and *packardi*, occur within the distribution of *T. jerryblatti*, but both are cave-limited, eyeless, and have 30, not 28, trunk segments. Nevertheless, the close relationship of *Trichopetalum* and *Zygonopus* is affirmed by this new species' gonopods, and strongly suggests that both genera originated from a common ancestor that more closely resembled *Zygonopus* than *Trichopetalum*.

At Little Anthony Creek, *T. jerryblatti* was collected from litter under white pine, beech and maple. The Locust Springs Recreation Area is at an altitude of 3700–3900', in a forest of northern hardwoods with scattered spruce. Camp Creek State Forest, however, is a typical cove forest at about 2400' elevation, dominated by yellow poplar, oaks, and hickories.

Genus *Zygonopus* Ryder

Zygonopus Ryder 1881:527. Packard, 1883:194. McNeill, 1888:9.

Bollman 1893:158. Cook & Collins, 1895:59. Causey, 1960:70.

Trichopetalum (in part), Shear, 1972:277 (*Zygonopus* incorrectly synonymized with *Trichopetalum*).

Type species: *Zygonopus whitei* Ryder, by monotypy.

Included species: In addition to the genotype, *Z. krekeri* Causey 1960, *Z. packardi* Causey 1960, and *Z. weyeriensis* Causey 1960.

Diagnosis: Distinct from *Trichopetalum* and *Nannopetalum* in having 30, rather than 28, trunk diplosegments, lacking eyes, in the very robust sixth legpair of males, and in the poorly sclerotized, lobe-like colpocoxites; from *Trigenotyla* in the form of the male ninth legpair, which have the telopodites apically attached on the coxae, rather than on the sides; from *Causeyella* in having the telopodite of the ninth legpair swollen and never with vestigial distal segments; from *Scoterpes* in the shorter segmental setae and in not having the fimbriate branch of the gonopod arising apically on the colpocoxite. *Scoterpes* lacks microtrichia on the gonopod angiocoxites; these are present in *Zygonopus*.

Eyeless, depigmented, legs and antennae elongate in typical troglomorphic syndrome. Legpairs 3–7 of males enlarged (Figs. 43, 47–50), but pairs 3–5 and 7 only slightly so, pair 6 at least twice as large as postgonopodal legs, separated by a distinct gap from legpair 5, femora swollen, almost globular, and with ventroapical hook (Figs. 33, 35, 44, 49). Male legpair 2 with coxal hook above seminal duct opening (Fig. 42). Gonopods with angiocoxite deeply divided into lateral and mesal branches, branches simple, acuminate. Colpocoxites rounded to subquadrate, poorly sclerotized.

The name *Zygonopus* is compounded from Greek words, and means “feet that make a yoke,” a reference to the much enlarged sixth legpair in males (Ryder 1881).

Distribution: Found only in limestone caves along the boundary between the states of Virginia and West Virginia, from eastern Wythe Co., Virginia, in the south, to southern Shenandoah and Page Cos., Virginia, in the north; in West Virginia from Hardy, Mineral and Randolph Cos. in the north, to Mercer Co. in the south. It would appear that few caves in this well-defined area are without *Zygonopus* populations. The recent compendium of West Virginia cave fauna (Fong *et al.* 2007) presents maps of the distribution of *Zygonopus* species in West Virginia that are based, unfortunately, on some erroneous identifications. Although I am credited in the compendium as having provided the identifications, in fact only a few, relatively recently collected specimens were seen by me; the majority of the localities mapped are from the literature and based on determinations provided by others. A comparison of the map (Map 3) presented here with the maps in Fong *et al.*

(2007) and the detailed records given will illustrate the differences. A key point is that none of the species of *Zygonopus* appear to be sympatric, much less syntopic, anywhere in the generic range. However, I cannot claim to have seen all the specimens on which the maps in Fong *et al.* (2007) are based.

The generic distribution encompasses the Ridge and Valley physiographic region in Virginia and northern West Virginia (the “panhandle”), and the southwest-northeast trending valleys lying between the westernmost Ridge and Valley ridge and the escarpment of the Alleghany Plateau. The ridges are sandstone and shale, but erosion in the valleys has exposed Paleozoic limestones which are richly cavernous. While there are anomalies, the four species of *Zygonopus* are each more or less limited to specific drainage systems. Even terrestrial troglobionts may have distributions which follow drainage patterns, because the caves in which they live are formed by water and often contain active streams. In this region, stream valleys follow the softer limestone exposed under the hard siliceous caprock of the ridges, so individual valleys tend to be closed systems; the caprock limits cave formation in the underlying limestone, making underground dispersal between valleys impossible.

Zygonopus packardi occurs in the New and southwestern James River drainages, the James drainage occurrences possibly explicable by headwaters erosion leading to stream capture, specifically the capture by the Roanoke River of the Fincastle River in the early Pleistocene, which switched the Fincastle from the New to the James drainage (Ross 1969). The northeastern part of the James drainage is occupied by *Z. weyeriensis*. *Zygonopus whitei* occurs in the headwaters of the Potomac drainage system, specifically the South Branch and Shenandoah Rivers. The relatively few records of *Z. krekeleri* are from the region drained by the Shavers Fork and South Fork tributaries of the Cheat River, which in turn flows north into the Monongahela system. The ultimate outlet of the Monongahela and New River systems is the Gulf of Mexico via the Ohio and Mississippi Rivers, of the James and Potomac, Chesapeake Bay.

Given these distributional patterns, it is interesting that the maps for many other terrestrial troglobionts (primarily insects; see especially the maps for the beetle genus *Pseudanophthalmus* Jeannel, 1920) given for West Virginia by Fong *et al.* (2007) show very similar patterns; essentially a division into the same (or very similar) three to five broad regions congruent for a number of species. However, at least in the case of *Pseudanophthalmus*, each “zone” may contain more than one, and in some cases several, sympatric if not syntopic species of the genus.

Within this larger pattern it seems reasonable to postulate that each *Zygonopus* species has achieved its present distribution through relatively rapid underground dispersal within the valleys of the stream systems, based on the lack of significant morphological variation within each. Above-ground dispersal can be ruled out by the delicate nature of these animals, unable to withstand warm temperatures or low humidities. It is possible that an initial colonization by a single ancestral population, or a few ancestral populations, eventually gave rise to the closely related and similar species *packardi*, *weyeriensis* and *whitei*, and that the very different *krekeleri* represents a separate initial colonization. An alternative would be the nearly simultaneous colonization of multiple cave systems by separate epigeal ancestors of each population, but this would be expected to lead to substantial variation and even speciation between those populations, which does not seem to be the case. Distribution through the epikarst, the vast array of microcaverns overlying caves accessible to humans (Culver & Pipan 2009), seems the most likely route for *Zygonopus* species.

Molecular phylogenetic studies of *Zygonopus* would be very interesting and would provide an opportunity to test these hypotheses.

Notes: In 1972 I argued for the synonymy of *Zygonopus* with *Trichopetalum*, largely on the basis of a newly discovered Alabama species, *T. syntheticum* Shear, which on subsequent examination turned out to be a species of *Scoterpes*. I could hardly have been more confused! Reconsideration of the many consistent differences between the two genera (admittedly some due to troglomorphy, which could be convergent) now leads me to revalidate *Zygonopus* as an obviously monophyletic group of species. A close relationship with *Trichopetalum* and *Nannopetalum* is strongly indicated by the gonopod anatomy; indeed the gonopods of *T. stan-*

nardi and *T. jerryblatti* are very similar to *Zygonopus* gonopods, but the *Trichopetalum* and *Nannopetalum* species have the apomorphic character of sclerotized gonopod colpocoxites and lack the extreme modification of male legpair six—an apomorphy of *Zygonopus*. The common ancestor of the three genera was very likely to have strongly resembled *Z. weyeri* in the gonopods, had 30 trunk segments, but was an eyed, pigmented epigean species.

Causey (1960) revised the genus and described three of the four species. At that time she stated:

“The differences between *Z. packardi*, *Z. weyeri*, and *Z. whitei* are mainly quantitative. When these three species were first studied, it appeared that subsequent collections might yield forms that would connect them. Then Dr. Barr’s large collection with male specimens of three species from 12 additional caves was received. Some variations were found, but they are slight, and in no case can they be regarded as intergrades between the species (Causey, 1960, p. 73)”

Three years later, Causey (1963) had evidently rethought that conclusion, and wrote: “...the four species that I formerly assigned to it (Causey, 1960) are two species, of which one is composed of three subspecies.” I assume Causey meant that *packardi* and *weyeri* were subspecies of *whitei*.

She was right the first time. In studying many more specimens from many more localities, I found the three species Causey later thought to be subspecies of *Z. whitei* perfectly and unambiguously distinct from one another, with no evidence of intergradation and with well-defined, separate areas of distribution. The differences between them are by no means “quantitative” as Causey herself demonstrated with her excellent figures of the gonopods (Causey 1960). The category subspecies has a biological meaning; it designates a population that consistently differs from other populations of the same species, but which is not reproductively isolated from those populations. The lack of reproductive isolation is demonstrated by the presence of zones of intergradation between the populations. If such intermediates cannot be found, it is better, depending on circumstances, to either describe the variation without nomenclatorial status, or name the populations as species. After all, the proposal of a species is a hypothesis like any other, which we expect to be tested in the future by additional data, and supported or rejected (Shear 2003).

Key to species, based on males

- 1a. Sixth legpair greatly enlarged (Figs. 34, 36, 44) 2.
- 1b. Sixth legpair less strikingly enlarged (Fig. 49) *packardi*.
- 2a. Gonopod angiocoxite divided (Figs. 41, 45) 3.
- 2b. Gonopod angiocoxite single (Fig. 42) *krekeri*.
- 3a. Eight or nine angiocoxal setae robust, curved (Fig. 41) *whitei*.
- 3b. Three to five angiocoxal setae small, not curved (Fig. 45) *weyeri*.

Zygonopus whitei Ryder

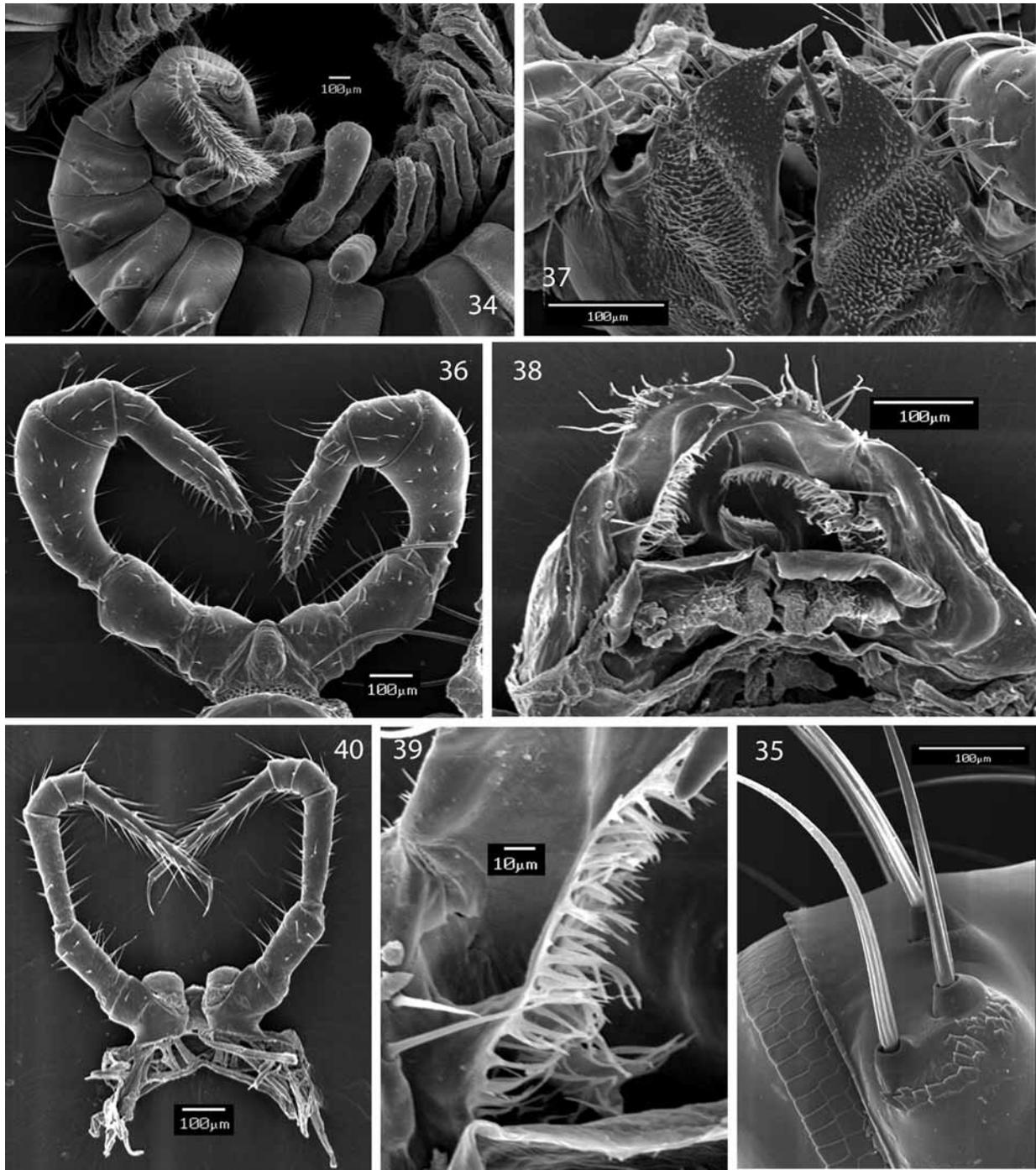
Figs. 34–41, Map 3

Zygonopus whitei Ryder 1881:527, figs. 1–3. Cook & Collins, 1895:60, figs. 14–21. Causey, 1960:73, figs. 2, 3.
Trichopetalum whitei, Shear, 1972:277.

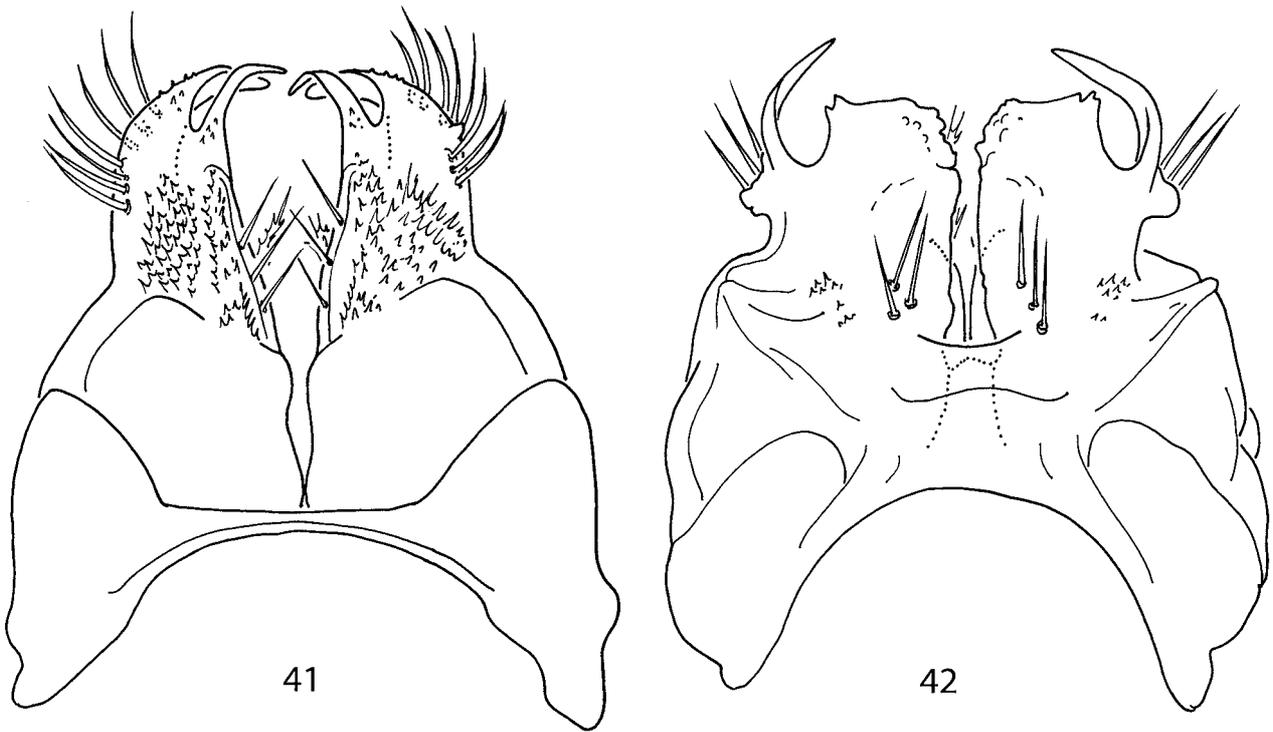
Types: The type locality is Luray Caverns, Page Co., Virginia. Since Ryder’s types were lost even at the time Cook & Collins (1895) did their revisionary work, I hereby designate a neotype male from a collection made

at Luray Caverns, 22 August 1958, by T. Barr and D. Egbert (FSCA). Cook & Collins (1895) based their detailed redescription on a single male collected in Luray Caverns by L. M. Underwood in 1887, but this specimen was thoroughly dissected and the parts mounted on microscope slides, which have since been lost.

Diagnosis: Distinct from other *Zygonopus* species in the row of numerous, strong, curved setae on the ectal surface of the gonopod angiocoxite.



FIGURES 34–40. *Zygonopus whitei* male, Scanning Electron Micrographs. 34. Anterior end of body, lateral view; note enlarged leg 6. 35. Segmental setae, lateral view. 36. Legpair 6, posterior view. 37. Gonopods, anterior view. 38. Same, posterior view; note poorly sclerotized colpocoxites have collapsed. 39. Gonopod fimbriate branch. 40. Legpair 10, posterior view.



FIGURES 41, 42. *Zygonopus* spp. 41. Gonopods of *Z. whitei*, anterior view. 42. Gonopods of *Z. krekeleri*, anterior view.

Etymology: Named by Ryder for C. A. White, a paleontologist, who obtained the original specimens from the owner of Luray Caverns, the actual collector (Ryder 1881).

