Systematics of the Subterranean Amphipod Genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States

JOHN R. HOLSINGER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 160

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ABSTRACT

Holsinger, John R. Systematics of the Subterranean Amphipod Genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States. *Smithsonian Contributions to Zoology*, number 160, 63 pages, 37 figures, 1974.—The subterranean amphipod genus *Stygobromus* is restricted to North America with the exception of one poorly known species from Siberia. *Stygobromus* is a member of the *Crangonyx* group of the family Gammaridae and is closely related to two other North American subterranean genera—*Apocrangonyx* and *Stygonectes*. It also has a close affinity with the Holarctic genus *Synurella*. Species of *Stygobromus* are widely distributed in cave waters and related ground water habitats throughout the greater part of the cavernous regions of the eastern, middle western, and far western United States.

A revised diagnosis of the genus is given, accompanied by a redescription of *S. hubbsi* Shoemaker from Oregon and the descriptions of 17 new species from the western United States. Of the 18 species recorded from the West, 15 belong to the newly erected *hubbsi* group. *Stygobromus putealis* (Holmes) from wells in Wisconsin is also assigned to this evolutionary group. Members of the *hubbsi* group are closely allied morphologically and are assumed to have been derived from a common ancestor. The western species inhabit a variety of subterranean biotopes, including limestone and lava caves, wells, springs, and one deep lake.

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Systematics of the Subterranean Amphipod Genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States

John R. Holsinger

Introduction

The subterranean amphipod genus *Stygobromus* was originally described by Cope (1872) on the basis of a single species (*S. vitreus*) collected from Mammoth Cave, Kentucky. Several workers subsequently placed this species in the genus *Crangonyx* (see Shoemaker, 1942a, for a historical review), but Schellenberg (1936) reassigned *vitreus* to *Stygobromus* after giving a brief diagnosis of this genus. *Crangonyx putealis,* a species described by Holmes (1909) from a well in Dodge County, Wisconsin, was also transferred to *Stygobromus* by Schellenberg (1936). Shoemaker (1942a) published a more thorough diagnosis of *Stygobromus* and redescribed *S. vitreus* from topotypes secured from Mammoth Cave. A third species (*S. hubbsi,* see later) was added to the genus by Shoemaker (1942b), followed by the descriptions of five new species of *Stygobromus* by Hubricht (1943). Two species previously described and placed in *Crangonyx* by Hubricht and Mackin (1940) were also assigned to *Stygobromus* in Hubricht's 1943 paper.

Only one species of *Stygobromus* has been reported from outside of the United States, this being *S. pusillus,* a blind, white species collected from Telelzkoye Lake in Siberia (USSR) and described by Martynov (1930). This species was originally placed in the genus *Eucrangonyx* (now considered invalid) by Martynov but later assigned to *Stygobromus* by Birstein (1940, 1950). Unfortunately it has so far been impossible to obtain types or additional specimens of this species and this, combined with the inadequacy of the original description, has made it difficult to determine the exact relationship of *S. pusillus* with the North American forms of the genus.

Prior to the present paper, *Stygobromus* contained 11 described species. An illustrated key to the 10 North American species was recently published (Holsinger, 1972), and the zoogeography of the Appalachian species (both described and undescribed) was discussed in an earlier paper (Holsinger, 1969a). In the present paper, 17 new species of *Stygobromus* from the western United States are recognized, bringing the total number of described species in the genus to 28. Approximately 35 additional species have been collected from other parts of the country and remain to be described.

The present study of *Stygobromus* is the fourth in a series designed to revise the systematics of the North American, subterranean amphipod genera of the family Gammaridae. Genera covered previously include *Stygonectes* (Holsinger, 1967), *Apocrangonyx* (Holsinger, 1969b), and *Allocrangonyx* (Holsinger, 1971). The study of the systematics of *Stygobromus* will be published in three parts: part

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I covers the western United States; part II will cover the Appalachian region; and part III will cover the central and middle-eastern United States (i.e., principally the Ozarks and the Interior Low Plateaus).

Species of *Stygobromus* are known primarily from cave habitats (e.g., small, mud-bottom pools and occasionally streams), although a few are found in groundwater-related biotopes such as seeps, springs, wells, and rarely deep lakes. The genus is represented in several of the major cave-bearing regions of North America, including: (1) Ozark Plateau and Arbuckle uplift of Arkansas, Missouri, and Oklahoma; (2) Interior Low Plateaus, from northern Alabama north to central and western Kentucky; (3) Appalachians, from southern Pennsylvania southwest to northwestern Georgia and northeastern Alabama; and (4) scattered limestone and lava cave areas of the western United States, principally in Arizona, California, Oregon, and Washington.

ACKNOWLEDGMENTS.—I am grateful to a number of persons who have collected and/or donated specimens and information used in this study. Contributions of specimens were made by Ronald Altig, William R. Elliott, Mark Grady, Richard E. Graham, Paul Hara, Francis G. Howarth, William Kruse, David McKenzie, James R. Reddell, Andrew L. Sheldon, Steve Shimek, and Richard D. Warren. Almo J. Cordone and Alvin McLane furnished some useful literature references on western amphipods, and R. E. Graham made available copies of field notes from his work in California caves. A. J. Cordone, W. R. Elliott, F. G. Howarth, A. L. Sheldon, and members of the Bower Cave Diving Group provided important ecological data from their observations in the field. Jack R. Schroeder is thanked for his assistance with the preparation of the figures. Thomas E. Bowman was kind enough to read the manuscript and make helpful comments.

Procedures

In two recent papers on North American freshwater amphipods (Holsinger, 1967, 1972), I attempted to standardize the terminology used in the descriptive morphology of these animals. One additional change to my proposed terminology is being made in this paper. The term "pleonal plate" has been adopted in lieu of "abdominal side plate." Pleonal plate is a shorter term that more clearly describes the paired lateral plates of the pleonites.

In the past, several amphipod workers, including myself, have designated the transverse rows of setae on the inner surface of the gnathopodal propods as lateral setae. Since these setae are, technically, medial instead of lateral in position, they have been designated medial setae (i.e., inferior and/or superior medial setae).

All measurements were made in millimeters to the nearest 0.10 with the aid of a calibrated micrometer disc. Total lengths refer to the length of the body excluding appendages, i.e., length from base of antenna 1 to base of telson. The figures were prepared with the aid of a Leitz drawing tube and a Rayoscope microprojector from appendages mounted in Hoyer's medium on glass slides.

Most of the specimens used in this study are either deposited in the National Museum of Natural History (Smithsonian Institution) under the catalog numbers of the United States National Museum (USNM) or in the collection of the author (JRH). Three collections are deposited in the Bernice P. Bishop Museum of Hawaii (BBM).

Cave names and locations correspond to those in published cave surveys or in other speleological publications. State cave surveys have been published for California (Halliday, 1962) and Washington (Halliday, 1963). Additional information is available on caves in Oregon (Greeley, 1971), and supplementary information on Washington caves was published recently in the "Guidebook of the 1972 Convention of the National Speleological Society."

Stygobromus Cope

Stygobromus Cope, 1872:422

DIAGNOSIS.—Without eyes or pigment; of subterranean facies. Size of sexually mature animals generally ranging from 2.5 to 12.0 mm. Antenna 1 longer than antenna 2; small, slender calceoli usually present on most primary flagellar segments; accessory flagellum 2-segmented. Interantennal lobe rounded anteriorly. Mandible with well-developed incisor and lacinia mobilis; molar triturative; palp well developed, 3-segmented. Maxilla 1: inner plate with long, plumose setae apically; outer plate with 7 (rarely 8) serrate spines apically; palp 2-seg-

mented, bearing a few stiff setae and small spines distally. Maxilla 2, inner plate broader than outer plate, bearing row of long, obliquely placed plumose setae on inner margin. Maxilliped: inner plate with thick spines and stiff setae apically; outer plate bearing coarse setae on apex and inner margin and often 1 (or rarely 2) bladelike spines apically; palp well developed, segment 2 the longest. Outer lobes of lower lip broadest proximally, narrowing distally; inner lobes varying from vestigial or absent to small and distinct.

Propod of gnathopod 1 usually smaller than (or rarely equal to) second propod, palm armed with double row of distally notched spine teeth. Palm of gnathopod 2 armed with double row of distally notched spine teeth. Pereopods 3 and 4 subequal, except coxal plate of 4 a little broader than 3. Pereopod 6 a little longer than pereopod 7 (nearly equal in length in a few species), always longer than pereopod 5. Biarticulate coxal gills present on pereopods 2–6, present or absent on pereopod 7. Sternal processes usually present but variable.

Pleonal Plates: Posterior margins usually slightly convex, with 1 to several setae; distoposterior corners if distinct, tiny and rounded; ventral margins of plates 2 and 3 usually with 1 to several spines, plate 1 with or without ventral spines. Pleopods decreasing in length posteriorly, inner rami slightly longer than outer; peduncles with 2 coupling hooks each on inner margins distally. Uronites free, not fused; dorsal margins without spines. Uropod 1 of male with distal peduncular process. Uropod 3 short, uniramous; ramus shorter than peduncle, armed with 1 to several apical spines. Telson usually longer than broad; apical margin entire or emarginate (but not deeply cleft), armed with spines.

TYPE-SPECIES (by monotypy).—*Stygobromus vitreus* Cope, 1872.

RELATIONSHIPS.—The genus *Stygobromus* is a member of the *Crangonyx* group of the family Gammaridae and is related to five other genera assigned to this group from North America (Holsinger, 1967, 1972). *Stygobromus* is closely allied morphologically and ecologically with both *Stygonectes* and *Apocrangonyx* and some of the similarities and differences between these three genera have been pointed out in earlier papers (Holsinger, 1967, 1969a, 1969b, 1972). Aside from the fact that these genera are exclusively subterranean, they share a number of important morphological characters: similarity in mouthparts; slender calceoli on antenna 1; double row of distally notched spine teeth on the palms of the gnathopodal propods; sternal processes (variable in some species); distoposterior corners of the pleonal plates usually small or indistinct but not produced; reduced, uniramous uropod 3; uropod 1 of male with a distal peduncular process (absent in some species); and a comparatively small telson which may or may not be emarginate but never deeply cleft.

With the exception of a few aberrant species, *Stygobromus* can be distinguished from *Stygonectes* by: gnathopodal propod 2 being larger than propod 1; pereopod 6 being slightly longer than pereopod 7; and the uronites being free (articulate) and not coalesced. In a few species of each genus, however, the size of the gnathopodal propods and the lengths of pereopods 6 and 7 are about equal, but the fusion of the uronites appears to be consistent among species of *Stygonectes* (although this fusion is not always complete between uronites 1 and 2). The presence of rastellate setae (see Holsinger, 1967) on segment 5 of the gnathopods and the presence of bifurcate lateral sternal processes on pereonites 6 and 7 are much more common among species of *Stygonectes* than among species of *Stygobromus*. As a rule, species of *Stygonectes* reach greater lengths at sexual maturity, and a number of species (approximately 25 percent) exceed 15.0 mm as adults. Species of *Stygobromus,* on the other hand, rarely exceed 10.0 mm at sexual maturity, most being smaller than this as adults.

The genus *Apocrangonyx* is not as easily distinguished because some species have characters that overlap with species in the other two genera. The origin of *Apocrangonyx* is probably polyphyletic (Holsinger, 1969a, 1969b), and, although the taxonomic status of this genus is somewhat obscure, several of its species will probably be reassigned to *Stygonectes* (viz, *A. ephemerus* and *A. parvus*) and *Stygobromus* (viz, *A. nortoni*) after further study. The character combination used to separate *Apocrangonyx* includes: gnathopodal propod 2 larger than propod 1, pereopod 7 slightly longer than pereopod 6, fusion of the uronites, lateral sternal processes usually bifurcate, and extreme reduction or loss of the ramus of uropod 3. In two or three species of *Apocrangonyx* the distal peduncular process of the first uropod of the male

is present but vestigial; in the other species it is absent. The size reached at sexual maturity is usually quite small for species in this genus, the largest species being 7.0 mm and the smaller ones (some undescribed) only about 2.5 mm.

Stygobromus is also closely allied morphologically with *Synurella,* a genus represented by 4 epigean species in North America and about 14 epigean and subterranean species in Europe and Asia (Holsinger, 1972). Three of the four North American species inhabit epigean habitats (chiefly springs, ponds, sloughs, bogs, etc.) in the southeastern United States and are stocky-bodied, eyed, pigmented forms with rather deeply cleft telsons (split more than 50 percent the distance of the base) and strongly produced, acuminate posterior corners of the pleonal plates. Species of *Synurella* are further distinguished by having the uronites fused (with the exception of one species) and lacking a distal peduncular process on uropod 1 of the male. The fourth North American species of *Synurella* occurs in Alaska (in tundra pools and streams) and is apparently more closely related to the Eurasian species of the genus in having a less deeply incised telson (split only about 30 to 35 percent the distance to the base) and weaker (less produced) posterior corners of the pleonal plates. Thus, with respect to the telson and the pleonal plates, the Alaskan and Eurasian species of *Synurella* appear to be more closely allied morphologically with species of *Stygobromus* than do species from the southeastern United States. The phylogenetic relalationship of *Stygobromus* and *Synurella* is still unclear, however, and the problem is open for further study. The morphological similarities between the two genera may be the result of parallel evolution or may imply that one group has descended from the other.

Key to the Western Species of *Stygobromus*

1. Simple, lateral sternal processes present on pereonites 6 and 7 2
   Sternal processes absent 3
2. Gnathopodal propods subequal in size, 1st perhaps slightly larger than 2nd; bases of pereopods 5–7 narrow, not expanded proximally; telson incised nearly one-fourth the distance to base. ..... 18. ***S. obscurus***
   Gnathopodal propod 2 larger than 1; bases of pereopods 5–7 broader proximally than distally; telson with shallow notch. ..... 17. ***S. montanensis***
3. Coxal plate of pereopod 4 reaching more than half the length of segment 2; bases of pereopods 5–7 broadly expanded, distoposterior lobes large; telson nearly twice as long as broad, distinctly tapering distally. ..... 16. ***S. mysticus***
   Coxal plate of pereopod 4 reaching up to half the length of segment 2 but usually less; bases of pereopods 5–7 not broadly expanded, usually rather narrow, distoposterior lobes small or lacking; telson not twice as long as broad, not much broader proximally than distally ..... (*hubbsi* group) 4
4. Inner plate of maxilla 1 with 10 to 16 apical, plumose setae; inner plate of maxilla 2 with oblique row of 13 to 15 plumose setae on inner margin; inner plate of maxilliped with 8 to 13 apical spines 5
   Inner plate of maxilla 1 with 6 to 9 apical, plumose setae; inner plate of maxilla 2 with oblique row of 6 to 10 plumose setae on inner margin; inner plate of maxilliped with 4 to 8 apical spines 8
5. Gnathopodal propod 2 of mature female nearly twice (or more) the size of propod 1, palm with double row of 9 to 13 spine teeth 6
   Gnathopodal propod 2 of mature female only a little larger than propod 1, palm with double row of 5 spine teeth ..... 7. ***S. gradyi***
6. Palms of gnathopodal propods of mature female with double row of 13 spine teeth, ventral margin of pleonal plate 1 with spines, ventral margin of plate 3 with 7 spines ..... 9 ***S. wengerorum***
   Palms of gnathopodal propods of mature female with double row of 10 or less spine teeth; ventral margin of pleonal plate 1 without spines, ventral margin of plate with 4 or 5 spines 7
7. Inner marginal spines of posterior angle of gnathopodal propod 1 of mature female mostly forked; gnathopodal propod 2 of mature male proportionately smaller than female; coxal plate of pereopod 4 extending about half the length of segment 2 with 13 marginal

setae ..... 6. ***S. grahami***

Inner marginal spines of posterior angle of gnathopodal propod 1 of mature female mostly unforked; gnathopodal propod 2 of mature male proportionately larger than female; coxal plate of pereopod 4 extending about one-third the length of segment 2, with 7 marginal setae ..... 8. ***S. harai***

8. Length of sexually mature female not exceeding 5.0 mm; bases of pereopods 5–7 distinctly broader proximally than distally; peduncle of uropod 2 of mature female with 3 spines; ramus of uropod 3 with 2 or 3 apical spines; apical margin of telson with small notch (never deeply notched) 9

Length of sexually mature females usually exceeding 5.0 mm (excepting *S. arizonensis*); bases of pereopods 5–7 often not much broader proximally than distally; peduncle of uropod 2 of mature female with more than 3 spines (excepting *S. sierrensis*); ramus of uropod 3 with 3 or more spines (excepting *S. arizonensis*); apical margin of telson usually emarginate (notched one-fourth the distance to base in *S. arizonensis*) 10

9. Inner plate of maxilliped with 6 to 8 apical spines; gnathopodal propod 2 of male only slightly longer than 1st propod; ramus of uropod 3 with 2 apical spines 12. ***S. sheldoni***

Inner plate of maxilliped with 4 apical spines; gnathopodal propod 2 of male about one-fourth longer than 1st propod; ramus of uropod 3 with 3 apical spines. . 10. ***S. mackenziei***

10. Posterior margins of bases of pereopods 5–7 convex midmarginally, distoposterior lobes lacking; ramus of uropod 3 with 2 apical spines; apical margin of telson incised one-fourth the distance to base ..... 15. ***S. arizonensis***

Posterior margins of bases of pereopods 5–7 not convex midmarginally, distoposterior lobes lacking or not; ramus of uropod 3 with 3 or more apical spines; apical margin of telson usually with shallow notch, but not incised one-fourth the distance to base. 11

11. Bases of pereopods 5–7 broader proximally than distally, posterior margins slightly convex, distoposterior lobes small, distinct 12

Bases of pereopods 5–7 not much broader proximally than distally, posterior margins nearly straight or irregular but not convex, distoposterior lobes small and distinct or lacking 13

12. Palm of gnathopodal propod 2 convex with double row of 16 spine teeth; pleonal plates with small, subacute posterior corners; telson with 15 or 16 apical spines . . . 4. ***S. oregonensis***

Palm of gnathopodal propod 2 convex distally, concave proximally, with double row of 12 spine teeth; pleonal plates with small, rounded posterior corners; telson with 12 to 14 apical spines ..... 14. ***S. lacicolus***

13. Uropods 1 and 2 heavily spined, uropod 1 with 52 spines, uropod 2 with 34 spines; telson with 16 apical spines, 4 of which are up to twice the length of the others. . 3. ***S. puteanus***

Uropods 1 and 2 not as heavily spined, uropod 1 with usually less than 38 spines, uropod 2 with usually less than 27 spines; apical spines of telson mostly subequal in length 14

14. Outer plate of maxilla 1 with 8 serrate spines apically; inner margin of palpal segment 2 of maxilliped elongate and heavily setose; posterior margins of bases of pereopods 5–7 often irregular; sexually mature females reaching 9.5 mm in length ..... 5. ***S. elliotti***

Outer plate of maxilla 1 with 7 serrate spines apically, inner margin of palpal segment 2 of maxilliped not elongate or heavily setose; posterior margins of bases of pereopods 5–7 typically straight or nearly so; sexually mature females not exceeding 7.0 mm in length 15

15. Distoposterior lobes of bases of pereopods 5–7 lacking; telson broader than long 2. ***S. tritus***

Distoposterior lobes of bases of pereopods 5–7 small but distinct; telson as long as, or usually longer than broad 16

16. Pleonal plates 2 and 3 with 2 ventral spines each; ramus of uropod 3 about one-fourth the length of peduncle; apical margin of telson with very slight emargination. . 11. ***S. sierrensis***

Pleonal plates 2 and 3 with at least 4 ventral spines each; ramus of uropod 3 about one-third the length of peduncle; apical margin of telson with small but usually distinct notch 17

17. Gnathopodal propod 2 of mature female up to one-third larger than 1st propod, palm with double row of 11 or 12 spines teeth; apical margin of telson of mature male and female with distinct notch and usually 8 spines ..... 1. ***S. hubbsi***

Gnathopodal propod 2 of mature female only a little larger than 1st propod, palm with double row of 7 or 8 spine teeth; apical margin or telson of mature male and female with very shallow notch (sometimes almost indistinct), male with 6 spines, female with 10 spines ..... 13. ***S. tahoensis***

The *hubbsi* group

DIAGNOSIS.—Posterior margin of gnathopodal propod 1 without setae or rarely with 1 submarginal seta just below defining angle. Gnathopodal propod 2 usually much broader proximally (near base), especially in females; outer margin of palm often with a few more spine teeth than inner margin toward area of posterior angle; posterior margin comparatively short, especially in females. Bases of pereopods 5–7 rather narrow, not much expanded posteriorly; distoposterior lobes often small, poorly developed, or occasionally absent. Sternal processes absent. Sternal blisters (small ventral humps) sometimes present on pereonites 2–7. Telson usually as long as broad or frequently a little longer than broad; apical margin with a small notch (except in some specimens of *S. elliotti*).

COMMENTS.—As defined above, the *hubbsi* group is composed of 15 species, geographically distributed from Washington, Oregon, and Montana southward through California and Nevada to southern Arizona. Two other western species of *Stygobromus*—*S. mysticus* and *S. montanensis*—are probably distantly related to the *hubbsi* group, but their morphological affinities are unclear, and they are not being assigned to this group at the present time.

Stygobromus putealis, a species recorded from five wells in southeastern Wisconsin (see Holsinger, 1972), is closely allied morphologically with members of the *hubbsi* group (i.e., especially in the structure of the gnathopodal propods, the absence of sternal processes and the presence of sternal blisters). Although this species is geographically far removed to the east and will not be redescribed until part III of the generic revision, it should nevertheless be regarded as a member of the *hubbsi* group.

1. *Stygobromus hubbsi* Shoemaker

FIGURE 1

Stygrobromus hubbsi Shoemaker, 1942b:1–6, figs. 1–2.—Hubricht, 1959:878.—Nicholas, 1960:128.—Bousfield, 1961: 2–3.—Holsinger, 1972:68–69, 72, fig. 26f.

MATERIAL EXAMINED.—OREGON. Harney Co.: Malheur Cave, holotype male (USNM 98404) and 104 paratypes (USNM 98405 and 80528), Carl L. Hubbs, 27 July 1928; additional specimens collected include 1 female by Virginia M. Tipton, 9 Aug. 1969 (JRH) and 2 juveniles by W. R. Elliott et al., 9 Aug. 1972 (JRH).

DIAGNOSIS.—A medium-sized cavernicolous species bearing a close morphological affinity with the cave species of east-central California (especially *S. grahami, S. harai,* and *S. wengerorum*) but distinguished by having fewer plumose setae on the inner plates of maxillae 1 and 2; fewer apical spines on the inner plate of the maxilliped; only 8 or 9 apical spines on the telson; and other characters noted in the descriptions below. Largest females, 6.5 mm; largest males, 5.5 mm.

This description corresponds to Shoemaker's (1942b) with the following additions and modifications: Antenna 1 about 45 percent as long as body, 50 percent longer than antenna 2; primary flagellum with up to 15 segments. Antenna 2, flagellum with 5 or 6 segments. Maxilla 1, inner plate with 8 or 9 apical, plumose setae. Maxilla 2, inner plate with 9 or 10 obliquely placed, plumose setae on inner margin. Maxilliped: inner plate armed apically with 4 or 5 bladelike spines, several stiff setae and 2 or 3 plumose spines; outer plate with 1 bladelike spine and a number of stiff setae apically and subapically.

Gnathopod 1: Propod palm slightly convex, armed with double row of 9 or 10 spine teeth; posterior angle with 1 long and 3 shorter spine teeth on outside, 5 spine teeth (some forked) on inside; posterior margin comparatively short, about one-third the length of palm, without setae or spines. Coxal plate of gnathopod 1 longer than broad, with 4 or 5 marginal setae. Gnathopodal propod 2 up to one-third larger than 1st, about 50 percent longer than broad; palm long, oblique, slightly concave proximally, with double row of 11 or 12 spine teeth, plus 3 additional spine teeth on outside; posterior angle with 1 long, curved spine and several long setae on outside, 3 shorter spine teeth on inside; posterior margin with 2 or 3 sets of long setae; superior medial setae singly and doubly inserted, inferior medial setae singly inserted; dactyl long and curved, nail rather long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 8 to 10 marginal setae; coxal plate of pereopod 4 about as broad as long, with 12 marginal setae. Pereopod 6 about 50 percent longer

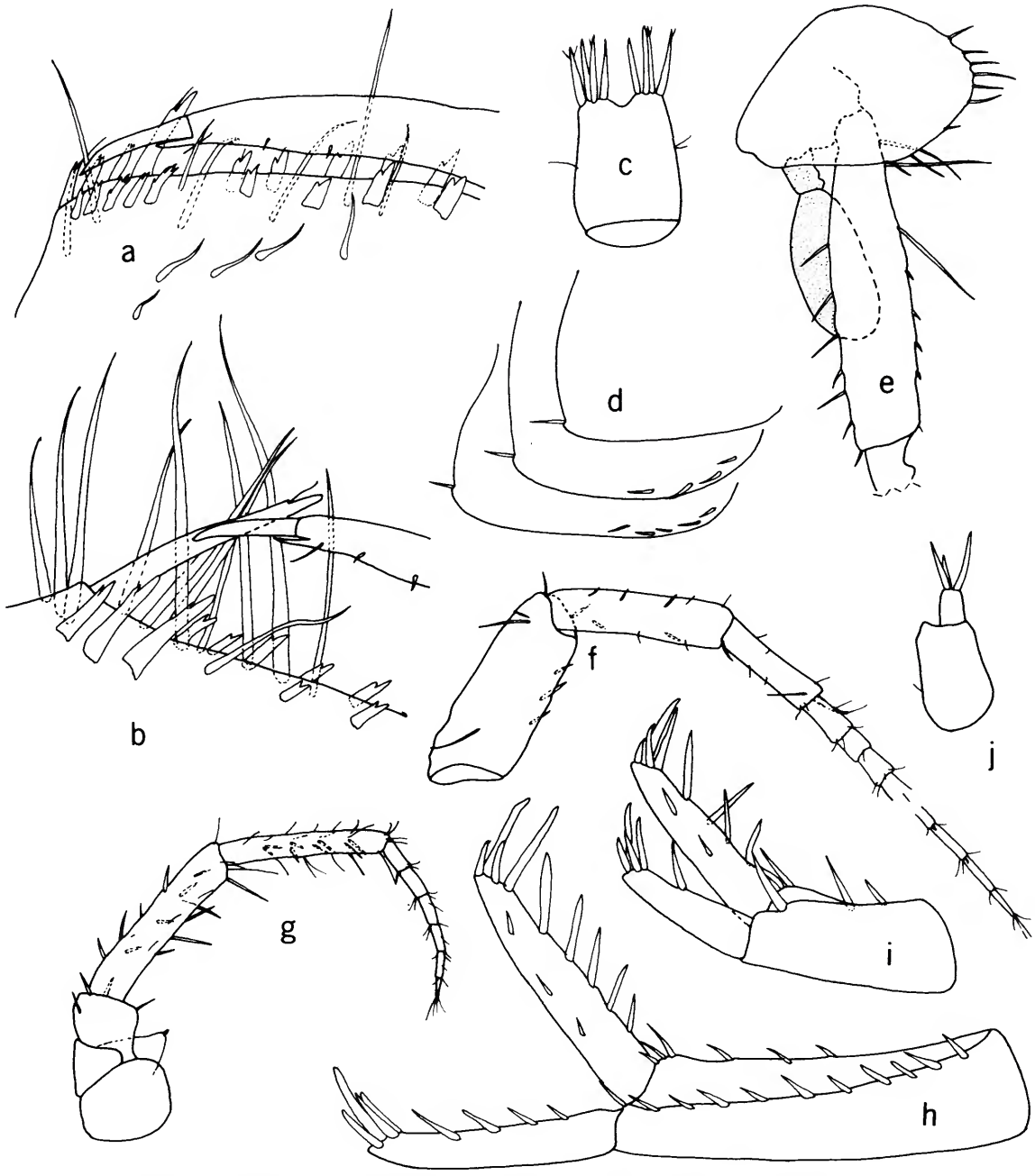

FIGURE 1.—*Stygobromus hubbsi* Shoemaker, female paratype (6.0 mm), Malheur Cave Oregon: *a*, *b*, palms of gnathopodal propods 1.2; *c*, telson; *d*, pleonal plates; *e*, pereopod 3 (in part); *f,g*, antennae 1,2; *h,i,j*, uropods 1,2,3.

than body, slightly longer than pereopod 7, 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 rather narrow, a little broader proximally than distally; distoposterior lobes small, rounded; dactyls comparatively long, about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins slightly convex and bearing 1 seta each; posterior corners broadly rounded; ventral margin of plate 1 without spines, ventral margins of plates 2 and 3 with 4 and 5 spines, respectively. Uropod 1 of female: inner ramus shorter than peduncle, slightly longer than outer ramus, armed with 12 spines; outer ramus with 8 spines; peduncle with 17 or 18 spines. Uropod 2 of female: inner ramus about as long as peduncle, about one-third longer than outer ramus, armed with 10 spines; outer ramus with 5 spines; peduncle with 5 spines. Uropods 1 and 2 of male with a few less spines; distal peduncular process of uropod 1 rather short and triangular. Uropod 3: ramus about one-third the length of peduncle, armed apically with 3 slender spines. Telson longer than broad; apical margin with shallow notch; apical lobes usually with 4 (or rarely 5) spines each.

TYPE-LOCALITY.—Malheur Cave, Harney County, Oregon. The type-locality is a lava tube formed in basalt of Late Cenozoic age. The original type-series and subsequent topotypes were collected from a lake over a thousand feet within the cave. Malheur Cave is also the type-locality (and only known locality) for the unique troglobitic planarian *Kenkia rhynchida,* described by Hyman (1937) and discussed more recently by Kenk (1972). In addition, the cave contains a tiny, white, eyeless isopod of the genus *Asellus.* The isopod, presumably undescribed, is known only from three females (1 ovigerous) collected along with two specimens of *S. hubbsi* by W. R. Elliott et al. in August 1972. The material is deposited in the National Museum of Natural History.

DISTRIBUTION AND ECOLOGY.—*Stygobromus hubbsi* is known only from its type-locality, where it is associated with the troglobitic planarians and isopods noted above. The majority of specimens collected have been females, but none were ovigerous and nothing is known about the life history of this species.

COMMENTS.—Although Shoemaker's 1942 description of this species was adequate, I found it necessary to give more detailed figures of some of the appendages as shown. In my recent identification manual of freshwater amphipods (Holsinger, 1972), I inadvertently misplaced the location of Malheur Cave on the distribution map for *S. hubbsi.* The location shown on the map in Figure 36 (herein) is correct.

2. *Stygobromus tritus,* new species

FIGURES 2, 3

MATERIAL EXAMINED.—MONTANA. Ravalli Co.: well at Victor Crossing, holotype female (USNM 142818) and 14 paratypes (USNM 142819), 19 Oct. 1952 (collector unknown); 11 paratypes (USNM 142820), Ocie Hessling, 11 Oct. 1952.

DIAGNOSIS.—A rather small subterranean species distinguished by the palms of the gnathopodal propods, which are slightly concave and have short spine rows; comparatively narrow propod of gnathopod 2; slender bases of pereopods 5–7 without distoposterior lobes; rather long marginal spines on the inner ramus of uropod 2; short telson (broader than long); and proportionately short ramus of uropod 3. Sexes generally similar. Largest females, 5.0 mm; largest males, 4.5 mm.

DESCRIPTION.—Antenna 1, 60 percent as long as body, 50 percent longer than antenna 2, with up to 14 segments in primary flagellum. Antenna 2, flagellum with 6 segments. Mandibles similar to those of *S. hubbsi.* Maxilla 1: inner plate with 6 apical, plumose setae; palp with 4 short spines and 2 setae apically. Maxilla 2, inner plate with oblique row of 7 or 8 plumose setae on inner margin. Maxilliped: inner plate with 3 serrate spines, 3 plumose spines and 2 stiff setae apically; outer plate with 1 small spine and several stiff setae apically to subapically on inner margin. Lower lip, inner lobes indistinct, vestigial or absent.

