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SYSTEMATICS OF THE SUBTERRANEAN AMPHIPOD GENUS *STYGOBROMUS* (CRANGONYCTIDAE): SPECIES OF THE OZARKS AND ADJACENT REGIONS

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Abstract

Three new species of the subterranean amphipod genus *Stygobromus* are described: *Stygobromus gardneri*, n. sp., from numerous localities in Arkansas and Missouri; *Stygobromus acicularis*, n. sp., from the Smittle Caves, Wright County, Missouri; and *Stygobromus arbucklensis*, n. sp., from Dip Cave, Murray County, Oklahoma. Eleven previously described species are discussed, several with detailed redescriptions, and new localities are presented. These are *Stygobromus onondagaensis* (Hubricht and Mackin), *S. heteropodus* Hubricht, *S. iowae* Hubricht, *S. putealis* (Holmes), *S. elatus* (Holsinger), *S. montanus* (Holsinger), *S. barri* (Holsinger), *S. clantoni* (Creaser), *S. ozarkensis* (Holsinger), *S. bowmani* (Holsinger), and *S. alabamensis* (Stout).

SYSTEMATICS

The *exilis* group

Diagnosis.—Adult size range small to medium, ca. 3.0–9.0 mm. Mature female larger than mature male. Gnathopod propods moderately small (not enlarged). Gnathopod 1: posterior margin of propodus subequal in length to palm, with row of singly inserted setae; few weakly developed rastellate setae usually present on article 5. Gnathopod 2: propodus little larger (longer) than propodus of gnathopod 1, subrectangular in shape; proportionately broader in male; palm and posterior margin subequal in length. Pereopod 6 little longer than pereopod 7. Pereopods 5–7: bases of pereopods 5–7 relatively broad, but not greatly expanded, posterior margins typically convex; dactyls comparatively long and slender. Pereopod 7 coxal gill present or absent (variable). Lateral sternal gills simple (not bifurcate). Pleonal plates: posterior margins with 1 setule each inserted at or just above distoposterior corner; corners rounded and sometimes indistinct. Uronites free. Ramus of uropod 3 distinct (never vestigial or absent), bearing 1 or more apical spines. Telson as long as broad but typically longer than broad, generally broadest proximally; apical margin usually unnotched (except one species as presently known).

Remarks.—This group is largely cavernicolous, known primarily from drip and other pools, occasionally small streams, and rarely from seeps or wells. The group was mentioned, but not formally designated or described, by Holsinger (1978) in a discussion of the affinities of *S. fecundus* from Gregory's Cave in Blount County, Tennessee. It is widely distributed, ranging from extreme upper east Tennessee westward to central Missouri, with *S. biggersi* disjunct in the Appalachian Valley and Ridge (northwestern Virginia to southern Pennsylvania) (Holsinger, 1978).

Composed of 10 species: one in the Great Smoky Mountains of eastern Tennessee; six in the Interior Low Plateaus (Cumberland Plateau, Highland Rim and Central Basin); one in the Central Lowlands in southwestern Ohio; one in the Ozark Uplift of Missouri, northern Arkansas and northeastern Oklahoma and east-central Kansas, and one in the Appalachian Valley, as noted above. The *exilis* group is closely allied morphologically with the *gardneri* group, which occurs in central and southwestern Missouri and south-central Oklahoma and overlaps with the former in south-central Missouri.

Stygobromus onondagaensis (Hubricht and Mackin)

Crangonyx onondagaensis Hubricht and Mackin, 1940: 202–203, fig. 9 [in part].

Stygobromus onondagaensis (Hubricht and Mackin).—Hubricht, 1943: 699, 701 [in part]; Dearolf, 1953: 228; Barnard, 1958: 74 [in part]; Hubricht, 1959: 878 [in part]; Nicholas, 1960: 129 [in part]; Holsinger, 1972: 71, fig. 27; Karaman, 1974: 115 [in part]; Pflieger, 1974: 36; Craig, 1975: 4; Craig, 1977: 83, 85, 87; Holsinger, 1977: 262; Barnard and Barnard, 1983: 441, map 16; Fitzpatrick, 1983: 147; Gardner, 1986: 17; Holsinger, 1986: 546.

Stygobromus sp.—Black, 1971: 8.

Stygobromus sp. A.—Black, 1973: 15.

Stygobromus n. sp. 1, *onondagaensis* group.—Gardner, 1986: 17 [in part].

Stygobromus n. sp. 3, *onondagaensis* group.—Gardner, 1986: 17.

Material examined.—ARKANSAS. Benton Co.: Arkansas Archeological Survey Site 3BE532 (cave), 1♀, M. Slay, S. Allen, 12 Apr 2000; Big Spring, 1♀, G. O. Graening, M. Slay, 7 Jul 2000; Cave Springs Cave, 1♀, J. E. Cooper et al.,

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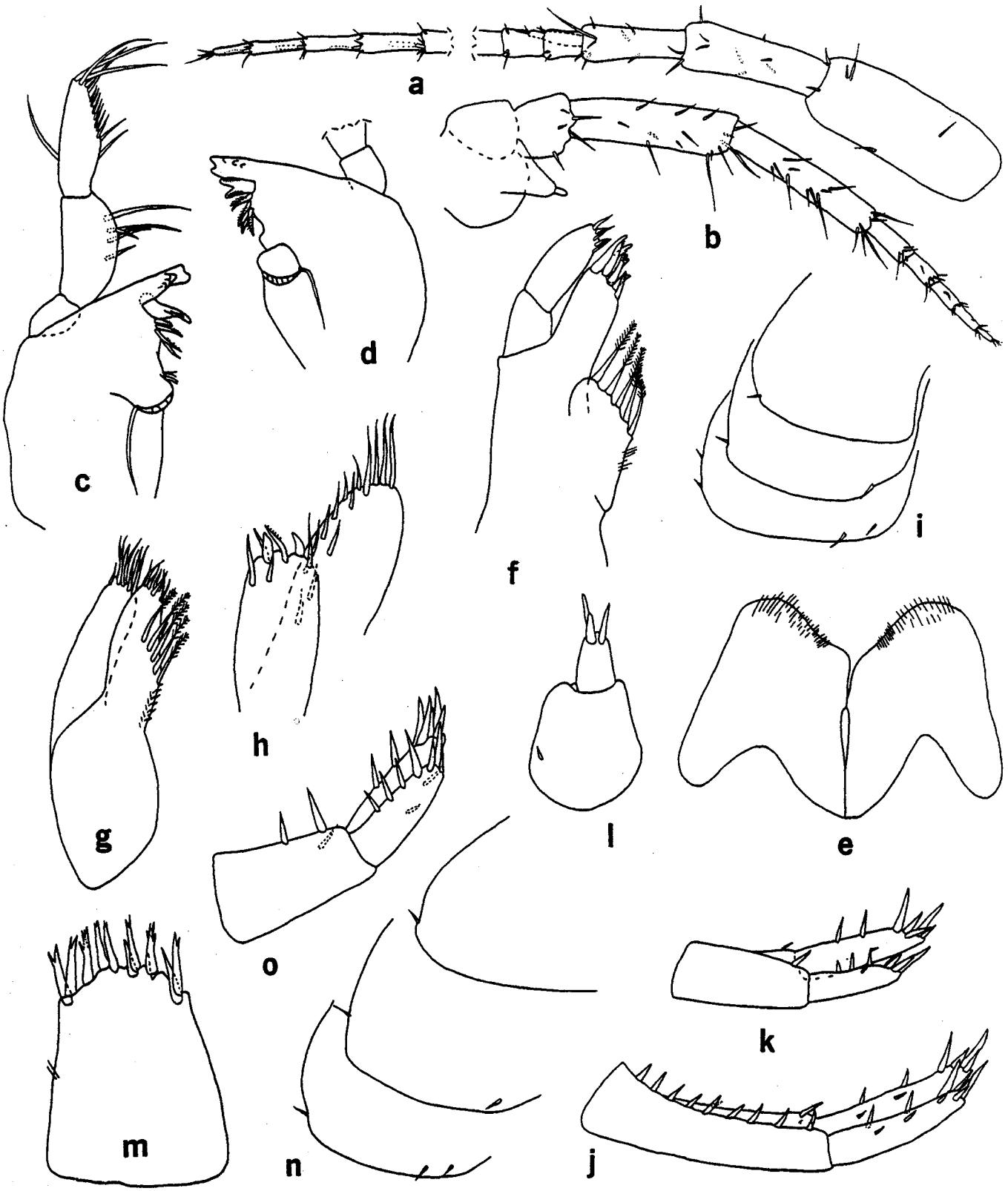

Figure 1. *Stygobromus onondagaensis* (Hubricht and Mackin). Female cotype (4.8 mm), Onondaga Cave, Missouri: a, b, antennae 1, 2; c, left mandible; d, dentate part of right mandible; e, lower lip; f, g, maxillae 1, 2; h, inner and outer plates of maxilliped; i, pleonal plates 1-3; j, k, l, uropods 1, 2, 3; m, telson. Female cotype (4.5 mm), Onondaga Cave: n, pleonal plates 1-3; o, uropod 2. (All mouthparts to same scale except plates of maxilliped to larger scale; antennae to same scale, pleonal plates to same scale.)

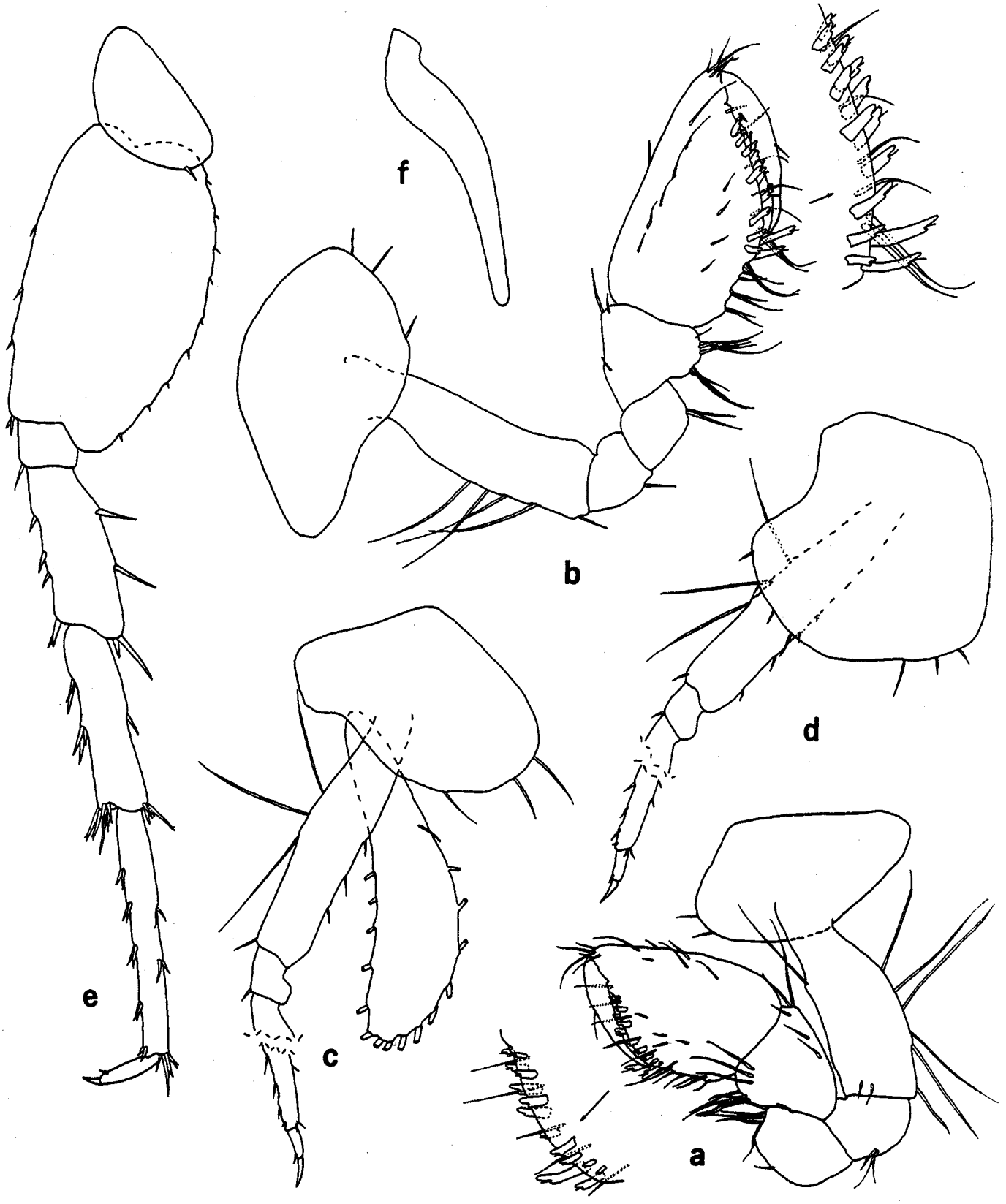

Figure 2. *Stygobromus onondagaensis* (Hubricht and Mackin). Female cotype (4.8 mm), Onondaga Cave: a, b, gnathopods 1, 2 (palmar margins enlarged); c, d, pereopods 3, 4 (in part); e, pereopod 7; f, lateral sternal gill. (Gnathopods and pereopods to same scale.)

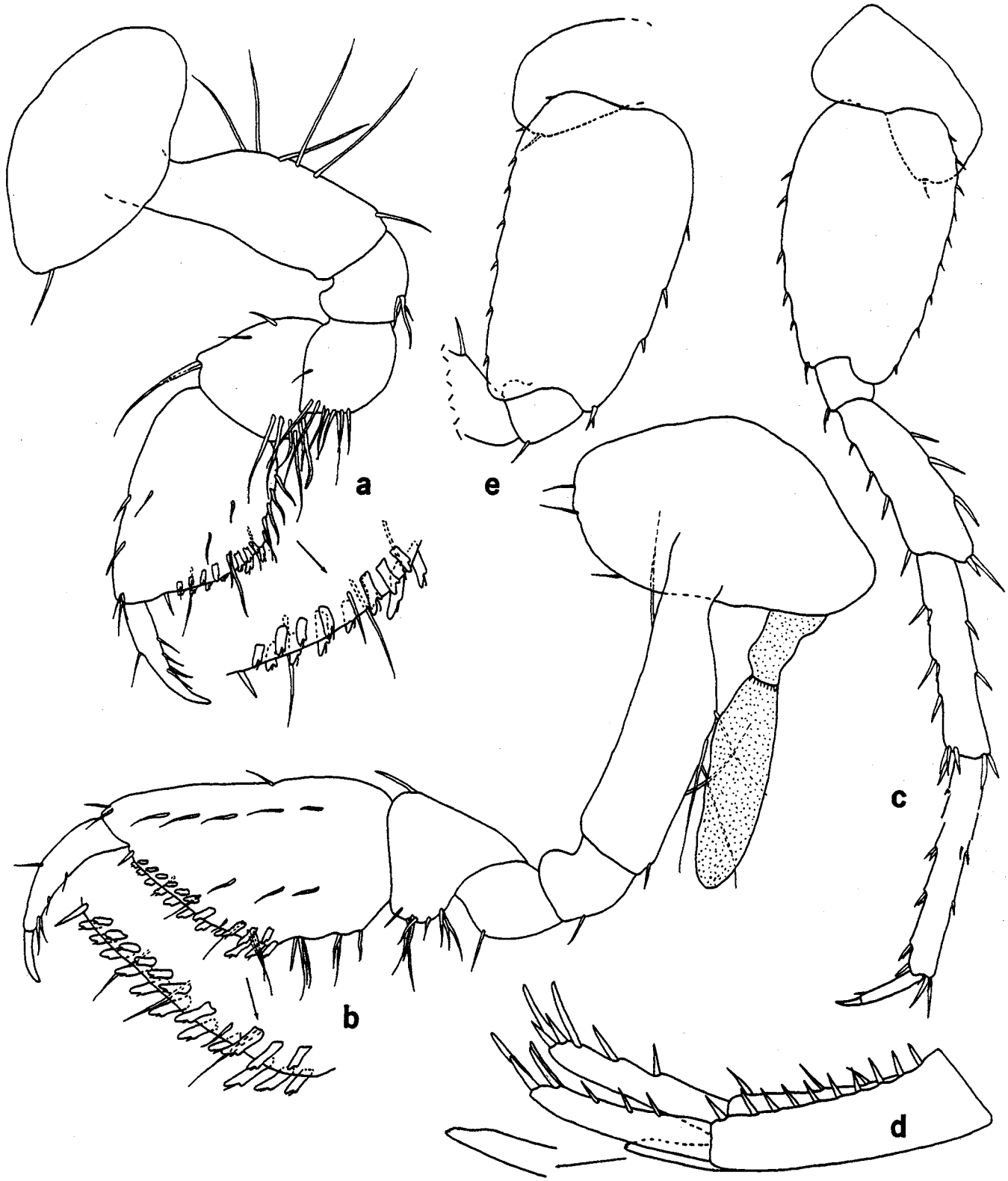

Figure 3. *Stygobromus onondagaensis* (Hubricht and Mackin). Male cotype (4.0 mm), Onondaga Cave: a, b, gnathopods 1, 2 (palmar margins enlarged); c, pereopod 6; d, uropod 1 (peduncular process enlarged). Male cotype (4.0 mm), Onondaga Cave: e, pereopod 6 (in part). (All structures to approximately same scale.)

22 Aug 1968; Tanyard Creek Nature Trail Cave, 1♂, G. O. Graening, S. McGinnis, 6 Jan 2003. KANSAS. Butler Co.: well at Purity Springs, near Augusta, 1♀ (USNM), L. Hubricht, 18 May 1942; well at Purity Springs, 1♀, J. J. Lewis, 1 Aug 1973; Cowley Co.: well on Rozar farm 11.2 km of Cedar Vale, 1♀, A. L. Metcalf, Oct 1970. MISSOURI. Camden

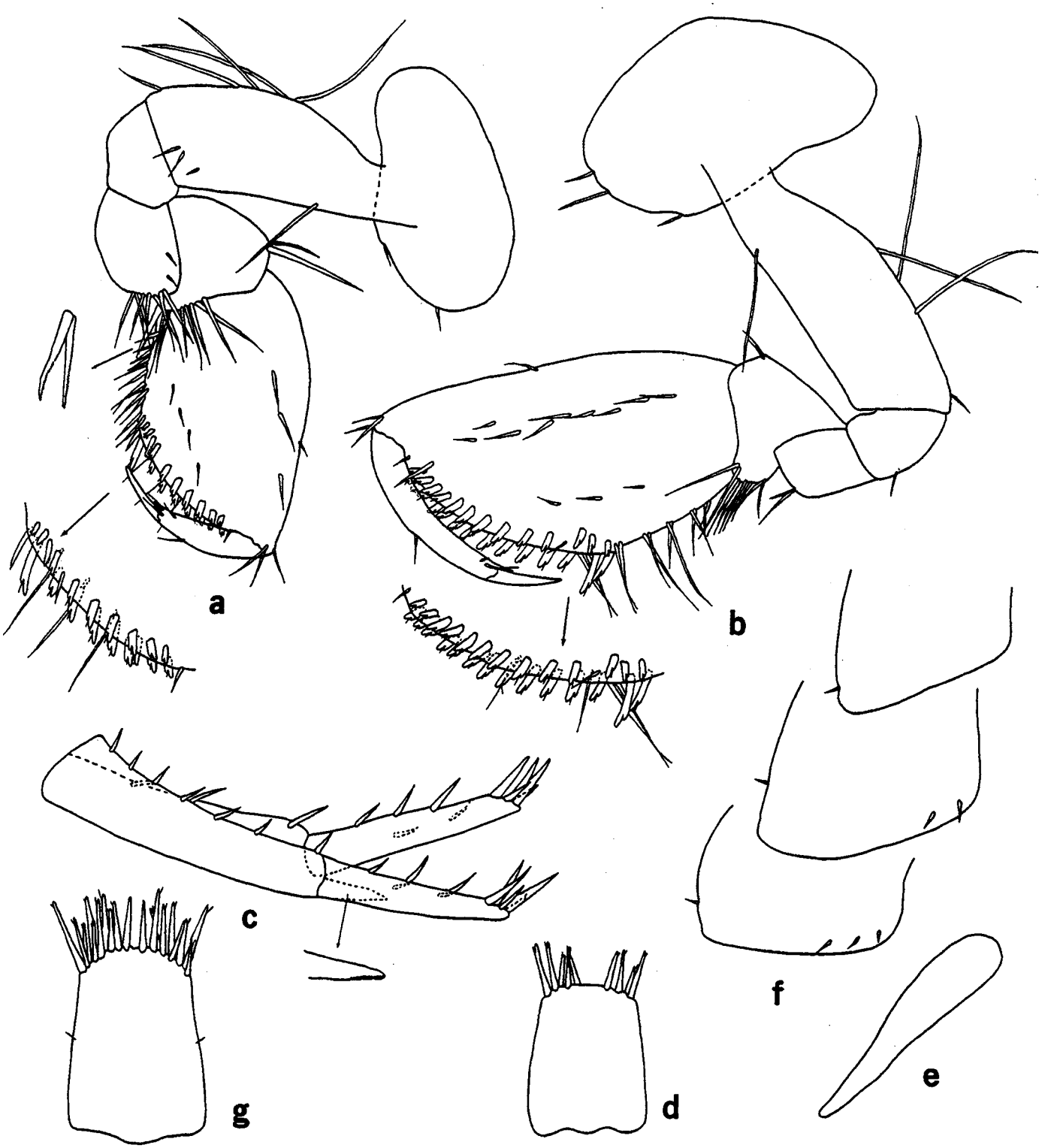

Figure 4. *Stygobromus onondagaensis* (Hubricht and Mackin). Male (4.0 mm), Tumbling Creek Cave, Missouri: a, b, gnathopods 1, 2 (palmar margins enlarged); c, uropod 1 (peduncular process enlarged); d, telson. Female (5.5 mm), Tumbling Creek Cave: e, lateral sternal gill; f, pleonal plates 1-3; g, telson. (Gnathopods to same scale; uropod and telsons to approximately same scale.)

Co.: River Cave, Hakatonka State Park, 25♀♂ (USNM), L. Hubricht, 4 Aug 1940; same locality, 8♀, 5♂, J. J. Lewis, T. Lewis, 5 Aug 1979; same locality, 2♀, 1♂, J. E. Gardner, 14 Apr 1981; Crawford Co.: Fleming Cave, 2♀♂, S. Samoray, N. Forbes, 26 Jan 2005; Moonshine Cave, 1♀, J. E. Gardner, 13 Mar 1982; Onondaga Cave, 2♀ (USNM), K. Dearolf, 17 Jun 1938, 7♀, 1♂ cotypes (USNM 77800) and 15♀, 13♂ cotypes (USNM acc. no. 270464), L. Hubricht, 24 Sep 1938, 4♀, 1 juvenile, J. L. Craig, K. Craig, 30 May 1974; same locality, 15♀, J. E. Gardner, 5 Jan 1982; Onyx Cave, 5♀, 1♂

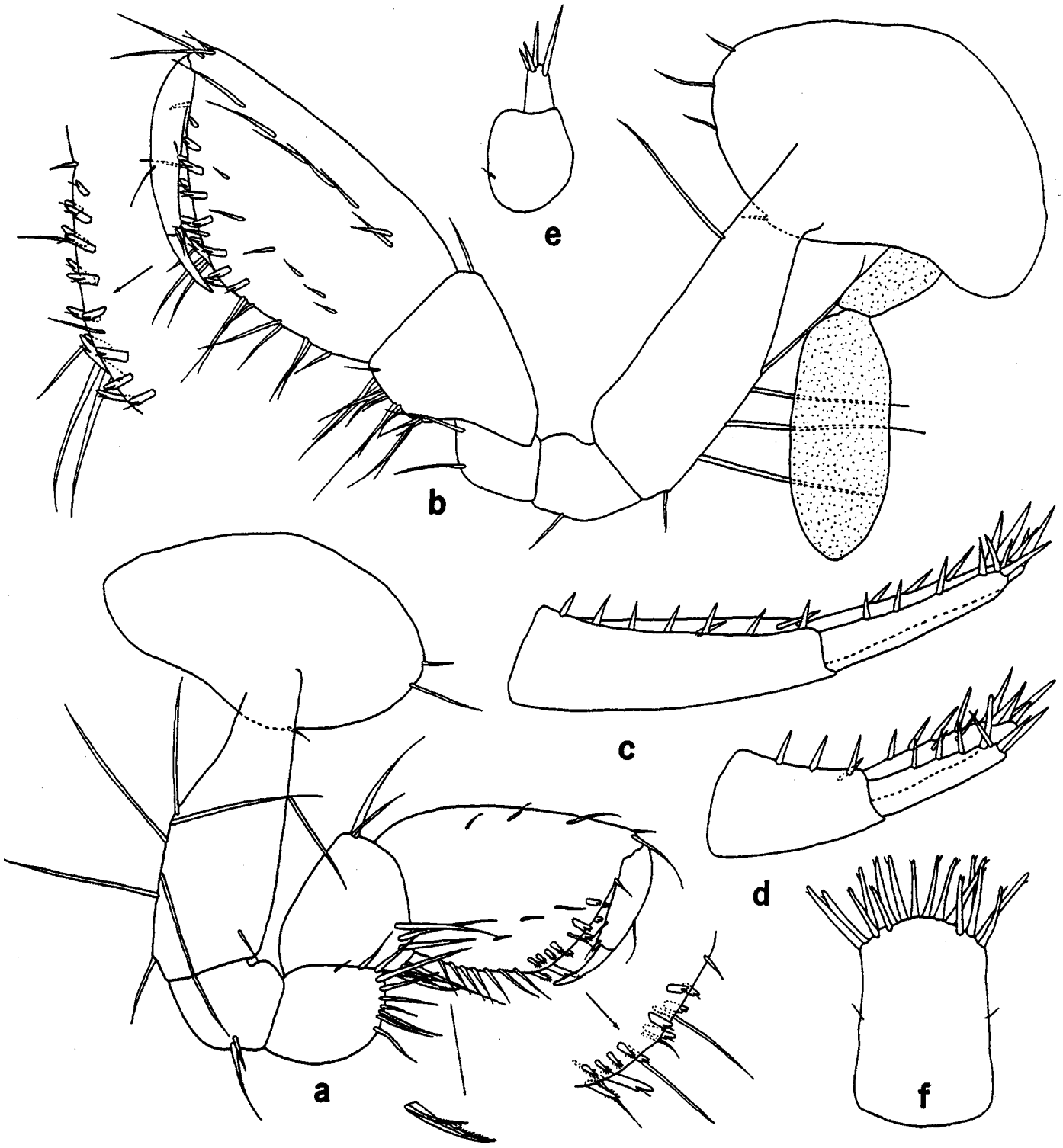

Figure 5. *Stygobromus onondagaensis* (Hubricht and Mackin). Female (5.5 mm), well in Cowley Co., Kansas: a, b, gnathopods 1, 2 (palmar margins enlarged); c, d, e, uropods 1, 2, 3; f, telson. (Gnathopods to same scale; uropods and telson to same scale.)