Male from Luray Caverns, Virginia: Length, 8.5 mm, width, 0.7 mm. Eyeless and without pigment. Leg-pairs 1 and 2 reduced in size, pairs 3–5 somewhat enlarged, with 5 the largest; distinct gap between pair 5 and 6 (Fig. 34), legpair 6 (Fig. 36) greatly enlarged, femora swollen, almost spherical; legpair 7 of normal size. Gonopods (Figs. 37–39, 41) in anterior view with dense patches of acute trichomes scale-like near midline, longer laterally; angiocoxite divided, lateral branch 2–3 times as broad as mesal branch, lateral branch with single row of 7–9 stiff, curved setae. Colpocoxites subglobular, lightly sclerotized, fimbriate branches (Fig. 39) small, somewhat concealed in posterior view. Ninth legpair typical. Tenth (Fig. 40) and eleventh legpairs with coxal glands.

Female from Luray Caverns, Virginia: Length, 9.0 mm, width, 0.85 mm. Nonsexual characters as in male.

Distribution: See Map 3 for selected records. Each of the following records verified by the examination of at least one male. **VIRGINIA:** *Page Co.:* Luray Caverns, 14 August 1939, L. Hubricht (FSCA), 22 August 1958, T. Barr, D. Egbert (FSCA). *Rockingham Co.:* 3-D Maze Cave, 3 mi SW Broadway, 27 June 1974, J. Holsinger (VMNH); Cedar Hill Cave, 3 April 1999, D. Hubbard (VMNH); Melrose Cave, 22 May 2000, D. Hubbard (VMNH); Ponderosa Fissure Cave, 20 February 2000, D. Hubbard (VMNH); Stephen's Cave, 23 September 1961, J. Holsinger (FSCA). *Shenandoah Co.:* Endless Caverns, New Market, 31 August 1937, K. Dearolf (FMNH), 7 May 1961, J. Holsinger (VMNH, FSCA); New Market Cave, 30 August 1937, K. Dearolf (FMNH), date and collector unknown (USNM); Madden's Cave, date and collector unknown (FSCA). **WEST VIRGINIA:** *Grant Co.:* Elkhorn Mountain Cave, 14 July 1962, J. Holsinger (VMNH). *Pendleton Co.:* Hell Hole Cave, 25 March 1961, collector unknown (FSCA); Kenny Simmons Cave, 8 April 1962, J. Holsinger (FSCA); Stratosphere Balloon Cave, 7 August 1962, J. Holsinger (FSCA), 31 August 1958, T. Barr (AMNH); Trout Rock Cave, 1 June 1935, K. Dearolf (FMNH).

Notes: The Grant Co., West Virginia, record is a new county record but close to the well-established localities in Pendleton Co. Grant Co. caves have not been well-explored and I would expect many of them to harbor *Z. whitei*. The distribution of *Z. whitei* seems divided into two discrete areas: the Shenandoah Valley from just north of Harrisonburg, Virginia, northwestward to Luray, Virginia, and the valley of the South Branch of the Potomac River from just south of Franklin, West Virginia, to Moorefield, West Virginia, where the North and South Forks of the South Branch unite. The two regions are on either side of Shenandoah Mountain, which is capped by erosion-resistant sandstones and shales. Specimens from these two regions show no distinctions in the gonopods. There is a gap between the southernmost records of *whitei* in Rockingham County and the northeastmost record of *Z. weyeri* along the Rockingham-Augusta Co. boundary. It is likely that *weyeri* is to be found in the extreme southeast corner of Rockingham Co., in caves near Grottoes, Virginia. There are many caves in southern Rockingham and northern Augusta Counties, and these should be explored to determine the distributional limits of the two species; Augusta Co., in particular, has not been well collected for *Zygonopus*. The distribution of the western populations of *whitei* in West Virginia is divided from the distribution of *Z. krekeleri* by the high sandstone-capped ridge of Allegheny Mountain, which includes Spruce Knob, the state's highest peak. As with Shenandoah Mountain, the rocks of this mountain are noncavernous sandstones and shales, and Allegheny Mountain marks the transition from the much-folded strata of the Ridge and Valley Province to the east and the tilted to nearly horizontal rocks of the Allegheny Plateau to the west.

***Zygonopus krekeleri* Causey**

Fig. 42, Map 3

Zygonopus krekeleri Causey 1960: 79, figs. 10, 11.

Types: Male holotype (AMNH) and male and female paratypes (FSCA) from Alpena Cave No. 1, Alpena, Randolph Co., West Virginia.

Diagnosis: The gonopods are highly distinctive, as the lateral branch of the angiocoxite is suppressed and the inner side of the coxite is drawn up into a strong, coarsely roughened lobe.

Etymology: Named by Causey for Carl H. Krekeler, a coleopterist who supplied her with specimens for her revision.

Male paratype: Length, 8.5 mm, width, 0.76 mm. Unpigmented, eyeless. Pregonopodal legs as described for *Z. whitei*. Gonopods (Fig. 42) robust; trichomes on anterior face of coxa suppressed, few in number; angiocoxite unbranched, 3 lateral coxal setae at base; median angle of coxite drawn into large, roughened subquadrate lobe; telopodite globose-quadrate, almost entirely concealing fimbriate branch. Ninth leg-pair as usual, tenth and eleventh legpairs with coxal glands.

Female paratype: Length, 9.1 mm, width, 0.79 mm. Nonsexual characters as in male.

Distribution: See Map 3 for selected records. Each of the following records verified by the examination of at least one male. WEST VIRGINIA: *Randolph Co.:* Alpena Cave No. 1, Alpena, 23 July 1957, C. Krekeler (AMNH, FSCA); Bowden Cave No. 1, 23 August 1966, J. Holsinger (FSCA); Crawford Cave, 23 July 1957, C. Krekeler (FSCA).

Literature Records: Causey (1960) reports *krekeleri* from Bennett and Mill Run Caves in southern *Tucker Co.*, WEST VIRGINIA. I did not find these specimens and the records (also mapped in Fong *et al.* 2007) are well south of the core distribution of the species. Fong *et al.* (2007) report *krekeleri* from Bonner Mountain Cave, Stewart Run Cave, and Stony Run Cave, *Randolph Co.*, WEST VIRGINIA, and from Bob White Cave and Red Run Cave, *Tucker Co.*, WEST VIRGINIA. I have not seen these specimens but the localities are tightly clustered in the core area for the species; they are mapped in Fong *et al.* (2007). FSCA has a sample

from Dyer's Cave, *Hardy Co.*, WEST VIRGINIA, that Causey had determined as *krekeleri*, but the male no longer has gonopods (they were slide-mounted and the slide has disappeared). This is a very unlikely record, around 40 miles east of the others, in the Potomac drainage on the west flank of Shenandoah Mountain, and within the distribution of *Z. whitei*, which is now known from Grant Co. (see above). The record should be checked.

Notes: *Zygonopus krekeleri* is a distinctive species found in the upper reaches of the Cheat River drainage and not closely related to its three congeners. More collecting is needed in Randolph and Tucker counties to delineate the distribution of *Z. krekeleri*.

***Zygonopus weyeri* Causey**

Figs. 43–47, Map 3

Zygonopus weyeri Causey 1960:75, figs. 4–7.

Zygonopus whitei, Packard 1883:194.

Types: Male holotype (AMNH) from Grand Caverns, 20 November 1958, collected by O. P. Estes.

Diagnosis: Closest to *Z. whitei* in the strikingly large sixth legpair, but easily distinguished by the lack of the characteristic strong, curved gonopod setae of that species and the longer, thinner divisions of the angiocoxite.

Etymology: The species name refers to the type locality; Grand Caverns was earlier known as Weyer's (pronounced "weers") Cave.

Male from Grand Caverns, Virginia: Length, 10 mm, width, 0.75 mm. Eyeless, unpigmented. Pregonopodal legs as described for *Z. whitei*; legpair 6 (Fig. 45) very much enlarged, femora nearly spherical. Gonopods (Fig. 46) with moderate vestiture of short, scale-like trichomes over anterior surface; inner coxal angle obtuse (margin not smooth); angiocoxites deeply divided, lateral branch about twice as wide as median branch, with 3–5 short, straight setae. Colpocoxites subglobular, not meeting in midline; fimbriate branches short but easily seen in anterior and posterior views. Ninth legpair (Fig. 47) as usual. Tenth and eleventh coxae with glands.

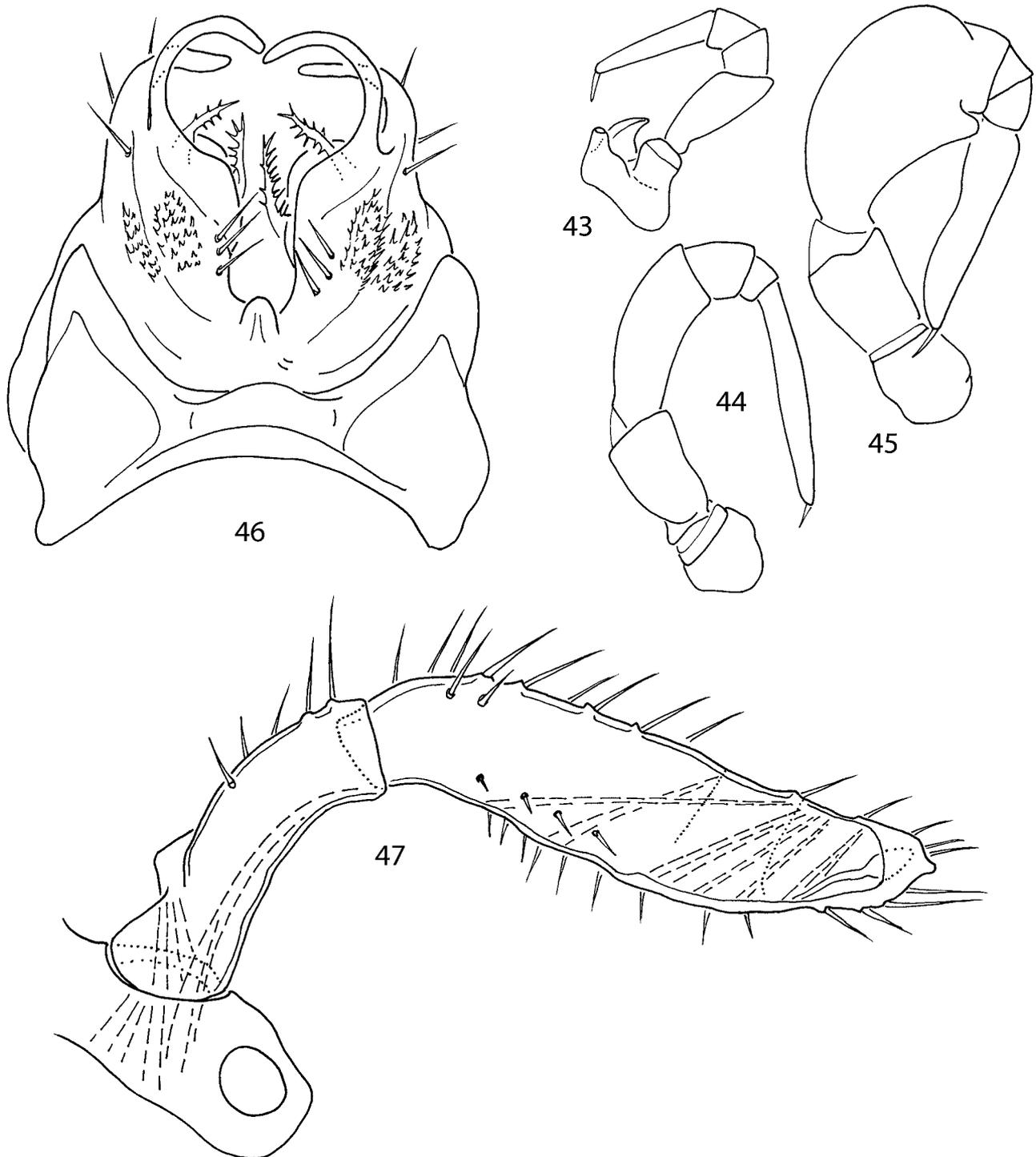
Female from Grand Caverns, Virginia: Length, 11 mm, width, 0.9 mm. Nonsexual characters as in male.

Distribution: See Map 3 for selected records. Each of the following records verified by the examination of at least one male. VIRGINIA: *Augusta Co.*: Grand Caverns (Weyer's Cave), 20 January 1958, P. Estes (FSCA); Madison Cave, no date or collector (FSCA); Madison's Saltpetre Cave, 5 March 1980, J. Holsinger *et al.* (VMNH). *Bath Co.*: Boundless Cave, 10 July 1967, J. Holsinger (FSCA), Breathing Cave Branch of Butler Cave, 28 August 1958, T. Barr (AMNH); Porter's Cave, no date or collector (FSCA); Starr Chapel Cave, no date or collector (FSCA). *Rockbridge Co.*: Graham's Cave, December 1970, J. Tichenor (VMNH). WEST VIRGINIA: *Greenbrier Co.*: General Davis Cave, 1 September 1975, G. Corbett (VMNH); Greenbrier Caverns System, 27 August 1966, G. Maus, S. Bauer (FSCA); Higgenbotham Cave, 17 August 1959, T. C. Barr (FSCA); Ludington Cave, 24 January 1962, J. Holsinger (FSCA); McClung Cave, 23 March 1966, G. Conrad (FSCA); McLaughlin-Unus Cave, 14 August 1966, J. Holsinger, B. Rogers (FSCA); The Hole, 27 January 1965, WVACS (FSCA). *Pendleton Co.*: Mystic Cave, 3 August 1958, 7 April 1962, T. Barr (FSCA). *Pocahontas Co.*: Linwood Cave, 22 August 1966, J. Holsinger (FSCA); Cass Cave, 14 October 1961, L. Conrad, J. Holsinger (FSCA).

Literature Records: Holsinger (1963, 1982) reported the species from Billy Williams Cave, *Rockbridge Co.*, VIRGINIA, and from Arbuckle, Benedict's, Culverson Creek, Organ, and Wade's Caves, *Greenbrier Co.*, WEST VIRGINIA. Holsinger, Baroody and Culver (1976) have *weyeri* from Hunt Cave, *Monroe Co.*, WEST VIRGINIA, but this needs to be checked as it impinges on the distribution of *Z. packardi*. Fong *et al.* (2007) repeat some of the above records; particularly notable are more records from *Pendleton Co.*: Keel

Spring Cave, Kenny Simmons Cave, and *Pocahontas Co.*: Cass Cave, Dreen Cave, Linwood Cave, My Cave. At least the Pendleton Co. records may refer to *weyeriensis*.

Notes: The records from Pendleton Co., West Virginia, seem out of place, well into the distributional area of *Z. whitei* in the South Branch Valley. I checked the specimens from Mystic Cave and Keel Spring Cave, and they are undoubtedly *Z. weyeriensis*. I have not seen the other specimens mentioned above as reported by Fong *et al.* (2007). Caves in Highland, Rockbridge, and Alleghany counties in Virginia need to be explored to clear up the full range of *weyeriensis*; as it stands the Greenbrier Co., West Virginia, records are quite isolated from the Virginia records. However, there is little variation in the gonopods of the species.



FIGURES 43–47. *Zygonopus weyeriensis* male. 43. Left leg 2, posterior view. 44. Right leg 5, posterior view. 45. Right leg 6, posterior view. 47. Right leg 9, anterior view; note vestigial segmentation and muscle remnants.

Zygonopus packardi Causey

Figs. 48–55, Map 3

Zygonopus packardi Causey, 1960:77, figs. 8, 9.

Trichopetalum packardi, Shear 1972:278: figs. 514, 515.

Types: Male holotype (AMNH) and male and female paratypes (FSCA) from Patton's Cave, 2 mi SE of Gap Mills, Monroe Co., West Virginia.

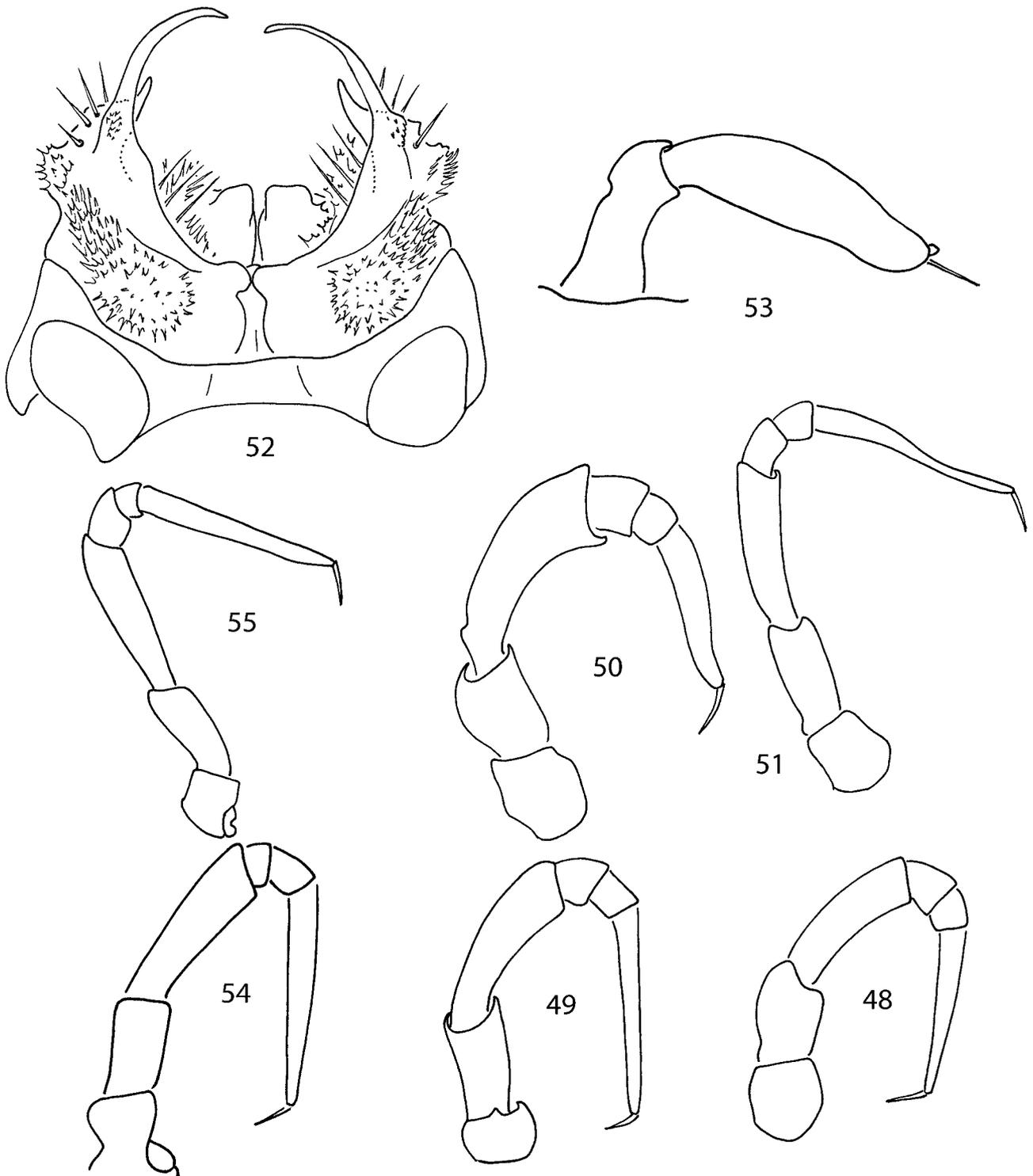
Diagnosis: Distinct from the other three species of the genus in much less enlarged sixth legpair (Fig. 50); the lateral branch of the gonopod angiocoxite is much shorter than the median branch, and closely appressed to it; the bases of the gonopod coxae are widely separated and the lateral margin of the coxa on each side is angular and roughened.