Gnathopod 1: Propod palm not oblique, rather straight, armed with double row of 5 spine teeth; posterior angle defined by 3 long spine teeth on outside, 4 shorter spine teeth on inside; posterior margin comparatively long, without setae; medial setae few in number, singly inserted; dactyl nail and accessory spine relatively long. Coxal plate of gnathopod 1 longer than broad, with 1 marginal

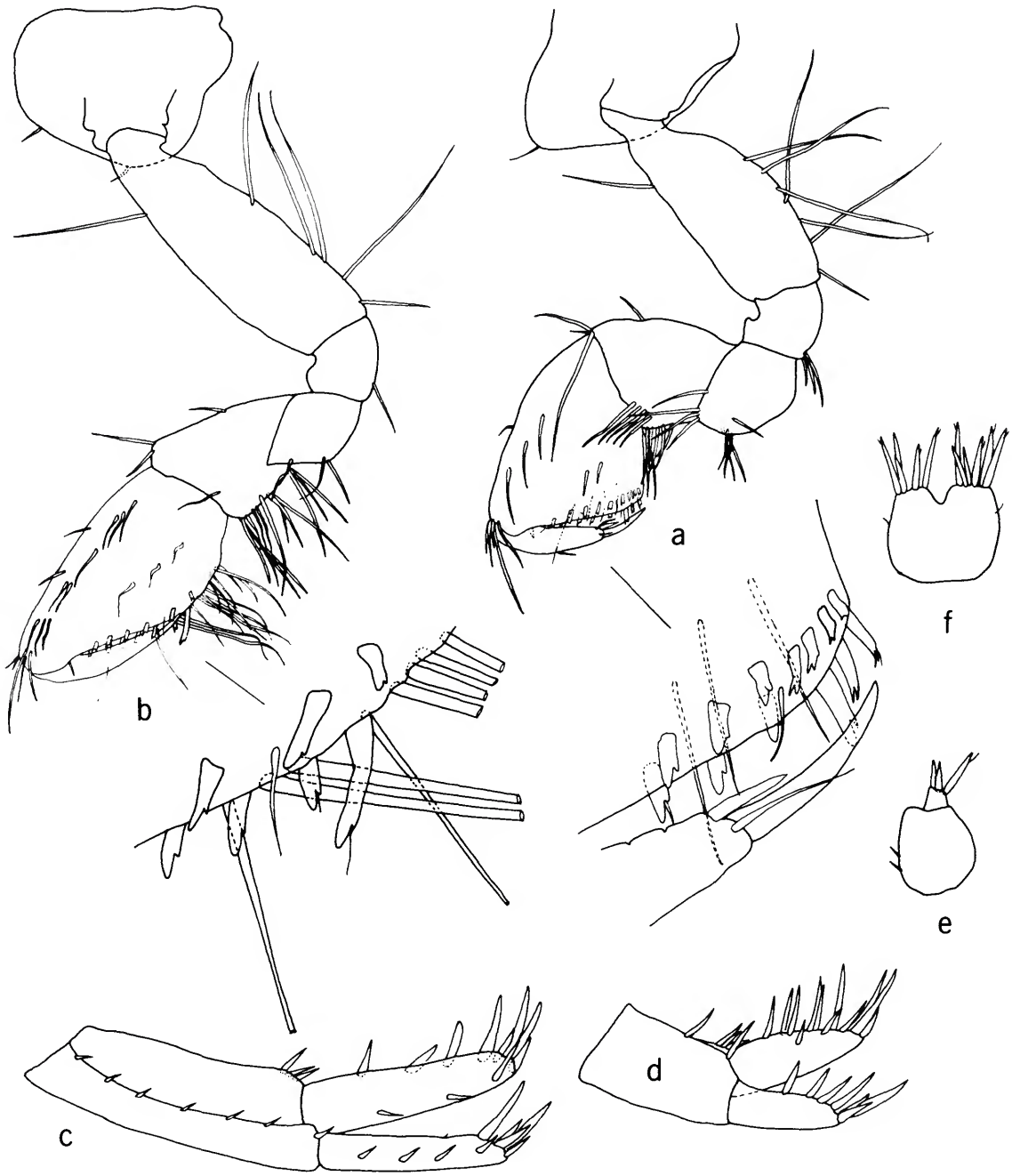

FIGURE 2.—*Stygobromus tritus*, new species, female paratype (5.0 mm), well at Victor Crossing, Montana: *a,b*, gnathopods 1,2; *c,d,e*, uropods 1,2,3,; *f*, telson.

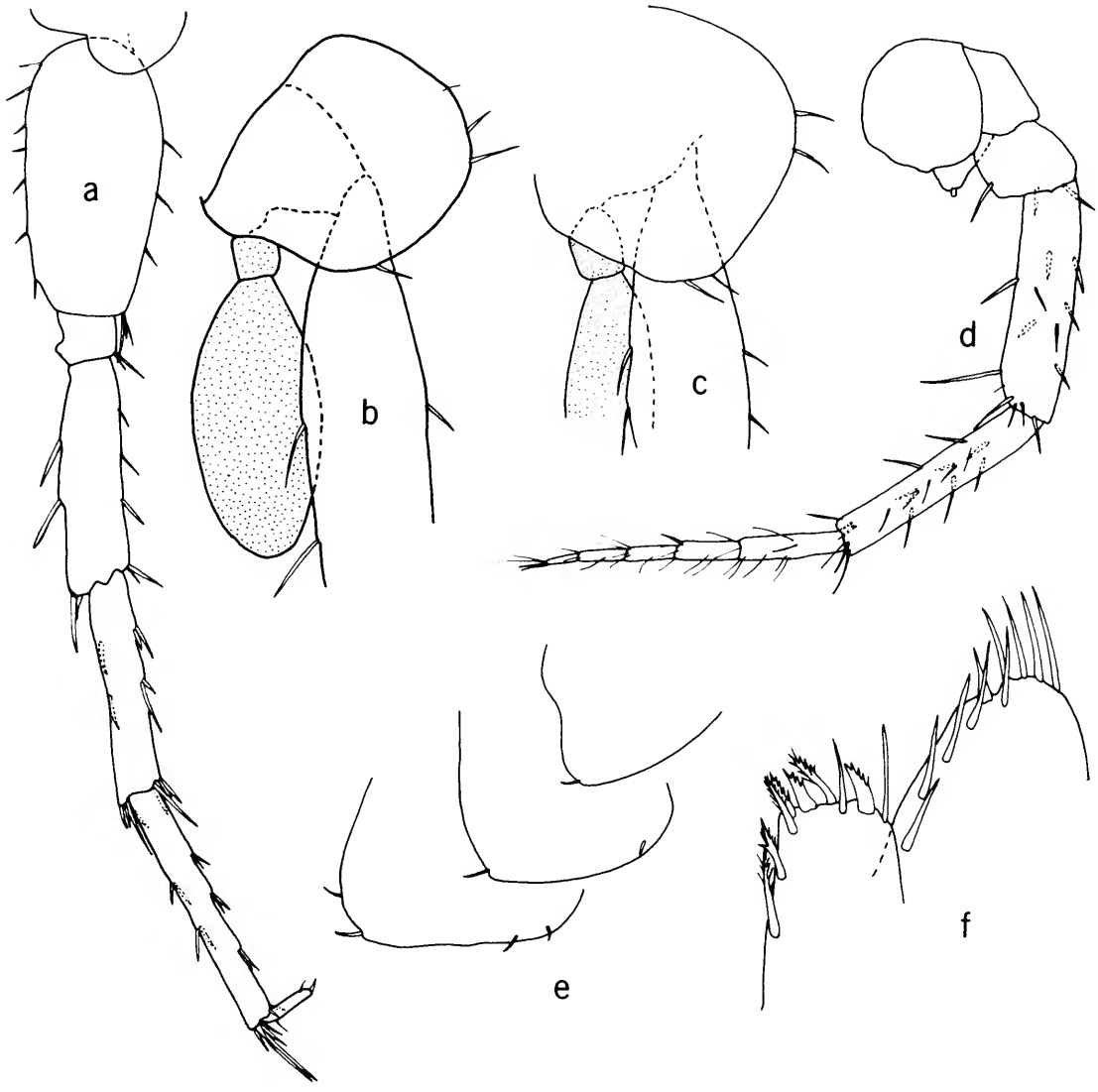

FIGURE 3.—*Stygobromus tritus*, new species, female paratype (5.0 mm): *a*, pereopod 6; *b,c*, pereopods 3,4 (in part); *d*, antenna 2; *e*, pleonal plates; *f*, apexes of inner and outer plates of maxilliped (greatly enlarged).

seta. Gnathopod 2: propod larger than 1st propod, nearly twice as long as broad; palm oblique, slightly concave, armed with double row of 6 spine teeth; posterior angle poorly defined, with 1 long spine tooth and 1 long seta on outside and 1 short spine tooth on inside; posterior margin rather long, uneven, with 3 sets of long setae; medial setae rather prominent, singly, doubly, and triply inserted; dactyl nail rather long. Coxal plate of gnathopod 2 rather shallow, with 2 marginal setae. Coxal plates of pereopods 3 and 4 broader than long, with 4 marginal setae each. Pereopod 6 slightly longer than pereopod 7, 50 to 55 percent as long as body, about 20 percent longer than pereopod 5. Bases of

pereopods 5–7 narrow, posterior margins with 6 or 7 setae, distoposterior lobes indistinct. Dactyls of pereopods 6 and 7 comparatively short, less than one-third length of corresponding propods. Coxal gills on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins convex, with 1 or 2 setae each; posterior corners tiny, rounded; ventral margins of plates 2 and 3 with 1 or 2 spines each. Uropod 1: inner ramus a little longer than outer ramus, shorter than peduncle, armed with 10 or 11 spines; outer ramus with 8 or 9 spines; peduncle with 9 or 10 spines. Uropod 2: inner ramus a little longer than outer ramus, about equal in length to peduncle, armed with 12 spines (some rather long); outer ramus with 7 spines; peduncle with 5 spines. Uropod 3: ramus comparatively short, only about 25 percent as long as peduncle, with 3 apical spines. Telson a little broader than long, apical margin with distinct notch, apical lobes with 5 or 6 spines each.

TYPE-LOCALITY.—A well at Victor Crossing, Ravalli County, Montana. The well is reported to be 20 feet deep and is located in or near the town of Victor, although a precise location was not given by the collector. This well is presumably excavated in Quaternary deposits which, according to geological maps, cover the floor of the valley formed by the Bitterroot River.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected at two different times in October 1952. The first sample, taken on 11 October, contained 11 specimens of *S. tritus,* 5 specimens of *S. montanensis* (described herein) and 2 specimens of *S. obscurus* (also described herein). The second sample (19 October) contained only 15 specimens of *S. tritus.* Females outnumbered males almost 3 to 1 in the two samples. Although several females had setose brood plates, none were ovigerous and nothing is known about the reproductive capacity of this species.

ETYMOLOGY.—The name *tritus* is from the Greek *tritos,* meaning "third."

3. *Stygobromus puteanus,* new species

FIGURES 4, 5

MATERIAL EXAMINED.—MONTANA. Gallatin Co.: well near Three Forks, holotype female (USNM 142799) and 3 paratypes (USNM 142800), C. A. Tryon, Jr., Feb. 1939.

DIAGNOSIS.—A medium-sized subterranean species apparently related to *S. tritus* but distinguished from that species by the straight to slightly convex palms of the gnathopodal propods; broader bases of pereopods 5–7; more spines on uropods 1 and 2; longer apical spines on uropod 3; and proportionately longer and more spinose telson with 16 apical spines (of which 4 are very long and slender). Largest females, 6.5 mm; male unknown.

DESCRIPTION.—Antenna 1, 45 to 50 percent as long as body, about 40 percent longer than antenna 2; primary flagellum with 19 or 20 segments. Antenna 2, flagellum with 5 segments. Mouthparts similar to those of *S. hubbsi.* Gnathopod 1: propod palm slightly convex, armed with double row of about 5 small spine teeth; posterior angle distinct, with 1 long and 2 short spine teeth on outside, 5 short spine teeth on inside; posterior margin without setae; medial setae few in number, singly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 about twice as long as broad, with 3 marginal setae. Gnathopod 2: propod up to one-third larger than 1st propod; palm oblique, nearly straight, armed with double row of 8 or 9 spine teeth; posterior angle defined by 1 long, curved spine tooth and 3 long setae on outside, 1 or 2 small spine teeth on inside; posterior margin convex, with 2 sets of long setae; inferior medial setae singly inserted, superior medial setae singly and doubly inserted; dactyl rather long, slightly curved, nail moderately long. Coxal plates of gnathopod 2 and pereopod 3 rather shallow, about as broad as long; plate 2 with 3 marginal setae, plate 3 with 6 marginal setae. Coxal plate of pereopod 4 broader than long, with 8 marginal setae.

Pereopod 6, 45 to 50 percent as long as body, slightly longer than pereopod 7, about 25 percent longer than pereopod 5. Bases of pereopods 5–7 rather narrow, slightly broader proximally than distally; posterior margins with 8 to 10 setae; distoposterior corners small, poorly defined. Dactyls of pereopods 6 and 7 nearly one-third the length of corresponding propods. Coxal gills on pereopods 2–6. Brood plates of mature females small and narrow. Pleonal plates: posterior margins convex; posterior corner of plate 1 rounded, corners of plates 2 and 3 indistinct; ventral margins of plates 2 and 3 with 3 spines each. Uropod 1: inner ramus

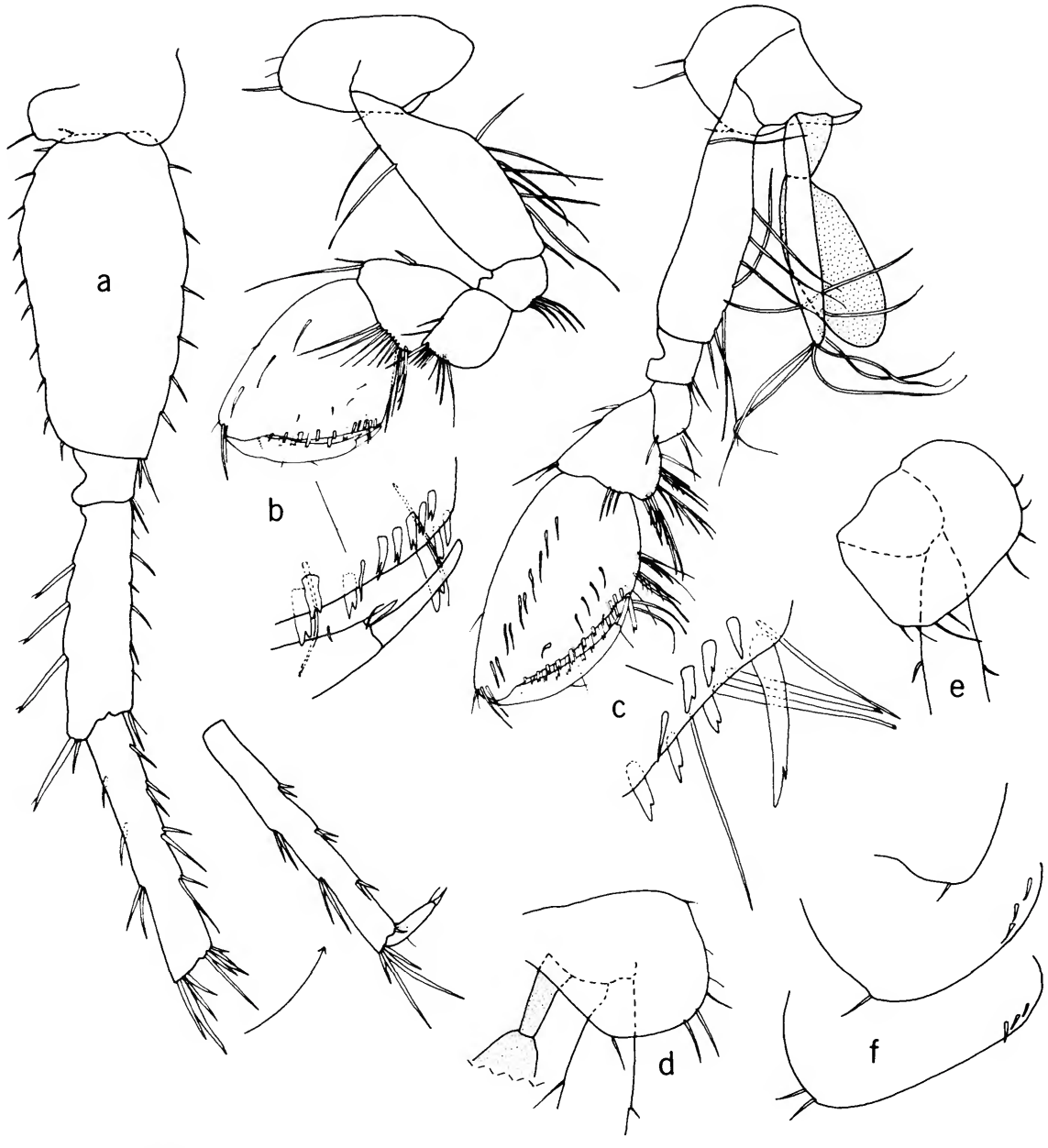

FIGURE 4.—*Stygobromus puteanus*, new species, female paratype (6.5 mm), well near Three Forks, Montana: *a*, pereopod 6; *b,c*, gnathopods 1,2; *d,e*, pereopods 3,4 (in part); *f*, pleonal plates.

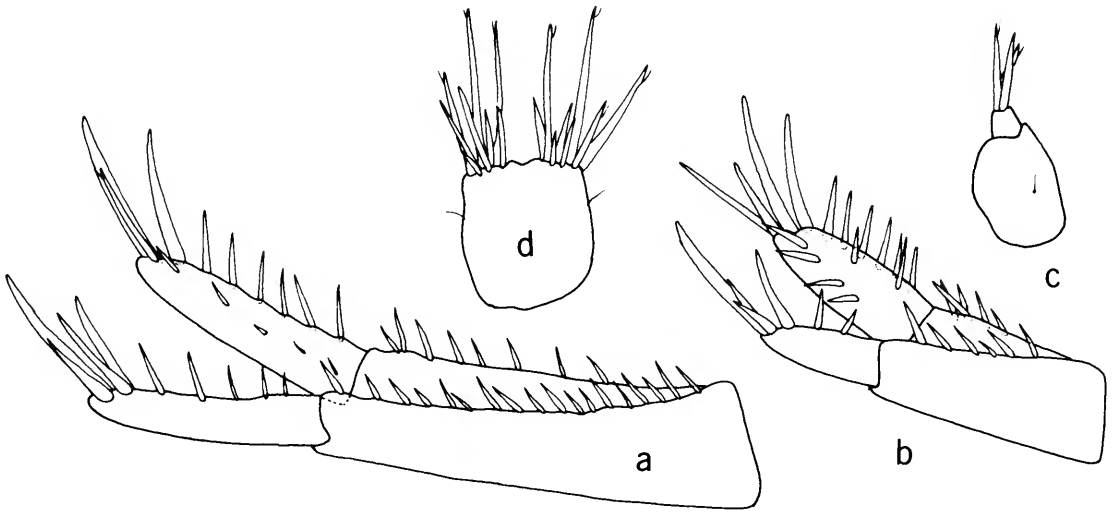

FIGURE 5.—*Stygobromus puteanus*, new species, female paratype (6.5 mm): *a,b,c*, uropods 1,2,3; *d*, telson.

slightly longer than outer ramus, about 60 percent as long as peduncle, armed with 13 or 14 spines, many of which are long and slender; outer ramus with 9 spines; peduncle with 25 spines. Uropod 2: inner ramus nearly twice as large as outer ramus, about 70 percent as long as peduncle, armed with 16 mostly elongate spines; outer ramus with 6 spines; peduncle with 12 spines. Uropod 3: ramus proportionately short, only about one-fourth the length of peduncle, armed with 3 long, apical spines. Telson a little longer than broad; apical margin with very tiny notch; apical lobes with 8 unequal spines each.

TYPE-LOCALITY.—A driven well, 80 feet deep, near Three Forks, Gallatin County, Montana. The exact location of this well was not specified by the collector, therefore it is impossible to determine the geological formation in which it occurs. Three Forks is situated in the Northern Rocky Mountains and the area surrounding the town is underlain by both sedimentary rocks of Early Paleozoic age and more recent deposits of Tertiary and Quaternary age.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality. The type-series contained four females, ranging in size from 6.0 to 6.5 mm. All four specimens had setose brood plates and were apparently sexually mature.

ETYMOLOGY.—The specific name is from the Latin, meaning "of a well."

4. *Stygobromus oregonensis*, new species

FIGURES 6, 7

MATERIAL EXAMINED.—OREGON. Douglas Co.: small cave near Roseburg, holotype female (USNM 142798) and 1 paratype (JRH), Jim Riggs, April (?) 1967.

DIAGNOSIS.—A relatively large cavernicolous species easily distinguished from other species of the *hubbsi* group by numerous long, stiff setae and slender spines on peduncular segments 4 and 5 of antenna 2; proportionately large propod of gnathopod 1 which has a very long, heavily spined palm; convex palm of gnathopodal propod 2 with double row of 16 spine teeth; doubly and triply inserted superior medial setae of the gnathopodal propods; convex posterior margins of the bases of pereopods 5–7; midlateral position of the posterior marginal setae of pleonal plates 2 and 3; small, subacute posterior corners of the pleonal plates; and comparatively large ramus of uropod 3 which has 5 rather long spines. Largest female, 11.0 mm; male unknown.

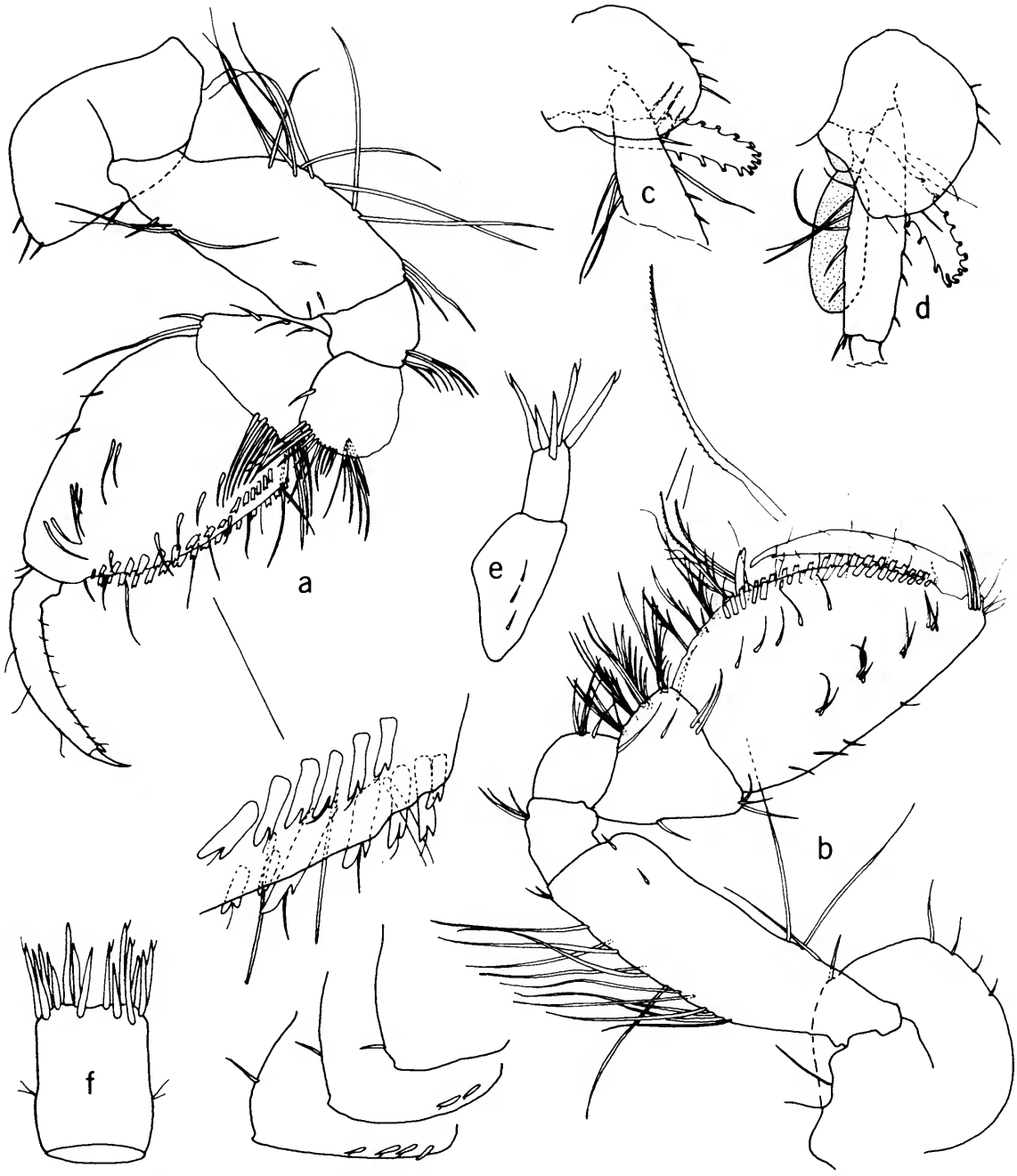

FIGURE 6.—*Stygobromus oregonensis*, new species, female paratype (9.5 mm), small cave near Roseburg, Oregon: *a,b*, gnathopods 1,2; *c,d*, pereopods 3,4 (in part); *e*, uropod 3; *f*, telson; *g*, pleonal plates.

DESCRIPTION.—Antenna 1, 45 percent as long as body, 40 to 45 percent longer than antenna 2, primary flagellum with up to 22 segments. Antenna 2, peduncular segments 4 and 5 with several prominent clusters of long spines and stiff setae; flagellum with 8 segments. Mandibles similar to those of *S. hubbsi*. Maxilla 1: inner plate with 8 or 9 apical, plumose setae; palp with 5 spines and 2 setae apically. Maxilla 2, inner plate with oblique row of 8 plumose setae. Maxilliped about like *S. hubbsi*, except outer plate with 1 or 2 bladelike spines subapically. Lower lip with tiny (vestigial) inner lobes.

Gnathopod 1: Propod much broader proximally than distally; palm long, slightly convex, armed with double row of about 14 or 15 spine teeth; posterior angle with 1 long seta but without prominent defining spines; posterior margin very short, without setae; superior medial setae mostly doubly inserted, inferior medial setae singly inserted; dactyl

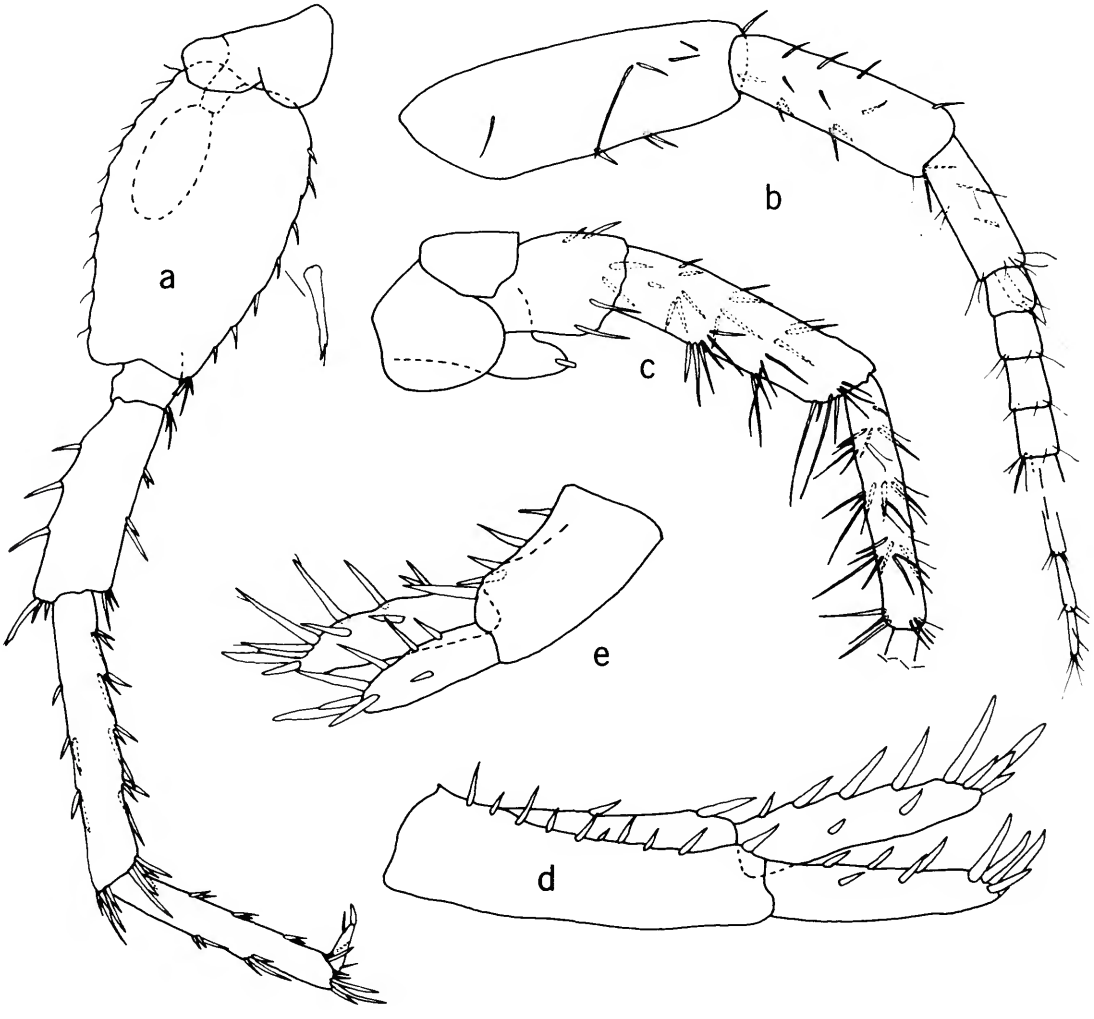

FIGURE 7.—*Stygobromus oregonensis*, new species, female paratype (9.5 mm): *a*, pereopod 6; *b,c*, antennae 1,2; *d,e*, uropods 1,2.

curved, nail rather long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopod 2: propod slightly larger than 1st propod; palm convex, armed with double row of 16 spine teeth; posterior angle defined by 1 long spine tooth and 2 sets of long setae on outside, 3 shorter spine teeth on inside; posterior margin with 3 sets of setae; superior medial setae mostly singly and doubly inserted, inferior medial setae singly inserted. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, with 5 marginal setae each; coxal plate of pereopod 4 slightly broader than long, with 5 marginal setae. Pereopods 6 and 7 about equal in length, about 40 percent as long as body, 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 broadest proximally; posterior margins convex, with about 10 setae each; distoposterior lobes rounded, distinct. Dactyls of pereopods about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins slightly convex, with 1 seta each; posterior corners small, distinct, subacute; ventral margins of plates 2 and 3 with 2 and 4 spines, respectively. Uropod 1: inner ramus slightly longer than outer ramus, about two-thirds the length of peduncle, armed with 11 spines; outer ramus with 10 spines; peduncle with 13 spines. Uropod 2: inner ramus longer than outer ramus, about as long as peduncle, armed with 8 to 10 spines; outer ramus with 7 or 8 spines; peduncle with 5 spines. Uropod 3: ramus more than one-half the length of peduncle, armed with 5 unequal, apical spines. Telson a little longer than broad; apical margin with very tiny median notch and 15 or 16 spines.

TYPE-LOCALITY.—A small cave near Roseburg, Douglas County, Oregon. This cave is a crevice in Lower Eocene basalt with water sometimes found 30 feet below the entrance (R. Altig, in litt.).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality in the Coastal Range of southwestern Oregon. The type-specimens, two females measuring 9.5 mm and 11.0 mm, had setose brood plates and appeared to be sexually mature.

5. *Stygobromus elliotti*, new species

FIGURES 8, 9

MATERIAL EXAMINED.—WASHINGTON. Skamania Co.: Deadhorse Cave, holotype female (USNM 142779) and 8 paratypes (JRH), W. R. Elliott et al., 22 Aug. 1972; 6 paratypes (BBM), F. G. Howarth and Lynn M. Ferguson, 14 Aug. 1972; other collections (in BBM) from Skamania Co. as follows: Upper Falls Creek Cave system, 1 female, F. G. Howarth and L. Nieuwenhuis, 24 Aug. 1972; Little Red River Cave, 7 females, Howarth and Nieuwenhuis, 26 Aug. 1972.

DIAGNOSIS.—A comparatively large cavernicolous species easily differentiated from other members of the *hubbsi* group and distinguished by the long and heavily setose palpal segment 2 of the maxilliped; 8 serrate spines on apex of inner plate of maxilla 1; broadly rounded outer lobes and short lateral processes of the lower lip; proportionately small gnathopodal propod of the male; typically uneven posterior margins of the bases of pereopods 5–7; presence or absence of sternal blisters; and frequently unnotched apical margin of the telson. Largest females, 9.5 mm; largest males, 7.0 mm.