(USNM), L. Hubricht, 28 Jul 1940; Dent Co.: Saltpeter Cave, 3♀, J. R. Holsinger, R. M. Norton, 10 Jun 1964; Franklin Co.: Mushroom Cave, 26♀, 1♂ (USNM in 2 vials), L. Hubricht, 5 Apr 1942; Wildcat Cave, 6♀, 3♂, 4 juveniles, J. E. Gardner, 12 Mar 1981; Howell Co.: Mud Spring Cave, 3♀, J. E. Gardner, 19 Jun 1979; Lawrence Co.: Turnback Cave, 9♀, 6♂, J. R. Holsinger, R. M. Norton, 11 Jun 1964, 1 juvenile ♀, J. E. Gardner, 24 Aug 1981, 3♀, W. R. Elliott, S. Samoray, M. Slay, 19 Nov 2004; McDonald Co.: unknown cave on Mikes Creek, 20♀♂, R. J. Sarver et al., 1 Oct 1997; Madison Co.: intermittent tributary of Twelve-mile Creek, 2♀ (USNM), L. Hubricht, 21 Apr 1938; Miller Co.: small stream in small cave,

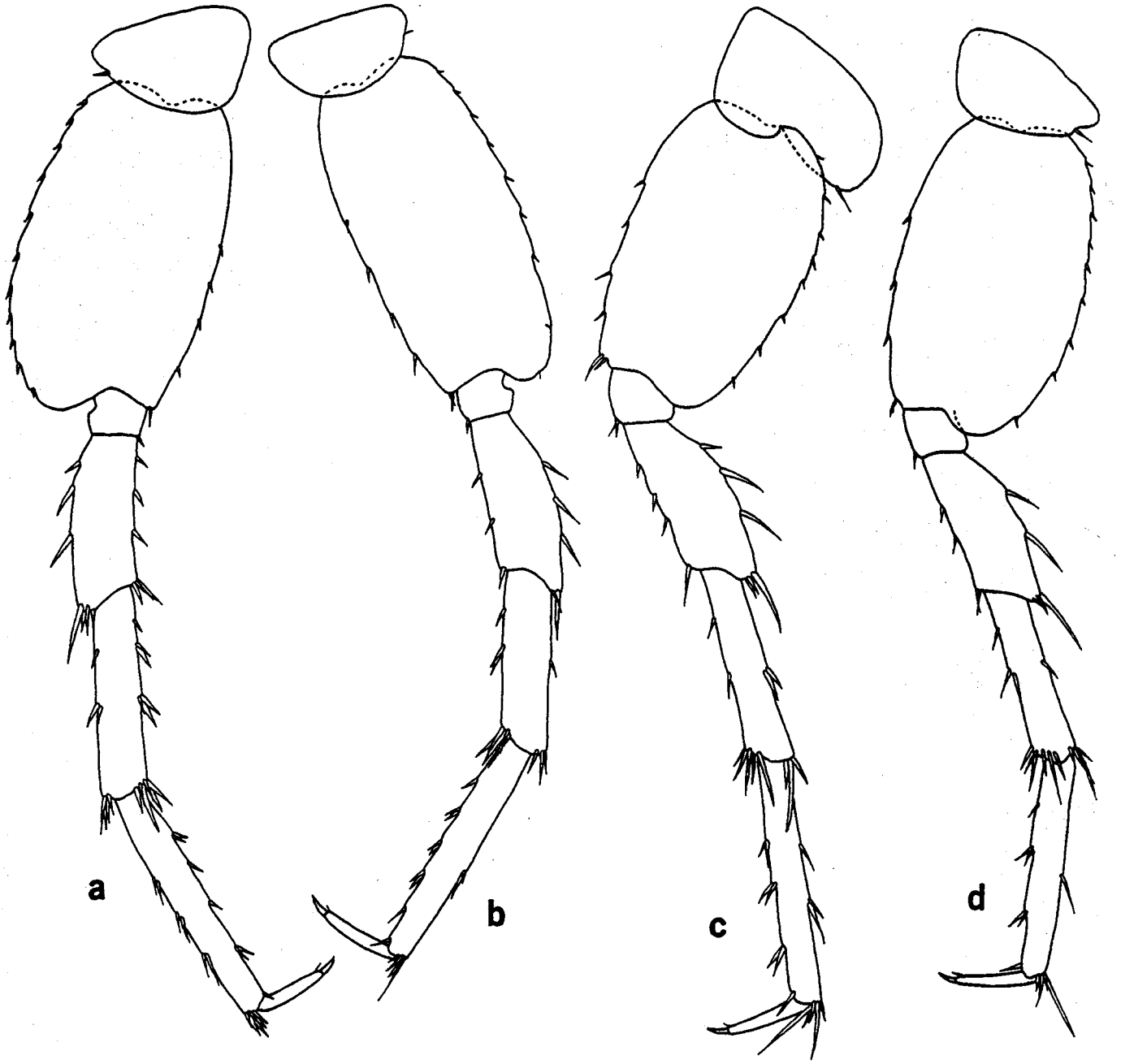

Figure 6. *Stygobromus onondagaensis* (Hubricht and Mackin). Female (5.5 mm), Tumbling Creek Cave, Missouri: a, pereopod 7. Male (4.0 mm), Tumbling Creek Cave: b, pereopod 7. Female (5.5 mm), well in Cowley Co., Kansas: c, d, pereopods 6, 7. (All pereopods to same scale.)

4.8 km SE of Tuscumbia, 14♀♂ (USNM), L. Hubricht, 24 Aug 1940; Morgan Co.: Richland Creek, 1♀, 1♂, R. J. Sarver et al., 28 Mar 2001; Oregon Co.: Barrett Spring Cave, 1♀, M. Sutton, 10 Mar 1991; Falling Spring Cave, 1♀, M. Sutton, 17 Nov 1990; Pipe Spring Cave, 2♀, 1 juvenile, M. Sutton, 15 Dec 1990; Thrasher Ford Cave, 2♀, M. Sutton, 1 Mar 1992; Willow Tree Cave, 3♀, J. E. Gardner, 6 Nov 1979; Ozark Co.: Bat Cave, 1♀, J. E. Gardner, 12 Jul 1979; Phelps Co.: Easter Cave, 1♂ (USNM), L. Hubricht, 26 Jul 1940; Spencer Cave, 1♀, J. R. Holsinger et al., 18 Aug 1968; Tree Root Cave, 6♀, J. E. Gardner, 2 Apr 1982; Pulaski Co.: Great Spirit (Inca, Maxey) Cave 100+♀♂ (AMNH 9159, USNM acc. 270464), L. Hubricht, 8 Oct 1939; same locality, 7♀, 3♂, J. E. Gardner, 22 Mar 1980; same locality, 2 juveniles, W. R. Elliott, 8 May 1999; Riden Cave, 2♀ (USNM), L. Hubricht, 7 Jun 1942; Spring Cave, 1 fragment (USNM), L. Hubricht, 17 Aug 1940; Shannon Co.: Branson Cave, 40♀♂ (USNM), L. Hubricht, 31 Aug 1940; same locality, 10♀, J. E. Gardner, 28 Nov 1982; same locality, 3 juveniles, M. Slay, W. R. Elliott, 9 Apr 2003; Hollow (Cave Hollow?) Cave, 1♀ (USNM), L.

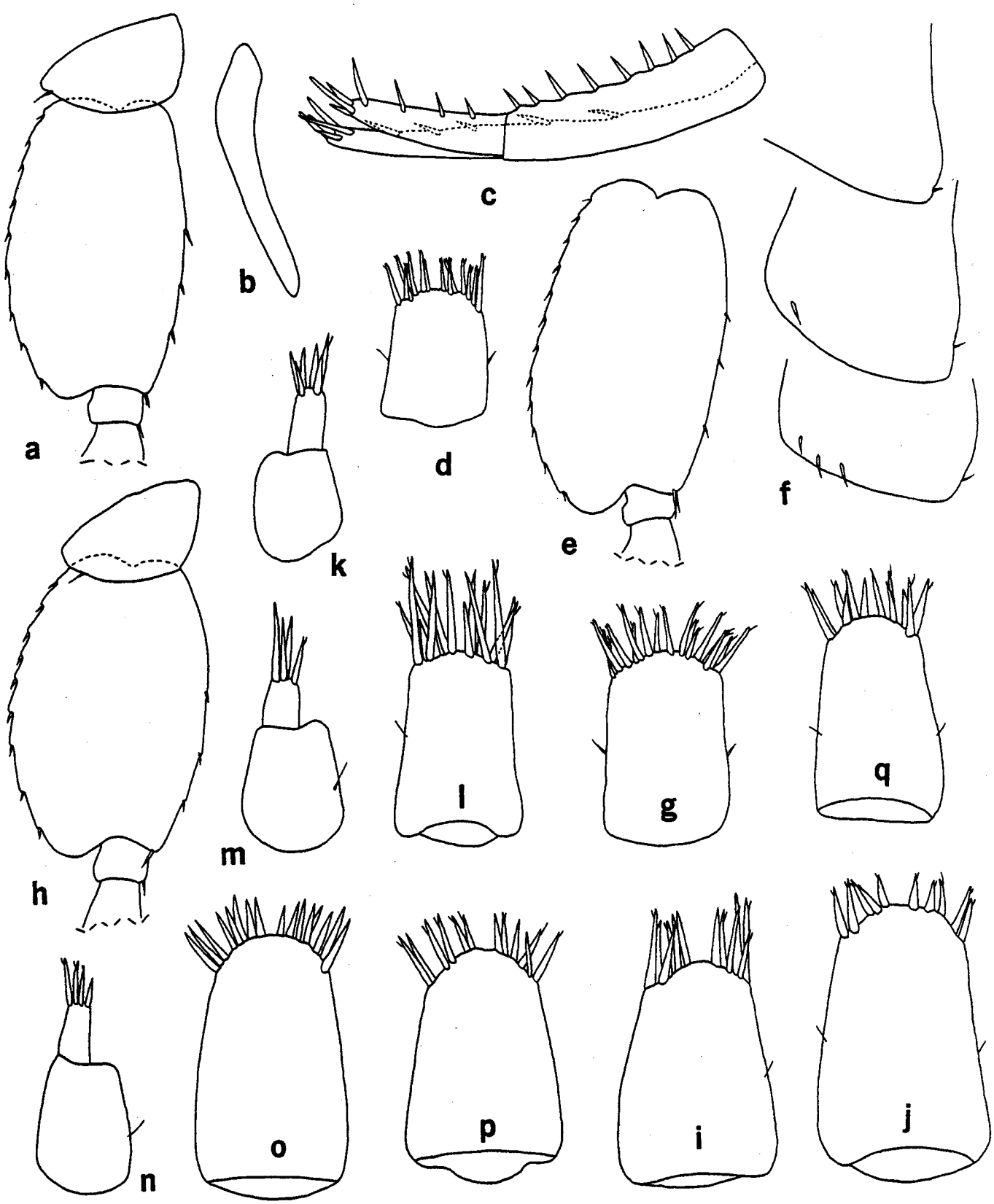

Figure 7. *Stygobromus onondagaensis* (Hubricht and Mackin). Female (4.5 mm), Turnback Cave, Missouri: a, pereopod 7 (in part); b, lateral sternal gill; c, uropod 1; d, telson. Female (6.0 mm), Dressler Cave, Oklahoma: e, uropod 7 (in part); f, pleonal plates 1-3; g, telson. Female (4.5 mm), River Cave, Missouri: h, pereopod 7 (in part); i, telson. Female (4.0 mm), River Cave: j, telson. Female (3.5 mm), well at Purity Springs, Kansas: k, uropod 3; l, telson. Female (4.5 mm), well at Purity Springs: m, uropod 3. Female (4.2 mm), small cave near Round Springs, Missouri: n, uropod 3; o, telson. Female (4.4 mm), Inca Cave, Missouri: p, telson. Female (4.0 mm), Miller Cave, Missouri: q, telson. (All pereopods to same scale; all uropods to same scale; all telsons to approximately same scale except d to smaller scale.)

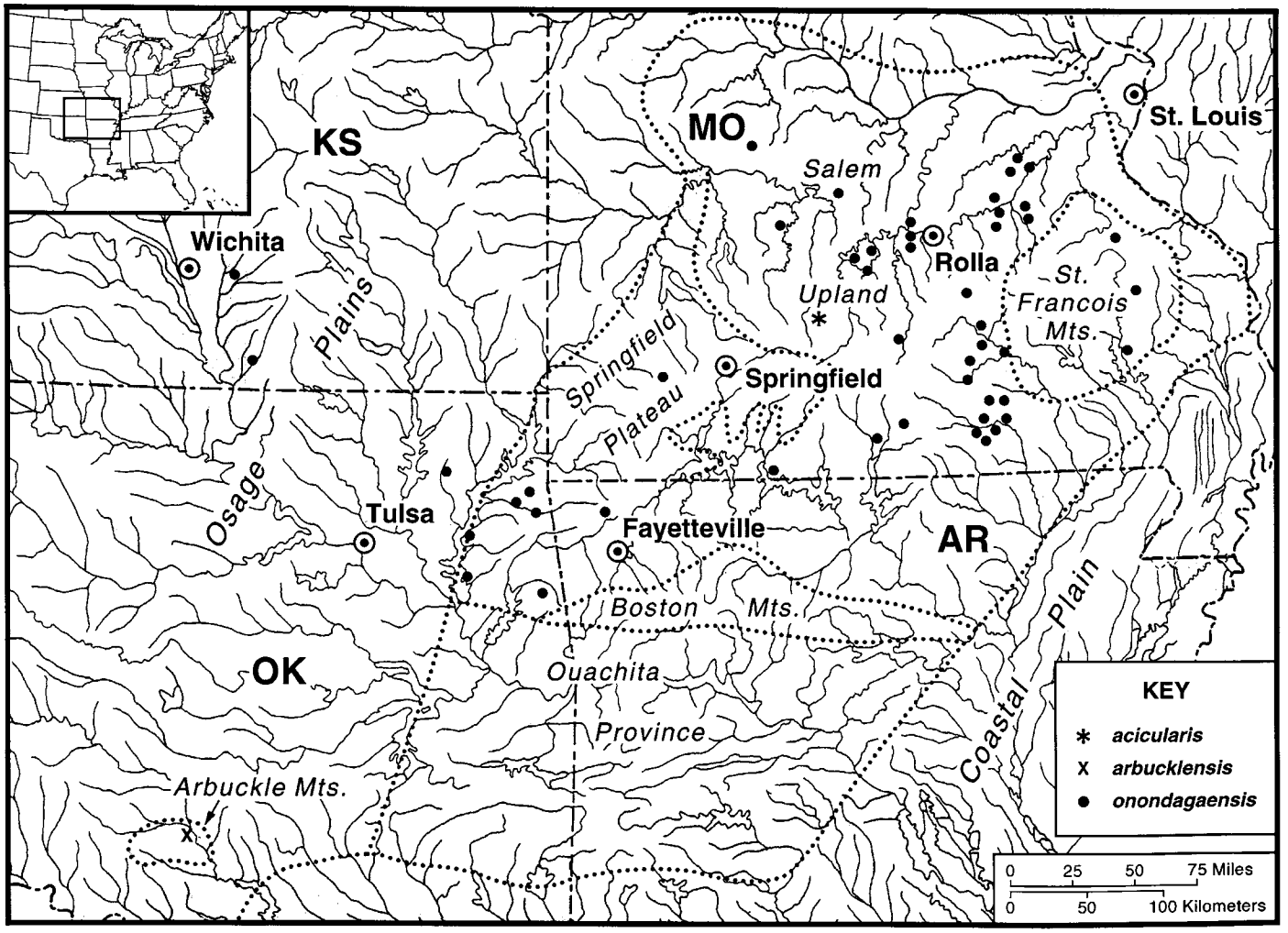

Figure 8. Geographic distribution of *Stygobromus* in the central United States: *S. onondagaensis* assigned to the *exilis* group, *S. acicularis* and *S. arbucklensis* in the *gardneri* group.

Hubricht, 6 Jul 1940; Davis Cave, 1♀, 1♂, 1 juvenile, M. Sutton, 19 Jan 1991; Forester Cave, 1♀, 1 juvenile, W. R. Elliott, 17 Oct 1998; Possum Trot Hollow Cave, 1♂, M. Sutton, 3 Dec 1990; Powder Mill Creek Cave, 4♀ (USNM), L. Hubricht, 2 Aug 1942; small cave near Round Spring, 7♀, 4♂ (USNM), L. Hubricht, 19 Jul 1942; Upper Spring Cave, 1♀, J. E. Gardner, 19 Jun 1984; St. Francois Co.: small spring 3.2 km NNE of Bismarck, 2♀ (USNM), L. Hubricht, 11 Jan 1941; Taney Co.: Blankenship Well, 6 collections (♂, ♀, juveniles), D. Ashley, P. Moss, M. Slay, 19 Dec 2002, 5 Apr 2003, 12 May 2004, 13 May 2004; Morel Cave, 2♀, M. Slay, A. Leary, 23 Apr 2003; plankton drift sample, 1 juvenile, collector/date unknown; Tumbling Creek Cave, 1♂, D. C. Culver, 30 Aug 1967; same locality, 15♀, 3♂, J. R. Holsinger, 22 Aug 1968; Texas Co.: West Piney Creek, 4♀♂, R. J. Sarver et al., 7 Mar 2000; Washington Co.: Brazil Pit Cave, 1♂, J. E. Gardner, 9 Apr 1982; Camp Branch Cave, 2♀, J. E. Gardner, 21 Aug 1980; Wayne Co.: Holmes Hollow Cave, 14♀♂ (USNM), L. Hubricht, 9 Jun 1940. OKLAHOMA. Adair Co.: Sams Pit (Duncan Field Cave system), 1♀, J. H. Black, 8 Nov 1970; Cherokee Co.: Dressler Cave, 2♀, J. H. Black, 2 Mar 1971; Delaware Co.: Bolton Cave, 1♀, C. C. Vaughn, 5 Oct 1991; Marian-Duncan Cave, 2♀, C. C. Vaughn, 9 Nov 1991; Stansberry-January Cave, 1♀, J. H. Black, 30 Jul 1971; Mayes Co.: seep at Girl Scout camp 5 km S of Locust Grove, 11♀ (USNM), L. Hubricht, 21 May 1942; Ottawa Co.: small cave/spring complex, 1♀, J. Waterbury, 28 Jun 2001; Rogers Co.: unnamed spring ca. 8 km NE of Chelsea, 1♀, J. J. Hoover and W. B. Milstead, 1 Jun 1981.

Diagnosis.—Small to medium-sized cavernicolous species, distinguished by the features of the *exilis* group, of which *S. onondagaensis* is the only Ozark representative. Most closely resembles the species of the morphologically very similar *gardneri* group, with which it is partially sympatric (with *S. gardneri* and *S. acicularis)*, but distinguished by the broader and less elongate telson, which usually has 10–20 spines. Largest males, 4.4 mm; largest female, 6.5 mm (rarely >5.5 mm).

Description: Female.—Antenna 1, 45–55 percent length of body, 45–55 percent longer than antenna 2; primary flagellum with 12–16 (rarely 18) articles. Antenna 2, flagellum with 4–5 articles.

Mandibles subequal, spine row with 4 plumose spines; palp article 2 with 4–5 setae, palp article 3 with 1 B seta, 2 C setae, row of D setae, 4 E setae, lacking A seta(e). Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 5 stiff setae/slender spines apically/subapically. Maxilla 2: inner plate with oblique row of 5 plumose setae on inner face. Maxilliped: inner plate with 2 bladespines, 1 plumose spine and 2 naked setae apically, and 2 setae subapically; outer plate with setae on apex and inner margin distally.

Gnathopod 1. Propod smaller than propod 2; palm subequal in length to posterior margin, weakly convex, armed with 8–10 spine teeth in unequal double row, a few of which on inside near defining angle may be plumose and not bifid; defining angle with 2 spine teeth on outside, 2 much shorter ones (sometimes plumose and not bifid) on inside; posterior margin with row of 6–7 setae; medial setae in 2 rows, singly inserted. Nail of dactyl moderately long but not reaching the end of defining angle spines. Article 5 with at least 1 rastellate seta. Coxa deeper than broad, ventral margin with 2 setae.

Gnathopod 2. Propod subrectangular, longer than broad, longer and little broader than propod 1; palm subequal in length to posterior margin, nearly straight or slightly convex, armed with 11–12 spine teeth in double row; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 4 sets of mostly doubly inserted setae; medial setae in 2 rows, singly inserted. Nail of dactyl moderately long but not reaching end of defining angle spines. Coxa deeper than broad, ventral margin with 3 setae.

Coxa of pereopod 3 deeper than broad, convex ventral margin with 3 longish setae. Coxa of pereopod 4 about as broad as deep, expanded distally, reaching about 60 percent length of corresponding basis; posterior margin with shallow concavity; convex ventral margin with 3 setae. Pereopod 6 little longer than pereopod 5, 40–50 percent length of body, 17–20 percent length of pereopod 5. Bases somewhat variable but typically moderately broad with convex posterior margins and well-developed distoposterior lobes; posterior margin of pereopod 7 basis convex, distally produced into broad, rounded, shallow lobe. Articles 4, 5, and 6 of pereopods with longish, slender spines. Dactyls of pereopods relatively long and slender, 35–45 percent length of corresponding propods. Coxal gills on pereopods 2–6. Two median sternal gills on pereonites 2 and 3; 2 pairs of simple, lateral sternal gills on pereonites 6 and 7, larger and sometimes bent on 7; sternal gills absent from pleonite 1. Brood plates expanded distally, longer than corresponding article 2 of pereopods 3 and 4.

Pleonal plates: posterior margins somewhat variable but usually weakly convex, each with 1 (rarely 2) setule near or above corner; distoposterior corners usually rounded off and indistinct but occasionally tiny and distinct; ventral margin of plate 2 with 1 or 2 spines, that of plate 3 with 2 or 3 spines. Uronites free. Uropod 1: inner ramus subequal to or little longer than outer ramus, 65–75 percent length of peduncle, armed with 6–8 spines; outer ramus with 7–10 spines; peduncle with 10–13 spines. Uropod 2; inner ramus longer than outer ramus, little shorter than peduncle, armed with about 8 spines; outer ramus with 8 or 9 spines; peduncle with 2 or 3 spines. Uropod 3: peduncle with 1 setule; ramus approximately 50 percent the length of the peduncle, bearing 3–4 apical spines. Telson longer than broad, slightly tapering distally; apical margin entire, weakly convex, bearing 10–20 spines (typically 12–16).

Male.—Differing from the female as follows. Gnathopod propod 2 proportionately larger, palm shorter than posterior margin, armed with 16–23 spine teeth in double row, posterior margin little longer than palm, with 3–5 sets of mostly doubly inserted setae. Peduncular process of uropod 1 about 40 percent length of outer ramus, with few minute serrations on distal end.

Variation.—Morphological variation is observed in populations extending across the species range from NE to SW. Rather significant differences are seen in structure of the telson and number of spines, bases of pereopods 7, and perhaps gnathopods.

Type-locality.—Onondaga Cave, 8 km southeast of Leasburg, Crawford County, Missouri, has both drip pools and a lower-level stream.

Distribution and ecology.—The range of *Stygobromus onondagaensis* is presented in Fig. 8. The ranges of *S. onondagaensis* and *S. gardneri* (see below) overlap in part in eight counties in eastern Missouri, but they have never been collected together from the same habitat or even the same cave. Also note several records of this species from surface streams, presumably inhabiting the hyporheos.

The *gardneri* group

Diagnosis.—Adult size range relatively small and incompletely known, 5.0–6.5 mm. Closely allied morphologically with the *exilis* group, but distinguished from the latter by the following differences: Propod of gnathopod 2 narrowing distally. Coxa 4 perhaps more broadly expanded distally. Pereopods 6 and 7 bases with broadly convex posterior margins and large, bluntly rounded distoposterior lobes; dactyls elongate and slender. Pereopod 7 without coxal gill. Pleonal plates produced distoposteriorly, especially 2 and 3; posterior margins with 1 setule each inserted well above

rounded-off and nearly indistinct distoposterior corners. Telson relatively narrow, distinctly longer than broad, sharply tapered distally.

This group is composed of three species: two occur in the Ozark region: *Stygobromus gardneri* being relatively common and widespread in eastern and central Missouri and northeastern Arkansas, while *S. acicularis* is rare and known only from two caves in southwestern Missouri. The third species, *Stygobromus arbucklensis*, is very rare and presently known only from a single cave in the Arbuckle Mountains in south-central Oklahoma.

***Stygobromus gardneri,* new species**

Crangonyx onondagaensis Hubricht and Mackin, 1940: 202–203 [in part].

Stygobromus onondagaensis (Hubricht and Mackin).—Hubricht, 1943: 699, 701 [in part]; Dearolf, 1953: 228; Barnard, 1958: 74 [in part]; Hubricht, 1959: 878 [in part]; Nicholas, 1960: 129 [in part]; Karaman, 1974: 115 [in part]; Gardner, 1986: 17 [in part].

Stygobromus sp.—Dearolf, 1953: 228.

S. new species.—Craig, 1977: 83, 85–87.

Stygobromus n. sp. 1 and n. sp. 2, *onondagaensis* group.—Gardner, 1986: 17.

Material examined (paratypes unless designated otherwise).—ARKANSAS. Carroll Co.: Blowing Springs Cave, 2♀1♂, 1 fragment, G. O. Graening et al., 28 Apr 2001; Independence Co.: Blevins Cave, 1♀, G. O. Graening et al., 5 Oct 2002; Chinn Springs Cave, 1♀, G. O. Graening, E. Corfey, B. Wagner, 10 Nov 2001; Dozens Den Cave, 1♀, 1♂, G. O. Graening et al., 12 Dec 2000; Madison Co.: Womack Spring Cave, 1♀ (not a paratype), G. O. Graening et al., 6 Dec 2000; Marion Co.: Reed Cave, 1♀, 1♂, G. O. Graening et al., 15 Nov 2001; Sharp Co.: Cave City (Crystal River) Cave, 1♀, G. O. Graening, D. Fenolio, 23 Nov 2002; Eckel Cave, 2♀, G. O. Graening, D. Fenolio, 22 Nov 2002; Stone Co.: Nesbitt Springs Cave, 1♀, M. Slay et al., 30 Mar 2002; Rowland Cave, 1♀, G. O. Graening, 12 Jun 2001. MISSOURI. Bollinger Co.: Little Whitewater River, 1 juv, R. J. Sarver et al., 19 Sep 2000; Carter Co.: Cave Spring Onyx Cavern, 1♀ (USNM 260782), L. Hubricht, 6 Jul 1940; Coalbank Cave, 3♀, J. E. Gardner, 18 Feb 1983; Lost Man Cave, 5♀, 2♂, J. E. Gardner, 14 Mar 1983; Crawford Co.: Cathedral Cave, 1♀ (USNM 260783), K. Dearolf, 7 Jun 1938; same locality, 1♀, J. E. Gardner, 24 Apr 1981; Dent Co.: Bounds Branch Cave, 2♀, J. E. Gardner, 20 Jun 1980; Franklin Co.: Fisher Cave, 8♀, 1♂, J. E. Gardner, 11 Mar 1982; Meramec Caverns, 16♀♂ and fragments (USNM 260784), L. Hubricht, 16 Dec 1939; same locality, 1♀, R. Oesch, Jan 1989, and 1♀/♂, M. Slay, 8 Oct 2002; Iron Co.: Railroad Cave on Big Creek, 2 juveniles, R. J. Sarver et al., 1 Oct 2002; Boulder Cave, 1♂, J. E. Gardner, 1 Jun 1982; Cave Hollow Cave, 2♀, J. E. Gardner, 2 Jun 1982; same locality, 1♀, W. Elliott, 6 Jun 1998; Jefferson Co.: Rice Cave, 1♀, 4♂ (USNM 260785), L. Hubricht, 18 Dec 1938; Oregon Co.: Blowing Spring Cave, 2♀, M. Sutton, 5 Apr 1992; New Liberty Cave, 1♂, M. Sutton, 5 Jan 1991; Onyx Cave, 1♀, M. Sutton, 3 May 1992; Statue Cave, 1♀, M. Sutton, 7 Dec 1991; Walters Spring Cave, 1, M. Sutton, 12 Oct 1991; Perry Co.: Schindler Cave, 21♀, 6♂, 3 fragments (USNM 260786), L. Hubricht, 20 Feb 1943; Phelps Co.: Marcellus Cave, 1♂, L. Hubricht, 1 Oct 1939; Saltpeter Cave, 3 juveniles (USNM 260787), L. Hubricht, 7 Oct 1939, 4♀, 1 juvenile (USNM 260788), L. Hubricht, 27 Jul 1941; same locality, 1♂, J. R. Holsinger et al., 18 Aug 1968; Shannon Co.: Brawley Cave, 2♀, M. Sutton, 7 Dec 1991; Marvel Cave, 1♀, J. E. Gardner, 29 May 1984; same locality, 1♀, L. Ireland, 18 Aug 2001; Medlock Cave, 2♀, 1♂ (USNM 260789), L. Hubricht, 31 Aug 1940; Spring Hollow Cave No. 1, 3♀, W. R. Elliott, K. Lister, R. Long, 20 Jan 1998; Sycamore Cave, 6♀, J. E. Gardner, 16 Nov 1982; St. Francois Co.: Falling Rock Spring Cave, 1♂, J. E. Gardner, 9 Apr 1982; Washington Co.: Great Scott Cave, 2♂, J. E. Gardner, 13 Sep 1979; Green Cave, 2♀, J. L. Craig, 12 Jul 1974; Hamilton Spring Cave, 1♀, 3♂, J. L. Craig, 13 Jul 1974, and 2♂, 2 fragments (USNM 260790), L. Hubricht, 20 Jul 1940; Mossy Spring Cave, 4♀, J. E. Gardner, 21 Aug 1980, and holotype ♀ (USNM 266488), 6♀, 3♂, J. E. Gardner, 14 Feb 1983.

Diagnosis.—A medium-sized cavernicolous species, closely allied morphologically and geographically with *S. onondagaensis*, but differing by having proportionately longer antennae, gnathopod propods, pereopods, uropods 1 and 2, and telson; more spines on palm of gnathopod propods; and reaching sexual maturity at larger size. The posterior corners of pleonal plates 1 and 2 are variably produced in some populations. Largest males, 5.0 mm; largest females, 6.5 mm.

Description: Female.—Antenna 1 about 60 percent length of body, 55 percent longer than antenna 2; primary flagellum with 16–17 articles. Antenna 2, flagellum with 5 articles. Mouthparts almost identical to those of *S. onondagaensis*, except that inner plates of maxillae each have 1 or 2 more plumose setae and apex of inner plate of maxilliped has 1 additional bladespine.

Gnathopod 1. Propod little smaller than propod of gnathopod 2; palm subequal to or little shorter than posterior margin, armed with 15 or 16 spine teeth in double row; defining angle with 1 long and 1 short spine tooth on outside, 2 short ones on inside; posterior margin rather long, nearly straight except near base, with row of 8 setae; medial setae sparse, singly inserted. Nail of dactyl about 1/3 length of dactyl, reaching end of defining angle spines. Article 5 with rastellate setae. Coxa slightly deeper than broad, convex ventral margin with 4 setae.

