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SYSTEMATICS OF THE NORTH AMERICAN SUBTERRANEAN AMPHIPOD GENUS *BACTRURUS* (CRANGONYCTIDAE)

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ABSTRACT

Bactrurus Hay is a relatively small generic group that inhabits caves and related groundwater habitats in parts of eastern and central USA. Two field trips, conducted in the spring of 1999, yielded important new locality records that give us a better knowledge of the distribution of the genus. The examination of fresh samples as well as older collection material has resulted in descriptions of four new species. Based on these descriptions and redescriptions of three previously known species, the taxonomy of the genus is revised. In addition, a phylogenetic analysis using morphological data is employed to examine the relationship of *Bactrurus* to 12 selected crangonyctid taxa, including its potential sister genus *Stygobromus* Cope. Five epigeal and hypogean amphipod taxa were chosen as outgroups for the analysis. For interspecific and intergeneric comparisons, pairwise sequence differences of the 18S (small subunit) rDNA gene are given for three species of *Bactrurus* and three of the outgroup taxa. Based on an updated, detailed distribution map the biogeography of *Bactrurus* is discussed with regard to possible dispersal and vicariant events. The evaluation of new data obtained by this study contributes to a more complete understanding of the evolutionary history of the genus.

Key words: biogeography, vicariance, phylogenetic reconstruction, taxonomic revision, cladistic analysis, groundwater, stygobiont, Amphipoda

INTRODUCTION

The crangonyctid genus *Bactrurus* is a comparatively small stygobiont group, restricted to hypogean environments in parts of eastern and central United States. Prior to this study, only three described species were known to science. *Bactrurus* was established by Hay (1902) who proposed a new genus for *Crangonyx mucronatus* Forbes, 1876. However, a generic diagnosis was

not given until 38 years later when Hubricht & Mackin (1940) introduced *B. brachycaudus* as the second species of the genus. A third species, *B. hubrichti*, was described by Shoemaker (1945). Although Holsinger (1972, 1977) discussed the morphological and biogeographic significance of *Bactrurus* as compared to its closest crangonyctid relatives and provided both familial and generic keys, the genus has not undergone a comprehensive taxonomic revision until now.

In the following revision of *Bactrurus*, a total of 235 locality records, comprising approximately 2500 specimens, have been examined or re-examined. The vast majority of these records belong to specimens of the three species currently assigned to the genus. A much smaller part of the collection material, however, contained several new species. In order to obtain additional samples of potentially new species, two collection trips were made in March and May, 1999. The field trips included excursions to caves and associated groundwater habitats in Alabama, Indiana, Illinois, Ohio, Missouri, Tennessee and Virginia. Some of these localities had not been investigated for more than 50 years. The evaluation of specimens obtained during the field trips as well as older collection material led to the descriptions of four new species of *Bactrurus* given in this paper. Moreover, several new and rather unusual records enabled us to fill in some of the gaps of inter- and intraspecific distribution patterns.

To investigate the phylogeny and biogeography of the genus *Bactrurus*, a cladistic analysis was performed on seven species of *Bactrurus* and 12 selected taxa of the family Crangonyctidae. Five epigeal and hypogean amphipod taxa were chosen as outgroups. Based on the phylogenetic analysis, the relationship of *Bactrurus* to its potential sister genus *Stygobromus* Cope, 1872, is reviewed and analyzed. In addition, pairwise sequence differences of the 18S (small subunit) rDNA gene are given for three species of *Bactrurus* and three of the outgroup taxa (adapted from Englisch & Koenemann, 2001). The evaluation of all data, as well as a detailed discussion of biogeographic and ecological characteristics of *Bactrurus*, provide new perspectives on the geographic distribution and evolutionary history of the genus in North America.

MATERIALS, METHODS AND DEFINITIONS

TAXONOMIC PROCEDURES. - The following redescriptions of *Bactrurus brachycaudus*, *B. hubrichti* and *B. mucronatus* are supplementary to the original descriptions. Because all species of the genus show a relatively high morphological resemblance, the description of *B. brachycaudus* was cho-

sen to serve as the basic model with regard to a variety of minor characters that show little or no variation among the other species, e.g., number of spines and setae on mouthparts and appendages. *Bactrurus brachycaudus* is, therefore, redescribed in greater detail. If a specific character is not explicitly mentioned for one of the other species, it can be assumed to be identical with that of *B. brachycaudus*.

The defining angles of propods of the first gnathopod were measured to facilitate interspecific comparisons between differently shaped propods. For these measurements, the palmar margin and the subangular (posterior) margin of the propod were considered two sides of an angle.

Nomenclature for setal patterns on segment 3 of the mandibular palp is based on the uppercase letter system first introduced by Stock (1974) (see also Fig. 2G).

Because vandalism and pollution have become major threats to many cave habitats, we have endeavored to protect these sensitive environments from further destruction by providing only cave names in the 'Material Examined' sections for each species. If more detailed information is needed on a particular locality, it can be obtained either from state geological surveys or from our database.

Species synonymies are complete for all references pertinent to the taxonomy and geographic distribution of taxa.

COLLECTION METHODS. - The following collection methods have been applied to different types of habitats:

Caves: in small bodies of water, e.g., drip pools and small streams, the animals were collected with the aid of modified pipettes and fine-meshed hand nets. Additionally, a Cvetkov net (closing net) was used if needed for less accessible waters (larger cave streams, deep lakes). Water bodies of greater depths were sampled with the assistance of baited traps.

Springs and wells: animals were collected utilizing either a Cvetkov net, a hand net with extended grip, or by hand-picking from the substrate.

Drainage outlets: pipe outlets of drainage systems beneath farm fields were sampled with the help of a hand net or by hand-picking from substrates.

In addition, the Karaman-Chappuis method (digging method) and a Bou-Rouch pump were employed to take samples of the groundwater fauna near surface streams, springs, and wells. The Bou-Rouch pump is specifically designed to collect small groundwater invertebrates from depths of 30-120 cm.

All collection samples were preserved in 90-95% ethanol. For the drawings, specimens were first dissected and mounted on microscope slides in Faure's medium. Holotypes of the new species are deposited in the National Museum of Natural History (Smithsonian Institution) under the catalogue numbers of the former United States National Museum. The following material is deposited in the Zoological Museum Amsterdam (ZMA), University of Amsterdam: *Bactrurus angulus*, one female paratype; *B. brachycaudus*, five specimens (both sexes); *B. hubrichti*, three specimens; *B. mucronatus*, five specimens (both sexes); *B. pseudo-mucronatus*, four paratypes (two of each sex); *B. wilsoni*, one male paratype.

DEFINITIONS AND NOMENCLATURE

GLACIAL DRIFT. - Sediments deposited by Quaternary glaciers; the repeated north-south movements of the ice sheets during the Pleistocene resulted in an accumulation of these deposits. In the Central Lowland Province, glacial drift is commonly composed of layers of sand, gravel, silt or clay.

RASTELLATE. - Term introduced by Holsinger (1967) to describe the comb- or brush-like spines or setae on the carpus of gnathopod 1 and/or 2.

ABBREVIATIONS FOR THE DEPOSITION OF MUSEUM SPECIMENS

AMNH American Museum of Natural History
JRH John R. Holsinger collection
KBS Kansas Biological Survey
USNM United States National Museum

TAXONOMIC PART

Genus *Bactrurus* Hay, 1902

Bactrurus Hay, 1902: 430; Hubricht & Mackin, 1940: 200; Shoemaker, 1945: 24; Holsinger, 1972: 73; 1977: 265; 1986a: 95; 1986b: 536; Barnard & Barnard, 1983: 435.

TYPE SPECIES (by monotypy). - *Crangonyx mucronatus* Forbes, 1876.

DIAGNOSIS.- Eyes absent. Body smooth, unpigmented. Uronites unfused. Coxal plates in stretched body position not overlapping; coxal plates 1 and 2 small; coxal plate 1 wider than long, coxal plates 2-4 slightly wider than long or as wide as long; plates 5-7 longer than wide; coxal plate of pereopod 5 with distinct anterodistal lobe, coxal plate of pereopod 6 with small anterodistal lobe, coxal plate of pereopod 7 ovate.

Antennae sometimes with aesthetascs on some peduncular segments and typically on most segments of primary flagellum. First antenna 49-92% of body length (usually 60-77%), primary flagellum longer than peduncle, with 24 to 59 segments in adult specimens; accessory flagellum two-segmented, short, as long as or slightly longer than first segment of primary flagellum. Second antenna without calceoli, 31-53% of length of antenna 1; flagellum approximately as long as peduncle, bearing 9 to 16 segments in adult specimens. Lower lip with small inner lobes. Mandibular palp three-segmented, third palp segment falcate, as long as or slightly longer than segment 2; molar prominent, triturative. Palp of maxilla 1 symmetrical, two-segmented (but weakly articulated); inner plate with up to five to eight plumose setae; outer plate with seven strong spines apically (bidentate and multidentate types). Inner plate of maxilla 2 wider than outer plate, bearing oblique row of five to ten strong, plumose setae. Inner plate of maxilliped bearing two to six blade-like spines apically (one of which sometimes modified as plumose spine; see Fig. 6C); outer plate with two to nine blade-like spines apically and subapically. Gnathopod 1 with expanded basis, basis of gnathopod 2 narrow; carpus of gnathopods triangular, bearing several strong, rastellate (brush-like) spines; propods of gnathopods 1 and 2 subequal (but propod of gnathopod 1 sometimes distinctly larger than that of gnathopod 2); propods with oblique palm; palmar margins with long and short, distally bifid spines; dactyls of both gnathopods with row of small setae on inner margin. Pereopods 3 and 4 subequal, with narrow bases; pereopods 5-7 gradually increasing in length, bases with posterior lobes, about as wide proximally as distally, poste-

rior margins convex, posterodistal lobes well developed, broadly rounded; pereopod 5 as long as or slightly shorter than pereopod 4; pereopod 7 subequal to or distinctly longer than pereopod 6. Coxal gills subovate, usually present on pereopods 2-7 (on pereopods 2-6 in *B. mucronatus*). Broodplates subovate, occurring on pereopods 2-5; exceeding length and width of bases on pereopods 2-4, greatly reduced on pereopod 5. Paired sternal processes proximolaterally on pereonites 6 and 7 and sometimes also on pleonite 1 (processes simple, non-bifurcate); sometimes single, median sternal (mediosternal) processes on pereonites 2 and 3 (absent in most species). Pleopods unmodified, biramous, with 5 to 18 segments per ramus (number of segments decreasing from pleopod 1 to 3; large specimens with up to 30 segments); outer ramus slightly shorter than inner ramus. Epimeral plates with rounded posterodistal corners, each of which bearing several short setae. Uropods unmodified, biramous, one-segmented; peduncles of uropod 1 and 2 without basiofacial (ventrolateral) spines; rami of uropod 3 reduced: inner ramus vestigial. Telson typically longer than wide (about 10% wider than long in *B. hubrichti*), apex with shallow excavation or V-shaped cleft (up to 23% cleft), bearing only apical spines (sometimes one to three small, subapical spines in *B. brachycaudus*). Several species with secondary sexual dimorphism of the male as follows: antenna 1 with longer flagellum; peduncle of uropod 1 distally with serrate process; telson slightly to extremely elongated (up to three times longer than female telson); telson with relatively short apical spines.

REMARKS. - *Bactrurus* is morphologically closely related to the crangonyctid genus *Stygobromus*. However, unlike *Bactrurus*, *Stygobromus* has a uniramous uropod 3, with a more greatly reduced outer ramus. In addition, most species of *Stygobromus* can also be differentiated from *Bactrurus* by absence of blade-like spines on the inner (apical and subapical) margin of the outer plate of the maxilliped, and in some species by bifurcate lateral sternal processes.

KEY TO THE SPECIES OF *BACTRURUS*

- 1a. Telson of male distinctly elongated, at least twice as long as uropod 3; female telson distinctly tapered, about twice

as long as broad (width less than 54% of length) 2
 b. Telson of male not distinctly elongated, shorter or slightly longer than uropod 3; female telson not tapered (or slightly tapered), usually not twice as long as broad (width in *B. brachycaudus* up to 58% of length) 3

- 2a. Coxal gill absent from pereopod 7; lateral sternal processes on pereopods 6 and 7 and on pleonite 1 (sometimes absent on pleonite 1); median sternal processes absent *B. mucronatus*
 b. Reduced coxal gill present on pereopod 7; lateral sternal processes on pereopods 6 and 7; median sternal processes on pereonites 2 and 3 *B. pseudomucronatus* n. sp.
- 3a. Lateral sternal processes on pereopods 6 and 7 and on pleonite 1; telson as wide as or wider than long, distinctly cleft (18-25%); merus of gnathopod 1 with plumose spine(s) *B. hubrichti*
 b. Lateral sternal processes on pereopods 6 and 7 (sometimes also on pleonite 1 in *B. brachycaudus*); telson longer than wide, cleft usually 1-12% of length of telson (sometimes up to 23%); merus of gnathopod 1 without plumose spine(s) 4
- 4a. Peduncle of male uropod 1 with serrate distal process; defining angle of gnathopod 1 propod distinct (120-140°); armature of telson sexually dimorphic 5
 b. Peduncle of male uropod 1 without serrate distal process; defining angle of gnathopod 1 shallow; armature of telson not sexually dimorphic *B. brachycaudus*
- 5a. Coxal gill of pereopod 7 only slightly smaller than coxal gill on pereopod 6; distal medial margin of carpus on gnathopod 2 with ca. three plumose setae; spines on anterior margin of basis of pereopod 5 relatively long *B. wilsoni* n. sp.
 b. Coxal gill of pereopod 7 less than half the size of coxal gill on pereopod 6; distal medial margin of carpus on gnathopod 2 with six to seven plumose setae; spines on anterior margin of basis of pereopod 5 short 6
- 6a. Palmar angle of propod of gnathopod 1 distinctly defined (ca. 120°); inner plate of maxilla 2 with oblique row of seven plumose setae; outer ramus of third uropod < 80% of length peduncle, bearing two to five subapical spines on both margins; peduncle of uropod 3 armed with one to two distal spines *B. angulus* n. sp.
 b. Palmar angle of propod of gnathopod 1 less distinct (135-140°); inner plate of maxilla 2 with oblique row of 10 plumose setae; outer ramus of third uropod > 80% of length peduncle, bearing four to eight subapical spines on both margins; peduncle of uropod 3 armed with three distal spines *B. cellulanus* n. sp.

Bactrurus brachycaudus Hubricht & Mackin, 1940

Figs. 1-5

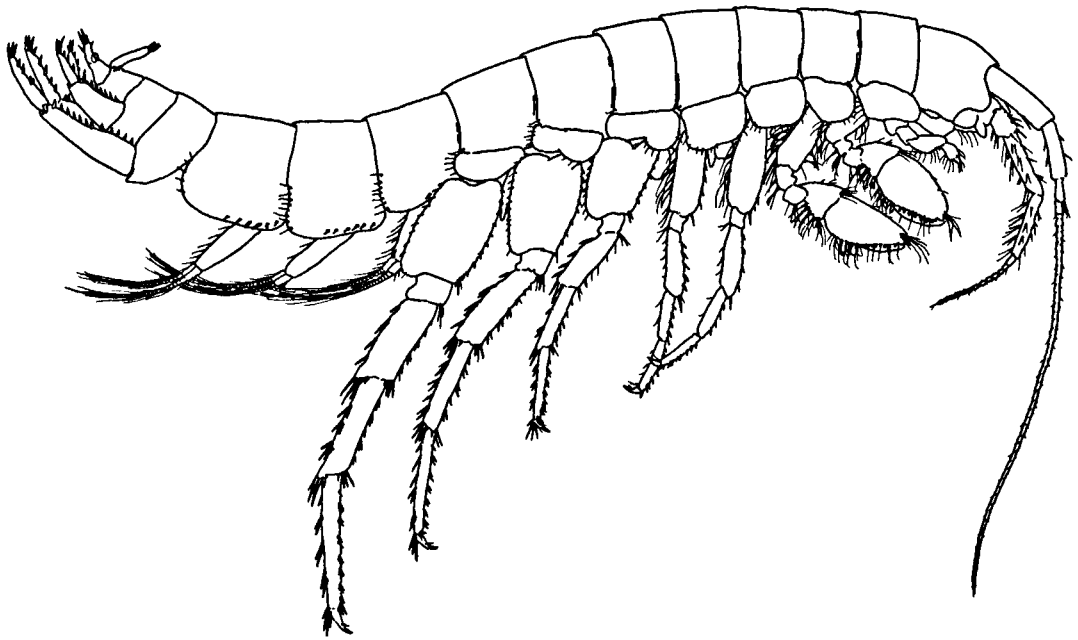


Fig. 1. *Bactrurus brachycaudus*. Syntype female (19.0 mm) from Keifer Creek (St. Louis County, Missouri).

Bactrurus brachycaudus Hubricht & Mackin, 1940: 201-202, figs. 8A-L; type locality: walled spring on Keifer Creek, 0.6 miles NW of Fern Glen (St. Louis County, Missouri); Hubricht, 1943: 693; 1959: 878; Barnard, 1958: 44; Nicholas, 1960: 127; Holsinger, 1972: 73, fig. 30c; 1977: 277; 1981: 93; 1986a: 95, fig. 6; 1986b: 542; Peck & Lewis, 1978: 45; Barnard & Barnard, 1983: map 12; Fitzpatrick, 1983: 44; Gardner, 1986: 15.

MATERIAL

ILLINOIS. - Adams Co.: well with pump, 10 mi. S of Quincy, 2 males, 6 females (JRH), J. G. Weise, 17-IX-1957. Greene Co.: spring on west edge of S14, 2.5 mi. W of Hillview, 2 males, 2 females (JRH), S. Peck, 22-IV-1966; spring at base of bluff, 3 mi W of Eldred, 5 males, 3 females (USNM), L. Hubricht, 8-IX-1940. Jackson Co.: Giant City State Park, 1 male, 3 females (JRH), J. A. Beatty, 27-IV-1971. Johnson Co.: Firestone Creek Cave (formerly called Vienna City Dump Cave), 1 female (JRH), J. Lewis, 3-III-1973; 1 juvenile (JRH), 15-XII-1973; Belknap Cave, 3 males, 3 females, 1 juvenile (JRH), J. Lewis, 19-V-1974. Monroe Co.: Camp Vandeventer Cave, 1 male (JRH), S. Peck, 27-XI-1965; Dane's Cave, 1 juvenile (JRH), J. Lewis and P. Moss, 5-IX-

1999; Fogelpole Cave, 2 males, 3 females (JRH), S. Peck, 25-VI-1965; 1 female (JRH), 16-VIII-1968; Frog Cave, 1 female (JRH), J. Lewis, S. Rafail, P. Moss and D. Tecic, 4-VII-1999; Fults Creek Cave, 1 female (JRH), S. Peck, 17-VIII-1968; Morrison (Burkesville) Cave, 1 female (USNM), L. Hubricht, 6-XI-1937; 2 males, 1 female (JRH), J. R. Holsinger and R. Norton, 13-VI-1965; Pautler Cave, 1 male (JRH), J. Lewis, S. Rafail, P. Moss and D. Tecic, 6-VII-1999; Rose Hole, 3 mi. WSW of Waterloo, 5 specimens (JRH), J. Lewis, S. Rafail, P. Moss and D. Tecic, 5-VII-1999; Schipp's Well, 0.25 mi. SW of New Hanover, 1 male (JRH), J. Lewis, S. Rafail, P. Moss and D. Tecic, 7-VII-1999; Seep, 2.8 mi. S of Valmeyer, 4 males, 5 females, 3 juveniles (USNM), L. Hubricht, 30-I-1943; small cave, 1 male (USNM), L. Hubricht, 30-I-1943; Terry Spring (Long Slash) Cave, 1 male (JRH), S. Peck, 27-XI-1965. Montgomery Co.: drain tile into concrete catchment basin, 5.2 mi. NW of Harvell, 3 specimens (JRH), S. Koenemann and U. Englisch, 15-V-1999; drain pipe, ca. 5 mi. E of Morrisonville, 9 specimens (JRH), S. Koenemann and U. Englisch, 15-V-1999. Pike Co.: Croxville Cave, 3 females (JRH), S. Peck, 15-VIII-1968; small spring, 1 mi SE of Pearl, 4 juveniles (USNM), L. Hubricht, 28-IV-1940; Twin Culvert Cave, 2 males, 2 females (JRH), S. Peck, 25-IX-1965. Sangamon Co.: drain pipe into Panther Creek, ca. 0.5 mi. W of Auburn, 14 specimens (JRH), S. Koenemann and U. Englisch, 16-V-1999. St. Clair Co.: Dashed Hopes Pit, 3.25 mi. ENE of

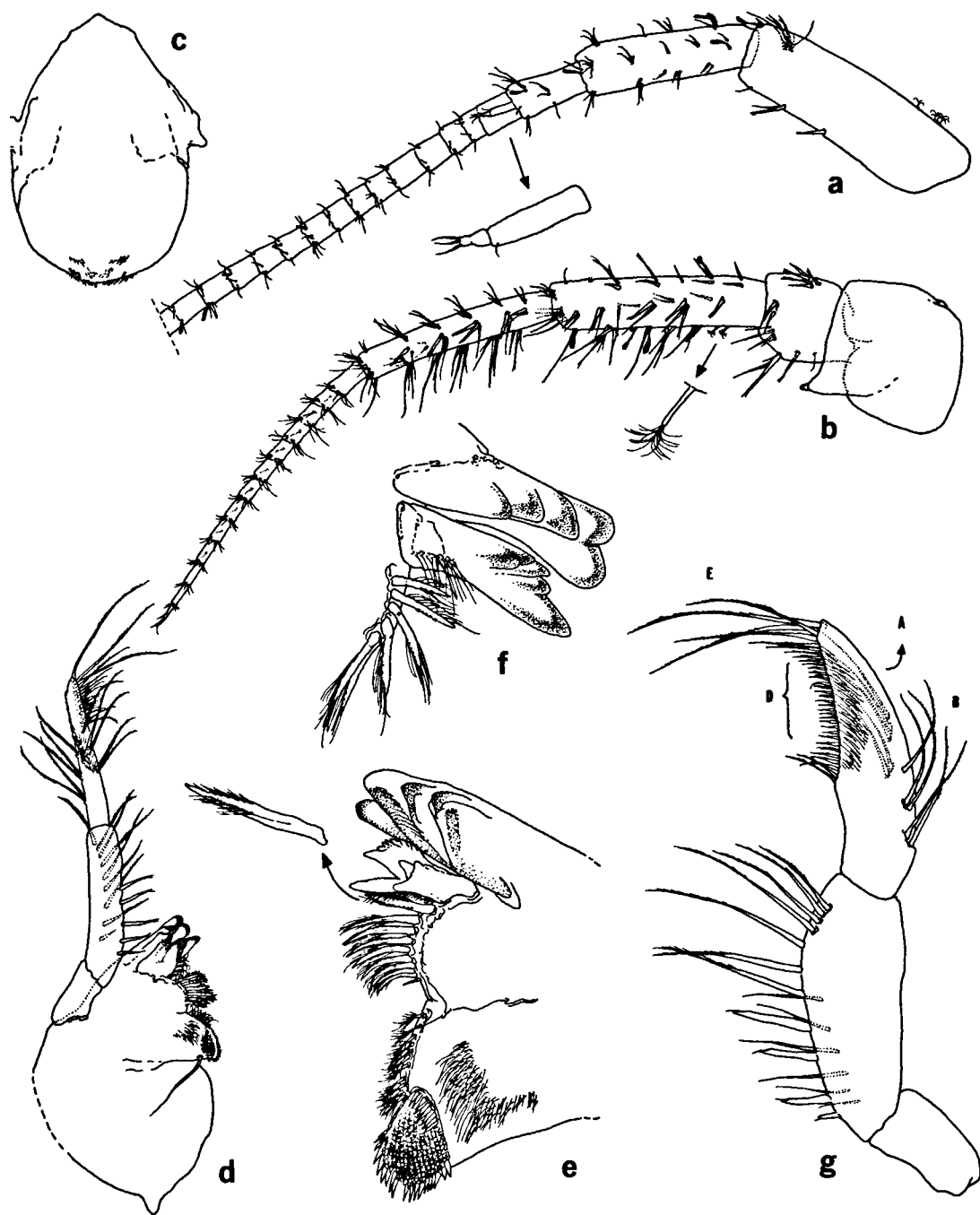


Fig. 2. *Bactrurus brachycaudus*. Female (19.9 mm) from Keifer Creek (St. Louis County, Missouri): A, antenna 1 (accessory flagellum enlarged). B, antenna 2 (plumose setule enlarged). C, upper lip. D, left mandible. E, detail of right mandible, with 1 spine enlarged. Male (19.0 mm) from same locality: F, dentate part of left mandible. G, palp of left mandible; note that setal types on segment 3 are designated by uppercase letters in accordance with Stock (1974).

Columbia, 1 male (JRH), J. Lewis, S. Rafail, P. Moss and D. Tecic, 3-VII-1999; small spring, 1 mi. S of Falling Spring, 7 males, 8 females (USNM), L. Hubricht, 18-IV-1937; Stemlers Cave, 1 female (USNM), L. Hubricht, 16-I-1938.

Union Co.: seep near McCann School, 2 females (USNM), L. Hubricht, 14-IV-1940; ditch along creek, 4 juveniles (JRH), J. Weise, 8-I-1952.

MISSOURI. - Bollinger Co: Blue Pond Natural Area, SW part

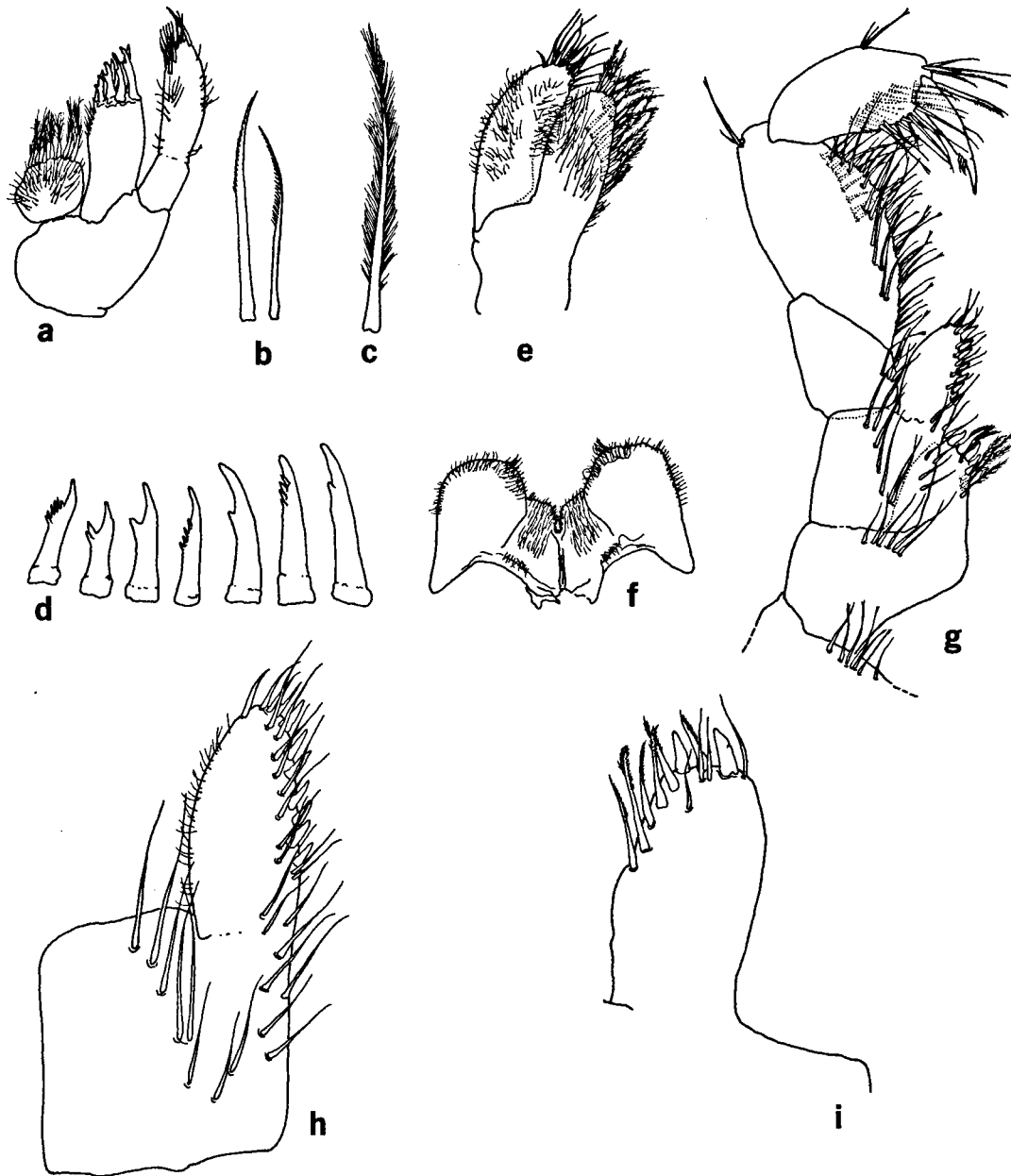


Fig. 3. *Bactrurus brachycaudus*. Female (19.9 mm) from Keifer Creek (St. Louis County, Missouri): A, maxilla 1. B, comb-like setae of mouthparts and gnathopods. C, plumose seta of mouthparts. D, spine types of outer plate of maxilla 1. E, maxilla 2. F, lower lip. G, maxilliped. H, outer plate of maxilliped. I, inner plate of maxilliped.

of county, 1 male (JRH), W. C. Pflieger, 23-III-1988. Boone Co.: Devils Icebox Cave, J. and T. Lewis, 2 juveniles (JRH), 4-VIII-1979; 4 males, 3 females (JRH), S. W. Schulte, XII-1980; 4 males, 4 females (JRH), J. E. Gardner, 29-I-1981; Hunted Cave, 26 specimens (USNM), L. Hubricht, 4-VIII-1940; Pollys Pot (Cave), 6 specimens (JRH), J. E. Gardner, 28-I-1981; seep near small creek, 4 mi. SE of Ashland, 9 specimens (USNM), L. Hubricht, 30-IV-1938; spring 4 mi.