Etymology: Named by Causey for Alphaeus S. Packard, the first American biologist to make a deliberate study of troglomorphic animals.

Male from Patton's Cave, West Virginia: Length, 8.2 mm, width, 0.75 mm. Eyeless, unpigmented. Pregonopodal legs as in figs. Legpair 6 (Fig. 50) only slightly larger than pairs 4 (Fig. 48), 5 (Fig. 49); femur somewhat enlarged distally, bowed; legpair 7 (Fig. 51) of nearly normal size. Gonopods (Fig. 52) with sternum bearing typical anterior swellings, coxae well-separated, heavily set with trichomes, trichomes triangular-acute near midline, become longer, scale-like, laterodistally; lateral angles of coxae acute, trichomes long; 4 lateral setae on each side short, straight. Angiocoxites divided, median branch 3–4 times longer than lateral branch, which is closely appressed to posterior side of median branch. Colpocoxites typical, fimbriate branches readily visible in both posterior and anterior views. Legpair 9 typical (Fig. 53). Legpairs 10 and 11 with coxal glands (Figs. 54, 55).

Female from Patton's Cave, West Virginia: Length, 9.1 mm, width, 0.8 mm. Nonsexual characters as in male.

Distribution: See Map 3 for selected records. Each of the following records verified by the examination of at least one male. VIRGINIA: *Alleghany Co.*: Blue Spring Cave, 11 April 1970, L. Ferguson (VMNH). *Bland Co.*: Coon Cave, 4.3 mi SW Mechanicsburg, 10 May 1981, J. Holsinger (VMNH); Hamilton Cave, 1 May 1971, L. Ferguson (VMNH), no date or collector (FSCA); Newberry Bone Cave, 3 mi SW Mechanicsburg, "winter" 1981, B. Koerschner (VMNH); Repass Saltpetre Cave, 10 May 1966, J. Holsinger (FSCA); Perry Saltpetre Cave, no date or collector (FSCA). *Craig Co.*: Loney's Cave, 18 April 1970, L. Ferguson (VMNH); Rufe Caldwell Cave, 1 July 1962, J. Holsinger (VMNH). *Giles Co.*: Canoe Cave, 25 February 1967, J. Holsinger, H. Steeves (FSCA); Clover Hollow Cave, 21 January 1962, J. Holsinger (FSCA); Doe Mountain Cave, 23 November 1999, D. Hubbard (VMNH); Echols Cave, 28 April 2000, D. Hubbard (VMNH); Giant Cave, October 1962, J. Holsinger (FSCA); Hopkin's Cave, 1 mi S Narrows, no date, C. Krekeler (FSCA); New River Cave, 24 October 1976, L. Ferguson (VMNH), 8 March 1970, L. Knight (VMNH); Stearns Cave, no date or collector (FSCA); Straley's Cave, no date or collector (FSCA); Tawney's Cave, 11 August 1954, C. Krekeler (FSCA), 7 July 1970, W. Muchmore (VMNH); *Montgomery Co.*: Old Mill Cave, 18–20 October 1971, L. Ferguson (VMNH). *Pulaski Co.*: Collier Cave, 22 June, 1997, D. Hubbard (VMNH); Fifty-foot Hell Cave, 3 mi NE Dublin, 5 October 1970, J. Holsinger (VMNH); Sam Bell's Cave, 0.8 mi NNW Dublin, 24 July 1970, J. Holsinger (VMNH). *Roanoke Co.*: Dixie Caverns, 23 November 1961, J. Holsinger (FSCA). *Wythe Co.*: Campbell Cave, 15 March 2000, D. Hubbard (VMNH); Early's Cave, 7 July 1997, D. Hubbard (VMNH); Gardner Cave, 6 September 1997, D. Hubbard (VMNH); Sam Six Cave, 25 August 1967, J. Holsinger (FSCA). WEST VIRGINIA: *Mercer Co.*: Beacon Cave, Bluefield, 5 December 1966, J. Holsinger (FSCA); Dyepot Cave, 5 December 1966, J. Holsinger (FSCA); Honaker Cave, 5 mi W Glen Lyn, 12 August 1957, C. Krekeler (FSCA). *Monroe Co.*: Fletcher's Cave, 31 August 1967, J. Holsinger (FSCA), "Ketcher's Cave (probably Fletcher's Cave)" no date or collector (FSCA); McClung Zenith Cave, 31 January 1967, J. Holsinger (FSCA); Patton's Cave, 2 mi SE Gap Mills, 7 August 1957, T. Barr (FSCA).



FIGURES 48–55. *Zygonpus packardi* male. 48–51. Right legs, posterior view. 48. Leg 4. 49. Leg 5. 50. Leg 6. 51. Leg 7. 52. Gonopods, anterior view. 53. Left leg 9, posterior view. 54. Right leg 10, posterior view. 55. Right leg 11, posterior view.

Literature records: Holsinger (1963) reports *Z. packardi* from VIRGINIA: *Bland Co.*; Newberry-Bane Caves; *Giles Co.*: Clover Hollow, Stearnes, Straley's, Tawney's Caves and Giant Caverns. Holsinger and Culver (1980) cite numerous localities in *Bland* and *Giles Cos.*, VIRGINIA, all already listed above. Holsinger, Baroody and Culver (1976) and Fong *et al.* (2007) report the following WEST VIRGINIA localities: *Mercer Co.*: Beacon, Caldwell, Dyepot, Honaker, and Panther Caves; *Monroe Co.*: Crossroad, Fletcher's, McClung

Zenith, and Patton Caves. Holsinger and Culver (1988) and Holsinger *et al.* (1976) cite numbers of caves in both Virginia and West Virginia as supporting *Zygonopus* populations, but males were not collected. For most of these caves, examination of the records given here for all four species allows good educated guesses as to the species present, but males are needed for confirmation.

Notes: Causey (1960), Holsinger *et al.* (1976), and Fong *et al.* (2007) cite *packardi* from Organ Cave and The Hole, Greenbrier Co., West Virginia. I was not able to find the specimens from Organ Cave and have not seen material from The Hole, but the records would be extremely unlikely since they are far out of range for *packardi* and well within the range of *Z. weyeriensis*. Organ Cave is a part of the Greenbrier Cave System, from which *weyeriensis* has been collected, and Holsinger and Culver (1988) report *Z. weyeriensis* from Organ Cave itself; Fong *et al.* (2007) list both *weyeriensis* and *packardi* from Organ Cave and The Hole. While syntopy of these two species is remotely possible, I have not seen any evidence for it and conclude that only *weyeriensis* occurs in these central Greenbrier County caves.

Genus *Scoterpes* Cope

Scoterpes Cope, 1872:414; Loomis, 1943:92; Shear, 1972:279; Hoffman, 2000:235.

Type species: *Spirostrephon (Pseudotremia) copei* Packard 1871, by original designation.

Included species: In addition to the genotype, *S. austrinus* Loomis 1943, *S. nudus* Chamberlin 1946, *S. ventus* Shear 1972, *S. syntheticus* (Shear) 1972, *S. sollmani* Lewis 2000, and the new species *alabama*, *blountensis*, *hesperus*, *jackdanieli*, *musicarustica*, *stewartpecki*, *tombbarri*, *tricornis* and *willreevesi*. *Scoterpes den-dropus* Loomis 1939 has been transferred to *Causeyella* Shear (Shear 2003).

Diagnosis: *Scoterpes* species lack coxal trichomes, which separates them from all other US trichopetalid genera. Blind, unpigmented, and with 30 segments, as in *Causeyella* and *Zygonopus*; in *Causeyella* the left and right gonopod angiocoxites are closely appressed to each other, while in *Scoterpes* they are widely separated; *Causeyella* also displays large, lamellate, fimbriate colpocoxite branches—in most *Scoterpes* these are thin with filamentous branches; in *Zygonopus* the fimbriate branch of the colpocoxite is relatively small and arises from its anterior surface, while in *Scoterpes* it arises apically and is a prominent feature of the gonopod. Animals (Fig. 56) range in size from 6 to 12 mm, generally larger than *Trichopetalum* individuals, but not so large as those of *Causeyella* species, which are up to 15 mm long. Segmental setae are very long and prominent (Fig. 55), from 80% of to slightly longer than the body width, longer than in any other genus of chordeumatidan millipeds. The lateralmost segmental setae are borne on prominent, paratnota-like knobs, the paralateral setae similarly but on a shorter knob, and the mesal setae on still lower mounds near the midline. Frequently blobs of secretion can be seen on the segmental setae (Fig. 57). Pregonopodal legs are only slightly enlarged or not different from postgonopodal legs. Legpairs 1–5 are notably shorter than subsequent pairs and the length difference is mostly in the femur, so that legpairs 6 and 7 appear abruptly longer. Legpair 6 sometimes has a slight ventral swelling on the femora (Fig. 58). Legpair 9 is typical for the subfamily (Fig. 59), with spindle-shaped telopodites that frequently have a vestigial claw, or rarely a few vestigial distal segments. This suggests that the telopodite article represents a coalescence of all articles distal to the prefemur, and not just the prefemur itself. The gonopods are typical of the family but with more obvious fusion of the coxae with the sternum and with each other. Coxal setae are in two groups, the mesoproximal group with three setae on each coxa, the distolateral group of variable number but always more than three. The angiocoxites are divided into two branches, mesal and lateral; the lateral branches are often complexly folded at their tips (Figs. 60, 61, 65, 67). The mesal branches may be reduced and sometimes are absent entirely. The colpocoxites are large, ovoid, and poorly sclerotized, with a single prominent fimbriate branch at the apex.

The name *Scoterpes* is compounded from the Greek words *skotos* and *herpeton*, and means “a crawler in darkness.” It is masculine in gender.

Distribution: Always in caves as troglobionts, ranging through southern Indiana, the interior plateaus and karst basins of Kentucky and Tennessee, the southern Blue Ridge in Tennessee and Georgia, and the southern Ridge and Valley Province in Alabama. Outliers are *S. sollmani* in southern Indiana, the only species occurring north of the Ohio River, but an obvious close relative (if not a synonym) of *S. copei* across the river in northern Kentucky, and *S. blountensis* n. sp., isolated far to the east of the main distribution in Blount Co., Tennessee, and of uncertain relationship. In western Kentucky and northcentral Tennessee, the Cumberland River bounds the distribution. South of where the Cumberland turns northwestward, the boundary is the Tennessee River, but these rivers are also nearly at the limit of the westward extension of karst (map in Barr 1961). Southeastward, *S. syntheticus* occurs farthest south, just north of Birmingham, Alabama, and *S. nudus* is found in the Etowah River valley, a little distance southeast of Rome, Georgia.

The central distribution or core area of the genus is the Cumberland Plateau in Tennessee, the Pennyroyal Plateau in Kentucky, and the interior karst basins, such as the Nashville Basin. Eastern Kentucky, arbitrarily defined as that part of the state east of the Kentucky and Rockcastle Rivers (equivalent to the Bluegrass and Eastern Coalfield physiographic regions), has karst but no *Scoterpes*; similarly, only the very isolated *S. blountensis* is to be found in Tennessee east of the Sequatchie River, despite the presence of abundant karst in the Ridge and Valley portion of that state (there is a Meigs Co., Tennessee, record of *S. copei*, but this is highly questionable).

In contrast, *Scoterpes* has found its way into the folded Appalachians in Georgia and Alabama, and there two of the most distinctive species are to be found, though I believe they are most closely related to the species of the Cumberland Plateau. The Cumberland Plateau of northern Alabama was recently shown to have the highest diversity of terrestrial troglobionts in North America (Culver *et al.* 2006), and at least six species of *Scoterpes* occur there.

Notes: Nell Causey worked extensively for many years on the large collections of *Scoterpes* made available to her by Barr, Peck, Holsinger, Steeves and others, but never published anything on them. She noted (in litt. 1972) that the situation was “hopelessly confusing.” In 1960, she estimated as many as 27 taxa in the genus (species and subspecies). Indeed although I have pushed ahead, and here describe nine new species in the genus, many difficulties remain. While species from the southern end of the generic range seem discrete, relatively homogeneous and limited geographically, at least two “species,” *S. copei* (Packard) and *S. ventus* Shear, have large ranges that transgress barriers known to separate species, or even genera, in other troglobiont taxa. Significant variation in gonopod anatomy can be detected within these species, but the variants seem to this eye to merge imperceptibly into one another. Based on her labelling, Causey discerned six subspecies of *copei* (though some labelling suggests she may have at times thought of these as species) and three subspecies of *ventus*. These hypothetical subspecies had some geographic coherence, but I cannot reliably separate them. Further, Lewis (2000) described *S. sollmani* from caves in Indiana, north of the Ohio River, but I do not see any significant differences between this species and *copei* south of the river and well south and east into Kentucky. I have no doubt that both *copei* and *ventus* are “superspecies,” groups of closely related populations that have reached the level of reproductive isolation, but a much more detailed analysis than I am willing to embark on would be required to test that hypothesis. With the increasing ease of the use of molecular methods to demonstrate reproductive isolation, the genus *Scoterpes*, and in particular the “species” *copei* and *ventus*, would present an ideal challenge to a student of molecular systematics. It may well be that Causey’s (1960) estimate of 27 species-level taxa in *Scoterpes* will turn out not to be far from the mark.

Therefore the account of *Scoterpes* species that follows is not really a definitive revision but only a “first pass” through the genus, in which I provide names for some obviously distinct populations and plant some signposts to mark out problems for future research.

Scoterpes differs from the other trichopetaline genera in the complete lack of the characteristic trichomes on the gonopod coxae and relative lack of modifications of the pregonopodal legs. It is difficult to say if these and other characters are apomorphic and due to a long history of troglobiosis, or represent truly plesiomorphic characters. If the latter, the genus is basal to the subfamily.

The presence of *Scoterpes* only in caves throughout its wide range, from Indiana south to Alabama and Georgia, and the high level to which they have developed troglomorphy, suggests to me that the most recent events of the Pleistocene, the Wisconsinian glacial advance and retreat, may not be responsible for the isolation in caves of this genus. Some of the species may be very ancient troglobionts. It is also unclear if underground dispersal or repeated isolation of surface populations dominates the history of the genus (see Culver and Pipan 2009, pp. 131–154, for an excellent discussion of these alternatives). In other words, were there numerous species of surface-dwelling proto-*Scoterpes* that independently became isolated in caves, or only a few species that have, since their isolation, speciated (and perhaps dispersed) underground? Likely either explanation can be invoked in different parts of the generic range—in the interior basins of Kentucky and Tennessee, where limestone strata are flat-lying and extensive and cave systems enormous and interconnected, far-reaching underground dispersal over millenia is at least possible. But in the southern end of the folded Appalachians in Georgia and Alabama, formidable barriers to underground dispersal exist. The dispersal and vicariance models of troglobiont evolution and distribution are not mutually exclusive. Vicariance (extinction of surface populations) may account in most cases for the original isolation of cave populations, and later, dispersal through continuous karst may explain the existing range of the species (Holsinger 2005; Culver and Pipan 2009).

Alternatively, the broad distribution of the possible “superspecies” *S. copei* and *S. ventus* could argue for their having reached this distribution as epigean/troglophilic species whose epigean populations have become extinct recently enough not to allow for conspicuous morphological (gonopod) change in the isolated cave populations. As an example from another taxon, the cleidogonid milliped species *Pseudotremia hobbsi* Hoffman, 1950, is found in the several counties along the Virginia/West Virginia border, both as epigean populations and as troglophiles in caves (Shear 1972, 2008). Were the epigean populations to be extirpated by climate change, the surviving cave populations would appear to be, after some evolutionary development in the direction of cave-related adaptations, a widespread trogobiotic species whose distribution could not be explained by underground dispersal. Furthermore it could be argued that when populations become isolated in caves, potential selective forces constraining gonopod anatomy are reduced, since such features need no longer isolate populations. In *Pseudotremia* several of the most troglomorphic species, unrelated to one another, have clearly converged on a highly simplified gonopod structure (Shear 1972). These are questions that cannot even be approached without more data on genetics, specifically gathered for the purpose. The work of Hedin (1997) on cave spiders of the genus *Nesticus* and that of Moulds *et al* (2007) on pseudoscorpions are pioneering preliminaries to more detailed analyses of the genetics of speciation and population structure in cave animals. While continuing to recognize morphological species, Hedin demonstrated that populations within these species were genetically coherent and distinct, and perhaps at some later time deserving of species status themselves. Such species, however, may only be identifiable by recourse to DNA sequences (see Bond and Sierwald 2002, 2003). As sequencing becomes more and more convenient with each passing year, it is not unreasonable to suppose that it might even be possible to do in the field in the relatively near future.

So despite my own dissatisfaction with what follows, I hope that at least some of the populations I hypothesize to be species will actually turn out to be so. But it cannot be denied that there are probably more species of *Scoterpes* than are named here, most of them concealed within my concepts of *copei*, *ventus*, and perhaps one or two others.