FEMALE.—Antenna 1: 55 to 60 percent as long as body, 55 to 60 percent longer than antenna 2; primary flagellum with 19 to 23 segments. Antenna 2: peduncular segment 3 with 7 slender spines, peduncular segments 4 and 5 with numerous slender spines and long setae marginally; flagellum with 7 or 8 segments. Mandibles subequal; spine row with 9 spines; palpal segment 2 with 15 setae on inner margin, segment 3 with row of short setae on inner margin and 5 long setae apically. Maxilla 1: inner plate with 9 apical, plumose setae; outer plate with 8 apical, serrate spines; palp with 7 spines and 6 setae apically and subapically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin, numerous short setae on apex; outer plate with numerous long, apical setae. Maxilliped: inner plate with 3 bladelike spines, 3 plumose spines and 3 setae apically and 5 plumose spines on inner margin; outer plate with 2 bladelike spines and 9 setae apically and double row of short setae on inner margin; segment 2 of palp with numerous long setae on inner margin. Lower lip with broad outer lobes and bluntly rounded lateral processes, inner lobes lacking.

Gnathopodal Propod 1: Palm long, oblique,

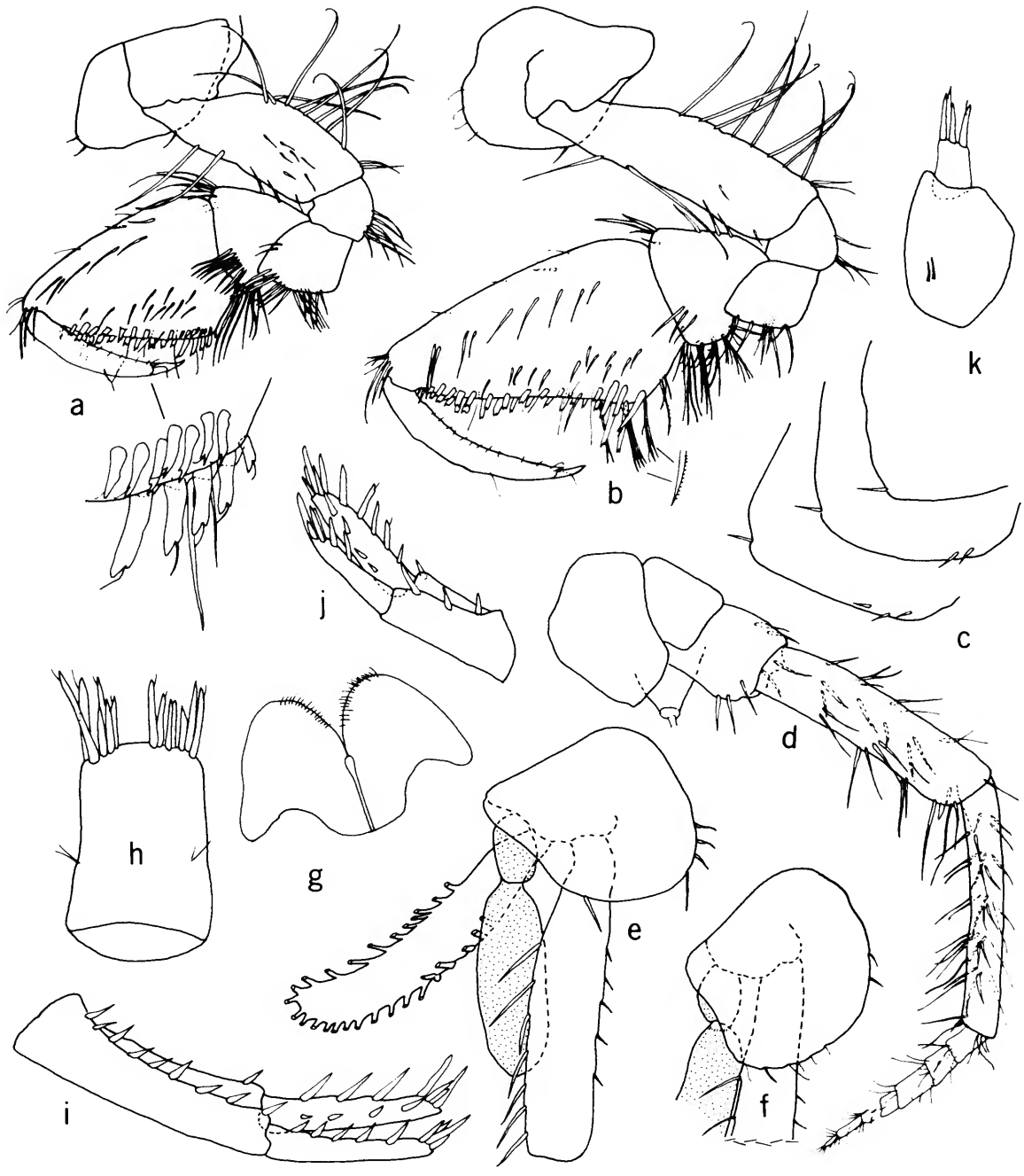

FIGURE 8.—*Stygobromus elliotti*, new species, female paratype (9.0 mm), Deadhorse Cave, Washington: *a,b*, gnathopods 1,2; *c*, pleonal plates; *d*, antenna 2; *e,f*, pereopods 3,4 (in part); *g*, lower lip; *h*, telson; *i,j,k*, uropods 1,2,3.

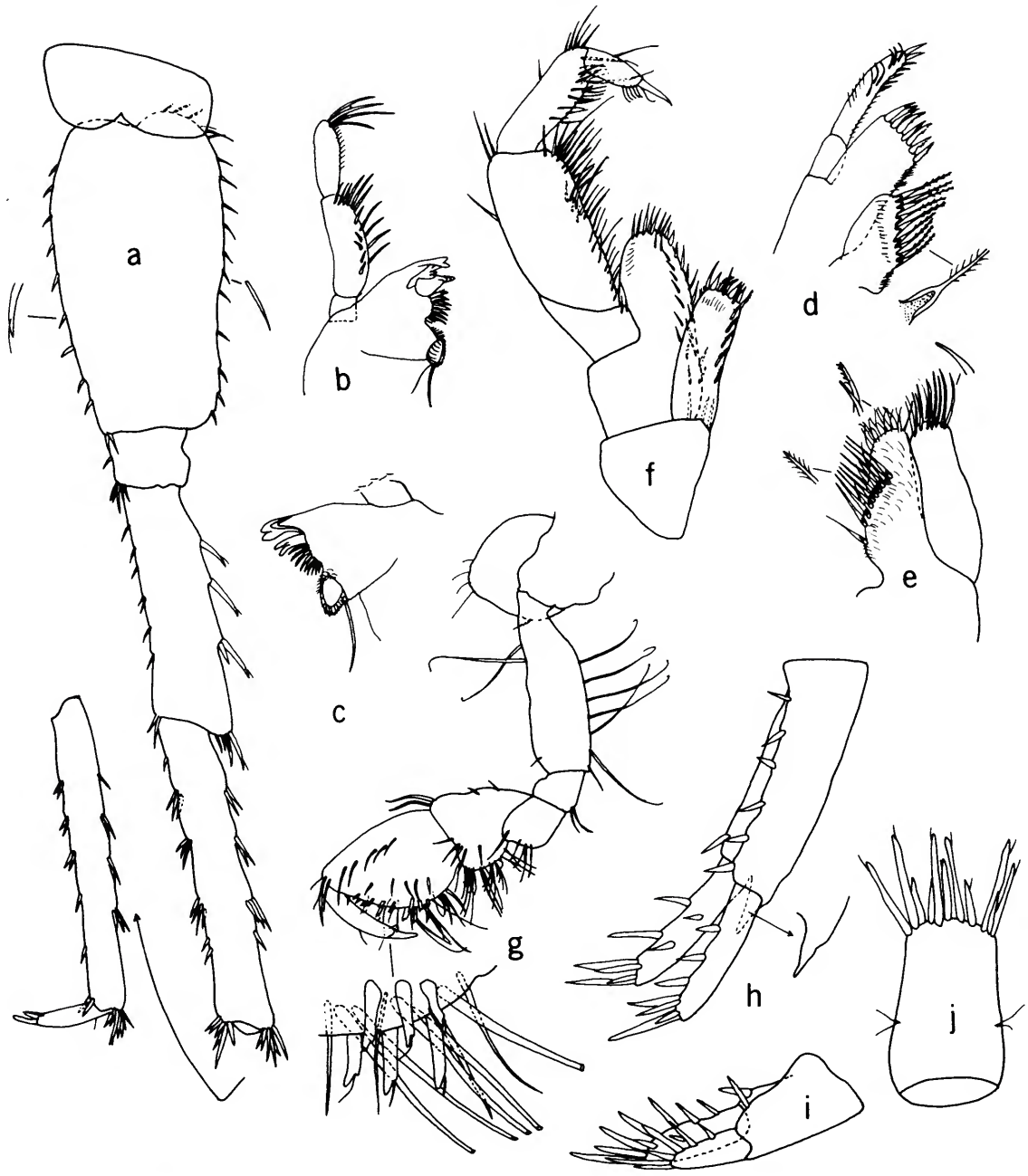

FIGURE 9.—*Stygobromus elliotti*, new species. Female paratype (9.0 mm): *a*, pereopod 6; *b*, left mandible; *c*, dentate part of right mandible; *d,e*, maxillae 1,2; *f*, maxilliped. Male paratype (7.0 mm), Deadhorse Cave: *g*, gnathopod 2; *h,i*, uropods 1,2; *j*, telson.

straight, armed with double row of about 8 spine teeth; posterior angle with 5 spine teeth and 2 setae on outside, 7 spine teeth on inside; posterior margin rather short, without setae; medial setae singly inserted; dactyl not reaching to defining angle. Coxal plate of gnathopod 1 longer than broad, with 2 short, marginal setae. Gnathopodal propod 2: palm long, oblique, slightly concave, armed with double row of 12 or 13 spine teeth; posterior angle with 2 long spine teeth and 2 sets of long setae on outside, 3 long spine teeth on inside; posterior margin with 1 set of 3 setae; medial setae mostly singly inserted; dactyl rather long and curved, nail short. Coxal plates of gnathopod 2 and pereopods 3 and 4 about as broad as long, plates 2 and 3 with 5 marginal setae each, plate 4 with 8 marginal setae. Pereopod 6 a little longer than pereopod 7, 50 to 55 percent as long as body, about 20 percent longer than pereopod 5. Bases of pereopods 5–7 not much broader proximally than distally; posterior margins nearly straight or slightly irregular, with 12 setae on pereopod 7 and 16 setae each on pereopods 5 and 6; distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6. Small sternal blisters sometimes present ventrally on pereonites 2–7, more obvious on pereonites 5–7. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins nearly straight to slightly convex; posterior corners poorly developed, rounded; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uropod 1: inner ramus slightly longer than outer ramus, about two-thirds the length of peduncle, armed with 10 to 12 spines; outer ramus with 10 spines; peduncle with 10 or 11 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 12 to 16 spines; outer ramus with 6 or 7 spines; peduncle with 4 spines. Uropod 3: ramus about 40 percent as long as peduncle, armed with 3 to 5 apical spines. Telson longer than broad; apical margin often entire, sometimes slightly emarginate, armed with 12 to 16 spines.

MALE.—Differing from the female as follows: Gnathopodal propod 1 with fewer spine teeth on palm. Gnathopodal propod 2 proportionately much smaller, not much larger than 1st propod; palm not very oblique, slightly convex, armed with double row of 4 spine teeth; posterior angle with 3 long spine teeth and several long setae on outside, 3 shorter spine teeth on inside; posterior margin with 5 or 6 long setae. Pereopods 5–7 with few less spines. Uropod 1: inner ramus slightly longer than outer ramus, about two-thirds the length of peduncle, armed with 8 spines; outer ramus with 7 spines; peduncle with 7 spines and distal process. Uropod 2: inner ramus longer than outer ramus, equal in length to peduncle, armed with 10 spines; outer ramus with 5 spines; peduncle with 2 spines. Telson with 10 or 11 apical spines.

VARIATION.—Slight variation in the structure and number of spines of the telson, the number of spines on uropod 3 and the presence or absence of sternal blisters was noted. A few females in the samples from both Deadhorse and Little Red River caves had a tiny notch in the apical margin of the telson. Most of the females from Little Red River Cave had 3 apical spines on the ramus of uropod 3 and 14 to 16 apical spines on the telson, while, in comparison, most of the females from Deadhorse Cave had 4 or 5 apical spines on uropod 3 and 12 to 14 apical spines on the telson. The presence or absence of sternal blisters was variable in each population.

TYPE-LOCALITY.—Deadhorse Cave, 7 miles northwest of Trout Lake, Skamania County, Washington. The type-locality is a relatively large, complex lava cave formed in the Mount Adams pahoehoe lava flow. The type-series was collected from a stream and stream pools (water temperature = 5°C) in association with an undescribed species of troglobitic isopod (*Asellus*) and eyed planarians of the family Dendrocoelidae.

DISTRIBUTION AND ECOLOGY.—This species is recorded from three lava caves in Skamania County. The specimens from Upper Falls Creek and Little Red River caves were collected from streams and pools (water temperature = 5°C). Upper Falls Creek Cave, located about 15 miles south-southwest of Deadhorse Cave, is also developed in pahoehoe lava of the Mount Adams flow. Little Red River Cave is located about 25 miles west-northwest of Deadhorse Cave and is developed in pahoehoe lava of the Mount St. Helens flow. Some of the females, ranging in size from 5.0 to 9.5 mm, had setose brood plates, and one female (8.0 mm) from Little Red River Cave was ovigerous with 12 embryos in the brood pouch. Out of the 23 specimens studied, only two were males.

ETYMOLOGY.—It is a pleasure to name this species in honor of its collector, William R. Elliott.

6. *Stygobromus grahami*, new species

FIGURES 10, 11

MATERIAL EXAMINED.—CALIFORNIA. Calaveras Co.: Cave of the Catacombs, holotype female (USNM 142781) and 17 paratypes (USNM 142782), R. E. Graham, 22 Aug. 1963; Sink Cave, 5 paratypes (JRH), P. Hara, 7 June 1971; Cave City Cave, 1 paratype (USNM 142783), collector unknown, 7 Feb. 1954; Cave of the Quills, 10 paratypes (JRH), R. E. Graham, 14 May 1960; Shaws Cave, 2 collections of paratypes (JRH), R. E. Graham, 15 Aug. 1962 and 21 Aug. 1963; Amador Co.: Soldier Creek Cave, 2 paratypes (JRH), R. E. Graham, 3 Sept. 1961.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished from other species of the *hubbsi* group described above by 15 or 16 plumose setae on the apex of the inner plate of maxilla 1 and on the inner margin of the inner plate of maxilla 2; 12 or 13 apical spines on the inner plate of the maxilliped; row of forked spine teeth on the inside margin of the posterior angle of gnathopodal propod 1; proportionately large gnathopodal propod 2 of the female with distally concave palm (excepting *S. hubbsi*); deep coxal plates of gnathopod 2 and pereopods 3 and 4; more spines on the ventral margins of pleonal plates 2 and 3 (excepting *S. hubbsi*); and the presence or absence of sternal blisters (excepting *S. elliotti*). Largest females, 9.0 mm; largest males, 5.0 mm.

FEMALE.—Antenna 1: 60 to 65 percent as long as body, 40 to 55 percent longer than antenna 2; primary flagellum with 20 to 24 segments. Antenna 2: peduncular segments 4 and 5 with numerous slender spines and stiff setae marginally; flagellum with 8 or 9 segments. Mandibles subequal; spine row with 10 or 11 spines; palpal segment 2 with 9 long setae on inner margin; palpal segment 3 with row of very short setae on inner margin, 5 long setae on apex. Maxilla 1: inner plate with 15 or 16 plumose setae apically; palp with 7 small spines and 4 or 5 setae apically and subapically. Maxilla 2: inner plate with 7 bladelike (some serrate) spines, 5 or 6 plumose spines and 3 or 4 setae apically and row of plumose spines (or stiff setae) on inner margin; outer plate with 1 or 2 bladelike spines and 7 or 8 setae apically. Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm oblique, convex, armed with double row of 7 or 8 spine teeth; posterior angle with 4 spine teeth on outside, 6 forked spine teeth on inside; posterior margin with 1 short seta submarginally just below defining angle; medial setae mostly singly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopodal propod 2 up to 3 times size of 1st propod; palm long, oblique, convex proximally, concave distally, armed with double row of 9 spine teeth plus 4 additional spine teeth on outside; posterior angle with 1 long spine tooth and several setae on outside, 2 shorter spine teeth on inside; posterior margin short, less than one-half the length of palm, with short row of long setae just below defining angle; inferior medial setae singly inserted, superior medial setae singly and triply inserted; dactyl long and curved, nail short. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 8 or 9 marginal setae each. Coxal plate of pereopod 4 rather deep, about half the length of segment 2, about as broad as long, expanded distally, with 13 marginal setae. Pereopod 6 a little longer than pereopod 7, 55 to 60 percent as long as body, 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 broader proximally than distally; posterior margins slightly convex; distoposterior lobes poorly developed, bluntly rounded. Dactyls of pereopods 6 and 7 relatively short, about one-fourth the length of corresponding propods. Coxal gills on pereopods 2–6. Small sternal blisters present or absent on pereonites 2–7. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins nearly straight, plate 1 with 2 setae, plates 2 and 3 with 1 seta each; posterior corners small, rounded; ventral margins of plate 2 with 5 spines, that of plate 3 with 4 spines. Uropod 1: inner ramus equal in length to outer ramus, about two-thirds the length of peduncle, armed with 11 spines; outer ramus with 8 or 9 spines; peduncle with 12 spines. Uropod 2: inner ramus longer than outer ramus, equal in length to peduncle, armed with 11 spines; outer ramus with 8 spines; peduncle with 5 spines. Uropod 3: ramus rather broad, about one-half the length of peduncle, with 4 or 5 apical spines. Telson

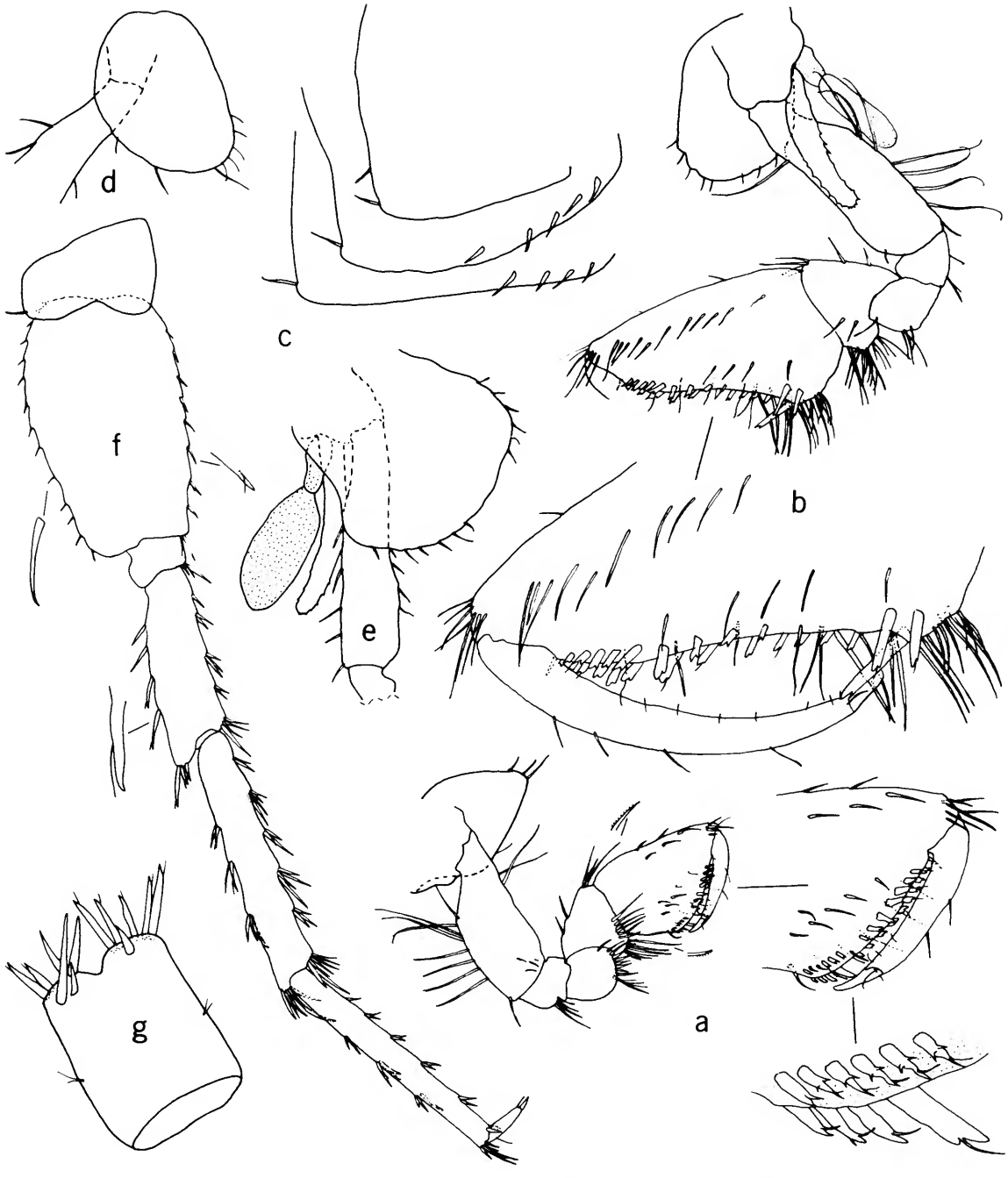

FIGURE 10.—*Stygobromus grahami*, new species, female paratype (8.0 mm), Cave of the Catacombs, California: *a,b*, gnathopods 1,2; *c*, pleonal plates; *d,e*, pereopods 3,4 (in part); *f*, pereopod 6; *g*, telson.

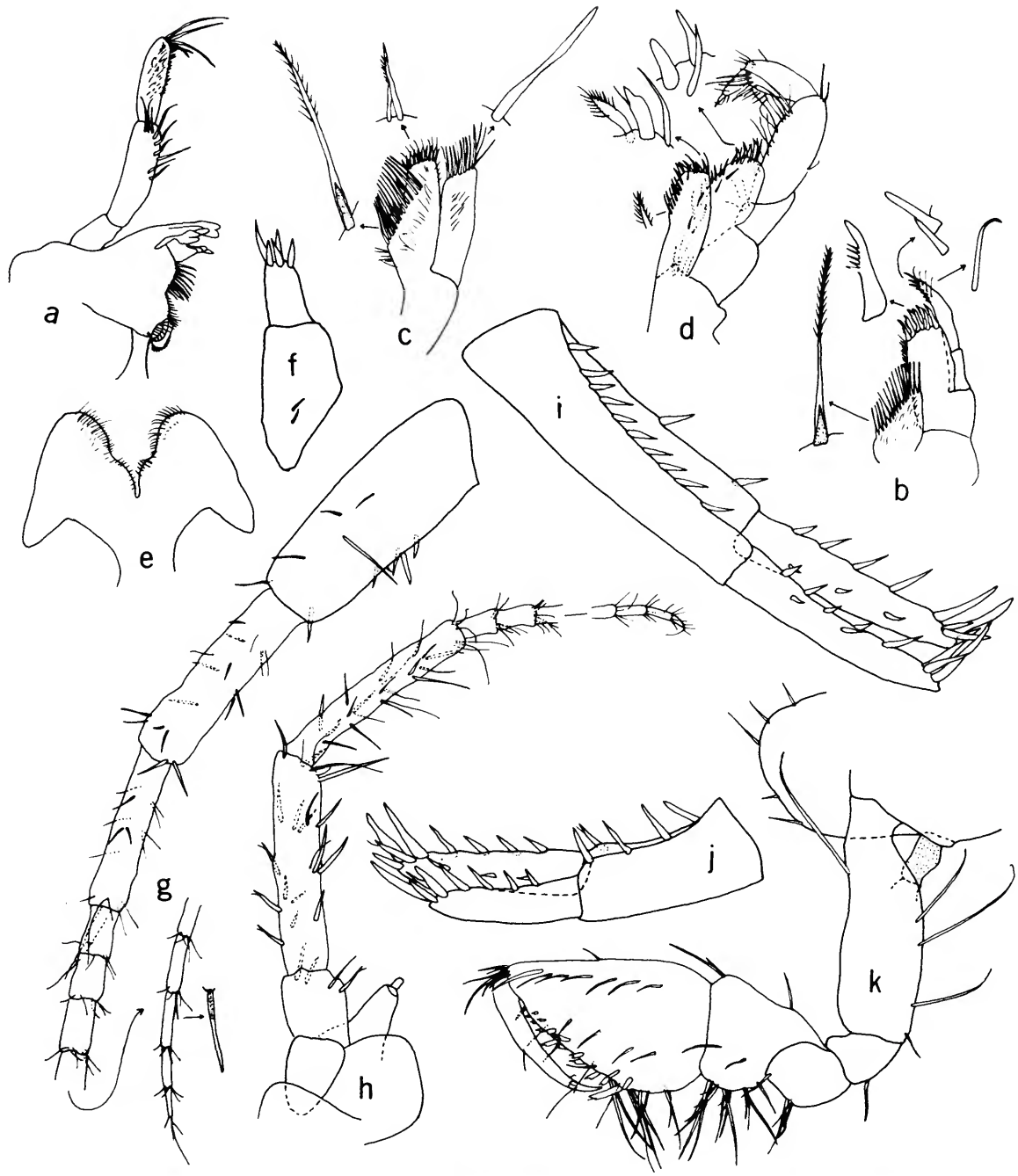

FIGURE 11.—*Stygobromus grahami*, new species. Female paratype (8.0 mm): *a*, left mandible; *b,c*, maxillae 1,2; *d*, maxilliped; *e*, lower lip; *f*, uropod 3; *g,h*, antennae 1,2; *i,j*, uropods 1,2. Male paratype (5.5 mm), Cave of the Catacombs: *k*, gnathopod 2.

nearly as broad as long; apical margin with small, V-shaped notch; apical lobes with 6 spines each.

MALE.—Differing from the female as follows: Antenna 1, 50 percent as long as body, 40 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2, flagellum with 7 segments. Gnathopod 1, palm of propod with double row of 5 spine teeth. Gnathopodal propod 2 less than one-half larger than 1st propod; palm oblique, nearly straight, armed with double row of 6 spine teeth plus 2 additional spine teeth on outside; posterior angle with 1 long spine tooth and 1 seta on outside, 1 shorter spine tooth on inside; posterior margin about two-thirds length of palm, with row of several setae just below defining angle and 1 set of 2 long setae about one-half the distance to base of propod; medial setae mostly singly inserted. Coxal plate of gnathopod 2 with 5 marginal setae. Pereopods 5–7 with few less spines; pereopod 6 a little longer than pereopod 7, 50 percent as long as body, 15 to 20 percent longer than pereopod 5. Sternal blisters not present in material examined. Uropods 1 and 2 with 6 or 7 fewer spines each. Peduncular process of uropod 1 not serrate distally.

VARIATION.—The size of gnathopodal propod 2 varies from 2 to 3 times the size of gnathopodal propod 1 in the female, apparently increasing allometrically in older (and larger) animals. Sternal blisters were not present on females collected from Shaws and Soldier Creek caves.

TYPE-LOCALITY.—Cave of the Catacombs, Mother Lode cave region, Calaveras County, California. A specific location, description, and map of this cave were published by Halliday (1962). The type-series was collected from a lake of fluctuating water in August 1963.

DISTRIBUTION AND ECOLOGY.—This species is known from five caves in central Calaveras County and one cave about 16 miles to the north in Amador County. All of these caves are formed in Middle Paleozoic limestones or marble of the Calaveras formation and are situated along tributaries draining west to the San Joaquin River. According to R. E. Graham (in litt.), most of these caves are developed in isolated lenses of steeply dipping or near vertically bedded limestone and the amount of cave interconnectivity is generally very low.

Most of the animals were found in pools or "lakes," some of which fluctuate seasonally or with precipitation. Out of 53 specimens studied, 43 were females, 3 were males, and 15 were newly hatched young (about 1.5 mm long). Samples were available from the months of February, May, June, August, and September, and all but the February sample (1 specimen) contained sexually mature females with setose brood plates. The May sample from Cave of the Quills contained 1 female with 8 newly hatched young in the brood pouch and an August sample from the Cave of the Catacombs contained 7 free, newly hatched young. These data indicate that *S. grahami* reproduces at least during the spring and summer.

ETYMOLOGY.—It is a pleasure to name this species in honor of Dr. Richard E. Graham, a pioneer in the biological study of California caves, who collected most of the specimens of this species and furnished valuable observations on its ecology.

7. *Stygobromus gradyi*, new species

FIGURES 12, 13

MATERIAL EXAMINED.—CALIFORNIA. Tuolumne Co.: Crystal Palace Cave, holotype female (USNM 142780) and 6 paratypes (JRH), Mark Grady, 15 Aug. 1968.

DIAGNOSIS.—A medium-sized cavernicolous species closely related to *S. grahami* but differing from that species by being smaller at sexual maturity; lacking inner lobes on the lower lip; proportionately smaller gnathopodal propod 2 of female with shorter and slightly convex palm; fewer spines on ventral margins of pleonal plates 2 and 3; and distally serrate peduncular process of male uropod 1. Largest females, 7.0 mm; largest males, 4.5 mm.

FEMALE.—Antenna 1: 50 percent as long as body, about 55 percent longer than antenna 2; primary flagellum with 14 to 17 segments. Antenna 2: peduncular segments similar to *S. grahami;* flagellum with 6 or 7 segments. Mandibles similar to *S. grahami* except for few less spines in spine row. Maxilla 1: inner plate with 12 or 13 plumose setae apically; palp with 5 spines and 3 or 4 setae apically and subapically. Maxilla 2: inner plate with oblique row of 14 plumose setae on inner margin. Maxilliped like that of *S. grahami.* Lower lip without inner lobes.

Gnathopodal Propod 1: Palm not very oblique, slightly concave, armed with double row of 5 spine

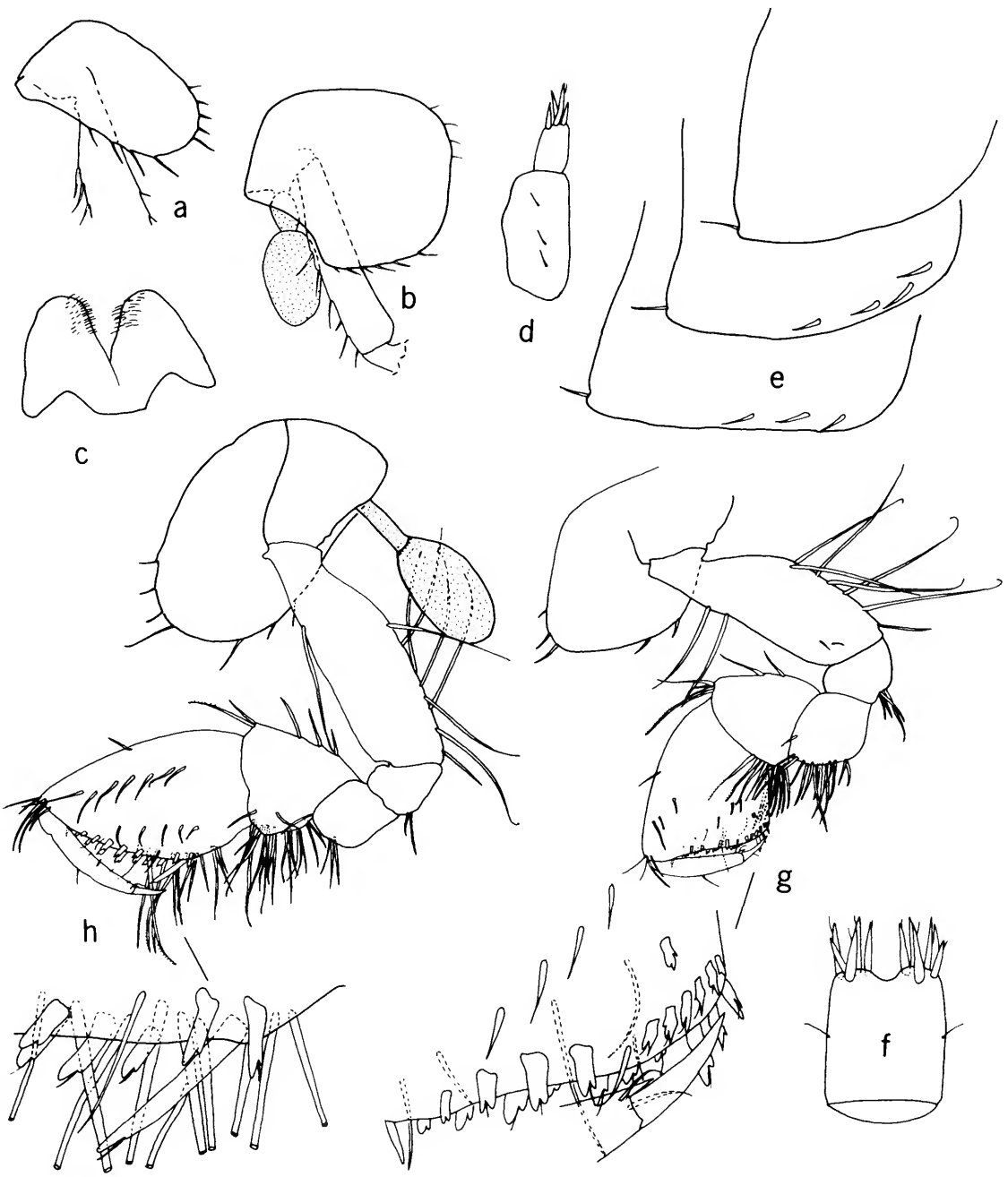

FIGURE 12.—*Stygobromus gradyi*, new species, female paratype (7.0 mm), Crystal Palace Cave, California: *a,b*, pereopods 3,4 (in part); *c*, lower lip; *d*, uropod 3; *e*, pleonal plates; *f*, telson; *g,h*, gnathopods 1,2.