E of Ashland, on Brushy Creek, 5 specimens (USNM), L. Hubricht, 14-V-1936. Crawford Co.: Jagged Canyon Cave, 1 juvenile (JRH), J. L. Craig, 16-XII-1973; 1 male (JRH), 5 females, 12-IV-1974; nameless Cave, 5 females (JRH), B. Harris, 3-VII-1976; 1 male (JRH), J. Craig, 16-II-1974. Narrows Cave, 1 male, 1 female (JRH), J. E. Gardner, 7-VIII-1980. Dent Co.: Bounds Branch Cave, 2 males, 2 females (JRH), J. E. Gardner, 20-VI-1980. Franklin Co.:

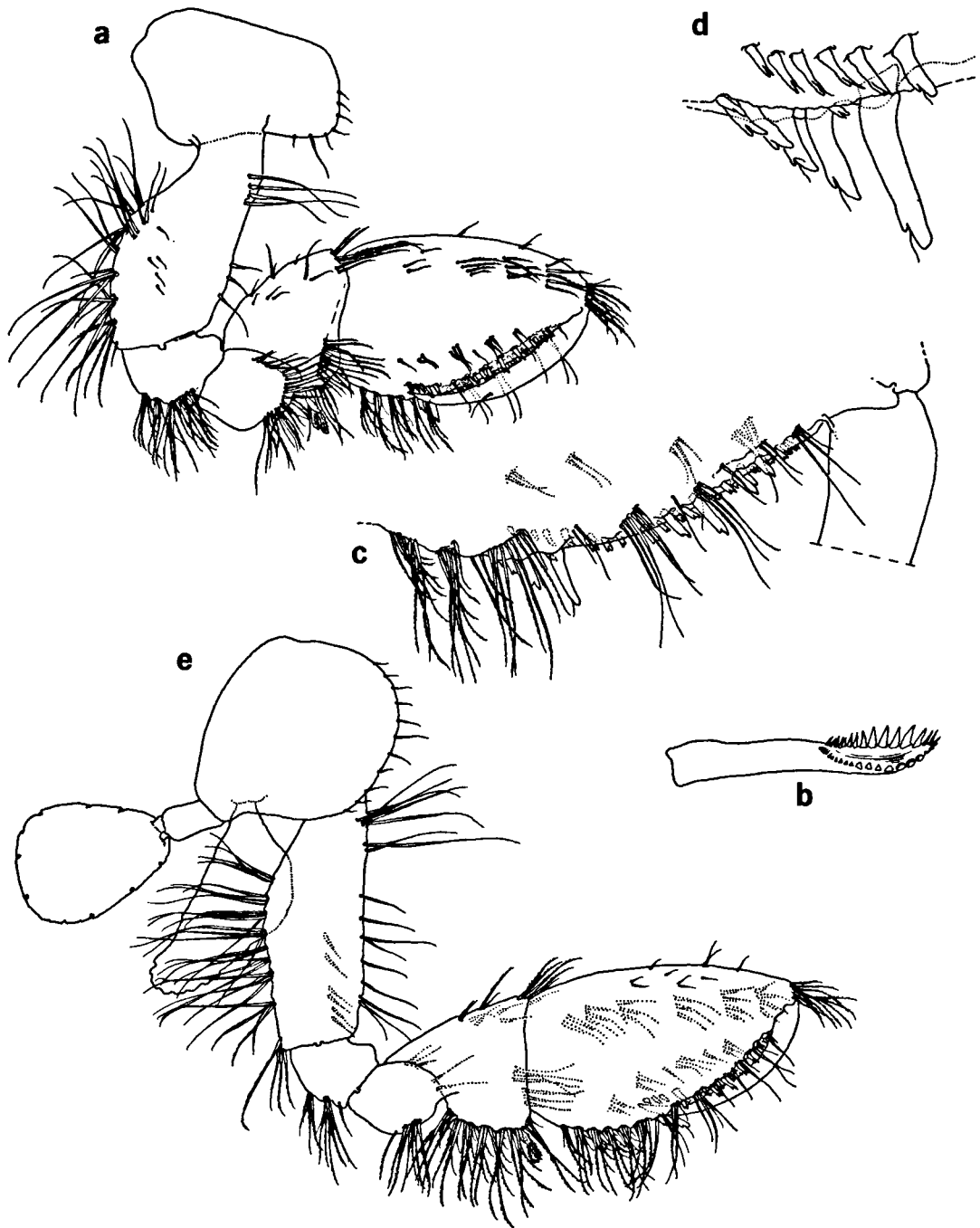


Fig. 4. *Bactrurus brachycaudus*. Female (19.9 mm) from Keifer Creek (St. Louis County, Missouri): A, gnathopod 1 (medial view). B, rastellate spine on carpus of gnathopod 1. C, palm of gnathopod 1 (lateral view). D, defining angle (corner) spines of propod (gnathopod 1, medial view). E, gnathopod 2 (lateral view).

Fisher Cave, 11 specimens (JRH), J. E. Gardner, 11-III-1982. Meramec Caverns, 1 male, 7 females (USNM), L. Hubricht, 16-XII-1939; Sheep Cave, 1 female (JRH), J. E. Gardner, 17-III-1981. Iron Co.: Boulder Cave, 3 males (JRH), J. E. Gardner, 1-VI-1982; Cave Hollow Cave, 1 male,

2 females (JRH), J. E. Gardner, 2-VI-1982. Jefferson Co.: Anderson Cave, >25 specimens (USNM), L. Hubricht, 24-IX-1939; Becker's spring, 0.5 mi. E of Seckman, 1 male (USNM), L. Hubricht, 6-VI-1937; Hoffarth's well, Antonia, 4 females (USNM), collected by Hoffarth, 16-X-1938;

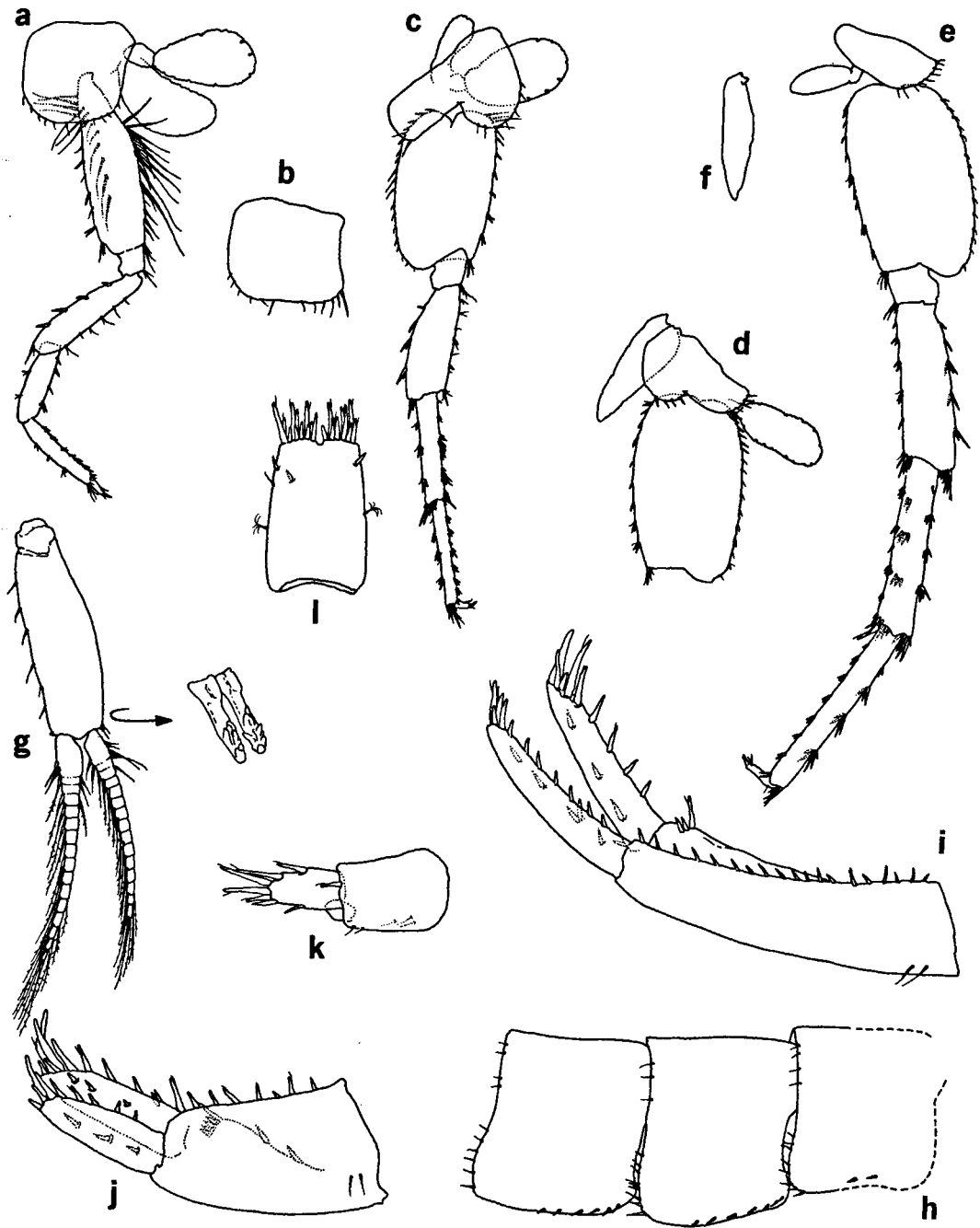


Fig. 5. *Bactrurus brachycaudus*. Female (19.9 mm) from Keifer Creek (St. Louis County, Missouri): A, left pereopod 3. B, coxal plate of pereopod 4. C, right pereopod 5. D, proximal part of left pereopod 6. E, left pereopod 7. F, lateral sternal process of pereonite 7. G, pleopod 1 (retinaculæ enlarged). H, epimeral plates 1-3. I-K, uropods 1-3. L, telson.

Pleasant Valley Cave, 1 male (JRH), D. and M. Bechler, 20-III-1977; Rice's Cave, 5 specimens (USNM), L. Hubricht, 31-X-1937; 1 female (JRH), D. Bechler and M. Harder, 30-I-1977; Sims Cave, 3 males, 3 females, 1 juvenile (JRH), T. Marsh, 27-III-1966; small spring on bluff, 0.5 mi. NW of

Selma, 52 specimens (USNM, in 2 vials), L. Hubricht, 10-V-1936; small spring at foot of hill, on tributary of Selma Creek, 0.7 mi. NNW of Selma, 16 specimens (USNM), L. Hubricht, 23-I-1938; small spring on bluff, 1 mi. W of Selma, 9 specimens (USNM), L. Hubricht, 2-VI-1937;

spring house on hillside, 2.2 mi. E of Antonia, 4 females (USNM), L. Hubricht, 6-VI-1937; small spring on bluff, 2 mi. E of Antonia, 1 female (USNM), L. Hubricht, 6-VI-1937; seep, 5 mi. S of Antonia, 26 specimens (USNM), L. Hubricht, 2-VI-1940; small spring, 5 mi. N of Antonia, 11 female (USNM), L. Hubricht, 6-VI-1937; seep near large spring, 2 mi. S of Platt, 3 specimens (USNM), L. Hubricht, 14-I-1942; spring on Antire Creek, 3.5 mi. E of Eureka, 2 females (USNM), L. Hubricht, 30-IV-1939. Lincoln Co.: Aker's Cave, 3 males, 2 females (USNM), L. Hubricht, 24-I-1943; Creech Cave, 1 female (JRH), J. E. Gardner, 15-IV-1982. Madison Co.: small intermittent stream (tributary of Twelvemile Creek), 7 mi. S of Fredericktown, 1 male, 1 female, 1 juvenile (USNM), L. Hubricht, 21-IV-1938. Perry Co.: Crevice Cave, 1 male (JRH), S. Peck, 23-IX-1961; 1 male, 2 females (JRH), J. R. Holsinger, 9-VI-1964; Mystery Cave (north upper passage, stream entrance to Spider Pit), 2 males (JRH), J. Lewis, 20-V-1972, and 1 juvenile (JRH), 31-III-1974; Tom/Berome Moore Cave, 1 male (USNM), L. Hubricht, 14-IX-1969; 1 male, 1 female (JRH), J. Lewis, 30-XI-1973; 2 males, 1 female, 1 juvenile (JRH), T. L. Saberton and S. Trimbley (donated by D. L. Bechler), date not given. Pike Co.: Cave N of Frankford, 9 specimens (USNM), L. Hubricht, 21-VI-1941. Ralls Co.: fisher's Cave, 1 male, 4 females (USNM), L. Hubricht, 21-VI-1941; 2 females (JRH), J. G. Weise (?), 21-IV-1953; 1 male, 1 female (JRH), J. G. Weise, 16-X-1954. Reynolds Co.: spring, 3 mi. WSW of Ellington, ca. 95 specimens (USNM), L. Hubricht, 3-V-1942. Scott Co.: spring seeps along gravel road, 1.75 mi. NW of Illmo (T30N, R14E, S29), 6 males, 11 females (JRH), W. L. Pflieger and G. McDonald, 27-II-1976. St. Charles Co.: Dingleline Cave, 1 male, 5 females (JRH), J. Holsinger, 9-VI-1964. St. Francois Co.: Shaver Cave, 2 juveniles (USNM), L. Hubricht, 20-VII-1941. St. Genevieve Co.: Kohm's Cave, 6 males, 2 females (USNM), L. Hubricht, 24-VIII-1941; 1 male, 1 female (JRH), D. and M. Bechler, 6-II-1977; Saltpetre Cave, 9 specimens (USNM), L. Hubricht, 24-VIII-1941; small spring, 4.6 mi. SW of St. Genevieve, 14 specimens (USNM), L. Hubricht, 9-III-1941. St. Louis Co.: Biffle's bunker spring, Tyson Research Center, 1 male (JRH), J. C. Walker, 21-II-1996; 1 male, 14-III-1996; 4 males (JRH), E. C. Biffle, Apr.-May 1996; 12 specimens (JRH), S. Koenemann and U. Englisch, 17-V-1999; Crystal Springs, Babler State Park, 1 male (JRH), S. Koenemann and U. Englisch, 17-V-1999; Cherokee Cave, 1 male (JRH), A. R. Templeton, 19-I-1984; basement of Biology Dept., St. Louis University, 1 male (JRH), D. L. Bechler, 1 male, 1977; 1 male (JRH), 12-VIII-1977; 1 male, 1 female (JRH), D. L. Bechler and J. Rice, 16-II-1978; Cliff Cave, 1 male (USNM), L. Hubricht, 25-IV-1938; cave, Kirkwood, juvenile (USNM), L. Hubricht, 13-VI-1937; small cave, Fern Glen, 1 male (USNM), L. Hubricht, 23-IV-1939; small cave (10-15 m long), NW of Eureka, 3 males, 1 female (JRH), J. and T. Lewis, 9-VIII-1979; Woods Cave, 12 specimens (JRH), J. E. Gardner, 17-VII-1979; spring, Monarch, 4 females (USNM), L. Hubricht, 23-V-1937; walled spring on Keifer Creek, 0.6 mi. NW of Fern Glen, 1 female and 5 male SYNTYPES (AMNH 9158), 23 male, 44 female and 5 juvenile SYNTYPES (USNM 74846) (2 specimens mounted on perma-

nent slides in JRH collection), L. Hubricht, 17-IV-1937; ca. 50 topotypes (USNM), L. Hubricht, 22-III-1942; small spring on bluff, 0.7 mi. S of Grimsby, 30 specimens (USNM), L. Hubricht, 29-II-1936; outlet of drain, Osage Hills Country Club, Kirkwood, 4 specimens (USNM), L. Hubricht, XII-1931; small spring near old quarry, Kirkwood, Osage Hills, 1 male (USNM), L. Hubricht, 23-IV-1939. Texas Co.: Bat Cave, 5 males, 13 females, 2 juveniles (USNM), L. Hubricht, 5-VII-1940; 1 female (JRH), W. R. Elliott, 14-XII-1999.

DIAGNOSIS. - A medium-sized to very large species without marked secondary sexual dimorphism. Propod of gnathopod 1 slightly shorter than propod of gnathopod 2. Pereopod 5 slightly longer than pereopod 4 (about 8%). Coxal gills on pereopods 2-7 (reduced on pereopod 7). Lateral sternal processes on pereonites 6 and 7; median sternal (mediosternal) processes usually absent. Telson entire or slightly emarginate, longer than wide. Largest male 31 mm, largest females up to 24 mm.

DESCRIPTION. - The description is based on several adult specimens of both sexes (19.0 mm female, Fig. 1); 23.5 mm female; 19.0 mm male; 20.5 mm male; 13.0 mm male).

Antenna 1 (Fig. 2A) up to 75% length of body. Second peduncular segment 74% length of peduncular segment 1; third peduncular segment 42% length of peduncular segment 2; several plumose setules dorsoproximally on peduncular segment 1. Aesthetascs sometimes on peduncular segments 2 and 3 and on most segments of main flagellum. Primary flagellum with up to 59 segments; accessory flagellum two-segmented.

Antenna 2 (Fig. 2B) about 40% length of antenna 1. Third peduncular segment 96% length of peduncular segment 2. Aesthetascs and several plumose setules on peduncular segment 4. Flagellum with up to 15 segments.

Upper lip (Fig. 2C) rounded apically, with small setae along distal margin.

Mandibles (Figs. 2D-G) subequal. Molar strong, triturate, with row of 10 to 12 small plumose setae on anterior outer margin. Row of eight to ten plumose spines between molar and lacinia mobilis. Left lacinia mobilis four-dentate (Fig. 2F); right lacinia irregular, with serrate distal margin (Fig. 2E). Palp segments 2 and 3 subequal in length; palp segment 2 with five to eight short

naked setae on lateral margin and seven to twelve plumose setae on medial margin (two to four of which can be slender spines in some males; see Fig. 2G); palp segment 3 bearing apically three to four long, plumose E-setae, a row of about 22 short, plumose D-setae, five to six long, plumose B-setae, four to five long, plumose A-setae, and faint, small setae on medial surface. Because there are two types of plumose setae on mouthparts and gnathopods the plumose setae of the mandibular palp are referred to as comb-type setae (Fig. 3B).

Maxilla 1 (Fig. 3A): palp two-segmented, articulation of segments faint; palp segment 2 bearing apically and subapically up to 14 naked setae and one or two long plumose setae (comb-type, Fig. 3B). Outer plate with seven strong spines, three to four of which bidentate and three to four multi-dentate (Fig. 3D). Inner plate with six to eight apical, plumose setae (Fig. 3C).

Maxilla 2 (Fig. 3E): outer plate bearing apically up to 18 setae, some of which faintly plumose (comb-type, Fig. 3B). Inner plate with oblique row of eight to ten strong, plumose setae on inner margin and 20 to 26 plumose, apical and subapical setae (all plumose setae of same type, Fig. 3C). Lower lip (Fig. 3F) bearing small setae on margins of outer lobes and on inner lobes; inner lobes very small; mandibular lobes short, with slightly rounded, pointed corners.

Maxilliped (Figs. 3G-I): outer plate with row of six to nine blade-like spines and up to 23 naked setae on inner margin. Inner plate with two to four naked, blade-like spines (one of which sometimes modified as plumose spine) and four to eight plumose setae on apical and subapical inner margin (brush-type setae, Fig. 3C; compare with mandible).

Gnathopod 1 (Figs. 4A-D): basis bearing up to 29 long, naked setae on posterior margin, two to six plumose setae on posterodistal corner, four to five long, naked setae on anteroproximal margin, three to four setae on anterodistal margin and six or seven short setae on medial surface. Carpus triangular, with 12 to 13 plumose setae on distal margin and up to nine (usually three to four) rastellate spines on posterodistal corner (Fig. 4B). Propod slightly shorter than propod of gnathopod 2; palm almost even, short part of distal margin finely serrate, armed with up to 17 spines on

lateral margin and seven spines on medial margin; defining angle rounded, shallow, with six short spines medially and five spines (long and short) on lateral corner (Fig. 4D); posterior (subangular) margin about 31% length of propod, with three to six sets of plumose setae (naked at defining angle); anteromedial surface bearing five rows of plumose setae (with two to five setae per row). Dactyl reaching about 79% length of propod. Coxal plate wider than long, with six to seven setae. All plumose setae of gnathopod 1 belong to comb-type (Fig. 3B).

Gnathopod 2 (Fig. 4E): basis with nine sets of two to four long setae on posterior margin (all naked, except two distal sets with plumose setae), up to seven long, naked setae on anteroproximal margin, up to nine setae on anterodistal margin and six to seven short setae on medial surface. Carpus triangular, with seven to ten sets of plumose setae on posterior margin, ca. seven plumose setae on distal margin and up to nine (usually five) rastellate spines on posterodistal corner (Fig. 4B). Palm of propod slightly rounded, short part of distal margin finely serrate, bearing 18 to 22 spines on lateral margin and up to 24 spines on medial margin; defining angle rounded, very shallow, with four to five short spines medially and three to five spines (long and short) on lateral corner; proximal (subangular) margin about 35% length of propod, with eight to nine sets of plumose setae (naked at defining angle); anteromedial surface bearing seven rows of plumose setae. Dactyl reaching about 70% length of propod. Coxal plate round, as wide as long, bearing nine or ten setae on distal margin. All plumose setae of gnathopod 1 belong to comb-type (Fig. 3B).

Pereopod 3 (Fig. 5A): basis with up to 10 long setae on proximoposterior margin (excluding posterodistal corner), two to six long setae on anteroproximal margin and six to ten long setae on medial surface. Coxal plate slightly wider than long, distal margin with up to 14 setae.

Pereopod 4 subequal to pereopod 3; coxal plate slightly wider than long, distal margin bearing up to 11 setae and one slender spine (Fig. 5B).

Pereopods 5-7: plumose setae absent. Dactyls relatively short, typically about 15% length of corresponding propod. Anterior lobe of coxal plate of pereopod 5 bearing four to seven setae; posterodistal corner with one slender spine (Fig. 5C).

Pereopods 6 and 7 subequal, but pereopod 6 reaching only 69% length of pereopod 7. Anterior lobe of coxal plate of pereopod 6 with two to four setae; posterior margin bearing two to four setae and one slender spine (Fig. 5D). Coxal plate of pereopod 7 ovate, with six to nine setae on posterior margin (Fig. 5E).

Coxal gills subovate, present on pereopods 2-7 (Figs. 4E, 5A, C-E), greatly reduced on pereopod 7. Two pairs of pointed sternal processes present on pereonites 6 and 7 (Figs. 5D, F).

Brood plates on pereopods 2-5 (Figs. 4E, 5A, C; not fully developed in specimen illustrated), distinctly smaller on pereopod 5.

Pleopods biramous (Fig. 5G); pleopod 3 slightly shorter than pleopods 1 and 2, which are subequal in length. Peduncle of pleopod 1 shorter than peduncles of pleopods 2 and 3; width of peduncles gradually increasing from pleopod 1 to 3. Inner rami about 12% longer than outer rami; first three to six proximal segments of both rami fused to form a single segment; both rami with subequal number of segments; number of unfused segments slightly decreasing from pleopods 1-3 (average number of rami segments: 16 in pleopod 1, 14 in pleopod 2 and 12 in pleopod 3; can be as many as 30 in large specimens). Epimeral (pleonal) plates (Fig. 5H): posterodistal margins bearing four to eight setae (one to three of which can be small spines on corner); ventral margins with two spines on plate 1 and four to seven spines on plate 2 and 3, respectively.

Uropod 1 (Fig. 5I): peduncle with up to 21 spines on laterodorsal margin and three to four spines on mediodistal corner. Rami subequal, about 57% length of peduncle; inner ramus with five apical spines, and seven to nine spines on dorsal surface. Outer ramus with four to six apical spines and 8 to 12 spines on dorsal surface.

Uropod 2 (Fig. 5J): peduncle with up to nine spines on laterodorsal margin, one or two spines on mediodorsal margin (sometimes absent), and a row of five to six spines near mediodistal corner. Inner ramus slightly longer than outer ramus, about 68% length of peduncle, with five to six apical spines, and seven to nine spines on dorsal surface. Outer ramus with four apical spines and five to seven spines on dorsal surface.

Uropod 3 (Fig. 5K): peduncle bearing one spine on distal margin (sometimes two spines). Inner

ramus vestigial, unarmed, about 37% length of outer ramus. Outer ramus short (approximately 71% length of peduncle), bearing up to six (usually three to four) apical spines and one to five subapical spines.

Telson slightly tapered apically (Fig. 5L); width 58-73% of length (usually about 68%); lateral margins with one small plumose seta each (see enlarged seta of Fig. 2B); apical margin entire or slightly emarginate (1-2% cleft), bearing 16 to 20 spines.

SEXUAL DIMORPHISM AND VARIATION. - As already noted, the majority of specimens did not show any marked secondary sexual dimorphism. However, the propods of both gnathopods appeared to have somewhat sinusoid palmar margins in some of the larger males (> 25 mm). The propod of gnathopod 1 was noticeably larger than the propod of gnathopod 2 in some large males. One 26 mm male (with sinusoid palmar margins on propods of gnathopod 1 and 2) had a double (U-shaped) row of 12 rastellate spines on the carpus of gnathopod 2.

No marked morphological variation could be observed in the majority of the specimens examined. Minor variation occurred in the number of aesthetascs on both antennae, which were strongly reduced or absent in some specimens. Palp segments 1 and 2 on maxilla 1 were weakly articulated in most specimens, apparently indicating an early stage of fusion. The strong apical, plumose spine on the inner plate of the maxilliped appears to be a plumose seta (brush-type, Fig. 3C) in some specimens. Variation was also found in the number of subapical, lateral spines on the telson (some specimens had one to three subapical spines) and the width/length ratio of the telson.

Marked variation, however, was found only in two populations at opposite edges of the distribution range of *B. brachycaudus*: 39 specimens, collected from drain pipe outlets in central Illinois (Montgomery and Sangamon Co.), showed sexual dimorphism in the width/length ratio of the telson. The majority of adult males had telsons that were about 20% longer than those of the female. The same sexually dimorphic width/length ratio could be observed in a cavernicolous population from central Missouri (Texas Co.). In addition, these specimens had median

sternal (mediosternal) processes on pereonites 2 and 3. Both populations were characterized by a relatively small average body size of adult specimens (9-13 mm), resulting in a proportionate reduction of segments and armature of some appendages, for example, the number of flagellar segments in antennae 1 and 2 and the number of spines and setae on mouthparts and pereopods. Most of diagnostic characters, however, left no doubt that both populations were geographic variants and belonged to *B. brachycaudus*. This assumption was supported by relative differences of DNA sequence data (Table 2).

REMARKS. - With some large specimens reaching up to 31 mm in length, *B. brachycaudus* is one of the largest subterranean amphipod species known to science and the largest freshwater amphipod on the North American continent. The species is reported from various subterranean habitats in Illinois and Missouri, including mostly caves, but also springs and seeps, and, as the May 1999 collection trip revealed, drainage systems in glaciated areas (see Fig. 28). To date, formerly glaciated areas in Ohio, Indiana, Illinois, Iowa and Michigan were assumed to be inhabited by only one species of the genus, *B. mucronatus*. Remarkably, these are the first recorded occurrences of *B. brachycaudus* from drain pipe outlets in glacial drift areas. In one locality (Montgomery Co., Illinois), *B. mucronatus* and *B. brachycaudus* were found together in the same drain pipe catchment basin, marking first collection of these species from the same locality.

Bactrurus mucronatus and the new species *B. pseudomucronatus* can be differentiated from *B. brachycaudus* by an exceptionally long telson and a tapered outer ramus on uropod 3, bearing only a few spines. *Bactrurus hubrichti* differs from *B. brachycaudus* by having a distinctly emarginate telson with relatively long apical spines and the presence of plumose spines on the merus of gnathopod 1. The presence of a serrate peduncular process on the male uropod 1 distinguishes *B. brachycaudus* from the new species *B. wilsoni*, *B. angulus* and *B. cellulanus*.

Aquatic crustacean fauna associated with *B. brachycaudus* includes the amphipods *Gammarus troglophilus*, *Crangonyx forbesi*, *Stygobromus* n. sp.

(Holsinger, in ms.), *B. mucronatus*, *Crangonyx packardii*, *G. pseudolimnaeus*, and the isopods *Caecidotea* spp.

SEX RATIOS. - The sex ratio of 72 specimens of *B. brachycaudus* from Fern Glen (St. Louis County, Missouri) was female biased (61%). Approximately 3/4 of other *Bactrurus* species with sample sizes of 10 or more specimens also showed a differential sex ratio favoring females. A study of sex ratios in 12 species of *Stygobromus* yielded similar data (Culver & Holsinger, 1969).

A female biased sex ratio may be related to the unique properties of subterranean habitats, which are typically characterized by limited food resources and restricted habitat space. Species with low dispersal abilities are more easily subjected to inbreeding, which in turn leads to 'local mate competition' (Krebs & Davies, 1993). If habitat space is limited, a female will increase her reproductive success if she produces just as many sons as needed to fertilize her daughters. From an energy economy point of view, any additional sons are wasted since they compete with their brothers for mating opportunities with available females from the same brood. As a result, populations affected in this way tend to develop female biased sex ratios.

***Bactrurus hubrichti* Shoemaker, 1945**
Figs. 6-8

Bactrurus hubrichti Shoemaker, 1945: 27, fig. 2; type locality: well at Topeka (Shawnee County, Kansas); Barnard, 1958: 44; Hubricht, 1959: 828; Nicholas, 1960: 127; Holsinger, 1972: 74, fig. 30d; 1977: 277, figs. 8c, 14j, 15d; 1986a: 95, fig. 6; 1986b: 542; Barnard & Barnard, 1983: figs. 18f, 20d, 21b, map 12; Fitzpatrick, 1983: 144.

MATERIAL

KANSAS. - Bourbon Co.: seep, 2.3 mi. S of Bronson, 3 males, 2 females (USNM), L. Hubricht, 17-V-1942. Butler Co.: Hourglass Cave, 4 males, 6 females (JRH and KBS), W. H. Busby and J. J. Young, 7-IX-1991; 1 male (JRH), W. H. Busby and D. Figg, 3-V-1989. Chautaugua Co.: Mill's Cave, 1 male (JRH), W. H. Busby and J. J. Young, 30-VI-1991; Dry Crawl Cave, 3 males, 4 females (JRH and KBS), W. H. Busby and J. J. Young, 30-VI-1991. Clay Co.: Spring, ca. 1 mi. NNW of rt. 82 and Knollwood in Wakefield, 1 male

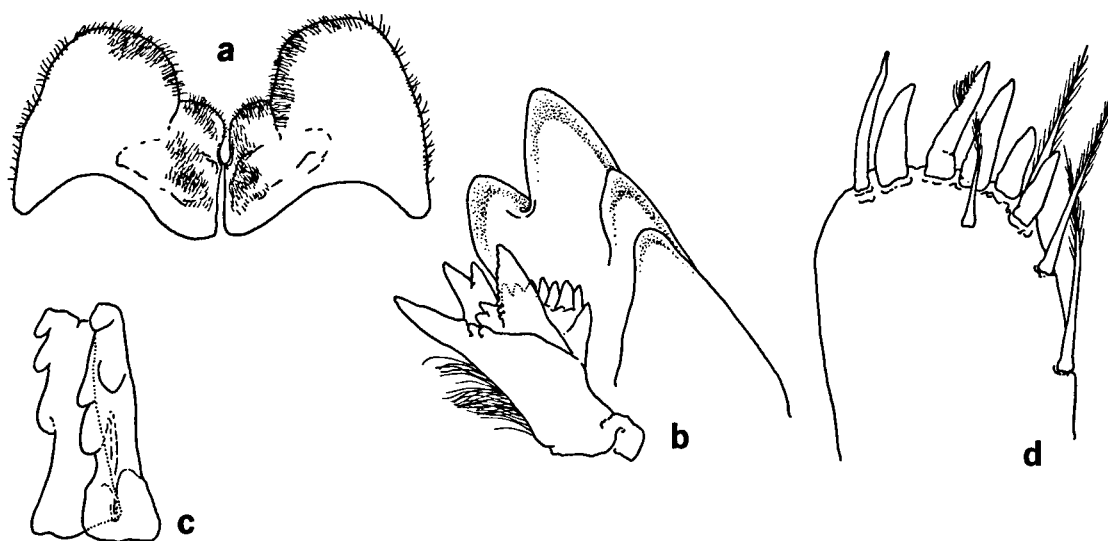


Fig. 6. *Bactrurus hubrichti*. Female (19.5 mm) from an abandoned well (Cowley County, Kansas): A, lower lip. B, dentate part of right mandible. C, retinaculæ of pleopods. Male (17.5 mm) from same locality. D, distal part of inner plate of maxilliped.