Three fairly distinct species groups can be recognized in *Scoterpes*, and two species have gonopods divergent enough that they cannot be comfortably placed in any of the three groups. The groups are formed largely by my impression of overall gonopod similarity, but a few characterizing remarks can be made. The largest group by far, occupying most of the generic range in Kentucky and Tennessee, is the Copei Group. The broadly similar gonopods of this group usually feature branched and/or folded lateral angiocoxites, and there seems to be a tendency for the median angiocoxites to be reduced. The Alabama Group appears to be a derivative of the Copei Group, in which both sets of angiocoxites have grown quite long and have become

simplified; one of the two species in Alabama group has evidently lost the median angiocoxites. One species occurs in southcentral Tennessee, the other in northern Alabama. The Austrinus Group is composed of two species, very closely related to each other, in northern Georgia. *Scoterpes willreevesi*, n. sp., from northern Georgia and adjacent Alabama, has highly complicated gonopods which, while they are obviously on the *Scoterpes* plan, are unlike any others. Finally, *S. syntheticus* Shear is a small species with correspondingly small gonopods that have become extremely simplified; it occurs in northcentral Alabama and is the most southerly distributed of the species.

Key to Species, Based on Males

- 1a. Less than 7 mm total length *syntheticus*.
- 1b. Greater than 9 mm total length..... 2.

- 2a. Coxae of gonopods with apical group of hook-like crochets (Figs. 79, 80) *ventus*.
- 2b. Without such crochets 3.

- 3a. Median angiocoxites of gonopods fused and U-shaped (Fig. 76)..... *blountensis*.
- 3b. Median angiocoxites otherwise, or absent 4.

- 4a. Lateral angiocoxites of gonopods long, rod-like, not expanded, branched or folded at the tip (Figs. 83, 84) 5.
- 4b. Lateral angiocoxites relatively short, expanded, branched or folded at the tip 6.

- 5a. Median angiocoxites of gonopods present, equal to lateral angiocoxites (Fig. 83)..... *alabama*.
- 5b. Median angiocoxites of gonopods absent (Fig. 84) *jackdanieli*.

- 6a. Lateral angiocoxites apically expanded, T-shaped (Figs. 81, 82) 7.
- 6b. Lateral angiocoxites apically folded, often with lateral branch (Figs. 67, 69)..... 8.

- 7a. Lateral angiocoxites with array of small microteeth or denticles (Fig. 82) *nudus*.
- 7b. No such denticles (Fig. 81) *austrinus*.

- 8a. Median angiocoxites equal in length to lateral angiocoxites (Fig. 62) *copei* and *sollmanni*.
- 8b. Median angiocoxites absent or shorter than lateral angiocoxites (Figs. 75, 78) 9.

- 9a. Median angiocoxites low-triangular to one-half length of lateral angiocoxites 10.
- 9b. Median angiocoxites absent 12.

- 10a. Median angiocoxites as low, triangular projections (Fig. 74)..... *hesperus*.
- 10b. Median angiocoxites about one-half length of lateral angiocoxites..... 11.

- 11a. Lateral group of coxal setae tightly clustered (Fig. 75) *tombarri*.
- 11b. Lateral group of coxal setae more linearly arranged (Fig. 72)..... *musicarustica*.

- 12a. From caves in central Tennessee *tricornis*.
- 12b. From caves in northern Alabama *stewartpecki*.

The Copei Group

Scoterpes copei (Packard)

Figs. 56–67, Map 5

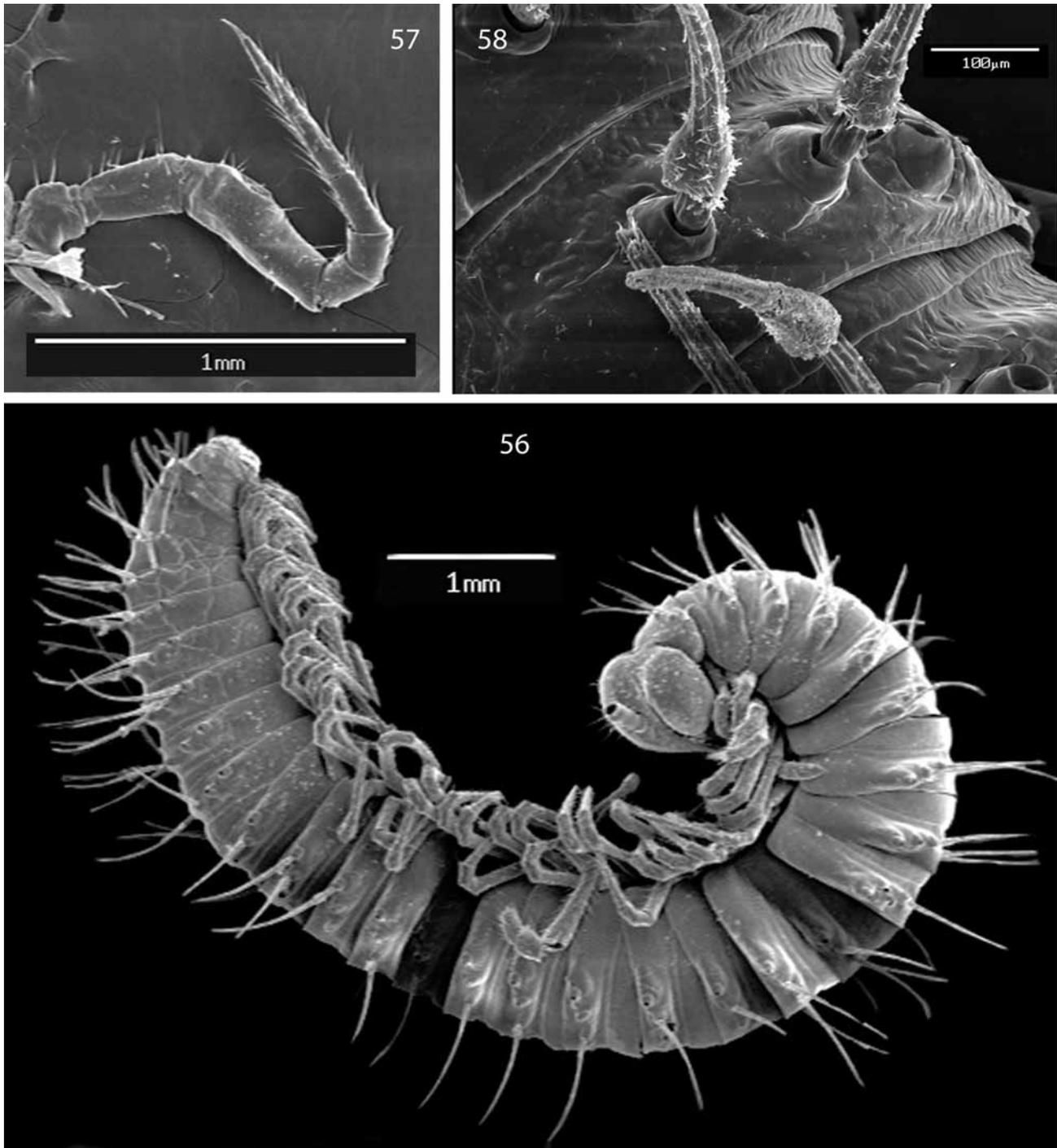
Spirostrephon (Pseudotremia) copei Packard, 1871, p. 748.

Scoterpes copei, Cook & Collins, 1895, p. 55. Shear, 1972, P. 279. Hoffman, 2000. P. 235.

Types: Male holotype and paratypes (MCZ) from Poynter's Cave, Edmonson Co., Kentucky, examined in 1971.

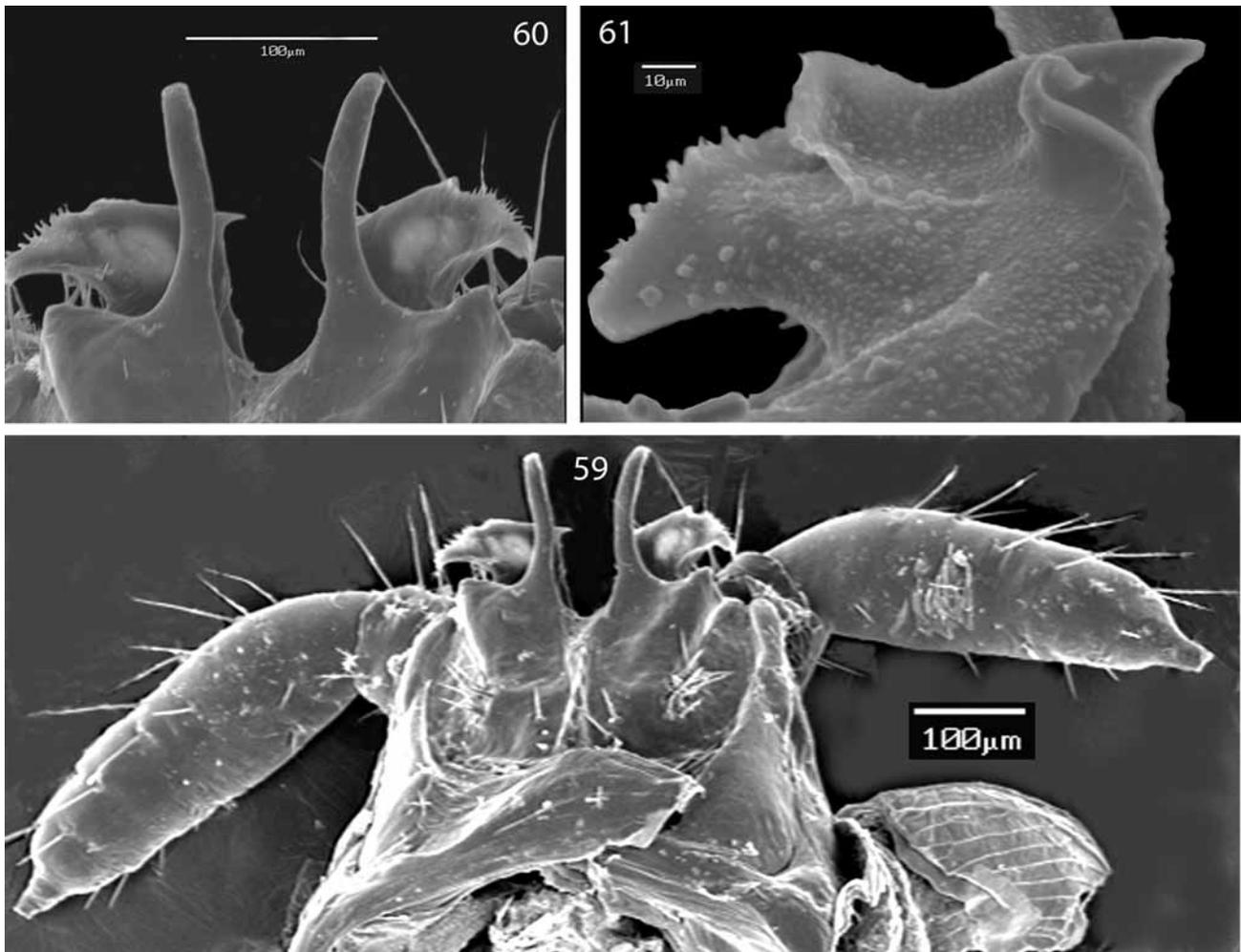
Diagnosis: *Scoterpes copei*, *S. tombarri* and *S. musicarustica* share the characteristic of long median angiocoxites with at least a short lateral branch (Figs. 72, 75), but *copei* has relatively shorter lateral angiocoxites, about equal in length to the medians. In the other two species, the lateral angiocoxites are considerably longer than the medians.

Etymology: Named for Edward Drinker Cope, a pioneer in American vertebrate paleontology, who, as an anatomist, also studied some of the adaptations of cave-dwelling animals, and described a few millipeds.



FIGURES 56–58. *Scoterpes copei* male, specimen from Mammoth Cave, Edmonson Co., KY. 56. Whole animal, lateral view. 57. Bases of segmental setae; note blobs of secretion. 58. Left leg 6, anterior view.

Male from Mammoth Cave, Kentucky: Length, 11.5 mm, width, 1.1 mm (Fig. 56). Nonsexual characters typical for genus. Gonopods (Figs. 59–67) with coxae fused to sternum, projecting anteriorly, median coxal setae in compact linear group, about 10 setae in lateral group, remote from distal edge of coxa; median angiocoxites long, flattened, lateral angiocoxites no longer than medians, complexly folded distally, with lateral branch thin, finely toothed; fimbriate branch of colpocoxite highly variable, usually feathery, prominent. Ninth, tenth and eleventh legpairs typical.



FIGURES 59–61. *Scoterpes copei* male, specimen from Mammoth Cave, Edmonson Co., KY. 59. Gonopods, anterior view. 60. Gonopod angiocoxites, anterior view. 61. Ectal coxite, lateral view.

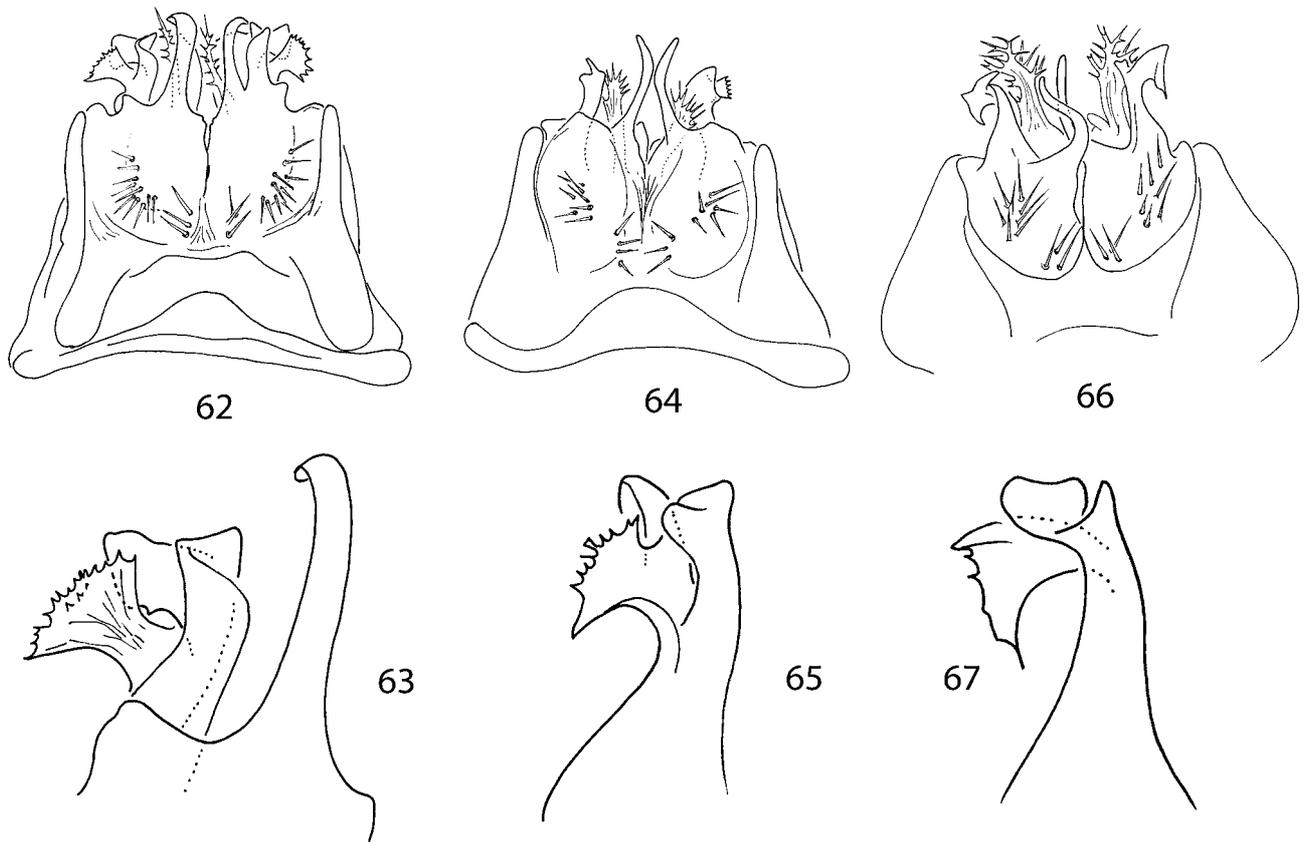
Female from Mammoth Cave: Length, 12 mm, width 1.3 mm. Nonsexual characters as in male.