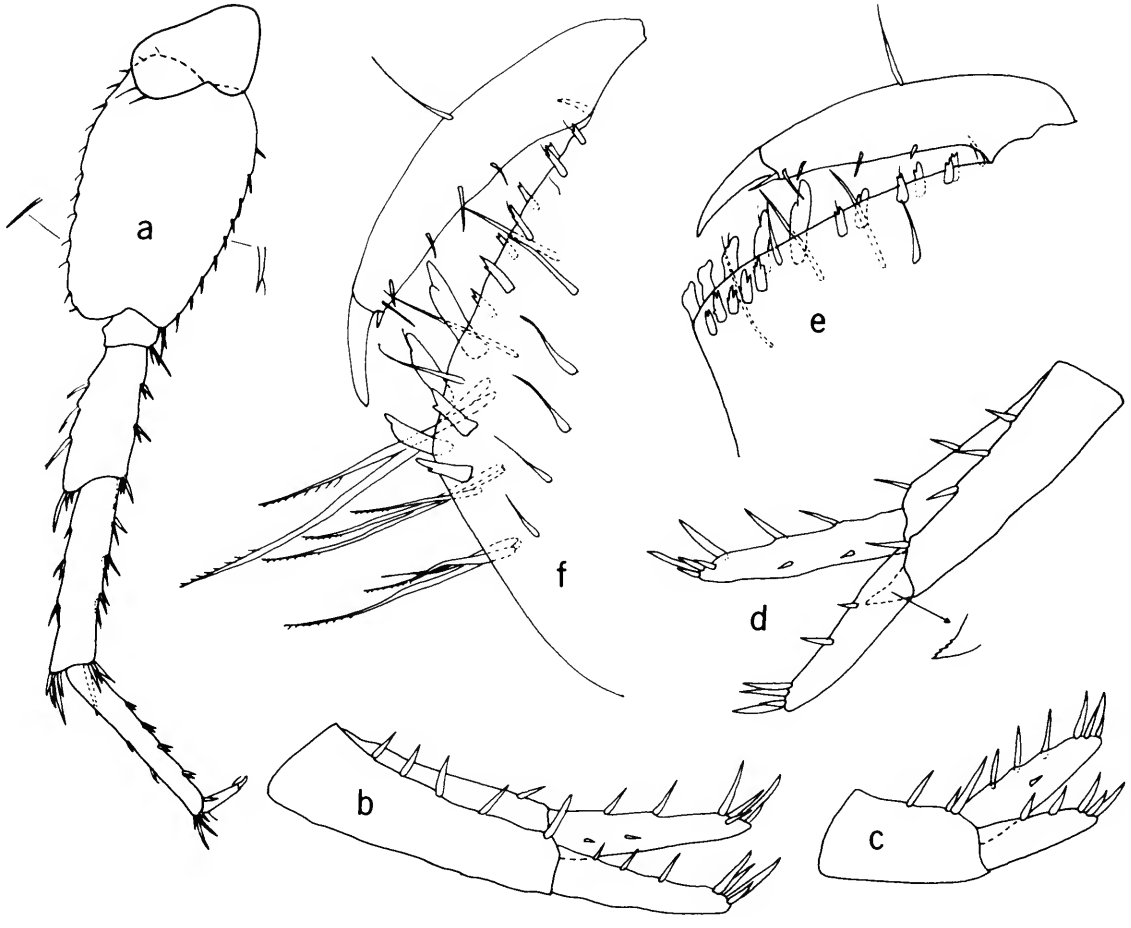

FIGURE 13.—*Stygobromus gradyi*, new species. Female paratype (7.0 mm): *a*, pereopod 6; *b,c*, uropods 1,2. Male paratype (4.5 mm), Crystal Palace Cave: *d* uropod 1; *e,f*, palms of gnathopodal propods 1,2.

teeth plus 2 additional spine teeth on outside; posterior angle with 3 long spine teeth on outside, 6 forked spine teeth on inside; posterior margin without setae; medial setae few in number, mostly singly inserted; dactyl nail long. Coxal plate of gnathopod 1 rather deep, longer than broad, with 5 marginal setae. Gnathopodal propod 2 a little longer than 1st propod; palm oblique, slightly convex, armed with double row of 5 spine teeth plus 2 additional spine teeth on outside; posterior angle with 1 long spine tooth and 6 setae on outside, 2 shorter spine teeth on inside; posterior margin with 1 set of 3 setae; medial setae singly inserted; dactyl nail rather long. Coxal plates of gnathopod 2 and pereopod 3 deep, nearly twice as long as broad, with 7 marginal setae on plate 2 and 9 on plate 3. Coxal plate of pereopod 4 deep, expanded distally (as in *S. grahami*), with 10 marginal setae. Pereopod 6 a little longer than pereopod 7, 45 to 50 percent as long as body, 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 broader proximally than distally; posterior margins slightly convex; distoposterior lobes distinct, rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6.

Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins of 2 and 3 slightly produced distally, that of 1 nearly straight; posterior corners small, distinct, rounded; ventral margin of plate 2 with 4 spines, that of plate 3 with 3 spines. Uropod 1: inner ramus a little longer than outer ramus, about two-thirds the length of peduncle, armed with 8 spines; outer ramus with 6 or 7 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, equal in length to peduncle, armed with 7 or 8 spines; outer ramus with 5 or 6 spines; peduncle with 3 spines. Uropod 3: ramus about 40 percent as long as peduncle, with 4 or 5 apical spines. Telson slightly longer than broad; apical margin with shallow notch; apical lobes with 5 or 6 spines per lobe.

MALE.—Differing from the female slightly in the structure of the gnathopodal propods and uropod 1 as follows: Gnathopodal propod 1: palm nearly straight, armed with double row of 3 small and 1 large spine teeth; posterior angle with 3 spine teeth on outside, 5 forked spine teeth on inside. Gnathopodal propod 2: palm not as oblique, nearly straight, armed with unequal double row of 4 small spine teeth plus 2 large spine teeth on outside; posterior angle with 1 spine tooth and 5 setae on outside, 2 spine teeth on inside. Peduncular process of uropod 1 with fine serrations on upper margin toward distal end.

TYPE-LOCALITY.—Crystal Palace Cave, about 10 miles east of Angels Camp, Tuolumne County, California. This cave is just north of the South Fork of the Stanislaus River and was described in detail by Halliday (1962). It is developed in steeply dipping marble or limestone of the Calaveras formation and contains two small streams. Crystal Palace Cave lies about 12 miles southeast of the cluster of caves in central Calaveras County which contain *S. grahami.*

DISTRIBUTION AND ECOLOGY.—This species is known only from five females and two males collected in August 1968 from intermittent stream pools in the upper section of Crystal Palace Cave. Two of the females (measuring 6.0 to 7.0 mm) had setose brood plates and were sexually mature.

ETYMOLOGY.—This species is named in honor of its collector, Mark Grady.

8. *Stygobromus harai,* new species

FIGURES 14, 15

MATERIAL EXAMINED.—CALIFORNIA. Tuolumne Co.: Pinnacle Point Cave, holotype female (USNM 142784) and 4 paratypes (JRH), P. Hara, 27 Nov. 1971; mine tunnel near Pinnacle Point Cave, 3 paratypes (USNM 142785), P. Hara, 27 Nov. 1971.

DIAGNOSIS.—A medium-sized cavernicolous species, closely related to *S. gradyi* and *S. grahami* but differing from these two species as follows: smaller size of sexually mature females; fewer apical spines on inner plate of maxilliped; inner margin of posterior angle of gnathopodal propod 1 with mostly unforked spine teeth; gnathopodal propod 2 of male proportionately a little larger than 2nd propod of female, with double row of 13 spine teeth on palm; coxal plates of gnathopod 2 and pereopods 3 and 4 not as deep; ramus of uropod 3 with 3 apical spines; and proportionately longer telson which is about one-third longer than broad. Largest females, 7.5 mm; largest males, 7.0 mm.

FEMALE.—Antenna 1: 40 to 45 percent as long as body, 40 to 45 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2: peduncular segments with fewer spines and setae than *S. grahami;* flagellum with 7 segments. Mandibles like those of *S. gradyi* (with fewer spines in spine row than *S. grahami*). Maxilla 1: inner plate with 10 or 11 plumose setae apically; palp with 4 spines and 2 setae apically and subapically. Maxilla 2: inner plate with oblique row of 13 plumose setae on inner margin. Maxilliped: inner plate with 3 or 4 bladelike spines (some with small bristles), 5 plumose spines and 3 setae apically and row of plumose spines (or heavy setae) on inner margin; outer plate like that of *S. grahami.* Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm rather long, convex, armed with double row of 8 or 9 spine teeth; posterior angle with 6 spine teeth on outside, 7 smaller spine teeth on inside; posterior margin with 1 seta submarginally just below defining angle; medial setae singly inserted. Coxal plate of gnathopod 1 longer than broad, with 4 marginal setae. Gnathopodal propod 2 nearly twice the size of 1st propod; palm long, oblique, convex distally, concave proximally, armed with double row of 10 spine teeth plus 3 additional spine teeth on outside; posterior angle with 1 long, curved spine tooth and 5

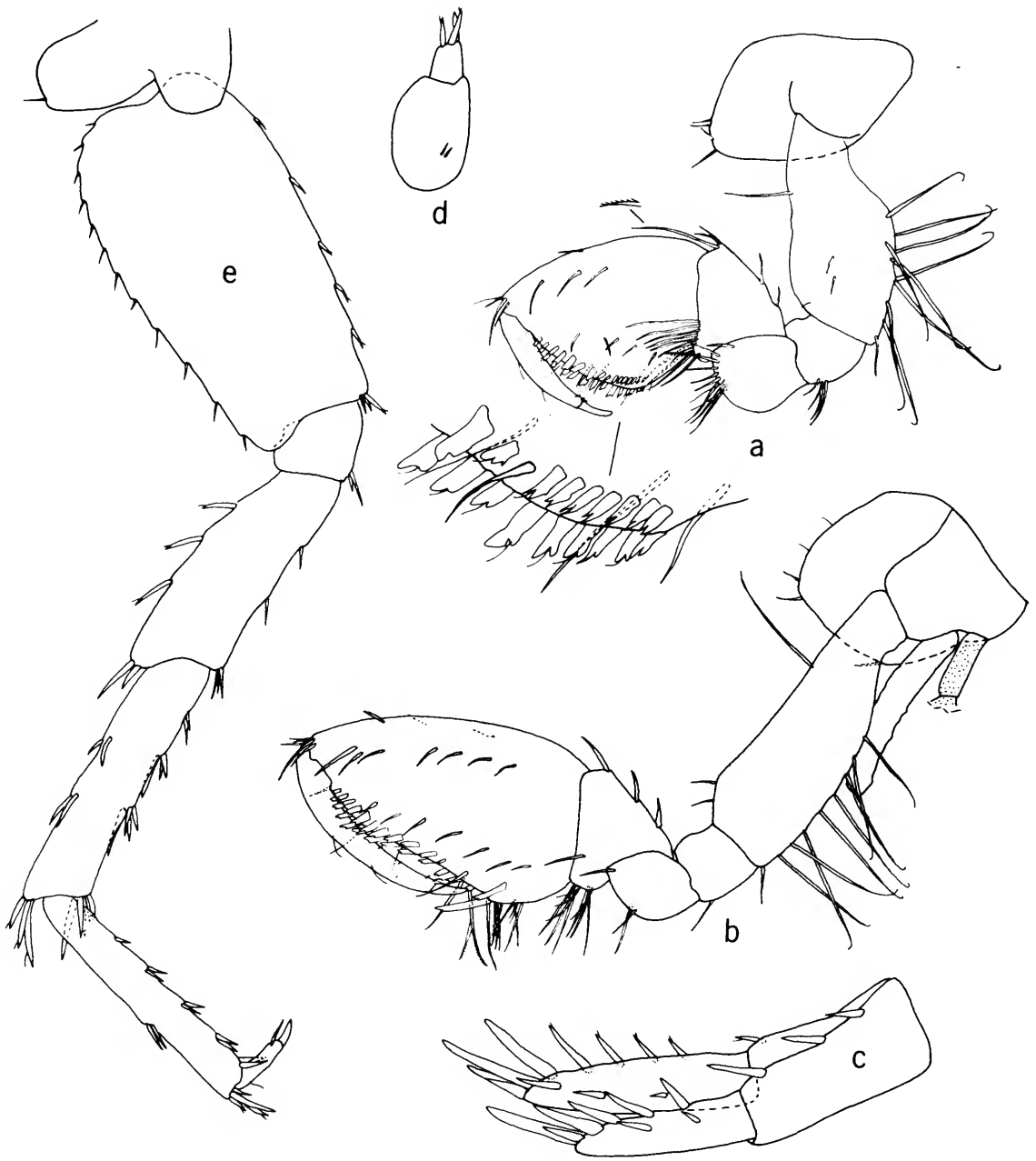

FIGURE 14.—*Stygobromus harai*, new species, female paratype (7.5 mm), Pinnacle Point Cave, California: *a,b*, gnathopods 1,2; *c,d*, uropods 2,3; *e*, pereopod 6.

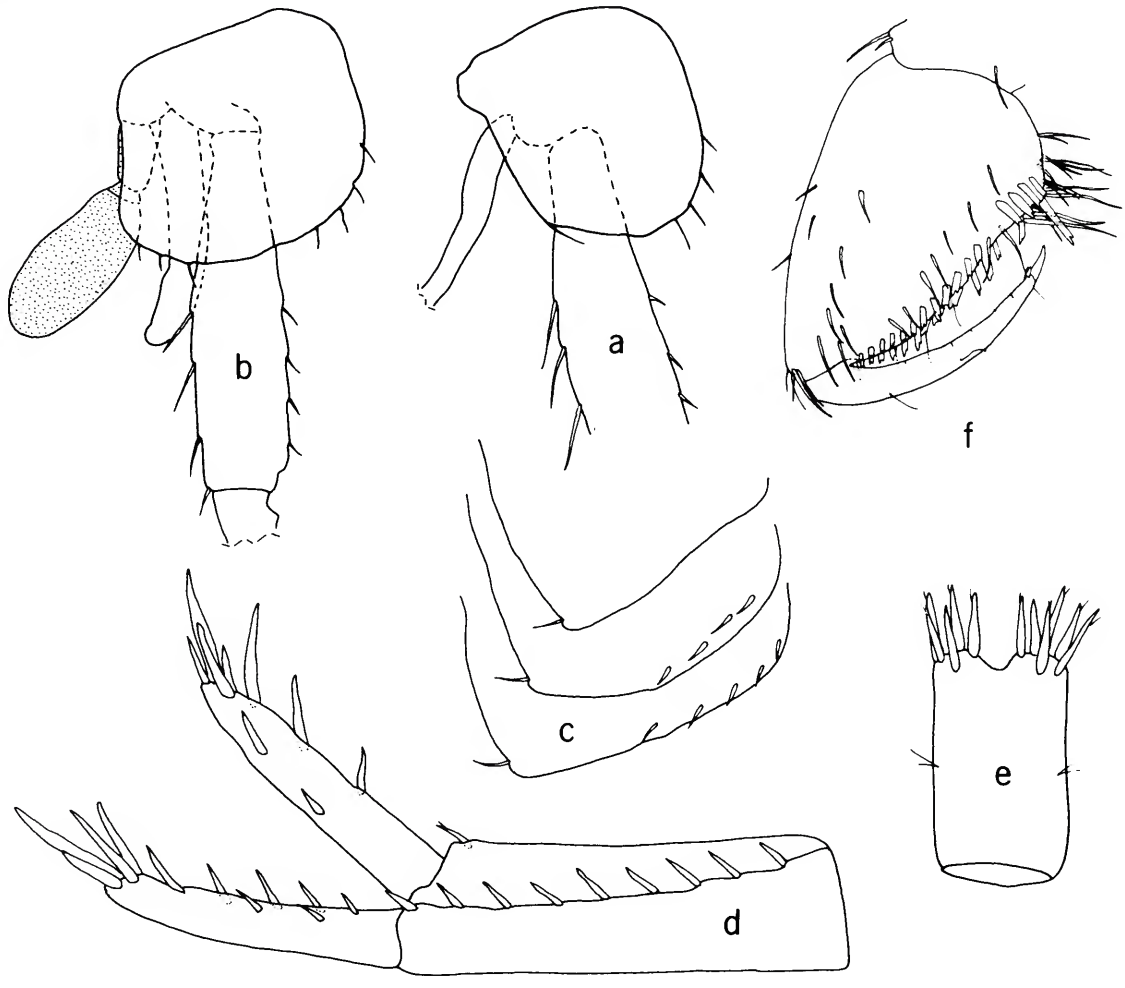

FIGURE 15.—*Stygobromus harai*, new species. Female paratype (7.5 mm): *a,b*, pereopods 3,4 (in part); *c*, pleonal plates, *d*, uropod 1. Male paratype (7.0 mm), Pinnacle Point Cave: *e*, telson; *f*, gnathopodal propod 2 (same scale as female).

setae on outside, 1 shorter spine tooth on inside; posterior margin with 1 set of setae; medial setae mostly singly inserted; dactyl long, curved, nail not reaching to defining angle. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, with 5 marginal setae each; coxal plate of pereopod 4 about as broad as long, about one-third as long as segment 2, with 7 marginal setae. Pereopod 6 equal in length or slightly longer than pereopod 7, 40 to 50 percent as long as body, 30 to 35 percent longer than pereopod 5. Bases of pereopods 5–7 a little broader proximally than distally; posterior margins slightly convex; distoposterior lobes small, distinct, rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins slightly convex; posterior corners small, distinct, rounded; ventral margin of plate 2 with 4 spines, that of plate 3 with 5 spines. Uropod 1: inner and outer rami equal in length, about two-thirds the length of peduncle;

inner ramus with 8 or 9 spines; outer ramus with 9 or 10 spines; peduncle with 10 or 11 spines. Uropod 2: inner ramus about 20 percent longer than outer ramus and peduncle, armed with 10 or 11 spines; outer ramus with 8 or 9 spines; peduncle with 3 or 4 spines. Uropod 3: ramus about 40 percent as long as peduncle, with 3 apical spines. Telson subrectangular, about one-third longer than broad; apical margin with small notch; apical lobes with 5 or 6 spines each.

MALE.—Differing from the female in the structure of gnathopodal propod 2 and uropod 1 as follows: Gnathopodal propod 2 proportionately a little larger; palm with double row of 13 spine teeth; posterior angle with 1 long spine tooth and 5 setae on outside, 3 shorter spine teeth on inside; posterior margin with 2 sets of setae; dactyl nail rather short. Peduncular process of uropod 1 not finely serrate as in *S. gradyi*.

TYPE-LOCALITY.—Pinnacle Point Cave, about 10 miles east of Valecito, Tuolumne County, California. The type-locality is located about 5 miles east-southeast of Crystal Palace Cave and on the south side of the Stanislaus River. This cave, like many others in the Mother Lode cave region, is developed in marble or limestone of the Calaveras formation and was described by Halliday (1962). The type-series, consisting of three males and two females, was collected from a small lake in the cave.

DISTRIBUTION AND ECOLOGY.—This species is known from its type-locality and a nearby mine tunnel. The November collection from the mine tunnel contained one male and two females. One of these females (6.0 mm long) had two embryos in the brood pouch. A third embryo was found loose in the collecting vial. A single female (7.0 mm long) from the type-locality had setose brood plates but was not ovigerous.

ETYMOLOGY.—This species is named in honor of its collector, Paul Hara.

9. *Stygobromus wengerorum*, new species

FIGURES 16, 17

MATERIAL EXAMINED.—CALIFORNIA. Mariposa Co.: Bower Cave, holotype female (USNM 142821) and 5 paratypes (JRH), Steve Shimek, 16 May 1971; 3 paratypes (USNM 142822), Bill Kruse, 16–18 July 1971.

DIAGNOSIS.—A relatively large cavernicolous species, closely related to, but distinguished from, other cavernicolous species of the Mother Lode region by proportionately larger gnathopodal propods with more spine teeth on palms, and more spines on the ventral margins of the pleonal plates. Largest females, 10.0 mm; male unknown.

DESCRIPTION.—Antenna 1: 55 percent as long as body, 50 percent longer than antenna 2; primary flagellum with 18 to 20 segments. Antenna 2: peduncular segments 3 and 4 with numerous slender spines and long setae (as in *S. grahami*); flagellum with 7 segments. Mandibles subequal, about like *S. grahami* except for few less spines in spine row. Maxilla 1: inner plate with 11 plumose setae apically; palp with 6 spines and 2 setae apically and subapically. Maxilla 2: inner plate with oblique row of 14 or 15 plumose setae on inner margin. Maxilliped: inner plate with 5 bladelike spines (some with small bristles), 3 or 4 plumose spines and 3 setae apically and row of plumose spines or stiff setae on inner margin; outer plate like that of *S. grahami*. Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm long, oblique, slightly convex, armed with double row of 13 spine teeth; area of posterior angle long, with 7 spine teeth (some forked) and 2 setae on outside, 8 mostly forked spine teeth on inside; posterior margin short, about one-fourth the length of palm; medial setae singly inserted. Coxal plate of gnathopod 1 longer than broad, with 2 marginal setae. Gnathopodal propod 2 proportionately large, more than twice the size of 1st propod, 10 percent as long as body in larger females; palm very long, oblique, convex distally, concave proximally, armed with double row of 13 spine teeth, plus 4 additional spine teeth on outside; posterior angle with 1 long spine tooth and 5 setae on outside, 3 spine teeth on inside; posterior margin proportionately short, about one-third the length of palm, with 1 set of 5 setae just below defining angle and 1 short seta about half the distance to base; medial setae mostly singly inserted; dactyl long, curved, nail rather short. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, plate 2 with 6 marginal setae, plate 3 with 9 marginal setae; coxal plate of pereopod 4 about as long as broad, with 9 marginal setae. Pereopod 6 a little longer than pereopod 7, 55 to 60 percent as long as body, 20 percent longer than pereopod 5. Bases of pereopods 5–7 rather long, a

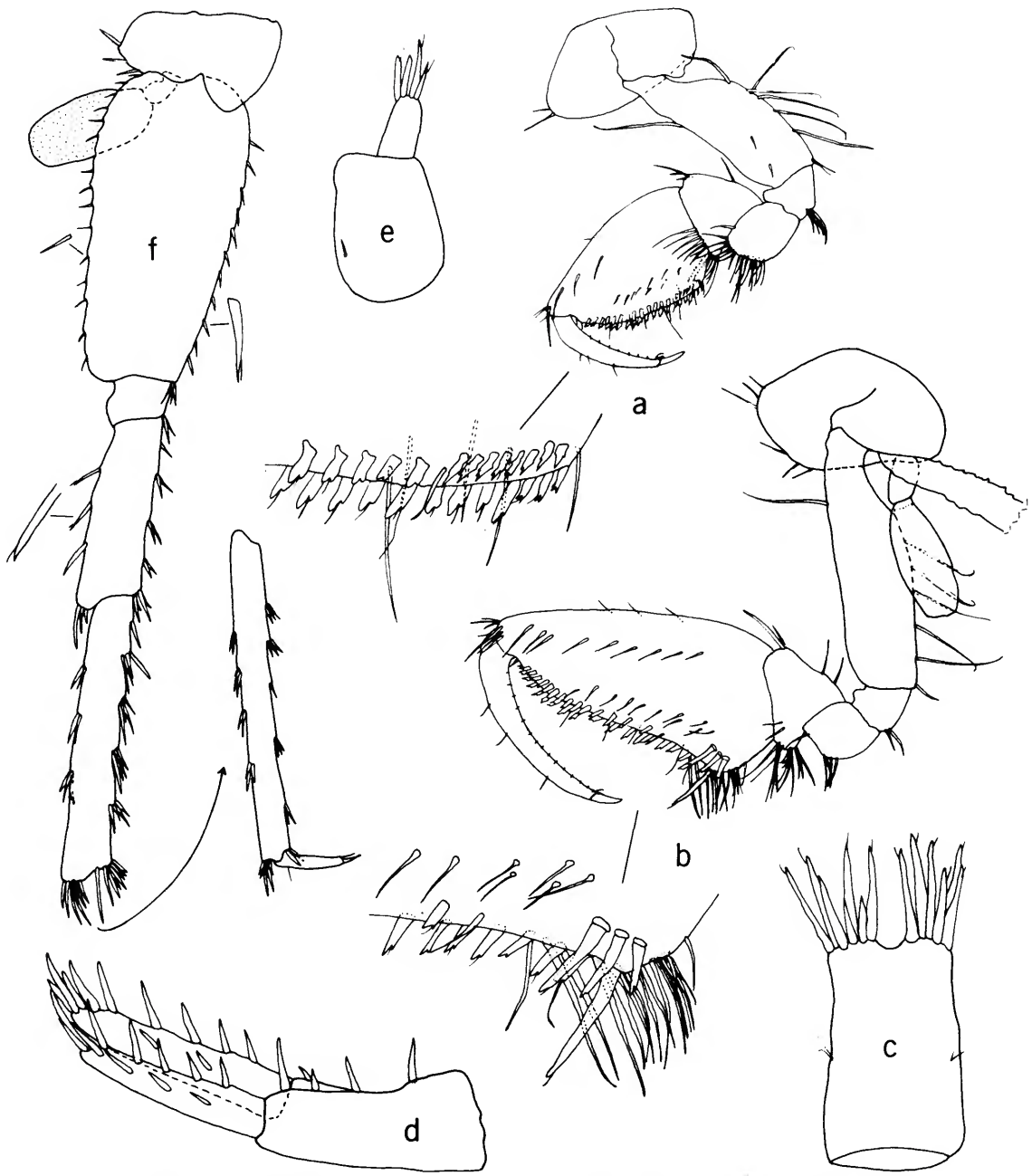

FIGURE 16.—*Stygobromus wengerorum*, new species, female paratype (9.0 mm), Bower Cave, California: *a,b*, gnathopods 1,2; *c*, telson; *d,e*, uropods 2,3; *f*, pereopod 6.

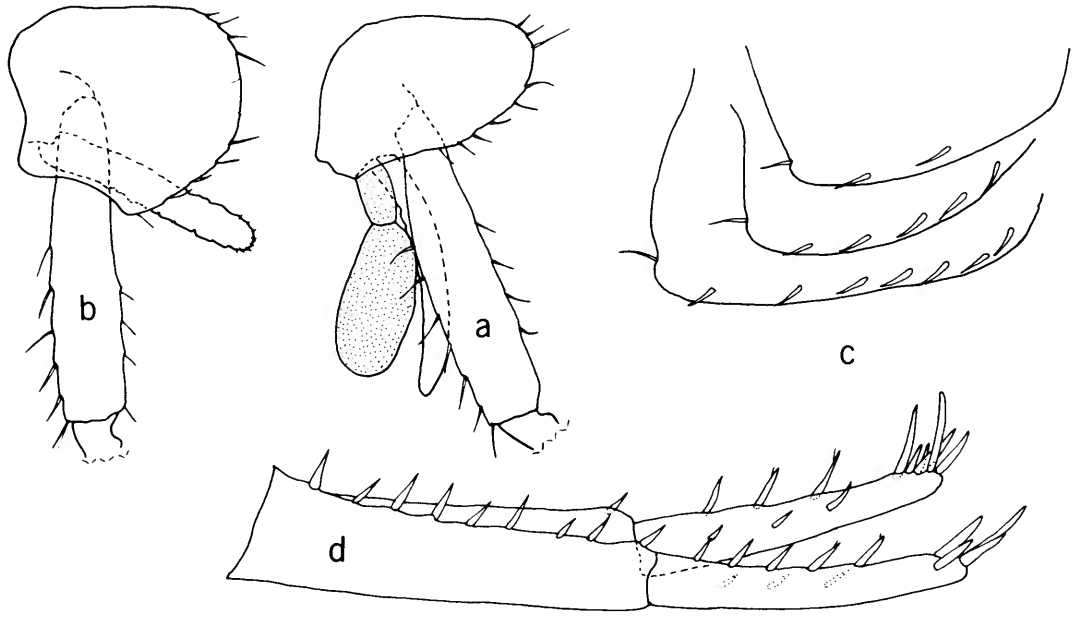

FIGURE 17.—*Stygobromus wengerorum*, new species, female paratype (9.0 mm): *a,b*, pereopods 3,4 (in part); *c*, pleonal plates; *d*, uropod 1.

little broader proximally than distally; distoposterior lobes rather small, distinct, bluntly rounded. Dactyls of pereopods 6 and 7, 25 to 30 percent as long as corresponding propods. Coxal gills present on pereopods 2–6. Sternal blisters present on pereonites 2–7. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins of plates 1 and 2 nearly straight, that of plate 3 convex; posterior corners distinct, rounded; ventral margin of plate 1 with 2 spines, plate 2 with 5 spines, plate 3 with 7 spines. Uropod 1: inner ramus subequal in length to outer ramus, about three-fourths the length of peduncle, armed with 12 or 13 spines; outer ramus with 12 or 13 spines; peduncle with 10 to 12 spines. Uropod 2: inner ramus a little longer than outer ramus, equal in length to peduncle, armed with 11 or 12 spines; outer ramus with 11 spines; peduncle with 5 spines. Uropod 3: ramus slightly less than half the length of rather broad peduncle, with 4 apical spines. Telson about one-third longer than broad; apical margin with shallow notch; apical lobes with 6 or 7 spines each.

TYPE-LOCALITY.—Bower Cave, about 8 miles east of Coulterville, Mariposa County, California. The type-locality is a deep, partly water-filled cave developed in vertically bedded marble or limestone of the Calaveras formation (Halliday, 1962). For the past several years this cave has been extensively explored by members of the Bower Cave Diving Group of Palo Alto, California. The May sample of six females was collected from a depth of 125 feet beneath the surface of the cave lake, where numerous specimens had been attracted by liver bait. The July sample of three females was collected at depths of 65 to 125 feet on the silt-covered floor of the main passage of the cave. The cave lake is also inhabited by an undescribed, troglobitic species of the planarian genus *Sphalloplana* (Roman Kenk, pers. comm.).

DISTRIBUTION AND ECOLOGY.—This species is known only from the type-locality, although according to Steve Shimek (in litt.), a small population of amphipods (probably *Stygobromus*) has been seen in nearby Centipede Cave. Three females with setose brood plates were observed in the May collection (size = 9.0 to 10.0 mm) and two were

observed in the July collection (size = 8.0 and 8.5 mm).

ETYMOLOGY.—At the request of the Bower Cave Diving Group, I have named this species in honor of the venerable Clara and George Wenger who have made significant contributions to the study of Bower Cave.