(JRH), N. W. Youngsteadt, 20-V-1980. Cowley Co.: shallow, hand-dug well, ca. 8 mi. SE of Dexter (on Metcalf farm), 13 males, 5 females, 7 juveniles (JRH), A. C. Metcalf, 1968-1970; abandoned well, 4 mi. S of Burden, 4 males, 6 females (JRH and KBS), W. A. Busby and J. J. Young, 30-VI-1991. Neosho Co.: hand-dug well, 1 mi. N of Parson's Reservoir dam, 1 female (JRH), J. Danoff-Burg, 13-VII-1991. Riley Co.: Endler Spring, Konza Prairie Research Natural Area, 1 male, 1 female (JRH), W. Dobbs, 8-VI-1995; spring, north fork of Kings Creek, Konza Prairie Research Natural Area, 9 specimens (KBS), M. Moffett, 28-V-1981; shallow well flow, Konza Prairie Research Natural Area (in Flints Hills area), 1 female (JRH), M. Whiles and K. Hooker, 20-VI-1986; 3 females (JRH), 23-VII-1986. Shawnee Co.: well at Topeka, 12 specimens (paratypes in USNM) collected by A. Popenoe as follows: 1 female, 9-VI-1911; 1 male, 15-II-1912; 1 male, 11-II-1912; 1 female, 23-II-1912; 2 males, 1 female, 25-II-1912 (2 samples); 2 females, 5-IV-1912; 1 female, 9-IV-1912; 1 male, 4-V-1912; 1 male, 25-IX-1913.

MISSOURI. - Miller Co.: Klugs Cave, 2 males, 3 females, 2 juveniles (USNM), L. Hubricht, 24-VIII-1940.

OKLAHOMA. - Muskogee Co.: well, near Connors State College, Warner, 1 female (USNM), A. Seamster, 6-I-1939. Rogers Co.: unnamed spring, ca. 3.5 mi. S of Oolagah, 1 male, 1 juvenile (JRH), J. J. Hoover and W. B. Milstead, 1-VI-1981.

DIAGNOSIS. - *Bactrurus hubrichti* is a medium-sized to large species without marked secondary sexual dimorphism. Propod of gnathopod 1 distinctly larger than propod of gnathopod 2. Pereopod 5 as long as or slightly longer than pereopod 4 (5-

14%). Coxal gills on pereopods 2-7; coxal gill on pereopod 7 only slightly reduced. Three pairs of lateral sternal processes on pereonites 6 and 7 and pleonite 1; median sternal processes absent. Telson cleft, wider than long. Largest male 22.0 mm, largest female 20.5 mm.

DESCRIPTION. - *Bactrurus hubrichti* is morphologically closely allied with *B. brachycaudus*. The following description is based on an adult female (19.5 mm) and adult male (17.5 mm).

Antenna 1 72-92% length of body (sometimes exceeding length of body). Primary flagellum with up to 40 segments.

Antenna 2 about 37% length of antenna 1. Flagellum with up to 14 segments.

Lower lip subequal to that of *B. brachycaudus* (Fig. 6A).

Mandibles: spine row with seven to nine plumose spines. Right lacinia mobilis with row of irregular, relatively long denticles on distal margin (Fig. 6B). Palp segment 2 without spines, bearing up to 17 setae on lateral and medial margins; palp segment 3 bearing up to 33 short, plumose D-setae, about three long, plumose B-setae and two to four long, plumose A-setae.

Maxilla 1 subequal to that of *B. brachycaudus*. Inner plate with five to six apical, plumose setae.

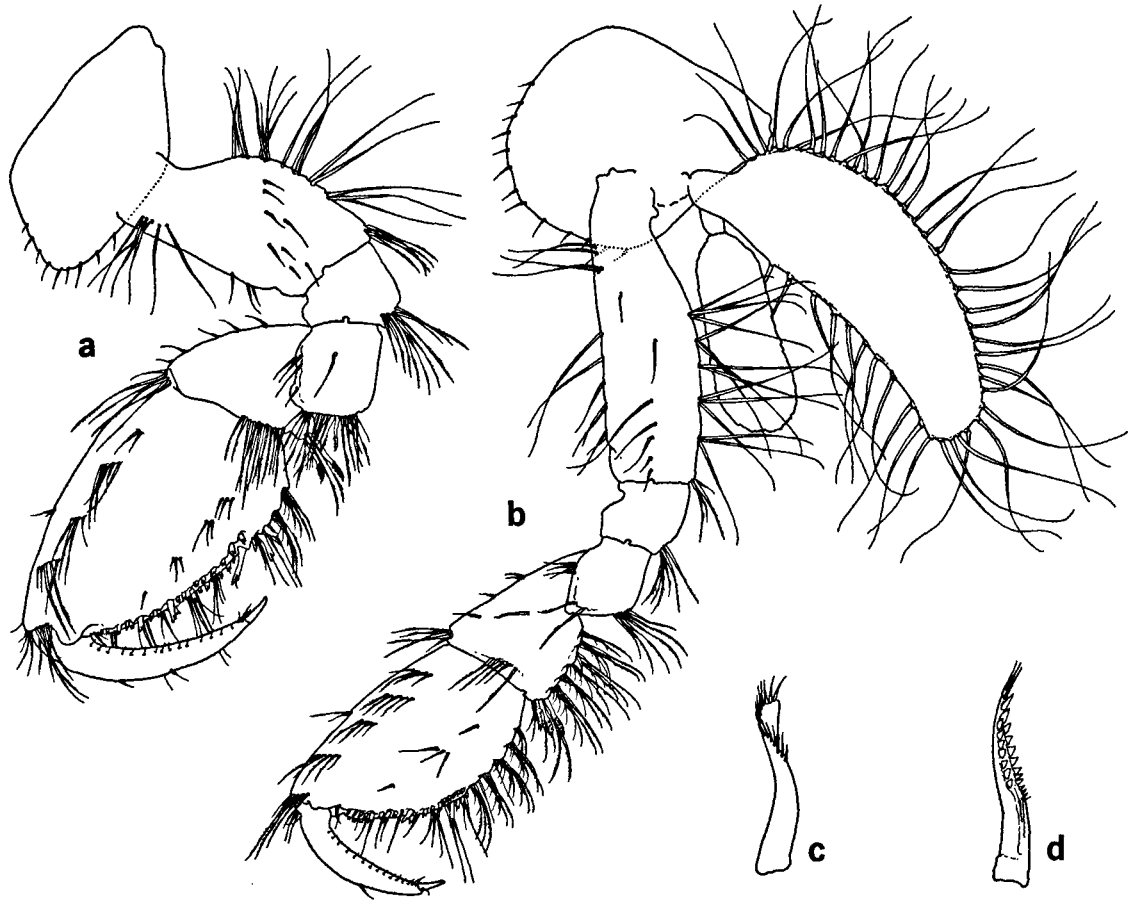


Fig. 7. *Bactrurus hubrichti*. Female (19.5 mm) from an abandoned well (Cowley County, Kansas): A, gnathopod 1 (medial view). B, gnathopod 2 (medial view). C, dentate spine of merus of gnathopod 1. D, rastellate spine of carpus of gnathopods 1 and 2.

Maxilla 2 subequal to that of *B. brachycaudus*. Inner plate with oblique row of six to seven strong, plumose setae.

Maxilliped: outer plate with five to seven blade-like spines on inner margin. Inner plate with three to six naked, blade-like spines (one of which sometimes modified as plumose spine) and three to four plumose setae on apical and subapical inner margin.

Gnathopod 1 (Fig. 7A): basis with six to eight sets of long, naked setae on posterior margin (with up to 17 setae in total), about four plumose setae on posterodistal corner, five to six long, naked setae on anteroproximal margin, three shorter setae on anterodistal margin and up to eight short setae on medial surface. Merus with two to three plumose spines (Fig. 7C). Carpus bearing 11 plumose setae

on distal margin and two to three rastellate spines on posterodistal margin (Fig. 7D). Propod wider and longer than propod of gnathopod 2; palm slightly convex, at least 2/3 of palmar margin finely serrate, bearing 17 to 20 spines on lateral margin and 11 to 15 spines on medial margin; defining angle distinct (ca. 135°), with two to three spines medially and three to six spines on lateral corner; posterior (subangular) margin 24% length of propod, with four sets of plumose setae; anteromedial surface bearing five rows of plumose setae. Dactyl reaching about 77% length of propod. Coxal plate bearing six to eight setae. Gnathopod 2 (Fig. 7B): basis with five to seven sets of two to three long setae on posterior margin, ca. four plumose setae on posterodistal corner, about four long, naked setae on anteroproxi-

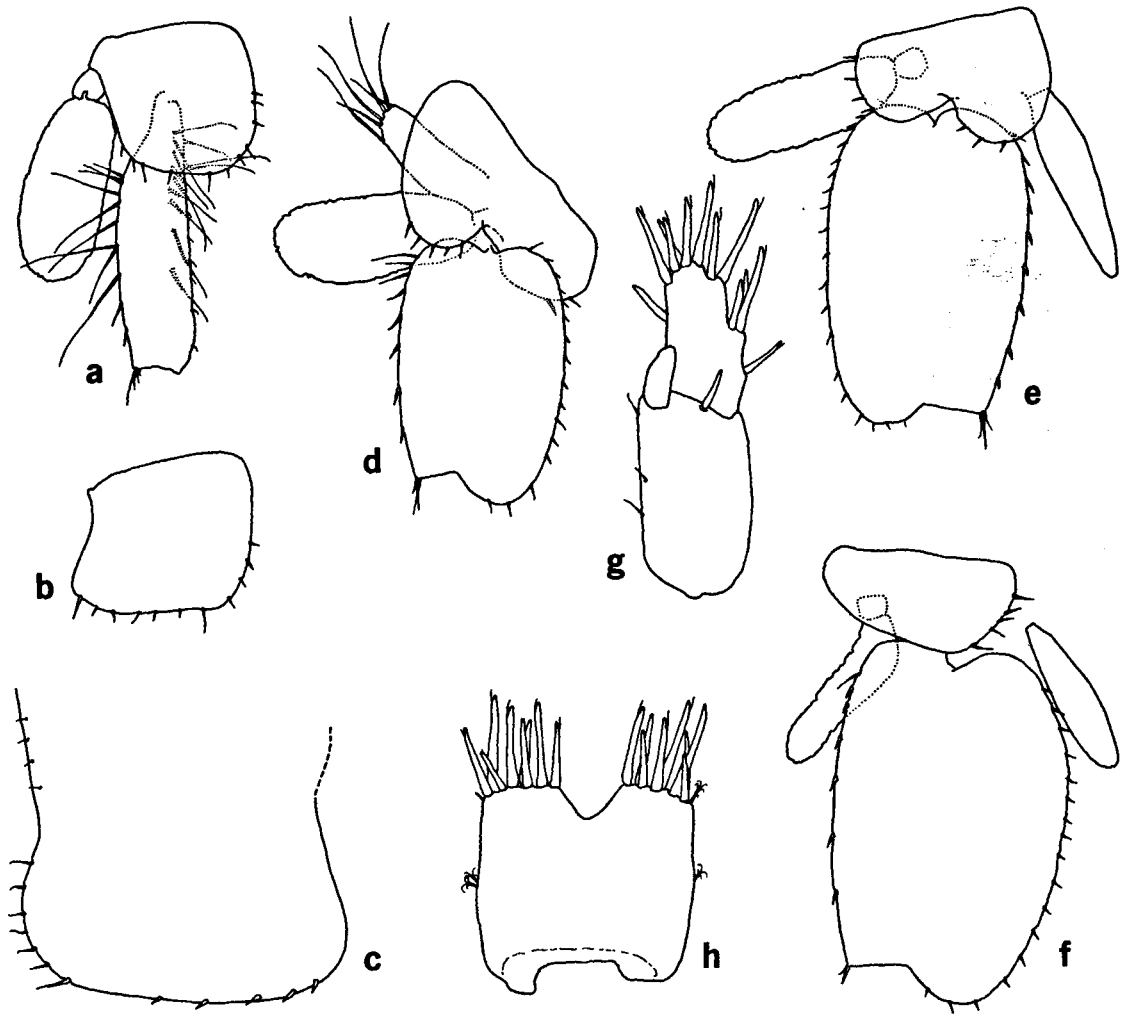


Fig. 8. *Bactrurus hubrichti*. Male (17.5 mm) from an abandoned well (Cowley County, Kansas): A, right pereopod 3. B, coxal plate of pereopod 4. C, epimeral plate 2. Female (19.5 mm) from same locality: D, left pereopod 5. E, right pereopod 6. F, left pereopod 7. G, uropod 3. H, telson.

mal margin, six to seven (mostly short) setae on anterodistal margin and a row of seven (mostly) short setae on medial surface. Carpus with six to seven sets of plumose setae on posterior margin, about five plumose setae on distal margin and up to four or five rastellate spines on posterodistal corner (Fig. 7D). Palm of propod slightly rounded, finely serrate along whole margin, with 13 to 17 spines on lateral margin and 12 to 14 spines on medial margin; defining angle rounded, very shallow, with row of five to six spines on medial corner and a row of four spines on lateral corner; proximal (subangular) margin ca. 42% length of propod, with five sets of plumose setae; antero-

medial surface bearing five rows of plumose setae. Dactyl 70% length of propod. Coxal plate round, as wide as long, bearing 11 to 15 setae on distal margin.

Pereopod 3 (Fig. 8A): basis with up to eight long setae and two short setae on proximoposterior margin, six short setae on anterior margin and 11 long setae on medial surface. Coxal plate with up to 11 setae.

Pereopod 4: coxal plate with 10 setae and one slender spine (Fig. 8B).

Pereopods 5-7: coxal plate of pereopod 5 with five setae on anterodistal lobe, posterodistal corner with one slender spine and one seta (Fig. 8D).

Coxal plate of pereopod 6 with three setae on anterodistal lobe, posterior margin with four setae (Fig. 8E). Coxal plate of pereopod 7 with five setae on posterior margin (Fig. 8F).

Coxal gill on pereopod 7 only slightly reduced (Fig. 8F). Three pairs of pointed, lateral sternal processes present on pereonites 6 and 7 and pleonite 1 (Figs. 8E, F).

Pleopods: number of unfused segments of outer and inner ramus as follows: pleopod 1 with 15 to 18 segments, pleopod 2 with 15 segments and pleopod 3 with 10 segments. Retinaculæ subequal to those of *B. brachycaudus* (Fig. 6C).

Epimeral plates: posterodistal margins bearing six to eight short setae; ventral margins: plate 1 without spines, plates 2 and 3 with four to five spines, respectively (Fig. 8C).

Uropod 1: peduncle with about 18 spines along laterodorsal margin and row of four spines on mediiodistal corner. Inner ramus with three to four apical spines and about 11 spines on dorsal surface. Outer ramus 59% of length peduncle, with three to four apical spines and up to 17 spines on dorsal surface.

Uropod 2: peduncle with ca. six spines on laterodorsal margin, and a row of three to five spines near mediiodistal corner. Inner ramus slightly longer than outer ramus, 74% of length peduncle, bearing four apical spines and nine to eleven spines on dorsal surface. Outer ramus with three to four apical spines and five to eleven spines along dorsal surface.

Uropod 3 (Fig. 8G): peduncle with one spine on distal margin (sometimes absent). Inner ramus about 45% length of outer ramus. Outer ramus ca. 73% length of peduncle, bearing four to seven apical spines, two to eight subapical spines on lateral margin and one spine on medial margin (sometimes absent).

Telson subquadrate, usually 11-14% wider than long (sometimes as long as wide), cleft 18-25% length of telson; apical lobes with six to ten spines each.

SEXUAL DIMORPHISM AND VARIATION. - The specimens examined did not show any secondary sexual dimorphism or marked morphological variation.

REMARKS. - *Bactrurus hubrichti* occurs in caves,

springs, seeps and wells in eastern Kansas, central Missouri and northeastern Oklahoma. It can be easily distinguished from all other *Bactrurus* species by a distinctly cleft telson, which is usually wider than long, and the presence of plumose spines on the merus of gnathopod 1.

Aquatic crustacean fauna associated with *B. hubrichti* includes the amphipods *Stygobromus clantoni*, *Crangonyx packardi*, and the isopod *Caecidotea* sp.

A single, 9.2 mm male specimen (USNM 81545) was found in a vial with a label that read: 'well at Fairview, Loudon Co., VA, ca. 6 mi. from Bull Run Mtn., Aug. 5, 1924, Mr. March'. The specimen was in a bad condition, but it perfectly matched the description of *B. hubrichti*. Because *B. hubrichti* occurs in the mid-western US without any known occurrence East of the Mississippi River, we have concluded that the Virginia collection was mislabeled.

***Bactrurus mucronatus* (Forbes, 1876)**

Figs. 9-13

Crangonyx mucronatus Forbes, 1876: 6, 21, figs. 1-7; type locality: well, Normal (McLean County, Illinois); O. P. Hay, 1882: 241; Schellenberg, 1936: 34.

Eucrangonyx mucronatus (Forbes); Stebbing, 1899: 423, 1906: 388; Weckel, 1907: 29, fig. 2.

Bactrurus mucronatus (Forbes); W. P. Hay, 1902: 430; Hubricht & Mackin, 1940: 200; Hubricht, 1943: 693; Shoemaker, 1945: 24, fig. 1 (redescription); Barnard, 1958: 44; Hubricht, 1959: 878; Nicholas, 1960: 127 [in part]; Holsinger, 1972: 75, fig. 30d, 1977: 265, figs. 8c, 14j, 15d; 1981: 93; 1986a: 95-96, fig. 6; 1986b: 542; Peck & Lewis, 1978: 45; Barnard & Barnard, 1983: map 12; Fitzpatrick, 1983: 144; Lewis, 1983: 36.

MATERIAL

ILLINOIS. - Champaign Co.: big concrete drain pipe into drainage ditch, 3.2 mi. N of Mayview, 7 specimens (JRH), S. Koenemann and U. Englisch, 13-V-1999; old well, Champaign, 1 male NEOTYPE (USNM 81546), 3 males, 7 females and 1 juveniles (USNM), collector not given, 29-III-1902; drainage ditch, Savoy; 2 females (USNM), H. J. Van Cleave, 9-V-1942; old well, Urbana, 4 males, 12 females (USNM), J. G. Mackin, date not given; drain tile discharge (at T20N, R10E, 529+35), 15 males, 25 females, 2 juveniles

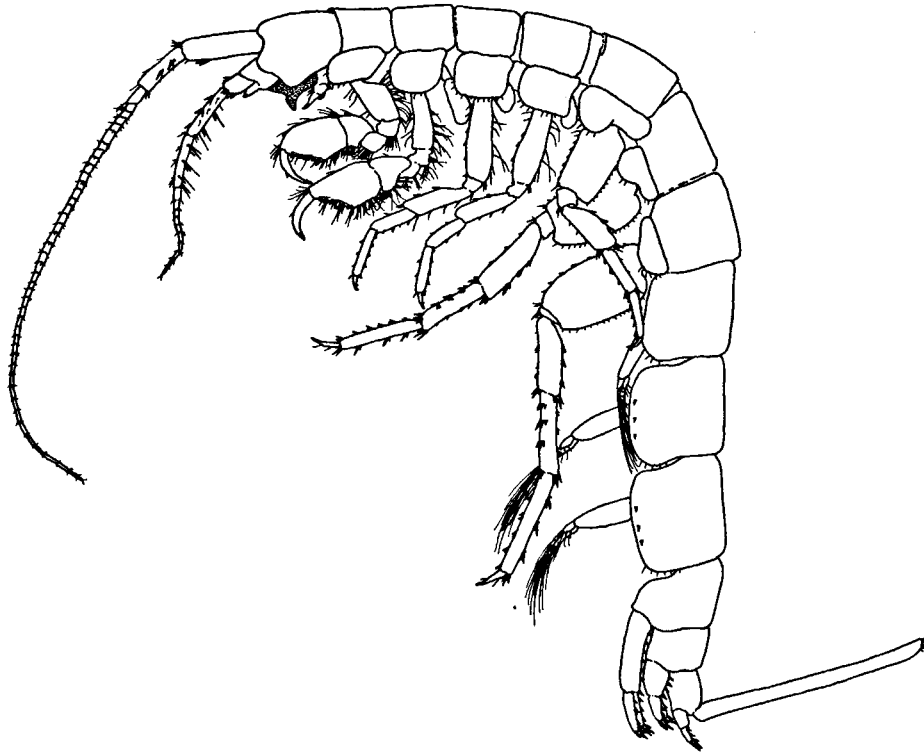


Fig. 9. *Bactrurus mucronatus*. Male (15.5 mm) from an old well near Champaign (Champaign County, Illinois).

(JRH), A. Seidenberg, 28-II-1967. Coles Co.: drain pipes into ditch or little stream, ca. 6 mi. N of Charleston, 15 specimens (JRH), S. Koenemann and U. Englisch, 13-V-1999. Fulton Co.: outlet of drain, 1.4 mi. S of Avon, 13 specimens (USNM), L. Hubricht, 4-V-1941. Gallatin Co.: drain pipes, ca. 5 mi. S of Omaha, 1 female (JRH), S. Koenemann and U. Englisch, 15-V-1999. Henderson Co.: outlet of drain, 3.0 mi. E of Biggsville, over 10 specimens (USNM), L. Hubricht, 25-IV-1942. Knox Co.: outlet of drain, 2 mi. N of Abingdon, 1 male (USNM), L. Hubricht, 4-V-1941; outlet of drain, 3.1 mi. N of St. Augustine, ca. 50 specimens (USNM), L. Hubricht, 4-V-1941; outlet of drain, 1.5 mi. SE of Williamsfield, >50 specimens (USNM), L. Hubricht, 3-V-1941. La Salle Co.: outlet of drain, Gustave Engelhaupt farm, just N of Peru, >50 specimens (USNM), L. Hubricht, 4-V-1941. McDonough Co.: outlet of drain, 4.8 mi. N of Macomb, >100 specimens (USNM), L. Hubricht, 4-V-1941; outlet of drain, 3.0 mi. S of Colmar, >125 specimens (in 2 lots) (USNM), L. Hubricht, 4-V-1941. Montgomery Co.: big iron drain pipe into catchment basin (high volume output), ca. 5 mi. W of Morrisonville, 1 male (JRH), S. Koenemann and U. Englisch, 15-V-1999. Moultrie Co.: old concrete drainage catchment basin, ca. 5 mi. WSW of Mattoon, 8 specimens (JRH), S. Koenemann and U. Englisch, 13-V-1999. Peoria Co.: outlet of drain, 1.5 mi. E of Laura, 7 specimens (USNM), L. Hubricht, 4-V-1941. Saline Co.: Equality

Cave (Cave Hill Cave), 26 specimens (USNM), L. Hubricht, 22-VI-1940; 3 males, 6 females (JRH), J. Holsinger and R. Norton, 14-VI-1965; 1 female (JRH), S. Peck, 23-X-1965; 3 males, 2 females (JRH), D. A. Hubbard, Jr., 8-VIII-1992; 8 specimens (JRH), S. Koenemann and U. Englisch, 14-V-1999. Vermillion Co.: outlet of drain, 1.0 mi. W of Fairmont, >50 specimens (USNM), R. W. Larimore, 11-IV-1952. Warren Co.: outlet of drain, 5.2 mi. E of Biggsville, >25 specimens (USNM), L. Hubricht, 25-IV-1942; outlet of drain, 2 mi. SE of Cameron, 5 females (USNM), L. Hubricht, 25-IV-1942.

INDIANA: Grant Co.: outlet of drain, 5 mi. W of Jonesboro, 4 specimens (USNM), L. Hubricht, 27-IV-1941; drain pipes at little bridge, ca. 5 mi. W of Jonesboro, ca. 40 specimens (JRH), S. Koenemann, U. Englisch and J. Lewis, 10-V-1999. Henry Co.: drain tiles, 3.2 mi. W of Knightstown, 11 specimens (JRH), S. Koenemann, U. Englisch and J. Lewis, 10-V-1999; outlet of drain, 3.8 mi. W of Knightstown, >25 specimens (USNM), L. Hubricht, 17-IV-1942; outlet of drain, 3.5 mi. W of Knightstown, 4 males, 4 females (in 2 lots) (USNM), L. Hubricht, 17-IV-1942. Marion Co.: well or swamp (?), Irvington, 4 males, 12 females (USNM), W. P. Hay, date not given. Montgomery Co.: drain tiles, ca. 1/2 mi. E of jct. 47/234, ca. 75 specimens (JRH), S. Koenemann and U. Englisch, 11-V-1999. Noble Co.: outlet of drain, 1.4 mi. W of Wawaka, 1 female (USNM), L. Hubricht, 19-IV-

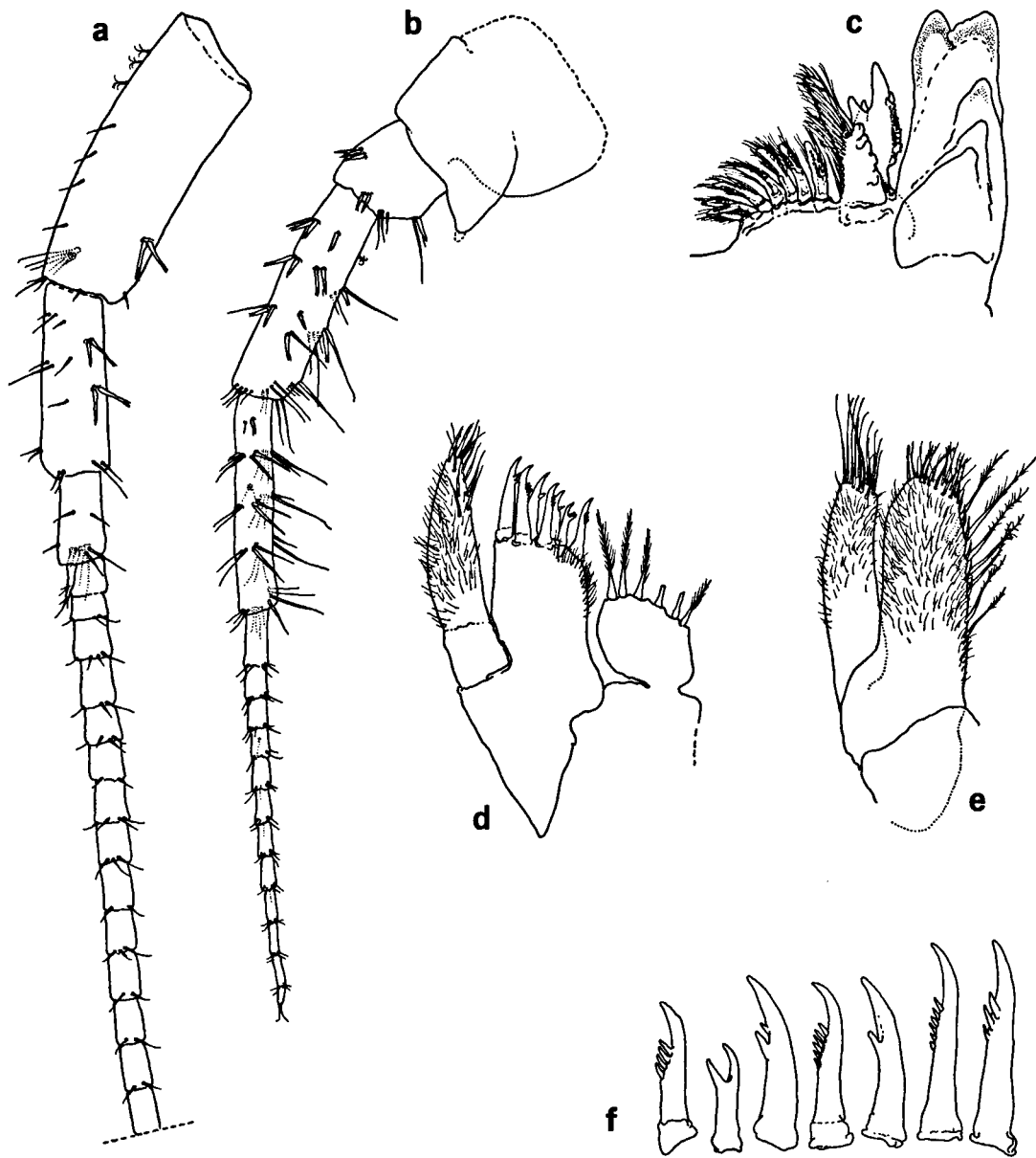


Fig. 10. *Bactrurus mucronatus*. Female (12 mm) from Equality Cave (Saline County, Illinois): A, antenna 1. B, antenna 2. C, dentate part of right mandible. D, maxilla 1. E, maxilla 2. Male (14 mm): F, spine types of inner plate of maxilla 1.

1942. Shelby Co.: drain tile, 3-4 mi. N of Hope, 1 male (JRH), S. Koenemann, U. Englisch and J. Lewis, 10-V-1999. IOWA. - Des Moines Co.: outlet of drain, 0.2 mi. NW of Danville, 4 males, 3 females (USNM), L. Hubricht, 24-IV-1942. Henry Co.: outlet of drain, 1.7 mi. S of Swedesburg, >100 specimens (in 2 lots) (USNM), L. Hubricht, 24-IV-1942; outlet of drain, 1.4 mi. S of New London, 23 specimens (USNM), L. Hubricht, 24-IV-1942. Washington Co.: outlet of drain, 0.5 mi. S of Haskins, 12 specimens (USNM), L. Hubricht, 24-IV-1942; outlet of drain, 1.0 mi. S of Haskins, >10 specimens (USNM), L. Hubricht, 24-IV-1942.

MICHIGAN. - Berrien Co.: Bear Cave, just N of Buchanan, 1 male, 2 females (JRH), D. A. Hubbard, Jr., 28-XII-1993. Monroe Co.: outlet of drain, 0.5 mi. N of Ottawa Lake, >25 specimens (USNM), L. Hubricht, 18-IV-1942; outlet of drain, 1.5 mi. WSW of Dundee, 18 specimens (USNM), L. Hubricht, 18-IV-1942.