Distribution: See Map 5 for selected records. All listed records supported by males; specimens FSCA unless noted. **KENTUCKY:** *Adair Co.* Cue’s Cave, 24 July 1964, T. C. Barr. *Allen Co.* Carpenter Cave, 4 January 1966, collector unknown. *Barren Co.* Duval Saltpetre Cave, 0.7 mi W of Beckton, 16 February 1957, L. Hubricht (VMNH); Edmunds Cave, 7 mi W of Glasgow, 27 August 1971, S. B. Peck; Indian Cave, “1881,” collector unknown (USNM); Indian Cave, 4 mi W of Cave City, 21 October 1958, L. Hubricht (VMNH); Mitchell Cave, Glasgow, 4 July 1958, L. Hubricht; 2 December 1959, T. C. Barr; Skaggs Saltpetre Cave, Temple Hill, 31 July 1963, T. C. Barr. *Breckenridge Co.* Boot Heel Cave, 30 June 1965, T. C. Barr; Norton Valley Cave, 19 October 1963, T. C. Barr; Thornhill Cave, 2 mi E of Big Spring, 15 August 1964, T. C. Barr. *Edmonson Co.* Blowing Spring Cave, Mammoth Cave National Park (MCNP), 1 December 1965, L. Hubricht (VMNH); Buzzard Cave, MCNP, 3 mi NE of Mammoth Cave, 20 June 1957, S. Krekeler; Diamond

Caverns, 1 January 1966, S. B. Peck; Dixon Cave, MCNP, 23 June 1956, L. Hubricht (VMNH); Floyd Collins Crystal Cave, 29 July 1956, L. Hubricht (VMNH); Mammoth Cave, MCNP, 1 July 1925, collector unknown (USNM); 1 July 1928, S. C. Bishop (USNM); 26 June 1937, collector unknown (FMNH); 15 January 1956, L. Hubricht (VMNH); 25 August 1957, N. B. Causey; Martin's Cave, MCNP, 13 October 1956, L. Hubricht (VMNH); Proctors Cave, MCNP, 23 September 1949, L. Hubricht (VMNH); small cave near Floyd Collins Crystal Cave, 29 July 1956, L. Hubricht (VMNH); White's Cave, MCNP, 28 May 1956, L. Hubricht (VMNH). *Green Co.* Montgomery Cave, 2 mi NW of Black Gnat, 25 August 1963, T. C. Barr. *Hardin Co.* Unnamed cave 1.3 mi W of Star Mills, 13 January 1957, L. Hubricht (VMNH); Saltpetre Cave, 10 May 1963, collector unknown; Great Onyx Cave, Cave City, 22 August 1935, collector unknown (FMNH). *Hart Co.* Buckner Hollow Cave, 30 August 1963, T. C. Barr; Chatlin Cave, 2 mi W of McMinnville, 11 August 1967, L. Hubricht (VMNH); Cooch Webb Cave, 2 November 1963, T. C. Barr; Copelin Cave, 2 mi E of Millerstown, 24 August 1964, L. Hubricht (VMNH); Cub Run Cave, 2 mi W of Cub Run, 29 December 1956, L. Hubricht (VMNH); Hogan Cave, 3 mi N of Cave City, 4 May 1957, L. Hubricht (VMNH); Ronald's Cave, 2.6 mi N of Cave City, 4 May 1957, L. Hubricht (VMNH); Saltpetre Cave, 1.5 mi E of Lone Star, 24 February 1957, L. Hubricht (VMNH). *Meade Co.* Rock Haven Cave, 8 July 1961, T. C. Barr. *Metcalfe Co.* Devil's Den, 3 mi S of Center, 25 September 1966, T. C. Barr. *Monroe Co.* Bromfield Cave, 2 mi SE Persimmon, 30 April 1964, T. C. Barr. *Pulaski Co.* Hydens Cave, 1.3 mi E of Bluejohn, 10 June 1964, T. C. Barr; Old Kentucky Cave, 8 mi SSE of Somerset, 29 January 1967, T. C. Barr; Richardson's Cave, 2.5 mi E of Somerset, 4 February 1962, T. C. Barr; 25 June 1957, S. Krekeler. *Rockcastle Co.* Teamer's Cave, 1 September 1963, T. C. Barr. *Warren Co.* Wolfe Creek Sink, Bowling Green, 12 October 1974, A. Likowski (FMNH). *Wayne Co.* Blowing Cave, 4 mi SSE of Powersburg, 6 September 1964, R. Norton; 28 September 1969, T. C. Barr; Hog Cave, 3 mi E of Mill Springs, 3 October 1959, T. C. Barr; Jesse Cave, 13 June 1964, T. C. Barr; Steale Cave, 3 October 1959, T. C. Barr; Wind Cave, 4 mi SE of Powersburg, 26 November 1959, T. C. Barr. TENNESSEE: *Fentress Co.* Sells Cave, 7 March 1959, T. C. Barr. *Macon Co.* Ann White Cave, 27 September 1956, T. C. Barr; Saltpetre Cave, 6 January 1966, T. C. Barr. *Meigs Co.* Sensabaugh Cave, 4 January 1963, R. Norton. *Overton Co.* Coleman Cave, near Pickett Co. line, 24 January 1960, T. C. Barr; Raven Bluff Cave, 28 February 1959, 8 April 1960, T. C. Barr.

Notes: I am as unsatisfied as others will undoubtedly be with this treatment of *Scoterpes copei* as a very widespread, polymorphic species distributed from near the Ohio River in the north to north-central Tennessee in the south, as well as its occurrence in two distinct karst regions, the Western Pennyroyal and Eastern Pennyroyal. The former dips into Tennessee as the western part of the Highland Rim, and the latter continues deep into Tennessee as the Cumberland Plateau province. Nell Causey seemed equally frustrated, judging from her specimen labels. She recognized no less than six subspecies of *S. copei*, but I find that I cannot reliably separate them based on the specimens she regarded as typical, and some of them lacked geographical coherence. However, it may be useful to review her thoughts here. "Copei proprius" was from a single record in Adair Co., and is in the far eastern part of the Western Pennyroyal, almost exactly between the proposed distributions of two other subspecies, "copei copei," occupying the Western Pennyroyal heartland, and "copei inexpectatus" in the northern Eastern Pennyroyal. In turn, "copei inexpectatus" blends into "copei rarus" in the southern Eastern Pennyroyal and Tennessee's Cumberland Plateau. There are no obvious barriers or natural breaks in the ranges of the latter two. The designation "copei remotus" was given to specimens from Hardin and Breckenridge counties north of the Rough River; these specimens most closely resemble *S. sollmanni* from Indiana (see below). Finally, "copei paganus" refers to a single collection from Meigs Co., Tennessee; Meigs Co. is in the Appalachian Ridge and Valley Province of Tennessee, far, far removed from any other *copei* records, and aside from the very isolated *blountensis* in karst windows in the Unaka Mountains, represents the only *Scoterpes* in Tennessee east of the Sequatchie Valley. I think it may be mislabelled, but only repeat collecting can solve the dilemma. *Scoterpes* species do occur southward in this Province in Georgia and Alabama, but they belong to different species groups, or cannot be assigned to a group.

The illustrations presented here are meant to show the range of variation in the gonopods of *copei*. Some intraspecific variation, particularly in the terminus of the lateral angiocoxites and in the fimbriate branch of the colpocoxites, is also present. After nearly 10 years of intermittent study, I cannot recover Causey's subspecies nor can I recognize groups of populations that are consistently distinct from those in the core area around Mammoth Cave National Park in Edmonson and Hart counties, Kentucky. Specimens from Hart County caves are surprisingly diverse in gonopod details. While I think there are cryptic species to be recognized in this complex, it will take a major collecting effort to obtain new material, suitable for genetic analysis, to finally work out the problems. Barr (1967) studied this species' ecology in Mammoth Cave.



FIGURES 62–67. *Scoterpes copei* males. Figs. 62, 63. Specimen from Mammoth Cave, Edmonson Co., KY. 62. Gonopods, anterior view. 63. Angiocoxites, lateral view. Figs. 64, 65. Specimen from Edmonds Cave, Barren Co., KY. 64. Gonopods, anterior view. 65. Angiocoxites, lateral view. Figs. 66, 67. Specimen from Rock Haven Cave, Meade Co., KY. 66. Gonopods, anterior view. 67. Angiocoxites, lateral view.

Scoterpes sollmani Lewis

Scoterpes sollmani Lewis 2000, p. 117. Shear, 2003, p. 7.

Types: Male holotype and male and female paratypes from Binkley Cave, Harrison Co., Indiana, 1.3 mi SSE of Corydon, collected 23 August 1998 by J. J. Lewis and T. P. Sollman (VMNH).

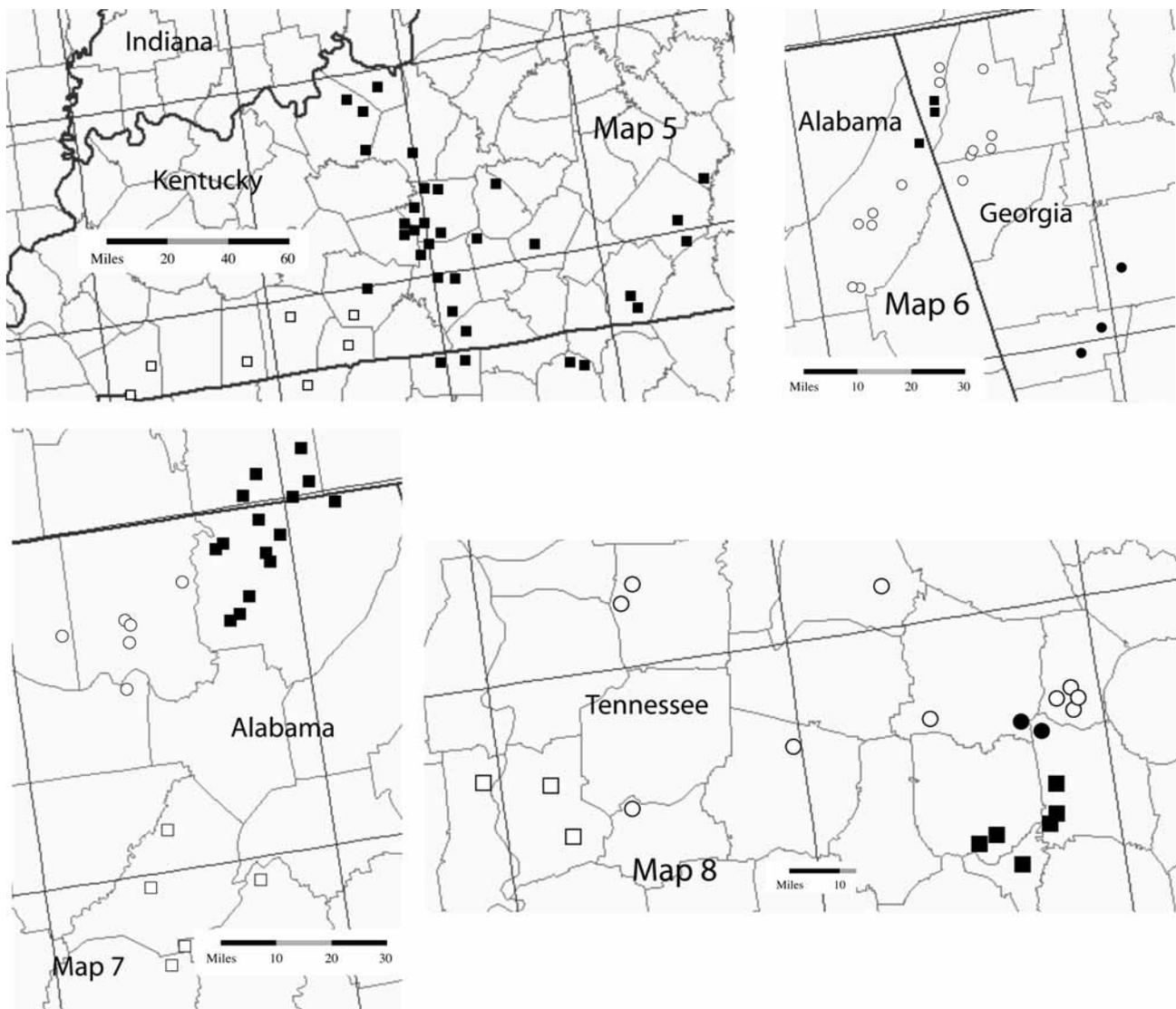
Notes: Through the kindness of J. J. Lewis, I examined specimens of this species from the type localities. I found that the material I examined was within the range of variation I accept for *Scoterpes copei*, which occurs extensively south of the Ohio River in Kentucky and Tennessee. Lewis (2000), in describing the species, focused his diagnosis on the form of the fimbriate branch of the gonopod, but I have found this very

complicated feature to be highly variable within *copei* populations. The Ohio River separates the two, but the karst regions of Indiana are continuous with the Western Pennyroyal karst plateau in Kentucky, and, as mentioned above in the notes on *S. copei*, specimens of that species from Breckinridge Co., Kentucky, just over the river from Indiana, closely resemble the Indiana specimens. But in view of the strong possibility that *S. copei* actually represents a complex of cryptic or difficult-to-separate species, I am not placing this name in the synonymy of that species without further data, perhaps derived from comparative DNA studies. There is a good chance that *S. sollmani* is a name that could be applied to the populations Causey called “*copei remotus* (see above).”

The species also occurs in BB Hole, 3.25 mi NE Leavenworth, Crawford Co., Indiana.

The southern Indiana karst region is interesting because the terrestrial troglobiotic fauna there has links to the karst regions of Kentucky, across the barrier of the Ohio River (*i.e.*, Hoffman and Lewis 1998; Lewis 2000, 2003, 2005; Shear, Lewis and Farfan, 2007).

Illustrations of *S. sollmani* are not provided here; they can be found in Lewis (2000).



Maps 5–8. Selected records of *Scoterpes* species. Map 5. Western Kentucky and north central Tennessee. *S. copei*, filled squares; *S. tombarri*, open squares. Map 6. Northeastern Alabama and northwestern Georgia. *S. austrinus*, open circles; *S. nudus*, filled circles; *S. willreevesi*, filled squares. Map 7. Northwestern Alabama and southcentral Tennessee. *S. stewartpecki*, filled squares; *S. syntheticus*, open squares; *S. alabama*, open circles. Map 8. Central Tennessee. *S. hesperus*, open squares; *S. jackdanieli*, filled squares; *S. musicarustica*, open circles; *S. tricornis*, filled circles.

Scoterpes tricorner, n. sp.

Figs. 68–71, Map 8

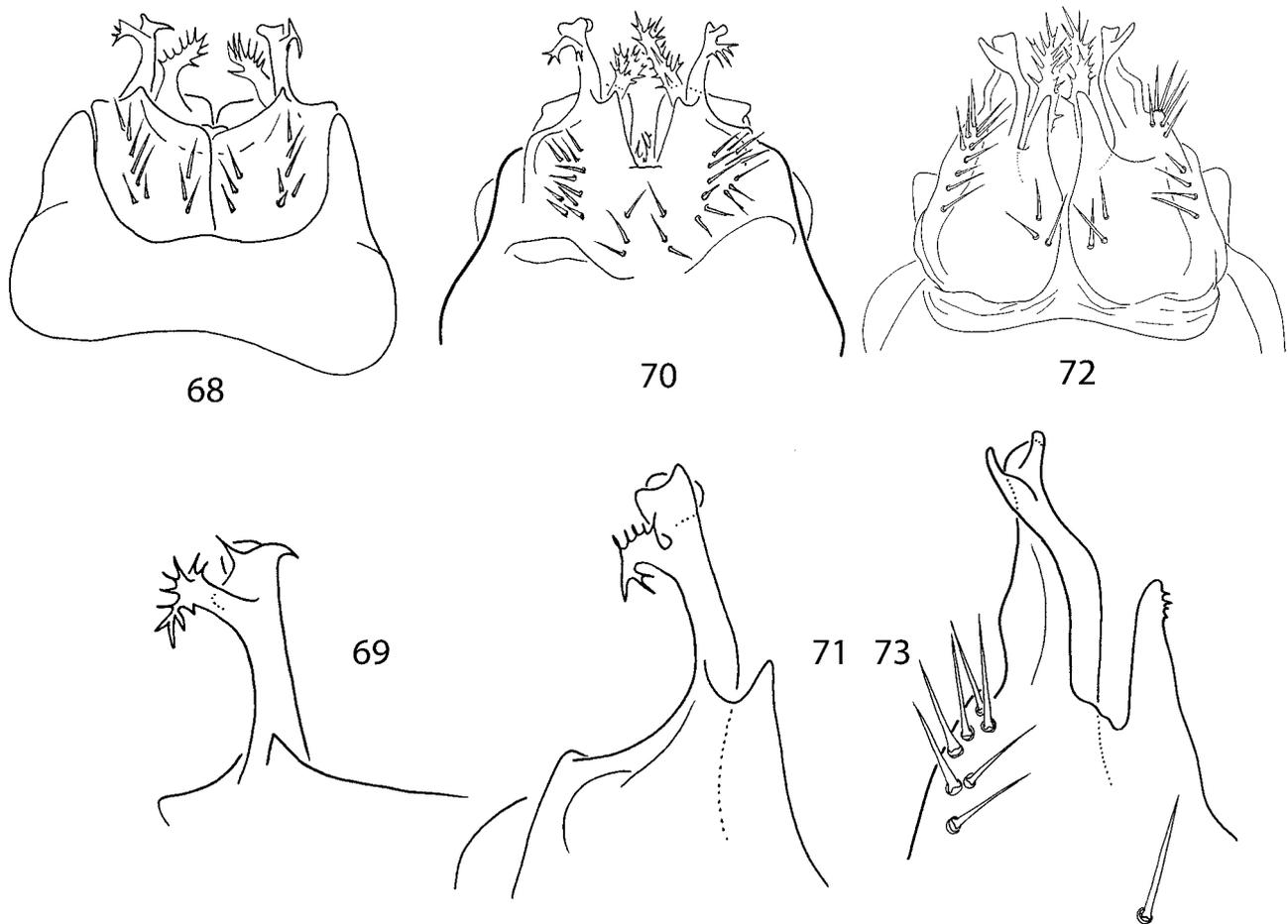
Types: Male holotype and female paratype (USNM) from Herring Cave, 1 mi NW of Lacassas, Rutherford Co., Tennessee, collected 14 October 1985 by A. Wynn and J. Jacobs.

Diagnosis: Similar to both *S. stewartpecki*, n. sp., and *S. musicarustica*, n. sp., and occurring on the southeast periphery of the range of the latter, this species is a member of the southern *copei* group. Distinct from *stewartpecki* in the small, triangular mesal angiocoxal branch, absent in that species, and from *musicarustica*, in which the mesal angiocoxal branch is two to three times as long as wide.

Etymology: The species epithet is a noun in apposition and refers to the narrow distribution of the species near the boundaries of Cannon, Rutherford and Coffee Counties, Tennessee.

Description of male from Herring Cave: Length, 9.0 mm, width, 0.85 mm. Nonsexual characters typical of genus. Gonopods (Figs. 68–71) with coxosternum completely fused; mesal setal group linear, three setae; distal group with 8–14 setae in elongate group nearly adjacent to mesal group. Mesal angiocoxal branch low or nearly absent; lateral branch with complex folding at posterior tip, anterior branch with several fine teeth. Colpocoxite of moderate size, fimbriate branch brushlike, not much subdivided. Ninth and tenth legs typical.

Female from Herring Cave: Length, 9.0 mm, width, 0.9 mm. Nonsexual characters as in male.



FIGURES 68–73. *Scoterpes* spp. males. 68–71. *S. tricorner*. 68, 69. Specimen from Burk Cave, Coffee Co., TN. 68. Gonopods, anterior view. 69. Angiocoxites, lateral view. 70, 71. Specimen from Herring Cave, Rutherford Co. TN. 70. Gonopods, anterior view. 71. Angiocoxites, lateral view. 73, 73. *S. musicarustica*. 72. Gonopods, anterior view. 73. Angiocoxites, lateral view.