10. *Stygobromus mackenziei,* new species

FIGURES 18, 19

MATERIAL EXAMINED.—CALIFORNIA. Santa Cruz Co.: Empire Cave, holotype female (USNM 142791) and 5 paratypes (JRH), David McKenzie, 28 May 1967.

DIAGNOSIS.—A small cavernicolous species, only distantly related to the cave species of the Mother Lode region of California and distinguished by having 4 apical spines on the inner plate of the maxilliped, lightly spined palms of the gnathopodal propods (especially the 2nd), relatively large, deep coxal plates of the gnathopods and pereopods 3 and 4, proportionately broad bases of pereopods 5–7, lightly spined peduncles of uropods 1 and 2, and 8 apical spines on the telson. Largest females, 4.7 mm; largest male, 4.0 mm.

FEMALE.—Antenna 1, about 45 percent as long as body, about 30 percent longer than antenna 2; primary flagellum with 10 to 12 segments. Antenna 2, flagellum with 5 or 6 segments. Mandibles subequal; spine row with 5 or 6 spines; palpal segment 2 with 6 setae toward distal end; palpal segment 3 comparatively short, about two-thirds the length of segment 2, with row of short setae on inner margin and 4 long setae apically. Maxilla 1: inner plate with 8 or 9 plumose setae apically; outer plate with 5 slender spines and 3 setae apically to subapically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: apex of inner plate with 4 serrate spines and 4 or 5 stiff setae, inner margin with 2 or 3 plumose setae; outer plate with 1 bladelike spine and a number of stiff setae apically. Lower lip without inner lobes.

Gnathopodal Propod 1: Palm not very oblique, slightly convex, armed with double row of 4 or 5 small spine teeth; posterior angle with 2 large spine teeth and 1 long setae on outside, 2 shorter spine teeth on inside; posterior margin without setae; medial setae few in number, singly inserted. Coxal plate of gnathopod 1 nearly twice as long as broad, with 2 marginal setae. Gnathopodal propod 2 about one-fourth longer than 1st propod; palm oblique, slightly concave, armed with double row of 5 spine teeth plus 2 additional spine teeth on outside toward posterior angle; posterior angle with 1 long spine tooth and several long setae on outside, 2 short spine teeth on inside; posterior margin with 2 sets of setae distally; medial setae mostly singly inserted; dactyl nail rather large. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 4 marginal setae each; coxal plate of pereopod 4 about as broad as long, with 5 marginal setae. Pereopod 6 a little longer than pereopod 7, 45 to 50 percent as long as body; 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 broader proximally than distally; posterior margins convex, distoposterior lobes small, bluntly rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills on pereopods 2–6. Sternal blisters on pereonites 2–7. Broad plates of mature females small and narrow.

Pleonal Plates: Posterior margins nearly straight to slightly convex; posterior corners broadly rounded; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines. Uropod 1: inner ramus slightly longer than outer ramus, about two-thirds the length of peduncle, armed with 8 spines; outer ramus with 7 spines; peduncle with 6 or 7 spines. Uropod 2: inner ramus about one-fourth longer than outer ramus, about four-fifths the length of peduncle, armed with 7 spines; outer ramus with 6 spines; peduncle with 3 spines. Uropod 3: ramus about one-half the length of peduncle, with 3 apical spines. Telson longer than broad; apical margin with small notch; apical lobes with 4 spines each.

MALE.—Generally similar to female with the following exceptions: Uropod 1: inner ramus a little longer than outer ramus, 60 to 65 percent as long as peduncle, armed with 6 spines; outer ramus with 7 spines; peduncle with 5 spines and small distal process. Uropod 2: inner ramus nearly twice the length of outer ramus, about equal in length to peduncle, armed with 5 or 6 spines; outer ramus with 4 spines; peduncle with 1 or 2 spines. Uropod 3: ramus with 2 or 3 spines. Telson only slightly longer than broad.

TYPE-LOCALITY.—Empire Cave, Santa Cruz

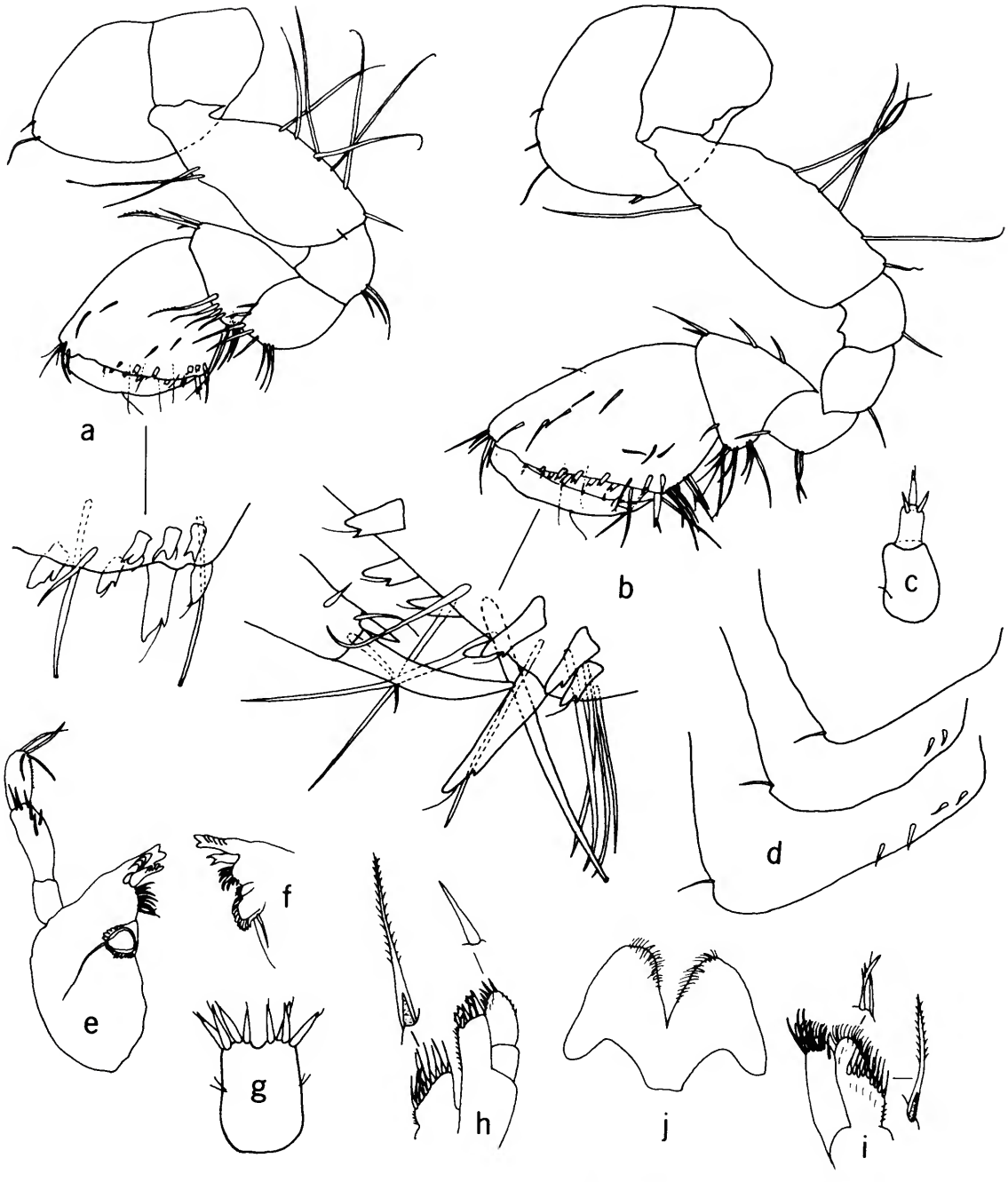

FIGURE 18.—*Stygobromus mackenziei*, new species, female paratype (4.7 mm), Empire Cave, California: *a,b*, gnathopods 1,2; *c*, uropod 3; *d*, pleonal plates; *e*, left mandible; *f*, dentate part of right mandible; *g*, telson; *h,i*, maxillae 1,2; *j*, lower lip.

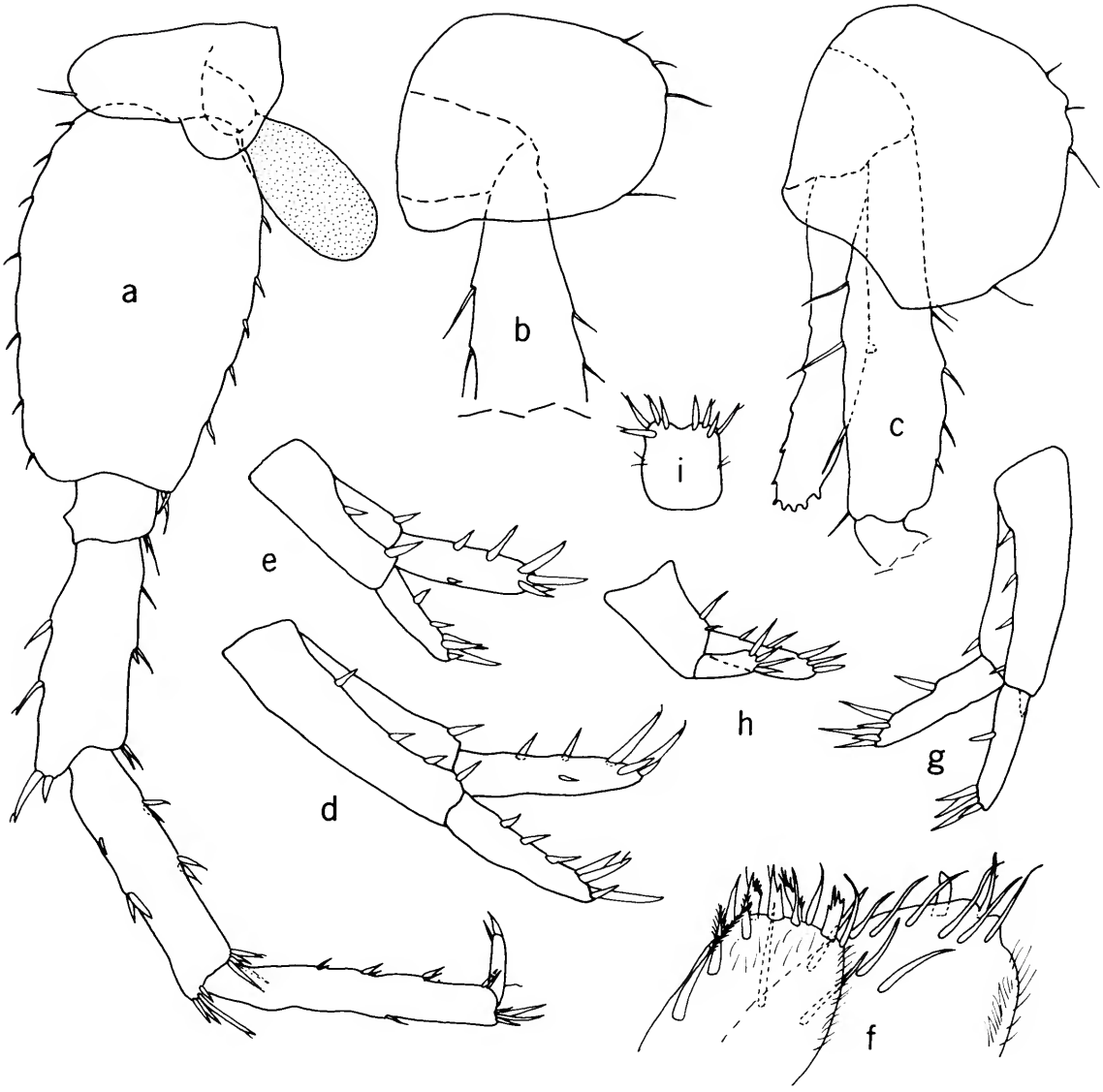

FIGURE 19.—*Stygobromus mackenziei*, new species. Female paratype (4.7 mm): *a*, pereopod 6; *b,c*, pereopods 3,4 (in part); *d,e*, uropods 1,2; *f*, apexes of inner and outer plates of maxilliped (greatly enlarged). Male paratype (4.0 mm), Empire Cave: *g,h*, uropods 1,2; *i*, telson.

County, California. The type-locality is a small cave located in or near the city of Santa Cruz and, according to Halliday (1962), is developed in metamorphosed limestone of unknown geologic age. Although the cave is subject to intermittent flooding, it does not contain a permanent stream but contains gours which are often filled with water (Halliday, 1962).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality. The type-series consisted of one male and five females. One of the females, measuring 3.6 mm, was ovigerous and

contained three eggs in the brood pouch. The remaining females ranged in size from 4.0 to 4.7 mm and most had setose brood plates.

ETYMOLOGY.—This species is named in honor of its collector, David McKenzie.

11. *Stygobromus sierrensis*, new species

FIGURES 20, 21

MATERIAL EXAMINED.—CALIFORNIA. Sierra Co.: spring in Trosi Canyon (6100 ft elevation), holotype female (USNM 142803) and 4 paratypes (JRH), A. L. Sheldon, 10 May 1966.

DIAGNOSIS.—A medium-sized groundwater species, resembling *S. hubbsi* in the number of spines and setae on the mouthparts and *S. grahami* in the shape and armature of gnathopodal propod 2 of the female, but generally distinguished by the shallow coxal plates of gnathopod 2 and pereopods 3 and 4; 2 ventral spines each on pleonal plates; proportionately short ramus of uropod 3; and near absence of a notch in the apex of the telson. Largest female, 7.0 mm; largest male, 5.2 mm.

FEMALE.—Antenna 1: 45 percent as long as body, 40 percent longer than antenna 2; primary flagellum with 11 to 13 segments. Antenna 2: peduncular segments 3, 4, and 5 with a number of long, slender spines and long, stiff setae marginally; flagellum with 5 or 6 segments. Mandibles and maxillipeds similar to *S. hubbsi*. Maxilla 1: inner plate with 6 plumose setae apically; palp with 4 spines and 2 setae apically. Maxilla 2: inner plate with oblique row of 9 or 10 plumose setae on inner margin. Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm long, oblique, slightly convex, armed with double row of about 7 spine teeth; posterior angle with 2 rather large spine teeth on outside, 4 shorter spine teeth on inside; posterior margin rather short, without setae; medial setae few in number, singly and doubly inserted; dactyl nail long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopodal propod 2 up to one-third longer than 1st propod; palm long, oblique, nearly straight or slightly concave, armed with double row of 5 or 6 spine teeth toward distal end and single row of 3 spine teeth toward posterior angle; posterior angle with 1 long, curved spine tooth and 3 long setae on outside, 2 shorter spine teeth on inside; posterior margin relatively short, with 1 set of 4 setae just below angle; inferior medial setae singly inserted, superior medial setae singly and doubly inserted; dactyl long and curved, nail long and slender. Coxal plates of gnathopod 2 and pereopod 3 rather shallow, about as broad as long, with 3 or 4 marginal setae each; coxal plate of pereopod 4 broader than long, with 5 marginal setae. Pereopod 6 equal to or slightly longer than pereopod 7, about 45 percent as long as body, 20 percent longer than pereopod 5. Bases of pereopods 5–7 not much broader proximally than distally; posterior margins nearly straight, with 7 to 10 setae; distoposterior lobes small, bluntly rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills present on pereopods 2–6. Brood plates of mature female small and narrow.

Pleonal Plates: Posterior margins convex; posterior corners rounded, nearly indistinct; with 1 seta each; ventral margins of plates 2 and 3 with 2 spines each. Uropod 1: inner ramus a little longer than outer ramus, about two-thirds the length of peduncle, armed with 8 spines; outer ramus with 7 spines; peduncle with 7 spines. Uropod 2: inner ramus about one-third longer than outer ramus, equal in length to peduncle, armed with 11 spines; outer ramus with 5 or 6 spines; peduncle with 3 spines. Uropod 3: ramus about one-fourth the length of peduncle, with 3 or 4 apical spines. Telson slightly longer than broad; apical margin only slightly emarginate; apical lobes with 7 or 8 spines each.

MALE.—Differing from female in a few minor ways as follows: Gnathopodal propod 2: palm oblique, nearly straight to slightly convex, armed with double row of 7 spine teeth; posterior angle with 1 long spine tooth and 1 long seta on outside and 1 shorter spine tooth on inside; posterior margin with 2 sets of setae just below posterior angle. Uropod 1 with distal peduncular process. Uropod 2: inner ramus with 8 spines; outer ramus with 3 spines; peduncle with 2 spines. Apical lobes of telson with 6 spines each.

TYPE-LOCALITY.—Spring in Trosi Canyon, Sierra County, California. This spring is located in the Sierra Nevada Mountains at an elevation of 6100 feet and drains into a stream system that flows west to join the Sacramento River.

DISTRIBUTION AND ECOLOGY.—This species is

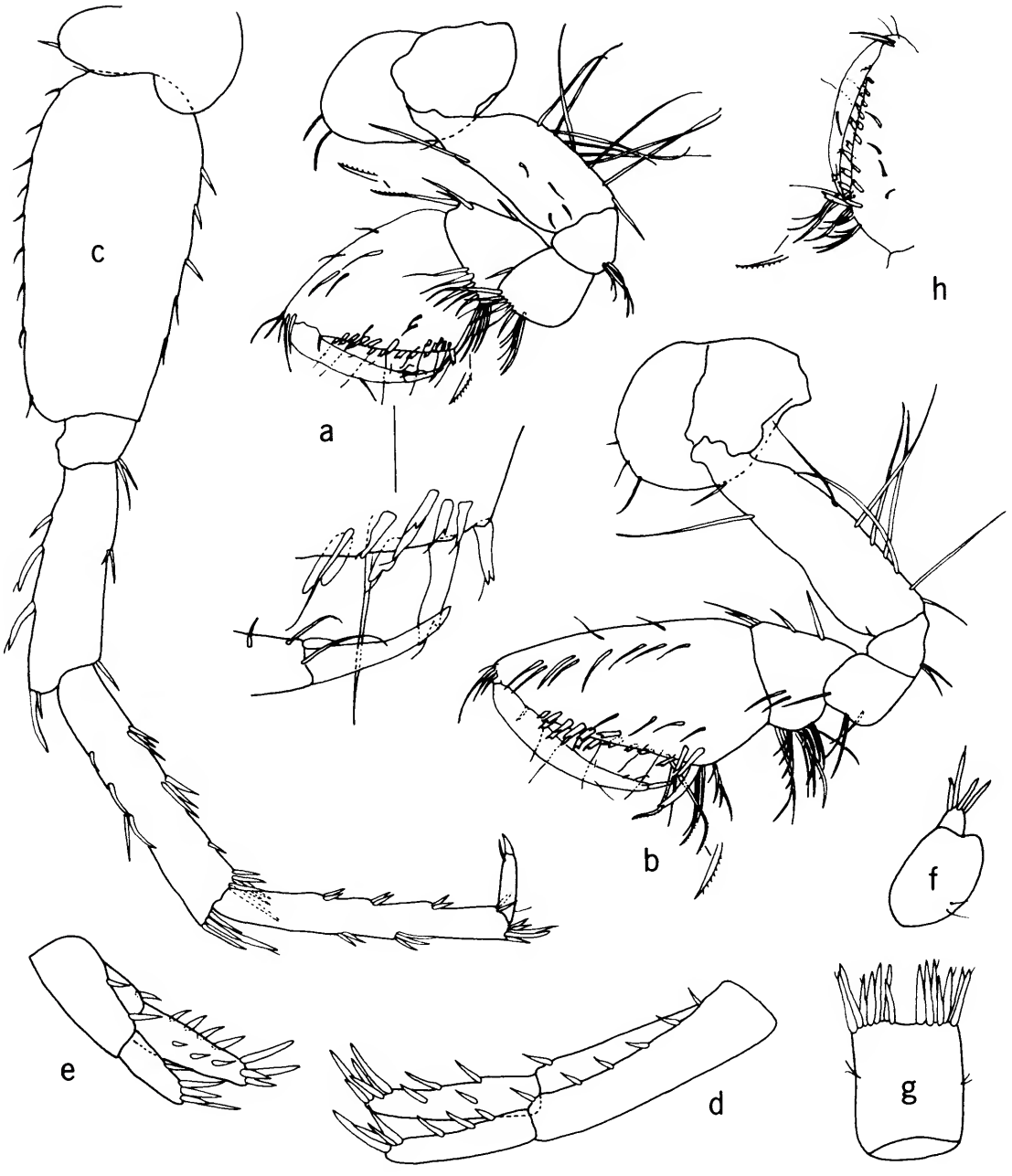

FIGURE 20.—*Stygobromus sierrensis*, new species. Female paratype (7.0 mm), spring in Trosi Canyon, California: *a,b*, gnathopods 1,2; *c*, pereopod 6; *d,e,f*, uropods 1,2,3; *g*, telson. Male paratype (5.0 mm), same locality: *h*, palm of gnathopodal propod 2.

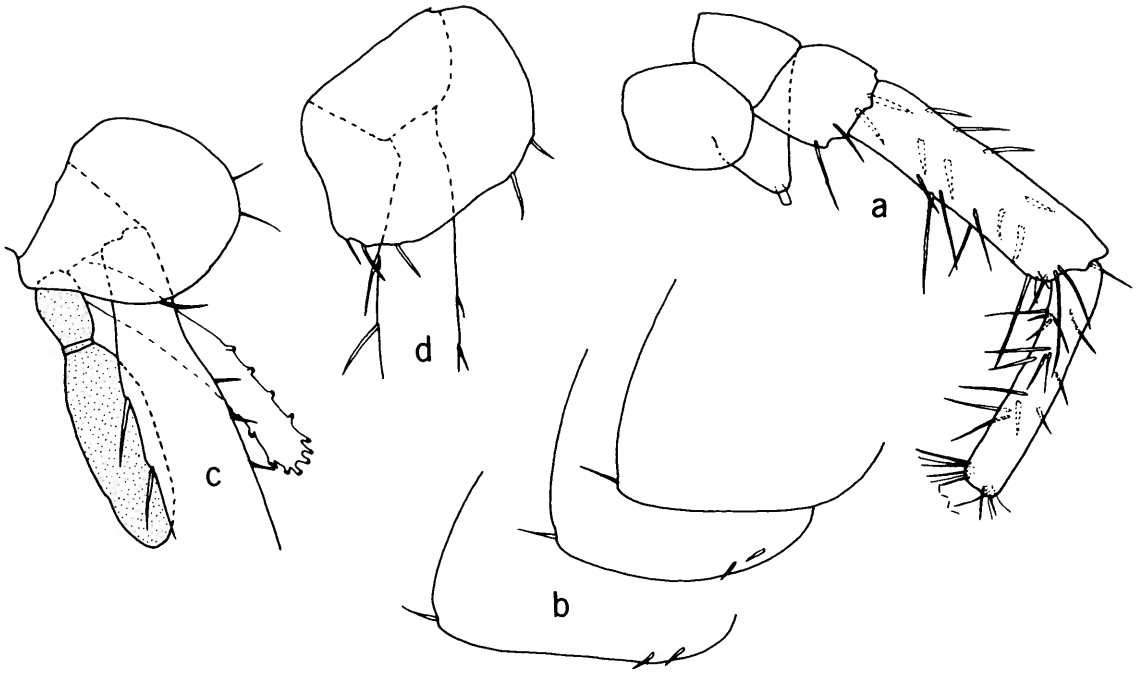

FIGURE 21.—*Stygobromus sierrensis,* new species, female paratype (7.0 mm): *a,* antenna 2 (in part); *b,* pleonal plates; *c,d,* pereopods 3,4 (in part).

known only from its type-locality on the basis of three males and two females. Both females (measuring 5.5 and 7.0 mm) had setose brood plates and were sexually mature.

12. *Stygobromus sheldoni,* new species

FIGURES 22, 23

MATERIAL EXAMINED.—CALIFORNIA. Nevada Co.: bog spring tributary to Sagehen Creek (6300 ft elevation), holotype female (USNM 142801) and 65 paratypes (USNM 142802), A. L. Sheldon, 11 April 1966; 8 additional collections (all paratypes deposited in JRH) made from the same locality by A. L. Sheldon between 6 Oct. 1965 and 23 Aug. 1966; Station spring (6400 ft elevation) to Sagehen Creek near Hobart Mills, 9 paratypes (JRH), A. L. Sheldon, 13 Sept. 1965; spring tributary to Sagehen Creek (7700 ft elevation), 4 paratypes (JRH), A. L. Sheldon, 5 Nov. 1965; spring tributary to Sagehen Creek in Kiln Meadow (6450 ft elevation), 4 paratypes (JRH), A. L. Sheldon, 19 July 1966.

DIAGNOSIS.—A small groundwater species (smallest in the *hubbsi* group) probably closely related to both *S. mackenziei* and *S. sierrensis,* but differing from the latter species in being smaller at sexual maturity, fewer spine teeth on the palms of the 1st gnathopod propods of both sexes, proportionately smaller gnathopodal propod 2 of male, proximally broader bases of pereopods 5–7, presence of sternal blisters, and 2 apical spines on ramus of uropod 3. Largest females, 4.0 mm; largest males, 3.0 mm.

FEMALE.—Antenna 1, 45 to 50 percent as long as body, 40 to 45 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2, flagellum with 6 segments. Mandibles and maxillipeds similar to those of *S. hubbsi.* Maxilla 1: inner plate with 6 to 8 plumose setae apically; palp with 2 spines and 3 setae apically. Maxilla 2: inner plate with oblique row of 7 to 9 plumose setae on inner margin. Lower lip with tiny inner lobes.

Gnathopodal Propod 1: Palm long, oblique, nearly straight, armed with double row of about

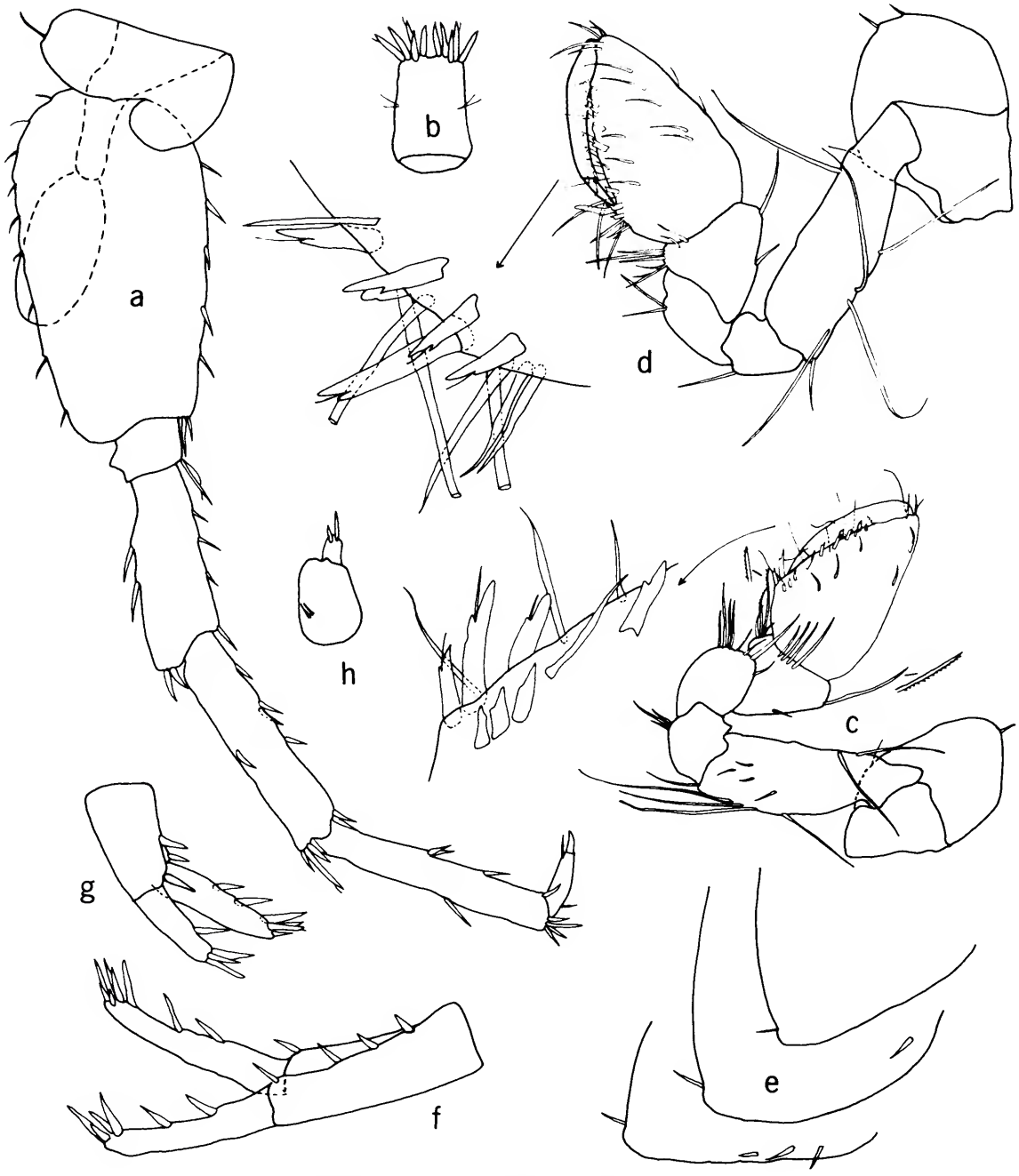

FIGURE 22.—*Stygobromus sheldoni*, new species, female paratype (4.0 mm), Bog Spring, tributary to Sagehen Creek, California: *a*, pereopod 6; *b*, telson; *c,d*, gnathopods 1,2; *e*, pleonal plates; *f,g,h*, uropods 1,2,3.

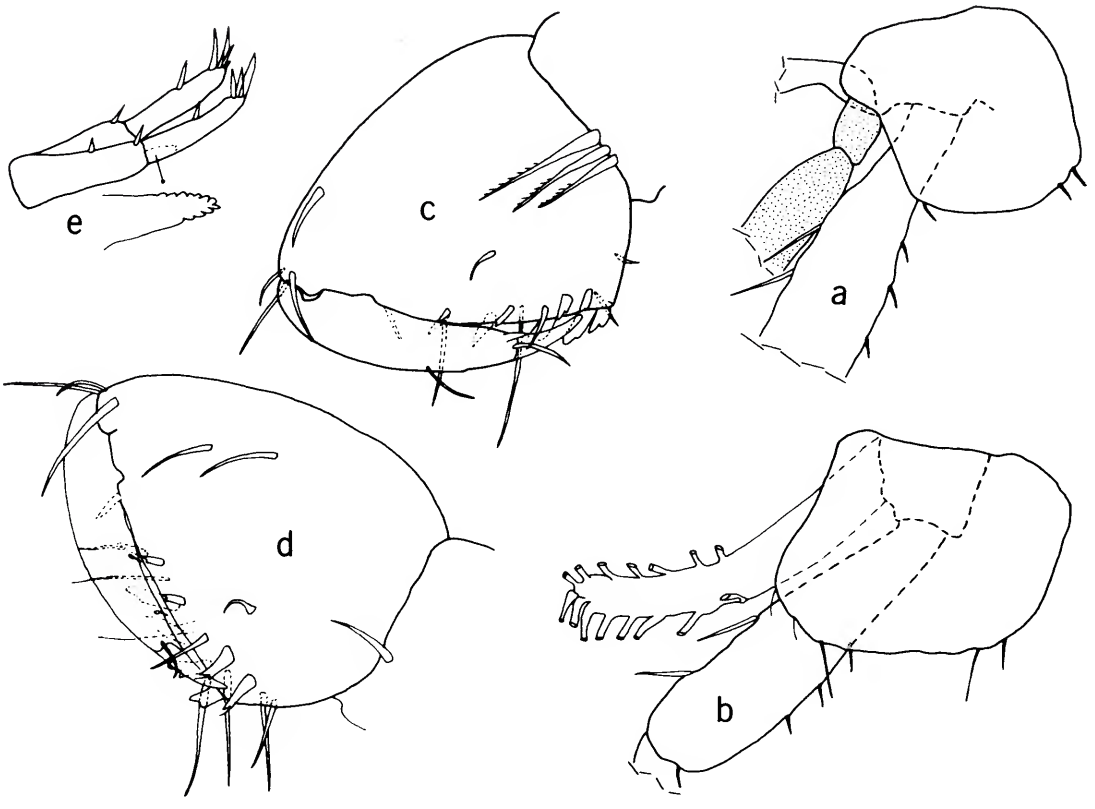

FIGURE 23.—*Stygobromus sheldoni*, new species. Female paratype (4.0 mm): *a,b*, pereopods 3,4 (in part). Male paratype (2.5 mm), Bog Spring, tributary to Sagehen Creek: *c,d*, gnathopodal propods 1,2; *e*, uropod 1.