OHIO. - Butler Co.: dug well, Francis farm at Shandon, 1 male, 1 female (USNM), S. R. Williams, date not given. Clinton Co.: 15 foot-deep well, Starbucktown, Liberty Turnpike, 1 male (USNM), collector not given, 19-X-1939. Logan Co.: drain pipe outlet, 2.4 mi. SW of Middlesboro, 2

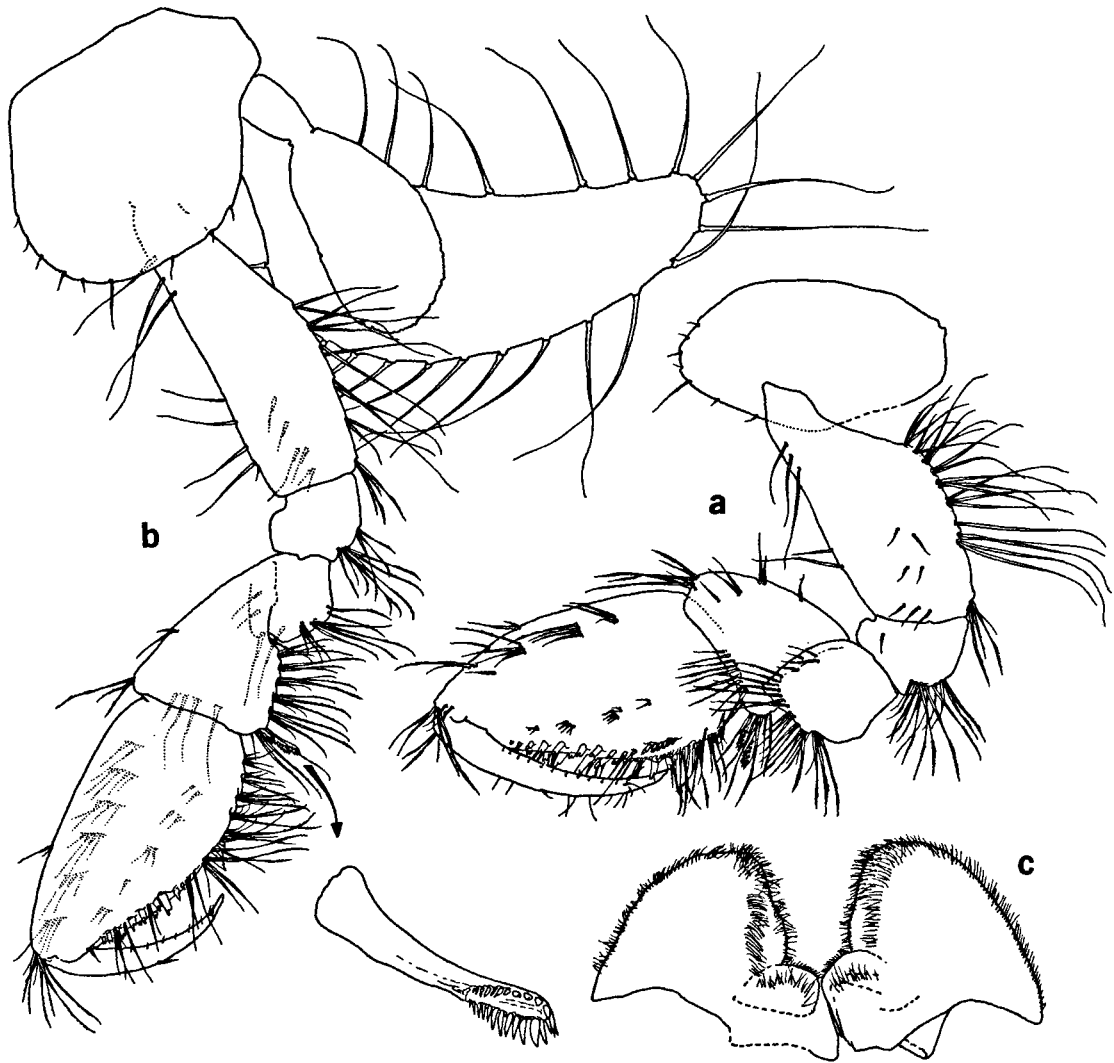


Fig. 11. *Bactrurus mucronatus*. Female (12 mm) from Equality Cave (Saline County, Illinois): A, gnathopod 1 (medial view). B, gnathopod 2 (lateral view, with rastellate spine of carpus enlarged). C, lower lip.

males, 1 female (USNM), L. Hubricht, 17-IV-1942. Lucas Co.: drain pipe outlet, 1.3 mi. S of Reynolds Corner, >10 specimens (USNM), L. Hubricht, 18-IV-1942. Marion Co.: high pressure groundwater pumps at sewage construction site, ca. 2-3 mi. S of Marion, 2 males, 1 female, 3 juveniles (JRH), S. Koenemann and U. Englisch, 6-V-1999; drain pipe outlet, 8.6 mi. SSW of Marion, 2 males (USNM), L. Hubricht, 18-IV-1942. Montgomery Co.: driven well, Phillipsburg, 1 male (USNM), J. S. Hauser, II-1930; drain pipe outlet, 4.4 mi. E of New Lebanon, 9 specimens (USNM), L. Hubricht, 17-IV-1942. Preble Co.: drain pipe, 5 mi. W of Eaton, 13 specimens (JRH), S. Koenemann and U. Englisch, 8-V-1999; >20 specimens (USNM), drain pipe outlet, 0.2 mi. NW of New Hope, L. Hubricht, 17-IV-1942. Wayne Co.: Crayfish burrow, Wooster, (at R14W, T20N,

Sec. 25), 1 male, 1 female (JRH), A. Weaver, 21-IV-1960. Wood Co.: drain pipe outlet, 1.3 mi. SE of Perrysburg, ca. 100 specimens (USNM), L. Hubricht, 18-IV-1942. County ? (not given): drilled well, 2 females (USNM), collector and date not given.

DIAGNOSIS. - *Bactrurus mucronatus* is a medium-sized species with conspicuous secondary sexual dimorphism in the telson: telson in adult males distinctly elongate, reaching 34% length of body (up to three times longer than female telson). Propods of gnathopod 1 and 2 subequal in size. Pereopod 5 slightly shorter than pereopod 4 (8-

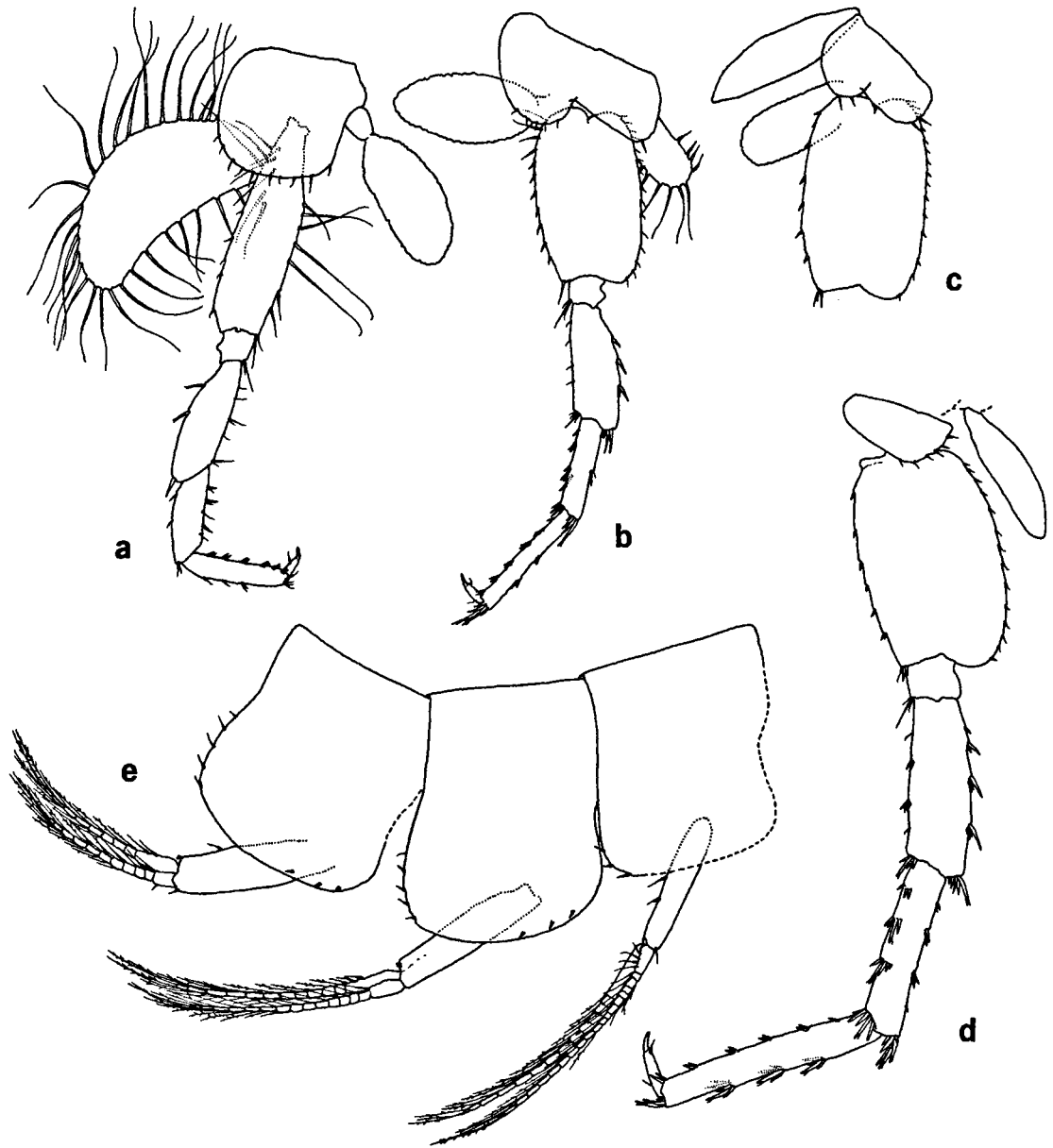


Fig. 12. *Bactrurus mucronatus*. Female (12 mm) from Equality Cave (Saline County, Illinois): A, left pereopod 3. B, left pereopod 5. C, proximal part of left pereopod 6. D, left pereopod 7. Male (14 mm): E, epimeral plates and pleopods 1-3.

9%). Coxal gills on pereopods 2-6. Three pairs of lateral sternal processes on pereonites 6, 7 and pleonite 1 (sometimes absent on pleonite 1); median sternal processes absent. Telson entire or slightly emarginate (2%); width of female telson ca. 54% of length. Most adult specimens 6.0-9.0 mm; largest male 15.5 mm, largest female 12.0 mm.

DESCRIPTION. - Based on adult male (15.5 mm; Fig. 9) and adult female (12.0 mm; Figs. 10-13). Antenna 1 73-75% length of body (Fig. 10A). Primary flagellum with up to 39 segments. Antenna 2 about 41-50% length of antenna 1 (Fig. 10B). Flagellum with up to 12 segments. Lower lip with short mandibular lobes (Fig. 11C) Mandibles: row of eight plumose spines between molar and lacinia mobilis; distal margin of right

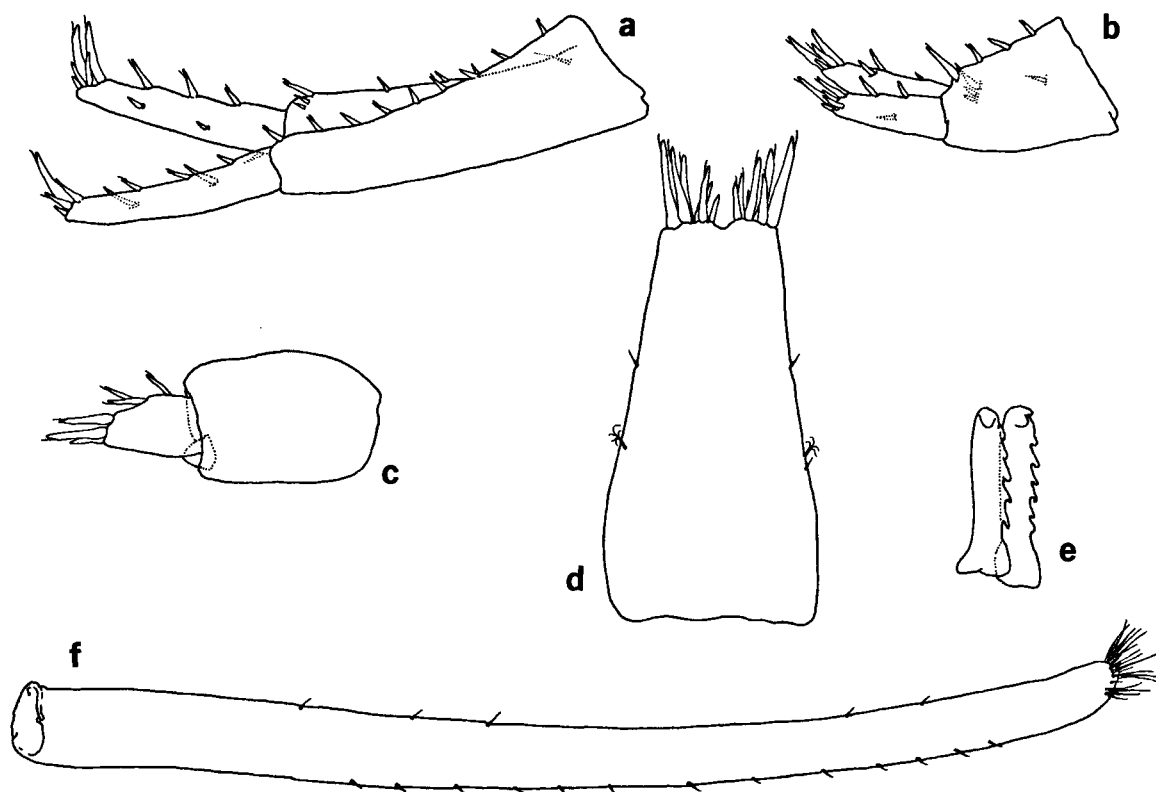


Fig. 13. *Bactrurus mucronatus*. Female (12 mm) from Equality Cave (Saline County, Illinois): A-C, uropods 1-3. D, telson. E, retinaculæ of pleopods. Male (14 mm) from same locality: F, telson.

lacinia mobilis irregularly serrate (Fig. 10C). Palp segment 2 usually without spines, bearing nine to eleven setae on lateral and medial margins (one female with two spines and nine setae); palp segment 3 with ca. 28 short, plumose D-setae, about three long, plumose B-setae and two to four long, plumose A-setae.

Maxilla 1 (Fig. 10D, F): palp segment 2 bearing apically and subapically eight to twelve naked setae and one or two stronger, plumose setae (comb-type, Fig. 3B). Inner plate with six to eight apical, plumose setae.

Maxilla 2 (Fig. 10E): inner plate with oblique row of six to seven strong, plumose setae.

Maxilliped: outer plate armed with five to eight blade-like spines on inner margin. Inner plate apically with three to six naked, blade-like spines (one of which sometimes modified as plumose spine) and three to seven plumose setae apically and subapically.

Gnathopod 1 (Fig. 11A): basis with five to nine

sets of long, naked setae on posterior margin (with up to 20 setae in total), ca. four plumose setae on posterodistal corner, three to four long, naked setae on anteroproximal margin, two shorter setae on anterodistal margin and six to seven short setae on medial surface. Carpus with up to four rastellate spines on posterodistal margin and nine plumose setae on distal margin. Propod subequal in size to propod of gnathopod 2; palmar margin slightly concave, finely serrate at proximal and distal ends, bearing 12 to 14 spines on lateral margin and approximately 10 spines on medial margin; defining angle rounded, shallow (sometimes distinct in adult males: 140°), with six spines medially, five to six short spines on lateral corner and three strong spines between medial and lateral corner spines; posterior (subangular) margin 28% length of propod, with about 17 plumose setae (naked at defining angle); anteromedial surface bearing five to eight rows of plumose setae. Dactyl ca. 81% length of propod.

Coxal plate with six to seven setae.

Gnathopod 2 (Fig. 11B): basis with five to seven sets of long setae on posterior margin (with 13 to 18 setae in total), ca. four plumose setae on posterodistal corner, three to four long, naked setae on anteroproximal margin, one to four naked setae on anterodistal margin (sometimes absent) and a row of six short setae on medial surface. Carpus with approximately five sets of plumose setae on posterior margin, three to seven plumose setae on distal margin and three to four rastellate spines on posterodistal corner (see enlargement of Fig. 11B). Palm of propod almost even (sometimes slightly concave), finely serrate at distal and proximal ends, armed with ca. nine spines on lateral margin and seven to nine spines on medial margin; defining angle rounded, with row of four to five spines on medial corner, two to three spines on lateral corner (long and short spines) and two to four spines between medial and lateral corner spines; proximal (subangular) margin ca. 33% length of propod, bearing seven to nine sets of plumose setae; anteromedial surface bearing seven rows of plumose setae. Dactyl 69% length of propod. Coxal plate round, as wide as long, bearing nine to twelve setae.

Pereopod 3 (Fig. 12A): basis with ca. five long setae and two short setae on proximoposterior margin, five short setae on anterior margin and five long setae on medial surface (sometimes additionally one to three long setae on anteroproximal margin). Coxal plate with nine to ten setae. Pereopod 4: subequal to pereopod 3.

Pereopods 5-7: coxal plate of pereopod 5 with five setae on anterodistal lobe and one seta (or slender spine) on posterodistal corner (Fig. 12B). Coxal plate of pereopod 6 bearing two to three setae on anterodistal lobe and two setae on posterior margin (Fig. 12C). Coxal plate of pereopod 7 with four to five setae on posterior margin (Fig. 12D).

Coxal gill absent from pereopod 7. Most specimens with paired sternal processes present on pereonites 6 and 7 and pleonite 1 (Figs. 12C, D). Pleopods (Fig. 12E): peduncles subequal to those of *B. brachycaudus*. Number of unfused rami segments: pleopod 1 with 12 to 16 segments, pleopod 2 with 11 to 14 segments and pleopod 3 with eight segments. Retinaculæ with unilateral row of hooks (Fig. 13E).

Epimeral plates (Fig. 12E): posterodistal margins bearing five to seven short setae; ventral margins: plate 1 without spines, plates 2 and 3 with two to five spines, respectively.

Uropod 1 (Fig. 13A): peduncle with nine to twelve spines on laterodorsal margin, two to four slender spines on mediodorsal margin and two to three spines on mediodistal corner. Rami subequal, about 61% length of peduncle; inner ramus with four to five apical spines and five to seven spines on dorsal surface. Outer ramus with four to five apical spines and six to seven spines on dorsal surface.

Uropod 2 (Fig. 13B): peduncle with four spines on laterodorsal margin, one spine on mediodorsal margin (sometimes absent) and two to three spines near mediodistal corner. Inner ramus slightly longer than outer ramus, ca. 79% of length peduncle, bearing four to five apical spines and nine to eleven spines on dorsal surface. Outer ramus with four apical spines and two to four spines along dorsal surface.

Uropod 3 (Fig. 13C): peduncle without spines. Inner ramus vestigial, bud-like, about 32% length of outer ramus. Outer ramus distinctly reduced, only about 54% length of peduncle, with three to four apical spines and one to three subapical spines on lateral margin.

Telson sexually dimorphic. Female telson entire or slightly emarginate (2%), tapered, width about 54% of length, armed with approximately 14 apical spines (Fig. 13D). Male telson extremely elongated (Fig. 13F), reaching 34% length of body in adult specimens (about three times longer than female telson), with ca. 22 apical setae and few small setae on lateral margins.

SEXUAL DIMORPHISM AND VARIATION. - Apart from the telson and a longer antenna 1 in most male specimens, the propods of gnathopod 1 and 2 had concave palmar margins in some adult males (opposed to almost even or slightly concave palms in females).

The majority of specimens examined (86%) had two pairs of lateral sternal processes on pereopods 6 and 7 and a smaller pair on pleonite 1. Seven records, exclusively from Illinois, consisted of specimens with paired sternal processes on pereonites 6 and 7 but no processes on pleonite 1. Although three of these seven records occurred

in an isolated cluster in southern Illinois (two records from Equality Cave, Saline Co., and one record from a drain pipe in Gallatin Co.), the remaining four collections seemed to be randomly distributed in north-central Illinois. Their localities were in close proximity to samples with specimens that had sternal processes on pereonites 6 and 7, and pleonite 1. Thus, no apparent geographic separation into morphologically different subpopulations (three pairs vs. two pairs of sternal processes) could be observed.

REMARKS. - *Bactrurus mucronatus* lives in ground-water habitats associated with glacial drift areas of Ohio, Indiana, Illinois, Iowa and Michigan. Although the majority of recorded localities of this species are mainly outlets of farm field drainage systems, a few are dug or drilled wells. The only exceptions are Equality Cave in southeastern Illinois (specimens collected from a small, vadose stream), and Bear Cave in southwestern Michigan. The latter, located near Lake Michigan, has about 100 m of passage developed in Kansan-aged travertine deposits. The specimens were collected from epikarstic drip pools (D. A. Hubbard, pers. com.). In almost all of the drain pipe samples, *B. mucronatus* was accompanied by the stygobiont isopod *Caecidotea kendeighi*. In one instance, *B. mucronatus* was collected together with *B. brachycaudus* from the same drainage catchment basin (see 'Sexual Dimorphism and Variation' and 'Remarks' under *B. brachycaudus*).

Bactrurus mucronatus is easily distinguished from most other *Bactrurus* species by the absence of coxal gills on pereopod 7 and the extremely elongate male telson. However, even in female specimens, the width length ratio of the apically tapered telson is a unique, distinguishing character.

Aquatic crustacean fauna associated with *B. mucronatus* includes the amphipods *Crangonyx forbesi*, *Crangonyx packardii*, *Synurella dentata* and the isopods *Caecidotea kendeighi*, *Caecidotea* sp. and *Lirceus* sp.

***Bactrurus pseudomucronatus* n. sp.**

Figs. 14-15

Bactrurus subsp.(?); Holsinger, 1972: 75-76.

Bactrurus n. sp. or subsp.; Gardner, 1986: 15.

Bactrurus sp.; Holsinger, 1986a: 95.

TYPE LOCALITY. - Mansell Cave (Randolph County, Arkansas).

MATERIAL

ARKANSAS. - Lawrence Co.: deep cistern, 5.5 mi. S of Imboden, 1 male (USNM), B. C. Marshall, 16-IX-1940. Randolph Co.: Mansell Cave, HOLOTYPE male (8.5 mm, on 2 slide mounts; USNM 296423), allotype female (8.5 mm; USNM acc. nr. 330764) and 102 paratypes (USNM), D. Barnett, 5-I-1970.

MISSOURI. - Carter Co.: Jayco Hole Cave, 6 specimens (JRH), J. E. Gardner, 16-IX-1980; Norris Cave, 4 females (JRH), J. E. Gardner, 29-I-1979; Secesh Cave, 2 males, 4 females (JRH), J. E. Gardner, 23-VII-1979; Spout Spring Cave, 2 males, 1 female (JRH), J. E. Gardner, 10-XI-1972; seeps along bluff of Current River, at mouth of Mill Creek, 4 mi. NW of Van Buren, >25 specimens (USNM), L. Hubricht, 3-V-1942. Douglas Co.: seep, 1.5 mi. W of Roosevelt, 7 males, 24 females, 1 juvenile (USNM), L. Hubricht, 1-V-1940. Oregon Co.: Bluehole Cave, 1 male (JRH), J. E. Gardner, 7-VII-1981; Kelly Hollow Cave, 3 females (JRH), J. Craig, 10-II-1973; 2 males, 1 female (JRH), M. Sutton, 20-I-1991; 5 specimens (JRH), S. Koenemann and U. Englisch, 20-V-1999; New Liberty Cave, 1 male (JRH), M. Sutton, 5-I-1991. Shannon Co.: Benton Stretch Cave, 3 males, 9 females (JRH), J. E. Gardner, 22-III-1984; Bootlegger Cave, 1 male (JRH), J. E. Gardner, 20-IV-1983; Douglas Hollow Cave, 2 males, 1 juvenile (JRH), J. E. Gardner, 15-III-1983; Fillchew Cave, 1 female (JRH), J. E. Gardner, 20-III-1984; Forester Cave (formerly known as Bloom Hollow Cave?), 17 specimens (JRH), S. Koenemann and U. Englisch, 19-V-1999; Jam-Up Cave, 1 female (USNM), L. Hubricht, 1-IX-1940; Packrat Cave, 3 females (JRH), J. E. Gardner, 18-IV-1984; cave in Powder Mill Hollow, 23 specimens (USNM), L. Hubricht, 2-VIII-1942; small cave in Searey Hollow, 2 males, 1 female (USNM), L. Hubricht, 1-IX-1940.

DIAGNOSIS.- *Bactrurus pseudomucronatus* is a medium-sized species that shows a high superficial morphological resemblance to *B. mucronatus*. Like the latter, the male telson of *B. pseudomucronatus* is extremely elongate, although at 16-28% of body length, it is proportionally not quite as long as in *B. mucronatus*. Propods of gnathopods 1 and 2 subequal in size. Coxal plate of gnathopod 2 wider than long. Coxal gills on pereopods 2-7 (distinctly reduced on pereopod 7). Two pairs of lateral sternal processes on pereonites 6 and 7; single median sternal processes on pereonites 2 and 3. Telson entire or slightly emarginate (2%); width of female telson 52% of length. Most adult

specimens 5.0-10.0 mm; largest male 13.5 mm, largest female 12.0 mm.

DESCRIPTION. - Based on an allotype female (8.5 mm; Figs. 14, 15A-G) and holotype male (8.5 mm; Fig. 15H).

Antenna 1 49-73% length of body (Fig. 14A). Primary flagellum with up to 24 segments.

Antenna 2 about 43-53% length of antenna 1 (Fig. 14B). Flagellum with nine to eleven segments.

Lower lip subequal to that of *B. mucronatus*.

Mandibles: row of six plumose spines between molar and lacinia mobilis; distal margin of right lacinia mobilis weakly serrate (Fig. 14C). Palp segment 2 with about eight setae on lateral and medial margins; palp segment 3 with approximately 21 short, plumose D-setae, four long, plumose B-setae and two long, plumose A-setae.

Maxilla 1 subequal to that of *B. mucronatus*. Segment 2 of palp with nine naked spines apically (two of which are strong and plumose).

Maxilla 2 subequal to that of *B. mucronatus*. Inner plate with oblique row of five to seven strong, plumose setae.

Maxilliped: outer plate armed with five to six blade-like spines on inner margin. Inner plate with two to five naked, blade-like spines (one of which sometimes modified as plumose spine or spine with jagged margins) and four to six plumose setae.

Gnathopod 1 (Fig. 14D): basis with four sets of long, naked setae on posterior margin (with about nine long setae in total), four plumose setae on posterodistal corner, three to four long, naked setae on anteroproximal margin, one seta on anterodistal margin and two to three setae on medial surface. Carpus with two rastellate spines on posterodistal margin and five plumose setae on distal margin. Palmar margin of propod slightly concave, with faint serrations on proximal and distal ends, bearing seven to nine spines on lateral margin and five to eight spines on medial margin; defining angle rounded, with four to five spines medially and a row of three to four short spines on lateral corner; posterior (subangular) margin 30% length of propod, with about nine plumose setae (naked at defining angle); anteromedial surface with three rows of plumose setae. Dactyl ca. 78% length of propod. Coxal plate

with four to five setae.

Gnathopod 2 (Fig. 14E): basis with five sets of long setae on posterior margin (with about 11 long setae in total), ca. three plumose setae on posterodistal corner, three long, naked setae on anteroproximal margin, three naked setae on anterodistal margin and three to four short setae on medial surface. Carpus with three sets of plumose setae on posterior margin, two plumose setae on distal margin and three rastellate spines on posterodistal corner. Palm of propod slightly concave, with faint serrations at distal and proximal ends, with eight to ten spines on lateral margin and four to five spines on medial margin; defining angle rounded, shallow, bearing three to four spines on medial corner and two spines on lateral corner; proximal (subangular) margin ca. 39% length of propod, bearing four sets of plumose setae; anteromedial surface bearing five rows of plumose setae. Dactyl 71% length of propod. Coxal plate wider than long, with five to seven setae.

Pereopod 3 (Fig. 15A): basis with six to eight long setae on proximoposterior margin (excluding setae on posterodistal corner), five short setae on anterior margin, two to three long setae on anteroproximal margin and two to four long setae on medial surface. Coxal plate with nine to eleven setae.

Pereopod 4: subequal to pereopod 3.

Pereopods 5-7: anterior margins of bases with only five to seven short spines. Coxal plate of pereopod 5 with three to four setae on anterodistal lobe and one seta on posterodistal corner (Fig. 15B). Coxal plate of pereopod 6 subequal to that of *B. mucronatus* (Fig. 15C). Coxal plate of pereopod 7 with four setae on posterior margin (Fig. 15D).

Coxal gills on pereopods 2-7, distinctly reduced on pereopod 7 (less than half the size of coxal gill on pereopod 6). Lateral sternal processes present on pereonites 6 and 7 (Figs. 15C, D).