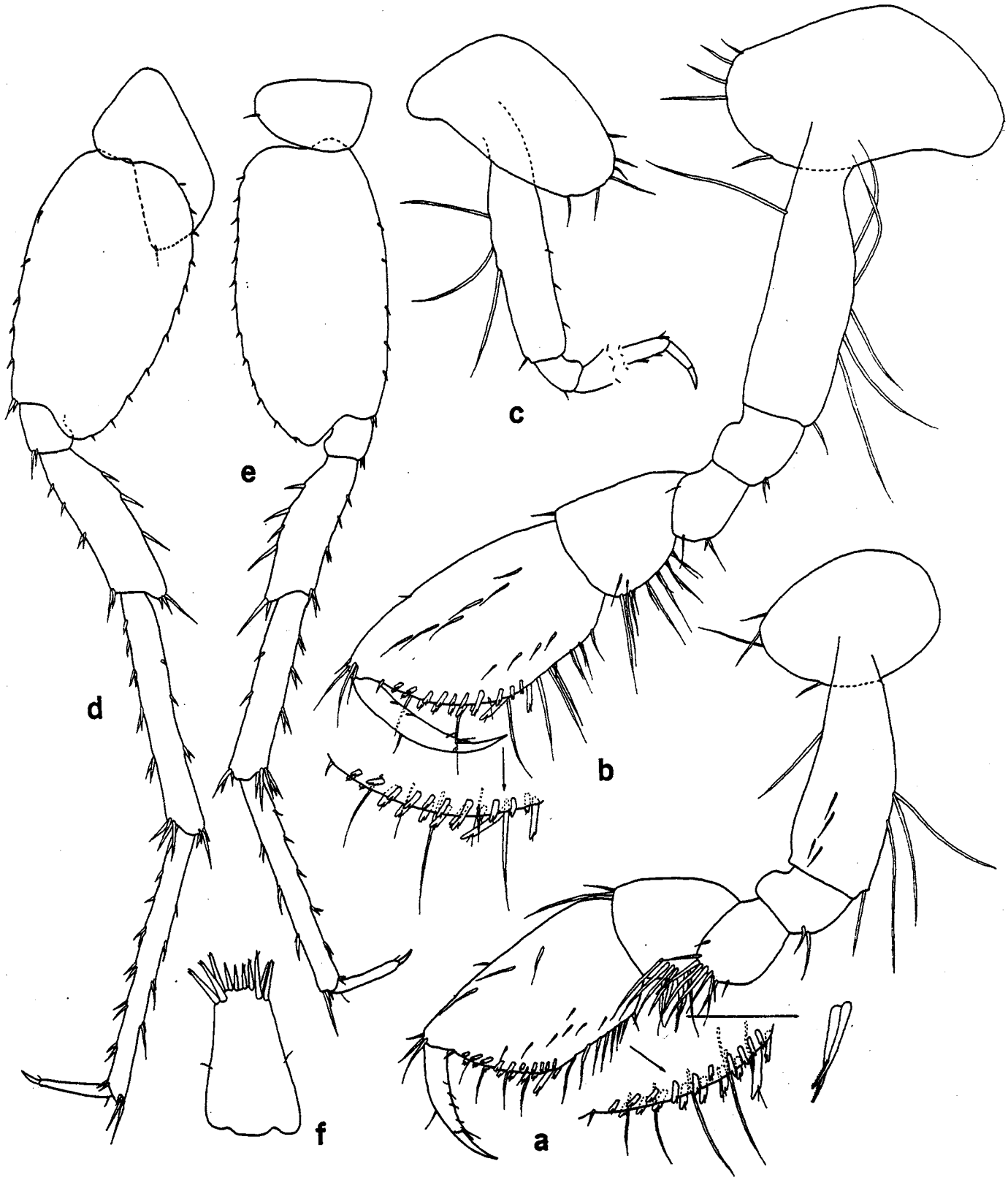

Figure 9. *Stygobromus gardneri*, new species, female paratype (5.5 mm), Mossy Spring Cave, Missouri: a, b, gnathopods 1, 2 (palmar margins and rastellate setae enlarged); c, pereopod 3 (in part); d, e, pereopods 6, 7; f, telson. (Gnathopods and pereopods to same scale.)

Gnathopod 2. Propod rather narrow, longer than broad, subrectangular; palm oblique, slightly convex, subequal in length to posterior margin, armed with 16 spine teeth in double row; defining angle with 2 longish spine teeth on outside, 2 or 3 shorter ones on inside; posterior margin relatively long, with 4 or 5 sets of singly and doubly inserted setae;

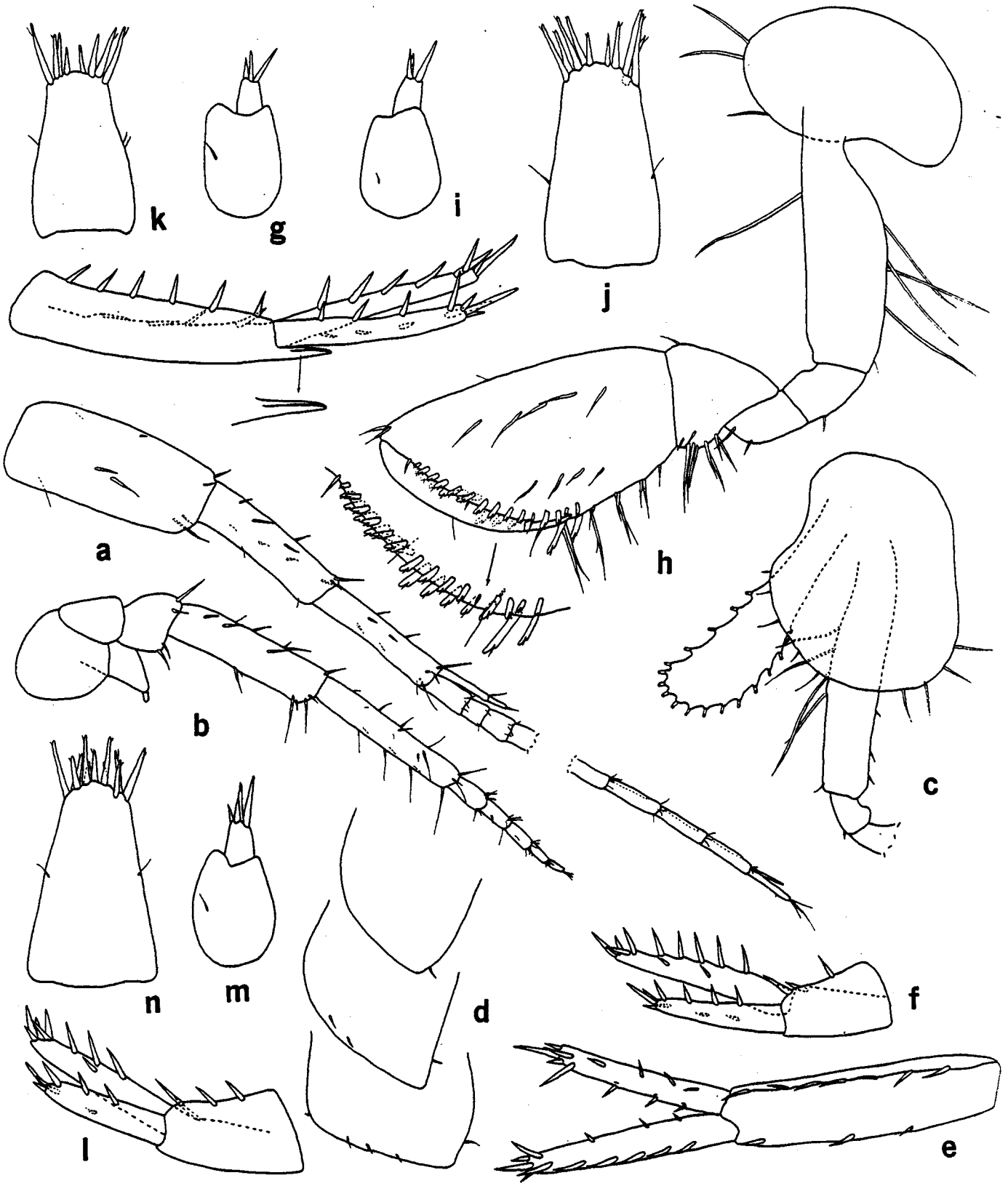

Figure 10. *Stygobromus gardneri*, new species, female paratype (5.5 mm), Mossy Spring Cave, Missouri: a, b, antennae 1, 2; c, pereopod 4 (in part); d, pleonal plates 1-3; e, f, g, uropods 1, 2, 3. Male paratype (4.0 mm), Mossy Spring Cave: h, gnathopod 2 (palmar margin enlarged); i, uropod 3; j, telson. Male paratype (3.2 mm), Great Scott Cave, Missouri: k, telson. Female paratype (5.5 mm), Lost Man Cave, Missouri: l, m, uropods 2, 3; n, telson. (Antennae to same scale; uropods 1 and 2 to same scale; uropods 3 and telsons to approximately same scale.)

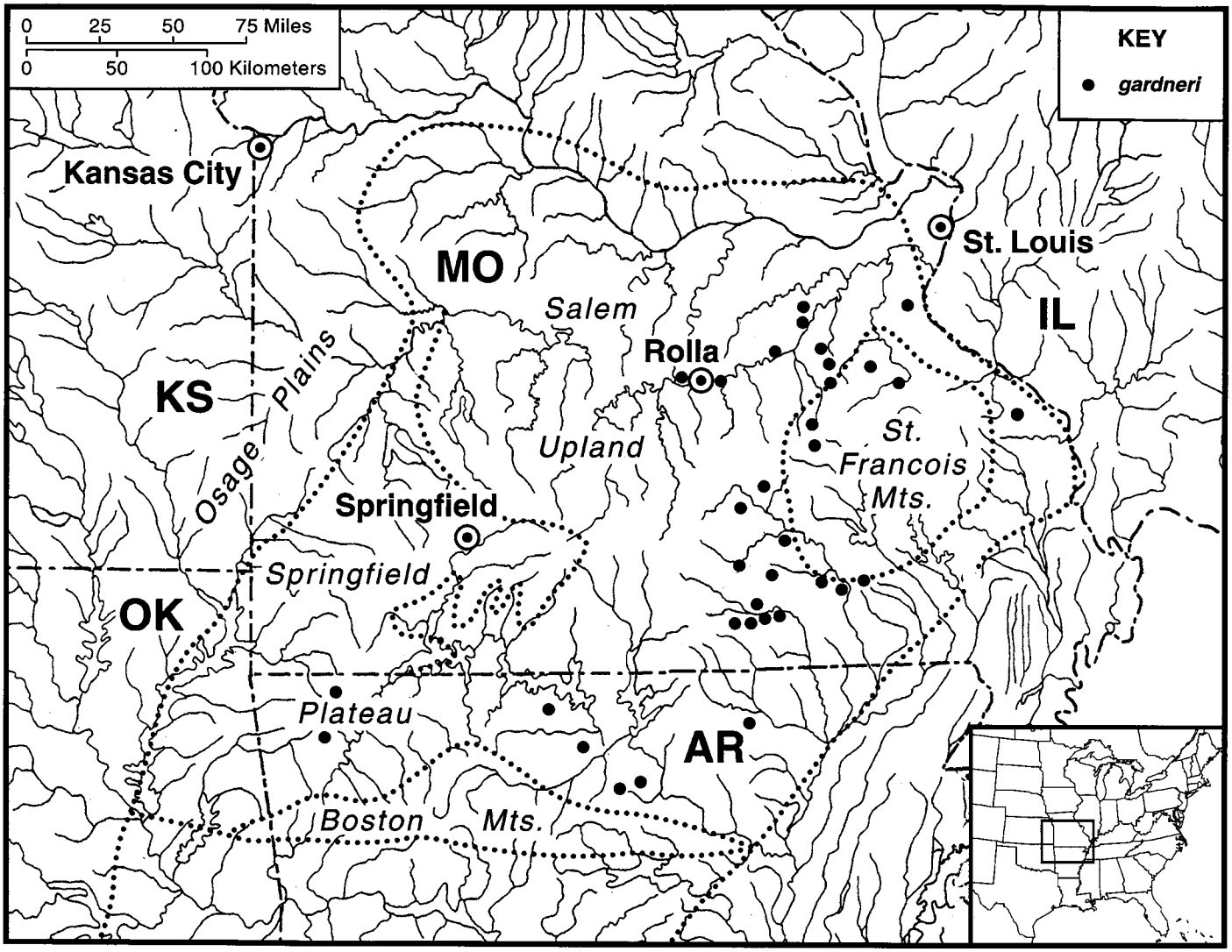

Figure 11. Range map of *Stygobromus gardneri*, new species.

medial setae in 2 rows, singly inserted. Dactyl nail moderately long. Coxa deeper than broad, convex ventral margin with 3–5 setae.

Coxa of pereopod 3 deeper than broad, margin with 6 setae. Coxa of pereopod 4 about as deep as broad, expanded distally, reaching about 60 percent length of corresponding basis; posterior margin with very shallow concavity; broad, convex ventral margin with 10 setae. Pereopod 6 little longer (about 10 percent) than pereopod 7, 58–63 percent length of body, about 15 percent longer than pereopod 5. Bases of pereopods 5–7 rather long, about as broad proximally as distally, posterior margins convex but not much expanded; distoposterior lobes broadly rounded but not deep. Dactyls of pereopods 5–7 relatively slender and elongate, those of pereopods 5 and 6 about 36–38 percent length of corresponding propods, that of pereopod 7 about 45 percent as long. Coxal gills present on pereopods 2–6, absent from 7. Two median sternal gills on pereonites 2 and 3; 2 pairs simple, lateral sternal gills on pereonites 6 and 7, structurally similar to those of *S. onondagaensis*; sternal gills absent from pleonite 1. Brood plates somewhat expanded distally and similar to those of *S. onondagaensis*.

Pleonal plates: plate 2 (and sometimes plate 1) produced posteroventrally, posterior margins of plates 1 and 3 weakly convex, that of plate 2 straight; each margin with 1 setule, setules on 2 and 3 well above corners, that of 1 close to corner; distoposterior corners weakly rounded; ventral margins of plates 2 and 3 with 2 or 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, armed with 10–13 spines; outer ramus with 10–12 spines; peduncle with 10 spines. Uropod 2: inner ramus relatively long, longer than outer ramus, longer than peduncle (sometimes up to 40 percent), armed with 9–11 spines; outer ramus with 7–10 spines; peduncle with 3–4 spines. Uropod 3: peduncle with 1 setule; ramus 1/3 to 1/2 length of peduncle, bearing 3–4 apical spines.

Telson rather narrow, longer than broad, tapering distally; apical margin entire, sometimes weakly convex, armed with 8–10 spines.

Male.—Differing from female as follows. Gnathopod propod 2 proportionately a little larger, palm armed with 23 spine teeth in double row, posterior margin with 4 sets of setae, singly, doubly and triply inserted. Peduncular process of uropod 1 about 1/3 length of outer ramus, narrowing to a point distally, with minute serrations on upper margin.

Variation.—The propod of gnathopod 2 appears to be slightly broader in females in some populations. The peduncle of uropod 2 may also be shorter in some populations. The single female specimen from Womack Spring Cave in Madison County, Arkansas, differs from most other members of this species in having a proportionately shorter first antenna and, for this reason, is not designated a paratype.

Type-locality.—Mossy Spring Cave, 18 km south-southwest of Richwoods in Washington County, Missouri. The type-material was collected from isolated drip pools.

Distribution and ecology.—Note the overlap in range with *S. onondagaensis* (see comments under that species above). *Stygobromus gardneri* is endemic to the Ozarks in the Salem Plateau region in southeastern Missouri and northern Arkansas in the Boston Mountains (Fig. 11), where it is an inhabitant of caves.

Remarks.—Although Hubricht and Mackin (1940) pointed out that their material from Rice Cave in Jefferson County possibly differed from the specimens they described as *S. onondagaensis*, they nevertheless assigned it to that species. Examination of this material clearly indicates that it warrants recognition as the species described above under the name *S. gardneri*. As indicated above, six caves listed by Hubricht and Mackin (1940) and Hubricht (1943) as localities for *S. onondagaensis* appear to be localities for *S. gardneri*.

Etymology.—It is a pleasure to name this species in honor of James E. Gardner in recognition of his many fine collections of amphipods from Missouri caves in the early 1980s.

***Stygobromus acicularis*, new species**

Material examined.—MISSOURI. Wright Co.: Smittle Cave, holotype ♀ (in part on slide mount) (USNM 266489); Little Smittle Cave, 1♂ paratype (in part on slide mount), J. R. Holsinger et al., 19 Aug 1968, and 2♀♂, M. Slay, W. R. Elliott, 14 Nov 2002.

Diagnosis.—A small, rare cavernicolous species closely allied with *S. gardneri*, but distinguished from that species by proportionately smaller and narrower gnathopod propods; and further distinguished by the rather long slender dactyls of pereopods 5–7, and relatively long, distally tapered telson with 8–10 spines with minute distal setule. Largest and only known male (possibly immature), 2.4 mm; largest and only known female, 3.5 mm.

Description: Female.—Antenna 1 relatively long, about 60 percent length of body, approximately 50 percent longer than antenna 2; primary flagellum with up to 12 articles. Antenna 2, flagellum with 3 articles.

Mouthparts closely similar or identical to those described for *S. gardneri* and *S. exilis*.

Gnathopod 1. Propod subrectangular, approximately twice as long as broad; palm relatively short, only about 65 percent length of posterior margin, armed with 4 spine teeth in double row; defining angle with 2 longish spine teeth on outside, 2 shorter ones on inside; posterior margin relatively long, bearing row of 4 setae; medial setae sparse, in 2 rows of 2 each and singly inserted. Dactyl nail long, reaching end of defining angle spines. Article 5 with rastellate setae. Coxa twice as deep as broad, convex ventral margin with 3 setae.

Gnathopod 2. Propod little larger (longer) than propod 1, subrectangular, more than twice as long as broad; palm oblique, shorter than posterior margin, armed with 6 spine teeth in double row; defining angle with 2 longish spine teeth on outside, 2 shorter ones on inside; posterior margin proportionately long, with few singly/doubly inserted setae; medial setae sparse, in 2 rows of 2 each and singly inserted. Nail of dactyl comparatively long and slender. Coxa deeper than broad, broadly convex ventral margin with 4 setae.

Coxa of pereopod 3 deeper than broad, margin with 4 setae. Coxa of pereopod as broad as deep, expanded distally, reaching about 60 percent length of corresponding basis; posterior margin with shallow concavity; broadly convex ventral margin with 7 setae. Pereopod 6 about 57 percent length of body, little longer than pereopod 7, 20 percent longer than pereopod 5. Bases of pereopods 5–7 moderately broad; posterior margins convex but not greatly expanded; distoposterior lobes broadly rounded but weakly produced. Articles 4, 5 and 6 of pereopods 5–7 bearing longish, slender spines. Dactyls of pereopods 5–7 long and slender, 50–55 percent length of corresponding propods. Coxal gills present on pereopods 2–6, absent from pereopod 7. Two small median sternal gills on pereonites 2 and 3; two pairs simple, lateral sternal gills on pereopods 6 and 7; sternal gills absent from pleonite 1. Brood plates expanded distally, longer than corresponding article 2 on pereopods 3 and 4.

Pleonal plates: posterior margin of plate 2 produced posteroventrally, posterior margins of plates 1 and 3 slightly convex, that of plate 2 nearly straight; each margin with 1 setule, setules on 2 and 3 well above corners, that of 1 close to corner; distoposterior corners of plates 1 and 3 rounded off and indistinct, that of plate 2 less rounded, more distinct; ventral margins of plates 2 and 3 each with 1 or 2 spines. Uronites free. Uropod 1: inner ramus little longer than outer

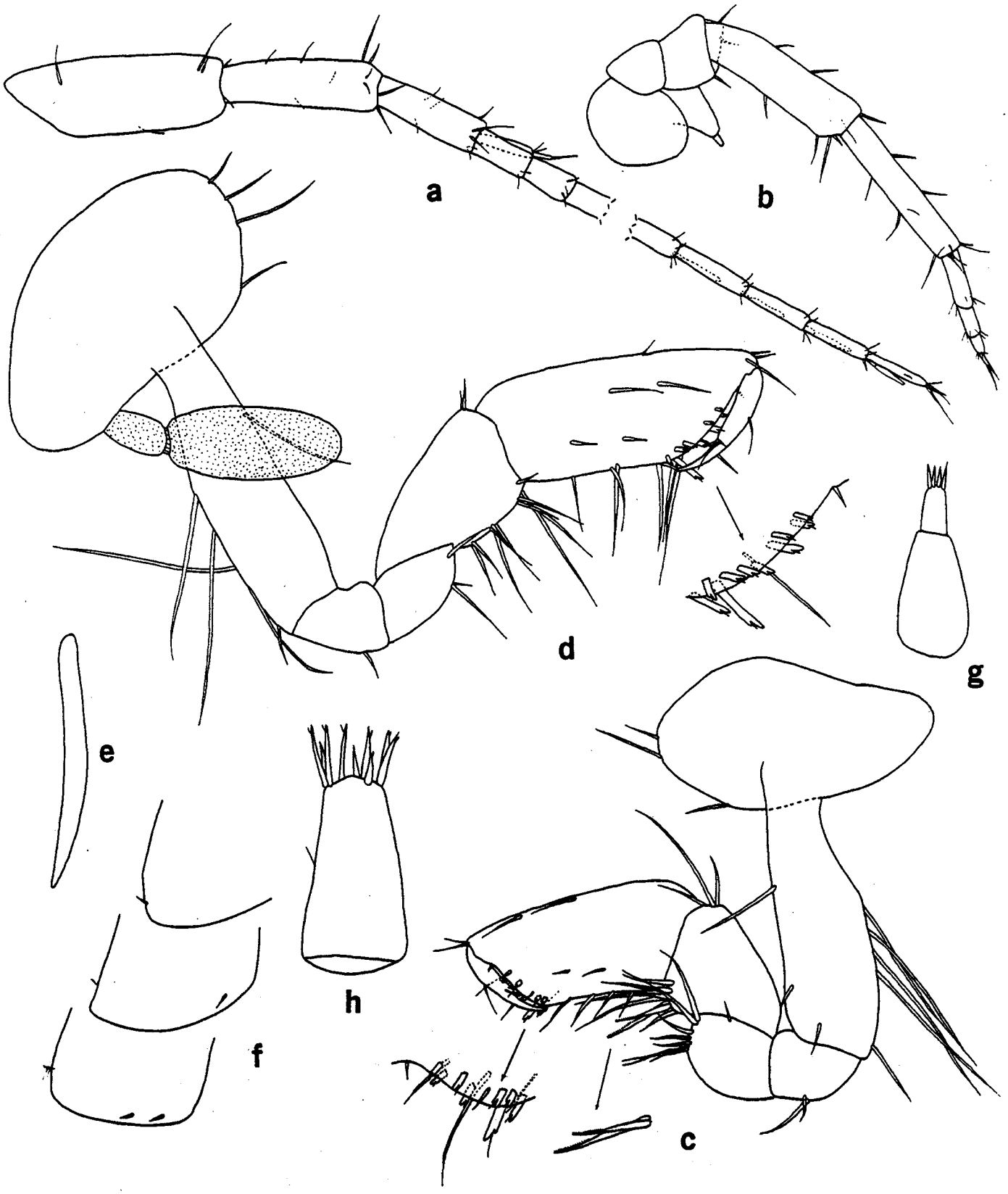

Figure 12. *Stygobromus acicularis*, new species, female holotype (3.5 mm), Smittle Cave, Missouri: a, b, antennae 1, 2; c, d, gnathopods 1, 2; e, lateral sternal gill; f, pleonal plates 1-3; g, uropod 3; h, telson. (Antennae and gnathopods to approximately same scale; other structures to different scales.)

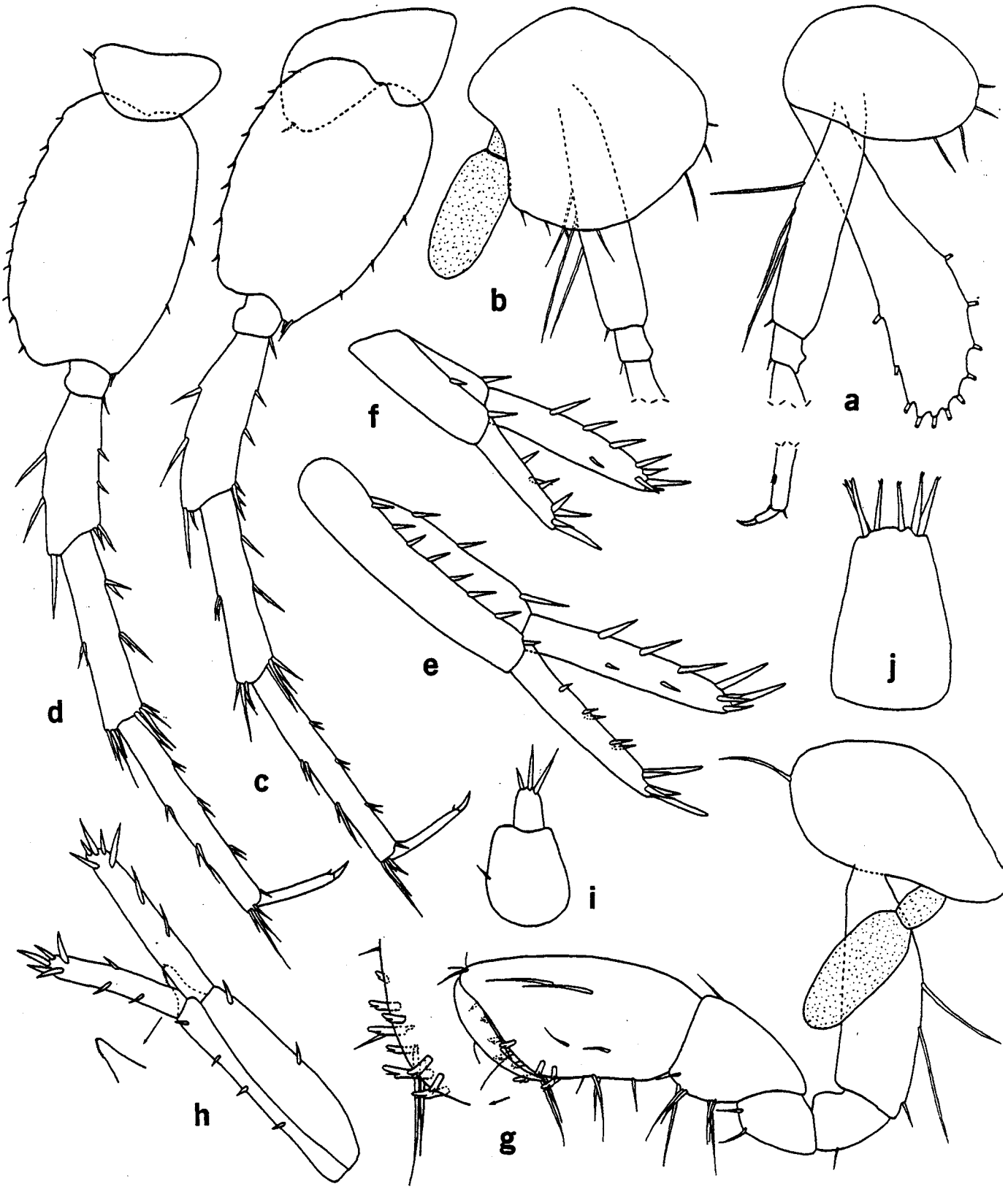

Figure 13. *Stygobromus acicularis*, new species, female holotype (3.5 mm), Smittle Cave, Missouri: a, b, pereopods 3, 4 (in part); c, d, pereopods 6, 7; e, f, uropods 1, 2. Male paratype (2.4 mm), Little Smittle Cave, Missouri: g, gnathopod 2 (palmar margin enlarged); h, uropod 1 (peduncular process enlarged); i, uropod 3; j, telson. (Pereopods to same scale; uropods 1 and 2 to same scale, uropod 3 and telson to larger scale.)

ramus, 75–80 percent length of peduncle, armed with 10 spines; outer ramus with 9 or 10 spines; peduncle with 10 or 11 spines. Uropod 2: inner ramus longer and thicker than outer ramus, 20 percent longer than peduncle, armed with 9 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: peduncle with setule; ramus about 50 percent length of peduncle, apex with 3–4 spines. Telson 35–40 percent longer than broad, narrowing distally; apical margin entire, weakly convex, bearing 8–10 spines.

Male.—Differing from female as follows. Propod of gnathopod 2 little broader and slightly less elongate. Peduncular process of uropod 1 about 30 percent length of outer ramus, narrowing distally, margin near end with very fine serrations. Fewer spines on uropods and telson.

Type-locality.—Smittle Cave, located approximately 40 km northeast of Marshfield, is developed in limestone or dolomite of lower Ordovician age on the Salem Upland of the Ozark Plateau.