Distribution (Map 8): All specimens FSCA; all records supported by at least one male. TENNESSEE: *Rutherford Co.* “Heron” Cave, near Lascassas, 5 January 1966, T. C. Barr. *Coffee Co.* Burk Cave, 16 July 1972, T. C. Barr.

Notes: *Scoterpes tricorner* from Burk Cave was labeled by Causey as “setosus” and from Herring Cave as “hostilis.” The “setosus” specimens have the median angiocoxal branch somewhat more reduced (Fig. 68) than in the Herring Cave specimens (Fig. 70), but the records are very close to each other and the specimens as a group quite distinctive, so I consider this to be one species. Further confusion surrounds the localities. “Heron” Cave, as the FSCA specimens are labeled, is undoubtedly a mistaken transcription for Herring Cave from a handwritten label; no “Heron” Cave is listed for Tennessee. There are two different Burk Caves in the immediate region (Barr 1961); one in Coffee Co., and the other in Rutherford Co. Since the collection from Burk Cave was made by Barr and labeled as Coffee Co., I assume that Barr, author of *Caves of Tennessee* (1961), knew the difference.

***Scoterpes musicarustica*, n. sp.**

Figs. 72, 73, Map 8

Types: Male holotype and male and female paratypes (VMNH) from Fisher Cave, Cannon Co., Tennessee, collected 1 July 1973 by S. B. Peck.

Diagnosis: Distinct from *S. tricorner*, n. sp., and *S. jackdanieli*, n. sp., in the much longer median colpocoxites and larger size of adults; the posterior branch of the lateral angiocoxite is simple, not branched.

Etymology: This species is endemic to the Central, or Nashville, Basin, and the species epithet, a noun in apposition, refers to the uniquely American music style (“country music”) that has its headquarters in the city of Nashville.

Description of male from Fisher Cave: Length, 11.2 mm, width, 0.9 mm. Nonsexual characters typical of genus. Gonopods (Figs. 72, 73) with coxae loosely fused to sternum; distal setal group linear and lateral, about 10 setae, proximal group mesal, 3 setae. Medial angiocoxite 3–4 times as long as basally broad, bluntly pointed; lateral angiocoxite with simple, anteriorly projecting branch, not folded. Ninth legs as usual for genus.

Female from Fisher Cave: Length, 12 mm, width 1.0 mm. Nonsexual characters as in male.

Distribution: See Map 8 for selected records. All specimens FSCA; all records supported by males. TENNESSEE: *Cannon Co.* Bob Williams Cave, 19 December 1956, T. C. Barr; Davenport Cave, 2.5 mi S of Woodbury, 22 August 1967, S. B. Peck; Espy Cave, 2 March 1957, T. C. Barr; Henpeck Mill Cave, 1.7 mi NE Woodbury, 22 August 1967, S. Peck, A. Fiske. *Davidson Co.* Mill Creek Cave, 12 June 1957, T. C. Barr. *Dickson Co.* Columbia Caverns, 5 February 1957, T. C. Barr; Jewel Cave, 30 October 1957, T. C. Barr. *Lewis Co.* DePriest Cave, 10 February 1957, T. C. Barr. *Maury Co.* Godwins Cave, 8 June 1957, T. C. Barr. *Rutherford Co.* Echo Cave, 27 November 1956, T. C. Barr.

Notes: Causey labeled specimens of what I consider to be this species with three different names. The Bob Williams Cave specimens (Cannon Co.) were labeled “barri cautus.” “Barri” was the name used by Causey for *Scoterpes ventus* Shear 1971 before that species was described, but she also used the name for a species from Kentucky unrelated to *S. ventus*, which I have formally named *tombarri* below. Espy Cave specimens (Cannon Co.) were labeled “cautus geminus,” and all Davidson, Dickson, Lewis, Maury and Rutherford Cos. specimens were labeled “barri incisus.” *Scoterpes ventus* is a species of the Cumberland Plateau, Sequatchie Valley, and Eastern Highland Rim. All records of *S. musicarustica* are from the Central, or Nashville, Basin; these are discrete physiographic provinces. The records of *musicarustica* outline a rough triangle, with its right angle in northern Lewis Co., extending east to an acute point in Cannon Co., thence northwest to northwestern Dickson Co. Any caves within this area likely support *musicarustica* populations.

The two caves known to have populations of *S. tricorner*, n. sp., are just west of the several Cannon Co. records of *musicarustica*.

***Scoterpes hesperus* n. sp.**

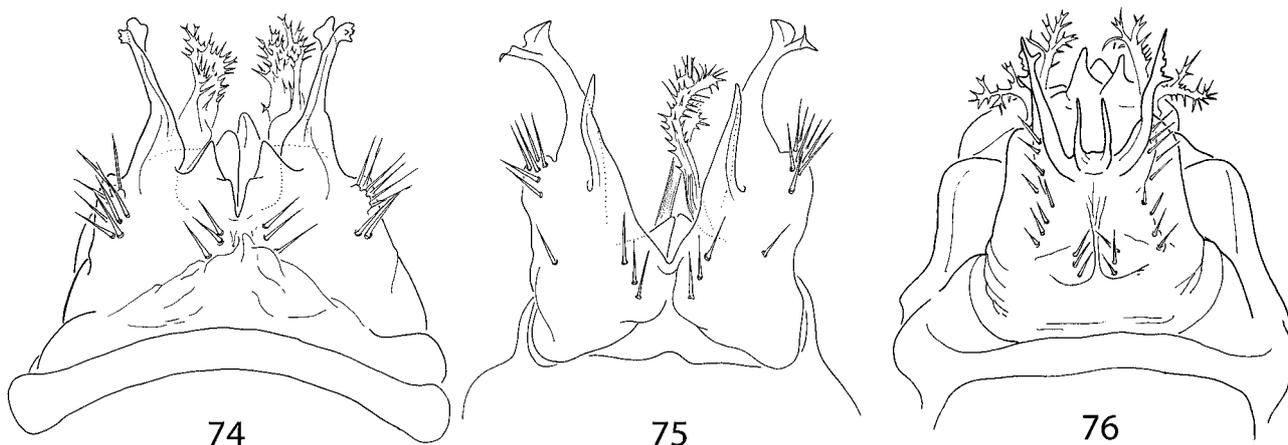
Fig. 74, Map 8

Types: Male holotype and female paratype (NCSM) from Jaybird Hollow Cave, Perry Co., Tennessee, collected 18 August 1971, by W. Henne.

Diagnosis: Most similar to *S. musicarustica*, n. sp., but distinct in the much narrower lateral angiocoxites and the triangular median angiocoxites.

Etymology: The species epithet is a noun in apposition, the Latin name of the evening star, but often used to refer to the west in general; this species is the most westerly occurring of all *Scoterpes*.

Description of male from Jaybird Hollow Cave: Length, 11.2 mm, width, 0.9 mm. Nonsexual characters typical of genus. Gonopods (Fig. 74) with coxae loosely fused to sternum; distal setal group clumped, lateral, about 8 setae, proximal group mesal, 3 setae. Medial angiocoxite broad basally, subtriangular, bluntly pointed; lateral angiocoxite not folded apically, with anteriorly projecting branch tipped with small nodules, seen in anterior view longer, thinner than in *S. musicarustica*. Colpocoxite fimbriate branches semilamillate, strongly fringed apically. Ninth legs as usual for genus.



FIGURES 74–76. *Scoterpes* spp. males, anterior view of gonopods. 74. *S. hesperus*. 75. *S. tombarri*. 76. *S. blountensis*.

Female from Jaybird Hollow Cave: Length, 12.0 mm, width 1.6 mm. Nonsexual characters as in male.

Distribution (Map 8): All localities with at least one male; all specimens NCSM. TENNESSEE: *Decatur Co.* Baugus Cave, 7 December 1971, W. Henne. *Perry Co.* No further locality, 11 August 1971, W. Henne.

Notes: This species links the closely related species *S. tricorner* and *S. musicarustica*; the three species form a fairly compact “Southern Copei Group,” the name coming from their obvious closeness to *S. copei* of Kentucky and northern middle Tennessee. It is notable that the Baugus Cave record of this species is the only record of *Scoterpes* west of the Tennessee River; the river does not mark the exact westernmost extension of the karst of the Western Highland Rim, but cuts its valley just within the Rim province. Baugus Cave is in a small tributary valley of the Tennessee River. *Scoterpes hesperus* is also found in Perry Co., east of the river, suggesting either that the river is no barrier to these species, or that the western bank record may be due to a change in the river’s course after the species’ dispersal.

***Scoterpes tombarri*, n. sp.**

Figs. 75, Map 5

Types: Male holotype and male and female paratypes (FSCA) from Plano Saltpetre Cave, 20 mi S of Bowling Green, Warren Co., Kentucky, collected 18 June 1973 by S. B. Peck.

Diagnosis: Most similar to *S. hesperus*, n. sp., but differing in the longer, more bladelike median angiocoxites and the slightly branched anterior processes of the lateral angiocoxites; the fimbriate branches of the colopocoxites generally appear smaller, but this character is variable.

Etymology: Named for Thomas C. Barr, dean of American speleobiologists, professor emeritus at the University of Kentucky, and author of *Caves of Tennessee*.

Description of male from Plano Saltpetre Cave: Length, 10.0 mm, width, 0.95 mm. Nonsexual characters typical of genus. Gonopods (Fig. 75) with coxae loosely fused to sternum; distal setal group clumped on obvious lateral shoulder, about 6 or 7 setae, single isolated seta near base; proximal group mesal, 3 setae. Medial angiocoxite narrow, bladelike, acute; lateral angiocoxite slightly folded apically, with anteriorly projecting branch bearing several small, acute subbranches, seen in anterior view longer, thinner than in *S. musicarustica*. Colpocoxite fimbriate branches linear, strongly fringed apically and along length. Ninth legs as usual for genus.

Female from Plano Saltpetre Cave: Length, 11.0 mm, width 1.0 mm. Nonsexual characters as in male.

Distribution: See Map 5 for selected records. All specimens FSCA; all records supported by at least one male. KENTUCKY: *Logan Co.* Collier Cave, 25 June 1957, T. C. Barr; Cooks Cave, 25 June 1957, T. C. Barr; Mud River Cave, 3 August 1967, collector unknown. *Simpson Co.* Hoy Cave, 2 mi N of Franklin, 2 January 1958, T. C. Barr. *Todd Co.*: Glover Cave, 9 June 1957, T. C. Barr. *Trigg Co.* Hardy Cave, 3 mi SSW Caledonia, 12 August 1965, T. C. Barr, J. Holsinger. *Warren Co.* Horseshoe Cave, 17 August 1963, T. C. Barr. TENNESSEE: *Robertson Co.* Buzzard Cave, 16 August 1957, T. C. Barr. *Stewart Co.* Tobaccoport Saltpetre Cave, 16 July 1957, T. C. Barr.

Notes: Yet another species of the Copei Group, *Scoterpes tombarri* was assigned the name "barri" on labels by Nell Causey, though later she relabeled some specimens as "ventus barri." The region of Kentucky where this species is found is the western part of the Cumberland Plateau (*sensu lato*) referred to in Tennessee as the Western Highland Rim; in Kentucky it is called the Pennyroyal Plateau, "Pennyrile (by local inhabitants)," or more formally the Mississippian Plateau. The distribution of *S. tombarri* is separated from that of *S. copei* on the east by the Barren River, and from that of *S. musicarustica* on the south by the Cumberland River, although additional collecting will be required to definitively establish that these rivers are actually barriers.

It is interesting that this species and a population of *S. copei* were examined using electrophoretic techniques (Laing, Carmody & Peck 1976). *Scoterpes tombarri* was sampled from State Trooper Cave, Bowling Green, Warren Co., Kentucky, and *S. copei* from White's Cave, Mammoth Cave National Park, Hart Co., Kentucky. The two caves are separated by about 43 km and as stated above, by the Barren River. At the time, Laing et al (1976) assumed that both populations represented *S. copei*. Unfortunately no voucher specimens were kept, and I have seen no additional specimens from State Trooper Cave, but I am quite sure that the geography of the situation supports the hypothesis that *S. tombarri* would be found in that cave. The results of the electrophoretic study showed that of the 10 loci that could be measured, six had become fixed for different alleles in the two populations, and that at two polymorphic loci, the two populations possessed completely different alleles. The authors concluded the two populations represented two different species (Rogers coefficient of 0.217), and that conclusion is supported here by gonopod morphology.

***Scoterpes blountensis*, n. sp.**

Fig. 76

Types: Male holotype and male and female paratypes (VMNH) from Gregory's Cave, Cade's Cove, Great Smoky Mountains National Park, Blount Co., Tennessee, collected 2 November 1998 by W. Reeves.

Diagnosis: *Scoterpes blountensis* cannot be confused with any other *Scoterpes* species because of its unique gonopods and its isolated distribution, more than 100 miles to the east of the nearest record of *S. ventus*, with no reliable *Scoterpes* records known from the intervening region.

Etymology: This species appears to be limited to Blount Co., Tennessee, adjacent to and within the Great Smoky Mountains National Park (GSMNP).

Male from Gregory's Cave: Length, 12.0 mm, width 1.0 mm. Nonsexual characters typical of genus. Gonopods (Figs.76) small relative to size of animal, coxae loosely fused to sternum; lateral setal group linear, 9–11 setae; mesal group of 3 setae; mesal angiocoxites small, thin, acute, bases close together, forming a U-shaped figure; lateral angiocoxites unbranched, with posterior irregular lamellate extensions, not folded; colpocoxites large, subglobular, fimbriate branch strongly dendritic. Legpair 9 typical, but in many specimens with 1 or 2 vestigial distal articles, obvious coxal gland.

Female from Gregory's Cave: Length, 12.5 mm, width 1.0 mm. Nonsexual characters as in male.

Distribution: All records supported by males. TENNESSEE: *Blount Co.* Bull Cave, Cade's Cove, GSMNP, 2 August 2000, W. Reeves, M. Hedin (VMNH); Calf Cave #1, Rich Mountain, GSMNP, 15 September 1999, W. Reeves (VMNH); Gregory's Cave, GSMNP, 5, 23 August 1965, S. B. Peck (FSCA), 2 April 1958, A. Stupka, V. Gilbert (FSCA), 13 June 2000, J. Mays (VMNH); Rich Cave near Townsend, GSMNP, 10 April 1958, S. B. Peck (FSCA), White Oak Blowhole Cave, 12 August 1999, W. Reeves (VMNH), Tuckaleechee Caverns, Townsend, 18 April 1959, 25 August 1960, T. C. Barr (FSCA).

Notes: While distantly related to the Copei Group, this species' occurrence so far from the nearest other species of the group is difficult to explain. How did *Scoterpes blountensis* come to be so distant from all other *Scoterpes* species? The Cade's Cove region is one of a few small karst windows in the western flanks of the Unaka Mountains, which includes the deep, broad valleys of Cade's Cove itself, White Oak Sink, and Tuckaleechee Cove. The limestone is exposed along the Unaka thrust fault. Other caves occur in the flanks of Rich Mountain just to the west of Tuckaleechee Cove in the same exposures of limestone (Barr 1961). Another small karst window, evidently not explored biologically as yet, is located near Cosby, a few miles northeast, in Sevier Co. Northwestern Blount Co. and the adjoining regions of Sevier and Monroe Cos., as well as the GSMNP to the south have no karst, and though karst does occur in these counties as they extend into the Ridge and Valley province to the west, no *Scoterpes* millipeds have been collected there, only species of the distantly related *Pseudotremia* (Cleidogonidae).

***Scoterpes stewartpecki*, n. sp.**

Figs. 77, 78, Map 7

Types: Male holotype and male and female paratypes (FSCA) from Jess Elliott Cave, 3 mi. E of Hytop, Jackson Co., Alabama, collected 3 September 1965 by S. B. Peck.

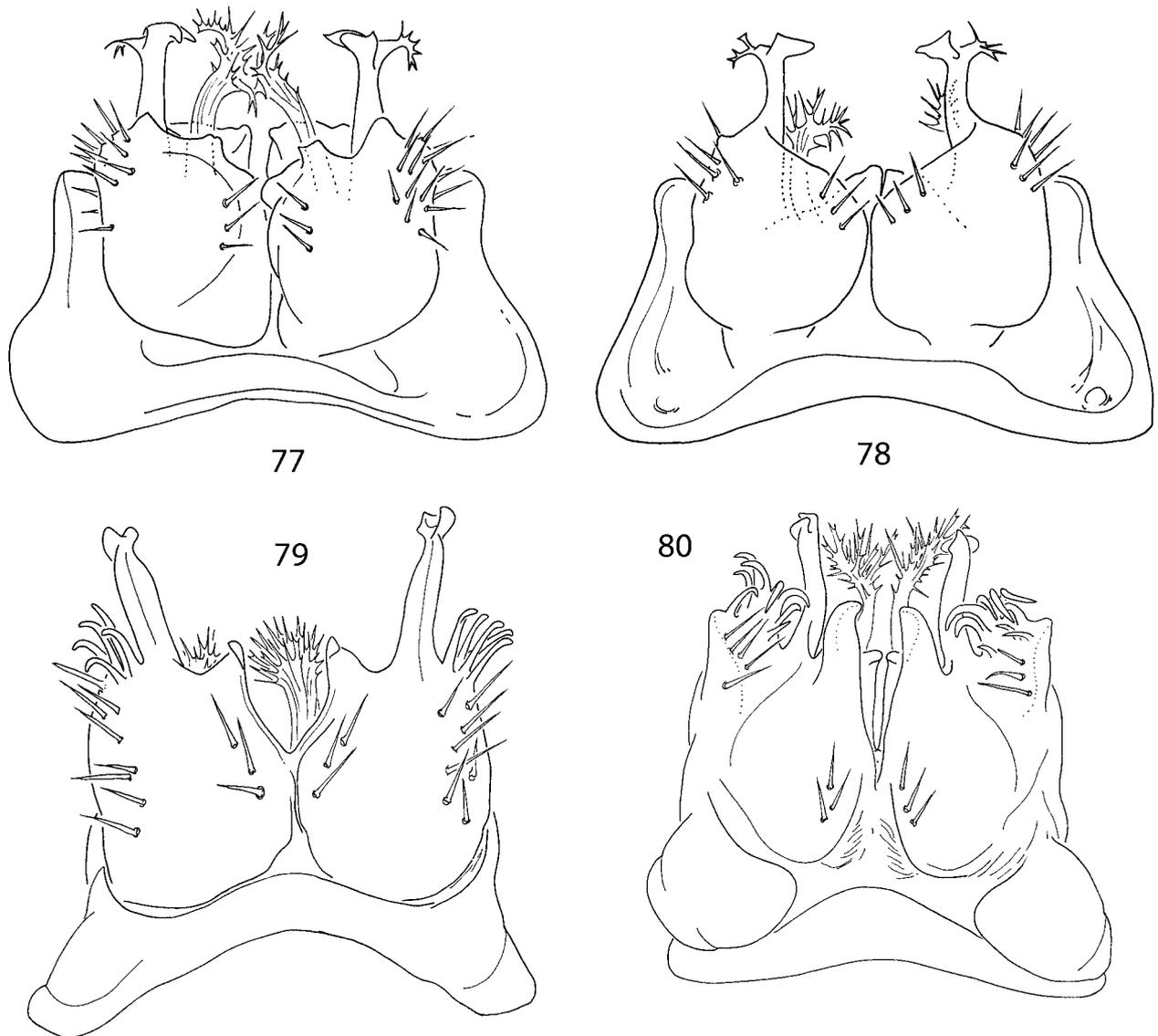
Diagnosis: Closest to *S. tricorner*, but distinct in the proportionally larger lateral angiocoxites and the nearly complete reduction of the median angiocoxites.