Pleopods: number of unfused rami segments (for outer and inner rami): pleopod 1 with nine to twelve segments, pleopod 2 with seven to nine segments and pleopod 3 with five segments. Retinaculae subequal to those of *B. brachycaudus* (Fig. 15E)

Epimeral plates (Fig. 15F): posterodistal margins bearing two to five short setae each; ventral mar-

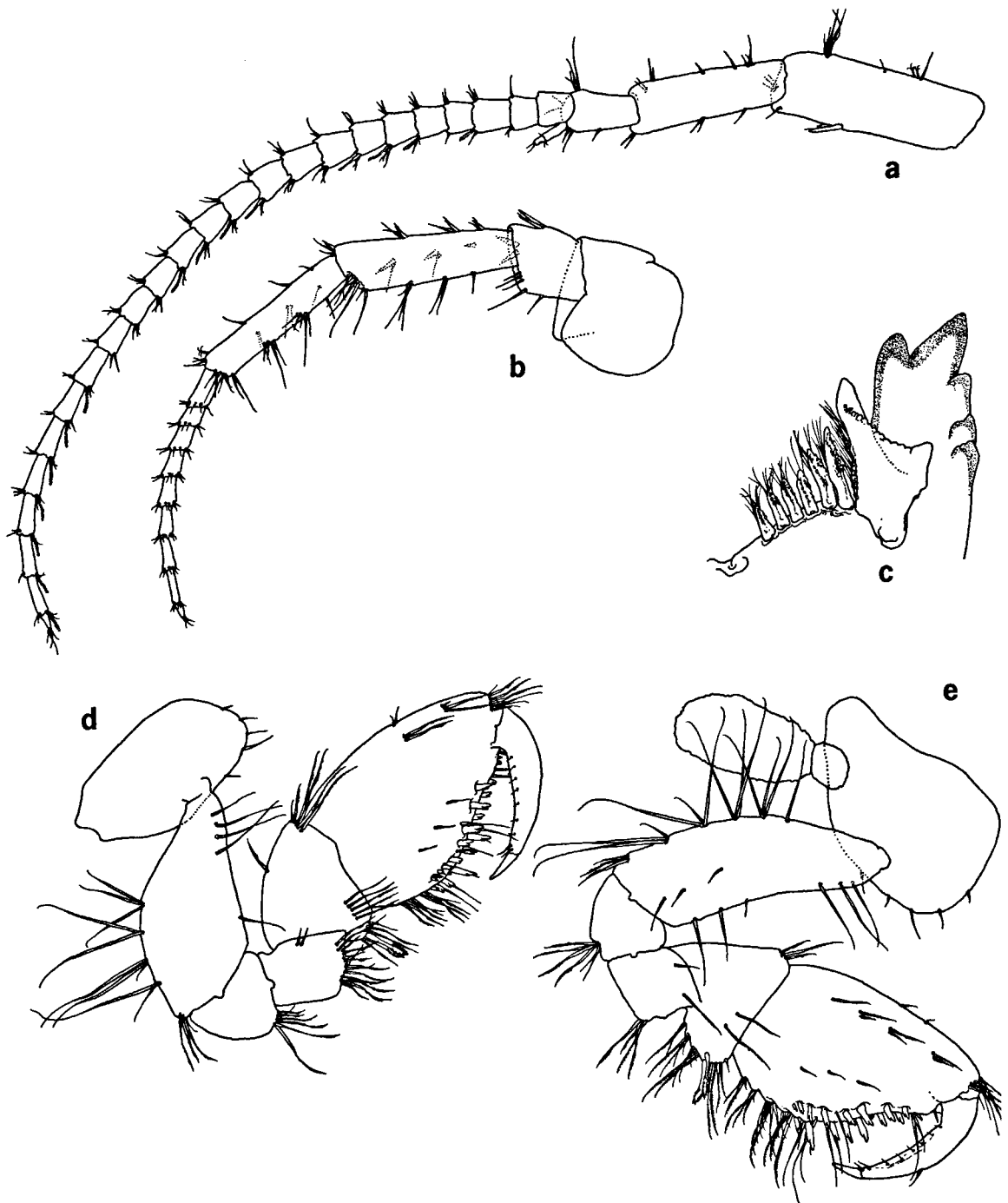


Fig. 14. *Bactrurus pseudomucronatus* n. sp. Allotype female (8.5 mm) from Mansell Cave (Randolph County, Arkansas): A, antenna 1. B, antenna 2. C, dentate part of right mandible. D, gnathopod 1 (medial view). E, gnathopod 2 (medial view).

gins: plate 1 with two to three spines, plate 2 with three spines and plate 3 with two to four spines. Uropod 1: peduncle with seven to nine spines on laterodorsal margin, two setae on mediodorsal

margin and two spines on mediodistal corner. Length peduncle/outer ramus and armature of inner ramus subequal to that of *B. mucronatus*. Outer ramus with four to five spines on dorsal

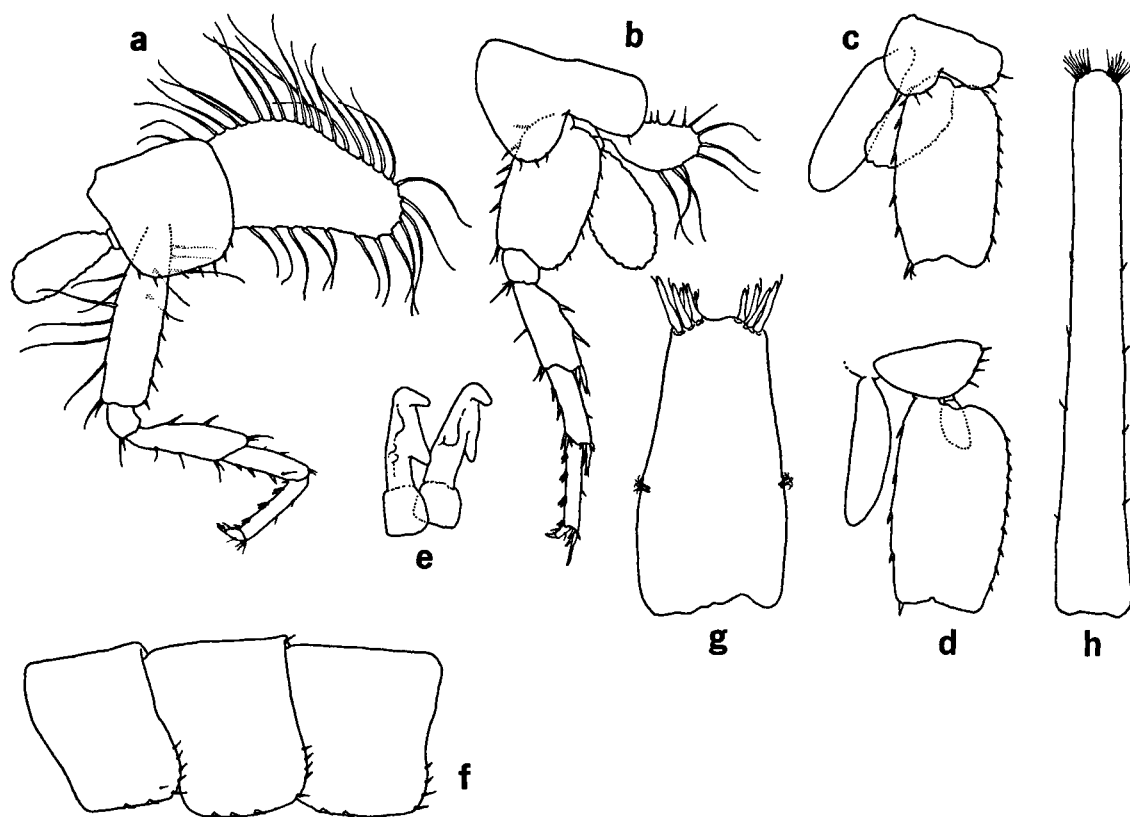


Fig. 15. *Bactrurus pseudomucronatus* n. sp. Allotype female (8.5 mm) from Mansell Cave (Randolph County, Arkansas): A, left pereopod 3. B, left pereopod 5. C-D, proximal parts of pereopods 6 and 7. E, retinaculæ of pleopods. F, epimeral plates 1-3. G, telson. Holotype male (8.5 mm) from same locality: H, telson.

surface.

Uropod 2: peduncle with two to three spines on laterodorsal margin and three spines near mediiodistal corner. Length peduncle/outer ramus subequal to that of *B. mucronatus*. Inner ramus with three to four spines on dorsal surface. Outer ramus bearing two to five spines along dorsal surface.

Uropod 3: subequal to that of *B. mucronatus*. Outer ramus bearing two to three apical spines and one to two subapical spines on lateral margin.

Telson sexually dimorphic. Female telson (Fig. 15 G) entire or slightly emarginate (2%), slightly tapered, width about 52% of length, bearing 10 apical spines. Male telson (Fig. 15H) extremely elongate, reaching 16-22% length of body in adult specimens, with about 20 apical setae (in two clusters) and few small setae on lateral mar-

gins.

SEXUAL DIMORPHISM AND VARIATION. - As in *B. mucronatus*, the only noticeable secondary sexual dimorphism was observed in the telson and in the length of the male antenna 1. No marked morphological variation was noted otherwise.

REMARKS. - The range of *B. pseudomucronatus* is restricted to karst areas in the Salem Upland section of the Ozark Plateaus. The species typically occurs in caves and seeps in southern Missouri (several caves, a few seeps) and northern Arkansas (one cave, one deep cistern).

The type locality, located in Eleven Point River Valley (White River drainage), is developed in Cotter limestone of Ordovician age. The type series consisted of 109 specimens collected from a small, shallow pool approximately 10 m from

the entrance (D. E. Barnett, pers. com.).

Bactrurus pseudomucronatus can be distinguished from *B. mucronatus* by the characters given in the diagnosis (see also: *B. mucronatus*, 'Remarks').

Aquatic crustacean fauna associated with *B. pseudomucronatus* includes the amphipod *Stygobromus* n. sp. (Holsinger, in ms.) and the isopod *Caecidotea tridentata*.

ETYMOLOGY. - The epithet *pseudomucronatus*, meaning 'false *mucronatus*', alludes to the morphological similarity of *B. pseudomucronatus* to *B. mucronatus* (*B. pseudomucronatus* was sometimes falsely identified as *B. mucronatus*).

***Bactrurus wilsoni* n. sp.**

Figs. 16-19

Bactrurus sp.; Holsinger, 1986a: 95.

TYPE LOCALITY. - Well in Culwell residence, Hayden (Blount County, Alabama).

MATERIAL

ALABAMA. - Blount Co.: well in kitchen of Wilson residence (presently owned by Charlie and Jane Culwell), 2.1 mi. NE of Hayden, 1 male paratype, Jimmy Wilson, J. R. Wilson and L. M. Ferguson, 12-VIII-1982; allotype female (11.5 mm; JRH 3901), J. R. Wilson, V-1983; 1 male, 1 female, paratypes (JRH), J. R. Wilson, Jul.-Aug. 1983 (specimens donated to present study by L. M. Ferguson); **HOLOTYPE** male (16.0 mm; USNM 296424), J. Culwell, 9-VI-1999, and 1 male paratype (JRH), 12-VI-1999.

DIAGNOSIS. - A medium-sized species distinguished by sexual dimorphism in uropod 1 and telson. Distal margin of right lacinia mobilis with large, irregular denticles. Propod of gnathopod 1 distinctly wider and shorter than that of gnathopod 2. Pereopod 5 about as long as pereopod 4. Coxal gills on pereopods 2-7. Two pairs of lateral sternal processes on pereonites 6 and 7; median sternal processes absent. Peduncle of male uropod 1 with serrate distal process. Telson of adult male slightly longer than telson of female, apical spines shorter than those of female; telson entire or with V-shaped excavation (12-15% cleft), width 75-77% of length. Largest male 16.0 mm, largest female 15.5 mm.

DESCRIPTION. - Based on holotype male (16.0

mm), paratype male (15.5 mm; Figs. 16A, B, 17A, B, 18F, 19A-F) and paratype female (10.5 mm; Figs. 16C-E, 17C, 18A-E, 19G-J).

Antenna 1 subequal to that of *B. mucronatus*, reaching 58-78% length of body. Primary flagellum with up to 44 segments.

Antenna 2 about 31-47% length of antenna 1 (Fig. 16A). Flagellum with up to 12 segments.

Lower lip with relatively well-developed outer lobes (Fig. 16B).

Mandibles: row of five to seven plumose spines between molar and lacinia mobilis; distal margin of right lacinia mobilis with large, irregular denticles (Fig. 16C). Palp segment 2 with 10 to 11 setae on lateral and medial margins; palp segment 3 with 19 to 22 short, plumose D-setae, about four long, plumose B-setae and one long, plumose A-seta (sometimes absent).

Maxilla 1: palp segment 2 bearing apically and subapically six to seven naked setae. Outer plate with seven bidentate and multidentate spines (bidentate spines sometimes absent; Fig. 16D).

Inner plate with five to six apical, plumose setae. Maxilla 2: outer plate bearing apically 10 to 11 mostly naked setae. Inner plate with oblique row of seven strong, plumose setae on inner margin and 17 plumose, apical and subapical setae.

Maxilliped: outer plate armed with two to three blade-like spines and 10 to 19 naked setae on inner margin (Fig. 16E). Inner plate apically with about three blade-like spines and five plumose setae.

Gnathopod 1 (Fig. 17A): basis with five to seven sets of long, naked setae on posterior margin plus row of four to six long, naked setae on proximo-posterior margin (with about 16 setae in total), four plumose setae on posterodistal corner, two to three long, plumose setae on anteroproximal margin, two to three setae on anterodistal margin and two short setae on medial surface. Carpus with two rastellate spines on posterodistal margin and five to eight plumose setae on distal margin. Propod slightly shorter and wider than propod of gnathopod 2; palmar margin almost even, crenulated, bearing 10 to 14 spines on lateral margin and seven to ten spines on medial margin; angle well-defined (ca. 135°), with four spines medially and four to five spines on lateral corner; posterior (subangular) margin 20% length of propod, with two to three sets of plumose setae; antero-

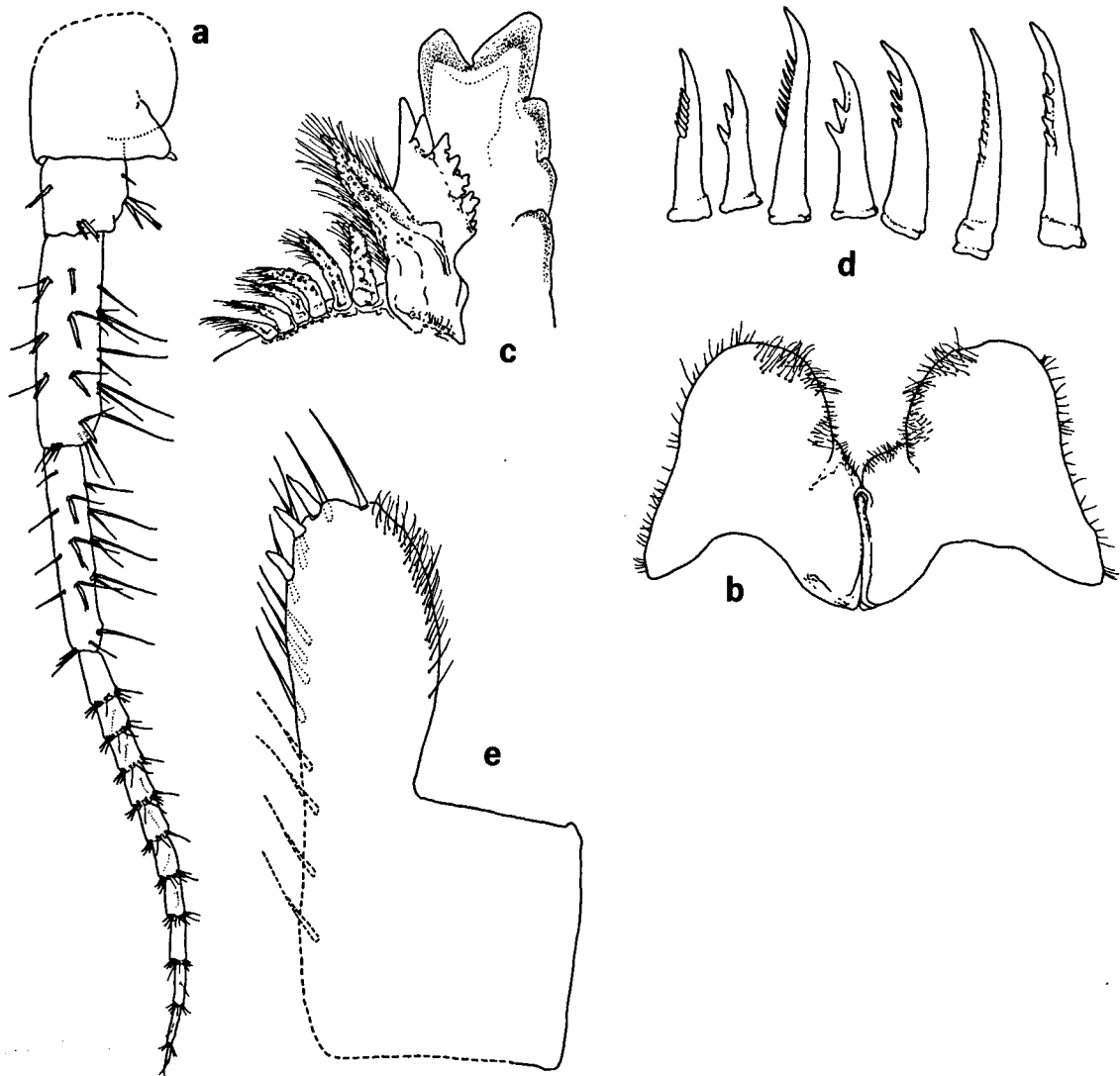


Fig. 16. *Bactrurus wilsoni* n. sp. Paratype male (15.5 mm) from well in Hayden (Blount County, Alabama): A, antenna 2. B, lower lip. Paratype female (10.5 mm) from same locality: C, dentate part of right mandible. D, spine types of inner plate of maxilliped. E, outer plate of maxilliped.

medial surface bearing four rows of plumose setae. Dactyl ca. 86% length of propod. Coxal plate with three setae.

Gnathopod 2 (Fig. 17B): basis with six to seven sets of long setae on posterior margin (with about 13 setae in total), three plumose setae on posterodistal corner, two long, naked setae on antero-proximal margin, five naked setae on anterodistal margin and two short setae on medial surface. Carpus with three to four sets of plumose setae on posterior margin, three plumose setae on dis-

tal margin and four to five rastellate spines on posterodistal corner (see enlargement of Fig. 17B). Palm of propod almost even, surface crenulated, bearing eight to twelve spines on lateral margin and 10 to 12 spines on medial margin (no distinct separation between corner spines and palmar spines on medial margin); defining angle ca. 135° , with about two spines on lateral corner; proximal (subangular) margin ca. 36% length of propod, bearing four sets of plumose setae; anteromedial surface bearing six rows of plumose

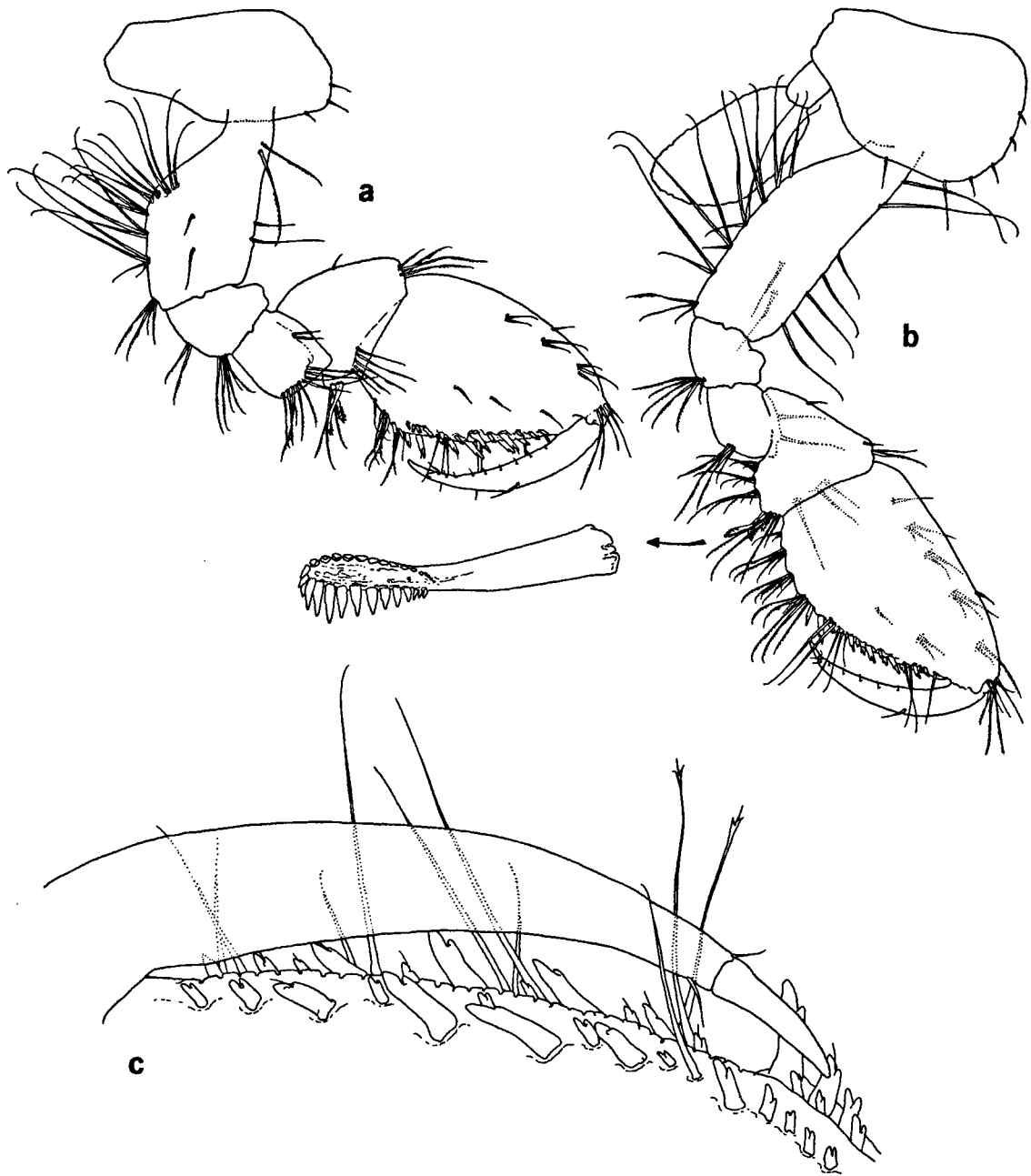


Fig. 17. *Bactrurus wilsoni* n. sp. Paratype male (15.5 mm) from well in Hayden (Blount County, Alabama): A, gnathopod 1 (medial view). B, gnathopod 2 (lateral view, with rastellate spine of carpus enlarged). Paratype female (10.5 mm) from same locality: C, palm of propod of gnathopod 1 (medial view).

setae. Dactyl 74% length of propod. Coxal plate wider than long, bearing five to six setae.

Pereopod 3 (Fig. 18A): basis with ca. five long setae and one to two short setae on posterior margin, four to five short setae on anterior margin,

two to three long setae on anteroproximal margin and one to two long setae on proximomedial surface. Coxal plate with four to six marginal setae.

Pereopod 4: subequal to pereopod 3. Coxal plate with six marginal setae (Fig. 18F).

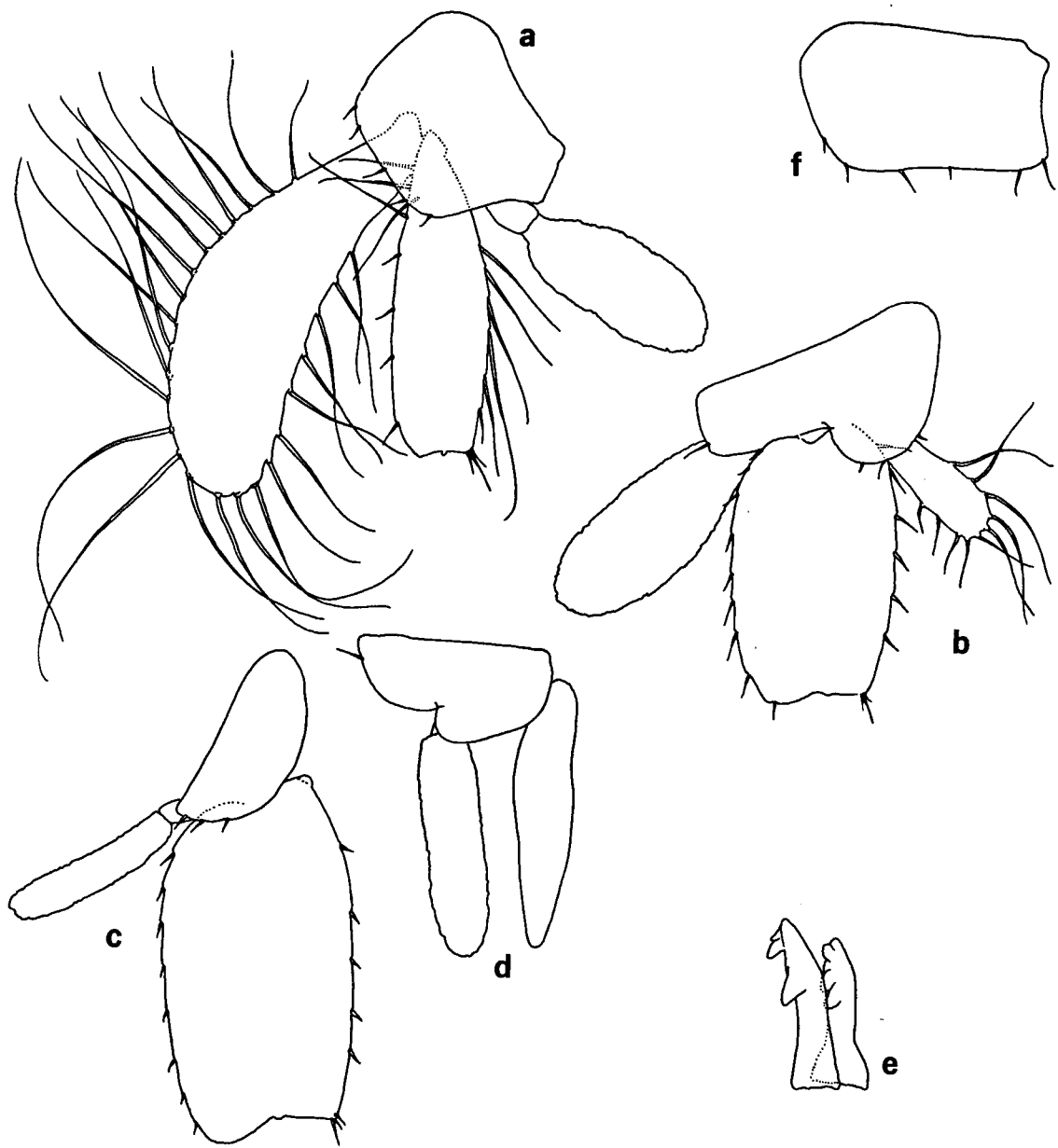


Fig. 18. *Bactrurus wilsoni* n. sp. Paratype female (10.5 mm) from well in Hayden (Blount County, Alabama): A-C, proximal parts of pereopods 3, 5 and 7. D, coxal plate, with coxal gill and lateral sternal process of pereonite 6. E, retinaculum of pleopods. Paratype male (15.5 mm) from same locality: F, coxal plate of pereopod 4.

Pereopod 5 (Fig. 18B): anterior margin of basis with six relatively long, slender spines; posterior margin with seven to nine setae. Coxal plate with three setae on anterodistal lobe and one slender spine on posterodistal corner.

Pereopods 6 and 7: anterior margins of bases with four to five short spines; posterior margins bearing eight to twelve short setae. Coxal plate of

pereopod 6 with one seta on posterodistal lobe (Fig. 18D). Coxal plate of pereopod 7 with three setae on posterior margin (Fig. 18C).

Coxal gills on pereopods 2-7, only slightly reduced on pereopod 7. Lateral sternal processes present on pereonites 6 and 7 (Fig. 18D).

Pleopods (Figs. 19A-C): width of peduncles gradually increasing from pleopod 1 to 3. Number of

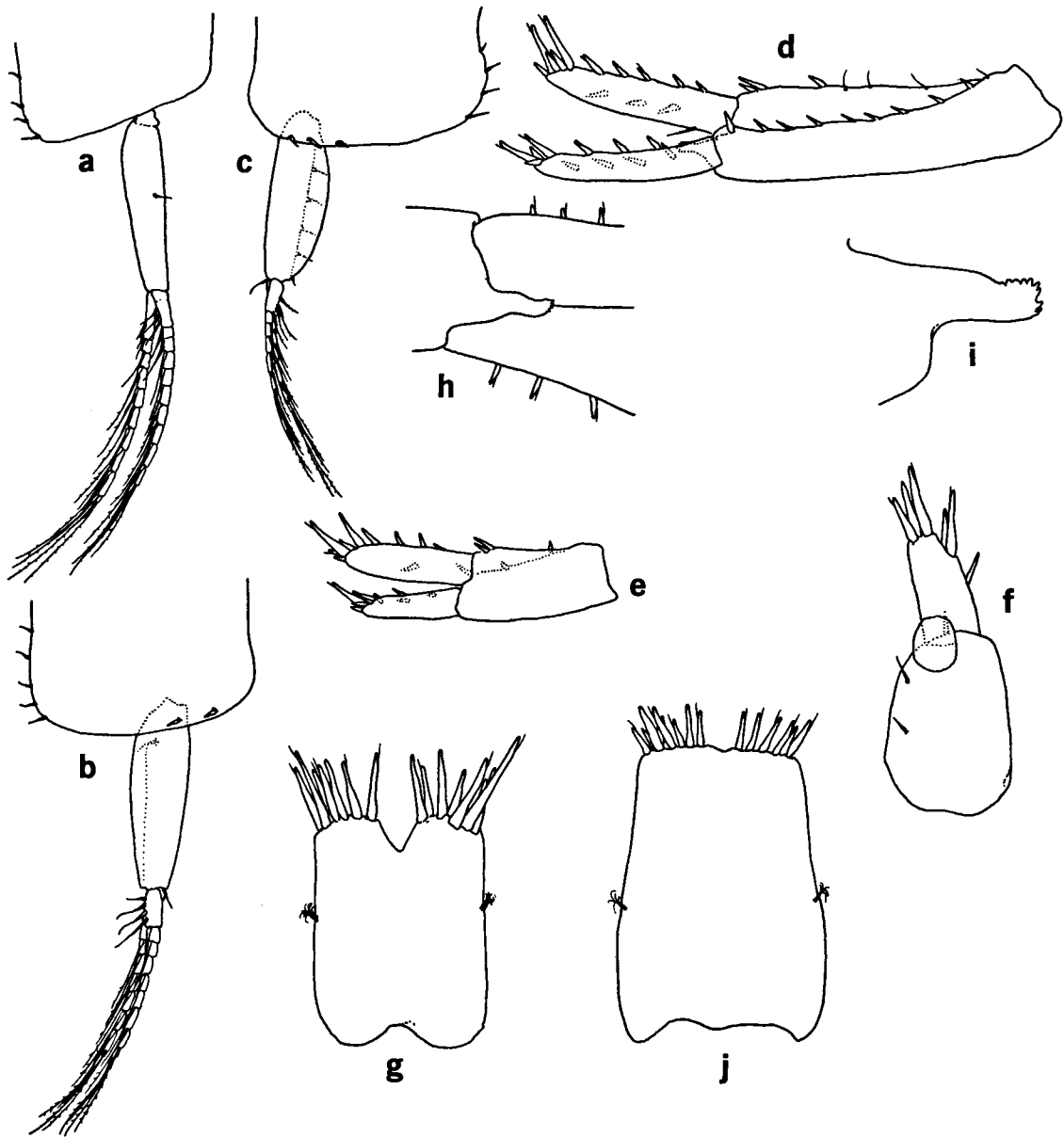


Fig. 19. *Bactrurus wilsoni* n. sp. Paratype male (15.5 mm) from well in Hayden (Blount County, Alabama): A-C, pleopods 1-3. D-F, uropods 1-3. Paratype female (10.5 mm) from same locality: G, telson. Male (16.0 mm). H-I, enlarged peduncular process of uropod 1. J, telson.

unfused rami segments: pleopod 1 with eight to ten segments, pleopod 2 with eight segments and pleopod 3 with six to seven segments. Retinaculae subequal to those of *B. brachycaudus* (Fig. 18E). Epimeral plates (Fig. 19A-C): posterodistal margins bearing three to five short setae; plate 1 without spines, plates 2 and 3 with two to three spines, respectively.

Uropod 1 (Fig. 19D): peduncle with eight to nine spines on laterodorsal margin, one spine on mediodorsal margin (sometimes absent) and two to three spines on mediodistal corner. Rami about 56% length of peduncle; inner ramus with five apical spines and seven to eight spines on dorsal surface. Outer ramus with four to five apical spines and about seven spines on dorsal sur-

face. Peduncle of male with ventrodorsal, serrate process (Figs. 19H, I).

Uropod 2 (Fig. 19E): peduncle with three to four spines on laterodorsal margin and two to four spines near mediodistal corner. Inner ramus longer than outer ramus, about 83% of length peduncle, bearing five apical spines and four to five spines on dorsal surface. Outer ramus with five apical spines and three to four spines on dorsal surface.

Uropod 3 (Fig. 19F): peduncle with one spine on distal margin. Inner ramus vestigial, about 48% length of outer ramus. Outer ramus reduced, about 64% length of peduncle, with three to four apical spines and one to five subapical spines on lateral margin.

Telson sexually dimorphic; apical margin entire or with V-shaped excavation (12-15% cleft), armed with six to nine apical spines per lobe; width about 75% of length in examined males and 77% of length in females; spines of female telson (Fig. 19G) distinctly longer than spines of male telson (Fig. 19J).

SEXUAL DIMORPHISM AND VARIATION. - The telson of the holotype male had an entire distal margin, whereas those of all other specimens had a V-shaped excavation (12-15% cleft). Secondary sexual dimorphism occurs in both uropod 1 and telson.

REMARKS. - To date, *B. wilsoni* is known only from a single groundwater aquifer on the Cumberland Plateau in northern Alabama. The type locality, a drilled well approximately 17 m deep, is apparently in Bangor limestone of Mississippian age. Specimens from the well were collected with a bucket-and-rope system through an opening in the kitchen floor of the Culwell house. One of the first samples (May 1983) also contained three specimens of the stygobiont amphipod *Stygobromus* n. sp. (Holsinger, in ms.).

Bactrurus wilsoni is morphologically very similar to the new species *B. angulus* and *B. cellulanus*, both of which have a serrate peduncular process on male uropod 1.

ETYMOLOGY. - The species is named in honor of Mr Johnny R. Wilson, who helped with collecting the first specimens in 1982 and also assisted with

the field work in the spring of 1999.

***Bactrurus angulus* n. sp.**

Figs. 20-22

Bactrurus sp.; Holsinger, 1986a: 95; 1986b: 540, fig. 2; Holsinger & Culver, 1988: 25-26.