Distribution and ecology.—This species is known only from the Smittle caves in northwestern Wright Co., Missouri (Fig. 8). The female holotype was ovigerous, with 1 embryo and 2 juveniles in the brood pouch. One specimen was collected from a shallow stream with a mud bottom in Smittle Cave, whereas the other was from a shallow stream with a gravel substrate in nearby Little Smittle Cave. Both caves also had other species of amphipods (*Stygobromus ozarkensis* and/or *Crangonyx forbesi*), isopods (*Caecidotea antricola*), and salamanders (*Eurycea nerea*).

Etymology.—The epithet *acicularis* is from Latin, meaning “like a needle,” which is descriptive of the long, slender dactyls of pereopods 5, 6 and 7.

***Stygobromus arbucklensis,* new species**

Stygobromus sp. B.--Black, 1973: 16.

Material examined.—OKLAHOMA. Murray Co.: Dip Cave, holotype ♂ (partly on slide mounts) (USNM 266490), R. M. Norton, J. R. Holsinger, 24 Jun 1964.

Diagnosis.--A relatively small subterranean species, bearing morphological similarity with *S. gardneri* and *S. acicularis* (described above), but easily distinguished from these species by: narrower gnathopod propods; deep, narrow coxae 1–3; deeper coxa 4; expanded bases of pereopods 5–7, especially 7; pleonal plates produced distoposteriorly; uropod 3 with tiny ramus and two large spines on peduncle; and very narrow, elongate telson. Largest and only known male, 4.0 mm; female unknown.

Description: Male.—Antenna 1, 53 percent length of body, about 48 percent longer than antenna 2; primary flagellum with 12 articles. Antenna 2, flagellum with 4 articles.

Mandibles subequal; spine row with 3 plumose spines; palp article 2 with 4 setae of unequal lengths; palp article 3 with 1 B setae, row of D setae, 4 E setae, lacking A and C setae. Inner lobes of lower lip small. Maxilla 1: inner plate with 4 plumose setae; palp with about 5 short setae apically/subapically. Maxilla 2: inner plate with oblique row of 4 plumose setae on inner face. Maxilliped: inner plate with 2 bladespines, 1 plumose seta, 1 naked seta apically, and 3 setae subapically; outer plate with many setae on apex and distal half of inner margin.

Gnathopod 1. Propod relatively narrow; palm shorter than posterior margin, armed with 12 spine teeth in unequal double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin longer than palm, with row of 6 or 7 singly inserted setae; medial setae sparse, in 2 rows, singly inserted. Dactyl rather short, not reaching to end of defining angle. Article 5 with rastellate setae. Coxa narrow, deep, more than 2x deeper than broad, narrow convex ventral margin with 3 longish setae.

Gnathopod 2. Propod longer than propod 1, relatively narrow, subrectangular, 2x longer than broad; palm little shorter than posterior margin, slightly convex, armed with 15 spine teeth in double row; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 3 sets of doubly/triply inserted setae. Medial setae in 2 rows, singly inserted. Dactyl short, nail not reaching to defining angle. Coxa narrow, deep, more than 2x deeper than broad, narrow convex ventral margin with 4 setae.

Coxa of pereopod 3 deep and narrow, closely similar to those of gnathopods, with 4 marginal setae. Coxa of pereopod 4 deeper than broad, reaching about 80 percent length of corresponding basis; posterior margin with shallow excavation of proximal 1/3; distal half of posterior margin and ventral margin with 6 setae and 3 setules. Pereopods 6 and 7 subequal in length, 50 percent length of body, only about 10 percent longer than pereopod 5. Bases of pereopods 5–7 broad: anterior margins convex, bearing rows of small spines; posterior margins of pereopods 5 and 6 nearly straight, that of 7 expanded distally into large, shallow, broadly rounded distoposterior lobe; distoposterior lobes of pereopods 5 and 6 also shallow and broadly rounded but not as large as that of pereopod 7. Dactyls of pereopods 5–7 slender, elongate, about 50 percent length of corresponding propods. Coxal gills on pereopods 2–6, absent from pereopod 7. Median sternal gills and pleonite sternal gills absent; 2 pairs simple (small) lateral sternal gills present on pereonites 6 and 7.

Pleonal plates: posterior margins produced into broadly rounded distoposterior corners, margins each with 1 setule set above corner; ventral spines set well above respective margins, plates 2 and 3 each with 1 or 2 such spines. Uronites free. Uropod 1: inner ramus longer than outer ramus, about 90 percent length of peduncle, bearing 8 spines;

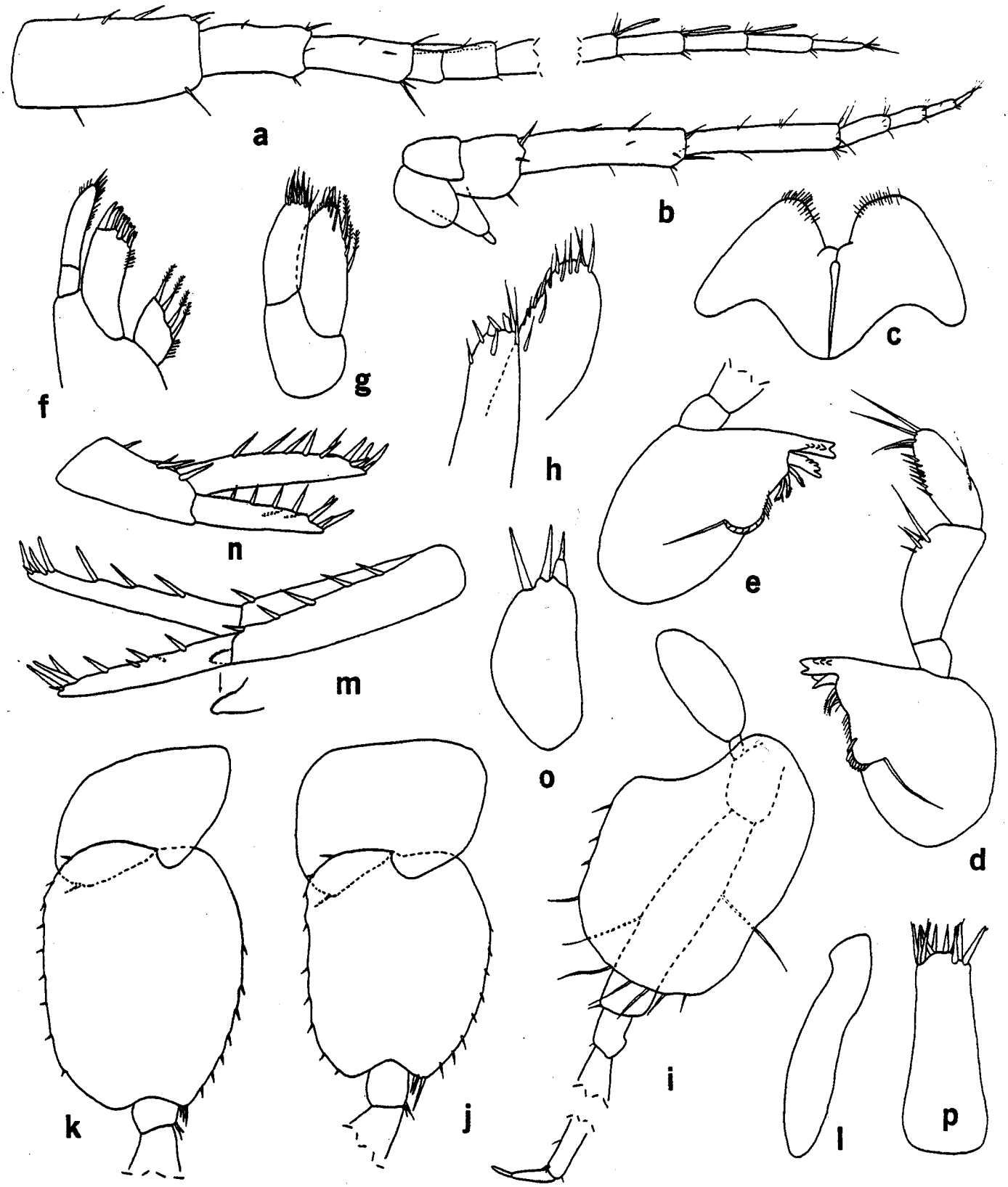

Figure 14. *Stygobromus arbucklensis*, new species, male holotype (4.0 mm), Dip Cave, Oklahoma: a, b, antennae 1, 2; c, lower lip; d, right mandible; e, left mandible (in part); f, g, maxillae 1, 2; h, inner and outer plates of maxilliped; i, pereopod 4 (in part); j, k, pereopods 5, 6 (in part); l, lateral sternal gill; m, n, o, uropods 1, 2, 3 (peduncular process of 1 enlarged); p, telson. (Antennae to same scale; mouthparts to same scale except maxilliped plates to larger scale; pereopods to same scale; uropods 1, 2 and telson to same scale, uropod 3 to larger scale.

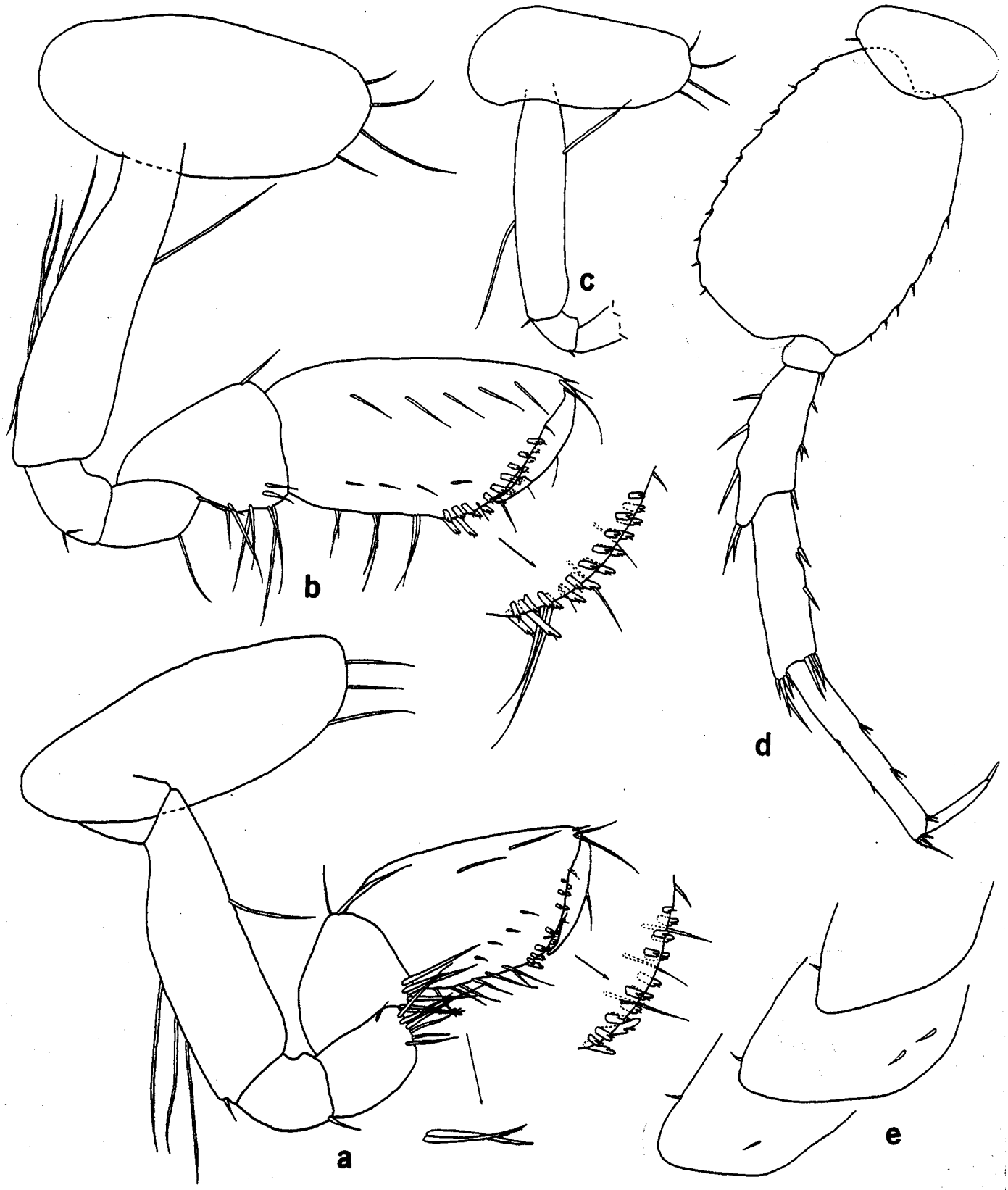

Figure 15. *Stygobromus arbucklensis*, new species, male holotype (4.0 mm), Dip Cave, Oklahoma: a, b, gnathopods 1, 2 (palmar margins and rastellate setae enlarged); c, pereopod 3 (in part); d, pereopod 7: e, pleonal plates 1-3. (Gnathopods to same scale; pereopods and pleonal plates to same scale.)

outer ramus with 9 spines; peduncle with 6 spines; peduncular process about 1/6 length of outer ramus, narrowing distally, upper margin minutely serrated. Uropod 2: inner ramus about 25 percent longer than outer ramus and peduncle, armed with 11 spines; outer ramus with 10 spines; peduncle with 4 spines. Uropod 3: peduncle much larger than ramus, with 2 longish spines apically; ramus reduced, about 20 percent length of peduncle, with an apical spine. Telson long, narrow, tapering distally, at least 2x longer than broad; apical margin entire, convex, bearing 10 spines.

Type-locality.—Dip Cave, located near Bitter Enders Cave and approximately 3.2 km upstream from Turner Falls, is a very small cave developed in lower Ordovician or upper Cambrian limestone. It is located adjacent to the surface creek that ultimately feeds the falls downstream. The single specimen was collected from submerged wood in a pool at the rear of the cave, where it was associated with a subterranean isopod, probably *Conasellus acuticarpus*.

Distribution and ecology.—This species is known only from the type-locality, Dip Cave, which is located in the Arbuckle Mountains of south-central Oklahoma (Fig. 8). The species has so far proven to be very rare, but with diligent searching it is likely to be found in other caves or associated karst groundwater habitats in the vicinity of Turner Falls.

Remarks.—The collection and examination of additional specimens, especially a mature female, would help in more precisely defining the taxonomic affinities of this species and clarify its group status.

Etymology.—The specific name refers to the occurrence of this species in the Arbuckle Mountains.

The *heteropodus* group

Diagnosis.—Distinguished by huge male gnathopod propod 2 with notched palm, sexual dimorphism, bases of pereopods 5–7, and other features. As presently known, the group contains three species, with distributions restricted to *Stygobromus heteropodus* in eastern Missouri and two undescribed species in central Kentucky and Harrison County, Indiana.

Stygobromus heteropodus Hubricht

Stygobromus heteropodus Hubricht, 1943: 701–703.—Barnard, 1958: 74; Hubricht, 1959: 878; Nicholas, 1960: 128; Holsinger, 1972: 68, 72; Karaman, 1974: 112; Pflieger, 1974: 8; Craig, 1975: 4; Holsinger, 1977: 262; 1978: 123; Peck and Lewis, 1978: 46, fig. 5; Barnard and Barnard, 1983: 409, map 14; Fitzpatrick, 1983: 146; Holsinger, 1986: 545.

Material examined.—MISSOURI. Ste. Genevieve Co.: small spring under ledge, Pickle Springs, 16♀, 12♂ cotypes (USNM 1093227; 10♂♀ under cat. no. USNM 79412) (several on slide mounts in part), L. Hubricht, 9 Mar 1941. Diagnosis.—A medium-sized stygobiont species, distinguished by pronounced sexual dimorphism in the male, which includes the large 2nd male gnathopod propod with palmar notch, shape of bases of pereopods 5–7, and long setae on pereopods 6 and 7. Largest male, 7.0 mm; largest female, 6.5 mm.

Description: Male.—Antenna 1, 40–45 percent length of body, about 45 percent longer than antenna 2; primary flagellum with 15 articles, accessory flagellum reaching end of second article of primary flagellum; aesthetascs 2/3 length of corresponding flagellar article. Antenna 2: peduncular articles 4 and 5 with a number of long setae; flagellum with 6 articles.

Gnathopod 1. Propod only about 1/3 times as large as propod of gnathopod 2; palm moderately convex, little longer than posterior margin, armed with unequal double row of 13 spine teeth (8 on outside, 5 on inside); defining angle area with 2 relatively large spine teeth on outside, 3 shorter, non-bifid spine teeth on inside; posterior margin with row of about 7 singly inserted setae; medial setae inferior, singly inserted. Dactyl nail long, reaching end of defining angle spines. Carpus with 2 very weak rastellate setae. Coxa approximately 2 times deeper than broad, convex ventral margin with 6 setae of unequal length.

Gnathopod 2. Propod enlarged, at least 3 times size of propod of gnathopod 1; palmar margin oblique, approximately twice length of posterior margin, nearly straight, with conspicuous, but very shallow, concave gap in spine row; double row of spine teeth very irregular with 6 on inside and 8 on outside; those distal to gap not bifid; defining angle area with 2 relatively small spine teeth on inside, apparently none on outside; posterior margin convex, bearing 3 sets of setae, mostly doubly or triply inserted; medial setae few in number, most in inferior row, singly inserted. Dactyl robust, strongly bent just beyond junction with propod, inner margin with row of tiny setules, nail very short but reaching small spines on defining angle. Coxa longer than broad, convex ventral margin with 8 setae/setules of unequal length.

Coxa of pereopod 3 subrectangular, nearly twice as deep as broad, margin with 10 setae of unequal length. Coxa of pereopod 4 greatly expanded, broader than deep; proximal half of posterior margin weakly concave; irregularly convex posteroventral margin bearing about 22 relatively short setae.

Pereopod 6 little longer than pereopod 7, 40–45 percent longer than pereopod 5, approximately 50 percent length of body. Basis of pereopod 5 greatly expanded, as broad as long, posterior margin lined with spines, which are longest on distoposterior lobe; basis of pereopod 6 narrowing distally, both anterior and posterior margins lined with spines; basis of pereopod 7 with broadly convex posterior margin, lined with spines, anterior margin also lined with spines, distoposterior lobe absent. Posterior margins of propods of pereopods 6 and 7 each with 1 set of 2 longish setae, and distal

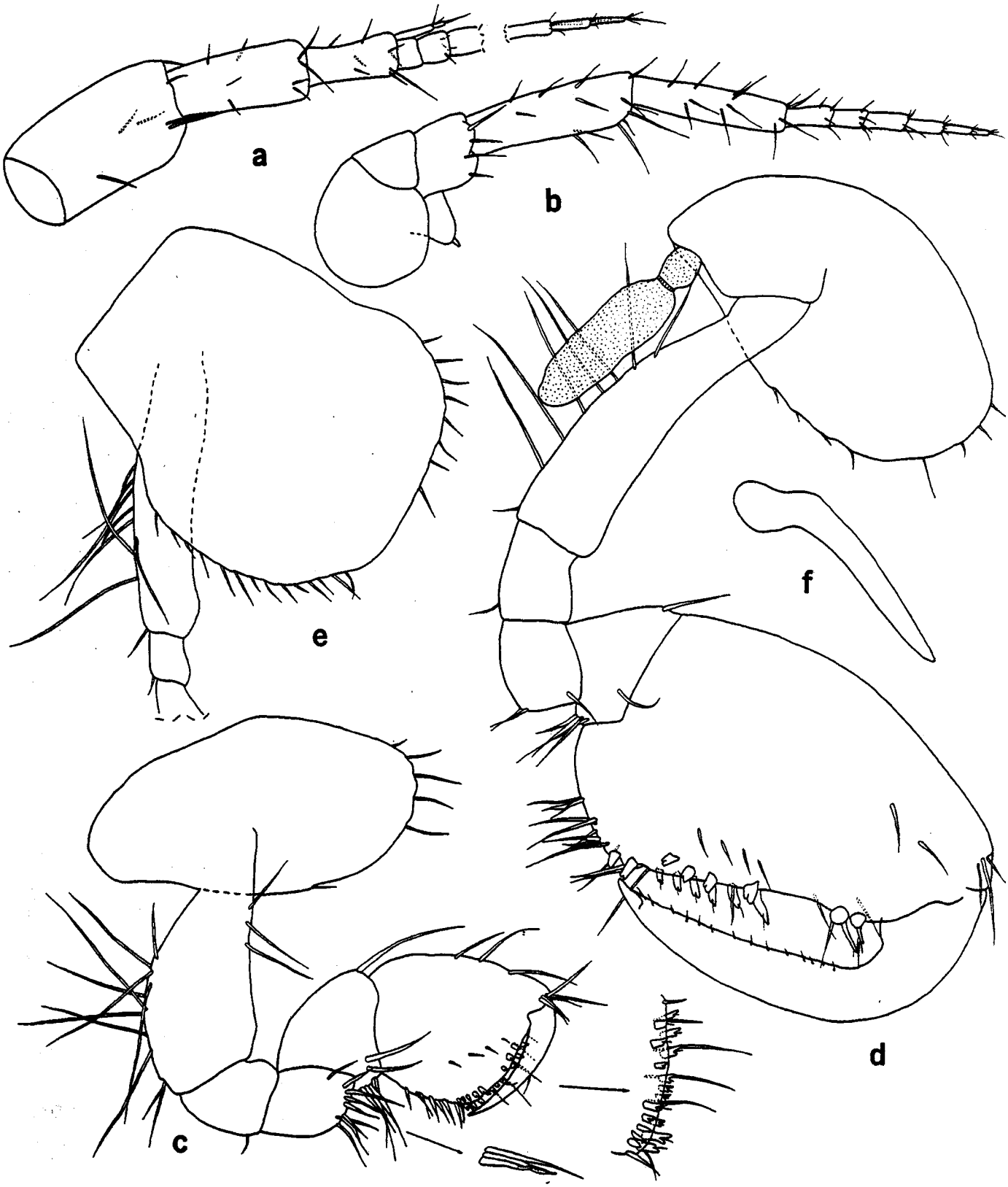

Figure 16. *Stygobromus heteropodus* Hubricht. Male cotype (6.2 mm), Pickle Springs, Missouri: a, b, antennae 1, 2; c, d, gnathopods 1, 2 (palmar margin and rastellate setae of 1 enlarged); e, pereopod 4 (in part); f, lateral sternal gill. (All structures to same scale except sternal gill to larger scale.)

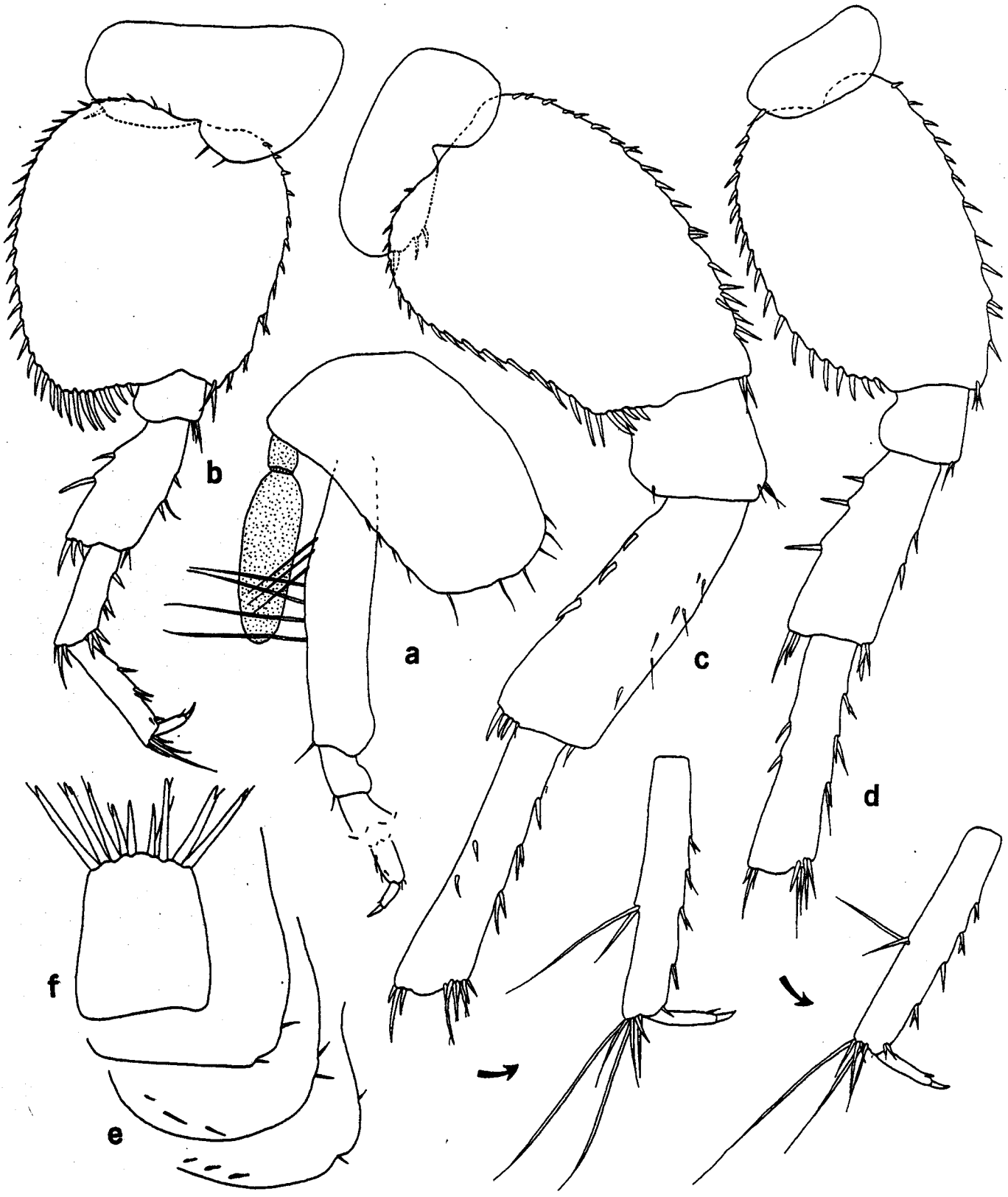

Figure 17. *Stygobromus heteropodus* Hubricht. Male cotype (6.2 mm), Pickle Springs: a, pereopod 3 (in part); b, c, d, pereopods 5, 6, 7; e, pleonal plates 1-3. Male cotype (5.5 mm), Pickle Springs: f, telson. (Pereopods to same scale; other structures to different scale.)

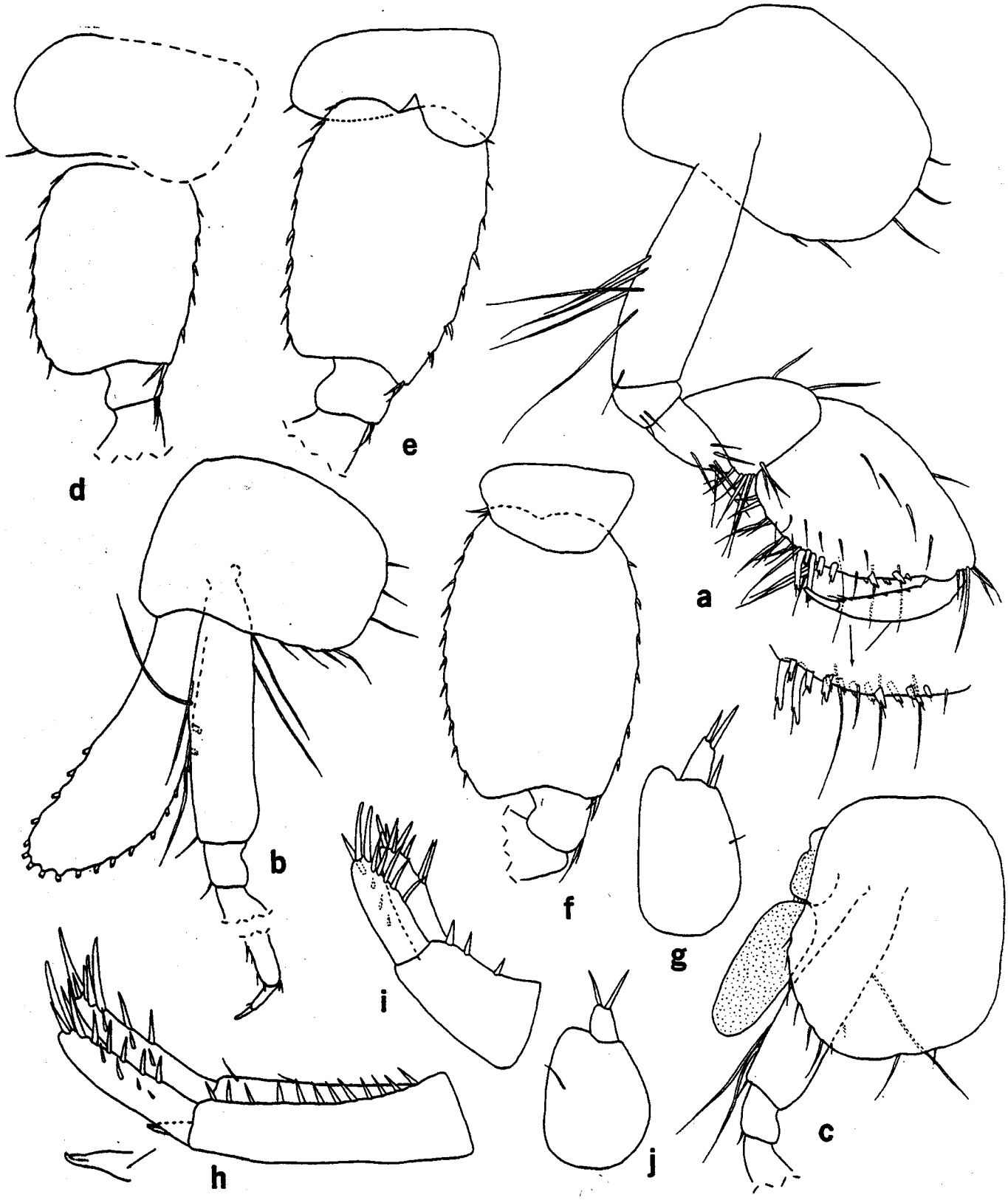

Figure 18. *Stygobromus heteropodus* Hubricht. Female cotype (5.5 mm), Pickle Springs: a, gnathopod 2 (palmar margin enlarged); b, c, d, e, f, pereopods 3, 4, 5, 6, 7 (in part); g, uropod 3. Male cotype (6.2 mm): h, i, uropods 1, 2 (peduncular process of 1 enlarged). Male cotype (5.5 mm), Pickle Springs: j, uropod 3. (All structures to same scale except uropod 3 to larger scale.)