5 spine teeth; posterior angle with 3 long spine teeth and 1 seta on outside, 3 shorter spine teeth on inside; posterior margin rather short, without setae; medial setae few in number, singly inserted; dactyl nail not reaching defining angle. Coxal plate of gnathopod 1 longer than broad, with 2 or 3 marginal setae. Gnathopodal propod 2 a little broader and longer than 1st propod; palm long, oblique, slightly convex, armed with unequal double row of about 5 spine teeth plus 2 additional spine teeth on outside toward posterior angle; posterior angle with 1 long spine on outside, 2 shorter spine teeth on inside; posterior margin short, less than one-half the length of palm, with 1 set of setae; medial setae singly inserted; dactyl nail rather large. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, with 3 marginal setae each; coxal plate of pereopod 4 broader than long, extending about one-half the length of segment 2, with 5 marginal setae. Pereopod 6 a little longer than pereopod 7, 50 percent as long as body, 30 percent longer than pereopod 5. Bases of pereopods 5–7 a little broader proximally than distally; posterior margins nearly straight to slightly convex; distoposterior lobes small, broadly rounded. Dactyls of pereopods 6 and 7 rather long, about 40 percent as long as corresponding propods. Coxal gills on pereopods 2–6. Small sternal blisters on pereonites 2–7. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins slightly convex; posterior corners distinct, bluntly rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 3 spines. Uropod 1: inner ramus a little longer than outer ramus, a little shorter than peduncle, armed

with 7 or 8 spines; outer ramus with 6 spines; peduncle with 5 spines. Uropod 2: inner ramus about one-third longer than outer ramus, a little longer than peduncle, armed with 6 spines; outer ramus with 4 or 5 spines; peduncle with 3 spines. Uropod 3: ramus about one-third the length of peduncle, with 2 apical spines. Telson about one-fourth longer than broad; apical margin with very tiny notch; apical lobes with 5 spines each.

MALE.—Differing from the female as folows: Antenna 1, 40 percent as long as body, about 30 percent longer than antenna 2; primary flagellum with 9 segments. Antenna 2, flagellum with 4 segments. Gnathopodal propod 1 about as broad as long; palm rather oblique, nearly straight, armed with only 2 spine teeth on either side; posterior angle with 2 spine teeth and 1 short seta on outside, 2 shorter spine teeth on inside; posterior margin short, with 1 tiny seta submarginally; medial setae 3 in number, singly inserted; dactyl nail relatively large but not reaching defining angle. Coxal plate of gnathopod 1 longer than broad, with 1 marginal seta. Gnathopodal propod 2 similar in shape to 1st propod but slightly larger; palm long, oblique, slightly convex, armed with double row of 3 or 4 unequal spine teeth; posterior angle with 1 heavy spine tooth and 1 seta on outside, 1 slender spine tooth on inside; posterior margin rather short, with 1 set of 2 setae; medial setae 4 in number, singly inserted; dactyl nail rather long. Coxal plate of gnathopod 2 longer than broad, with 1 marginal seta.

Pereopod 6 about 50 percent as long as body, about 25 percent longer than pereopod 5. Sternal blisters absent in specimens studied. Uropod 1: inner ramus subequal in length to outer ramus, a little shorter than peduncle, armed with 5 or 6 spines; outer ramus with 5 spines; peduncle with 3 spines and distal process. Uropod 2: inner and outer rami with 5 spines each; peduncle with 2 spines. Telson with small apical notch, apical lobes with 3 or 4 spines each.

TYPE-LOCALITY.—Bog spring, tributary to Sagehen Creek, Nevada County, California. This spring is located in the Sierra Nevada Mountains at an elevation of 6300 feet. Sagehen Creek is a part of the Truckee River system which drains east to brackish Pyramid Lake in nearby Nevada (A. L. Sheldon, in litt.).

DISTRIBUTION AND ECOLOGY.—This species has been collected from four springs in Nevada County, California. Nine of the 12 collections were made from the type-locality; the remainder were from nearby springs ranging in elevation from 6400 to 7700 feet. According to A. L. Sheldon, who made periodic collections of this species from September 1965 to August 1966, late afternoon August temperatures in the springs ranged from 3.5° to 6.5° C. The springs are fed by water that flows through morainal material and have a substantial discharge with a steep gradient just below the springheads. The amphipods were usually found in tufts of moss exposed to strong currents. *Stygobromus sierrensis* presumably occupies a similar spring habitat in nearby Sierra County. *Stygobromus spinosus* (Hubricht and Mackin), an inhabitant of springs at higher elevations in the Blue Ridge Mountains of northern Virginia, also occupies a similar biotope.

With the exception of January, monthly samples were available for a full year and each sample contained a few mature females (size range, 3.0 to 4.0 mm) with setose brood plates. None of the samples contained ovigerous females, however, but mature males (2.5 to 3.0 mm long) were found in all samples except October, November, and July. Juveniles (under 2.0 mm in length) were also found in most of the samples, and this, combined with the constant presence of mature females, may indicate that breeding takes place throughout the year. The absence of ovigerous females from all of the samples, however, may further indicate that reproduction takes place beneath the ground.

ETYMOLOGY.—This species is named in honor of Dr. Andrew L. Sheldon, whose diligent collections and observations have provided much useful information.

13. *Stygobromus tahoensis*, new species

FIGURES 24, 25

Stygobromus hubbsi Shoemaker.—Frantz and Cordone, 1966: 7 (in part).

MATERIAL EXAMINED.—All material from Lake Tahoe at the indicated locations and depths. CALIFORNIA. Placer Co.: between Skunk Harbor and Tahoe City (1534–1623 ft), holotype female (USNM 142804) and 96 paratypes (USNM 142805), T. C. Frantz et al., 14 Dec. 1962; approximately 450 additional paratypes (USNM 142806–142817) as fol-

lows—Placer Co.: 2 collections off McKinney Bay (820–840 ft and 1255 ft), A. J. Cordone and T. C. Frantz, 24 Sept. 1962; Tahoma (455–460 ft), Frantz and Curran, 21 Dec. 1962; El Dorado Co.: Emerald Bay (116–198 ft), Frantz, Curran, and Saake, 11 July 1962; South Tahoe shelf (250–425 ft), Frantz, Curran, and Saake, 20 Aug. 1962. NEVADA. Washoe Co.: 2 collections from Crystal Bay (410–444 ft), Frantz, Curran, and Saake, 13 Aug. and 20 Dec. 1962; Douglas Co.: dredge from bottom in Cave Rock area (245–264 ft), T. C. Frantz, 22 May 1962; 2 collections at Logan Shoals (618–630 ft and 1165 ft), Frantz and Cordone, 16 Aug. 1962; 2 collections at Cave Rock (215–501 ft and 245 ft), Frantz, Curran, and Saake, 17 July and 27 Oct. 1962.

DIAGNOSIS.—A medium-sized, deep-lake dwelling species, apparently related to *S. sierrensis* and *S. sheldoni,* but differing from these species in the female which has proportionately more narrow gnathopodal propods with longer posterior margins and more spines on the peduncle of uropod 1; in the male by the short outer ramus of uropod 2 and the proportionately smaller telson with only 6 apical spines; and in both sexes by having fewer ventral spines on pleonal plates 2 and 3 and 2 setae each on the posterior margins of these plates. Largest females, 6.5 mm; largest males, 5.0 mm.

FEMALE.—Antenna 1, about 45 percent as long as body, about 50 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2, flagellum with 5 segments. Mandibles subequal; spine row with 6 spines; palpal segment 2 with 7 long setae on inner margin; palpal segment 3 with 4 short setae on inner margin, 5 long setae apically. Maxilla 1: inner plate with 6 plumose setae apically; palp with 3 spines and 3 setae apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 2 serrate spines and 4 setae apically; outer plate with 1 bladelike spine and several setae apically. Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm about as long as posterior margin, armed with double row of 4 spine teeth, plus 2 additional spine teeth on outside; posterior angle with 3 spine teeth and 1 long setae on outside; 6 spine teeth on inside; posterior margin without setae; medial setae mostly singly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopodal propod 2 a little longer than 1st propod; palm oblique, slightly convex, armed with double row of 7 or 8 spine teeth; posterior angle rounded, with 1 long spine tooth and 5 setae on outside, 2 shorter spine teeth on inside; posterior margin with 1 set of 3 long setae; medial setae mostly singly inserted; dactyl nail rather long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 3 or 4 marginal setae each; coxal plate of pereopod 4 about as broad as long, with 5 marginal setae. Pereopod 6 a little longer than pereopod 7, about 45 percent as long as body, about 20 percent longer than pereopod 5. Bases of pereopods 5–7 rather narrow, not much broader proximally than distally; distoposterior lobes poorly developed, broadly rounded. Dactyls of pereopods 6 and 7 relatively long, about 40 percent as long as corresponding propods. Coxal gills on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins of plates 1 and 3 convex, that of plate 2 nearly straight; margins of plates 2 and 3 with 2 setae each; posterior corners distinct, bluntly rounded; ventral margins of plates 2 and 3 with 4 spines each. Uropod 1: inner ramus a little longer than outer ramus, about two-thirds the length of peduncle, armed with 11 spines; outer ramus with 8 spines; peduncle with 11 or 12 spines. Uropod 2: inner ramus about one-third longer than outer ramus, equal in length to peduncle, armed with 10 spines; outer ramus with 7 spines; peduncle with 4 spines. Uropod 3: ramus about one-third the length of peduncle, with 3 or 4 apical spines. Telson about as long as broad; apical margin with tiny notch; apical lobes with 5 spines each.

MALE.—Differing from the female as follows: Antenna 1, 35 to 40 percent as long as body, primary flagellum with 8 segments. Antenna 2, flagellum with 5 segments. Gnathopodal propod 1 with few less spines at defining angle. Gnathopodal propod 2 proportionately stouter, only about one-fourth longer than broad; palm slightly convex; posterior angle better defined; posterior margin with row of 6 setae just below posterior angle. Distoposterior lobes of bases of pereopods 5–7 better developed, not as broadly rounded. Uropod 1 with fewer spines and large, distally acute peduncular process. Uropod 2: inner ramus rather broad and proportionately long, 50 percent longer than outer ramus and about 25 percent longer than peduncle, armed with 6 spines; outer ramus with 4 spines; peduncle with 2

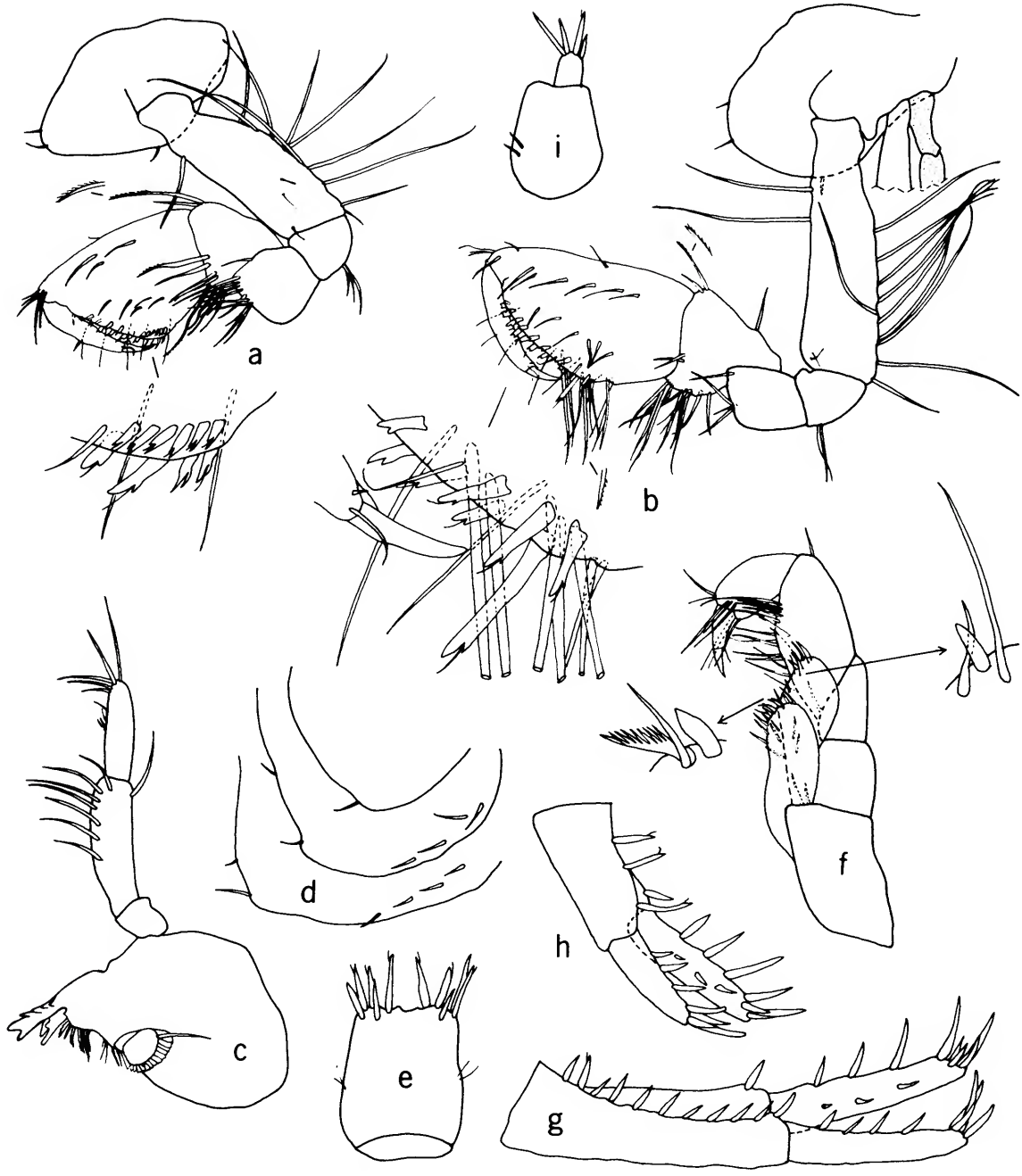

FIGURE 24.—*Stygobromus tahoensis*, new species, female paratype (6.5 mm), Lake Tahoe, between Skunk Harbor and Tahoe City, California: *a,b*, gnathopods 1,2; *c*, right mandible; *d*, pleonal plates; *e*, telson; *f*, maxilliped; *g,h,i*, uropods 1,2,3.

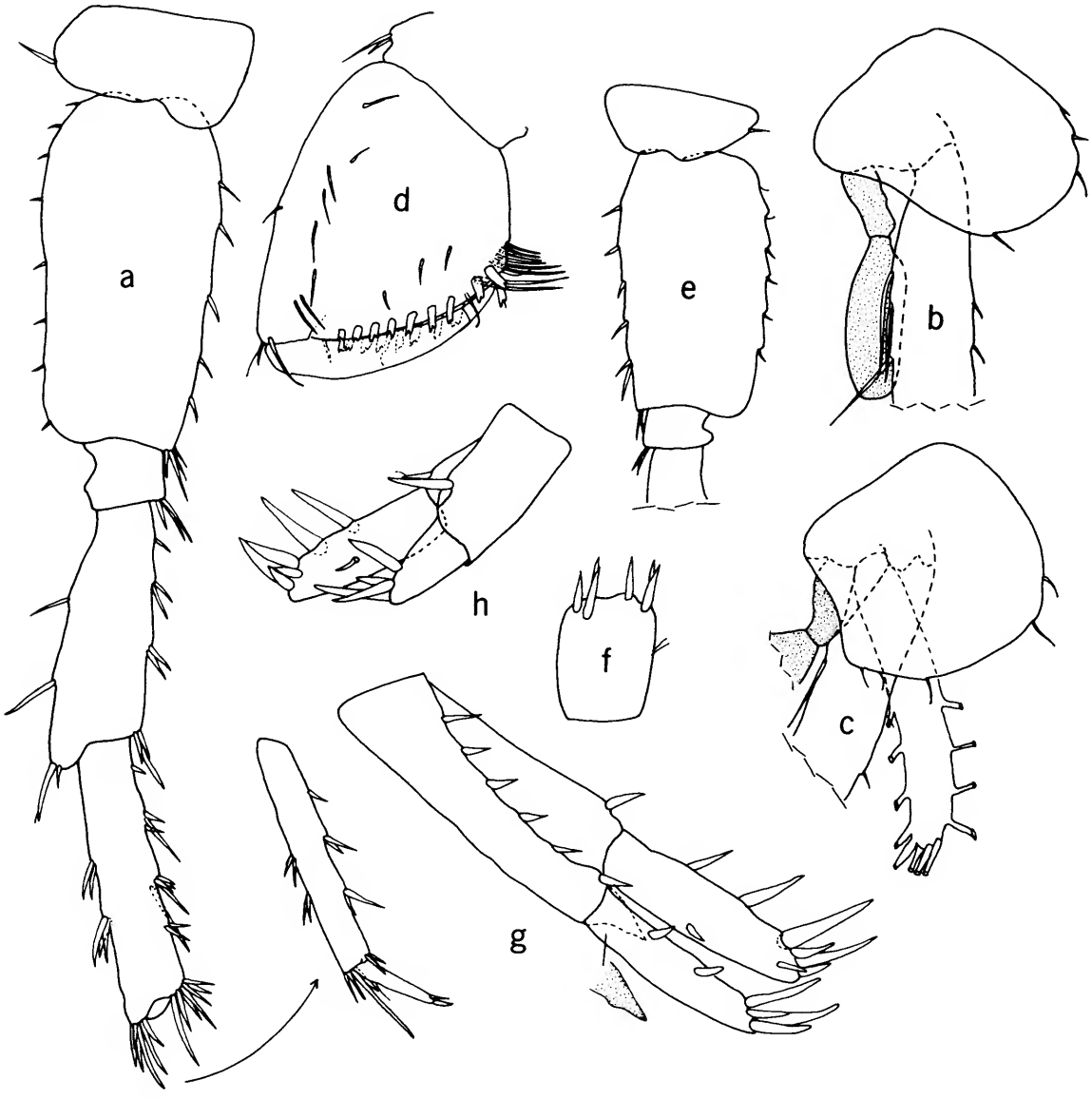

FIGURE 25.—*Stygobromus tahoensis*, new species. Female paratype (6.5 mm); *a*, pereopod 6; *b,c*, pereopods 3,4 (in part). Male paratype (5.0 mm), Lake Tahoe, between Skunk Harbor and Tahoe City: *d*, gnathopodal propod 2; *e*, pereopod 7 (in part); *f*, telson; *g,h*, uropods 1,2.

spines. Telson about one-fourth longer than broad; apical margin nearly entire or with very shallow emargination; apical lobes with 3 spines each.

VARIATION.—Smaller ovigerous females (about 4.5 to 5.0 mm) have a few less spines on the palm of gnathopodal propod 2 and 1 or 2 fewer setae on the posterior margins of the bases of pereopods 5–7 than larger ovigerous females (about 5.5 to 6.5 mm).

TYPE-LOCALITY.—Lake Tahoe between Skunk Harbor and Tahoe City (depth = 1534 to 1623 ft), Placer County, California.

DISTRIBUTION AND ECOLOGY.—This species is known only from Lake Tahoe, where it was extensively sampled in the early 1960s by T. C. Frantz and A. J. Cordone during a limnological survey of the lake. Two reports by these workers (Frantz and Cordone, 1966, 1967) usefully summarized the animal and plant life of the lake and included a detailed map showing the collecting sites. The records for this species (and for *S. lacicolus*, described later) are the first reported occurrences for blind, white amphipods from a deep, oligotrophic lake in the United States, although species of similar subterranean facies have been reported previously from deep lakes in Europe (e.g., *Niphargus foreli*) and Siberia (*Stygobromus pusillus*). In addition to the two species of *Stygobromus*, a blind, white planarian (*Dendrocoelopsis hymanae*) was also collected on this survey and was described by Kawakatsu (1968).

Approximately 550 specimens of *S. tahoensis* were represented in a series of 13 samples taken from the lake periodically from May to December 1962. The majority of specimens were taken at depths ranging from 200 to 1623 feet; only one sample (July) was obtained at less than 200 feet. The talitrid amphipod *Hyalella azteca* (Saussure) was also sampled but was almost exclusively restricted to depths less than 200 feet. Two of the 13 samples also contained *Stygobromus lacicolus* (see below) and three additional samples contained only the latter species. The substrate preference of *Stygobromus* in Lake Tahoe is apparently not living plants, since, as shown by Frantz and Cordone (1967), plants were most concentrated at depths of 200 to 350 feet, beyond which only small quantities were found at 400 feet and none were taken at 500 feet or deeper. The greatest concentrations of *Stygobromus* were found at depths of 600 to 900 feet and again at 1500 to 1623 feet (Frantz and Cordone, unpublished data).

Out of the approximately 550 specimens studied, 51 were ovigerous females ranging in size from 3.8 to 6.5 mm ($\bar{x}$ = 4.8 mm). The number of eggs and/or embryos per female ranged from 1 to 5 ($\bar{x}$ = 2.25). Ovigerous females were found in samples taken during May, July, August, September, October, and December. Males and juveniles were also found in most of these samples, but females were always the most abundant.

COMMENTS.—On the basis of a mistaken determination, Frantz and Cordone (1966) listed the *Stygobromus* from Lake Tahoe as *S. hubbsi*. They also indicated the presence of two species of *Hyalella*—*H. azteca* and *H. inermis*. The latter species, however, is usually regarded as a synonym of the former.

14. *Stygobromus lacicolus*, new species

FIGURES 26, 27

Stygobromus hubbsi Shoemaker.—Frantz and Cordone, 1966: 7 (in part).

MATERIAL EXAMINED.—All material from Lake Tahoe at the indicated locations and depths. NEVADA. Douglas Co.: Cave Rock (215–501 ft), holotype male (USNM 142786), T. C. Frantz et al., 17 July 1962; Logan Shoals (1165 ft), 5 paratypes (USNM 142787), T. C. Frantz and A. J. Cordone, 16 Aug. 1962; El Dorado Co.: Homewood to Rubicon Bay (18–197 ft), 1 paratype (USNM 142789), Cordone and Frantz, 30 May 1962; Sugar Pine Point (480 ft), 1 paratype (USNM 142790), Frantz, Curran, and Saake, 18 July 1962. CALIFORNIA. Placer Co.: Tahoe City area (392 ft), 3 paratypes (USNM 142788), Frantz, Curran, and Saake, 24 July 1962.

DIAGNOSIS.—A medium-sized, deep-lake dwelling species, occuring sympatrically with *S. tahoensis* but differing from that species in gnathopodal propod 1 of the male which has a longer palm and more spine teeth, gnathopodal propod 2 of both sexes which has a longer palm and is broader proximally (strongly resembling *S. wengerorum*), deeper coxal plates of pereopods 3 and 4, broader bases of pereopods 5–7, fewer spines and setae on pleonal plates 2 and 3, fewer spines on uropods 1 and 2, smaller peduncular process (with serrate apex) of uropod 1 of the male, proportionately longer ramus of uropod 3, and proportionately longer telson with more apical spines. Largest female, 6.0 mm; largest males, 5.5 mm.

MALE.—Antenna 1, 40 to 45 percent as long as body, about 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2, flagellum with 6 segments. Mouthparts similar to *S. tahoensis* except maxilliped differing slightly as follows: inner plate with 3 serrate spines, 2 bladelike spines, and several setae apically; outer plate

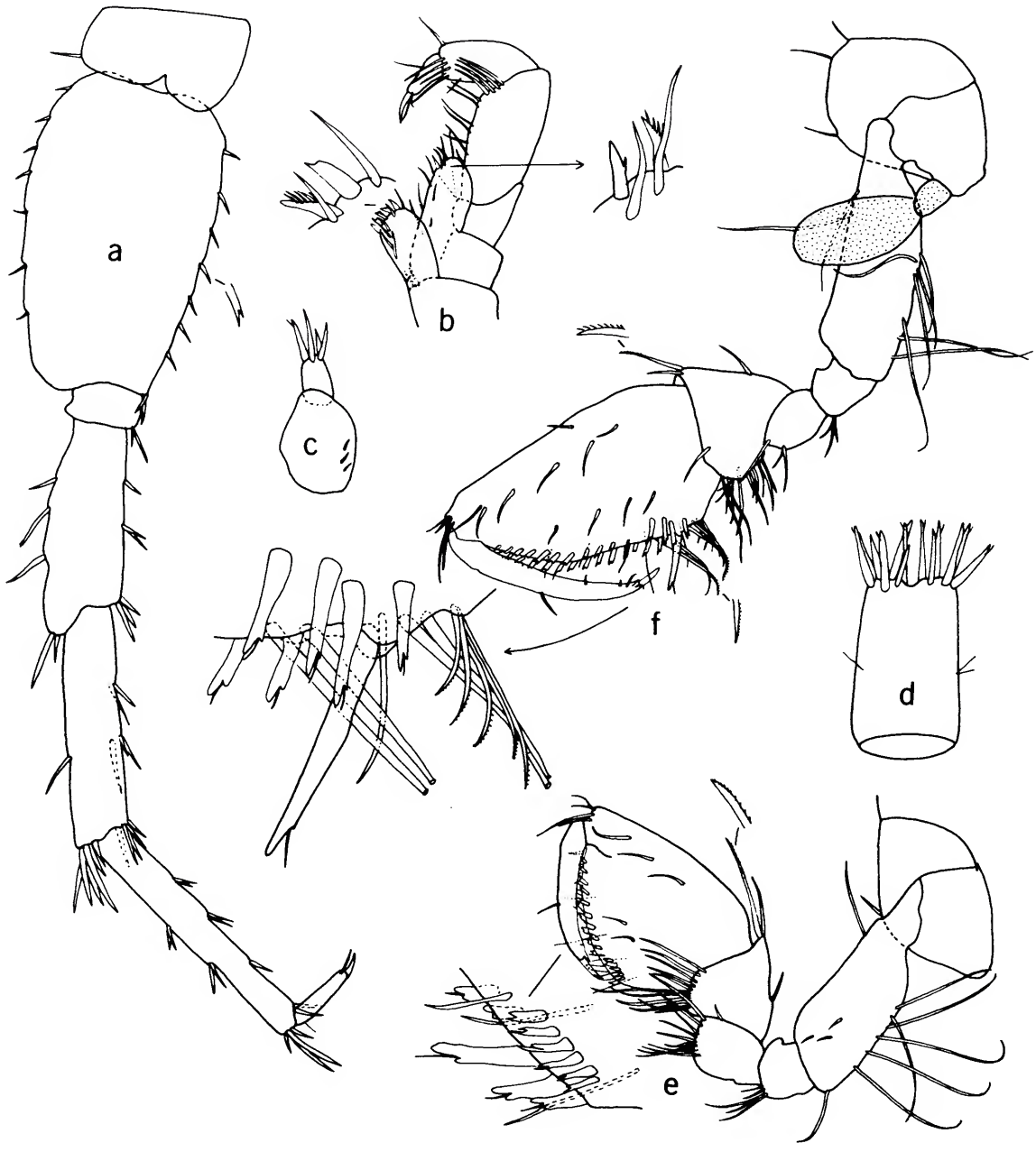

FIGURE 26.—*Stygobromus lacicolus*, new species, male paratype (5.5 mm), Lake Tahoe, Sugar Pine Point, California: *a*, pereopod 6; *b*, maxilliped; *c*, uropod 3; *d*, telson; *e,f*, gnathopods 1,2.

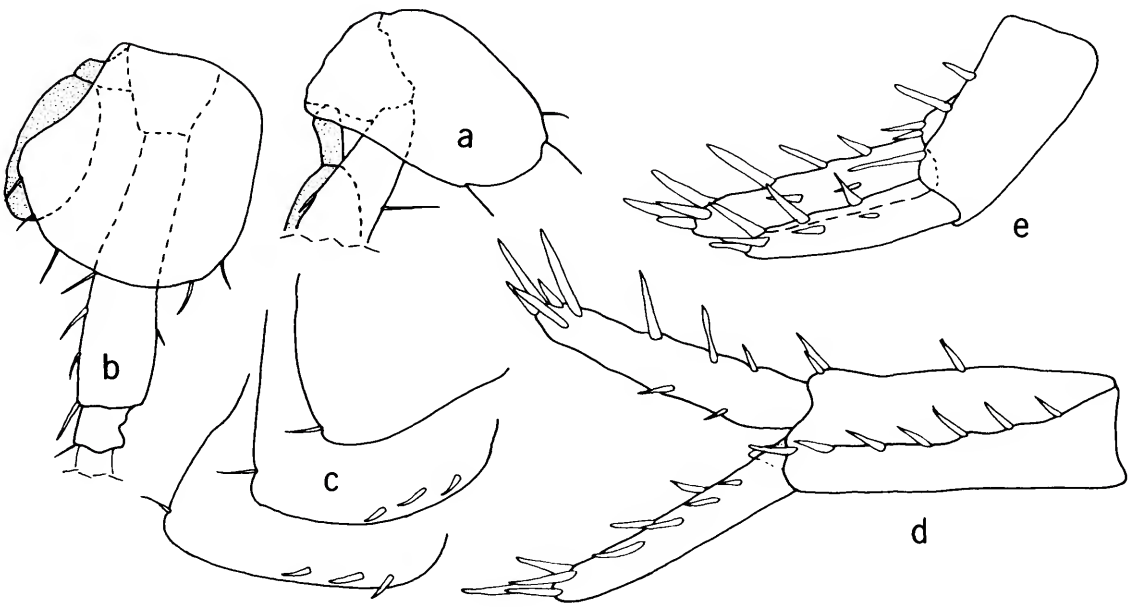

FIGURE 27.—*Stygobromus lacicolus*, new species, male paratype (5.5 mm): *a,b*, pereopods 3,4 (in part); *c*, pleonal plates; *d,e*, uropods 1,2.

with 1 bladelike spine, 1 serrate spine, and 3 setae apically. Gnathopodal propod 1: palm long, convex, armed with double row of 9 or 10 spine teeth; posterior angle with 3 spine teeth on outside, 5 shorter spine teeth on inside; posterior margin about half the length of palm, without setae; medial setae singly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 longer than broad, with 2 marginal setae. Gnathopodal propod 2: nearly twice the size of 1st propod; palm long, oblique, convex distally, concave proximally, armed with double row of 12 spine teeth plus 2 additional spine teeth on outside; posterior angle with 1 long spine tooth and 3 setae on outside, 2 shorter spine teeth on inside; posterior margin short, with 1 set of setae just below posterior angle; medial setae mostly singly inserted; dactyl rather long, nail comparatively short. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 3 marginal setae each; coxal plate of pereopod 4 rather deep, as broad as long, reaching about half the length of segment 2, with 5 marginal setae. Pereopod 6 a little longer than pereopod 7, 45 to 50 percent as long as body, 20 percent longer than pereopod 5. Bases of pereopods 5–7 broader proximally than distally; posterior margins convex; distoposterior lobes distinct, broadly rounded. Dactyls of pereopods 6 and 7 relatively long, about one-third the length of corresponding propods. Coxal gills on pereopods 2–6.

Pleonal Plates: Posterior margins straight to slightly convex; posterior corners rounded, distinct; ventral margins of plates 2 and 3 with 3 spines each. Uropod 1: inner ramus slightly longer than outer ramus, a little shorter than peduncle, armed with 10 spines; outer ramus with 10 spines; peduncle with 10 spines and small process with tiny apical serrations. Uropod 2: inner ramus about one-fourth longer than outer ramus and peduncle, armed with 9 or 10 spines; outer ramus with 7 or 8 spines; peduncle with 5 spines. Uropod 3: ramus about one-half the length of peduncle, with 4 or 5 apical spines. Telson more than one-third longer than broad; apical margin with small rounded notch; apical lobes with 6 or 7 spines each.

FEMALE.—Known only from a single, partly broken specimen but apparently generally similar to male.

TYPE-LOCALITY.—Lake Tahoe at Cave Rock (depth = 215 to 501 ft), Douglas County, Nevada.