TYPE LOCALITY. - Saur Kraut Cave, (Claiborne Co., Tennessee).

MATERIAL

TENNESSEE. - Claiborne Co.: Kings Saltpetre Cave, 2 female paratypes (JRH), J. R. Holsinger, 24-XI-1973; Saur Kraut Cave, HOLOTYPE male (16.7 mm; USNM 296421), J. R. Holsinger and D. C. Culver, 4-VIII-1977.

VIRGINIA. - Lee Co.: Cumberland Gap Saltpetre Cave, allotype female (11.2 mm; JRH 1994), 1 male and 2 female paratypes (JRH), J. R. Holsinger, V. M. Dalton (Tipton), et al., 15-VII-1979.

DIAGNOSIS. - A medium-sized species morphologically closely allied with *B. wilsoni*. It can be distinguished by the following characters: propod of gnathopod 1 noticeably wider and slightly shorter than that of gnathopod 2; defining angle of gnathopod 1 very distinct (ca. 120°). Pereopod 5 about as long as pereopod 4. Coxal gills on pereopods 2-7. Two pairs of lateral sternal processes on pereonites 6 and 7; median sternal processes absent. Peduncle of male uropod 1 with serrate distal process. Telson of adult males sometimes slightly longer than telson of female, apical spines shorter than those of female; telson with shallow notch or V-shaped excavation (5-19% cleft). Largest male 16.7 mm, largest female 14.0 mm.

DESCRIPTION. - Based on holotype male (16.7 mm; Figs. 21E, 22A-H), allotype female (11.2 mm; Figs. 20A-E, 21A-C, 22I) and paratype male (13.5 mm; Fig. 21D).

Antenna 1 subequal to that of *B. mucronatus*, about 66% length of body (Fig. 20A). Primary flagellum with up to 41 segments.

Antenna 2 approximately 43-47% length of antenna 1 (Fig. 20B). Flagellum with 11 to 12 segments.

Lower lip subequal to that of *B. wilsoni* (Fig. 20C). Mandibles: row of six to seven plumose spines between molar and lacinia mobilis; distal margin

of right lacinia mobilis with irregular serrations (Fig. 20D). Palp segment 2 with 12 to 13 setae on lateral and medial margins; palp segment 3 with 24 to 25 short, plumose D-setae, two to three long, plumose B-setae and two to three long, plumose A-seta.

Maxilla 1: palp segment 2 bearing apically and subapically seven to eight naked setae, one to two of which are stronger and plumose. Outer plate with seven bidentate and multidentate spines. Inner plate bearing five apical, plumose setae.

Maxilla 2: outer plate apically with 15 to 17 mostly naked setae. Inner plate with oblique row of seven plumose setae and up to 20 plumose setae apically and subapically.

Maxilliped: outer plate with four blade-like spines and 14 to 16 naked setae on inner margin. Inner plate apically with four naked, blade-like spines, one plumose apical spine, and three to four plumose setae on subapical inner margin (brush-type setae, Fig. 3C).

Gnathopod 1 (Fig. 21A): basis with five to seven sets of long, naked setae on posterior margin (with about 22 setae in total), three to five plumose setae on posterodistal corner, two naked setae on anteroproximal margin, three naked setae on anterodistal margin and three naked setae on medial surface. Carpus with three rastellate spines on posterodistal margin (see enlargement of Fig. 17B) and about 10 plumose setae on distal margin. Propod noticeably wider and slightly shorter and than propod of gnathopod 2; palmar margin almost even, surface crenulated, bearing ca. eight spines on lateral margin and nine to ten spines on medial margin; defining angle distinct (ca. 120°), with seven slender spines medially and row of five to six spines on lateral corner; posterior (subangular) margin 18% length of propod, with two sets of plumose setae; anteromedial surface bearing four rows of plumose setae. Dactyl ca. 95% length of propod. Coxal plate with four setae.

Gnathopod 2 (Fig. 21B): basis with eight sets of long setae on posterior margin (with ca. 14 setae in total), three to five plumose setae on posterodistal corner, three long, naked setae on anteroproximal margin, three to five naked setae on anterodistal margin and two short setae on medial surface. Carpus with four to five sets of plumose setae on posterior margin, seven to nine

plumose setae on distal margin and four to five rastellate spines on posterodistal corner (see enlargement of Fig. 17B). Palm of propod crenulated, with 10 to 11 spines on lateral margin and 10 to 12 spines on medial margin; defining angle 135-140°, with two to four spines on lateral corner and row of four to five smaller spines on medial corner; proximal (subangular) margin ca. 31% length of propod, bearing four to five sets of plumose setae; anteromedial surface bearing six rows of plumose setae. Dactyl 81% length of propod. Coxal plate slightly wider than long, bearing six to seven setae.

Pereopod 3 (Fig. 22A): basis with five to six long setae and one to two short setae on posterior margin, five to six short setae on anterior margin and four to six long setae on anteroproximal margin and surface. Coxal plate with seven to eight setae.

Pereopod 4: subequal to pereopod 3. Coxal plate with six to nine setae (Fig. 22D).

Pereopod 5 (Fig. 22B): anterior margin of basis with five to seven short spines; posterior margin with nine to eleven setae. Coxal plate with three setae on anterodistal lobe and one seta on posterodistal corner.

Pereopods 6 and 7 subequal to those of *B. wilsoni*. (Figs. 22C, E).

Coxal gills on pereopods 2-7, distinctly reduced on pereopod 7 (less than half the size of coxal gill on pereopods 5 and 6; Fig. 22C). Lateral sternal processes present on pereonites 6 and 7 (Fig. 22C).

Pleopods: width of peduncles gradually increasing from pleopod 1-3. Number of unfused rami segments: pleopod 1 with 12 segments, pleopod 2 with nine to ten segments and pleopod 3 with eight segments. Retinaculae asymmetrical, with unilateral row of small hooks (Fig. 20E).

Epimeral plates: posterodistal margins with four to five short setae each; plate 1 without spines, plate 2 bearing two spines and plate 3 with three spines.

Uropod 1 (Fig. 22F): peduncle with eight to nine spines on laterodorsal margin, three to four spines on mediodorsal margin and two to three spines on mediodistal corner. Rami about 51% length of peduncle; inner ramus with four to five apical spines and about six spines on dorsal surface (some of which relatively long). Outer ramus with

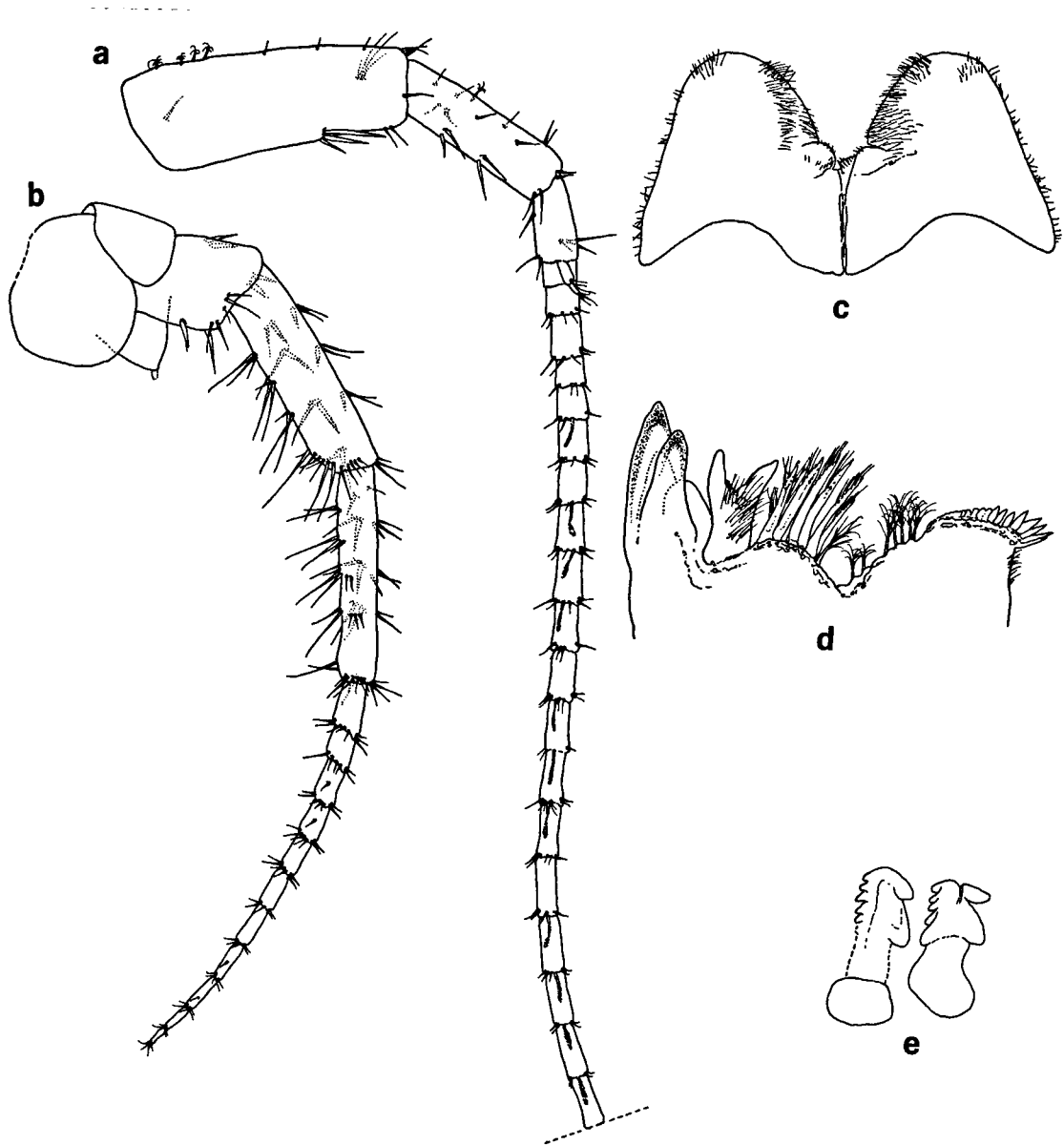


Fig. 20. *Bactrurus angulus* n. sp. Allotype female (11.2 mm) from Cumberland Gap Saltpetre Cave (Lee County, Virginia): A, antenna 1. B, antenna 2. C, lower lip. D, dentate part of right mandible. E, retinaculæ of pleopods.

five to six apical spines and ca. six spines on dorsal surface. Peduncle of male with ventrodistal, serrate process (Figs. 22F, G).

Uropod 2 (Fig. 22I): peduncle with three to four spines on laterodorsal margin, two spines on mediodorsal margin and three to four spines on mediodistal corner. Inner ramus longer than outer ramus, about 71% of length of peduncle, bearing four apical spines and five to six spines on dorsal surface. Outer ramus with five apical

spines and about three spines on dorsal surface. Uropod 3 (Fig. 22H): peduncle armed with two spines on distal margin. Inner ramus vestigial, only about 27% length of outer ramus. Outer ramus reduced, about 83% length of peduncle, with three to four apical spines, one to three subapical spines on lateral margin and one to two subapical spines on medial margin.

Telson (Figs. 21C-F): apical margin with shallow notch or V-shaped excavation (5-19% cleft), bear-

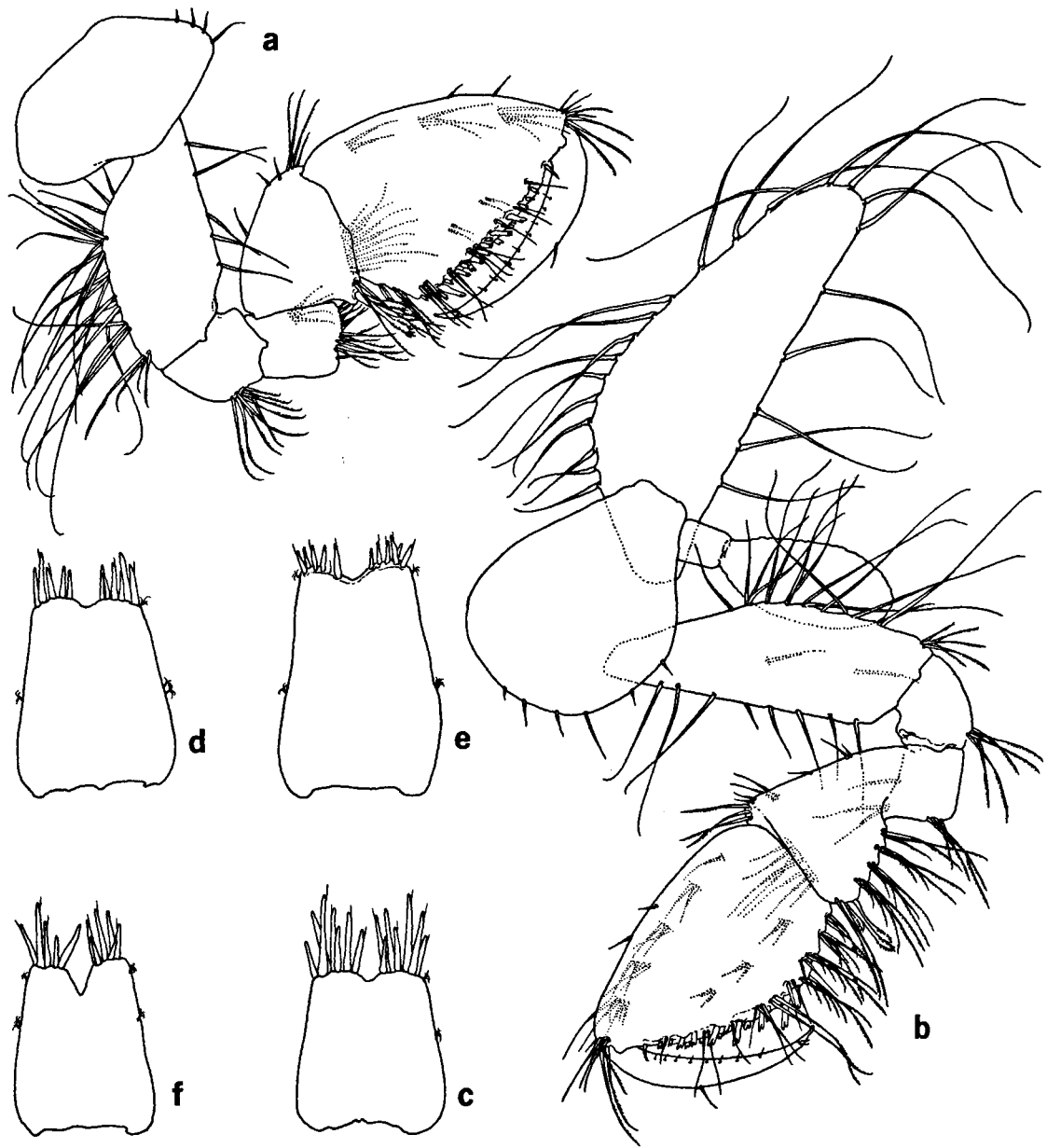


Fig. 21. *Bactrurus angulus* n. sp. Allotype female (11.2 mm) from Cumberland Gap Saltpetre Cave (Lee County, Virginia): A, gnathopod 1 (lateral view). B, gnathopod 2 (lateral view). C, telson. Male (13.5 mm): D, telson. Holotype male (16.7 mm) from Saur Kraut Cave (Claiborne County, Tennessee): E, telson. Paratype female (12 mm) from King's Saltpetre Cave (Claiborne County, Tennessee): F, telson.

ing 11 to 14 apical spines. Width of male telson 73-87% of length, with relatively short apical spines; width of female telson 85-106% of length, apical spines distinctly longer than spines of male telson.

SEXUAL DIMORPHISM AND VARIATION. - One of

the two examined males had a telson which was distinctly longer than wide (holotype male), whereas the telsonic width/length ratio of the smaller male did not differ from those of the females. With the exception of one female telson showing a distinct, V-shaped excavation (19% cleft), the majority of the specimens examined

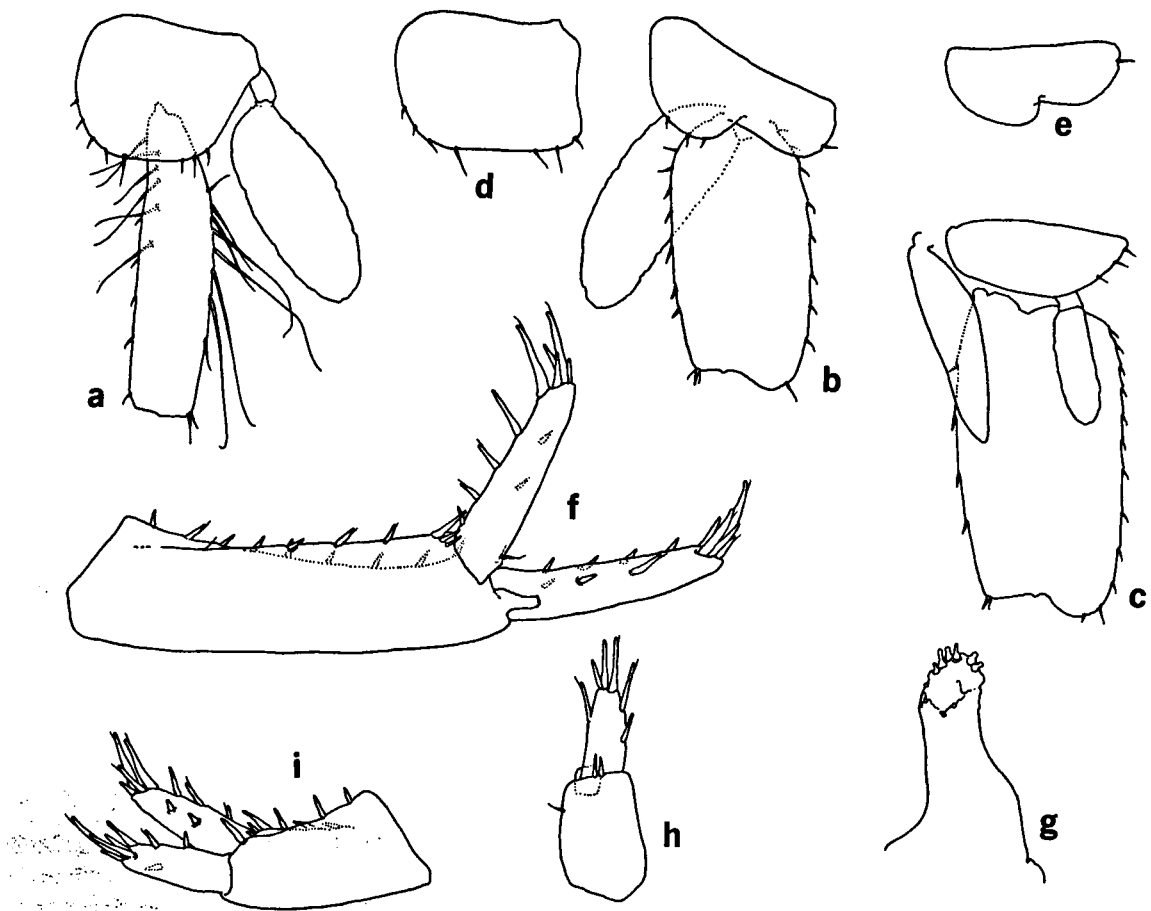


Fig. 22. *Bactrurus angulus* n. sp. Holotype male (16.7 mm) from Saur Kraut Cave (Claiborne County, Tennessee): A-C, proximal parts of pereopods 3, 5 and 7. D-E, coxal plates of pereopods 4 and 6. F, uropod 1. G, enlarged peduncular process of uropod 1. H, uropod 3. Allotype female (11.2 mm) from Cumberland Gap Saltpetre Cave (Lee County, Virginia): I, uropod 2.

had a telson with a shallow distal notch (5-7% cleft). Secondary sexual dimorphism was found in uropod 1 and telson.

REMARKS. - *Bactrurus angulus* is presently known only from two caves in northeastern Tennessee and one cave in southwestern Virginia. This species is very rare and several attempts to collect additional specimens have been unsuccessful (1996 and 1997). The type locality, located south of Powell River and northeast of Tazewell, contains about 100 m of passages and is developed in Middle Ordovician limestone. Despite two visits to the cave, only a single male (holotype) has been found to date. The specimen was collected from a shallow, mud-bottom drip (seep-fed) pool in a short dead end passage.

Like *B. wilsoni*, *B. angulus* differs from most other *Bactrurus* species by a serrate peduncular process on male uropod 1. It can be distinguished from *B. wilsoni* by the following characters: absence of large denticles on lacinia mobilis of right mandible; distinct defining angle of propod on gnathopod 1; dactyl of gnathopod 1 ca. 95% length of propod (86% in *B. wilsoni*); mediodistal margin of carpus on gnathopod 2 with ca. seven plumose setae (three plumose setae in *B. wilsoni*); spines on anterior margin of basis of pereopod 5 short (relatively long in *B. wilsoni*); coxal gill on pereopod 7 distinctly reduced (less than half the size of coxal gill on pereopods 5 and 6); mediodorsal margin of peduncle on uropod 1 with three to four spines (one in *B. wilsoni*); length and armature of outer ramus on uropod 3 show-

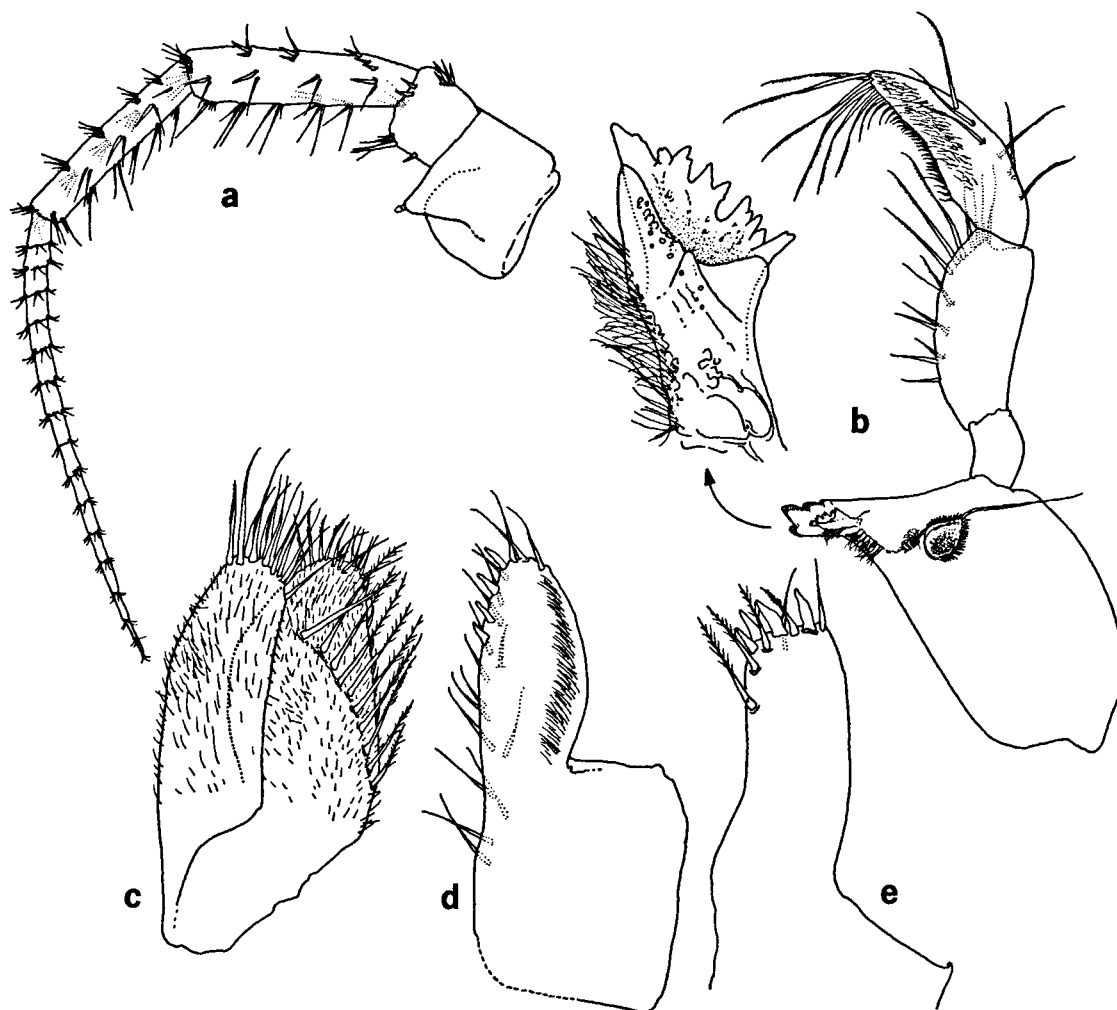


Fig. 23. *Bactrurus cellulanus* n. sp. Holotype male (15.8 mm) from seep (Monroe County, Indiana): A, antenna 2. B, right mandible (lacinia mobilis enlarged). C, maxilla 2. D-E, outer and inner plates of maxilliped.

ing less reduction than that of *B. wilsoni*.

The stygobiont amphipod *Crangonyx antennatus* was associated with *B. angulus* in small stream pools in Cumberland Gap Saltpetre and Kings Saltpetre caves.

ETYMOLOGY. - The epithet *angulus* (Latin for corner, angle) refers to the distinct defining angle of the propod of gnathopod 1.

***Bactrurus cellulanus* n. sp.**

Figs. 23-25

Bactrurus sp.; Holsinger, 1986a: 95.

TYPE LOCALITY. - Small spring- or seep-fed stream in unfinished basement of Jordan Hall on campus of Indiana University, Bloomington (Monroe County, Indiana).

MATERIAL

INDIANA. - Monroe Co.: seep-fed stream in basement of Jordan Hall, Indiana University, Bloomington, 1 female paratype (JRH), F. Young, XII-1962; HOLOTYPE male (15.8 mm, on two slide mounts; USNM 296422), and 1 male paratype (JRH), 8-I-1963 (specimens collected by Young donated to study by J. J. Lewis); allotype female (15.5 mm; USNM acc. nr. 395927), N. Hynes, I-1963.

DIAGNOSIS. - A medium-sized species morpho-

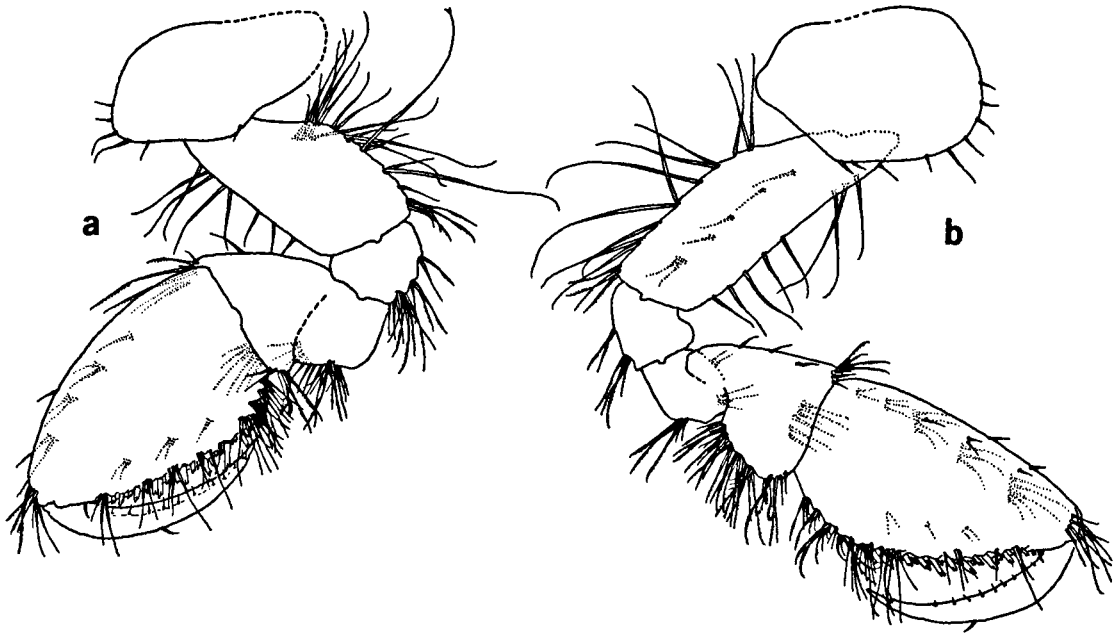


Fig. 24. *Bactrurus cellulanus* n. sp. Holotype male (15.8 mm) from seep (Monroe County, Indiana): A, gnathopod 1 (lateral view). B, gnathopod 2 (lateral view).

logically very similar to *B. wilsoni* and *B. angulus*. *Bactrurus cellulanus* can be distinguished by the following characters: distal margin of right lacinia mobilis with large, irregular denticles. Propods of gnathopod 1 and 2 subequal in length, propod of gnathopod 1 noticeably wider than propod of gnathopod 2; defining angle of gnathopod 1 distinct (ca. 140°). Pereopod 5 about as long as pereopod 4. Coxal gills on pereopods 2-7, distinctly reduced on pereopod 7 (less than half the size of coxal gill on pereopod 6). Two pairs of lateral sternal processes on pereonites 6 and 7; median sternal processes absent. Male uropod 1 with serrate peduncular process. Telson of adult male sometimes slightly longer than telson of female, apical spines shorter than those of female; telson with shallow notch or V-shaped excavation (5-19% cleft). Largest male 15.8 mm, largest female 15.5 mm.

DESCRIPTION. - Based on holotype male (15.8 mm; Figs. 23A-E, 24A, B, 25A-J) and allotype female (15.5 mm; Fig. 25K, L).

Antenna 1 subequal to that of *B. mucronatus*, 60-79% length of body. Primary flagellum with up to

47 segments.

Antenna 2 about 45-49% length of antenna 1 (Fig. 23A). Flagellum with up to 16 segments.

Lower lip subequal to that of *B. wilsoni*.

Mandibles (Fig. 23B): row of seven plumose spines between molar and lacinia mobilis; distal margin of right lacinia mobilis subequal to that of *B. wilsoni* (with large, irregular denticles; see enlargement Fig. 23B). Palp segment 2 with 13 to 14 setae on lateral and medial margins; palp segment 3 with 28 to 30 short, plumose D-setae, three to five long, plumose B-setae and two to four long, plumose A-seta.

Maxilla 1 subequal to that of *B. wilsoni*.

Maxilla 2 (Fig. 23C): outer plate apically with up to 19 setae. Inner plate with oblique row of 10 strong, plumose setae and up to 19 plumose setae apically and subapically.

Maxilliped: outer plate with four to five blade-like spines and ca. 12 naked setae on inner margin (Fig. 23D). Inner plate apically with four blade-like spines and three to four plumose setae (Fig. 23E).