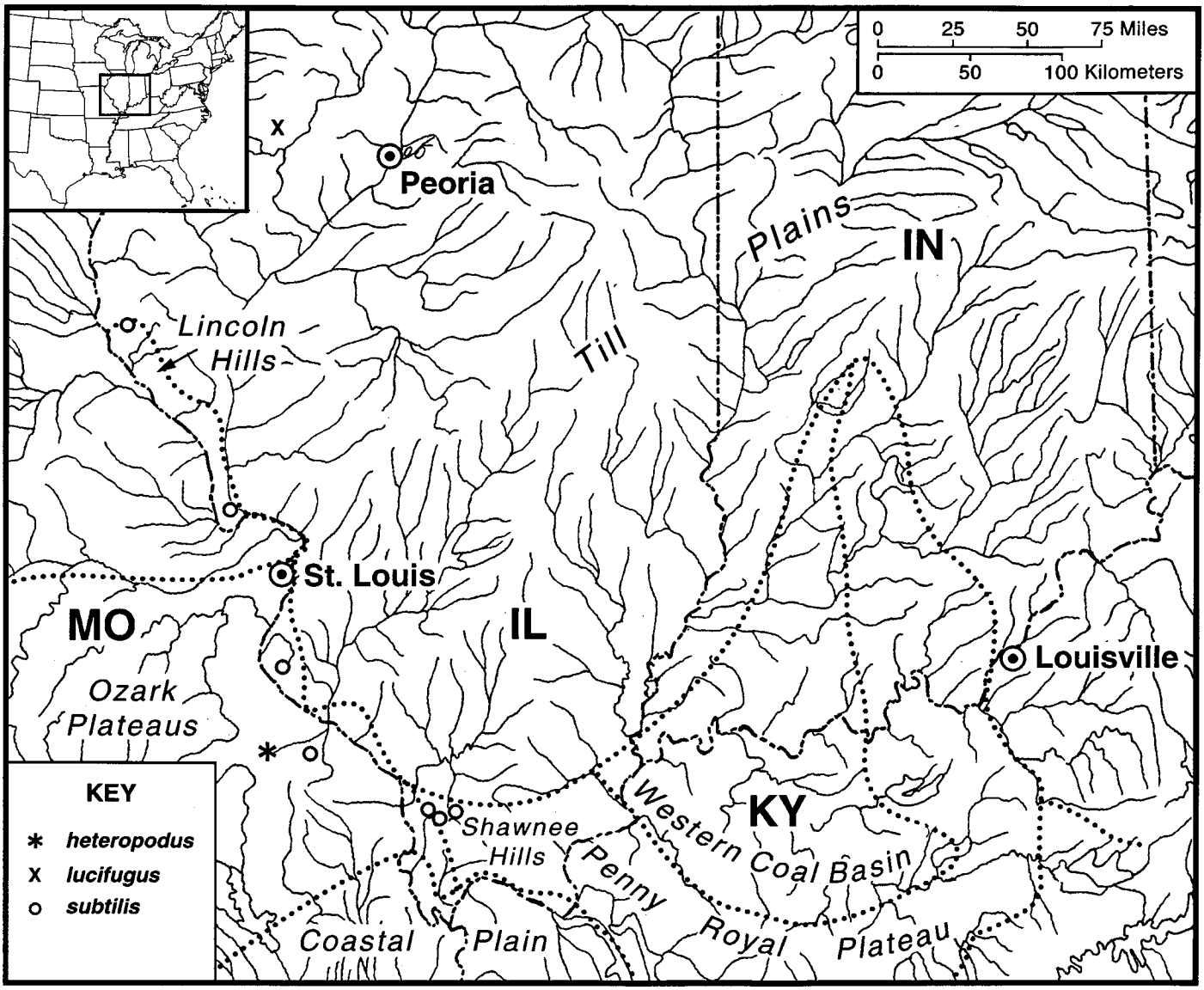

Figure 19. Geographic distribution of *Stygobromus* in the east-central United States: species of the *heteropodus* and *subtilis* groups — *S. subtilis* and its probable synonym, *S. lucifugus*, is not included herein.

ends near junction with dactyls bearing several long threadlike setae. Dactyls of pereopods 5–7 moderately elongate, about 35 percent as long as corresponding propods on pereopods 6 and 7, about 50 percent as long on pereopod 5. Coxal gills on pereopods 2–6, absent from pereopod 7. Two median sternal gills on pereonites 2 and 3; 2 pairs simple, bent (sickle-shaped) lateral sternal gills on pereopods 6 and 7, sternal gills absent from pleonite 1.

Pleonal plates: posterior margins convex, each bearing 2 setules; distoposterior corners rounded, indistinct, and weakly rounded; ventral margin of plates 2 and 3 with 3 spines each. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 60 percent length of peduncle, armed with about 10 spines; outer ramus with about 13 spines; peduncle with about 14 spines, some very weak; peduncular process about 30 percent length of outer ramus, distal end broadly narrowing and finely serrate. Uropod 2: inner ramus subequal in length to outer ramus, about 90 percent length of peduncle, armed with 8 spines; outer ramus with 10 or 11 spines; peduncle bearing 3 spines. Uropod 3: peduncle with 1 setule; ramus about 30 percent length of peduncle, bearing 2 apical spines. Telson little longer than broad, slightly tapered distally; apical margin unnotched, bearing 10 spines.

Female.—Differing significantly from the male in the following ways. Propod of gnathopod 2 normal, not greatly enlarged or sexually dimorphic; palmar margin of the propod oblique, convex, longer than posterior margin, armed with double row of 10 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; inferior and superior medial setae singly inserted; posterior margin weakly convex, with 3 or 4 sets of setae. Dactyl of gnathopod 2 normal, nail not shortened. Coxa 3 deeper than broad, but not 2 times deeper, margin with 7 setae of unequal length;

coxa 4 little deeper than broad but not greatly expanded distally, convex posteroventral margin with 8 setae of unequal length. Bases of pereopods 5–7 rather broad, posterior margins weakly convex, both anterior and posterior margins bearing short setae or small spines but conspicuously spinate. Distal ends of propods of pereopods 6 and 7 without elongate threadlike setae. Median, lateral, and pleonite sternal gills present. Brood plates moderately large, expanded distally, exceeding length of corresponding article 2 of gnathopod 2 and pereopods 3 and 4. Peduncle of uropod 3 with spine distally near ramus.

Type-locality.—According to Hubricht (1943), the type-specimens were "collected in a small spring under a ledge in the main valley, Pickle Springs, head of Pickle Creek." Both the spring and most of the creek occur within the Pickle Springs Natural Area, which is located near Hawn State Park approximately 18 km east-northeast of Farmington. According to information provided to JRH by the Missouri Department of Conservation, Pickle Spring is a small perennial spring under a rock ledge just to the left of Pickle Creek as one faces a waterfall from the nature trail. Presumably, this spring is the one from which Hubricht obtained the type-specimens in 1941. The area around the spring is composed of Cambrian-aged sandstone of the Lamotte formation. Several attempts by biologists in recent years to obtain additional specimens of this species from the Pickle Springs area have been unsuccessful.

Distribution and ecology.—Known only from cotypes collected from Pickle Springs in eastern Missouri (Fig. 19).

The *iowae* group

Diagnosis.—Closely similar to members of the *hubbsi* group and differing only by possession of lateral sternal gills.

***Stygobromus iowae* Hubricht**

Stygobromus iowae Hubricht, 1943: 702–703.—Barnard, 1958: 74; Hubricht, 1959: 878; Nicholas, 1960: 128; Holsinger, 1972: 70–71; Karaman, 1974: 113; Holsinger, 1977: 262; Barnard and Barnard, 1983: 440, map 16; Fitzpatrick, 1983: 146; Holsinger, 1986: 545; Peck and Christiansen, 1990: 75.

Material examined.—ILLINOIS. Carroll Co.: South Gate Spring, Mississippi Palisades State Park, 2♀ (INHS), M. J. Wetzel, 25 Apr 1995; Wellhouse Spring, 8 km NW of Mt. Carroll, 1♂ (INHS), M. J. Wetzel, D. W. Webb, 5 Apr 1997; Jo Daviess Co.: Nicholson Mine (California diggings), 1♀, S. B. Peck, 14 Nov 1965; same locality, 6♀, 30 Nov 1965. IOWA. Fayette Co.: spring, 1.1 km N of Fayette, 3♀ cotypes (USNM 79411), 3♀, 2♂ paratypes (USNM), L. Hubricht, 24 Apr 1942; Winneshiek Co.: Skunk Cave, 2♀, 1♂, K. A. Christiansen, 31 Jul 1963; Wonder Cave, 4♀, 3♂, 4 Oct 1964. MINNESOTA. Fillmore Co.: Niagara Cave, 1♀, D. A. Hubbard, Jr., 28 Jul 2003.

Diagnosis.—A medium-sized stygobiont species, closely similar to members of the *hubbsi* group but differing in having small, lateral sternal gills. Largest males, 5.5 mm; largest females, 6.0 mm.

Description: Female.—Antenna 1, 35–45 percent length of body, 45–50 percent longer than antenna 2; primary flagellum with 12–13 articles. Antenna 2: peduncular articles 4 and 5 with several long setae; flagellum with 5–6 articles.

Mandibles subequal, spine row with 7 plumose spines; palp article 2 with row of 6 setae on inner margin distally; palp article 3 bearing 1 B seta, short row of about 6 D setae, 5 E setae, lacking C and A setae. Lower lip: inner lobes vestigial. Maxilla 1: inner plate with 7 apical plumose setae; palp with 6 stiff setae or slender spines apically/subapically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner face. Maxilliped: inner plate with 3 or 4 bladespines (2 or 3 finely serrated) and 2 naked setae apically, and 3 setae (2 plumose) on inner margin and 2 on inner face; outer plate with 14 to 15 setae on apex, inner margin and inner face.

Gnathopod 1. Propod slightly smaller (shorter) than propod of gnathopod 2; palm longer than posterior margin, armed with 8–11 spine teeth in double; defining angle with 1 long and 2 shorter spine teeth on outside and 3 short spine teeth on inside; posterior margin without setae; medial setae in inferior and superior rows, singly inserted. Dactyl nail elongate, reaching to end of defining angle spines. Article 5 with cluster of weak rastellate setae. Coxa deeper than broad, convex ventral margin with 3 setae.

Gnathopod 2. Propod larger (longer) than first propod; palm longer than posterior margin, moderately oblique, palmar margin convex, armed with 14–17 spine teeth in double row; defining angle with 1 long spine tooth on outside, and 2 much shorter ones on inside; posterior margin with 2 or 3 sets of setae (typically doubly inserted); medial setae in two rows, all singly inserted. Dactyl nail elongate, reaching to end of defining angle spines. Article 5 with several rastellate setae on posterior margin. Coxa about as broad as deep, ventral margin with 4 setae.

Coxa of pereopod 3 little deeper than broad, ventral margin with 3 short setae. Coxa 4 about as broad as deep; posterior margin with very shallow concavity; ventral margin with 5 setae. Pereopod 6 little longer than pereopod 7, 40–45 percent length of body, 15–25 percent longer than pereopod 5. Bases of pereopods 5–7 not greatly expanded, little broader proximally than distally, distoposterior lobes broadly rounded but not large; posterior margin of basis of pereopod 7 convex, that of 6 tapered toward distal end. Dactyls of pereopods 5–7, 37–41 percent length of corresponding propods. Coxal gills on pereopods 2–6. Small, paired, simple lateral process present on pereonites 6 and 7; median and pleonite sternal processes absent. Brood plates not much expanded distally, about as long and broad as article 2

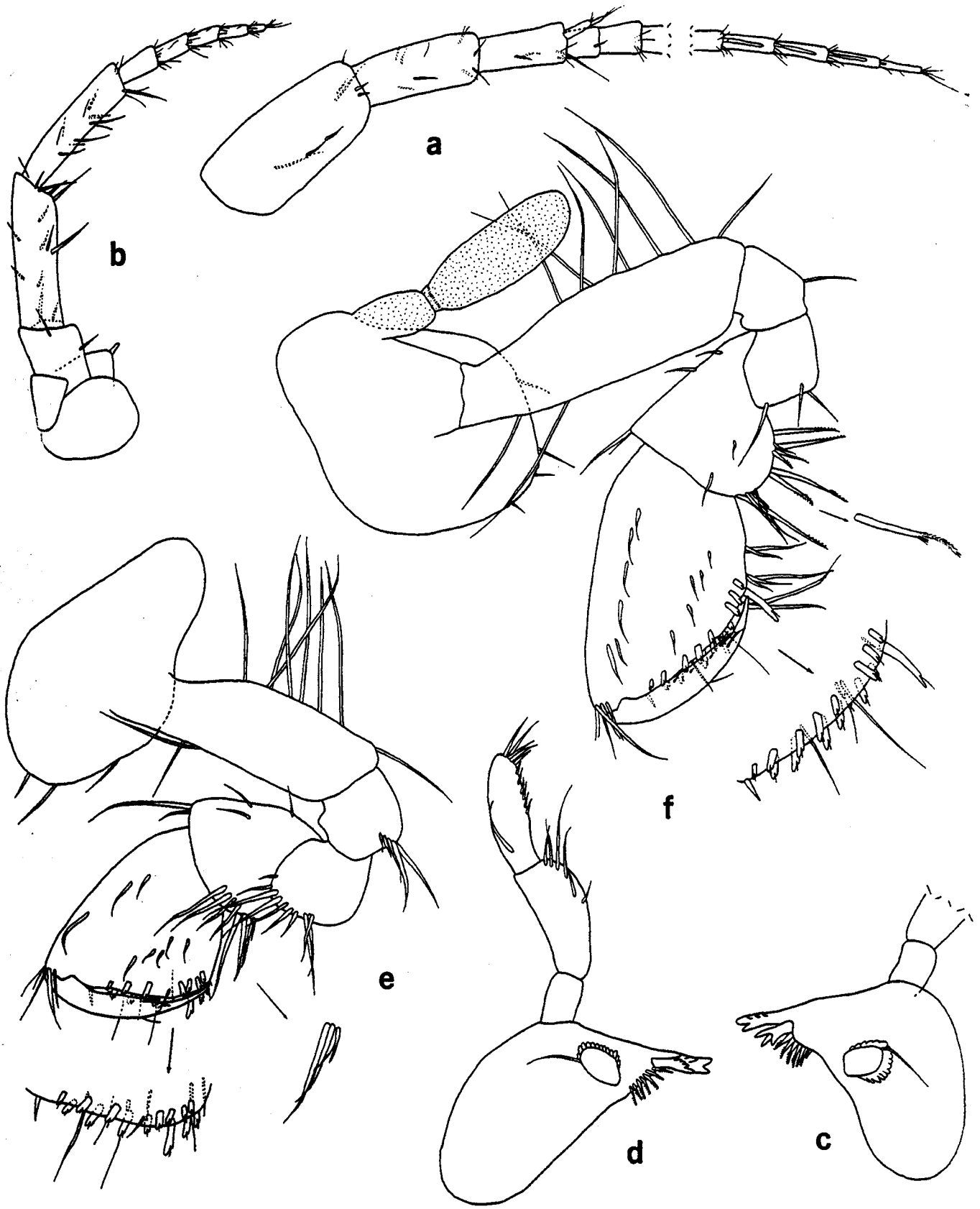

Figure 20. *Stygobromus iowae* Hubricht. Female (5.3.mm), Skunk Cave: a, b, antennae 1, 2; c, left mandible (in part); d, right mandible; e, f, gnathopods 1, 2 (palmar margins and rastellate setae enlarged). (Antennae to same scale; gnathopods to same scale.)

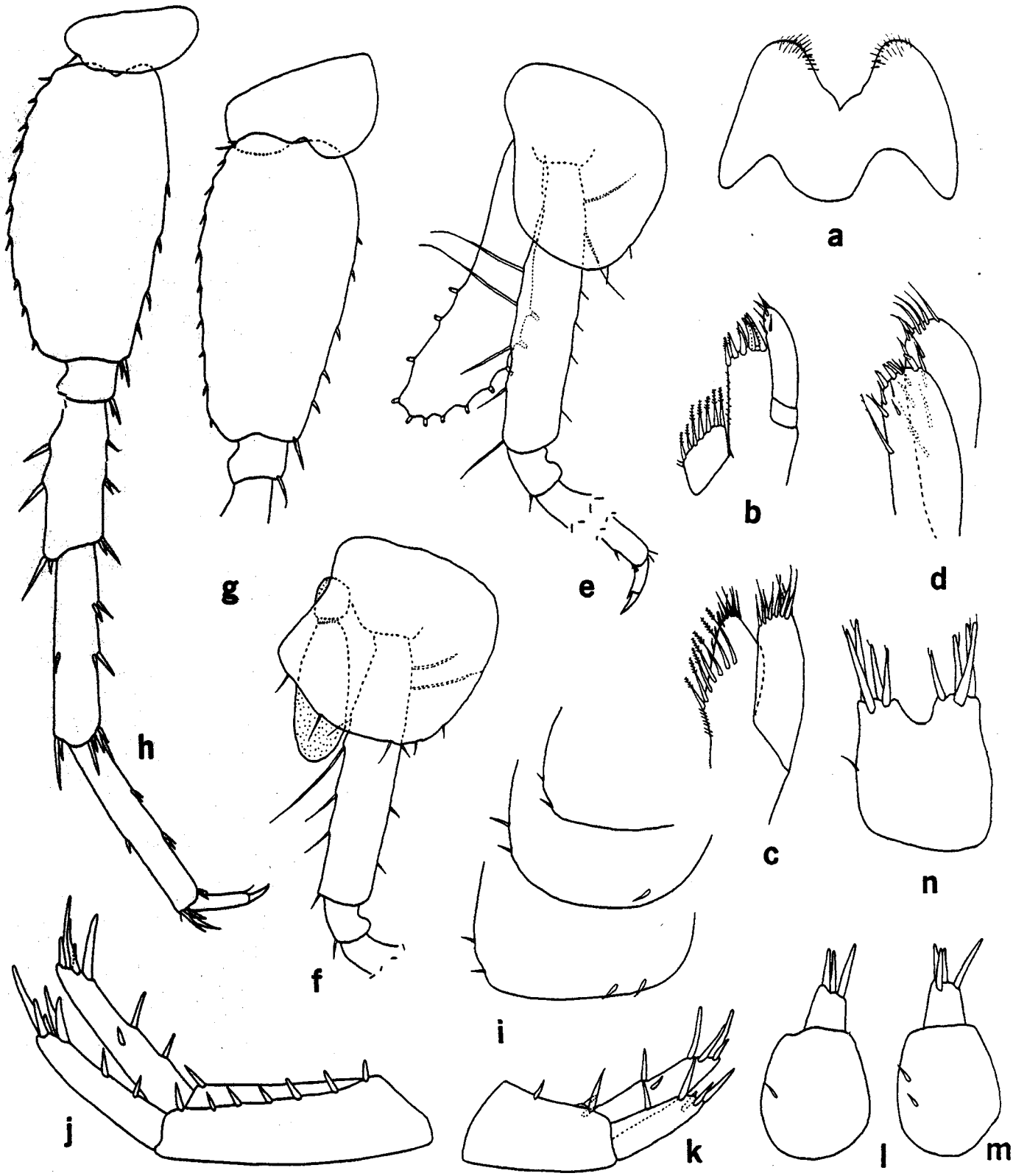

Figure 21. *Stygobromus iowae* Hubricht. Female (5.5 mm), Skunk Cave: a, lower lip; b, c, maxillae 1, 2; d, inner and outer plates of maxilliped; e, f, pereopods 3, 4 (in part); g, pereopod 6 (in part); h, pereopod 7; i, pleonal plates 1-3; j, k, uropods 1, 2; l, m, uropod(s) 3; n, telson. (Mouthparts, uropod 3 and telson to same scale; other structures to smaller scale.)

of gnathopod 2 and pereopods 3 and 4.

Pleonal plates: posterior margins weakly convex, with 2 setules each just above corners; distoposterior corners small, rounded, that of plate 2 indistinct; ventral margin of plate 2 with 1 spine, plate 3 with 2 spines. Uronites free.

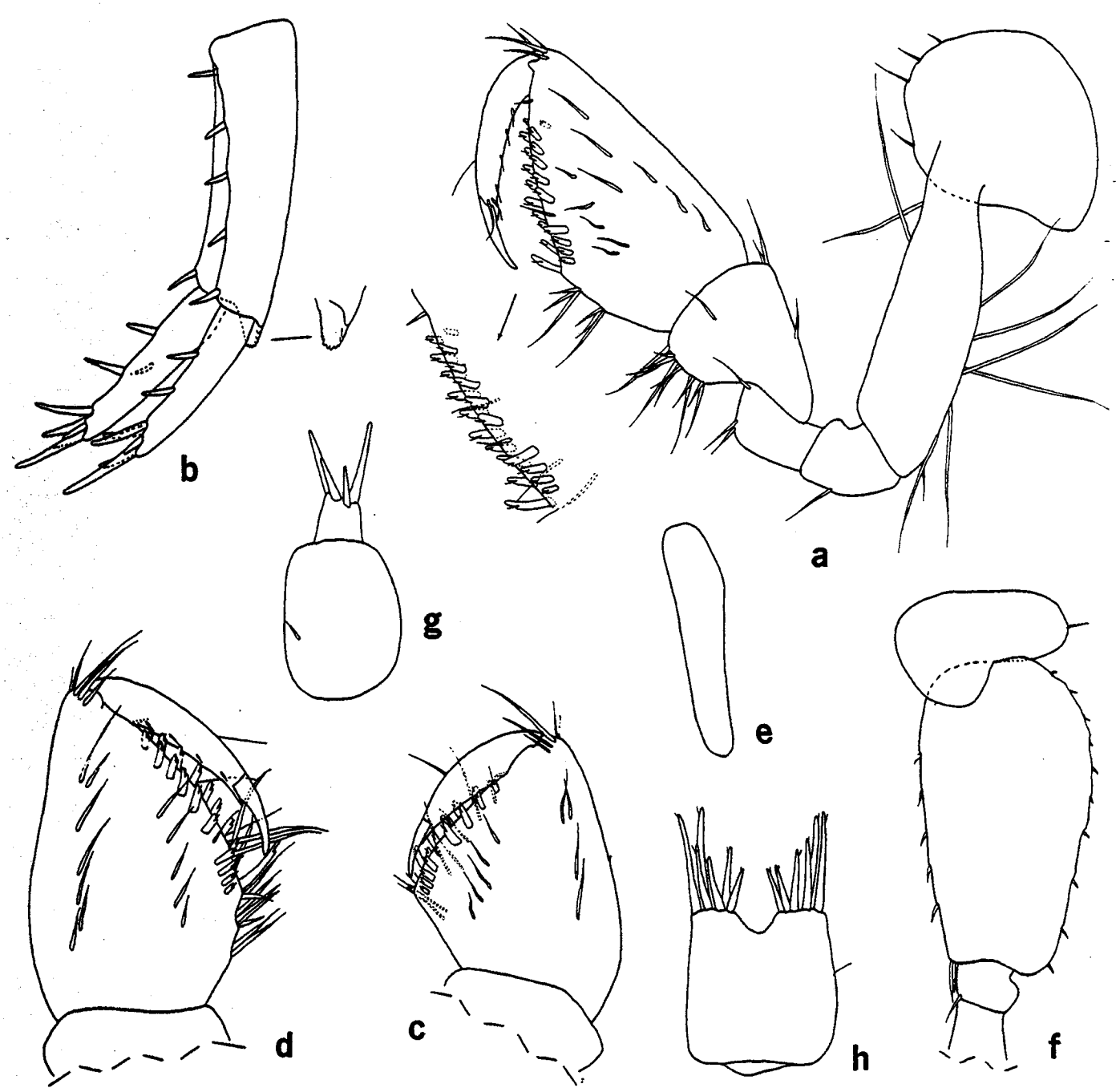

Figure 22. *Stygobromus iowae* Hubricht. Male (5.0 mm), Skunk Cave: a, gnathopod 2 (palmar margin enlarged); b, uropod 1 (peduncular process enlarged). Female (5.5 mm), Nicholson Mine, Illinois: c, d, gnathopods 1, 2 (in part); e, lateral sternal gill; f, pereopod 6 (in part); g, uropod 3; h, telson. (All structures to same scale except pereopod 6 to smaller scale.)

Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, armed with 8 spines; outer ramus with 7 spines; peduncle with 8 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 6 spines; outer ramus with 5 spines; peduncle with 4 spines. Uropod 3: peduncle with 1 setule; ramus about 1/3 the length of peduncle, with 3–4 apical spines. Telson subquadrate, about as broad as long; apex with shallow notch and bearing 8–10 (and sometimes 12) spines.

Male.—Differing from the female as follows. Propod of gnathopod 2slightly more elongate; palm more oblique and less convex, armed with approximately 16 spine teeth in double row; medial setae scattered (not in distinct rows). Peduncular process of uropod 1 short, only about 1/7 length of corresponding ramus, margin with distinct serrations.

Variation.—Minor morphological variation was noted in the Nicholson Mine population in Illinois. These specimens tend to have a few more spine teeth on the gnathopod propods and a few additional setae on the posterior margin of the

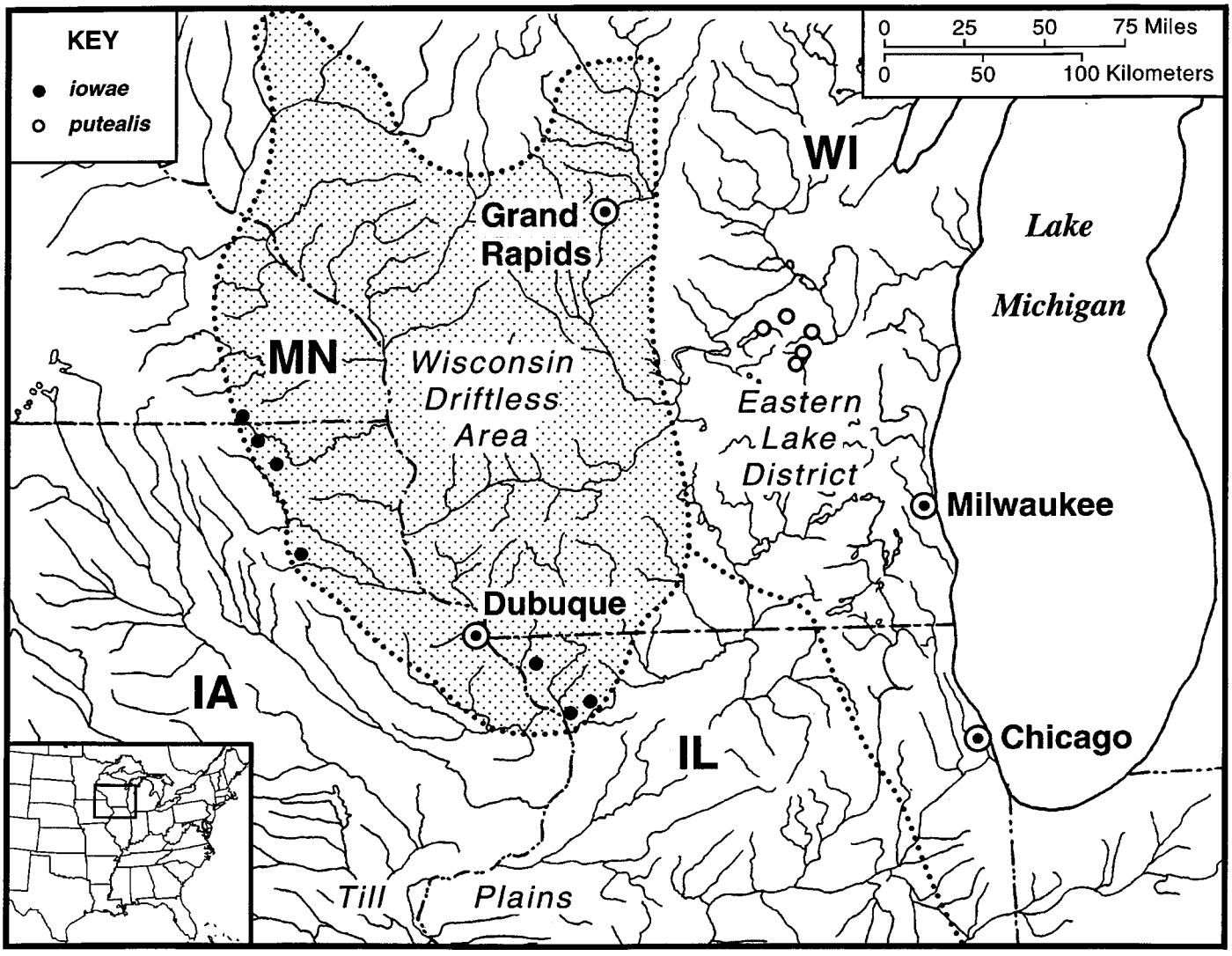

Figure 23. Geographic distribution of *Stygobromus* in the north-central United States: single species of the *hubbsi* and *iowae* groups in or near the Wisconsin Driftless Area (stippled). The approximate boundary of the Driftless Area shown here defines the region that is believed to have remained unglaciated during Wisconsin glaciation, however, earlier glaciation probably covered parts of this area, but perhaps never all of it.

propod of gnathopod 2. In addition, most of the specimens from the mine have 4 apical spines on the ramus of uropod 3 and 12 apical spines on the telson, as opposed to 3 spines on uropod 3 and 10 on the telson in specimens from the other populations in Illinois and Iowa. The width of the bases of pereopods 5–7 are also proportionately greater in one specimen from Nicholson Mine than in any other specimen from either the mine or the other localities.