DISTRIBUTION AND ECOLOGY.—This species is known only from Lake Tahoe, where it was collected during the previously mentioned limnological survey by Frantz and Cordone in the early 1960s. Of the 16 samples of *Stygobromus* studied from Lake Tahoe, 5 contained specimens of *S. lacicolus;* 3 of the 5 contained only this species and 2 had both this species and *S. tahoensis.* Of these two species, *S. lacicolus* appears to be far less abundant in the lake, as the five samples, representing the months of May, July, and August, contained only 11 specimens. Of these 11 specimens, 8 were males, 2 were juveniles and 1 was a female. The association of *Stygobromus* with Lake Tahoe is discussed in more detail under the description of *S. tahoensis.*

ETYMOLOGY.—The specific name is from the Latin *Lacus* (lake) and *colo* (to inhabit).

15. *Stygobromus arizonensis,* new species

FIGURES 28, 29

MATERIAL EXAMINED.—ARIZONA. Cochise Co.: small cave on Flying "H" Ranch near Fort Huachuca, holotype male (USNM 142778) and 1 paratype (JRH), J. L. Colehour, Sept. (?) 1963; mine in limestone near Paradise, 1 specimen (JRH), R. E. Graham, 24 July 1962.

DIAGNOSIS.—A relatively small cavernicolous species, distinguished by having only 4 apical spines on the inner plate of the maxilliped, the convex posterior margins of the bases of pereopods 5–7 which lack distoposterior lobes, the pleonal plates which have 2 long setae each on the posterior margins and only 1 or 2 small spines on the ventral margins of plates 2 and 3, the 2-spined ramus of uropod 3, and the rather deeply notched apical margin of the telson. Largest female, 3.7 mm; largest males, 5.0 mm.

DESCRIPTION.—Antenna 1, 45 to 50 percent as long as body, 40 percent longer than antenna 2; primary flagellum with 12 to 13 segments. Antenna 2, flagellum with 5 segments. Mandibles subequal; spine row with 6 spines; palpal segment 2 with 5 setae on inner margin distally; palpal segment 3 with row of short setae on inner margin distally and 4 long setae apically. Maxilla 1: inner plate with 6 plumose setae apically; outer plate with 4 slender spines and 3 setae apically and subapically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 4 thick, serrate or plumose spines and 3 or 4 setae apically; outer plate with 1 bladelike spine and about 6 setae apically. Lower lip with small inner lobes.

Gnathopodal Propod 1: Palm rather oblique, nearly straight, armed with double row of 5 spine teeth; posterior angle with 4 spine teeth and 1 long seta on outside, 4 shorter spine teeth on inside; posterior margin without setae; medial setae few in number, mostly singly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 longer than broad, with 2 marginal setae. Gnathopodal propod 2 about one-fourth longer than 1st propod; palm oblique, slightly convex, armed with double row of 8 or 9 spine teeth; posterior angle with 1 long, curved spine tooth on outside, 1 short spine tooth on inside; posterior margin about half the length of palm, with 1 set of 4 setae just below posterior angle; medial setae mostly singly inserted; dactyl nail and accessory spine rather long. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, with 3 marginal setae each; coxal plate of pereopod 4 about as broad as long, with 5 marginal setae. Pereopod 6 a little longer than pereopod 7, 60 percent as long as body, 30 to 35 percent longer than pereopod 5. Bases of pereopods 5–7 a little broader proximally than distally, posterior margins convex, with 5 to 8 setae each; distoposterior lobes indistinct. Dactyls of pereopods 6 and 7 less than one-third the length of corresponding propods. Coxal gills on pereopods 2–6. Brood plates of female small and narrow.

Pleonal Plates: Posterior margins nearly straight to slightly convex, with 2 rather long, stiff setae each; posterior corners tiny, rounded; ventral margin of plate 2 with 1 small spine, that of plate 3 with 2 small spines. Uropod 1: inner ramus slightly longer than outer ramus, about 60 percent as long as peduncle, armed with 8 or 9 spines; outer ramus with 6 spines; peduncle with 10 to 12 spines and distal process. Uropod 2: inner ramus longer than outer ramus, equal in length to peduncle, armed with 7 or 8 spines; outer ramus with 6 spines; peduncle with 3 spines. Uropod 3: ramus about one-half the length of peduncle, with 2 or 3 apical spines. Telson about one-fourth longer than broad; apical margin incised about one-fourth the distance to base; apical lobes with 4 spines each.

TYPE-LOCALITY.—Small cave on the Flying "H"

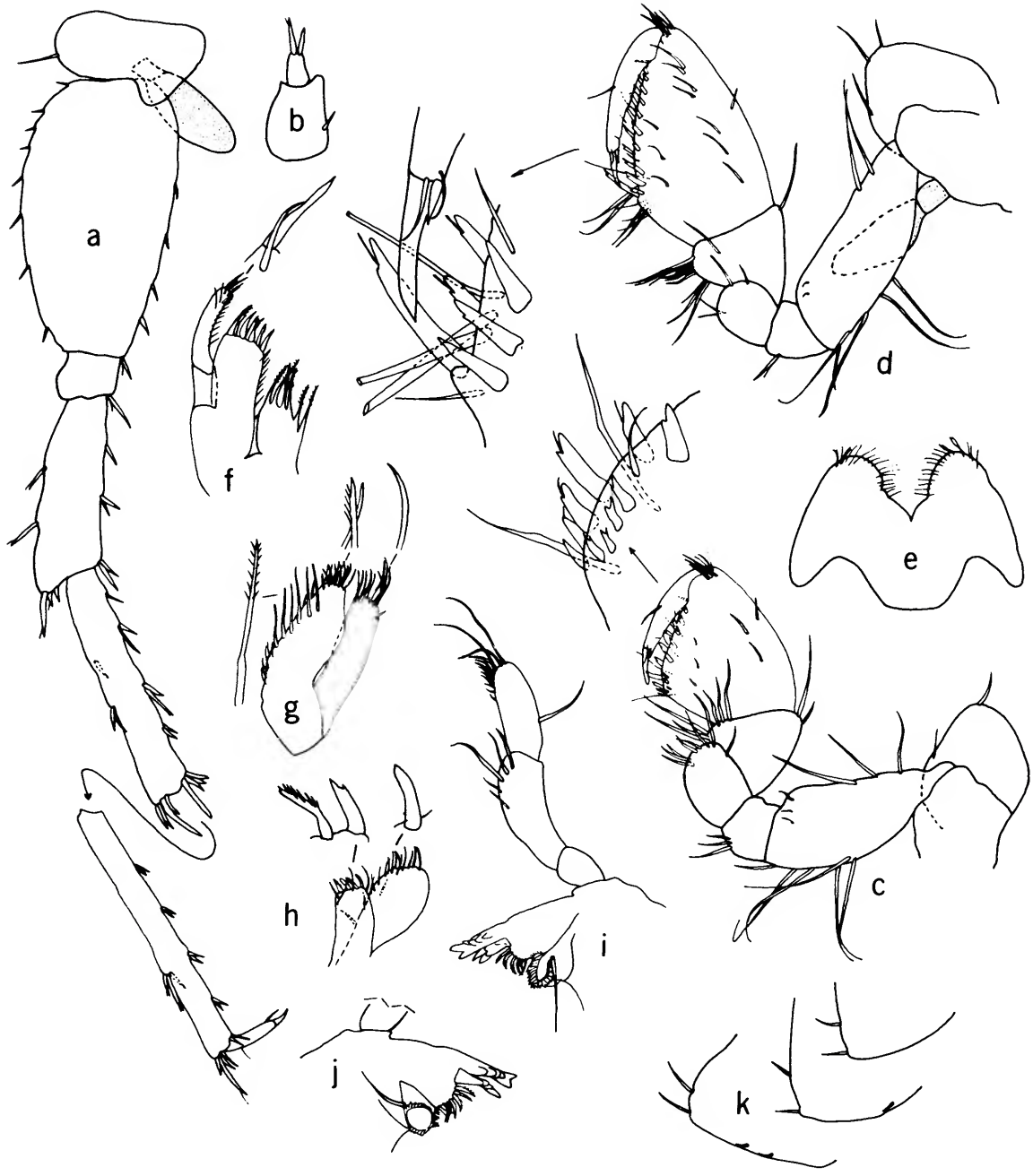

FIGURE 28.—*Stygobromus arizonensis*, new species, male paratype (5.0 mm), small cave on Flying "H" Ranch near Ft. Huachuca, Arizona: *a*, pereopod 6; *b*, uropod 3; *c,d*, gnathopods 1,2; *e*, lower lip; *f,g*, maxillae 1,2; *h*, apexes of inner and outer plates of maxilliped; *i*, right mandible; *j*, dentate part of left mandible; *k*, pleonal plates.

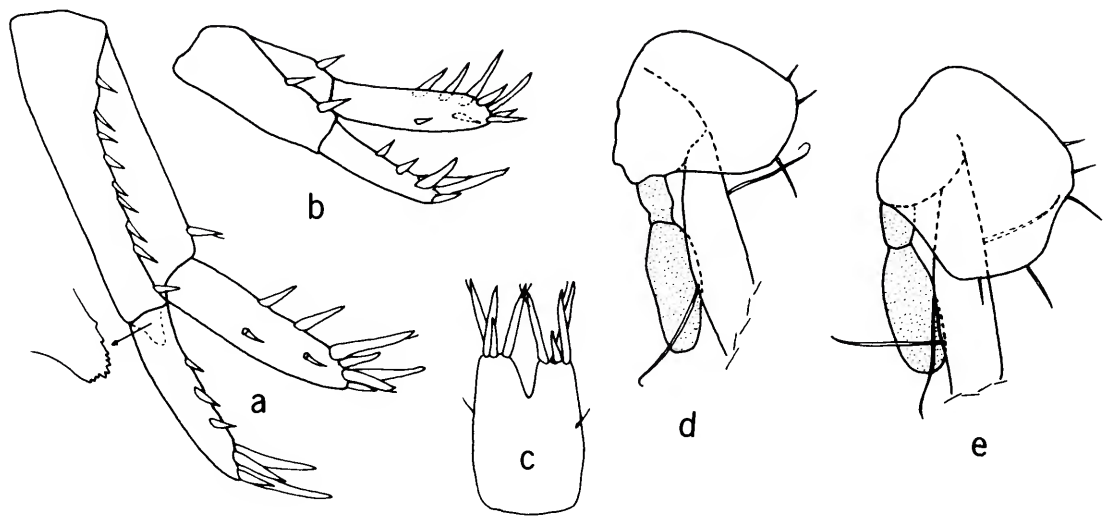

FIGURE 29.—*Stygobromus arizonensis*, new species, male paratype (5.0 mm): *a,b*, uropods 1,2; *c*, telson; *d,e*, pereopods 3,4 (in part).

Ranch near Fort Huachuca, Cochise County, Arizona. The cave is presumably developed in the Lower Paleozoic limestones which are exposed in the southwestern corner of the county. The type-specimens were collected at a depth of about 3 feet in a pool with a maximum depth of about 65 feet.

DISTRIBUTION AND ECOLOGY.—This species is known from two males collected in the type-locality and from one female collected from a small spring in a mine (in limestone) at Paradise. The latter locality is about 70 miles northeast of the type-locality. Although the single specimen from Paradise is generally similar in morphology to the Flying "H" Ranch specimens, I have not made it a paratype. The female from Paradise measured 3.7 mm and had setose brood plates.

Other Species

The following three species have not been assigned to the *hubbsi* group.

16. *Stygobromus mysticus*, new species

FIGURES 30, 31

MATERIAL EXAMINED.—CALIFORNIA. Siskiyou Co.: subterranean habitat at Greenview, holotype female (USNM 142794) and 24 paratypes (USNM 142795), W. E. Barrett (date of collection unknown).

DIAGNOSIS.—A rather unique, medium-sized subterranean species, probably distantly related to species of the *hubbsi* group and distinguished by proportionately small gnathopodal propods; deep coxal plates, especially plate 4, which is also broadly expanded; broadly expanded bases of pereopods 5–7 with convex posterior margins and large, rounded distoposterior lobes; narrow outer rami of uropods 1 and 2; and long, distally tapering telson with rather short apical spines. Largest females, 8.0 mm; male unknown.

DESCRIPTION.—Antenna 1: about 45 percent as long as body, 55 to 60 percent longer than antenna 2; primary flagellum with 15 or 16 segments. Antenna 2: peduncular segments 4 and 5 with a few spines and stiff setae; flagellum with 6 or 7 segments. Mandibles subequal; spine row with 7 spines; palpal segment 2 with 2 long setae; palpal segment 3 with row of short setae on inner margin and 4 long setae apically. Maxilla 1: inner plate with 9 or 10 apical, plumose setae; outer plate with 4 slender spines and 1 stiff seta on apex. Maxilla 2: inner plate with oblique row of 9 or 10 plumose setae on inner margin. Maxilliped: apex of inner plate with 1 bladelike spine, 3 plumose spines and

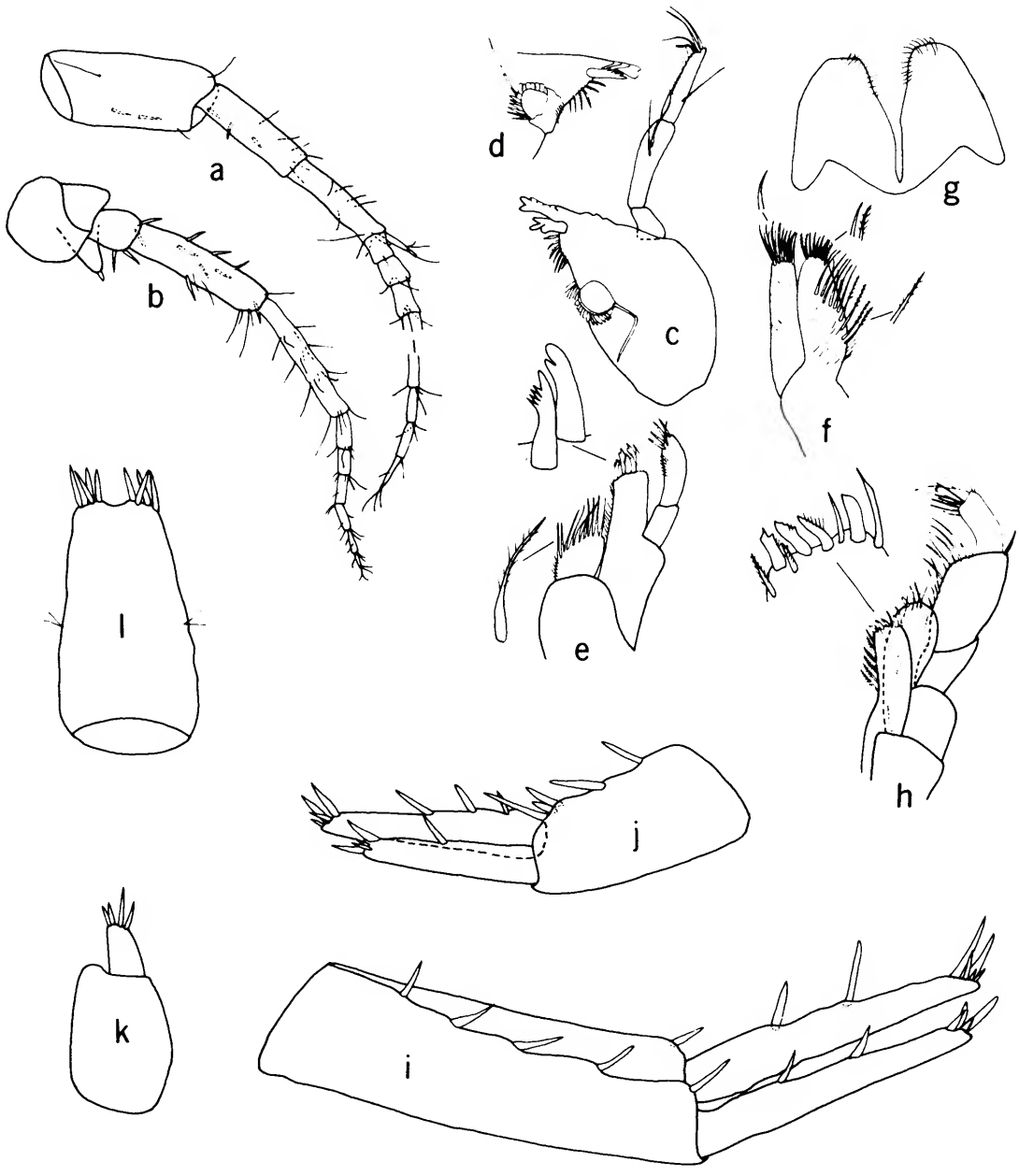

FIGURE 30.—*Stygobromus mysticus*, new species, female paratype (7.5 mm), Greenview, California: *a,b*, antennae 1,2; *c*, right mandible; *d*, dentate part of left mandible; *e,f*, maxillae 1,2; *g*, lower lip; *h*, maxilliped; *i,j,k*, uropods 1,2,3; *l*, telson.

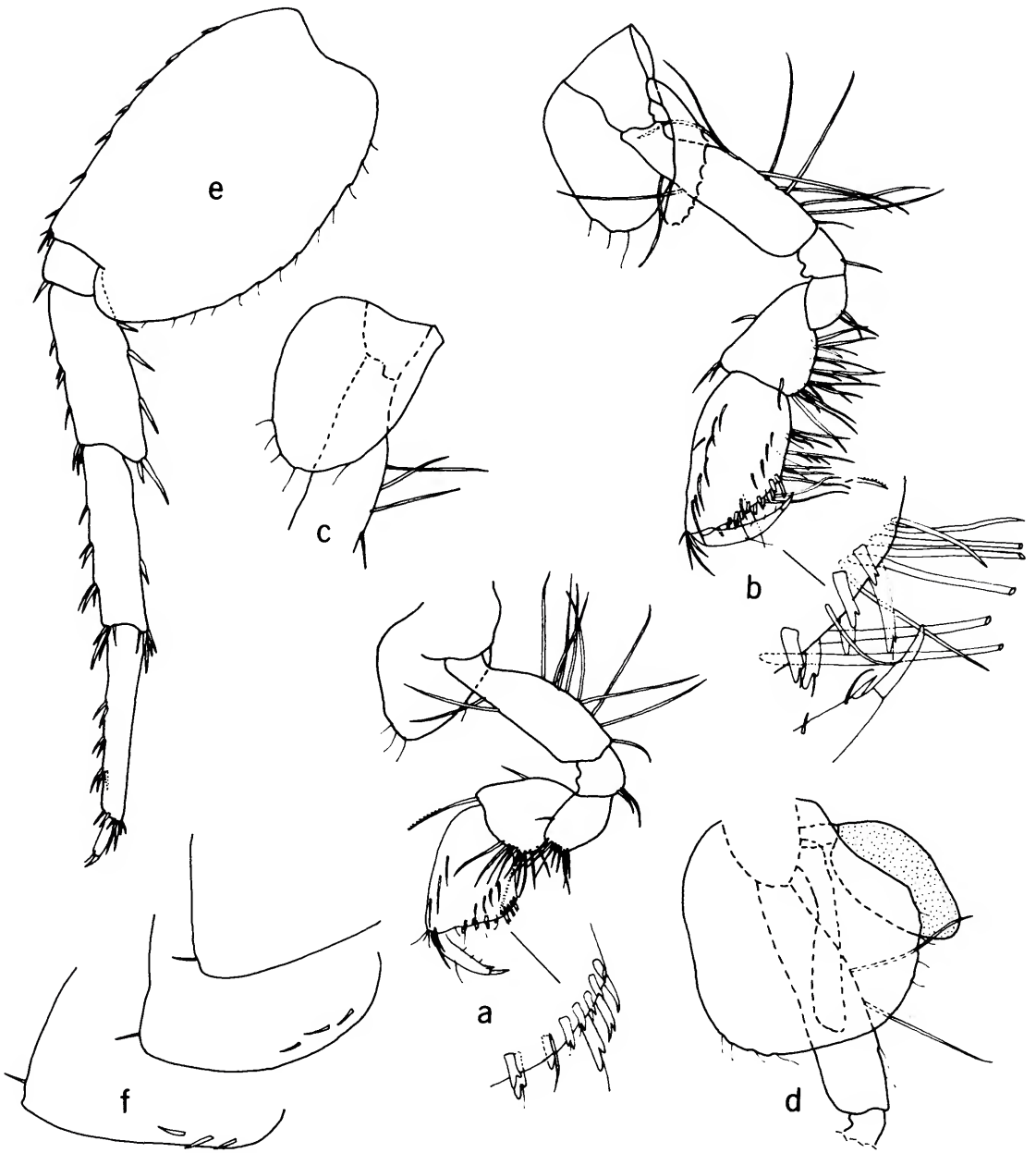

FIGURE 31.—*Stygobromus mysticus*, new species, female paratype (7.5 mm): *a,b*, gnathopods 1,2; *c,d*, pereopods 3,4 (in part); *e*, pereopod 7; *f*, pleonal plates.

3 or 4 setae, inner margin with 6 plumose setae; outer plate with 1 bladelike spine and about 6 stiff setae apically. Lower lip without inner lobes.

Gnathopodal Propod 1: Palm not oblique, nearly straight, armed with double row of 4 small spine teeth; posterior angle with 3 long spine teeth on

outside, 5 shorter spine teeth on inside; posterior margin without setae; medial setae singly inserted. Coxal plate of gnathopod 1 longer than broad, with 4 marginal setae. Gnathopodal propod 2 as broad as, but about one-fourth longer than, 1st propod; palm slightly convex, armed with double row of 6 spine teeth; posterior angle defined by 1 long spine tooth and several long setae on outside, 1 short spine tooth on inside; posterior margin about as long as palm, with 3 sets of 3 or 4 long setae each; medial setae mostly singly inserted; dactyl nail and accessory spine moderately long. Coxal plates of gnathopod 2 and pereopod 3 rather deep, about 30 percent longer than broad, with 4 or 5 marginal setae each; coxal plate of pereopod 4 broad and deep, reaching about two-thirds the length of segment 2, with 9 or 10 short setae marginally. Pereopod 6 a little longer than pereopod 7, about 40 percent as long as body, about 20 percent longer than pereopod 5. Bases of pereopods 5–7 broadly expanded; posterior margins convex; distoposterior lobes large, bluntly rounded. Dactyls of pereopods 6 and 7 about one-third the length of corresponding propods. Coxal gills on pereopods 2–6. Brood plates of mature females small and narrow.

Pleonal Plates: Posterior margins nearly straight; posterior corners of plates 1 and 3 tiny but distinct, that of plate 2 rounded and indistinct; ventral margins of plates 2 and 3 with 3 spines each. Uropod 1: inner ramus a little longer than outer ramus, about two-thirds the length of peduncle, armed with 7 spines; outer ramus with 5 spines; peduncle with 6 spines. Uropod 2: inner ramus about one-fourth longer than outer ramus, equal in length to peduncle, armed with 7 spines; outer ramus with 4 or 5 spines; peduncle with 5 spines. Uropod 3: ramus about one-third the length of peduncle, with 4 rather short, apical spines. Telson nearly twice as long as broad, tapering distally; apical margin with very shallow notch; apical lobes with 4 short spines each.

TYPE-LOCALITY.—A subterranean habitat at Greenview, Siskiyou County, California. The habitat is possibly a well, but this was not specified on the collection label. Greenview is located in the Klamath Mountains and the area surrounding the town is underlain by both metamorphic rocks of Paleozoic age and more recent deposits of Quaternary age.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality. Two of the larger females in the sample measured 7.5 to 8.0 mm and had setose brood plates.

ETYMOLOGY.—The specific name is from the Latin *mysticus,* meaning "secret," so named because of the secretive nature of this species, both in regard to its habitat and its relationship to other western species of the genus *Stygobromus.*

17. *Stygobromus montanensis,* new species

FIGURES 32, 33

MATERIAL EXAMINED.—MONTANA. Ravalli Co.: well at Victor Crossing, holotype female (USNM 142792) and 4 paratypes (USNM 142793), Ocie Hessling, 11 Oct. 1952.

DIAGNOSIS.—A small to medium-sized subterranean species, possibly related to species of the *hubbsi* group but differing in the possession of setae on the posterior margin of gnathopodal propod 1 and the presence of 2 pairs of tiny, simple, lateral sternal processes on pereonites 6 and 7. Largest female, 5.5 mm; male unknown.

DESCRIPTION.—Antenna 1, 50 percent as long as body, 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal; spine row with 7 spines; segment 2 of palp with 7 stiff setae on inner margin; segment 3 of palp with row of short setae on inner margin and 3 long setae on apex. Maxilla 1: inner plate with 7 plumose setae apically; outer plate with 3 apical spines and 3 or 4 setae subapically. Maxilla 2: inner plate with oblique row of 7 plumose setae; outer plate with about 15 long, stiff setae apically. Maxilliped: inner plate with 2 bladelike spines, 4 serrate spines and 3 setae apically; outer plate with 1 bladelike spine and 5 setae apically. Lower lip, inner lobes tiny or vestigial.

Gnathopodal Propod 1: Palm slightly convex, armed with double row of 6 spine teeth; posterior angle defined by 1 long and 2 short spine teeth and 1 long seta on outside, 3 short spine teeth on inside; posterior margin with 2 long and 2 or 3 short setae; inferior medial setae singly inserted, superior medial setae doubly inserted; dactyl nail rather long. Coxal plate of gnathopod 1 a little longer than broad, with 5 or 6 marginal setae. Gnathopod 2: propod larger than 1st propod; palm

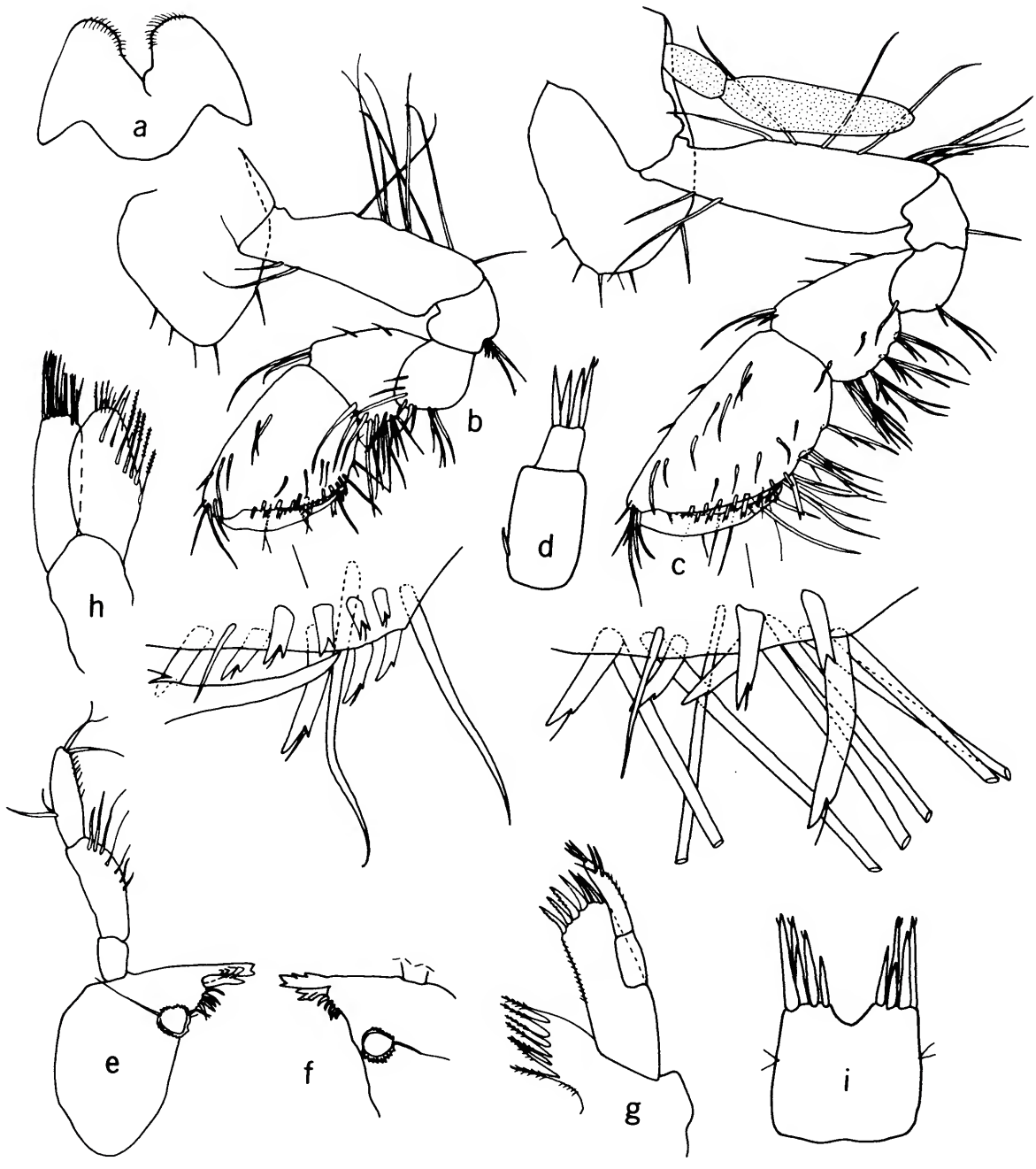

FIGURE 32.—*Stygobromus montanensis*, new species, female paratype (5.0 mm), well at Victor Crossing, Montana: *a*, lower lip; *b,c*, gnathopods 1,2; *d*, uropod 3; *e*, left mandible; *f*, dentate part of right mandible; *g,h*, maxillae 1,2; *i*, telson.

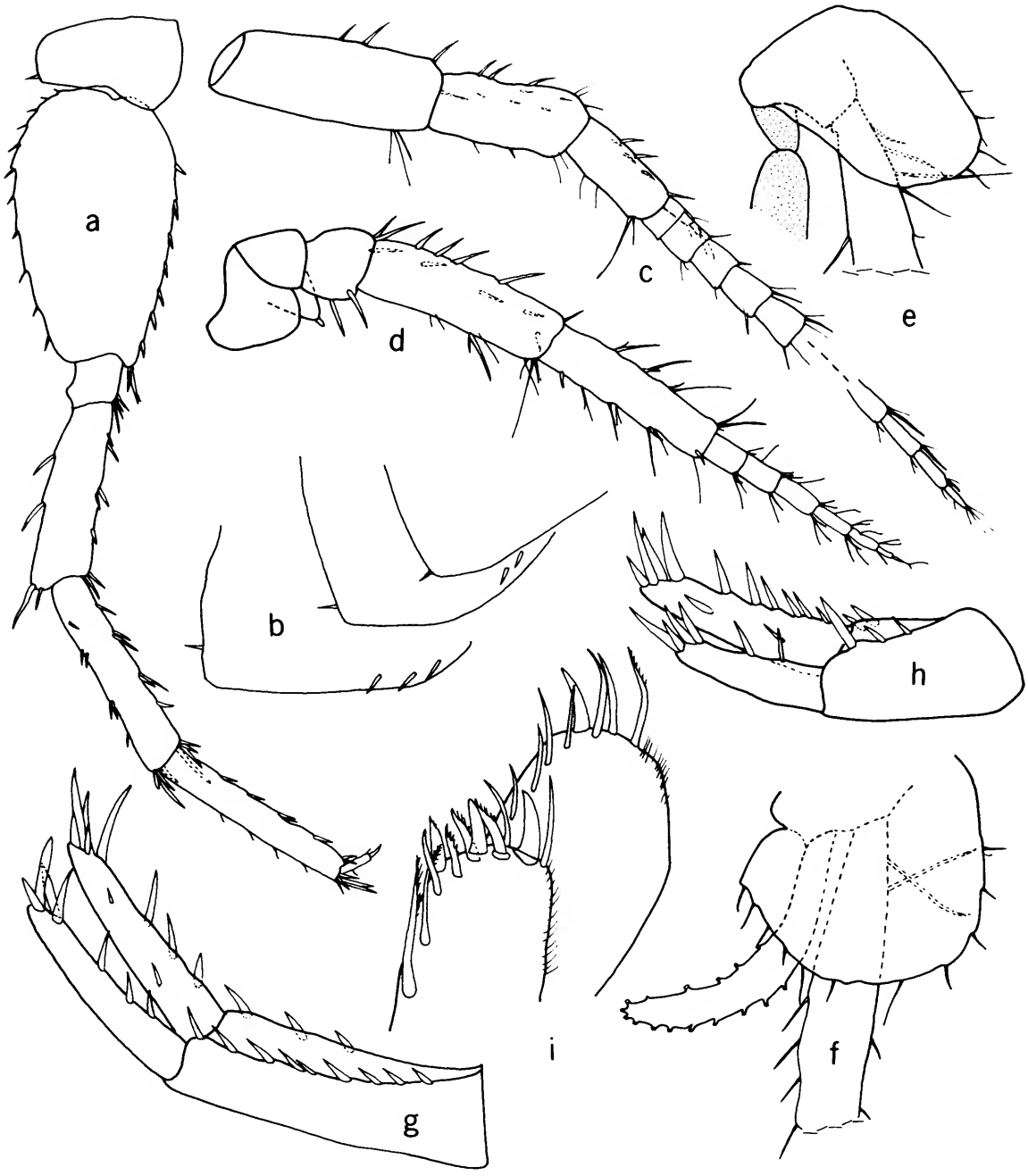

FIGURE 33.—*Stygobromus montanensis*, new species, female paratype (5.0 mm): *a*, pereopod 6; *b*, pleonal plates; *c,d*, antennae 1,2; *e,f*, pereopods 3,4 (in part); *g,h*, uropods 1,2; *i*, apexes of inner and outer plates of maxilliped (greatly enlarged).

oblique, convex, armed with double row of 6 or 7 spine teeth; posterior angle not well defined, with 1 long, curved spine tooth and 2 long setae on outside, 1 short spine tooth on inside; posterior margin about as long as palm, with 2 sets of long setae; inferior medial setae singly inserted, superior medial setae mostly doubly inserted; dactyl nail rather long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 6 marginal setae each; coxal plate of pereopod 4 about as broad as long, with 11 marginal setae. Bases of pereopods 5–7 broader proximally than distally; posterior margins convex; distoposterior corners small, bluntly rounded. Pereopod 6 slightly longer than pereopod 7, 50 to 55 percent as long as body, about 20 percent longer than pereopod 5. Dactyls of pereopods 6 and 7 rather short, about 25 percent as long as corresponding propods. Coxal gills on pereopods 2–6. Tiny, paired, simple lateral processes on pereonites 6 and 7. Brood plates of female small and narrow.