Gnathopod 1 (Fig. 24A): basis with approximately 18 long, naked setae on posterior margin, five

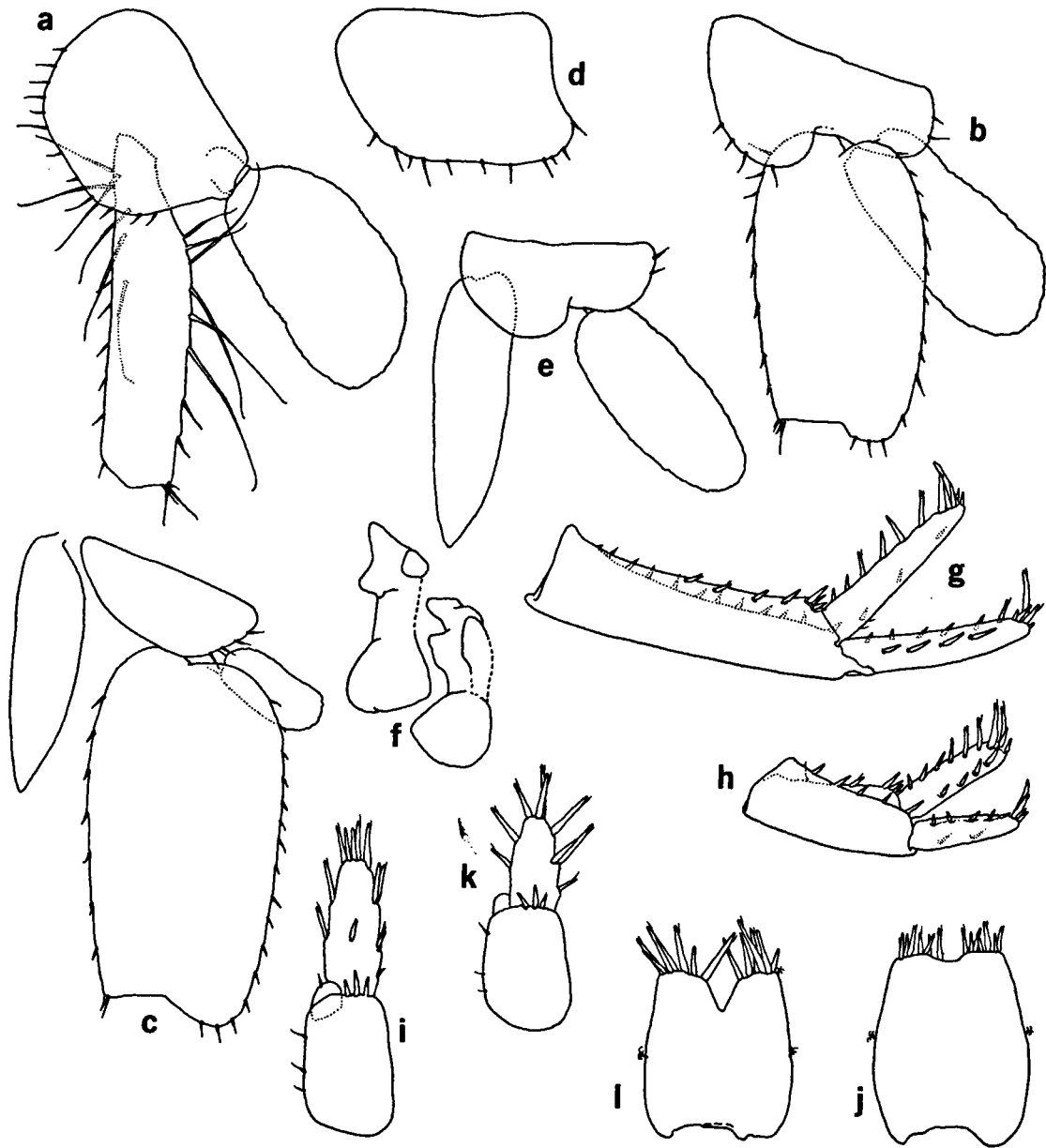


Fig. 25. *Bactrurus cellulanus* n. sp. Holotype male (15.8 mm) from seep (Monroe County, Indiana): A-C, proximal parts of pereopods 3, 5 and 7. D, coxal plate of pereopod 4. E, coxal plate, gill and lateral sternal process of pereopod 6. F, retinaculæ of pleopods. G-I, uropods 1-3. J, telson. Allotype female (15.5 mm) from same locality: K, uropod 3. L, telson.

plumose setae on posterodistal corner, seven to eight naked setae on anterior margin and five naked setae on medial surface. Carpus with two rastellate spines on posterodistal margin (see enlargement of Fig. 17B) and ca. six plumose setae on distal margin. Propod noticeably wider than propod of gnathopod 2 (but about equally long); palmar margin almost even, crenulated,

armed with 15 to 17 spines on lateral margin and about 21 spines on medial margin; defining angle distinct (ca. 140°), bearing a row of five spines medially and four spines on lateral corner; posterior (subangular) margin 23% length of propod, with four sets of plumose setae (distal set naked); anteromedial surface bearing five rows of plumose setae. Dactyl ca. 82% length of propod.

Coxal plate with six setae.

Gnathopod 2 (Fig. 24B): basis with seven to nine sets of long setae on posterior margin (with about 11 setae in total), four plumose setae on posterodistal corner, three long, naked setae on anteroproximal margin, five to six naked setae on anterodistal margin and six setae on medial surface. Carpus with six sets of plumose setae on posterior margin, five to six plumose setae on distal margin and four rastellate spines on posterodistal corner (see enlargement of Fig. 17B). Palm of propod almost even, crenulated, with 12 to 13 spines on lateral margin and about 14 spines on medial margin; defining angle rounded, with row of four spines on lateral corner; medial corner with row of four spines, accompanied by two long spines and one short spine; proximal (subangular) margin ca. 31% length of propod, bearing five sets of plumose setae; anteromedial surface bearing six rows of plumose setae. Dactyl 76% length of propod. Coxal plate wider than long, bearing five to seven setae.

Pereopod 3 (Fig. 25A): basis with six long setae and two short setae on posterior margin, five to seven short setae on anterior margin and four to seven long setae on anteroproximal margin and surface. Coxal plate with 10 to 11 marginal setae.

Pereopod 4: subequal to pereopod 3. Coxal plate with 11 marginal setae (Fig. 25D).

Pereopod 5 (Fig. 25B): anterior margin of basis with nine short spines; posterior margin with 15 short setae. Coxal plate with four to five setae on anterodistal lobe and two setae on posterodistal corner.

Pereopods 6 and 7 subequal. Anterior margins of bases with six to eight short spines; posterior margins bearing up to 16 setae (including two to three slender spines). Coxal plate of pereopod 6 with two setae on posterodistal lobe (Fig. 25E). Coxal plate of pereopod 7 with four setae on posterior margin (Fig. 25C).

Coxal gills on pereopods 2-7, distinctly reduced on pereopod 7 (less than half the size of coxal gill on pereopod 6; Fig. 25C). Lateral sternal processes present on pereonites 6 and 7 (Figs. 25C, E).

Pleopods: width of peduncles gradually increasing from pleopod 1-3. Number of unfused rami segments: pleopod 1 with nine to fifteen segments, pleopod 2 with 12 to 14 segments and

pleopod 3 with eight to twelve segments. Retinaculæ reduced, asymmetrical (Fig. 25F).

Epimeral plates: posterodistal margins with five to seven short setae each; plate 1 without spines, plates 2 and 3 bearing three spines, respectively.

Uropod 1 (Fig. 25G): peduncle with 12 spines on laterodorsal margin, four to five spines on mediodorsal margin and four spines on mediodistal corner. Rami about 62% length of peduncle; inner ramus with five apical spines and about eight to nine spines on dorsal surface. Outer ramus with five apical spines and eight to ten spines on dorsal surface. Peduncle of male with ventrodistal, serrate process.

Uropod 2 (Fig. 25H): peduncle with three to five spines on laterodorsal margin, one spine on mediodorsal margin (sometimes absent) and two to four spines on mediodistal corner. Inner ramus longer than outer ramus, about 71% of length peduncle, bearing four apical spines and seven to eleven spines on dorsal surface (some of which relatively long). Outer ramus with five apical spines and five to seven spines on dorsal surface.

Uropod 3 (Fig. 25I, K): peduncle armed with three spines on distal margin. Inner ramus vestigial, 24-25% length of outer ramus (sometimes with one tiny apical seta). Outer ramus reduced (but relatively long), 80-101% length of peduncle, bearing three to five apical spines, two to five subapical spines on lateral margin and two to three subapical spines on medial margin (sometimes one spine on dorsal surface).

Telson (Figs. 25J, L): width 90% of length. Apical margin entire or with V-shaped excavation (15-23% cleft), bearing 13 to 15 apical spines. Male telson (Fig. 25J) with relatively short apical spines; spines distinctly longer in female telson (Fig. 25L).

SEXUAL DIMORPHISM AND VARIATION. - Similar to *B. angulus*, variation was found in the excavation of the distal telsonic margin (one male with entire margin, other specimens with V-shaped excavation (15-23% cleft)). Secondary sexual dimorphism occurred as described in uropod 1 and telson.

REMARKS. - The type-locality is a small spring- or seep-fed stream in an unfinished basement beneath Jordan Hall on the campus of Indiana University. The terrain surrounding the seep is

karst developed on Mississippian-aged limestone and is believed to have been a sinkhole complex prior to construction of Jordan Hall. Four specimens of the new species were collected in December 1962 and January 1963, but *Bactrurus* was not seen on a visit to the seep by JRH in June 1965. More recently, the diversion of the small stream and other work in the basement has apparently destroyed the type-locality (J. J. Lewis, pers. com.).

In addition to *B. cellulanus*, stygobiont amphipods (*Crangonyx packardii*) and isopods (*Caecidotea jordani*), and an epigeal crayfish (*Cambarus*) have been collected from the seep-fed stream beneath Jordan Hall.

Bactrurus cellulanus is morphologically closely allied with *B. wilsoni* and *B. angulus*. Like the last two species, *B. cellulanus* has a serrate peduncular process on the male uropod 1. It can be further distinguished as follows: inner plate of maxilla 2 with oblique row of 10 strong, plumose setae (six to seven in most other species); outer ramus of uropod 3 relatively long, bearing several subapical spines on both margins; peduncle of uropod 3 armed with three distal spines (usually one to two spines in other species).

Bactrurus cellulanus differs from *B. angulus* by the following characters: 21 medial and 15 to 17 lateral spines on palmar margin of gnathopod 1 (nine to ten medial and eight lateral spines in *B. angulus*); defining angle of propod on gnathopod 1 less distinct; rami of uropod 1 with eight to ten spines on dorsal surface (six spines in *B. angulus*); dorsal margins of inner ramus on uropod with seven to eleven spines, some of which relatively long (five spines in *B. angulus*).

B. cellulanus can be distinguished from *B. wilsoni* as follows: outer plate of maxilliped with four to five blade-like spines (two to three in *B. wilsoni*); posterior margin of carpus on gnathopod 2 with six sets of plumose setae (three sets in *B. wilsoni*); proximal, subangular margin of propod on gnathopod 1 with four rows of plumose setae (less setose in *B. wilsoni*); anterior margin of basis on pereopod 5 with ca. nine short spines (six relatively long, slender spines in *B. wilsoni*); coxal gill of pereopod 7 less than half the size of coxal gill on pereopod 6 (only slightly reduced in *B. wilsoni*); mediadorsal margin of peduncle on uropod 1 with four to five spines (one spine or absent in *B.*

wilsoni); dorsal margins of inner ramus on uropod with seven to eleven spines, some of which relatively long (four to five spines in *B. wilsoni*).

ETYMOLOGY. - The epithet *cellulanus* (Latin for 'hermit' or 'recluse') refers to the 'reclusive' habitat in the basement of Jordan Hall, Indiana University.

PHYLOGENETIC ANALYSIS

CLADISTIC METHODS. - The phylogenetic analysis was performed using PAUP, version 3.0s. Initially, all characters were left unordered and unweighted. Subsequently, some characters were ordered and weighted through outgroup comparison (see 'Character Assessment' and Appendix 1). In the following text, these alternative runs will be referred to as 'unordered analysis' and 'partially ordered analysis'. During a Heuristic Search, the ancestral condition was left 'unknown' and the following search options were in effect: only minimal trees were kept, collapsing zero-length branches; TBR branch swapping was performed on minimal trees only (steepest descent by random stepwise addition). The trees obtained with these settings were used for subsequent runs, keeping all minimal trees (MULPARS option) that were as short as or shorter than those loaded into memory. These steps were repeated until no shorter trees could be found. A strict consensus tree was calculated from the trees generated by the Heuristic Search.

CHARACTER ASSESSMENT. - Except for the species of *Bactrurus* that were examined during the study, the assessment of character states is based on descriptions and drawings from the literature (see Appendix 1). During the partially ordered analysis, more complex characters were ordered and weighted, assuming that their evolution had to be more directed and less likely than the development of more simple structures. For example, the different stages of reduction of coxal gills in several crangonyctid and bogidiellid taxa suggest a stepwise, gradual evolution over a long period of time, whereas the occurrence or loss of spines and setae on appendages may have evolved much faster (Koenemann & Holsinger, 1999a).

Table 1. Character matrix. See Appendix 1 for a description of characters. Characters are numbered according to their listing in Appendix 1. Outgroup taxa of the partially ordered analysis are capitalized.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>GAMMARUS PULEX</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>GAMMARUS TROGLOPHILUS</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>NIPHARGUS FONTANUS</i>	1	0	1	2	0	0	0	0	0	1	0	1	0	0	0	2
<i>MEGAGIDIELLA AZUL</i>	1	0	2	2	0	0	1	0	1	0	0	0	1	0	1	3
<i>SPELAEOGAMMARUS SPINILACERTUS</i>	1	0	3	2	0	0	1	0	1	0	0	1	1	0	1	1
<i>Bactrurus brachycaudus</i>	1	1	0	1	0	1	1	0	2	1	0	1	2	1	1	2
<i>Bactrurus hubrichti</i>	1	1	0	0	0	2	1	0	2	1	0	0	1	1	1	2
<i>Bactrurus mucronatus</i>	1	1	1	2	0	2	1	0	2	1	2	1	2	1	1	2
<i>Bactrurus pseudomucronatus</i>	1	1	0	1	1	1	1	0	2	1	2	1	2	1	1	2
<i>Bactrurus wilsoni</i>	1	1	0	0	0	1	1	1	2	1	1	1	1	1	1	2
<i>Bactrurus angulus</i>	1	1	0	1	0	1	1	1	2	1	1	1	1	1	1	2
<i>Bactrurus cellulanus</i>	1	1	0	1	0	1	1	1	2	1	1	1	1	1	1	2
<i>Crangonyx forbesi</i>	0	0	0	1	1	2	1	0	2	1	0	0	1	1	0	2
<i>Crangonyx subterraneus</i>	1	0	1	2	0	2	1	0	2	1	0	0	1	1	0	2
<i>Lyurella</i>	0	0	0	?	1	1	1	0	5	2	0	1	1	1	0	2
<i>Stygobromus araeus</i>	1	0	1	2	1	1	1	0	4	2	1	1	2	1	1	2
<i>Stygobromus grahami</i>	1	0	1	2	0	0	1	1	3	2	0	1	2	1	1	2
<i>Stygobromus hoffmani</i>	1	0	0	0	1	1	1	1	3	2	0	1	2	1	1	2
<i>Stygobromus mackini</i>	1	1	0	1	1	1	1	1	3	2	0	1	1	1	1	2
<i>Stygobromus phreaticus</i>	1	1	1	2	0	1	1	1	4	2	0	0	1	1	1	2
<i>Stygobromus t. tenuis</i>	1	1	0	1	1	2	1	1	3	2	1	1	2	1	1	2
<i>Stygonyx courtneyi</i>	1	0	0	1	0	1	1	1	2	2	0	0	1	1	0	2
<i>Synurella a. ambulans</i>	0	0	0	?	1	2	1	0	3	2	1	1	1	1	0	2
<i>Synurella dentata</i>	0	0	0	1	1	2	1	0	2	2	0	1	0	1	0	2

TERMINAL TAXA. - The strength of phylogenetic analyses is strongly dependent on the quality and quantity of the data employed. For example, to investigate the relationship of *Bactrurus* to its potential sister genus *Stygobromus*, the morphological similarity of both genera has to be taken into consideration. In this case, the preferable approach was to analyze a selection of taxa that represent different species groups of *Stygobromus*. However, we also wanted to investigate the phylogenetic relationship of *Bactrurus* and *Stygobromus* to other genera of the family Crangonyctidae. Therefore, in addition to the seven species of *Bactrurus*, the following taxa were included to ensure that the analysis was as comprehensive as possible for the scope of this study (Table 1):

Stygobromus mackini Hubricht, 1943, and *Stygobromus hoffmani* Holsinger, 1978, occur primarily in limestone caves at the eastern margin of the *Bactrurus* distribution range (Fig. 26). Each represents a group of morphologically closely allied species, respectively: the *mackini* and *emarginatus* groups. *Stygobromus grahami* Holsinger,

1974, is a species of the *hubbsi* group found in the western United States. The 14 species of the *tenuis* group, represented in the analysis by *Stygobromus t. tenuis* (Smith, 1874), have the widest distribution range of all *Stygobromus* species groups. They are recorded from several states in eastern, southern, and central parts of the United States. *Stygobromus phreaticus* Holsinger, 1978, and *Stygobromus araeus* (Holsinger, 1969), are morphologically unique species that occur in shallow groundwater habitats in eastern Virginia.

Crangonyx forbesi (Hubricht & Mackin, 1940), a stygophile inhabitant of caves and related groundwater habitats, with reduced eyes and pigmentation, frequently co-occurs with *B. brachycaudus*. A large part of the range of *C. forbesi* overlaps with that of *Bactrurus*. *Crangonyx subterraneus* Bate, 1859, was chosen as a European representative of the genus *Crangonyx*.

Synurella dentata Hubricht, 1943, is an epigeal crangonyctid amphipod from the East-Central United States. Similar to *C. forbesi*, its range partly overlaps that of *Bactrurus*. *Synurella a. ambulans*

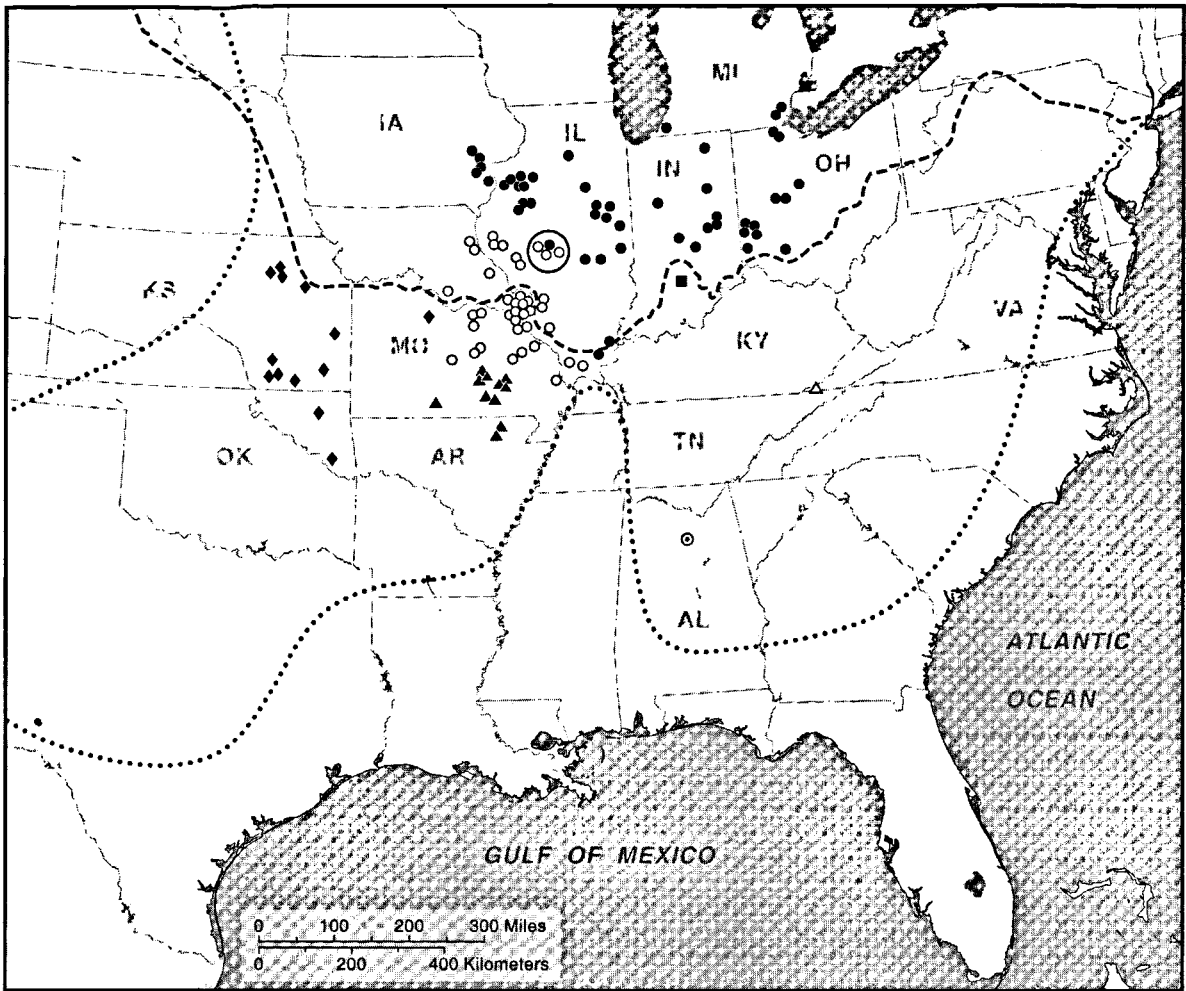


Fig. 26. Geographic distribution of *Bactrus* in eastern and central North America. Each symbol represents approximately one locality record (the actual number of records may be slightly higher in some of the densely clustered areas). Open circles: *B. brachycaudus*; filled diamonds: *B. hubrichti*; filled circles: *B. mucronatus*; filled triangles: *B. pseudomucronatus*; dot surrounded by circle: *B. wilsoni*; filled square: *B. cellulanus*; open triangle: *B. angulus*. The large open circle in the glacial drift area (Illinois) surrounds several localities: three are the first records for *B. brachycaudus* from glacial drift habitats; one is a locality occupied by both *B. brachycaudus* and *B. mucronatus* (see text). The maximum southern extent of Pleistocene glaciation is indicated by the black dashed line. The dotted line delineates the maximum extent of a continental marine embayment in the middle to late Cretaceous (adapted from Holsinger, 1993).

(Müller, 1846) was included as a European species of the genus.

The monotypic crangonyctid genus *Lyurella* Derzhavin, 1939, is endemic to the Caspian Sea region and shares several diagnostic characters with *Synurella*, e.g., coxal plates 1 and 2 longer than wide; presence of reduced eyes; telson longer than wide.

Stygonyx courtneyi Bousfield & Holsinger, 1989, is a monotypic crangonyctid genus known only from a single hypogean freshwater locality in the

state of Oregon. It is morphologically very similar to *Stygobromus*.

Gammarus pulex Linnaeus, 1758, and *G. troglophilus* Hubricht & Mackin, 1940, were chosen as outgroup taxa. *Gammarus pulex* is a common epigeal freshwater species in many parts of Europe and has been recorded as far East as Siberia, including Lake Baikal. *Gammarus troglophilus* is a stygophile that inhabits both epigeal and hypogean habitats in the central United States; its range overlaps that of *Bactrus*.

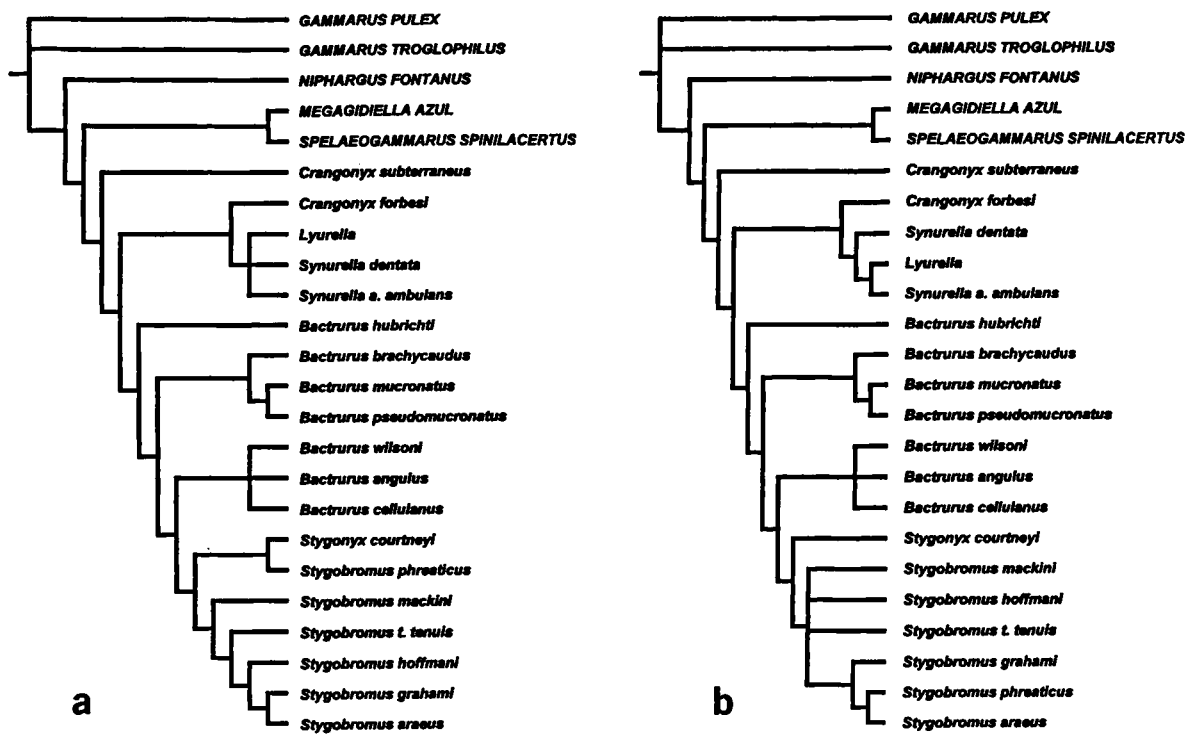


Fig. 27. Phylogenetic analysis of seven *Bactrurus* species, including selected crangonyctid genera and several outgroup taxa (capitalized). A, PAUP Strict Consensus tree; characters unordered and equally weighted (CI: 0.44; RI: 0.68; RC: 0.30; length: 65; min. possible length: 29; max. possible length: 143). B, PAUP Strict Consensus tree; characters partially ordered and weighted (CI: 0.43; RI: 0.70; RC: 0.30; length: 145; min. possible length: 63; max. possible length: 341).

The following stygobiont taxa were included as additional outgroups: *Niphargus fontanus* Bate, 1859 (widely distributed in Europe); *Spelaeogammarus spinilacertus* Koenemann & Holsinger, 2000, and *Megagidiella azul* Koenemann & Holsinger, 1999b, two genera of the family Bogidiellidae endemic to eastern and south-central Brazil, respectively.

RESULTS

Both unordered and partially ordered analyses produced strict consensus trees with well-resolved, very similar topologies (Fig. 27). Both trees have a single stem, with the species of *Gammarus* as basal sister group to all stygobiont and stygophile taxa. *Niphargus fontanus* appears as a sister group to both Bogidiellidae and Crangonyctidae. The small, monophyletic clade of the bogidiellids is a sister group to the Crangonyctidae. A somewhat unexpected result is that *Bactrurus* is not monophyletic. The genus is

subdivided into two smaller clades: a trichotomy with *B. wilsoni*, *B. angulus* and *B. cellulanus* (hereafter referred to as *wilsoni* group) and *B. brachycaudus* on a clade with the morphologically closely related *B. mucronatus* and *B. pseudomucronatus* (hereafter referred to as *brachycaudus* group). Interestingly, the analyzed data set renders *B. hubrichti* as a sister group of both *Bactrurus* and *Stygobromus*.

Although the crangonyctid taxa form a large, monophyletic clade in both consensus trees, the topology within the crangonyctids shows some interesting differences. The first point to note is that *Stygobromus* is not monophyletic in the consensus tree of the unordered analysis (Fig. 27A): a small clade with *Stygobromus phreaticus*, joined by *Stygonyx courtneyi*, appears as a sister group to the remaining *Stygobromus* species. In the partially ordered analysis, *Stygonyx courtneyi* has become the sister group to a monophyletic *Stygobromus* clade (Fig. 27B). The second difference between unordered and partially ordered analyses is a

small clade with both *Synurella* species and *Lyurella*. This clade remains unresolved in the unordered analysis, whereas *Synurella dentata* is a sister group to *Lyurella* and *Synurella a. ambulans* in the partially ordered analysis.

DISCUSSION

PHYLOGENETIC ANALYSIS. - The congruent sequence of outgroup taxa in both analyses suggest monophyly for the Crangonyctidae, with Niphargidae and Bogidiellidae as sister groups (Fig. 27). *Crangonyx* is paraphyletic, but both species included occur at basal positions of a large, monotypic crangonyctid clade. The phylogenetic relationships of the genera *Crangonyx*, *Lyurella*, *Synurella*, *Bactrurus* and *Stygobromus* is in agreement with Holsinger's cladogram of the Crangonyctidae (1986a). Both unordered and partially ordered analyses maintain *Lyurella* and *Synurella* on a single clade, suggesting a close relationship of *Lyurella* to *Synurella*, as postulated by Holsinger (1977, 1986a). However, the different topology within this clade in both trees fails to resolve the relationship of *Synurella* and *Lyurella*. The partially ordered analysis places *Lyurella* closer to the European *Synurella a. ambulans*. However, more data are needed to clarify the relationship of these genera.

Another difference of the unordered and partially ordered analysis affects the relationship of *Stygonyx courtneyi* with the *Stygobromus* taxa. Interestingly, the diagnostic distinction between both genera is mainly based on the comparatively longer outer ramus of uropod 3 in *Stygonyx*. Apart from this character, *Stygonyx* and *Stygobromus* are morphologically indistinguishable. Considering the comparatively greater variation of outer rami length on third uropods in *Bactrurus* (with *B. mucronatus* and *B. cellulanus* as the most extreme forms), the given topology probably correctly reflects the close phylogenetic relationship of *Stygonyx* and *Stygobromus*. A separate generic status for *Stygonyx courtneyi* is questionable and its assignment to the genus *Stygobromus* is perhaps justified (in this case, the analyses would imply monophyly for *Stygobromus*). But as in the case of *Lyurella/Synurella*, more data and certainly also additional records are needed to resolve the relationships of these genera.

In both trees, *Bactrurus* and *Stygobromus* are nested in a large clade, distinguished from the other crangonyctid taxa by two synapomorphies: character 2 (presence of rastellate spines on the carpus of gnathopod 2) and character 15 (coxal plates 1 and 2 wider than long). The paraphyly of *Bactrurus* is largely determined by two factors:

(1) The *wilsoni* group has become the sister group to the *Stygobromus/Stygonyx* clade because it shares a distinct synapomorphy with these genera (character 8: peduncle of male uropod 1 with serrate process).

(2) The *brachycaudus* group is separated by a homoplasious character 13 (telson not cleft), which is also found in a clade with four *Stygobromus* species in the tree of the unordered analysis (*S. t. tenuis*, *S. hoffmani*, *S. grahami* and *S. araeus*).

The fact that *Bactrurus* appears as a paraphyletic genus is not too surprising when we compare it morphologically with *Stygobromus*. The taxonomic discrimination between both genera is based primarily on two diagnostic characters:

(1) *Stygobromus* is distinguished from *Bactrurus* by the absence of an inner ramus and a more reduced outer ramus of uropod 3.

(2) The blade-like spines on the outer plate of the maxilliped are either absent or much reduced in number in most *Stygobromus* species.