Type-locality.—Spring, 1.1 km north of the town of Fayette in Fayette County, Iowa. The spring is apparently developed in Silurian-aged dolomite or marble.

Distribution and ecology.—The range of this species, which occurs just inside the southern and southwestern margins of the Driftless Area and covers a linear distance of approximately 215 km, extends from the northwestern corner of Winneshiek County in northeastern Iowa south to central Fayette County and then southeast to northwestern Carroll County in the northwestern corner of Illinois (Fig. 23). Although the species was originally described from specimens collected from a spring in Fayette Co., Iowa (Hubricht, 1943), it has since been found in cave pools elsewhere in Iowa, on rotting timbers in a flooded shaft in Nicholson Mine, and in two springs in northwestern Illinois. All localities for this species occur in Ordovician or Silurian carbonates: the caves are in Ordovician limestone, the mine in Galena Dolomite (Ordovician), and the springs in Silurian dolomites.

Nothing is known about the life history of this species, except that a single ovigerous female (5.3 mm in length) with two embryos was collected from a sample taken in July from Skunk Cave.

The *hubbsi* group

Diagnosis.—A diagnosis for the *hubbsi* group was presented by Holsinger (1974), the most salient characteristic being the absence of sternal processes. Most of the species of the *hubbsi* group occur in the western United States, except *S. putealis* and an undescribed species from a drain tile outlet in Floyd County, Indiana that will be described in a separate paper.

***Stygobromus putealis* (Holmes)**

Crangonyx putealis Holmes, 1909: 77-–78, plate 6.

Stygobromus putealis (Holmes).—Schellenberg, 1936: 37; Shoemaker, 1942a: 5; Hubricht, 1943: 701; Barnard, 1958: 74; Hubricht, 1959: 878; Nicholas, 1960: 129; Holsinger, 1972: 70–71; Holsinger, 1974: 6; Karaman, 1974: 117; Holsinger, 1977: 262; Barnard and Barnard, 1983: 441, map 16; Fitzpatrick, 1983: 146; Holsinger, 1986: 547; Holsinger and Shaw, 1986: 99; 1987: 2206; Peck and Christiansen, 1990: 75.

Material examined.—WISCONSIN. Dodge Co.: well (21.3 m deep) at Waupun, 2♀ cotypes (USNM 33479); wells, 1.6–3.2 km S of Waupun, 10♀, 10♂ (USNM), L. Hubricht, 21 Apr 1942; Fond du Lac Co.: wells, 805 m SE of Ripon, 4♂♀ (USNM), L. Hubricht, 21 Apr 1942; wells, Rosendale, 25♀, 11♂ (USNM 79413); same locality, 28♀, 27♂ (USNM), L. Hubricht, 21 Apr 1942; Duer's well (45 m deep), ca. 2.6 km NE of junction of routes 49 east and 151 in Waupun, 5♀, 8♂ (MPM), Q. Duer, 18 Jul 1986; same locality, 1♀, 2♂ (MPM), J. P. Jass et al., 20 May 1994; Green Lake Co.: Kutchin well at Maplewood Hotel, Green Lake, 3♀, 9♂, plus 4♂♀ (USNM, in 2 vials), C. Juday, 4 Sep 1923.

Diagnosis.—An obvious member of the *hubbsi* group, which otherwise occurs much farther west, as indicated by absence of sternal gills, possession of median sternal blisters, absence of setae on posterior margin of propod of gnathopod 1, relatively narrow bases of pereopods 5–7. Largest males, 4.0 mm; largest females, 6.0 mm.

Description: Female.—Antenna 1, 40–50 percent length of body, about 45 percent longer than antenna 2; primary flagellum with 12 articles; aesthetascs rather long, some up to 90 percent length of corresponding flagellar articles. Antenna 2, flagellum with 5 articles; peduncular articles 4 and 5 not heavily setose.

Mandibles subequal, spine row with 5–6 plumose spines; palp article 2 with 5 longish setae on inner margin toward distal end; palp article 3 with row of relatively long D setae and 5 E setae; A, B, and C setae absent. Lower lip with small, almost vestigial, inner lobes. Maxilla 1: inner plate with 8 apical plumose setae; palp with 6 slender or stiff setae spines apically-subapically. Maxilla 2: inner plate with oblique row of 10 plumose setae extending from medial margin onto inner face. Maxilliped: inner plate with 3 very lightly plumose bladelike spines, 4 or 5 naked setae apically, and about 3 naked setae subapically on inner margin; outer plate with uneven row of setae on apex and inner margin and 1 bladespine just below apex on inner margin.

Gnathopod 1. Propod broader but shorter than propod of gnathopod 2; palm rather long, nearly twice length of posterior margin, margin generally straight, armed with about 12 spine teeth in double row; defining angle with 4 spine teeth of variable length on outside, 4 smaller ones on inside; posterior margin lacking setae; medial setae mostly in superior row, all singly inserted. Dactyl nail relatively long, reaching to end of spines on defining angle. Article 5 without rastellate setae. Coxa broader than deep, ventral margin with 2 setae.

Gnathopod 2. Propod longer and proportionately little larger than propod of gnathopod 1;

palm oblique, almost twice length of posterior margin, palmar margin straight, armed with 14 or 15 spine teeth in uneven double row; defining angle with 1 long, prominent spine tooth on outside and 2 moderately long spines on inside; posterior margin relatively short, bearing 4 relatively long, singly inserted setae just below defining angle; medial setae in superior and inferior rows, all singly inserted. Dactyl nail rather long, closing just in front of large defining angle spine. Coxa broader than deep, ventral margin with 3 setae of unequal length.

Pereopods 3 and 4 subequal. Coxa 3 about as broad as deep, ventral margin with 3 setae. Coxa 4 broader than deep; posterior margin with very shallow concavity; ventral margin with 4 short setae. Pereopod 6 subequal in length to pereopod 7 or slightly longer, 40–50 percent length of body, 20–25 percent longer than pereopod 5. Bases of pereopods 5–7 relatively narrow, little broader proximally than distally, distoposterior lobe small and rounded. Dactyls of pereopods 5–7 approximately 33–36 percent length of corresponding propods. Coxal gills present on pereopods 2–6; absent from 7. Sternal processes absent, although some specimens with small ventral blister-like possible vestiges on pereonites 6 and 7. Brood plates rather small, sublinear, not as long as article 2 of pereopods 3 and 4.

Pleonal plates: posterior margins weakly convex, each with setule near corner; distoposterior corners rounded and almost indistinct; ventral margin of plate 2 with 1 spine, that of 3 with 2 spines. Uronites free. Uropod 1: inner ramus longer than outer ramus, about 80 percent length of peduncle, armed with 6 spines; outer ramus with 7 spines; peduncle with 8 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 7 spines; outer ramus with 4 spines; peduncle with 3 spines. Uropod 3: peduncle with 1 or 2 setules; ramus almost 50 percent length of peduncle, armed with 3 apical spines. Telson nearly twice as long as broad, narrowing slightly toward distal end; apical margin with tiny notch, armed with 8 spines.

Male.—Differing from female as follows. Propods of gnathopods 1 and 2 similar to female's, but proportionately

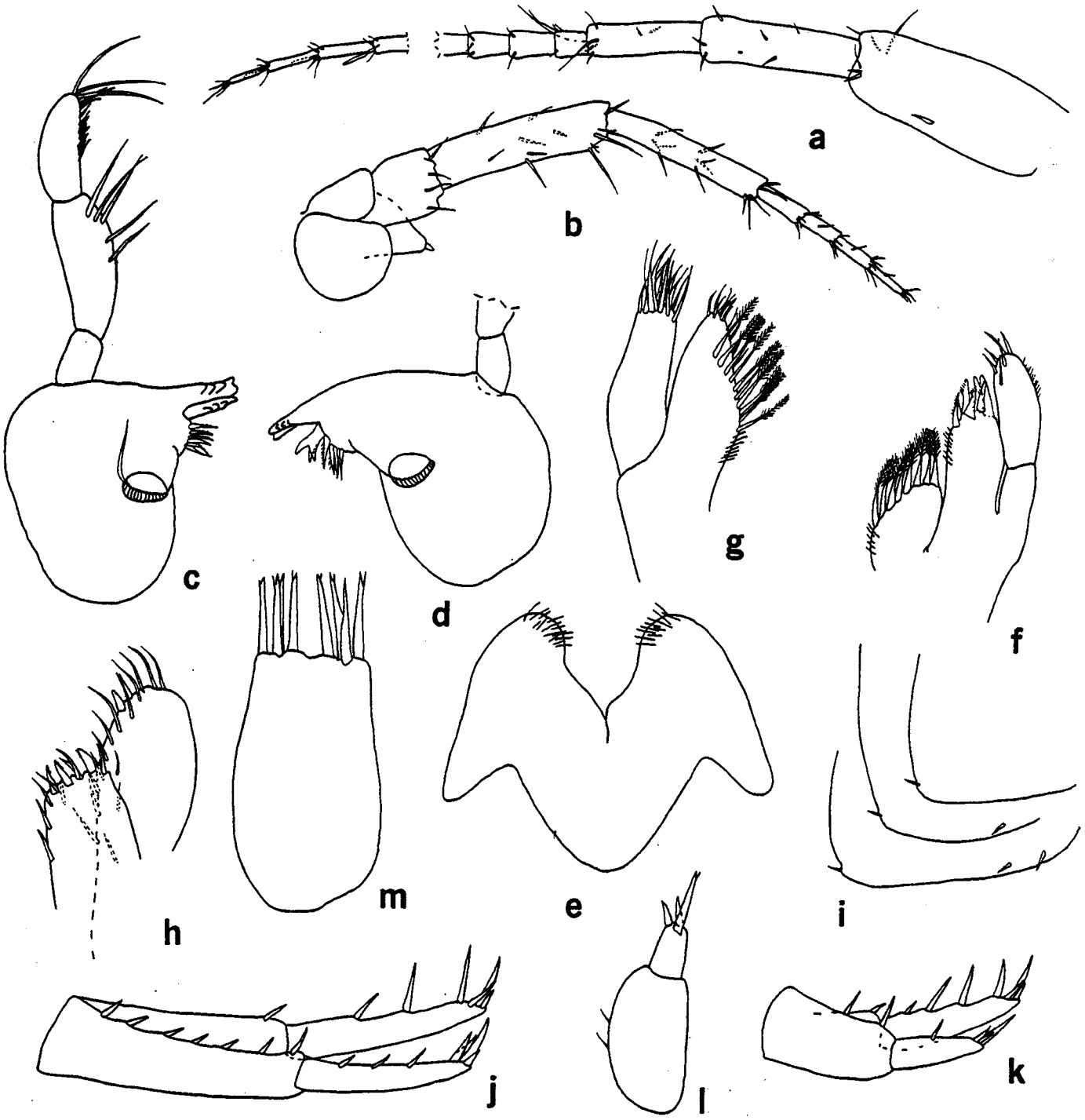

Figure 24. *Stygobromus putealis* (Holmes). Female (5.5 mm), wells, Rosendale, Wisconsin: a, b, antennae 1, 2; c, left mandible; d, right mandible (in part); e, lower lip; f, g, maxillae 1, 2; h, inner and outer plates of maxilliped; i, pleonal plates 1-3; j, k, l, uropods 1, 2, 3; m, telson. (Mouthparts to same scale except maxilliped plates to larger scale; antennae 1, 2 and uropods 1, 2 to same scale; uropod 3 and telson to larger scale.)

broader and bearing fewer spine teeth.Uropod 1 with slightly fewer spines; peduncular process about 35 percent length of corresponding ramus, narrowing distally with fine serrations. Uropod 2 with proportionately shorter peduncle. Telson with 6 apical spines.

Type-locality.—Well at Waupun, Dodge County, Wisconsin. Although Holmes (1909) failed to mention a type-specimen or name a type-locality in his description of this species, he did, however, deposit two female cotypes in the USNM collection labeled "*Crangonyx putealis* Holmes, Waupun, Wisconsin." The label also gave the depth of the well as 70

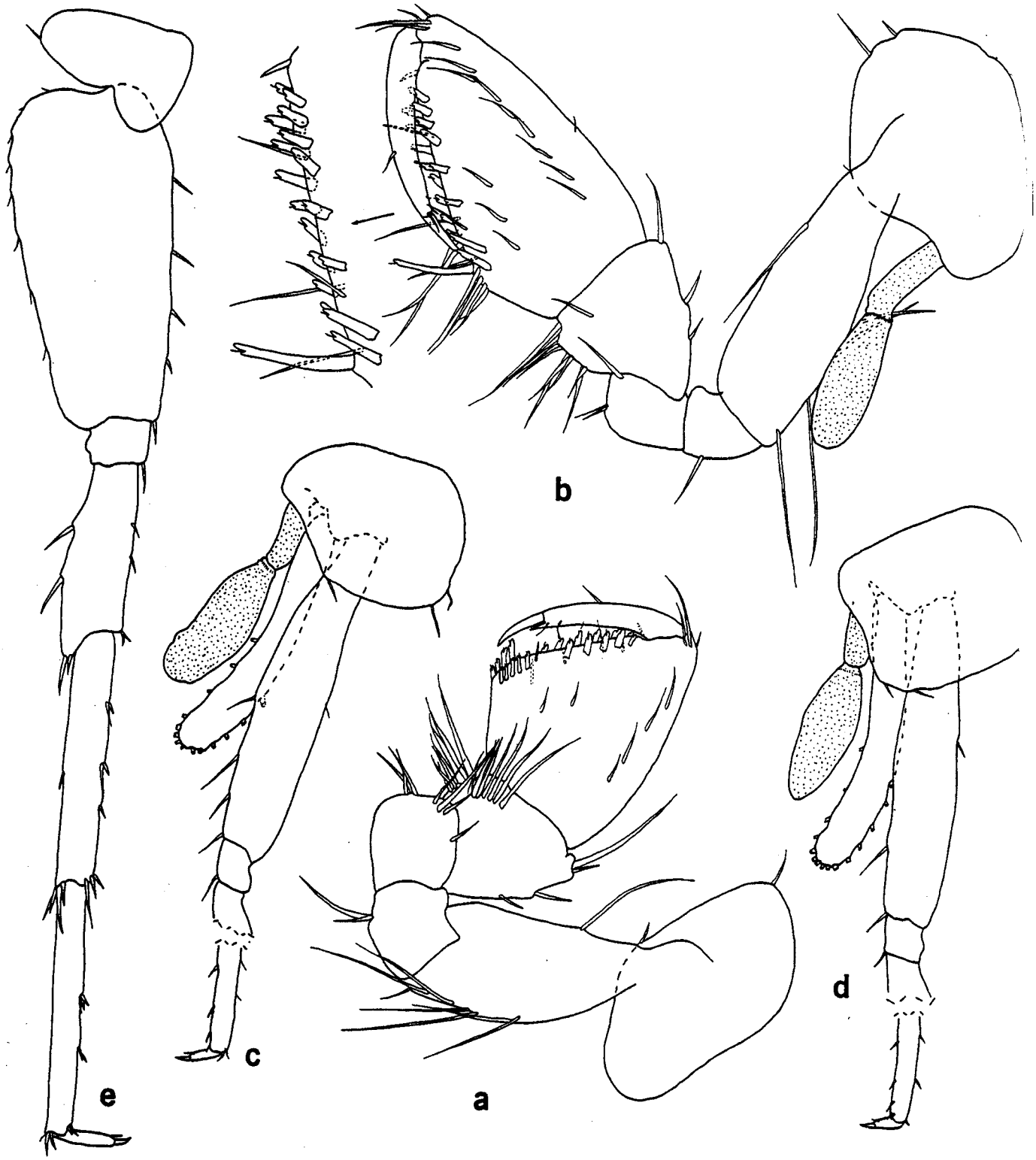

Figure 25. *Stygobromus putealis* (Holmes). Female (5.5 mm), wells, Rosendale: a, b, gnathopods 1, 2 (palmar margin of 2 enlarged); c, d, pereopods 3, 4 (in part); e, pereopod 6. (Gnathopods to same scale; pereopods to smaller scale.)

feet [= 21.3 m]. One of the wells just south of Waupun in Dodge County, from which Hubricht collected *S. putealis* in 1942 (see above), is apparently close to, or perhaps the same as, the type-locality.

Distribution and ecology.—To date all collections of this species have been from wells in a relatively small area in southeastern Wisconsin situated approximately 56 km east of the Driftless Area (Fig. 23). With the possible exception of the population recorded from Green Lake County, the range of this species falls within an area underlain by Gale-

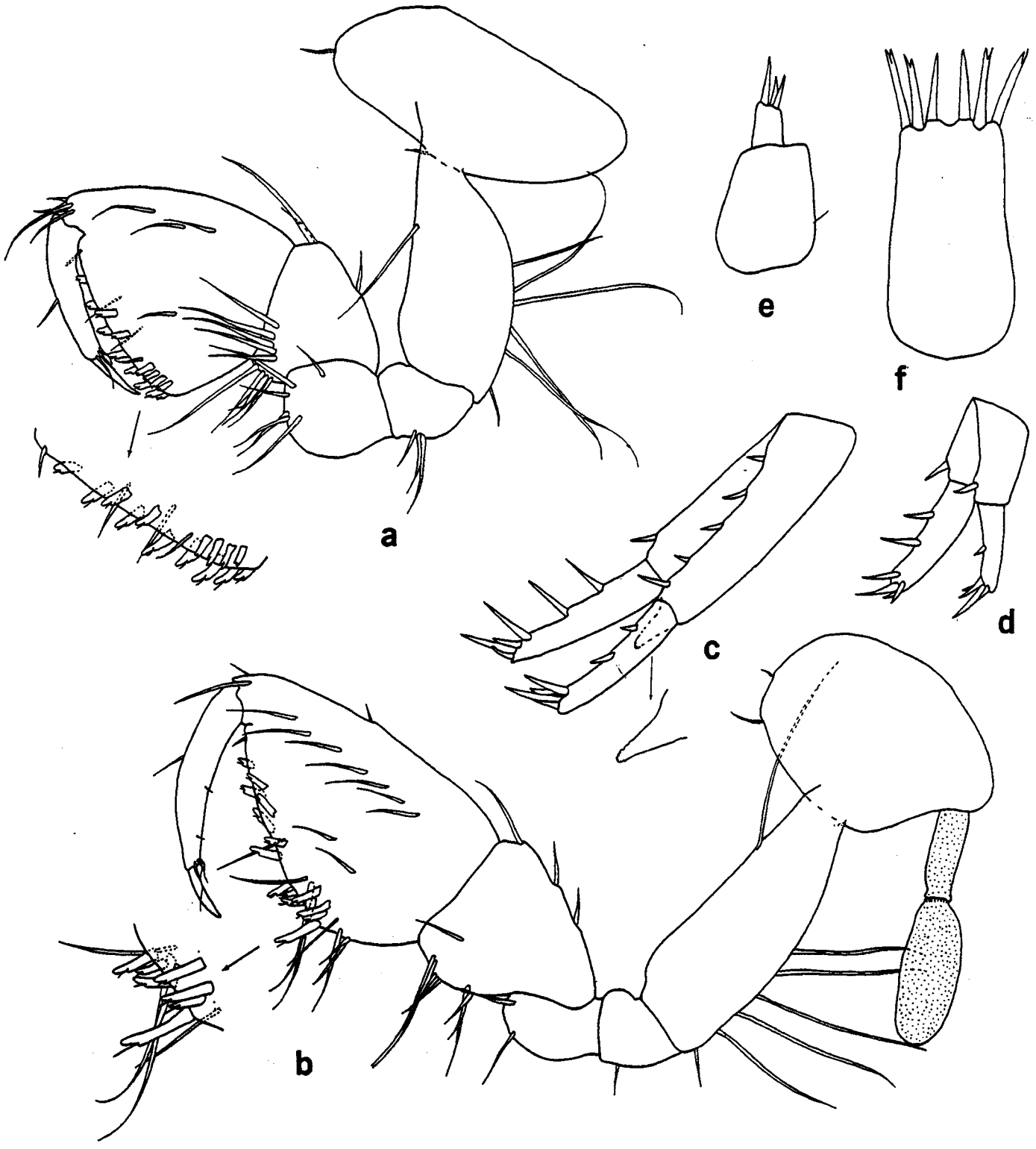

Figure 26. *Stygobromus putealis* (Holmes). Male (3.5 mm), well, Rosendale: a, b, gnathopods 1, 2 (palmar margin enlarged); c, d, e, uropods 1, 2, 3; f, telson. (Gnathopods and uropods 1 and 2 to same scale; uropod 3 and telson to larger scale.)

na Black River dolomite of Ordovician age. If the depths of the wells near Waupun are a good indication, the species probably inhabits relatively deep subterranean aquifers in the underlying dolomitic bedrock beneath the glacial drift that covers the surface in this area.

Very little data is available on the life history or biology of *S. putealis*; of the 74 female specimens collected to date,

none has been ovigerous, although many specimens 3–4.5 mm in length have setose brood plates.

Remarks.—The late Joan P. Jass, Curator of Zoology at the Milwaukee Public Museum, launched a project to locate and study additional populations of this rare species in order to learn more about its natural history. She believed that most, if not all, of the original collection sites for the species were either previously destroyed or are inaccessible to biologists. Even the only known site accessible at that time, the well on the Duer farm just northeast of Waupun in Fond du Lac County, was apparently threatened by the proposed relocation of Highway 26–151 (J. P. Jass, pers. comm.). [Addendum by JJL: This work was completed subsequent to Dr. Holsinger's completion of his draft manuscript, and Jass and Klausmeier (2011) reported a new population locality of *S. putealis* collected from a 45 meter well in Fond du Lac County, Wisconsin. Collections were made at the well in 1986 and 1994, reported here in the material examined. The site of the well was indeed covered by US Highway 151 and access was difficult because a manhole above the well was in the active roadway of the highway (Jass, pers. comm. to J. Lewis). Joan Jass passed away in 2012.]

During the preparation of this manuscript, Joan Jass called attention to a paper by Pearse (1917) that listed specimens of *Crangonyx vitreus* Cope in the University of Michigan Museum collected from a well at Randolph, Wisconsin (on the Dodge/Columbia County line just 24 km southwest of Waupun). These specimens are almost certainly *S. putealis*, but we were unable to locate them for verification, despite looking for them in the Smithsonian Institution collections, where the Michigan Museum crustacean collection was transferred some years ago.

The *tenuis* group

Diagnosis.—Morphologically, a relatively homogeneous group, distinguished by: sexually dimorphic males, which are larger than sexually mature females; gnathopod propod 1 a little larger than proportionately short pereopod 5, which is typically only 55 to 60 percent length of pereopod 7; pereopod 7 little longer than 6 (with one exception); lateral sternal gills typically bifurcate; apical margin of telson entire, with outermost apical spines often deflected laterally from the midline; and uronites partly or completely fused.

A total of 14 species have been assigned to this group in the past (see Holsinger, 1967, 1986), however, the group affinity of *Stygobromus reddelli* from Texas is doubtful and the taxonomic status of *S. elatus* from Arkansas is questionable (see below). The group is widely distributed, ranging from northeastern United States south to Alabama, then west-northwest to Arkansas and Missouri and west to central Texas. Two geographically disjunct undescribed species extend the distribution of this group into west-central Tennessee and southeastern Indiana.

The *tenuis* group includes some of the largest and most widely distributed *Stygobromus* species.Specimens of *S. clantoni* may reach 29.0 mm, making this species by far the largest reported for the genus and, along with the stygobiont *Bactrurus brachycaudus* Hubricht and Mackin, one of the two largest freshwater amphipods in North America (see below).

***Stygobromus elatus* (Holsinger)**

Stygonectes elatus Holsinger, 1967: 84–87.—Holsinger, 1972: 62; McDaniel and Smith, 1976: 58.

Stygobromus elatus (Holsinger); Karaman, 1974: 110; Holsinger, 1977: 261; Barnard and Barnard, 1983: 439, map 14; Fitzpatrick, 1983: 146; Holsinger, 1986: 544.

Remarks.—The taxonomic status of this species is questionable. Whether it simply represents a few aberrant specimens of *S. alabamensis* or is actually a separate species remains unresolved. *Stygobromus elatus* was originally described from three females (apparently mature) and one male (apparently immature) collected by Leslie Hubricht from a seep, 322 m (0.2 mi) east of the Lodge on Magazine Mountain in Logan County, Arkansas in 1940 (Holsinger, 1967). Although well within the geographic range of and closely similar to *S. alabamensis*, *S. elatus* differs from this species primarily in the structure of the gnathopod propods, which have straight palmar margins and more spine teeth (double row of 10 to 12), and the telson, which has 15 to 18 apical spines.

Collections subsequent to those of Hubricht from seeps and springs on Magazine Mountain contain specimens that appear to be within the morphological parameters of *Stygobromus alabamensis.* This observation, combined with the strong possibility that at least one of these recent collections came from or very near the site of the type-locality for *S. elatus* (Paul Hartfield, personal communication), casts even further doubt on the validity of this species.

***Stygobromus montanus* (Holsinger)**

Stygonectes montanus Holsinger, 1967: 82–84 (with references).—Holsinger, 1972: 62; McDaniel and Smith, 1976: 58.

Stygobromus montanus (Holsinger).—Karaman, 1974: 114; Holsinger, 1977: 262; Barnard and Barnard, 1983: 441, map 14; Fitzpatrick, 1983: 147; Holsinger, 1986: 546.

Material examined.—ARKANSAS. Polk Co.: springs on Rich Mt., 1♀, 1♂ (USNM), L. Hubricht, 26 Apr 1936; spring/seeps 68 m from Visitors Center and on Lover's Leap trail, Queen Wilhelmina State Park, Rich Mountain, 4♀, 4♂, K. Smith, J. Rettig, 22 Apr 1981.

Diagnosis.—Corresponding to the diagnosis given by Holsinger (1967). Closely allied morphologically with *Stygo-*

bromus alabamensis, but easily distinguished from that species by structure of uropod 3 and telson as follows: uropod 3 proportionately longer, approximately 75 percent length of telson, ramus 35–40 percent length of peduncle, with 2 or 3 apical spines (rarely 4); Telson proportionately longer and narrower, approximately 50 percent longer than broad. Largest male, 13.0 mm; largest female, 9.8 mm.

Distribution and ecology.—This species is known only from springs and seeps on Rich Mountain in Polk Co., Arkansas, where it was first collected in 1936 and again in 1981.

Remarks.—The material collected in 1981 by Smith and Rettig from groundwater outlets in Queen Wilhelmina State Park is identical to the type-material collected many years earlier; and therefore, provides further support for recognition of the Rich Mountain populations as a species distinct from the very common and widely distributed *S. alabamensis* (see Holsinger, 1967, 1972).

Stygobromus barri **(Holsinger)**

Stygonectes barri Holsinger, 1967: 87–90 (with references).—Holsinger, 1972: 63; Pflieger, 1974: 8; Craig, 1975: 4.

Stygobromus barri (Holsinger).—Karaman, 1974: 108; Holsinger, 1977: 261; Barnard and Barnard, 1983: 438, map 14; Fitzpatrick, 1983: 146; Holsinger, 1986: 543.

Material examined.—MISSOURI. St. Francois Co.: well in Farmington, 4♀ (USNM), D. H. Hazelwood, 8 May 1971.