Etymology: Named for the collector, Stewart B. Peck, Carleton University, Ottawa, a leading student of the biogeography and evolution of troglobionts and collector of most of the specimens of this species.

Description of male from Jess Elliott Cave, Alabama: Length, 10 mm, width 0.96 mm. Nonsexual characters typical of genus. Gonopods (Figs. 77, 78) with coxae distinct from sternum; mesal setal group linear,

three setae; distal group with 10–13 setae in compact group nearly well separated from mesal group. Mesal angiocoxal branch nearly or obviously absent; lateral branch with complex folding at posterior tip, anterior branch relatively long, with several fine teeth. Colpocoxite of large to moderate size, fimbriate branch brush-like, finely subdivided. Ninth and tenth legs typical.

Description of female from Jess Elliott Cave: Length, 10 mm, width 1.0 mm. Nonsexual characters as in male.



FIGURES 77–80. *Scoterpes* spp. males, anterior view of gonopods. 77, 78. *S. stewartpecki*. 77. Specimen from Eagle Cave, Jackson Co., AL. 78. Specimen from Salt River Cave, Franklin Co., TN. 79, 80. *S. ventus*. 79. Specimen from Allgood School Cave, Putnam Co., TN. 80. Specimen from Turkeyscratch Cave, Warren Co., TN.

Distribution: See Map 7 for selected records. All records supported by male specimens; all FSCA unless otherwise noted. ALABAMA: *Jackson Co.* Blowing Cave (Larkin Cave), off Larkin Fork, 5 September 1959, T. C. Barr; (unnamed) Cave, section 36, T25S/R5E, Mud Creek quadrangle, 27 November 1964, R. Brandon (VMNH); Crossing Cave, 1 mi N of Paint Rock, 5–13 August 1967, S. B. Peck; Driftwood Cave, 9 mi N of

Scottsboro, 9 November 1965, S. B. Peck; Cagle Cave, 4 mi NNW of Princeton, 20 August 1971, S. B. Peck; Hambrick Cave, 6 June 1970, W. Torode (NCSM); Horseshoe Cave, 2 mi E of Bridgeport, 3 August 1967, S. P. Peck, A. Fiske; Montague Cave, 5 November 1960, M. V. Kroeger; Pigent Russell Cave, Russell Cave National Monument, 17 August 1967, S. B. Peck; Rainbow Cave, 7 mi W of Stevenson, 16 August 1967, S. B. Peck; Russell Cave National Monument, 10 August 1960, W. B. Jones; Sheldon's Cave, 1 mi N of Scottsboro, 25 January 1967, S. B. Peck; Talley Ditch Cave, 5 mi NNW of Stevenson, 28 July 1957, T. C. Barr; 1 August 1967, S. B. Peck, A. Fiske; Tate Cave 3 mi E of Hytop, 3 September 1965, S. B. Peck; Tumbling Rock Cave, 27 May 1956, T. C. Barr; 14 March 1965, S. B. Peck. TENNESSEE: *Franklin Co.* Crownover Cave, undated, T. C. Barr; Lost Cove Cave, 13 April 1958, S. Lazell; Round Mountain Cave, 4 mi. NE of Estill (AL), 30 August 1967, S. B. Peck, A. Fiske; Salt River Cave, 27 November 1964, R. Brandon (VMNH).

Notes: Causey labeled this species "lazelli." Caves in Franklin Co, Tennessee, also support populations of *S. ventus*, but they are separated from those caves with *S. stewartpecki* by a drainage divide: the northern part of Franklin Co. is in the Elk River drainage, while the southern part (along the Alabama border), where *S. stewartpecki* is found, is in the drainage of Crow Creek and the Paint Rock River; both are tributaries of the Tennessee River. Peck (1984), in a study of the *Ptomophagus* beetle species of the region, has mapped most of the Alabama caves with *S. stewartpecki* in detail. These maps suggest that the species will eventually be collected in Madison and Marshall counties, Alabama, and in Marion County, Tennessee.

***Scoterpes ventus* Shear**

Figs. 79, 80, Map 4

Scoterpes ventus Shear 1972, p. 279, 280. Hoffman, 2000, p. 235.

Types: Male holotype and paratype from Blowing Cave, Sequatchie, Marion Co, Tennessee (MCZ), examined in 1971.

Etymology: The species name, a noun in apposition, is Latin for "wind" and refers to Blowing Cave, the type locality.

Diagnosis: Distinct from every other species of *Scoterpes* in the evident transformation of some of the lateral coxal setae of the gonopod into unsocketed crochets projecting from the distal coxal angles.

Description of male from Blowing Cave: Length, 10 mm, width 1.0 mm. Nonsexual characters as usual for genus. Legs 3–7 distinctly encrassate. Gonopods (Figs. 79, 80) with coxae fused to sternum; mesal setal group linear, three setae; distal group with 3–8 socketed setae proximal, 5–7 distal setae fused to coxal, sockets lacking, curved, hooklike. Mesal angiocoxal branch broadly triangular; lateral branch with slight folding at blunt posterior tip, anterior branch absent. Colpocoxite of large to moderate size, fimbriate branch brush-like, finely subdivided. Ninth and tenth legs typical.

Female from Cumberland Caverns: Length, 10.2 mm, width 10. Mm. Nonsexual characters as in male.

Distribution: See Map 4 for selected records. All records supported by males, all specimens FSCA unless noted. TENNESSEE: *Cannon Co.* Henpeck Mill Cave, 1.7 mi NE of Woodbury, 8 August 1967, S. B. Peck. *DeKalb Co.* Cripp's Mill Cave, 27 December 1956, T. C. Barr; Indian Grave Point Cave, 27 December 1956, T. C. Barr. *Franklin Co.* Caney Hollow Cave, 9 May 1959, T. C. Barr; Dry Cave, 10 January 1958, S. Lazell; 3 December 1960, H. Steeves; Thumping Dick #1 Cave, Suwannee, 22 March 1958, S. Lazell; Wet Cave, 20 July 1958, T. C. Barr. *Grundy Co.* Boyd Hollow Cave, 8 June 1958, T. C. Barr; Crystal Cave, 13 October 1956, 18 May 1957, T. C. Barr; Tom Campbell Cave, 14 April, 1958, T. C. Barr; Trussell Cave, 18 April 1958, T. C. Barr; Wonder Cave, 1.5 mi SE of Mountain View, 30 June 1937, collector unknown (FMNH); 18 May 1957, 28 December 1965, T. C. Barr; 26 June 1957, L. Hubricht. *Jackson Co.* Carter Cave, 20 April 1957, T.

C. Barr. *Overton Co.* Falling Springs Cave, 31 May 1958, T. C. Barr. *Putnam Co.* Allgood School Cave, 11 December 1960, T. C. Barr. *Smith Co.* John Fisher Cave, 18 July 1957, T. C. Barr; Piper Cave, 5 January 1957, T. C. Barr. *Van Buren Co.* McElroy Cave, 1.5 mi NE of Bone Cave Post Office, 23 June 1957, L. Hubricht (VMNH); Rice Cave, 18 March 1961, T. C. Barr. *Warren Co.* Cumberland Caverns, 13 March 1959, T. C. Barr; Higgenbotham Cave, 8 mi SE of McMinnville, 23 June 1957, L. Hubricht (VMNH); Hobbs Cave 8 June 1958, T. C. Barr; Hubbard Cave, 11 October 1956, T. C. Barr; John Green Cave, 31 May 1956, T. C. Barr; Turkeyscratch Cave, 5 September 1981, T. C. Barr (VMNH). *White Co.* Dairyhouse Cave, 15 October 1958, T. C. Barr; Lost Creek Cave, 30 August 1959, T. C. Barr; Moore Cave, 17 January, 20 June 1958, T. C. Barr; Sparkman Cave, 9 November 1958.

Notes: Causey labeled specimens of this species “barri barri” or “barri cautus” while one collection (Falling Springs Cave, Overton Co.) was labeled “similis.” Records for this species extend north to south virtually the entire width of Tennessee, and fall mostly in the Cumberland Plateau physiographic region, but the most westerly ones are in the Highland Rim region. The Sequatchie Valley bisects the southern part of the plateau; all records are west of the Sequatchie River, including the DeKalb County records, which are actually in the valley. With the exception of *S. blountensis* isolated far to the east, and a single, likely spurious, record of *S. copei* from Meigs Co., the distribution of *Scoterpes* as a genus in Tennessee stops at the Sequatchie River. Variation in the gonopods of *S. ventus* is seemingly chaotic; two extremes are shown. Given the broad occurrence of the species, it would not be a surprise to find that it actually consists of two or more cryptospecies.

The Austrinus Group

Scoterpes austrinus Loomis

Fig. 81, Map 6

Scoterpes austrinus Loomis 1943, p. 386. Shear, 1972, p. 279. Hoffman, 2000, p. 235.

Type: Male holotype from Manitou Cave, 1 mi. S of Ft. Payne, DeKalb Co., Alabama (MCZ), examined in 1971.

Diagnosis: The unfolded, winglike lateral angiocoxites are similar only to those of *S. nudus*, which differs in having a shorter, thinner mesal coxite and microteeth on the lateral angiocoxite.

Etymology: The species name refers to the southerly occurrence of this species compared originally to that of *S. copei*. And indeed, only *S. nudus* and *S. syntheticus* have been discovered further south.

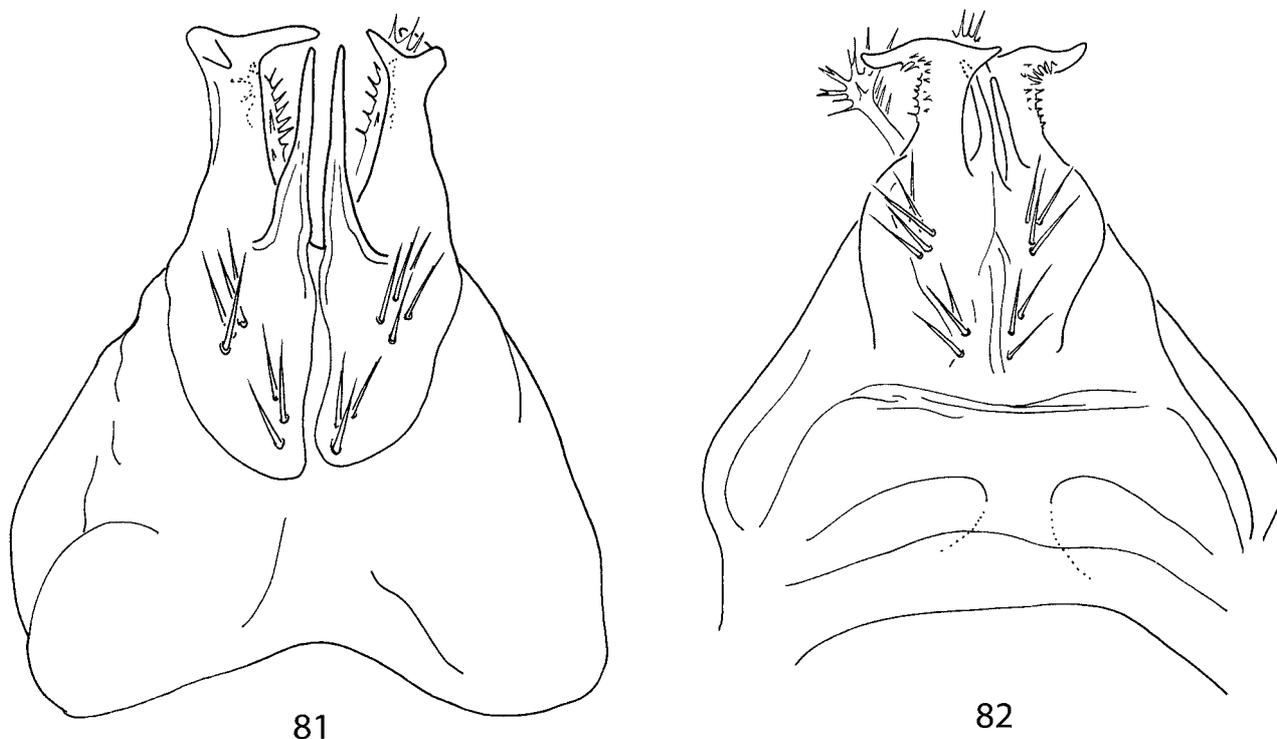
Description of male from Manitou Cave, Alabama: Length, 9.5 mm, width 0.90 mm. Nonsexual characters as described for genus. Gonopods (Fig. 81) with completely fused coxosternum; angiocoxal setal groups well-separated, distal group of 4–5 setae. Mesal angiocoxal branch nearly as long as lateral, smoothly acuminate. Lateral branch lamellate, T-shaped, lacking microteeth. Fimbriate branch moderately prominent. Ninth legs typical of genus.

Female from Manitou Cave, Alabama: Length, 9.8 mm, width 0.92 mm. Nonsexual characters as in male.

Distribution: See Map 6 for selected records. All specimens FSCA. The following records are supported by at least one male specimen. ALABAMA: *DeKalb Co.* Bartlett Cave, 1 mi SE Collinsville, 12 August 1958, J. Danielson, same locality, 27 August 1965, S. & J. Peck; Cherokee Cave, 4.5 mi NE Ft. Payne, 20 July 1965, S. Peck; Fort Payne Cave, 10 June 1967, “Jones & Daniel;” Kelly Girls Cave, 1 mi SE Colliersville, 25 August 1965, S. & J. Peck; Killian Cave, sec. 16, T8S, R8E, 6 December 1958, B. Killian *et al.*; Manitou Cave, Ft. Payne, 28 August 1965, S. Peck; Stankey Cave, 8 mi NE Ft. Payne, 16 July 1967, S. Peck, A. Fiske; Stanley-Carden Cave, Ft. Payne, 3 September 1967, J. & M. Cooper; Talley Cave, 30 July 1965, S. & J. Peck. GEORGIA: *Chatooga Co.* Blowing Spring Cave, 2.5 mi E Cloudland, 11 June 1967, J. Holsinger. *Dade Co.*

Johnson Creek Cave, 4.5 mi NE Rising Fawn, 19 June 1967, J. Holsinger; Morrison Cave, 2 mi E Trenton, 13 July 1967, S. Peck; Sittons Cave, 20 March 1959, T. Barr, 30 July 1967, S. Peck. *Walker Co.*: Bible Spring Cave, 2 mi NE Lookout, 11 June 1967, J. Holsinger, 12 July 1967, S. Peck; Harrisburg Cave, 4 mi W Centerpost, 12 August 1967, S. Peck; Horseshoe Cave, 4 mi SW Chickamauga, 10 June 1967, J. Holsinger *et al.*; Mountain Cove Cave, 1.5 mi E Lookout, 11 June 1967, J. Holsinger *et al.*; Pettijohn Cave, 5 mi SW Lafayette, 10 June 1967, J. Holsinger, 21 June 1967, S. Peck.

Notes: One of the specimens from Manitou Cave had an anomalously unreduced ninth legpair. *Scoterpes austrinus* occurs in the Lookout Mountain and Pigeon Mountain karst areas. The Dade County localities are very narrowly separated from those for *S. willreevesi*, which is found in the Fox Mountain karst. More exploration of caves in Sand Mountain is needed to clarify which species of *Scoterpes*, if any, occurs there. *Scoterpes austrinus* is not related to *S. willreevesi*, but closely related to *S. nudus* (see immediately below) and the two have very similar, but distinct, gonopods. The Oostanaula and Etoway Rivers, branches of the Coosa River, separate the ranges of the two species; *austrinus* is not found south of the Coosa in Alabama, or of the Chatooga River, another Coosa tributary, in Georgia. Karst occurs in the intervening region, but there are no *Scoterpes* records available.



FIGURES 81, 82. *Scoterpes* spp. males, anterior view of gonopods. 81. *S. austrinus*. 82. *S. nudus*.

***Scoterpes nudus* Chamberlin, new status**

Figs. 82, Map 6

Scoterpes austrinus nudus Chamberlin 1946, p. 52. Shear, 1972, p. 279. Hoffman 2000, p. 235.

Types: Male holotype from Saltpetre Cave [Kingston Saltpetre Cave], 4 mi S Kingston, Bartow Co., Georgia; whereabouts unknown.

Diagnosis: The gonopods of *S. nudus* are very similar to those of *S. austrinus*, but differ in the thinner, shorter mesal angiocoxites and the presence of fine cuticular teeth on the lateral angiocoxites.

Etymology: The name refers to Chamberlin's (1946) observation of the lack of a claw on the ninth leg of the holotype. The presence of a claw on Loomis' (1943) illustration of the ninth leg of *austrinus* represents an anomalous specimen; the claw is generally absent in both species.

Description of male from Kingston Saltpetre Cave: Length, 10.2 mm, width, 0.98 mm. Nonsexual characters as described for genus. Gonopods (Fig. 82) with completely fused coxosternum; angiocoxal setal groups well-separated, distal group of 4–5 setae. Mesal angiocoxal branch obviously shorter than lateral, thin and smoothly acuminate. Lateral branch lamellate, T-shaped, with prominent microteeth laterally. Fimbriate branch moderately prominent. Ninth legs typical of genus.