However, of these differences only the absence of the inner ramus on uropod 3 is a truly robust diagnostic character. The other two characters (length of outer ramus of uropod 3 and armature of outer plate of maxilliped) show a considerable amount of variation in both genera, so that a clear separation of two distinctly different degrees of reduction becomes nearly impossible. It appears that the length of the outer ramus of uropod 3 shows an almost continuous spectrum of reduction from *Crangonyx* to *Bactrurus* to *Stygobromus*. Similarly, there are additional diagnostic characters that cannot be used unambiguously to morphologically distinguish *Bactrurus* from *Stygobromus*. For example, pereopod 7 varies from little to distinctly longer than pereopod 6 in *Bactrurus*, whereas in *Stygobromus* it is shorter than, equal to, or a little longer than pereopod 6.

The employment of different or additional characters may produce trees with different topologies for *Bactrurus* and *Stygobromus*. However,

it is the relatively large amount of morphological variation, mainly within the genus *Stygobromus*, that is likely to complicate a character analysis and cloud its outcome. In the long run, the supplemental utilization of molecular and/or developmental data may be the best way to gain a more complete picture of the phylogeny within the Crangonyctidae.

The data used in the phylogenetic analysis support an ancient freshwater origin for the crangonyctids. Several taxa with distinct Holarctic distributions (*Crangonyx* and *Synurella*) appear at basal positions of a monophyletic Crangonyctidae. However, more data are needed to investigate the origin of crangonyctid amphipods in greater detail. A conclusive answer to this question will depend on whether or not we can establish monophyly for the Crangonyctidae.

The results of the phylogenetic analysis do not support *Bactrurus* as a monophyletic group. Furthermore, *Bactrurus* and *Stygobromus* do not appear as sister groups. However, both genera appear on a separate clade together with *Stygonyx courtneyi*. Although the cladograms rendered a stable topological separation of both genera, we cannot unambiguously infer if a close relationship is based on homoplasious similarity or common ancestry.

THE BIOGEOGRAPHY OF *BACTRURUS*. - The cladograms show an interesting branching pattern for *Bactrurus* that can be related to the geographic distribution of the individual species. *Bactrurus hubrichti* appears on a single branch as the sister group of the other two clades with three species each.

The first clade is composed of the three species of the *brachycaudus* group, each of which is relatively abundant and two of which have wide ranges. Together, they form a more or less continuous cluster of records, which embraces most of the range of *Bactrurus* (Fig. 26).

A second, polytomous clade is formed by the *wilsoni* group, which is composed of three highly endemic species that share several apomorphic characters. Typically, the localities of the *wilsoni* group species are disjunct and few in number.

The distribution of *B. hubrichti* is characterized by a pattern that differs from both the *brachycaudus* and *wilsoni* groups: it has a relatively wide range,

but many of the localities are disjunct. With the exception of a single record from central Missouri, the range of *B. hubrichti* is separated from the *brachycaudus* group by a distinct gap (Fig. 26).

1. THE *WILSONI* GROUP

The three species of the *wilsoni* group are endemic to isolated areas. Two species occur in the Appalachians and thus are far removed from all other species in the genus. *Bactrurus cellulanus* and *B. wilsoni* are recorded from single localities, whereas *B. angulus* is found in three caves within a small area (Fig. 26). The distances between the range of *B. angulus* and *B. wilsoni* and the main cluster of species in the physiographic provinces of the Central Lowland and Ozark Plateaus are remarkably large, with no recorded species in between. The greatly delimited range of *B. cellulanus* appears to be an exception to this pattern, inasmuch as it occurs in relatively close proximity to the extensive range of *B. mucronatus* in central and northern Indiana. However, all records of *B. mucronatus* in Indiana are from glaciated areas, whereas *B. cellulanus* was found in an unglaciated karst region south of the glacial drift areas. Hence, a dispersal barrier might exist between the range of *B. cellulanus* and the groundwater aquifers of the adjacent drift region to the north. Repeated efforts to find *B. cellulanus* in caves and related groundwater habitats in the greater Bloomington area surrounding the type locality have been unsuccessful to date, leading to the conclusion that this species represents an isolated relict on the periphery of the range of *B. mucronatus*.

In addition to their isolated distributions, species of the *wilsoni* group also share several unique morphological characters: the males of all three species have serrate peduncular processes on uropod 1, which are absent in the other species of *Bactrurus*, but very common in *Stygobromus* (see also 'Phylogenetic Analysis'). Moreover, the species of the *wilsoni* group have an almost identical form of sexual dimorphism of the telson (differing width/length ratios and armature). The possession of several unique synapomorphies suggests that species of this group descended from a common ancestor with a continuous distribution. The occurrence of the

wilsoni group in the Appalachians and Interior Low Plateau, at great distances from the extensive marine embayments of the Cretaceous (see Fig. 26), suggests that these species are probably remnants of a very old freshwater group, with a long since fragmented distribution pattern. Similarly, the other four species of *Bactrurus*, despite having comparatively much wider ranges, also occur in a part of the continent that was not exposed to marine waters during the Cretaceous. The evolutionary history of *Bactrurus* seems to be in accordance with that of other genera of the Crangonyctidae. The family is believed to be an 'ancient' freshwater group that was already established on Laurasia prior to the separation of North America and Eurasia in the early Mesozoic (see Holsinger, 1986a, 1986b, 1994).

2. THE *BRACHYCAUDUS* GROUP

2.1. *Bactrurus mucronatus*

In the *brachycaudus* group, two species also share a unique, conspicuous apomorphy: males of *B. mucronatus* and *B. pseudomucronatus* have an extremely elongate telson. However, the distributions of the two species are disjunct. *Bactrurus pseudomucronatus* occurs exclusively in karst groundwater habitats in parts of the Ozark Plateaus of southern Missouri and northern Arkansas, whereas *B. mucronatus* inhabits almost exclusively glacial drift areas of the Central Lowland Physiographic Province. The only exceptions for *B. mucronatus* appear to be a single karst locality in southern Illinois (Equality Cave), where the species has been regularly collected from a cave stream over the last 60 years, and Bear Cave near Lake Michigan (Berrier County, Michigan). Prior to this study, the occurrence of the population in Equality Cave was believed to be isolated by a considerable distance from the closest recorded drift population in central Illinois (Holsinger, 1986a). However, new locality records obtained in May 1999 helped to fill in this gap. They included a locality in the drift area approximately 16 km north of Equality Cave. The new records indicate a more continuous distribution of *B. mucronatus* in the Central Lowland, as well as a possible hydraulic connection of karst and drift aquifers in southern Illinois.

On the distribution map of *Bactrurus*, *B. mucronatus* is the only species of the genus that

occurs almost exclusively north the line that delineates the maximum extent of the Pleistocene glaciation (Fig. 26). Two alternative theories have been proposed to explain the occurrence of stygobiont crustaceans in glaciated areas:

(1) A few stygobionts survived periods of glaciation in groundwater refugia under the ice.

(2) Some stygobionts followed the receding ice northward at the end of the last Pleistocene glaciation and subsequently invaded and colonized newly available habitats in coarse sediments deposited by glaciers.

Because it was widely assumed that the Pleistocene ice sheets destroyed the hypogean biota they covered, most workers seemed to favor the second explanation (Holsinger, 1978; Lewis & Bowman, 1981). However, based primarily on the distribution of a number of *Stygobromus* species that occur north of the glacial boundaries, and which appear to be distantly related to those in unglaciated areas, Holsinger (1978, 1981, 1986a) discussed the possibility of subglacial refugia. Nevertheless, survival in subglacial refugia was considered improbable for *B. mucronatus* (Holsinger, 1986a). This assumption was based primarily on the occurrence of the morphologically close populations south of the glacial boundary, described herein as *B. pseudomucronatus*. *Bactrurus mucronatus* was believed to have split from an ancestral species (*B. pseudomucronatus*) by northward dispersal and subsequent geographic isolation. In this scenario, *B. mucronatus* originated from a region south of the maximum extent of the Pleistocene glaciations, e.g. southern Missouri and possibly southern Illinois, and followed the receding glaciers north to its present range. However, there are several biogeographic features of *B. mucronatus* that weaken the likelihood of lateral dispersal and invasion of glacial drift areas subsequent to glacial recession:

(1) The distribution range of *B. mucronatus* extends over a distance of approximately 650 km, from west to east. Given what are generally regarded as weak dispersal abilities of hypogean amphipods, a colonization of these dimensions is not very probable within the given time-frame (assuming that dispersal started at the end of the last glaciation, perhaps 10000 to 16000 BP; some peripheral dispersal, however, could have started at the end of Illinoian glaciation, as early as 100,000

BP).

(2) A lateral (horizontal) invasion and colonization of drift is assumed to have started from an area south of the glaciated regions, presumably originating by splitting into two lineages in proximity to the present range of *B. pseudomucronatus*. In this scenario, we should expect to find remnant populations between the center of dispersal and the present range. However, *B. mucronatus* and *B. pseudomucronatus* are separated by a gap, which is occupied by *B. brachycaudus* and there are no records of *B. mucronatus* in this area.

(3) The dispersal from a hypothetical center should also result in a typical, branch-like pattern, following major drainage systems with decreasing densities from center to outer margins. It is obvious from the distribution map that the present range of *B. mucronatus* does not show this kind of pattern.

(4) *Bactrurus brachycaudus* inhabits karst groundwater habitats much closer to the drift areas than *B. pseudomucronatus*. Yet, several new localities for the former species in glacial drift discovered during the recent field work appear to be exceptional occurrences. Thus, dispersal from karst into interstitial groundwater systems in western Illinois may be restricted or obstructed by physiographic barriers.

Rather than pointing towards a dispersal center south of its present range, the distribution of *B. mucronatus* extends in a belt-like fashion from east to west, with the most densely populated areas along a center axis, also roughly following an east-west stretch (Fig. 26). In glaciated areas, specimens are often common at the outlets of drainage systems in farm fields (Fig. 28). During wet periods, usually in late winter and spring, many outlet pipes discharge groundwater without interruption, continually flushing out stygobiont invertebrates (mostly *B. mucronatus* accompanied by the asellid isopod *Caecidotea kendeighi*). At several outlet catchment basins, one of us (SK) counted up to 200 flushed-out specimens of *B. mucronatus* and *C. kendeighi*. Large sample sizes (up to 100 specimens) from drain outlets were recorded in the early 1940s by Leslie Hubricht. This abundance is in sharp contrast to cave habitats that are typically sparsely populated. These findings suggest that the glaciated areas of the Central Lowland might have sheltered comparatively

large and stable populations of *B. mucronatus* for a long period of time, stretching well back into the Pleistocene. How can this be explained?

Much of the Central Lowland was profoundly affected by periods of continental glaciation over the last one to two million years. Glaciers repeatedly advanced and retreated across the surface, disrupting preglacial drainage patterns and eroding both bedrock and older, unconsolidated sediments. The moving ice sheets carried vast amounts of debris, which was mostly deposited as unsorted sediments (till). In some regions, however, the melting glaciers formed well-sorted layers of sands and gravels. Many of these deposits were subsequently covered by till. Quaternary deposits in the Central Lowlands are up to 120 m thick. Geologic investigations in Illinois have revealed a complex, three-dimensional network of groundwater aquifers in Quaternary drift (Larson et al., 1995, 1997). The distribution of subterranean aquifer systems depends on various hydrogeological factors, for example, stratigraphy and consistency of deposits, transmissivity and storage capacity of sediments, and also properties of the underlying bedrock (Larson et al., 1997).

The distribution of *B. mucronatus* in the Central Lowlands is apparently correlated with thicker Quaternary deposits (60-120 m) and/or deposits near major surface streams as shown in Fig. 29. Considering the complex distribution of shallow sand and gravel aquifers and deeper bedrock aquifers in the Central Lowland, the invasion of drift by *B. mucronatus* may have been an upward (vertical) rather than a lateral (horizontal) dispersal process. Since the permafrost during glaciation periods did not penetrate the ground deeper than approximately 5 m, the colonization of glacial deposits could have taken place much earlier than postulated by a lateral, post-glaciation dispersal model, i.e. between 10000 and 16000 BP. In a vertical dispersal scenario, the invasion of drift may have occurred during glacial and interglacial periods and date back as early as the onset of Pleistocene glaciation.

Bactrurus mucronatus is the most widespread and abundant species of the genus. Its distribution pattern suggests that the colonization of an extensive network of (newly) available interstitial habitats is the result of adaptive radiation. Moreover, groundwater aquifers in drift areas



Fig. 28. Two photographs showing outlets of drain pipes in central Illinois. Stygobiont amphipods and isopods are often found in these outlets, presumably having been flushed out of deeper, interstitial habitats and into drainage systems when groundwater tables are elevated during wet periods. Above, water is passing from a pipe into a ditch or small creek. Below, one can see the outlet pipe of a drainage system in a large, flat field. These systems are very common in glacial drift areas of the mid-west and in unconsolidated sediments on the eastern coastal plain. They consist of a series of perforated pipes, which are buried approximately 2 meters beneath the surface of poorly drained farm fields. In late winter and early spring, excess water from those fields is drained off in preparation for seasonal plowing and planting.

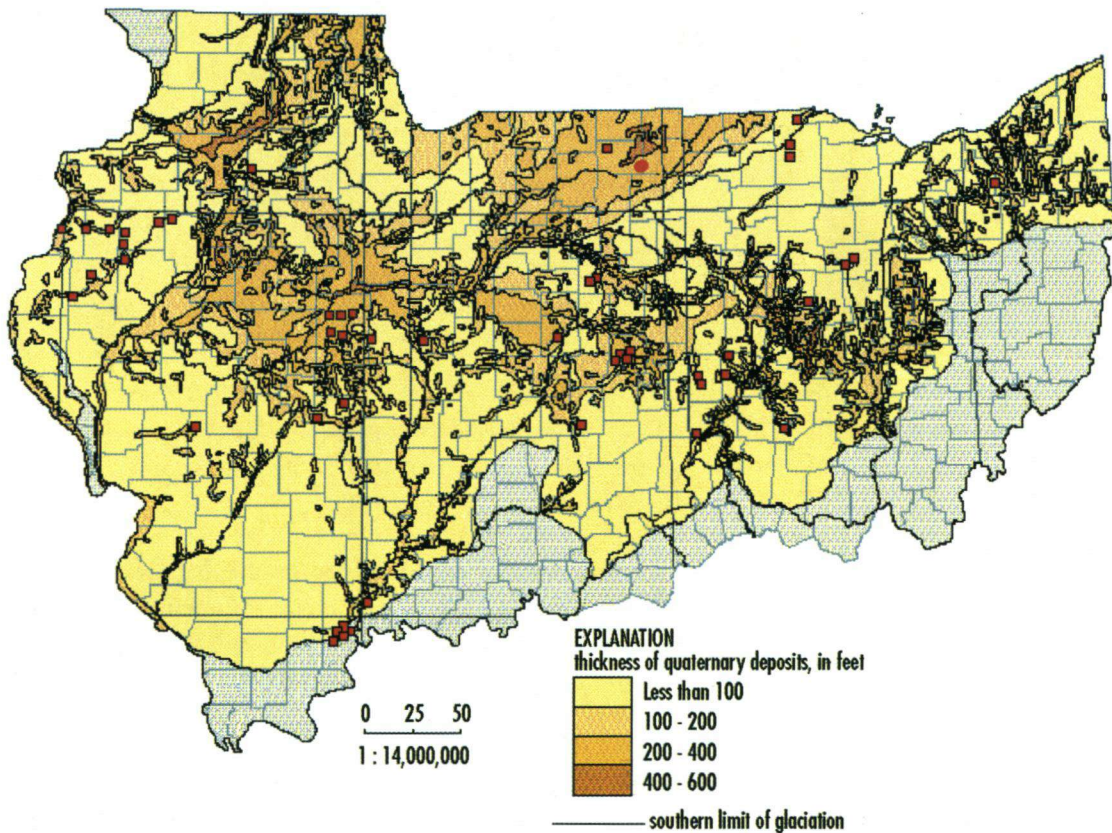


Fig. 29. Distribution of *B. mucronatus* in a part of the Central Lowland Physiographic Province that covers the states of Ohio, Indiana and Illinois. Each symbol (red squares) represents a collection record for this species. Quaternary deposits within pre-glacial bedrock valleys or along streams and rivers generally contain shallow sand and gravel aquifer systems. (Map modified, with kind permission of U.S. Geological Survey).

might have a considerably higher nutrient input in comparison with those in karst. The leaching of soluble constituents by precipitation is likely to play a more crucial role in the flat drift regions with extensive farm fields, where a relatively low run-off results in increased and more diffuse percolation and infiltration.

It is difficult to say whether *B. mucronatus* was already widespread in the Central Lowland before glacial deposits accumulated or whether it originated from ancestral relicts that were isolated somewhere within its present range in sub-glacial refugia and repeatedly re-invaded newly available aquifers. Larson et al. (1995, 1997) point out that some deep bedrock aquifers yield groundwater to overlying glacial drift. The hydraulic connections are maintained through fractured bedrock (carbonates) or permeable

units (sandstone). Vertical invasions from deeper bedrock aquifers into shallow sand and gravel habitats cannot be excluded as an important factor in the distribution of *B. mucronatus*.

2.2. *Batrachus brachycaudus*

Batrachus brachycaudus may be able to invade and colonize newly available habitats in much the same way as we have postulated for *B. mucronatus* above. An illustrative example of the rapid colonization of new habitat space was observed by one of us (SK) in May, 1999. In a karst area at Tyson Research Center (Missouri), a former U.S. Army bunker had been modified into an artificial cave habitat. Mr Earl Biffle, who designed and maintains the 'cave bunker', diverted part of the outflow of a natural spring, located on a slope just above the bunker. He let the spring water flow

Table 2. Pairwise sequence differences of 18S rDNA (small subunit) gene, calculated with Chi-square test in Paup 4.0. *Batrurus brachycaudus* (GD) = specimens from glacial drift area. Table adapted from Englisch & Koenemann (2001).

	<i>Batrurus mucron.</i>	<i>Batrurus pseudom.</i>	<i>Batrurus brachyc.</i> (GD)	<i>Crangonyx forbesi</i>	<i>Niphargus fontanus</i>	<i>Gammarus troglophilus</i>	<i>Gammarus pulex</i>
<i>Batrurus brachycaudus</i>	1.2%	1.0%	0.3%	7.6%	7.3%	9.9%	9.1%
<i>Batrurus mucronatus</i>	-	1.3%	1.2%	8.2%	7.8%	10.2%	9.4%
<i>Batrurus pseudomucronatus</i>	-	-	1.1%	7.8%	7.6%	9.9%	9.2%
<i>Batrurus brachycaudus</i> (GD)	-	-	-	7.8%	7.2%	10.0%	9.3%
<i>Crangonyx forbesi</i>	-	-	-	-	10.4%	13.3%	11.9%
<i>Niphargus fontanus</i>	-	-	-	-	-	9.4%	8.7%
<i>Gammarus troglophilus</i>	-	-	-	-	-	-	2.7%

through a simple pipe system, which entered the bunker at the back side. The interior of the bunker (ca. 5 x 20 m) was parted by a small, low wall that allowed the formation of a shallow pool (ca. 15 cm deep) and the discharge of excess water at the front of the bunker. After a long and thorough search at the mouth of the spring only one juvenile specimen of *B. brachycaudus* could be found, while the bunker itself was populated by several hundred individuals of that species. Interestingly, only a small number of specimens actually stayed in the artificial pool (which was also inhabited by epigeal gammarids and a few cave salamanders). Instead, swarms of juveniles and adults, many of which reached 30 mm in length, were crawling under aluminum foil covers outside the pool (!) in shallow puddles of water. Mr Biffle assured us that he did not provide any supplemental nutrients. However, he introduced the salamanders as natural predators to the artificial habitat.

Another significant discovery during the 1999 field work was a drain pipe sample that contained specimens of both *B. brachycaudus* and *B. mucronatus*. Not only is this the first record of *B. brachycaudus* from a non-karst habitat, it is also the first recorded co-occurrence of two *Batrurus* species from the same locality. The sample was taken at the outer, northeastern margin of the range of *B. brachycaudus* in Montgomery County, Illinois. The specimens from this locality showed minor morphological variation in several characters when compared with *B. brachycaudus* specimens from karst habitats (see *B. brachycaudus*, 'Remarks'). Yet, a conspicuous degree of sexual dimorphism was found in the telson, with male telsons up to 20% longer than those of females. It cannot be com-

pletely ruled out that these specimens are hybrids of a cross between *B. mucronatus* and *B. brachycaudus*.

The majority, if not all, of the localities of *B. brachycaudus* occur within the Mississippi River drainage system. This species is found in springs and caves in karst areas on both sides of the river, and it is possible that individuals of *B. brachycaudus* are occasionally carried into drift areas during extensive flooding of the Mississippi River.

A second case of a locally isolated population was found at the western margin of the range of *B. brachycaudus*. Similar to the specimens from the drift area in Illinois, a cave population from Texas Co. (Missouri) exhibited minor degrees of morphological variation, indicating possibly genetic isolation from the main population (see: *B. brachycaudus*, 'Sexual Dimorphism and Variation').

The range of *B. pseudomucronatus* is adjacent to that of *B. brachycaudus* and includes a few seeps and caves in karst areas of southern Missouri and northern Arkansas (see 'Remarks' under *B. pseudomucronatus*). *Batrurus pseudomucronatus* is less widespread and abundant than *B. mucronatus* and *B. brachycaudus*. However, similar to the other two species, its localities are probably interconnected hydrologically and population sizes may be much larger than the records suggest.

COMPARISON OF MOLECULAR SEQUENCE DATA. - The pairwise sequence differences of the 18S rDNA (small subunit) gene for *B. brachycaudus*, *B. mucronatus* and the new species *B. pseudomucronatus* shows differences between 1.0 to 1.3%, respectively (Table 2). Since intraspecific differences around 1% were found for different populations of *Gammarus pulex* (U. Englisch, pers. com.), the

low interspecific differences among species of the *brachycaudus* group may indicate a relatively recent splitting of this lineage.

The comparison of sequence differences reveals several noteworthy observations:

(1) The difference between *B. mucronatus* and *B. pseudomucronatus* (1.3%) is slightly larger than the difference between *B. brachycaudus* and *B. pseudo-mucronatus* (1.0%).

(2) The same tendency was found for the glacial drift population (Montgomery County, Illinois) of *B. brachycaudus*, which was found together with *B. mucronatus* in one locality.

(3) The slight difference of 0.3% between the glacial drift population and a specimen from the main range of *B. brachycaudus* seems to support the view that both specimens analyzed belong to the same species.

Moreover, the molecular data do not convincingly support a possible hybridization of *B. brachycaudus* and *B. mucronatus* in Montgomery County.

CONCLUSIONS

The geographic distribution of *Batrachus* is characterized by different patterns, which reflect both dynamic and static elements and are differentiated as follows:

(1) Three isolated, endemic relict species (*wilsoni* group).

(2) Three abundant and widespread species (*brachycaudus* group), all of which have more or less contiguous populations in hydrologically connected groundwater habitats.

(3) One species (*B. hubrichti*) is less widespread than the species of the *brachycaudus* group and has at least one population that is isolated by a distinct gap from other localities (Miller Co., Missouri).

The analysis of the biogeography of the seven species of *Batrachus* in eastern and central United States allows us to draw two final conclusions:

(1) The occurrence of all seven species in interior regions of the North American continent that were not covered by a shallow marine embayment during the Cretaceous suggests that the present distribution is composed of remnants of an ancient freshwater group, possibly dating back to

the late Paleozoic.

(2) The present distribution of *B. brachycaudus* and *B. mucronatus* was probably profoundly affected by glaciation and major drainage changes throughout the Pleistocene. Whereas the distribution of *B. brachycaudus* is largely in karst drained by the Mississippi River, *B. mucronatus* is distributed throughout the interstitial habitats of glacial drift. It is likely that relatively high nutrient and energy input, combined with extensive habitat space, has resulted in *B. mucronatus* being the most abundant and widespread species of the genus.

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APPENDIX 1.

LIST OF CHARACTERS AND CHARACTER STATES USED IN THE PHYLOGENETIC ANALYSIS. - If not explicitly indicated otherwise, a character was coded as unordered and unweighted (i.e., equally weighted with weight factor 1) for both unordered and partially ordered analysis (see 'Cladistic methods')

(1) Eyes: state 0 = eyes present; state 1 = eyes absent. Partially ordered analysis: weight factor 3. For this character, state 0 was assumed as the ancestral condition of an epigean predecessor. Although different degrees of reduction could be observed in some of the stygophile taxa, a differentiation into more than two states (absent and present) seemed doubtful because of the discrete appearance of this trait.

(2) Rastellate spines on carpus of gnathopod 2: state 0 = absent; state 1 = present. The occurrence of two to six rastellate spines (sometimes reduced to strong brush-like setae) on the posterodistal margin of the carpus of gnathopod 2 was considered an apomorphic condition. It is present in *Bactrurus* and most species of the genus *Stygobromus*. Rastellate spines and setae usually occur on both gnathopods. The only exception was *Stygobromus t. tenuis* which had no rastellate spines on the first gnathopod. To avoid overrating of this trait by scoring rastellate spines for both gnathopods as two independent characters, we decided to include the character 'rastellate spines' only once, for the second gnathopod.

(3) Coxal gills: state 0 = six pairs (present on pereopods 2-7); state 1 = five pairs (present on pereopods 2-6); state 2 = four pairs (present on pereopods 3-6); state 3 = three pairs (present on pereopods 4-6). Partially ordered analysis: ordered; weight factor 3. A progressive reduction of coxal gills was regarded as adaptation to subterranean environments and, therefore, state 0 was coded as plesiomorphic character state.

(4) Coxal gills on pereopod 7: state 0 = normal; state 1 = reduced; state 2 = absent. Partially ordered analysis: ordered. Similar as in character 3, a continuous reduction of this trait was hypothesized, with state 2 as apomorphic condition.

(5) Median sternal processes: state 0 = absent; state 1 = present. Median sternal processes occur in many crangonyctid taxa. More than 95% of *B. brachycaudus* specimens had no median sternal processes. According to the majority of occurrences, state 0 was chosen for this species (Majority Coding method; see also Koenemann & Holsinger, 1999a).

(6) Lateral sternal processes: state 0 = absent; state 1 = on pereonites 6 and 7; state 2 = on pereonites 6 and 7 and

pleonite 1. Partially ordered analysis: ordered; weight factor 3. The function of sternal processes is still unknown. We think that it may be an adaptation to life in cold subterranean freshwater environments and assume a linear, progressive evolution from state 0 to state 2. Approximately 86% of all *B. mucronatus* specimens examined had lateral sternal processes on pereopods 6 and 7 and on pleonite 1 (as opposed to sternal processes on pereopods 6 and 7 only). Therefore, state 2 was chosen for *B. mucronatus*.

(7) Uronites with dorsal setae: state 0 = present; state 1 = absent. The presence of dorsal spines on uronites 1-3 is common in *Gammarus* and considered the ancestral condition of an epigeic predecessor.

(8) Peduncle of male uropod 1 with distal process: state 0 = absent; state 1 = present. Partially ordered analysis: weight factor 3. A sexually dimorphic uropod 1 with peduncular process occurs in some species of *Bactrurus* and almost all species of *Stygobromus*. Modified uropods and/or pleopods are relatively common in the stygobiont family Bogdiellidae. Sexually dimorphic modifications of posterior appendages might be functionally related to reproductive success in hypogean environments and, therefore, are treated as apomorphic adaptation.

(9) Outer ramus of uropod 3: state 0 = two-segmented; state 1 = one-segmented, not reduced, with apical and subapical spines; state 2 = one-segmented, distinctly reduced, with few subapical spines; state 3 = one-segmented, strongly reduced, with no subapical spines; state 4 = one-segmented, scale-like, with only one to two apical spines; state 5 = absent. Partially ordered analysis: ordered; weight factor 3. Although a reduced outer ramus is common for both *Bactrurus* and *Stygobromus*, a distinction could be made between different degrees of reduction. The outer ramus is clearly more reduced in all *Stygobromus* taxa, bearing no subapical spines and with only one to three apical spines in the majority of species. In *Stygobromus*, the outer ramus reaches 10-42% of the length of the peduncle or it is sometimes absent. In *Bactrurus*, the most advanced reduction was observed in *B. mucronatus*, but even this species had an outer ramus that reached 54% of the length of the peduncle, with at least one or two subapical spines. The most developed outer ramus of all *Bactrurus* taxa was found in *B. cellulanus*. Because this outer ramus was very similar to those of both *Crangonyx* species, character state 2 was applied for *Bactrurus* and *Crangonyx*. In some specimens of *Stygobromus phreaticus*, the outer ramus of uropod 3 is absent. However, state 4 was applied since this reflects the condition in the majority of species.

(10) Inner ramus of uropod 3: state 0 = present, > 70% length of outer ramus; state 1 = present, < 35% length of outer ramus; state 2 = absent. Partially ordered analysis: ordered; weight factor 3. Similar to the reduction of the outer ramus, we hypothesized a progressive reduction for this character, with state 0 as ancestral condition.

(11) Sexual dimorphism of the telson: state 0 = absent; state 1 = present, but minor degree of dimorphism; state 2 = pre-

sent, distinct degree of dimorphism. Partially ordered analysis: ordered; weight factor 3. State 1 refers to the short apical spines found in males of *B. wilsoni*, *B. angulus* and *B. cellulanus* (*wilsoni* group), opposed to distinctly longer spines in females. In the *wilsoni* group, the female telson apparently also tends to be wider and shorter than the male telson. The same dimorphism, albeit much more extremely developed, occurs in *B. mucronatus* and *B. pseudomucronatus*. The differences between the male and female telson can be observed without optical aids: in adult males the telson reaches up to 1/3 of the body length. Since both character states 1 and 2 are sexually dimorphic, they may be related to the reproductive success of males.

(12) Length/width ratio of telson: state 0 = as wide as long or wider than long; state 1 = distinctly longer than wide. A telson scored as distinctly longer than wide was approximately twice as long as wide (length 150-200% of width). The lowest length/width ratio was found in *Stygobromus mackini* (110%). This condition still was easily distinguished from state 0.

(13) Cleft of telson: state 0 = cleft to base (90-100%); state 1 = cleft 5-40% of length of telson; state 2 = telson entire (cleft 0-2% of length of telson). *Bactrurus wilsoni*, *B. angulus* and *B. cellulanus* had dimorphic telsons: in some individuals, state 1 was observed while other specimens had state 2 (see Taxonomic part). Unfortunately, there were not enough specimens available to apply the Majority Coding method. In this case, the intermediate character condition (state 1) seemed to be the appropriate choice. Although the difference between the extremes of character state 1 (5%) and state 2 (2%) is only marginal, a distinction of two different states seemed justifiable because both values could be measured in only some specimens of a taxon, respectively. For example, the apical notch in *Stygobromus phreaticus* was 5-9%, whereas most specimens of *B. brachycaudus* had a convex apical margin or a very small notch (0-2%). The hypothesis that a deeply cleft telson is the plesiomorphic condition is speculative. For the analysis, we assumed a progressive reduction from a deeply cleft telson with subapical and apical spines to an elongated, entire telson with apical spines only. Therefore, the deeply to completely cleft telson was chosen as the ancestral condition.

(14) Subapical spines of telson: state 0 = absent; state 1 = present.

(15) Coxal plates 1 and 2: state 0 = longer than wide; state 1 = wider than long. Partially ordered analysis: ordered; weight factor 3. State 1 is a common condition for many stygobiont amphipods. The evolution of shorter coxal plates may be an adaptation to life in subterranean environments.

(16) Number of segments in accessory flagellum: state 0 = four to six segments; state 1 = three segments; state 2 = two segments; state 3 = one segment. State 0 occurred in the outgroup taxa only, all crangonyctid species analyzed had a two-segmented accessory flagellum.