Diagnosis.—Corresponding to the earlier diagnosis by Holsinger (1967). Closely similar to *S. alabamensis*, but clearly distinguished from that species by possession of lateral spines on the telson.

Distribution and ecology.—This rather poorly known species was previously recorded from two localities in two counties in southeastern Missouri. The new record listed above extends the range of the species 42 km to the north. The females in the Farmington sample ranged in size from 8.5 to 11.0 mm, whereas previously recorded females did not exceed 8.25 mm in length (Holsinger, 1967).

Stygobromus clantoni **(Creaser)**

Stygonectes clantoni (Creaser).—Holsinger, 1967: 102–106 (with references); 1972: 64; Pflieger, 1974: 8; Craig, 1975: 4.

Stygobromus clantoni (Creaser).—Karaman, 1974: 109; Holsinger, 1977: 261; Barnard and Barnard, 1983: 438, map 16; Fitzpatrick, 1983: 146; Holsinger, 1986: 544.

Material examined.—KANSAS. Anderson Co.: Honey Locust well (hand-dug) 6.4 km NE of Colony, 1 juv, W. H. Busby, 19 Apr 1991; Brecheisen well (hand-dug) 4.8 km NE of Colony, 2♂ (1 in KBS), J. Danoff-Burg, W. R. Brecheisen, 16 May 1991; Butler Co.: Bluestem well (drilled) 6.4 km SW of Cassody, 1♀, 3♂ (1 in KBS), 1 juv, J. Danoff-Burg, 20 Jul 1991; Hourglass Cave, 1 juv, W. H. Busby, D. Figg, 3 May 1989; same locality 4♀, 11♂ (1 in KBS), W. H. Busby, J. J. Young, 7 Sep 1991; Purity Springs near Augusta, 2♂, R. Kenk, 10 Jun 1970; well (27 m deep) at Purity Springs, 2♂, J. J. Lewis, 1 Aug 1973, same locality/collector, 2♂, 3 Aug 1973; Spring Cave (Rutherford Cave of Holsinger, 1967: 102), 1♀, 1♂ (KBS), W. H. Busby, D. Figg, 3 May 1989; same locality, 1♂, W. H. Busby, J. J. Young, 29 Jun 1991; same locality, 2♀ (1 in KBS), J. J. Young, 1 Sep 1991; Stone Cave, 1♂, W. H. Busby, D. Figg, 3 May 1989; same locality, 8♀ (1 in KBS), 5♂, 1 juv, W. H. Busby, J. J. Young, 7 Sep 1991; Chase Co.: Jack Spring Cave, 3♀ (1 in KBS), 4♂, 5 juveniles, W. H. Busby, 7 Sep 1991; Cowley Co.: Dutch Creek well (drilled) 12.9 km SW of Atlanta, 1♀, W. H. Busby, J. J. Young, 30 Jun 1991; Miami Co.: Cave Spring Cave, 1♀, 1 juvenile, W. H. Busby, J. J. Young, 13 Apr 1991. MISSOURI. Cass Co.: well (ca. 6 m deep) at Belton, 1♀, 2♂, J. Adamski, Apr 1982; Hickory Co.: seep 8 km W of Urbana, 1 juvenile, J. L. Craig, 16 Mar 1975; Jackson Co.: Scarrit Spring (walled) on Cliff Drive, S side of river in Kansas City, 2♀, E. F. Pembleton, 18 Jan 1973.

Notes on material examined.—In a status report on *Stygobromus clantoni* to the U.S. Fish and Wildlife Service, Busby and Danoff-Burg (1992) reported one large specimen from Nelson's well (hand-dug), ca. 3.2 km NE of Lane, Franklin Co., Kansas. This specimen was not examined during the present study. The Dunkak well, a previously reported locality for the species in Franklin County, is located 2.4 km NW of Lane, not NE as mistakenly stated by Holsinger (1967: 102).

Diagnosis.—A very large subterranean species, closely allied morphologically with *Stygobromus ozarkensis*, but differing from that species by: reaching greater size at sexual maturity; lacking median sternal gills; proportionately shorter ramus of uropod 3, which is ca. 33 percent length of peduncle, and bears fewer apical spines (2 or 3); having more apical spines on telson (>20); and rarely with few distolateral spines on telson in males >25.0 mm in length. Sexes generally similar. Largest male, 29.0 mm (typically ca. 27.0 mm); largest female, 22.5 mm (typically ca. 20.0 mm).

Corresponding to the redescription by Holsinger (1967), with the following additions and modifications.

Description: Male.—Mandibles subequal: spine row with 6 or 7 short plumose spines; palp article 2 with 7–11 setae on inner margin; palp article 3 with 2 B setae, 5–6 C setae, row of D setae, 3–4 E setae, lacking A setae. Maxilla 1: inner plate with 5–6 apical, plumose setae; palp article 2 with 9 slender spines or stiff setae apically/subapically. Maxilliped: inner plate with 5 bladelike spines and 2 or 3 naked setae apically, and 2 plumose setae subapically on inner margin; outer plate with row of setae on apex and inner margin distally, several of which near apex spine-like.

Gnathopod 1. Propod larger than propod of gnathopod 2; palm oblique, convex, at least twice length of posterior

Figure 27. *Stygobromus clantoni* (Creaser). Male (17.0 mm), well, Purity Springs, Kansas: a, left mandible; b, right mandible (in part); c, maxilla 1; d, inner and outer plates of maxilliped; e, gnathopod 2; f, g, h, uropods 1, 2, 3 (peduncular process of 1 enlarged); i, telson. (All structures to same scale except maxilliped plates to larger scale.)

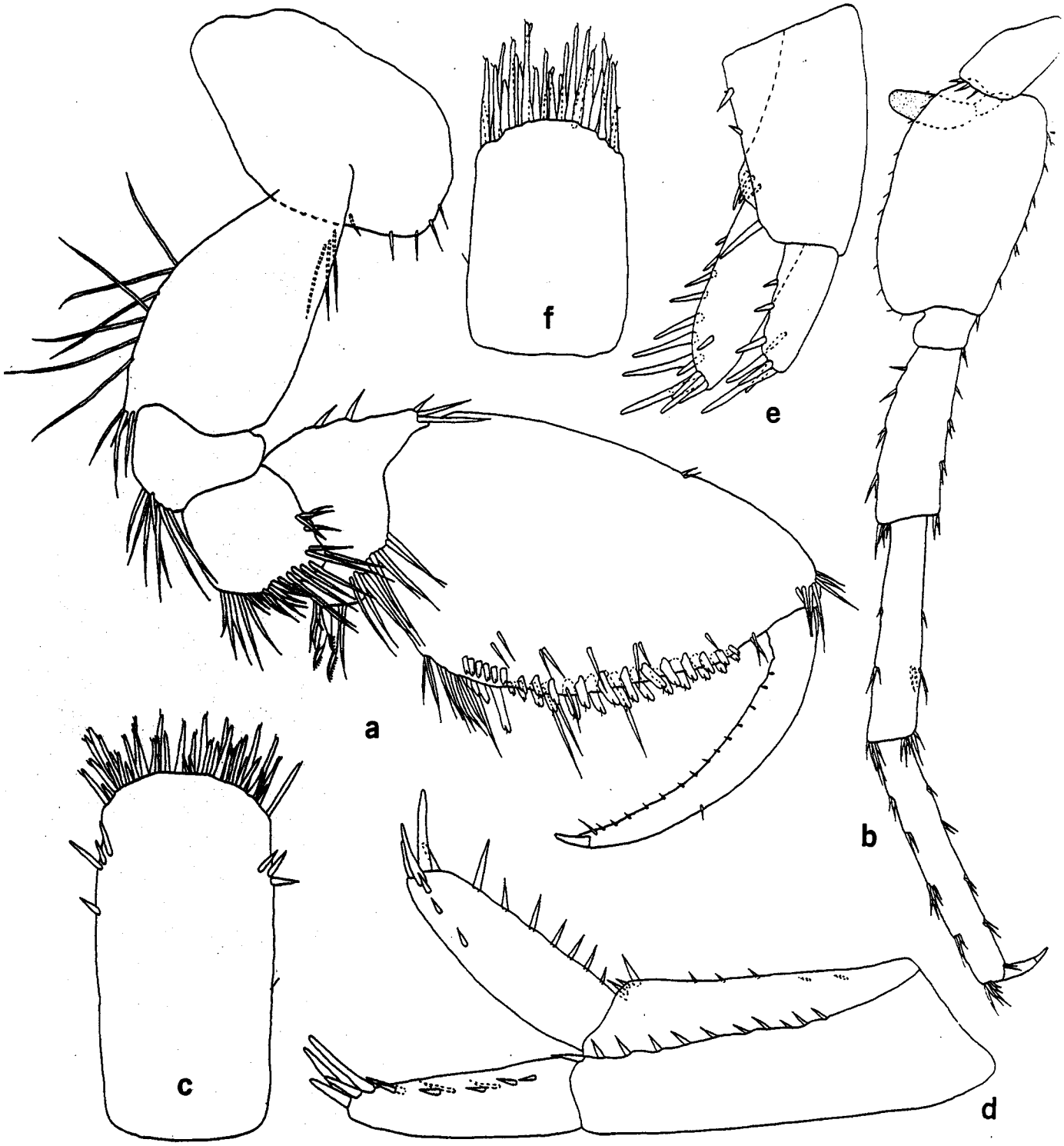

Figure 28. *Stygobromus clantoni* (Creaser). Male (17.0 mm), well, Purity Springs: a, gnathopod 1; b, pereopod 7. Male (26.5 mm), well, Purity Springs: c, telson. Female (18.0 mm), well, Purity Springs: d, e, uropods 1, 2; f, telson. (Gnathopod, uropods and female telson to same scale; pereopod and male telson to smaller scales).

margin, armed with 25 or 26 spine teeth in double row; defining angle with 5 spine teeth of variable length on outside (one longer) and 6 smaller ones on inside; posterior margin comparatively short, bearing short row of 6 tightly packed setae and a set of triply inserted setae just proximal to area of defining angle; medial setae in inferior row only, singly and doubly inserted. Dactyl with row of tiny setules on inner margin; nail short, closing into defining angle spines. Article 5 with cluster of 3 rastellate setae. Coxa deeper than broad, ventral margin with 5 short setae.

Gnathopod 2. Propod smaller than that of gnathopod 1; palm oblique, weakly convex, longer than posterior margin,

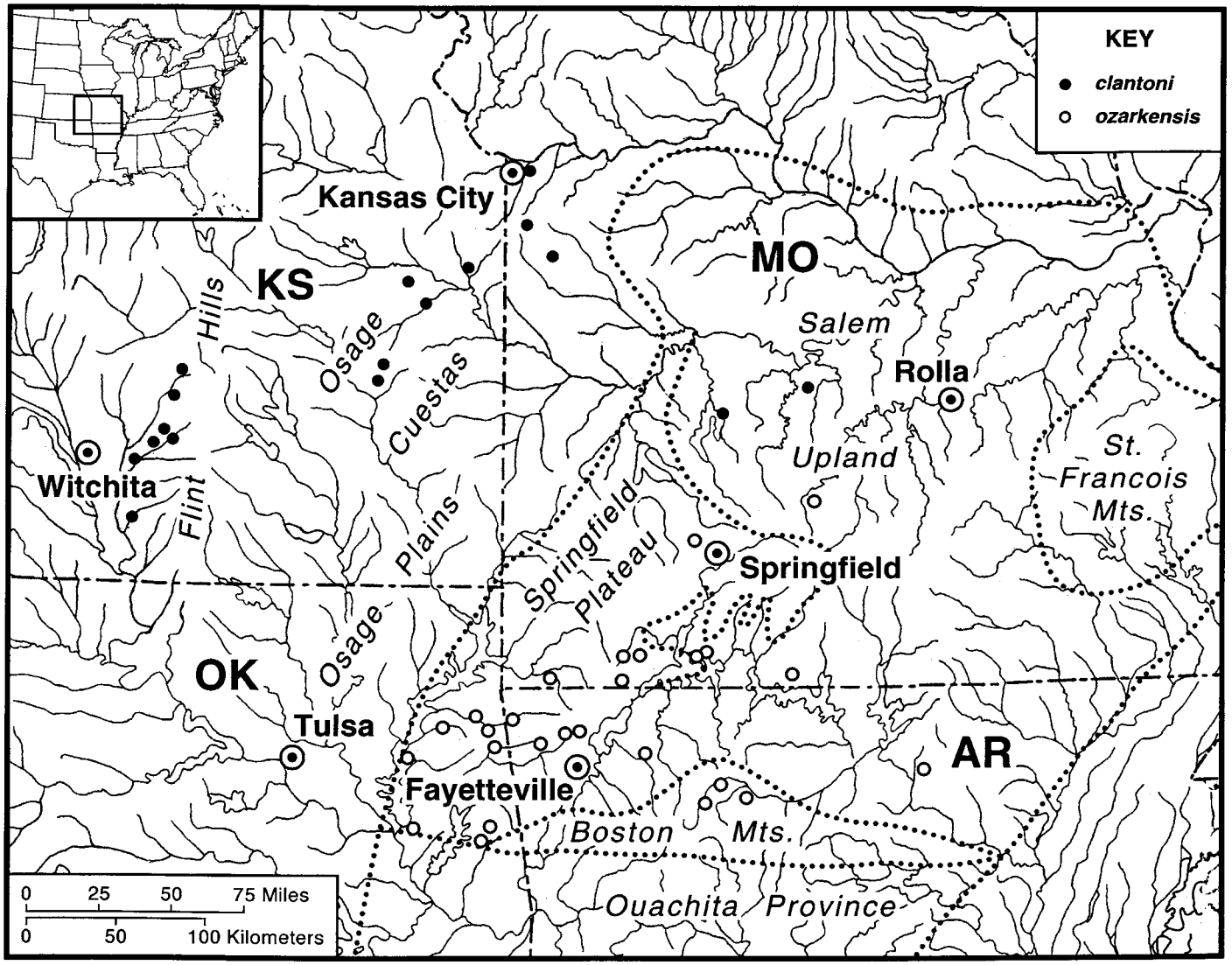

Figure 29. Geographic distribution of *Stygobromus clantoni* and *S. ozarkensis* from the Ozark Plateaus and Osage Plains in the central United States. Symbols represent single localities except that a single circle may represent two closely proximate localities for *S. ozarkensis* in Arkansas.

armed with 22–23 spine teeth in double row; defining angle with 5–7 spine teeth (1 or 2 longer) on outside, up to 7 smaller ones on inside; posterior margin weakly convex, bearing 5 sets of clusters of 4–5 setae; superior medial setae in sets of 3s and 4s, inferior medial setae fewer in number, doubly inserted. Dactyl with row of tiny setules on inner margin; nail short, closing defining angle spines. Article 5 with cluster of 5 rastellate setae. Coxa as deep as broad, broadly convex ventral margin with 4 short and 2 longer setae.

Coxal gills present on pereopods 2–7. Paired, bifurcate, lateral sternal gills on pereonites 6 and 7; median and pleonite sternal gills absent.

Uronites fused or nearly so. Uropod 1: inner ramus subequal in length to outer ramus, 65–70 percent as long as peduncle, armed with 13 spines; outer ramus with 13 spines; peduncle with 23 spines; peduncular process about 20 percent length of corresponding ramus, bluntly rounded distally with serrated margin. Uropod 2: inner ramus longer and broader than outer ramus, subequal in length to peduncle, armed with 12 spines; outer ramus with 7 spines; peduncle with 6 spines. Uropod 3: peduncle with 2 setules; ramus 30–33 percent length of peduncle, armed with 3 apical spines. Telson rather long, subrectangular, 35 to 50 percent longer than broad; lateral margins sometimes bearing few short spines near distal end (distolateral spines, see variation below); apical margin convex, armed with about 25 to 38 spines of variable length.

Female.—Differing from the male by absence of peduncular process on uropod 1.

Variation.—Variation in the length of antenna 1 and in the number of apical spines on uropod 3 were noted in an

earlier study of this species (Holsinger, 1967: 105). Examination of many additional specimens during the present study revealed the presence of distolateral spines on the telson of two out of the four largest males (25.0 mm) sampled from Butler Co., Kansas. Males from Bluestem well (25.5 mm) and Purity Springs well (26.5 mm) had distolateral spines, whereas males from Hourglass Cave (27.0 and 29.0 mm) did not possess this feature. The number of apical spines on the telson is also variable and apparently increases with overall size of the animal. Whereas most large specimens (ca. 16.0 to 18.0 mm) had approximately 25 apical spines, a very large male (26.5 mm) from Purity Springs, Butler Co., Kansas had 38 apical spines (Fig. 28c). There may also be size variation between populations from Flint Hills and the Osage Cuestas, as noted by Busby and Danoff-Burg (1992). In samples from the former, especially from the Butler County area, males are commonly over 20.0 mm, some reaching 29.0 mm, whereas some females reach 22.5 mm and several exceed 20.0 mm. In comparison, Osage Cuestas samples did not contain any males or females that exceed 19.5 mm. This comparison may be misleading, however, because the number of specimens available from Flint Hills is much greater.

Distribution and ecology.—The range of this species, which is highly disjunct and difficult to interpret biogeographically, covers parts of the Flint Hills in east-central Kansas (northern Cowley County north-northeast to southern Chase County), the Osage Cuestas in eastern Kansas and western Missouri (Anderson County north to Franklin County in Kansas and northeast to Jackson and Cass counties in Missouri), and the Salem Upland in central Missouri (Camden and Hickory counties) (Fig. 29). Arkansas records for this species from Clay Cave in Izard County (McDaniel et al., 1979), Fitton Spring Cave in Newton County (Lindsley and Welbourn, 1977), and John Eddings Cave in Newton County (Welbourn and Lindsley, 1979) are in error and refer to *Stygobromus ozarkensis*.

The geographic distribution of this species and potential threats to its existence were analyzed in some depth by Busby and Danoff-Burg (1992). A list of approximately 100 sites, including many wells in 19 counties of eastern Kansas, checked for the presence of *S. clantoni* by these workers during 1991 was provided. A majority of these sites did not yield specimens of this species.

In the Flint Hills, *S. clantoni* is recorded from wells and caves in limestones of Permian age. Most of these localities lie within 25 km of El Dorado in Butler County and occur in the Fort Riley limestone (Busby and Danoff-Burg, 1992; Young and Beard, 1993). Populations of this species recorded from the Osage Cuestas in eastern Kansas and western Missouri are separated from those in the Flint Hills by a geographic hiatus of 105 km. They inhabit subterranean groundwaters (primarily accessible through wells) in shales and limestones of Pennsylvanian age. Finally, the two populations in central Missouri are widely separated from those in the Osage Cuestas by a distance of approximately 200 km and are recorded from a cave and a seep developed in Ordovician limestones on the northwestern side of the Salem Upland.

Approximately half of the *S. clantoni* samples are from wells (both hand-dug and drilled), whereas the remainder are primarily from caves (stream riffles, pools, and occasional drip pools), and a few from springs/seeps. Despite the good efforts of Busby and Danoff-Burg (1992) to find *S. clantoni* in more localities in eastern Kansas, additional fieldwork should focus on the big gaps in the range of this species to determine whether they are true disjunctions or actually contain populations that have so far remained inaccessible to collectors.

Only one ovigerous female has been recorded. A specimen measuring 22.0 mm in length, collected on 7 Sep 1991 from Stone Cave, Butler Co., Kansas, was found with several juveniles in the brood pouch and had presumably released 17 others, which were found loose in the container. The juveniles measured ca. 3.0 mm in length.

Stygobromus clantoni has been collected with the stygobiont amphipod *Crangonyx packardi* (Zhang and Holsinger, 2003) from several different wells and caves, with the stygobiont amphipod *Bactrurus hubrichti* from Hourglass Cave on two occasions, and with *Stygobromus onondagaensis* from the well at Purity Springs, Kansas.

Remarks.—*Stygobromus clantoni* is the second largest amphipod recorded from North America freshwaters and potentially one of the largest stygobiont amphipods in the world. In North America, it is surpassed in size only by *Bactrurus brachycaudus*, another stygobiont crangonyctid recorded from caves and subterranean groundwaters in southwestern Illinois and eastern Missouri that may exceed the length of 30 mm (see also Holsinger, 1972; Koenemann and Holsinger, 2001).

***Stygobromus ozarkensis* (Holsinger)**

Stygonectes ozarkensis Holsinger, 1967: 107–109 (with references).—1972: 64; Black, 1971: 8; 1973: 16; Pflieger, 1974: 8; Craig, 1975: 4.

Stygobromus ozarkensis (Holsinger).—Karaman, 1974: 115; Holsinger, 1977: 262; Barnard and Barnard, 1983: 441, map 16; Fitzpatrick, 1983: 147; Gardner, 1986: 17; Holsinger, 1986: 546; Hobbs and Brown, 1987: 1044.

Material examined.—ARKANSAS. Benton Co.: Bear Hollow Cave, 1♀, M. Slay, G. O. Graening, 7 Dec 2000; Blowing Spring, 1♀, M. Slay et al., 27 Sep 2001; Cave Springs Cave, 1♀, T. L. Poulson, 1966 or 1967; same locality, 1♀, G. O. Graening, M. Slay, 30 Nov 2000; Civil War Cave, 1♀, 1 G. O. Graening, M. Slay, 23 Nov 1999; Dickerson Cave, 1♀,

Figure 30. *Stygobromus ozarkensis* (Holsinger). Female (18.0 mm), Clay Cave, Arkansas: a, left mandible; b, right mandible (in part); c, d, gnathopods 1, 2; e, lateral sternal gill; f, pereopod 7; g, uropod 3. (Gnathopods, mandibles and uropod to same scale; other structures to smaller scale.)

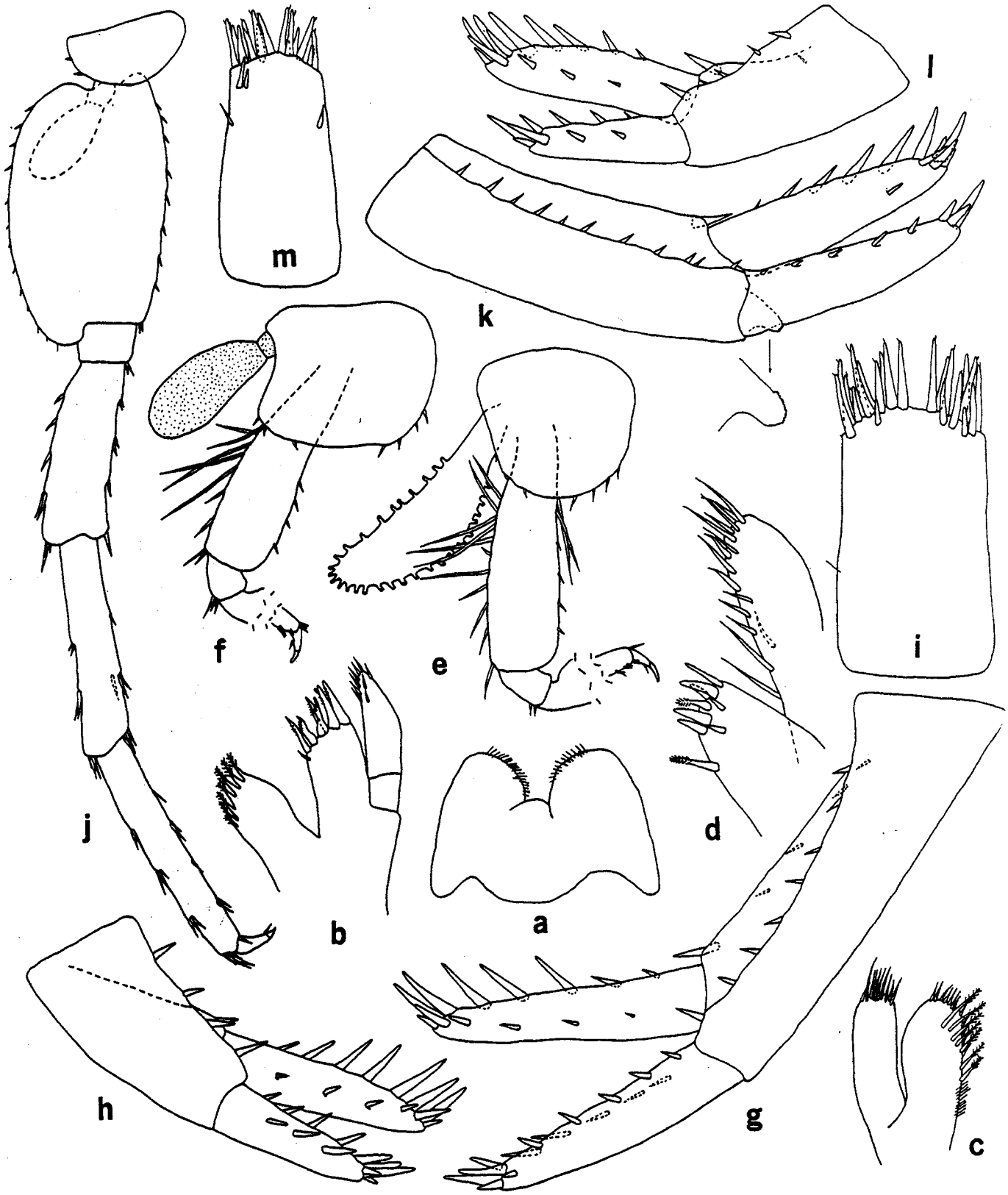

Figure 31. *Stygobromus ozarkensis* (Holsinger). Female (19.0 mm), Clay Cave: a, lower lip; b, c, maxillae 1, 2; d, inner and outer plates of maxilliped; e, f, pereopods 3, 4 (in part); g, h, uropods 1, 2; i, telson. Male (15.0 mm), Tumbling Creek Cave, Missouri: j, pereopod 7; k, l, uropods 1, 2 (peduncular process of 1 enlarged); m, telson. (Mouthparts except maxilliped plates, uropods, and telsons to same scale; pereopods to same but smaller scale; plates of maxilliped to larger scale.)

M. D. Schram, 25 Jul 1978; Old Pendergrass Cave, 1♀, G. O. Graening, M. Slay, 10 Dec 1999; Spavinaw Creek Cave, 2♀, M. Slay, 1 Sept 1999; War Eagle Cave, 1♀, 1♂, G. O. Graening, S. McGinnis, 11 Feb 2000; Carroll Co.: cave on Pond above Black Bass Lake, 1♂, G. O. Graening, 11 Oct 2002; Izard Co.: Clay Cave, 1♀, V. R. McDaniel, 26 Feb 1978; Needles Cave, 1♂, G. O. Graening, M. Slay, 2 Feb 2003; Madison Co.: Withrow Spring Cave, 2 juv, M. D. Schram, 6 Aug 1978; Madison Co.: Hunters Cave, 1♂, G. O. Graening et al., 28 Apr 2001; Marion Co.: Boat Creek Mine, 1♀, 1♂, M. Slay et al., 5 Aug 2002; Reed Cave, 1♀, G. O. Graening, S. McGinnis, 9 Mar 2002; Newton Co.: Fitton Cave, 2♀, 1 juvenile, G. O. Graening et al., 13 May 2001; Fitton Spring Cave (Buffalo National River), 1♀, 1 juvenile, W. C. Welbourn, 11 Sep 1979, 1♀ (ovigerous), 1 juvenile, 1 fragment, M. Slay, Chuck Bitting, Carol Bitting, 5 Oct 2000; John Eddings Cave (Buffalo National River), 2♀, 1♂, 11 juveniles, W. C. Welbourn, 9 Sep 1979; same locality, 1♀, G. O. Graening et al., 21 Sept 2000; Pretty Clean Cave, 1♀, M. Slay, C. Bitting, 7 Jul 2001; Sherfield Cave, 1♀, G. O. Graening, 10 Jun 2000; Walker Mountain Overflow Cave, 1 fragment, A. G. Grubbs, 19 Mar 1973; Stone Co.: Flittering Pit, 1♂, G. O. Graening et al., 24 Nov 2002; Washington Co.: Copperhead Cave, 4♀, M. Slay, J. Gunter, 28 Nov 2000. MISSOURI. Barry Co.: Chimney Rock Cave, 2♀, 1♂, J. E. Gardner, 14 Mar 1979 and 2♂, D. Figg, K. Lister, 22 Dec 1988; Mushroom Rock Cave, 3♀, 3♂, 2 juveniles, J. E. Gardner, 12 May 1981; Onyx Cave, 1♂, J. E. Gardner, 6 Mar 1979; Greene Co.: Fantastic Caverns, 1♂, J. R. Holsinger et al., 21 Aug 1968; Jasper Co.: Sarcoxie Cave, 1♂, M. Slay, S. Samoray and W. R. Elliott, 19 Nov 2004; Lawrence Co.: Turnback Cave, 1 juvenile, W. R. Elliott, 10 Nov 2001; McDonald Co.: unnamed cave (possibly Henson Cave) 0.8 km N of junction of state route 90 and US route 71, 1♂, D. Martin, 26 Jan 1969; Stone Co.: Hayes Spring Cave, 1 juvenile, W. R. Elliott, S. Samoray, M. Slay, 10 Aug 2004; Marvel Cave, 1♂ (AMNH 6082), 11 Sep 1927; seep 4.8 km NW of Silver Dollar City, 1♀, J. L. Craig, 10 May 1975; Wind Cave, 2♀, 2♂, 1 juvenile, M. Slay et al., 21 Nov 2002; Taney Co.: Tumbling Creek Cave, 3♀, 2♂, 30 Aug 1967; same locality, 1♀, 1♂, J. R. Holsinger et al., 22 Aug 1968; same locality, 3♀, 3♂ (USNM), L. Hubricht, 18 Sep 1969; Wright Co.: Smittle Cave, 1♀, J. R. Holsinger, 19 Aug 1968. OKLAHOMA. Adair Co.: Cave Spring ca. 3.2 km N of Bunch, 1♀, J. J. Hoover, W. B. Milstead, 4 Jun 1982; Three Forks Cave on Gittin Down Mountain, 2♀, 1 juvenile, J. H. Black, 1 Aug 1970; Cherokee Co.: Dressler Cave, 1♂, C. C. Vaughn et al., 26 Sep 1991; Delaware Co.: Marian Duncan Cave, 1♀, C. C. Vaughn, 9 Nov 1991; Nickel Preserve Cave, No. 4, 1♂, S. Hensley, 1 Jun 2001; Rodman Cave, 1 juvenile, C. C. Vaughn, 23 Nov 1991; Spavinaw Bat Cave, 1♀, C. C. Vaughn, 9 Nov 1991; Stansbury-January Cave, 1♀, 1♂, C. C. Vaughn, 26 Oct 1991; same locality, 1♀, D. Fenolio et al., 9 Oct 2001.