Pleonal Plates: Posterior margins nearly straight to slightly convex, with 1 seta each; distoposterior corners rounded, indistinct on plate 1; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uropod 1: inner ramus a little longer than outer ramus, about three-fourths the length of peduncle, armed with 10 spines; outer ramus with 7 spines; peduncle with 12 spines. Uropod 2: inner ramus about one-fourth longer than outer ramus, a little longer than peduncle, armed with 13 spines; outer ramus with 6 spines; peduncle with 5 or 6 spines. Uropod 3: ramus about 40 percent as long as peduncle, armed with 4 apical spines. Telson a little broader than long; apical margin with wide, shallow notch; apical lobes with 5, unequal spines each.

TYPE-LOCALITY.—Well at Victor Crossing, Ravalli County, Montana. See notes under the description of *S. tritus* for further details.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality on the basis of five females collected on 11 October 1952. The five specimens were taken in a sample containing two specimens of *S. obscurus* (described later) and 11 specimens of *S. tritus*. The females ranged in size from 5.0 to 5.5 mm and several had brood plates fringed with setae.

COMMENTS.—The presence of setae on the posterior margin of gnathopodal propod 1 and the possession of lateral sternal processes exclude this species from the *hubbsi* group. With the exception of these two characters, however, *S. montanensis* appears to be more closely allied with species of this group than with *S. obscurus*.

18. *Stygobromus obscurus*, new species

FIGURES 34, 35

MATERIAL EXAMINED.—MONTANA. Ravalli Co.: well at Victor Crossing, holotypes female (USNM 142796) and 1 paratype (USNM 142797), Ocie Hessling, 11 Oct. 1952.

DIAGNOSIS.—A rather unusual, medium-sized subterranean species, apparently unrelated to other known species of *Stygobromus* in the western United States and readily distinguished by the gnathopodal propods being subequal in size; shallow coxal plates of gnathopod 2 and pereopods 3 and 4; narrow bases of pereopods 5–7 which lack distoposterior lobes; possession of 2 pairs of simple, lateral sternal processes; absence of ventral spines on the pleonal plates; numerous long spines on the uropods; and by the apical margin of the telson which is narrowly incised about one-fourth the length to base and armed with 14 rather long spines. Largest female, 7.0 mm.

DESCRIPTION.—Antenna 1: about 50 percent as long as body, 35 percent longer than antenna 2; primary flagellum with 15 segments. Antenna 2: peduncular segments 4 and 5 with a number of slender spines and stiff setae; flagellum with 5 segments. Mandibles subequal; spine row with 5 spines; palpal segment 2 with 8 long, inner marginal setae; palpal segment 3 with row of short setae on inner margin and 5 long setae near apex. Maxilla 1: inner plate with 5 apical, plumose setae; outer plate with 4 spines and 2 setae apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin; outer plate with 8 to 10 stiff setae. Maxilliped: inner plate with 4 thick spines and 1 stiff seta apically; outer plate reaching only about one-fourth the length of palpal segment 2, apex with 2 spines and 1 seta, inner margin with 4 or 5 setae. Lower lip with prominent outer lobes and small but distinct inner lobes.

Gnathopod 1: Propod equal to or perhaps a little longer than 2nd propod; palm long, oblique, nearly straight, armed with double row of 13 spine teeth; posterior angle not well defined; posterior margin

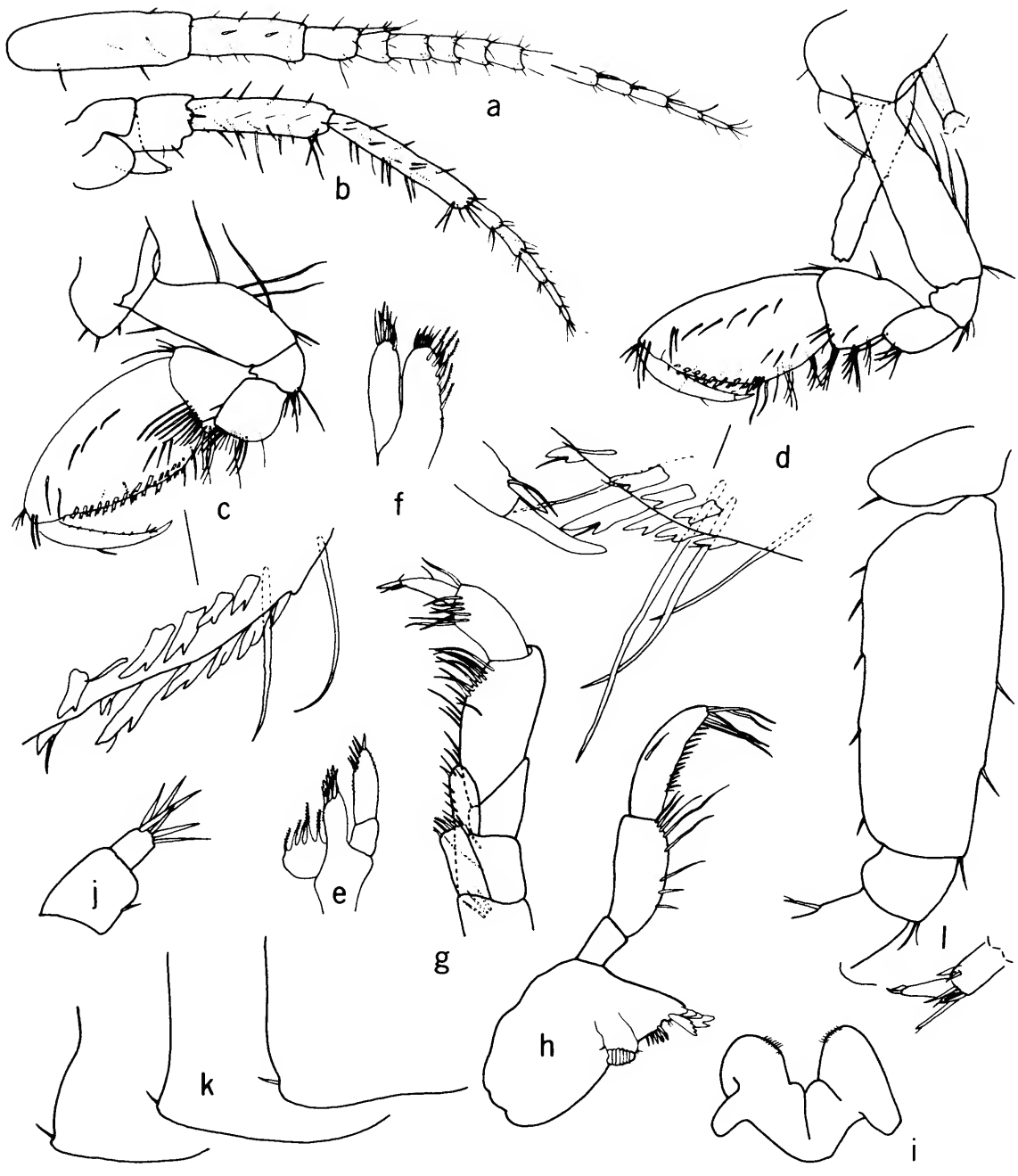

FIGURE 34.—*Stygobromus obscurus*, new species, female paratype (7.0 mm), well at Victor Crossing, Montana: *a,b*, antennae 1,2; *c,d*, gnathopods 1,2; *e,f*, maxillae 1,2; *g*, maxilliped; *h*, left mandible; *i*, lower lip; *j*, uropod 3; *k*, pleonal plates; *l*, pereopod 7 (in part).

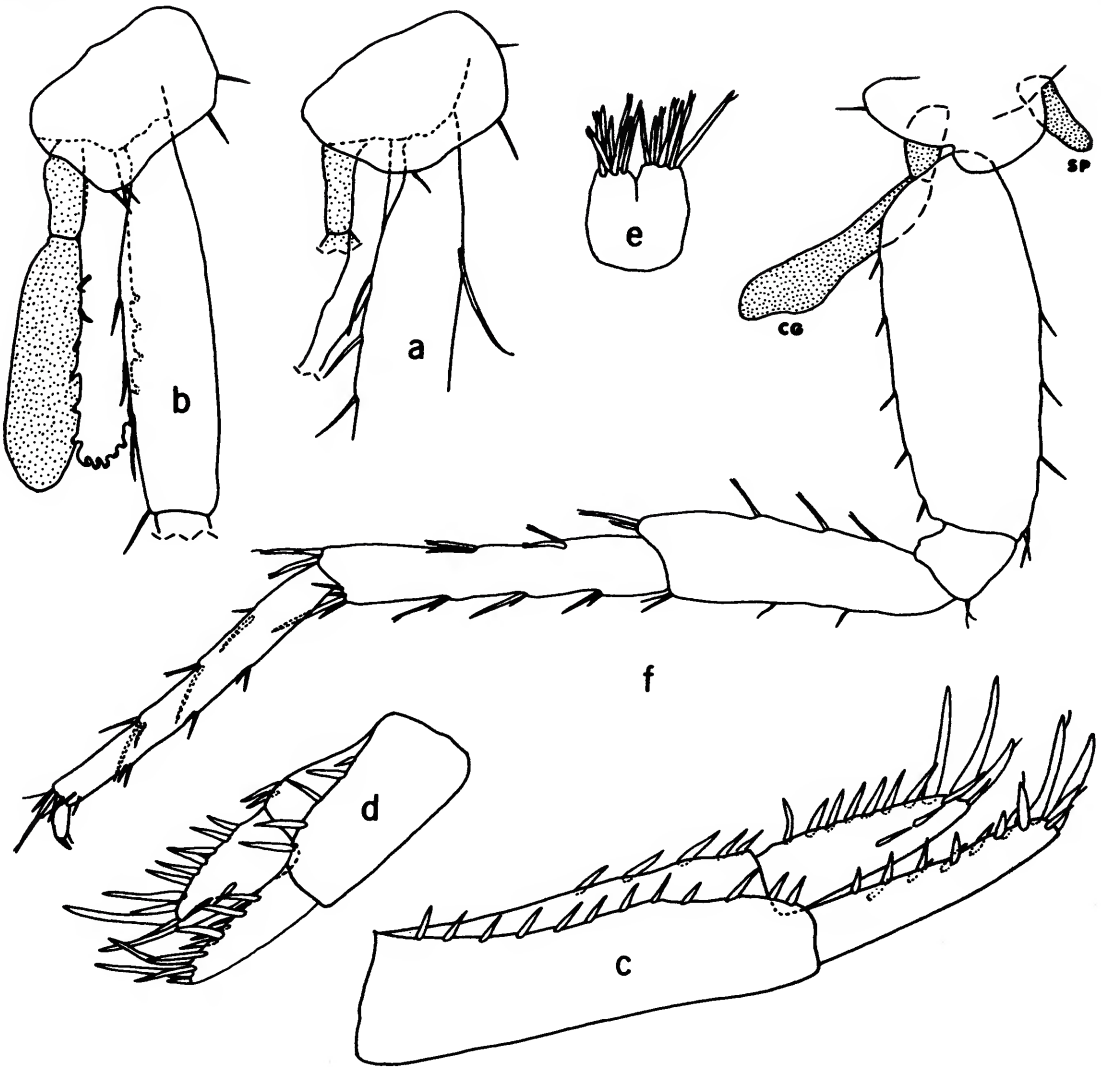

FIGURE 35.—*Stygobromus obscurus*, new species, female paratype (7.0 mm): *a,b*, pereopods 3,4 (in part); *c,d*, uropods 1,2; *e*, telson; *f*, pereopod 6 (note coxal gill, CG, and lateral sternal process, SP).

comparatively short, with 1 long seta; medial setae few in number, singly inserted. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopodal propod 2 about as long as, but not as broad as, 1st propod; palm convex, armed with double row of 7 or 8 spine teeth; posterior angle with 1 long and 3 short spine teeth and 2 long setae on outside, 3 short spine teeth on inside; posterior margin nearly as long as palm, with 2 sets of 4 long setae each; medial setae mostly singly inserted; dactyl nail rather short. Coxal plate of gnathopod 2 about as broad as long, with 3 marginal setae; coxal plates of pereopods 3 and 4 shallow, broader than long, with 3 or 4 marginal setae. Pereopods 6 and 7 about equal in length, about 45 percent as long as body, about 35 percent longer

than pereopod 5. Bases of pereopods 5–7 narrow, about as broad proximally as distally; distoposterior lobes indistinct; posterior margins with 5 or 6 short setae; anterior margins with 2 or 3 long, stiff setae. Dactyls of pereopods 6 and 7 comparatively short, only 15 to 20 percent as long as corresponding propods. Coxal gills on pereopods 2–6. Small, simple, paired lateral sternal processes on pereonites 6 and 7. Brood plates of female small and narrow.

Pleonal Plates: Posterior margins of 1 and 3 slightly convex, that of 2 concave; posterior corners small, distinct, rounded; ventral margins without spines. Uropod 1: inner ramus shorter and thicker than outer ramus, about one-half the length of peduncle, armed with 14 spines; outer ramus with 14 or 15 spines; peduncle with 17 spines. Uropod 2: inner ramus shorter and thicker than outer ramus, about two-thirds the length of peduncle, armed with 14 spines; outer ramus with 7 spines; peduncle with 7 spines. Uropod 3: ramus about one-half the length of peduncle, armed with 6 long, apical spines. Telson about as broad as long; apical margin incised about one-fourth the distance to base; apical lobes with 7 long spines each.

TYPE-LOCALITY.—A well as Victor Crossing, Ravalli County, Montana. See notes under the description of *S. tritus* for further details.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality on the basis of two females collected on 11 October 1952. The two specimens were found in a sample containing 11 specimens of *S. tritus* and 5 specimens of *S. montanensis*. The brood plates of the larger female (7.0 mm long) were fringed with setae, indicating sexual maturity.

COMMENTS.—This species differs from members of the *hubbsi* group by having gnathopodal propod 1 equal to or slightly larger than propod 2, possession of setae on the posterior margin of gnathopodal propod 1, possession of lateral sternal processes, equal length of pereopods 6 and 7, and heavily spinose uropods. With *S. montanensis*, it shares the possession of lateral sternal processes and setae on the posterior margin of gnathopodal propod 1, but in other characters it does not appear to be closely related. Were it not for the free uronites and its geographic distribution, *S. obscurus* could be assigned to the genus *Stygonectes*.

ETYMOLOGY.—The specific name is from the Latin *obscurus*, meaning "indistinct" or "obscure," so named because of the obscure relationship of this species to other members of the genus *Stygobromus*.

Zoogeography

In previous papers (Holsinger, 1966, 1967, 1971) I have discussed a possible mode of origin for some of the freshwater, subterranean amphipod genera of North America (north of Mexico), pointing out that these groups might have evolved from marine or brackish-water ancestors during periods of marine embayments. The major difficulties in tracing these freshwater groups to marine ancestors are the lack of a fossil record and the absence of a potential marine ancestral group living in the sea at the present time. Another cogent question is, namely, have contemporary subterranean genera like *Stygobromus, Stygonectes, Apocrangonyx, Allocrangonyx*, etc. evolved directly from blind, depigmented, brackish-water ancestors that were living in interstitial habitats at the onset of their invasion of continental freshwaters, or have these exclusively subterranean genera been derived from eyed, pigmented ancestral forms living in epigean habitats prior to their colonization of subterranean waters? Unfortunately, the present evidence does not allow a definitive answer.

Assuming, a priori, as I have done previously that the exclusively subterranean genera of North America were derived directly from brackish water, interstitial ancestors, such as has been rather convincingly shown to be the case with the evolution of the subterranean *Hadzia* group genera of the greater Caribbean region (Holsinger and Peck, 1968; Holsinger and Minckley, 1971; Holsinger, 1973), then one must look to past geologic times when parts of the North American land mass were inundated by shallow marine waters. As I have already pointed out, the extensive marine embayments of the Late Cretaceous and possibly the early Tertiary would have provided these conditions. During the inundation of North America in the Late Cretaceous, marine waters covered a significant portion of western and southern North America, with wide arms of the sea stretching from the Caribbean region north to the Arctic Ocean and across the Gulf and Atlantic Coastal plains (Dunbar, 1960; Kummel, 1961).

The ancestral stock of *Stygobromus*, as well as that of the other members of the generic complex

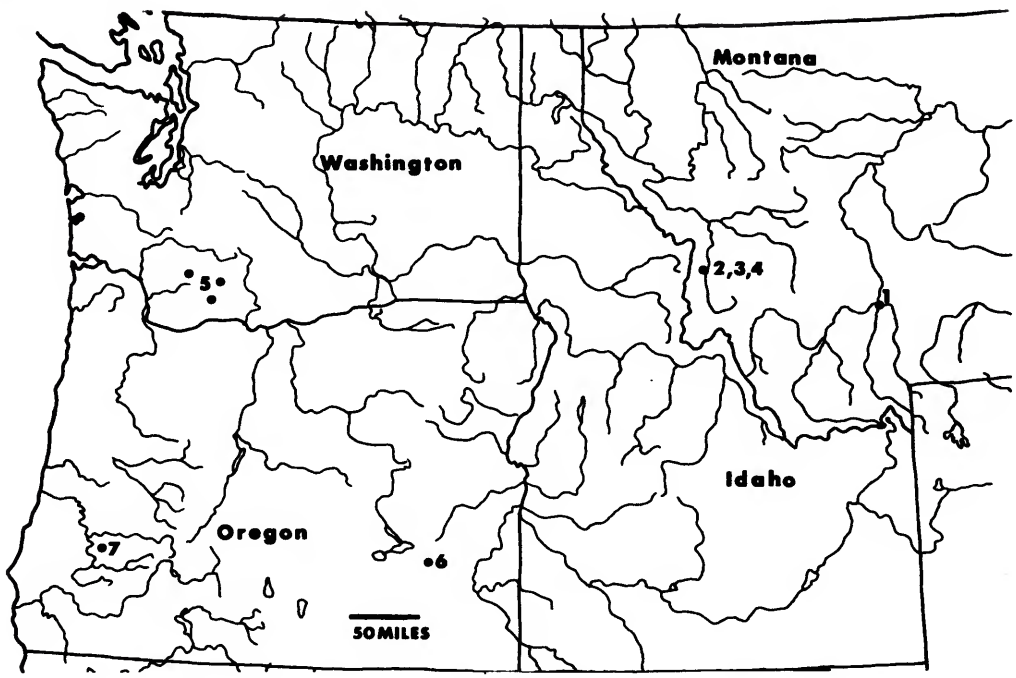

FIGURE 36.—Distribution of species of *Stygobromus* in Montana, Oregon, and Washington: 1, *S. puteanus;* 2,3, and 4, *S. montanensis, S. obscurus, S. tritus;* 5, *S. elliotti* (3 lava caves); 6, *S. hubbsi;* 7, *S. oregonensis.*

which includes *Stygonectes* and *Apocrangonyx* (see Holsinger, 1969a), might have been widespread in these shallow marine embayments. Gradual regression of marine waters from the continental land mass would have been accompanied by the formation of new freshwater habitats, thus affording the opportunity for the invasion of newly opened niches. Access by freshwater invaders to inland massifs such as the Appalachians, Interior Low Plateaus, Ozarks, and the western Cordillera would have been facilitated since none of these areas were far removed from ancient Cretaceous shorelines.

Another hypothesis for the origin of North American, subterranean amphipods, and one favored by some amphipodologists, is that these genera or their ancestors were already established in continental freshwaters by the middle of the Mesozoic (see for example, Bousfield, 1958:56). Acceptance of this hypothesis would assume perforce a marine to freshwater invasion much older than the Cretaceous, perhaps as early as the Late Paleozoic. The attractive features of this theory are that it diminishes the importance of the lack of an extant group of potential marine ancestors and makes the widespread, Holarctic distribution of the entire *Crangonyx* group easier to comprehend.

As shown in Figures 36 and 37, the geographic distributions of species of *Stygobromus* in the western United States are widespread and scattered. Many of these species display highly insular ranges and all but four are known only from a single locality. Even those species represented in two or more localities are restricted to small ranges and only one species, *S. arizonensis,* has a range possibly as wide as 70 to 75 miles. The present distributional patterns, however, may not reflect the true ranges of all species, nor can the number of species now recorded from the western United States be regarded as final. With the exception of many of the caves in the Mother Lode region of California, some of the lava tubes of Washington and other well studied spots such as Lake Tahoe, numerous potential *Stygobromus* habitats remain to be investigated in the rugged mountainous country of

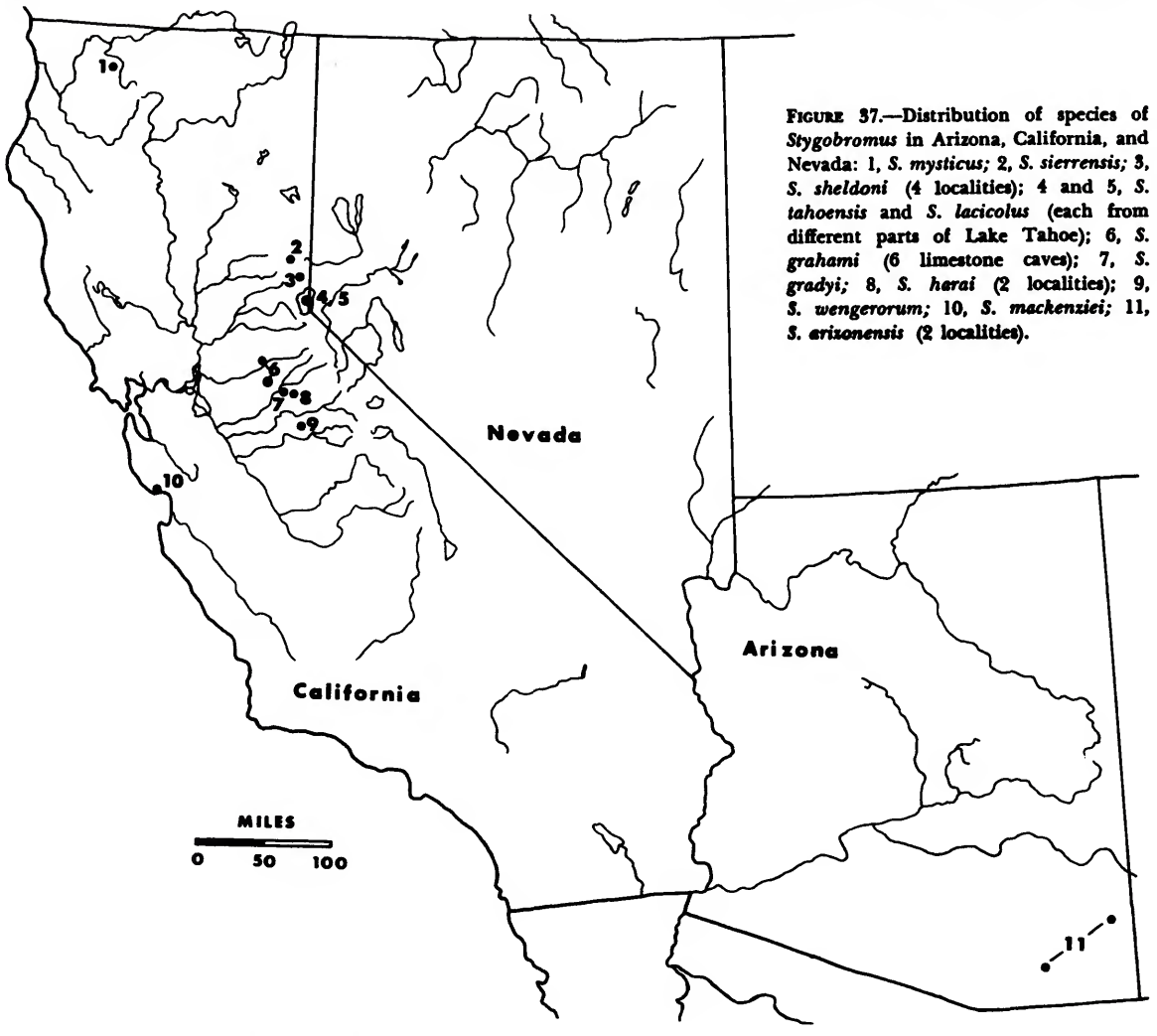

FIGURE 37.—Distribution of species of *Stygobromus* in Arizona, California, and Nevada: 1, *S. mysticus;* 2, *S. sierrensis;* 3, *S. sheldoni* (4 localities); 4 and 5, *S. tahoensis* and *S. lacicolus* (each from different parts of Lake Tahoe); 6, *S. grahami* (6 limestone caves); 7, *S. gradyi;* 8, *S. harai* (2 localities); 9, *S. wengerorum;* 10, *S. mackenziei;* 11, *S. arizonensis* (2 localities).

the west. Many habitats such as wells, seeps, and remote caves and springs in the more inaccessible regions of the Sierra Nevada and other mountain ranges may be expected to yield additional populations, if not new species, when they are finally checked. The reported sighting of amphipod crustaceans (presumably subterranean) in Devil's Hole, Nye County, Nevada, by La Rivers (1962) and other unconfirmed site records of subterranean amphipods strongly indicate that these animals are more common in the West than previously believed or than are borne out by the findings reported in the present paper. Moreover, the biological investigation of lava caves in the northwestern part of the country has just begun in earnest (F. G. Howarth, in litt.; Peck, in press) and continued study of these unique caves will almost certainly reveal additional populations of subterranean crustaceans.

The numerical distribution of species by physiographic province or subprovince is as follows (number of species in parentheses): Northern Rocky Mountains (4), Payette Section of the Columbia Plateaus (1), Northern Cascade Mountains (1), Oregon Coastal Range (1), Klamath Mountains (1), California Coastal Range (1), Sierra Nevada (8), and the Mexican Highland of the Basin and Range (1). Species are, in turn, numerically distributed by major biotope as follows: limestone or

marble caves (6), lava caves (3), wells (4 or 5), springs (2), and deep lake (2). Only one species, *S. puteanus,* occurs east of the Continental Divide, in an area that drains north and east to the Missouri River system. The remaining species occur west of the Continental Divide in drainage systems flowing west to the Pacific Ocean.

Of added zoogeographic interest is the occurrence of *S. putealis,* a member of the *hubbsi* group, in eastern Wisconsin, some 1100 miles east of the range of the western species. If one assumes that species of the *hubbsi* group were derived from a common ancestral species or a cluster of closely related species and that the similarity of *S. putealis* to western species is more than coincidental, then the presence in Wisconsin of a species belonging to a group otherwise known only from the far western United States must clearly be regarded as a relict distribution. Since the middle of the Cenozoic, climates have become increasingly arid in the west-central United States (i.e., across the Great Plains), and this area, north of central Texas, is practically devoid of freshwater amphipods, either epigean or hypogean. If there was a continuous distribution of *hubbsi* group progenitors across the west-central United States then it must have occurred prior to the Miocene while the climate in this region was still humid.

An extensive discussion of speciation within the genus *Stygobromus* must logically await the completion of the three part generic revision. However, based on knowledge of previously described species and my observations on many of the undescribed species of the genus, the *hubbsi* group appears to be a distinct evolutionary group within the genus. With the exception of *S. putealis* from Wisconsin, the *hubbsi* group (and the other three species described above) is geographically disjunct from all other species of *Stygobromus* and occupies a position well isolated from all other subterranean amphipod genera of North America.

The present distributional patterns of the western species have probably resulted from fragmentation of previously more widespread populations and concomitant isolation of gene pools. The western United States has been marked by a series of major geological changes and climatic shifts since the Laramide Revolution, but modern landforms and climates are the result of events in the middle to late Tertiary such as the Cascadian Revolution and extensive regional volcanism. According to King (1958), both regional and local relief and climatic contrasts have been greater in the Cordillera since the mid-Tertiary than at any other time. Many habitats presently occupied by species of *Stygobromus* are no older than the Pleistocene, if not, as in the case of the Oregon and Washington lava tubes, even more recent. As Pennak (1958:224) has pointed out for aquatic invertebrates in general: ". . . the western states appear to present a set of conditions that should encourage isolation and speciation, especially in certain taxa containing macroscopic forms, and the West should theoretically have a unique population of freshwater invertebrates."

Although the 15 species of the *hubbsi* group comprise a relatively homogeneous assemblage, several patterns of speciation are discernible. The most obvious pattern is demonstrated by the four closely related cave species of the Mother Lode region of California. The close morphological similarity of these species (especially in regard to their mouthparts and gnathopods), combined with their geographic proximity and similarity in habitat, is strongly indicative of their derivation from a recent common ancestor. The isolated nature of the limestone lenses containing caves in the Mother Lode region could easily provide dispersal barriers to troglobites (or phreatobites), thus effectively isolating populations to single caves or small clusters of caves.

Three other species—*S. hubbsi, S. sierrensis,* and *S. lacicolus*—appear to be closely related to the four cavernicolous species of the Mother Lode region. While these species differ in the structure of their mouthparts (i.e., having fewer plumose setae on the maxillae and fewer spines on the inner plate of the maxilliped), their gnathopodal propods are very similar to the Mother Lode species, and two of these species occupy habitats only 50 to 75 miles north of the California cave region. *Stygobromus hubbsi,* on the other hand, occurs in a lava cave approximately 350 miles north of the Mother Lode region. Moreover, aside from their smaller size and other minor differences, three other species from California—*S. tahoensis, S. mackenziei,* and *S. sheldoni*—also show affinity with the Mother Lode cave species as well as with *S. sierrensis* and *S. lacicolus.* The remaining five species of the *hubbsi* group differ more significantly from the

Mother Lode species, are far removed geographically, and occur on the periphery of the range of the group. Thus, it would appear that at least one major center of speciation within the *hubbsi* group has taken place in the east-central California region, producing species which have successfully colonized a diversity of groundwater habitats, including caves, springs, and at least one deep lake.

Only two instances of sympatry (or syntopy) are so far known among western species of *Stygobromus*. The first is the curious association of three species in the well at Victor Crossing in Ravalli County, Montana. Of the three species, however, only *S. tritus* is a member of the *hubbsi* group. A second member of the trio, *S. montanensis*, while showing a remote affinity with the *hubbsi* group, is at best only distantly related to *S. tritus*. The third member, *S. obscurus*, is unrelated to any of the other western species of the genus and, in addition, bears some affinity with the genus *Stygonectes*, a genus unknown from any farther west than central Texas. Unfortunately, very little is known about the well at Victor Crossing and it is not known whether these three species continuously share the same habitat or only occasionally come in contact. On the basis of the two samples removed from this well in October 1952, *S. tritus* appears to be by far the most common of the three species recorded from this habitat.

The other sympatric association occurs in Lake Tahoe, where both *S. tahoensis* and *S. lacicolus* were obtained in periodic samples made in the early 1960s. Of the 16 samples studied, however, the two species were found together only twice, and *S. tahoensis* appeared to be much more abundant than *S. lacicolus*.

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