Female from Kingston Saltpetere Cave: Length, 11.0 mm, width 1.0 mm. Nonsexual characters as in male.

Distribution (Map 6): All specimens FSCA. Each of the records below is supported by at least one male specimen. GEORGIA: *Bartow Co.* Kingston Saltpetre Cave, 4 mi S Kingston, 29 December 1955, T. C. Barr; 13 June 1967, J. Holsinger *et al.*. *Polk Co.* Deaton's Cave, 29 September 1967, "Iles;" River Cave, 20 February 1954, W. H. Gross; White River Cave, 3 mi. NE Rockmart, 13 June 1967, J. Holsinger.

Notes: This species was originally described by Chamberlin (1946) as a subspecies of *S. austrinus*, based only on the lack of a claw on the ninth leg in *nudus*. This is a trivial character, since the claw is missing in most specimens of male *Scoterpes*; Loomis' 1943 illustration happened to be of a specimen of *austrinus* that had a vestigial claw. In 1972, I speculated that the subspecific designation might not be valid; Hoffman (2000) then placed *nudus* in the synonymy of *austrinus*, citing my mention of a specimen of typical *austrinus* from White River Cave in Floyd County. Unfortunately we were both wrong; White River Cave is actually in Bartow County, but in any case is south of the Oostanula River and therefore geographically proves nothing about the identity of *nudus*. Distributional data aside from type localities was not available in 1971 or in 2000. I stated that I had not compared my specimens to the type of *nudus*, and did not formalize the synonymy, but my illustrations (1972: figs. 518–520) clearly depict *nudus* because of the microteeth on the lateral or ectal coxite; that distinction is made for the first time here. The two species are obviously very close, and subspecies designation for *nudus* may still prove to be correct if intermediate populations are found between the compact distributions now known for the two nominal species. At present, since both populations are distinct morphologically and geographically, regarding them both as full species best fits the evidence. Clearly Chamberlin (1946) did not have a modern view of the category subspecies, which at the time he wrote was still inextricably confused with the concept of "variety." Solving the status of the two populations would be a nice little problem for a local naturalist. For additional information, see the Notes on *S. austrinus*, immediately above.

The Alabama Group

Scoterpes alabama, n. sp.

Fig. 83, Map 6

Types: Male holotype and male and female paratypes (VMNH) from Shelta Cave, Huntsville, Madison Co., Alabama, collected 25 September 1966 by L. Hubricht.

Diagnosis: The gonopods of this species can be confused with no other; both angiocoxite branches are long and linear, and the colopocoxite, instead of being fimbriate as it is in all other species, is in the form of a long, prominent, apically serrate lamella.

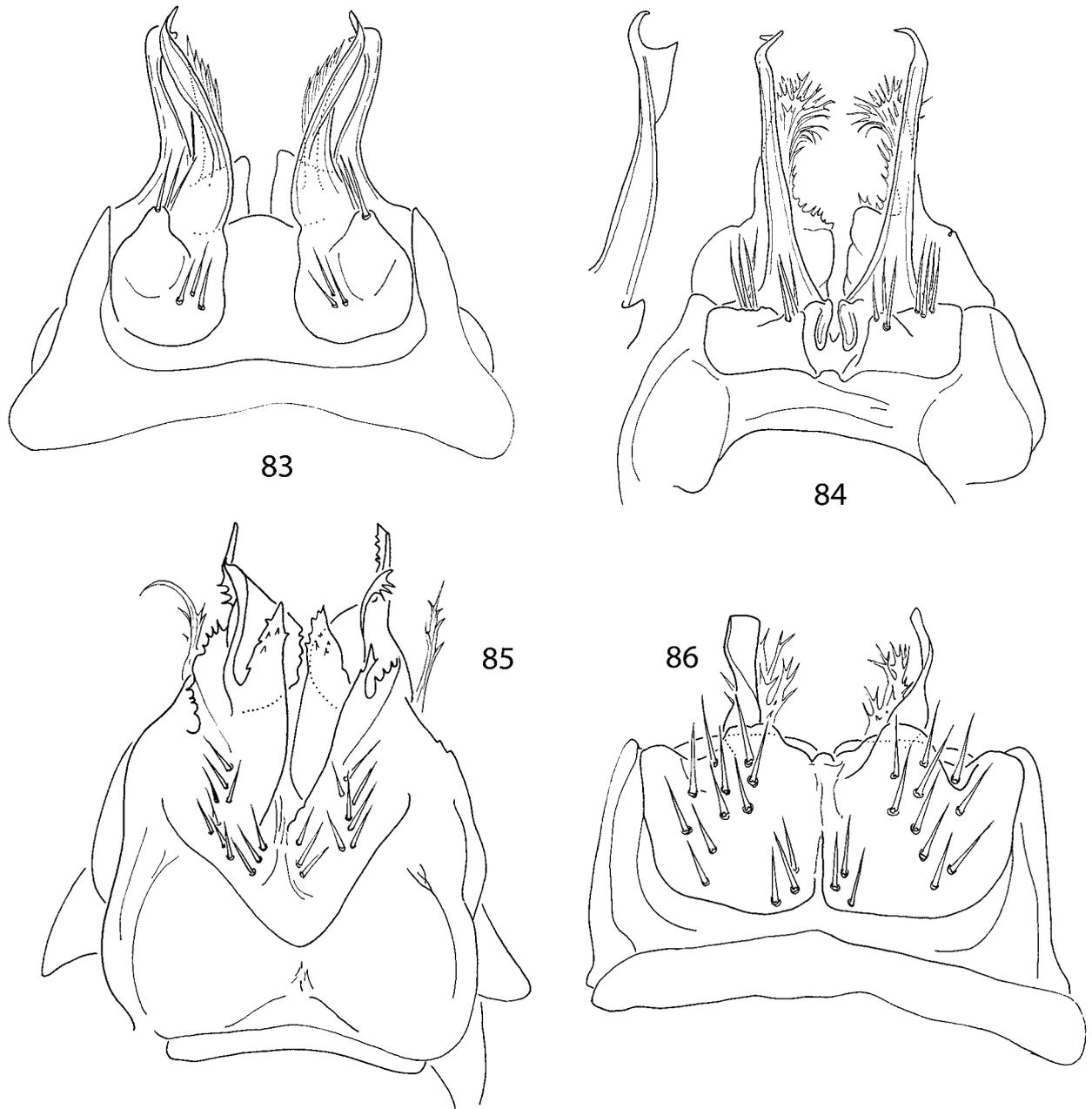
Etymology: The species epithet, a noun in apposition, refers to the state of Alabama.

Description of male from Shelta Cave, Alabama: Length, 7.5 mm, width, 0.7 mm. Nonsexual characters as described for genus. Gonopods (Fig. 83) with completely fused coxosternum; angiocoxal setal groups

well-separated, distal group of 3 setae. Mesal angiocoxal branch longer or equal to lateral, flat, bladeliike, slightly twisted, acuminate. Lateral branch more cylindrical, slightly decurved or knobbed apically. Fimbriate branch prominent, thin, lamellate, seemingly made of fused linear fibers, marginally and apically serrate. Ninth legs typical of genus.

Female from Shelta Cave: Length, 7.8 mm, width 0.75 mm. Nonsexual characters as in male.

Distribution: See Map 6 for selected records. All records supported by at least one male specimen; all FSCA unless noted otherwise. ALABAMA: *Madison Co.* Burwell Cave, 22 August 1965, S. Peck; Byrd Spring Cave, 21 June 1967; Oakwood Cave, 13, 21 March 1966, S. Peck; Shelta Cave, numerous collections from 1965–1969 by several collectors (some VMNH); Alladin Cave, numerous collections from 1951–1965 by several collectors (some VMNH). *Morgan Co.* Talucah Cave, 16 July 1965, S. Peck. *Limestone Co.* Indian Cave, 11 July 1971, W. Varnedoe, 19 August 1965, S. Peck.



FIGURES 83–86. *Scoterpes* spp. males, anterior view of gonopods. 83. *S. alabama*. 84. *S. jackdanieli*. 85. *S. willreevesi*. 86. *S. syntheticus*.

Notes: Madison, Morgan and Limestone Cos. are partially or wholly in the Highland Rim physiographic province of Alabama, while Jackson Co. is entirely in the Cumberland Plateau province. Shelta Cave, the type locality, is located directly beneath the National Speleological Society national headquarters in Huntsville, Alabama. Approximately 2500 feet (700 m) long, Shelta Cave serves as the NSS laboratory for cave biology. The cave has one of the most diverse underground faunas in the world (Culver and Sket 2000), with twelve species of troglobionts (terrestrial) and twelve species of stygobionts (aquatic). That the community was dependent for energy input on bat guano was tragically demonstrated when a “bat-unfriendly” gate was placed over the entrance; with the depletion of the bat population, the populations of cave-adapted invertebrate species also declined significantly and at least one species may have become locally extinct (Culver and Sket 200). Remarkably, the Shelta Cave *Scoterpes* has gone unnamed and undescribed until now. Causey had recognized this species, but I found it labeled under three different names in her collection: “facundus,” “honoratus,” and “haackeri;” these labels may have represented new thoughts about the names rather than implying the presence of three species. In my opinion only a single species, with some variability, is present.

Scoterpes jackdanieli, n. sp.

Fig. 84, Map 8

Types: Male holotype, male, female paratypes from Motlow Cave, Lynchburg, Moore Co. Tennessee (FSCA), collected 2 January 1960 by T. C. Barr.

Diagnosis: Similar to *S. alabama* n. sp., but differing in the absence of the mesal angiocoxites and the more fimbriate nature of the colpocoxite branch.

Etymology: The species epithet honors Jasper “Jack” Daniel (1850–1911), noted distiller of Jack Daniel’s Bourbon Whiskey, still made in Lynchburg, Tennessee, and a favorite libation of the author.

Description of male from Motlow Cave: Length, 6.7 mm, width 0.5 mm. Structure typical of genus. Gonopods (fig. 84) with completely fused coxosternum; coxal portions project anteriorly; angiocoxal setal groups close together, of 3 or 4 setae, mesal group on low prominence. Mesal angiocoxal branch absent; lateral branch erect, straight, distally tapering to slightly curved point, below which is posterior winglike extension. Colpocoxites large, bulky, fimbriate branch thick, brushlike. Ninth and tenth legpairs typical.

Female from Motlow Cave: Length, 6.8 mm, width 0.6 mm. Nonsexual characters as in male.

Distribution: See Map 8 for selected records. All specimens FSCA; all records supported by at least one male. TENNESSEE: *Bedford Co.* Campbell Cave, 27 August 1957, T. C. Barr, 28 December 1960, 17 January 1961, H. R. Steeves. *Friddle Cave*, 2 February 1964, H. R. Steeves. *Coffee Co.* Blowing Cave, 25 July 1972, T. C. Barr; *Carroll Cave*, 25 July 1957, 5 July 1972, T. C. Barr; *Crompton Creek Cave*, 6 July 1972, T. C. Barr; *Riley Creek Cave*, 6 July 1972, T. C. Barr. *Rutherford Co.* Bishop Cave, 17 January 1972, T. C. Barr.

Notes: Motlow Cave, a former commercial cave, is about 600 yards from the famous Jack Daniel Spring Cave, located on the Jack Daniel Distillery grounds, and from which the water used to brew the whiskey is taken. Motlow Cave reputedly connects with Jack Daniel Cave (Barr 1961, p. 337). Causey labeled specimens of this species as “rudis.” Clearly related to *S. alabama*, from Jackson, Madison and Limestone Counties, Alabama, this species is nonetheless distinct in lacking entirely the mesal colpocoxite branches. The distribution of *S. jackdanieli* is separated on the eastern side from that of *S. alabama* by caves in Franklin Co., Tennessee, that are occupied by the widespread species *S. ventus* Shear. However, in the more westerly part of the range, there are no *Scoterpes* records from the intervening Lincoln Co., Tennessee. All the currently known records for *S. jackdanieli* appear to be located in the Duck River drainage.

Ungrouped Species

Scoterpes willreevesi, n. sp.

Figs. 85, Map 6

Types: Male holotype and female paratype (VMNH) from Cemetary Cave (Cemetary Pit), Rising Fawn, Dade Co. Georgia, collected 10 May 1999 by Will Reeves.

Etymology: Named for the collector, entomologist and speleobiologist Will Reeves.

Diagnosis: The complexly folded angiocoxites of this species are unlike those of any other.

Male from Cemetary Cave: Length, 9.5 mm, width 0.85 mm. Nonsexual characters as described for genus. Gonopods (Fig. 85) with coxal setal groups narrowly separated. Mesal coxite branch flattened, irregularly toothed, acuminate; lateral branch complexly folded, with large lamina turned mesad posteriorly. Fimbriate branch of colpocoxite small, weak. Ninth legpair typical of genus.

Female from Cemetary Cave: Length, 10.0 mm, width 0.9 mm. Nonsexual characters as in male.

Distribution (Map 6) : All specimens FSCA; all records supported by males. GEORGIA: *Dade Co.* Byers Cave, 1.5 mi SW Rising Fawn, 18 June 1967, J. Holsinger *et al.*; same locality, 9 August 1967, S. Peck. ALABAMA: *DeKalb Co.* Sequoyah Caverns, Valley Head, 9 August 1967, S. Peck, male.

Notes: Cemetary Cave, or Pit, is a large, complex cave system that can only be entered by means of a 150-foot vertical drop. The adjoining areas of DeKalb Co., Alabama, and Dade Co., Georgia, are also home to *S. austrinus* Loomis, and the species both occur in the Rising Fawn area in caves no more than 5 miles apart, but in narrowly separated karst windows. Reeves (in litt.) says "...Sequoia [sic] Caverns is a commercial cave in Alabama near Rising Fawn, Georgia. It is on the same piece of limestone as Cemetary Pit, Rustys Cave, and all the other Fox Mountain sites." Cemetary Pit and other Fox Mountain caves are on a 332-acre preserve owned by the Southeastern Cave Conservancy. The property contains many other caves large and small, and these should be explored for new localities for *S. willreevesi*.

This species is probably, along with *S. syntheticus*, the most distinctive species of *Scoterpes* because of the large, complexly folded angiocoxites. It is nothing like the broadly sympatric *S. austrinus*. The specimens from Sequoyah Caverns and Byers Cave were labeled "latus" by Causey; this is an unpublished name.

Scoterpes syntheticus (Shear), new combination.

Fig. 86, Map 7

Trichopetalum syntheticum Shear, 1972, p. 278. **New Combination.**

Type: Male holotype from Crossings Cave, 1.5 mi N of Paint Rock, Jackson Co., Alabama (MCZ).

Etymology: This species was named in the mistaken belief that it provided evidence for the synonymy of *Zygonopus* with *Trichopetalum*.

Diagnosis: Distinct from all other *Scoterpes* species in its small size and evidently much reduced gonopods, which lack median angiocoxites and have short, simple, truncated lateral angiocoxites.

Description of male holotype: Length, 5.5 mm, width 0.6 mm. Nonsexual characters typical of genus. Pregonopodal legs not encrassate. Gonopods (Fig. 86) very small, coxae distinct from sternum, median coxal setae 3, tightly clustered, 10 setae in each lateral group, lateral group covers about half of each coxa; median angiocoxites absent, lateral angiocoxites very short, squared-off distally; fimbriate branch about as long as lateral angiocoxites. Legpair 9 typical, legpairs 10, 11 as usual.

Description of female from Paint Rock Cave: Length, 5.8 mm, width 0.6 mm. Nonsexual characters as in male.

Distribution: See Map 7 for selected records. All records supported by males, all specimens FSCA unless otherwise noted. ALABAMA: *Blount Co.* Bangor Cave, 1 mi N Bangor, 25 January 1961, W. R. Janks; 28 June 1967, S. B. Peck, A. Fiske; Bryant Cave, 19 March 1966, S. B. Peck; Catfish Cave, 1 mi SE Blount Springs, 5 April 1967, S. B. Peck; Randolph Cave, 12 December 1957, H. Steeves; 15 June 1967, T. Barr, R. Norton; Wildcat Cave, Blountsville, 17 May 1959, H. Steeves. *Jackson Co.* Blowing Cave, 15 March 1959, H. Steeves; Kennamer Cave, 15 March 1966, S. B. Peck; Paint Rock Cave, 0.5 mi W of Paint Rock, 20 December 1965, S. B. Peck. *Jefferson Co.* (unamed) cave 0.75 mi NE of Crystal Caverns, Clay, 10 September 1965, S. B. Peck; Crystal Caverns, 4 April 1959, H. Steeves; 18 November 1965, S. B. Peck. *Madison Co.* Cave Spring Cave, N of New Hope, 30 December 1965, S. B. Peck. *Marshall Co.* Kristy's Cave, 16 April 1970, W. Torode (NCSM). *St. Clair Co.* McGlendon Cave, 4 mi N of junction of US 11 and 131, 15 June 1967, S. B. Peck, A. Fiske.

Notes: I described this species in 1972 as a *Trichopetalum* largely based on the small size, simple gonopods, and a mistaken segment count—the single damaged male available was counted at 28 trunk segments. In fact that male probably had 30 segments, as do all the other males and females of the species. This is undoubtedly a *Scoterpes*. Causey, who evidently always considered the species in *Scoterpes*, labelled material “steevesi steevesi,” “steevesi merus,” and “steevesi pectus.” The distribution pattern is unusual and probably not an artifact of limited collecting. One group of populations occurs in Jackson, Madison and Marshall counties north of the Tennessee River, sympatrically with *S. stewartpecki*, in fact, in caves less than 1 km apart. The other group, in Blount, St. Clair and Jefferson counties south of the river represents the most southerly distribution of the genus (Crystal Caverns a little northwest of Birmingham is the southernmost record). Causey recognized Blount Co. records as “steevesi steevesi” and Jefferson and St. Clair Co. records as “steevesi merus,” but I cannot distinguish them and there are no obvious barriers except possibly the Locust Fork of the Black Warrior River. None of the specimens in the Causey collection from Jackson Co. had gonopods in the vials, but the type is from Jackson Co. and specimens from Madison and Marshall counties are *S. syntheticum*. Possibly further collecting will unite the populations across the Tennessee River, or it may be that more than one species is involved, despite my inability to distinguish them on the basis of gonopod anatomy.

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