Diagnosis.—Corresponding to the diagnosis and description by Holsinger (1967) with the following additions. A large subterranean species, closely allied morphologically with *Stygobromus clantoni*, but differing from that species by: reaching sexual maturity at smaller size; having median sternal gills; proportionately longer ramus of uropod 3, which is 5060 percent length of peduncle, and which typically bears more apical spines (3 to 6); having few lateral spines on the telson (variable); and fewer apical spines on telson (ca. 20). Largest males, 20.0 mm (typically ca. 18.0 mm); largest females, 20.0 mm (typically ca. 15.0 mm).

Description: Female.—Mandibles subequal: spine row with 7 plumose spines; molar relatively small, conical; lacinia mobilis well developed, multidentate; palp article 2 with 9 relatively long setae on inner margin; palp article 3 with 2 A setae, 1 B seta, 4 or 5 C setae, row of D setae, and 2 or 3 E setae. Lower lip: inner lobes small but distinct. Maxilla 1: inner plate with 7 apical plumose setae; palp article 2 with 9 slender spines or stiff setaeapically/subapically. Maxilla 2: inner plate with oblique row of 7 plumose setae extending from inner margin onto inner face. Maxilliped: inner plate with 4 bladespines, 1 plumose spine, and 3 naked spines apically, and 1 plumose spine subapically on inner margin; outer plate with row of setae on apex and inner margin.

Gnathopod 1. Propod larger than propod of gnathopod 2; palm very long, oblique, almost straight, armed with 24 spine teeth in double row; area of defining angle with 5 spines of variable length on outside and 3 on inside; posterior margin very short, less than 1/3 length of palm, with 2 sets of triply inserted setae just proximal to defining angle spines; inferior medial setae singly and doubly inserted, superior medial setae reduced to one small set. Dactyl with row of tiny setules on inner margin; nail comparatively short, closing on defining angle spines. Article 5 bears rastellate setae. Coxa deeper than broad, narrowing convex ventral margin with 5 short setae.

Gnathopod 2. Propod smaller than propod of gnathopod 1; palm oblique, weakly convex, longer than posterior margin, armed with 28–30 spine teeth in double row; defining angle area with 5 spines on outside and 5 on inside; posterior margin more than ½ length of palm, nearly straight, with 6 or 7 clusters of setae; inferior medial setae singly inserted, superior medial setae doubly and triply inserted. Dactyl with row of tiny setules on inner margin; nail short but closing at end of defining angle spines. Article 5 with set of 3 rastellate setae. Coxa only a little deeper than broad, broadly convex ventral margin with 3 to 5 setae.

Pereopods 3 and 4 subequal in length: coxa 3 about as broad as deep, ventral margin with 7 short setae; coxa 4 broader than deep, posterior margin with shallow concavity, ventral margin with 7 short setae. Bases of pereopods 5–7 moderately broad, posterior margins convex (especially 7); distoposterior lobes relatively well developed. Dactyls of pereopods 5–7 relatively short, 20–25 percent length of corresponding propods. Coxal gills present on pereopods

2–7. Two to 3 single median sternal gills present on pereonites 2–4; paired, bifurcate lateral sternal gills present on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates expanded distally, nearly as long as article 2 of pereopods 3 and 4.

Uronites fused or partly so. Uropod 1: inner ramus subequal in length to outer ramus, approximately 75 percent length of peduncle, armed with about 13 spines; outer ramus with 15 spines; peduncle with 13–14 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 13 spines; outer ramus with 12 spines; peduncle with 5–6 spines. Uropod 3: peduncle with 2 (rarely 3 or 4) setules; ramus about 55 percent as long as peduncle, bearing typically 3 apical spines, but sometimes 4 to 6. Telson rather long, subrectangular, more than 50 percent longer than broad; sometimes with 2 to 4 dorsolateral spines per side, sometimes without; apical margin weakly convex, armed with typically 20–21 spines of unequal length.

Male.—Differing from female in several minor ways as follows. Uropod 1: inner ramus subequal in length to outer ramus, 60–65 percent length of peduncle, armed with 12 spines; outer ramus with 8–13 spines; peduncle with 12–16 spines; peduncular process short, about 20 percent length of outer ramus, bluntly rounded apically with serrated margin. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 12–13 spines; outer ramus with 9 spines; peduncle with 6–7 spines. Telson 55 to 60 percent longer than broad, narrowing slightly toward the distal end; armed laterally with typically 1 small dorsolateral spine per side; apical margin weakly convex, armed with 18 to 20 spines.

Variation.—Both the number of apical spines on the ramus of uropod 3 and the presence or absence of dorsolateral spines on the telson vary in this species, sometimes even within a single population (Holsinger, 1967). The number of apical spines on uropod 3 varies from 3 to 6, although it rarely exceeds 5. Approximately half of the adult specimens examined in this study had 1 or 2, or rarely 3 or 4, dorsolateral spines on each side on the telson; the number of apical spines on the telson also varies but rarely exceeds 20. Variation was also observed in the number of spines on uropods 1 and 2, but it did not appear to be geographically structured.

Distribution and ecology.—This species is recorded from subterranean waters in north-central and northwestern Arkansas, south-central and southwestern Missouri, and northeastern Oklahoma, all within the Ozark Plateaus (Fig. 29). Most samples are from small streams in caves developed in Ordovician-aged limestones on the southwestern side of the Salem Upland and in Mississippian-aged limestones of the Springfield Plateau. In caves, *Stygobromus ozarkensis* has been observed to co-occur frequently with *S. alabamensis* or *Crangonyx packardi*, occasionally with *S. onondagaensis*, and rarely with *S. acicularis*. A few females with setose brood plates have been collected, but were not ovigerous, and nothing is known about the natural history of this species. *Stygobromus ozarkensis* is also reported from Logan Cave (11 km east of Siloam Springs), Benton Co., Arkansas by Hobbs and Brown (1987), where it was found with the crayfish *Cambarus aculabrum* and other aquatic organisms in the cave stream.

Remarks.—Although *S. ozarkensis* and *S. clantoni* are obviously closely allied sister species, their respective ranges, as presently known, are geographically separate. They come closest together in the Salem Upland of central Missouri, where the locality for *S. ozarkensis* in Wright County is within approximately 56 km of the localities for *S. clantoni* in Camden and Hickory counties. Elsewhere, their ranges are at least 200 km apart. However, because large disjunctions also occur within the range of *S. clantoni* itself (as noted above), the geographical hiatus between the ranges of these species may not be surprising or even significant. It would therefore be appropriate to focus future fieldwork in the area between the ranges of these species to determine whether they are geographically isolated or overlap and possibly hybridize. It is conceivable that some of the more variable populations of *S. ozarkensis*, especially on the western and northwestern periphery of its range, represent intergrading populations. However, this cannot be resolved without additional collections and probably genetic studies.

Stygobromus bowmani (Holsinger)

Stygonectes bowmani Holsinger, 1967: 110–113 (with references).—Holsinger, 1972: 64.

Stygobromus bowmani (Holsinger).—Karaman, 1974: 108–109; Holsinger, 1977: 261; Barnard and Barnard, 1983: 438, map 14; Fitzpatrick, 1983: 146; Holsinger, 1986: 544.

Diagnosis.—Distinguished by the diagnosis and description of Holsinger (1967).

Distribution and ecology.—This species is known only from a single groundwater seep in northeastern Oklahoma, where it was collected in the company of *S. ozarkensis* (Holsinger, 1967).

Stygobromus alabamensis (Stout), NEW STATUS

Stygonectes alabamensis alabamensis (Stout).—Holsinger, 1967: 75–79 (with references); Black, 1971: 81; Holsinger, 1972: 62; Black, 1973: 16; Craig, 1975: 4; McDaniel and Smith, 1976: 58.

Stygonectes alabamensis occidentalis Holsinger, 1967: 81 (with references).—Black, 1971: 81; Holsinger, 1972: 62; Black, 1973: 16.

Stygobromus alabamensis alabamensis (Stout).—Karaman, 1974: 105; Barnard and Barnard, 1983: 438, map 15; Fitz-

patrick, 1983: 146; Gardner, 1986: 16–17; Holsinger, 1986: 543.

Stygobromus alabamensis occidentalis (Holsinger).—Karaman, 1974: 105; Barnard and Barnard, 1983: 438, map 15; Fitzpatrick, 1983: 146; Holsinger, 1986: 543.

Stygobromus alabamensis (Stout).—Holsinger, 1977: 261.

Material examined.—ALABAMA. Clarke Co.: seep 3.2 km S of Suggsville, 16 ♀, 5♂, L. Hubricht, 14 May 1966; Lee Co.: well 1.6 km E of Auburn (type-locality), 2♂ (USNM), J. M. Robinson, 23 Apr 1940 and 2♀, 2♂ (USNM), G. C. Moore, 23 Apr 1941; Pike Co.: seep 6.4 km E of Spring Hill, 8♀, 1 juvenile, L. Hubricht, Mar 1961. ARKANSAS. Baxter Co.: Norfork Bat Cave, 5♀, 1♂, G. O. Graening, B. Wagner, 13 Sept 2000; Benton Co.: Cold Cave, 3♀♂, G. O. Graening, M. Slay, 10 Apr 2000; hyporheic of Little Sugar Creek, SE of Benton, 27♀♂, M. D. Schram, 3 Mar 1982; Boone Co.: Majors Cave, 1♀, N. W. Youngsteadt, J. O. Youngsteadt, Jul 1977; Carroll Co.: cave on Miner's Rock Trail, 1 fragment, G. O. Graening, 12 Aug 2000; same locality, 4♀♂, G. O. Graening, 20 Aug 2000; Huckleberry Cave, 1♀, D. Kampwerth, B. Wagner, 18 Sep 2002; hyporheic in Kings River (station 19), ca. 9 km E of Eureka Springs, 1 juvenile, A. Brown, 6 Mar 2002; Cleburne Co.: seep near North Fork Cadron Creek, 2♀, 1♂, 1 juvenile, D. M. Johnson, 19 Feb 1977; spring 9.6 km SSW of Drasco, 2♀ (MPM), D. Hildebrandt, M. Plonczynski, 21 Mar 197?; Conway Co.: spring/seep run, Petit Jean State Park., 6♀, 2 juveniles, A. W. Norden, 21 Mar 1984; Crawford Co.: USFS Cave 23010, 2♀, 1♂, 1 fragment, M. Slay, 9 Apr 2000; USFS Cave 23040, 1♀, M. Slay, J. Briggler, 9 Apr 2000; Garland Co.: Arbordale Spring, 1♀, R. Fox, no date; Independence Co.: Blowing Cave, 3♀, 2♂, T. C Barr, Jr., T. G. Marsh, 26 Sep 1967; Izard Co.: Bergren Cave, 1♀, G. O. Graening et al., 18 Aug 2002; Clay Cave, 1♂, R. R. Rockwell, 11 Oct 1974, 1♀, 8 Feb 1975, 1♂, V. R. McDaniel, 26 Feb 1978; Needles Cave, 2♂, K. Smith, 30 Aug 1975, 5♀♂, G. O. Graening, M. Slay, 2 Feb 2003; Jackson Co.: Masons Cave, 1♀, V. R. McDaniel, 8 Apr 1977; Johnson Co.: spring in Foot Print Bog East, N of Clarksville, 3♀, 3♂, 1 juvenile, H. W. Robison, 25 May 1993; Sandstone Crevice Cave, 1♀, G. Tucker, 5 Feb 1991; Logan Co.: dripping springs, in sphagnum moss, Magazine Mountain, 3♀, S. K. Tedder, 27 May 1987, 3♀, 25 Nov 1987; seep at Dripping Springs, Magazine Mountain, 12♀, 3♂, 4 juveniles, L. Hubricht, 26 May 1966; seep 322 m W of the Lodge, Magazine Mountain, 8♀, 3♂, K. Smith, 6 Apr 1980; seep at Brown Springs, Magazine Mountain, 9♀, 4♂, L. Hubricht, 26 May 1966, 3♀, 4♂, 21 May 1968, and 5♀, 2♂, P. Hartfield, G. Tucker, 13 Mar 1991; spring/seep 160 m W of the old Lodge site, Magazine Mountain, 2♂, 3 juveniles, P. Hartfield, G. Tucker, 13 Mar 1991; seep on N face of Magazine Mtn., 3♀, 2♂, 3 juveniles, P. Hartfield, G. Tucker, 13 Mar 1991; spring/seep on S face of Magazine Mountain. (possibly the type-locality of *Stygobromus elatus*), 3♀, 3♂, P. Hartfield, G. Tucker, 13 Mar 1991; spring on S side of Moss Back Ridge, Magazine Mountain, 3♀, 2♂, P. Hartfield, G. Tucker, 13 Mar 1991; Madison Co.: Simpsons Cave, 6 fragments, G. O. Graening, S. McGinnis, 9 Jul 2002; Wounded Knee Cave, 1♀ (ovigerous), 1♀, G. O. Graening, C. Brickey, 12 May 2001; Marion Co.: Coon Cave, 2♂, W. C. Welbourn, 14 Sep 1979; Dogman Cave, 1♀, M. Slay, 2 Jul 2002; Elm Cave, 1♀ (ovigerous), G. O. Graening, B. Sasse, 16 Nov 2002; Middle Creek Spring Cave, 1♂, D. Coons, Mar 1977; Newton Co.: Cave Mountain. Cave, 3♀, 1♂, M. Slay, C. Bitting, 29 Jun 2001; Chilly Bowl Cave, 1♂, M. Slay, C. Brickey, M. Covington, 4 Aug 2001; Copperhead Cave, 1♂, G. O. Graening, 15 Sep 1999; Corkscrew Cave, 1♀, N. W. Youngsteadt, J. O. Youngsteadt, Jul 1977; Friday the 13th Cave, 1 fragment, M. Slay and S. Allen, 15 Apr 2000; Lewis Spring Cave, 1♀, 1 juvenile, N. W. Youngsteadt, J. O. Youngsteadt, Feb 1978; Mr. Clean Cave, 1♂, M. Slay, C. Bitting, 6 Jul 2001; Saltpeter Cave, 1 juvenile ♀, M. Slay, M. Covington, 17 Mar 2002; Stillhouse Hollow Cave, 2♀, G. O. Graening et al., 23 Jun 2002; Tom Watsons Bear Cave, 4♀, M. Slay, C. Brickey, 28 Jan 2002; Wolf Creek Cave, 1♂, G. O. Graening, R. Redman, 14 Jan 2002; Pulaski Co.: seeps from crevice in granite in Little Rock, 5♀, 1♂, A. W. Norden, 24 Mar 1984; Searcy Co.: Big Creek Cave, 2♀, G. O. Graening, C. Brickey, 16 Mar 2002; small spring S of Witts Spring, 5♀, R. S. Fox, 20 Dec 1970; Stone Co.: Biology Cave, 1♀, J. A. Stanford, 23 Oct 1978; Blanchard Springs Caverns, 1♀, T. C. Barr, Jr., T. G. Marsh, 27 Sep 1967, 2♀, 1♂, D. A. Hubbard, 1 Jul 1994; Breakdown Cave, 1♀, W. C. Welbourn, 20 Jan 1980, 2♀, G. Graening, S. McGinnis, M. Hattenbach, 27 Jan 2001; Saltpeter (Party) Cave, 1♀, G. O. Graening et al., 31 Mar 2002; Wet (Allison) Cave, 2♀, V. R. McDaniel, 13 Jul 1974 and 1♀, 20 Jul 1974; Woods Hollow Cave No. 1, 2♀♂, G. O. Graening and C. Brickey, 16 Mar 2002; Van Buren Co.: seeps in sphagnum and mud near North Fork Cadron Creek, 1♀, 1 juvenile, D. M. Johnson, 19 Feb 1977; seep, 8.8 km N of Clinton, 18♀, 10♂, 4 juveniles, L. Hubricht, 2 May 1940; Washington Co.: Evans Seep, 1♀, G. O. Graening, M. Slay, 1 Mar 2002; seep 2.4 km N of Winslow, 35♀♂, L. Hubricht, 7 May 1940; seep in basement, Fayetteville, 9♀, 7 ♂, M. D. Schram, 2 Jun 1982; spring at Bradley Cave, 3♀, G. O. Graening, M. Slay, 2 Apr 2000; storm drain system at Physics Building, University of Arkansas, 2♀, G. O. Graening, D. Fenolio, 18 Feb 2003. KANSAS. Cherokee Co.: intermittent stream 1 km S of Baxter Springs, 4♀, 1♂ (KBS), F. C. Gilbert, 13 Jun 1979; spring run from cave at Schumerhorn Park, 18♀, 1♂ (KBS), P. Liechti et al., 18 Mar 1981; Douglas Co.: Washington Creek N of Lone Star Lake, 5♀, 2♂ (KBS), D. Huggins, Sep–Nov 1973; Marion Co.: Miller Spring, 6.4 km E of Florence, 1 juvenile ♀, R. Leichti et al., 8 Jan 1982. MISSISSIPPI. Clarke Co.: swamp S of Pachuta, 1 juvenile (USNM), L. Hubricht, 16 Mar 1963; Lauderdale Co.: seep in ravine 4 km SE of Whynot, 1♀, L. Hubricht, 3 Dec 1961; Wayne Co.: Pitts Cave near Waynesboro, 1♂, D. A. Hubbard, 15 Jun 1994. MISSOURI. Barry Co.: Bear Waller Cave, 3 juveniles, J. E. Gardner, 12 May 1981; Cave of the Winds, 1 juvenile, J. E. Gardner, 4 Apr 1981; Chimney Rock Cave, 2♀, 1♂, J. E. Gardner, 14 Mar 1979

and 2♀, 1♂, 22 Jan 1980; Piney Creek Cave, 4 juveniles, J. E. Gardner, 14 May 1981; Roaring River Spring and Cave, 4♀, R. J. Sarver et al., 2 Oct 1997; Sugar Silver Cave, 1♂, J. E. Gardner, 15 Mar 1979; Camden Co.: Boat Shelter Cave, 1♀, 2♂, J. E. Gardner, 16 Mar 1982; Toby Cave, 2♀♂, D. C. Ashley et al., 6 Mar 2004; Dallas Co.: Little Lindley Creek, 3♀, R. J. Sarver et al., 25 Sep 2002; Douglas Co.: Bryant Creek, 2 juveniles, R. J. Sarver et al., 22 Mar 1999; Greene Co.: James River, 1♀/♂, N. W. Youngsteadt, 17 Apr 1985; Pearson Creek, multiple samples with 1–2♀/♂ each, N. W. Youngsteadt, 2 and 3 Mar 1992, 25 May, 10 and 14 Sept 1999, 8 Mar, 26 Apr, 18 and 19 Oct 2001; Sequiota Creek, N. W. Youngsteadt, 1♀/♂, 26 Oct 2000; Sawyer Creek, N. W. Youngsteadt, 1♀/♂, 1 May 1984, 2♀♂, 17 Oct 1986, and 1♀/♂, 6 May 1988; Turner Creek, 1♀/♂, N. W. Youngsteadt, 25 Apr 1990, 2♀♂, 14 Nov 1990; Hickory Co.: intermittent stream below seep, 8 km W of Urbana, 2♀, 2♂, J. L. Craig, 23 Mar 1975; Jasper Co.: Jones Creek, 5♀, R. J. Sarver et al., 9 Apr 1998; Laclede Co.: Coffin Cave, 10♀, J. E. Gardner, 22 Dec 1980 and 21♀♂, D. C. Ashley et al., 20 Jul 2000; Lawrence Co.: Turnback Cave, 1 juvenile ♂, J. E. Gardner, 24 Aug 1981; Williams Creek, 2♀, R. J. Sarver et al., 18 Mar 1997; Wilson Cave, 5♀♂, W. R. Elliott, 2 Mar 2000; Miller Co.: Travertine Spring Cave, 7♀♂, J. E. Gardner, 20 May 1981; Ozark Co.: Onyx Cave, 3♀, J. E. Gardner, 18 May 1979; Willis Donley Cave, 2♀♂, D. Ashley, L. Thompson, 15 Jul 2001; Phelps Co.: Little Piney Cave, 5♀, J. E. Gardner, 15 May 1980; Tree Root Cave, 1♀, J. E. Gardner, 2 Apr 1982; Pulaski Co.: Little Cave, 2♀, 1♂, J. E. Gardner, 6 Dec 1978 and 1♀, 28 Dec 1978; Shannon Co.: Forester Cave, 1♀, W. R. Elliott, 17 Oct. 1998; Stone Co.: Marvel Cave, 1♀ (AMNH), 11 Sep 1927; Taney Co.: Morel Cave, 6♀♂, M. Slay, A. Leary, 23 Apr 2003; plankton drift sample, 1♀, collector/collection date unknown; Zoo Cave, 1♀, 1, J. E. Gardner, 16 May 1979; Webster Co.: James River, N. W. Youngsteadt, 1♀/♂, 6 Jun 1984; Panther Creek, N. W. Youngsteadt, 1♀/♂, 15 Nov 1990; Sawyer Creek, N. W. Youngsteadt, ♀/♂, 19 Sept 1989; same collector/locality, 1♀/♂, 12 Feb 1990. OKLAHOMA. Adair Co.: Cave No. AD-14, 1♀, W. Howard, 12 Oct 1996; Charley Owl Cave, 3♀, J. H. Black, 1976, 3♀, 7 May 1977, and 1♀/♂, W. Puckette, Aug–Sep 1992; Sams Pit Cave, 1♂, J. H. Black, 8 Nov 1970; Duncan Field Cave (system), 1♀, 2♂, D. L. Certain and W. Puckette, 7 Dec 1991; Three Forks Cave, 1♂, J. H. Black, 1 Aug 1970; Cherokee Co.: Spring Creek at Terresita Bridge, 3♀, R. K. Heth, 21 May 1996, 8♀♂, 12 Dec 1996; Choctaw Co.: cistern fed by spring, ca. 4 km NW of Hugo, 3♀, J. J. Hoover, W. B. Milstead, 5 Aug 1981 and 14♀♂, 14 Jul 1982; Delaware Co.: unnamed spring at West Siloam Springs, 1♀, J. J. Hoover, W. B. Milstead, 3 Jun 1982; Mayes Co.: intermittent south tributary to Snake Creek, 7♀, R. K. Heth, 7 Dec. 1996; Ottawa Co.: 5 Mile Creek, 80♀♂ (CMN), R. Craven, 9 Nov 1968; unnamed spring ca. 6.4 km E of Wyandotte, 1♀, J. J. Hoover and W. B. Milstead, 2 Jun 1981. TEXAS. Nacogdoches Co.: well at Chireno, 1♀, 4♂, D. C. Rudolph, 26 Mar 1980; Palo Pinto Co.: Manley Water Cave, 8♀, 1♂, J. R. Reddell and D. McKenzie, 26 Aug 1972.

Addendum by JJL: As a species with the type-locality in Alabama, consideration of *Stygobromus alabamensis* was initially deferred until the *Stygobromus* species of the southeastern United States were covered in a future publication. I have been persuaded to include *S. alabamensis* because, under its revised status, most of the material now considered as *S. alabamensis* originates from the Ozarks. I suspect that when a molecular genetic analysis of *S. alabamensis* has been conducted, the species will be demonstrated to be a complex of cryptic species. If this comes to pass, then *S. alabamensis* is likely to be restricted to a much smaller geographic area, and the status of *S. elatus* (on Magazine Mountain, Logan Co., Arkansas) which John Holsinger so strongly questioned herein, will prove to be distinct (along with *S. montanus*, in Polk Co., Arkansas). The Ozark and other populations will likewise have to be dealt with.

Also note that other than Figure 1 in the introduction to this monograph of the habitus of *Stygobromus alabamensis*, Dr. Holsinger's materials did not include any illustrations of the Ozark populations of the species. As discussed above, when this "species" is addressed and probably divided into a complex of related taxa, the morphological aspects can be revisited in detail.

Notes on material examined.—The single ovigerous female from the unnamed spring east of Wyandotte, Ottawa Co., Oklahoma is tentatively identified as *S. alabamensis*. It is in a poor state of preservation and smaller than any other known ovigerous female of this species.

The locality "Van Buren Co.: seep, 5.5 miles N of Winslow, May 7, 1940" listed under material examined by Holsinger (1967:77) was typographically garbled and inadvertently combined two different sites. As correctly indicated above, the seeps in Van Buren Co., Arkansas, are near North Fork Cadron Creek, whereas the seep north of Winslow is in Washington Co., Arkansas.

Diagnosis.—Corresponding to the diagnosis by Holsinger (1967), except the species is no longer regarded as being polytypic. Largest males, 13.5 mm; largest females, 13.0 mm.

Variation.—Whereas the number of spines on the apex of the telson is typically 7 or 8 in males (Holsinger, 1967), it may be up to 10 (or rarely 12) in larger females. The presence or absence of median and pleonite sternal gills and 7th pereopod coxal gills may also vary, although this variation is usually seen in populations on the western end of the range (see remarks below).

Distribution and ecology.—Despite the numerous new locality records listed above, both the geographic and eco-

logical distribution of this species remains approximately the same as described by Holsinger (1967). However, several new records from Texas (Nacogdoches and Palo Pinto counties) extend its range a little farther west and southwest. As presently understood, the range of *Stygobromus alabamensis* covers a linear distance of approximately 1,126 km, extending from eastern Alabama west to northcentral Texas, and northwest to eastern Kansas, southern Missouri, and northeastern Oklahoma. It covers parts of nine states and is approximately twice as extensive as any other species in the genus.

Stygobromus alabamensis is occasionally collected in the company of other species of crangonyctid amphipods, most commonly with *S. ozarkensis* and *Crangonyx* spp., and less often with *S. gardneri* or *S. onondagaensis*. It is also sometimes found with the amphipod *Gammarus minus* (Gammaridae) or asellid isopods. In addition to its presence in caves, Stygobromus has been documented in hyporheic gravel substrates of surface streams (e.g., the Randy Sarver collections). Similarly, collections were made by Norman W. Youngsteadt (personal communication) from rocky surface stream substrates in Greene and Webster counties in the vicinity of Springfield, utilizing a square foot Surber riffle sampler with a 3-inch base extension.

Based on previously published data (Holsinger, 1967) and observations on material examined during the present study, the size range for ovigerous females is 4.0 mm to 9.0 mm, with the average size being 6.0 mm, with average number of seven to eight eggs/embryos per female.

Remarks on synonymy.—*Stygobromus a. occidentalis* was originally erected for a few populations in east-central Oklahoma and northeastern Texas that consistently lacked median and pleonite sternal gills and coxal gills on pereopod 7 (Holsinger, 1967). However, subsequent examination of many additional collections of *S. alabamensis* from eastern Oklahoma, especially from the Ozark region, reveals considerable discordant variation in the presence or absence of sternal gills among populations and an overall trend toward loss of some or all of these gill structures in populations in the western part of the range of the species. Moreover, similar variation was also noted in populations along the northwestern periphery of the species range in Missouri (Holsinger, 1967). Therefore, based on these observations, separate subspecies status for populations on the extreme southwestern end of the range is no longer warranted.

Enigmatic *Stygobromus* species

A specimen from a population in the study area for this manuscript was examined from the hyporheic of the Illinois River, in Cherokee Co., Oklahoma. It was a single juvenile collected by C. C. Vaughn, 11 Jul 1995. The 3.5 mm long specimen has bifurcate lateral sternal gills and propod of gnathopod 1 larger than that of gnathopod 2, thus a probable member of the *tenuis* group. However, since the telson and uropod 3 are apparently different from all other species in this group, this specimen may represent an undescribed species. With only a single juvenile specimen known, additional material would be needed to ascertain the identity of this taxon.

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