Systematics of the Subterranean Amphipod Genus *Stygobromus* (Crangonyctidae), Part II: Species of the Eastern United States

JOHN R. HOLSINGER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 266

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Systematics of the Subterranean Amphipod Genus *Stygobromus* (Crangonyctidae), Part II: Species of the Eastern United States

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SMITHSONIAN INSTITUTION PRESS
City of Washington
1978

ABSTRACT

Holsinger, John R. Systematics of the Subterranean Amphipod Genus *Stygobromus* (Crangonyctidae), Part II: Species of the Eastern United States. *Smithsonian Contributions to Zoology,* number 266, 144 pages, 77 figures, 1978.—The amphipod genus *Stygobromus* is widespread in the subterranean waters of the United States and is recorded from a variety of groundwater habitats. A revised diagnosis of the genus is given and a tentative division into three subgeneric groups is proposed. The recently proposed synonymy of *Stygonectes* and *Apocrangonyx* with *Stygobromus* is reaffirmed. Forty-eight described species are herein recognized from the Appalachian and Coastal Plain regions of the eastern United States, of which 30 are newly described, three are completely redescribed, and new systematic data are given for the remainder. In addition, six populations are provisionally recognized as distinct species but are not described because of lack of adequate material. On the basis of morphology and geographic distribution, 12 species groups are recognized in the eastern United States, eight of these being newly established herein.

Ancestral stygobromids are now believed to have occurred earlier in the freshwater environment than originally suggested. Species of *Stygobromus* occupy a diversity of groundwater and groundwater-related habitats in the eastern United States, including primarily cave pools and streams, phreatic reservoirs and the hypotelminorheic media of seeps and small springs. Habitat selection is based on niche breadth and movement through shallow groundwater, both of which are believed to be significant factors in dispersal and geographic distribution. A number of species occur syntopically and/or sympatrically but most closely allied species have allopatric ranges. The possibility that several species are glacial relicts of the Pleistocene is raised.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Holsinger, John R.
Systematics of the subterranean amphipod genus Stygobromus (Gammaridae).
(Smithsonian contributions to zoology, no. 160, 266)
Vol. 2 has title: Systematics of the Subterranean amphipod genus Stygobromus (Crangonyctidae)
Bibliography: v. 1, p. 62–63; v. 2, p.
Contents: pt. 1. Species of the Western United States.—pt. 2. Species of the Eastern United States.
Supt. of Docs. no.: SI 1.27:266
1. Stygobromus—Classification. 2. Crustacea—Classification. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 160, 266 [etc.]
QL1.S54 no. 160, etc. 591'.08s [595'.371] 73–9808 [QL444M315]

Contents

Systematics of the Subterranean Amphipod Genus *Stygobromus* (Crangonyctidae), Part II: Species of the Eastern United States

John R. Holsinger

Introduction

Prior to recent papers by Karaman (1974) and Holsinger (1977), which suggested lumping *Stygobromus, Stygonectes,* and *Apocrangonyx,* 28 species had been assigned to the genus *Stygobromus* (Holsinger, 1974), 29 to the genus *Stygonectes* (Holsinger, 1967), and six to the genus *Apocrangonyx* (Holsinger, 1969b). In the present paper, 30 new species are described and the synonymy of *Stygonectes* and *Apocrangonyx* with *Stygobromus* is reaffirmed. The results of the present study bring the total number of species in *Stygobromus* to 93, making it one of the largest genera of freshwater amphipod crustaceans.

Stygobromus was previously considered a member of the family Gammaridae, but recently Bousfield (1973, 1977), Barnard (1976), and Holsinger (1977) have begun to subdivide this heterogeneous taxon into smaller, more discrete, monophyletic families which better represent evolutionary trends and world patterns of geographic distribution. Thus, *Stygobromus* and five other genera of the old *Crangonyx* group of Schellenberg (1936) are now assigned to the Holarctic family Crangonyctidae (emend.) (Holsinger, 1977).

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Part I of a series of three papers planned to revise the systematics of *Stygobromus* treated 18 species (17 newly described) from the western United States (Holsinger, 1974). The present paper, which is Part II of the series, treats 48 species: 30 are newly described, three previously described species are completely redescribed, and new data are given for the remaining 15. Of the 18 previously described species treated, 13 were originally assigned to *Stygonectes* (Holsinger, 1967, 1972), three to *Apocrangonyx* (Holsinger, 1969b, 1972), and two to *Stygobromus* (Holsinger, 1972). Part III, now in the early stages of preparation, will cover 26 previously described species and approximately 30 new (provisionally recognized) species from the central and east-central United States (principally the Interior Low Plateaus, Ozark Plateau, and Edwards Plateau).

On the basis of morphological alliance and geographic distribution, 41 of the species considered in Part II have been assigned to species groups; the remaining seven species are unassigned, pending further study. Of the 12 species groups currently recognized, eight are newly erected and four were previously established in my monograph on *Stygonectes* (Holsinger, 1967).

All species of *Stygobromus* occur in groundwater or groundwater-related habitats (e.g., caves, seeps,

small springs, wells, interstices, and rarely deep lakes) and are of subterranean facies (i.e., eyeless, unpigmented, and frequently with attenuated bodies). The majority of species in the eastern United States is cavernicolous, but several of the cave forms are also found in wells and spring/seeps. Ten species are predominately noncavernicolous and, with one exception, occur in groundwater biotopes outside of cave and karst areas. A more detailed discussion of habitat diversity is included in the terminal section on zoogeographical and ecological considerations.

The geographic region covered in this study includes the Appalachian plateaus (excluding the cavernous western margin of the Cumberland Plateau section), New England, Valley and Ridge, Blue Ridge, Piedmont, and Coastal Plain physiographic provinces. The first five provinces are major components of the Appalachian Highlands (= Applalachian region of this paper), whereas the Coastal Plain is a separate physiographic division. Species from the Cumberland Plateau in Kentucky, Tennessee, and parts of Alabama will be considered in Part III.

METHODS AND MATERIALS.—Conventional methods for collecting subterranean amphipods have been discussed by me in previous papers (Holsinger, 1967, 1972). In the laboratory all measurements were made in millimeters to the nearest tenth 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 from appendages mounted in Hoyer's medium on glass slides. Appendages are not drawn to any particular scale unless noted to the contrary.

Holotype specimens are deposited in the National Museum of Natural History (Smithsonian Institution) under the catalog numbers of the former United States National Museum (USNM). Paratypes are deposited in either the National Museum of Natural History or my personal collection (JRH), as indicated. All other material is in my personal collection unless noted otherwise.

Synonymies for species formerly assigned to *Stygonectes* and *Apocrangonyx* are complete only back to the time of my revision of these genera (i.e., 1967 for *Stygonectes* and 1969b for *Apocrangonyx*). All other synonymies are complete back to original descriptions. Unless indicated otherwise, the keys are based on mature females.

Cave names and locations correspond to those in published state or county surveys or in the unpublished files of state cave surveys. Published surveys utilized in this study cover all or parts of Alabama (Tarkington, Varnedoe, and Veitch, 1965; Varnedoe, 1973), Maryland (Franz and Slifer, 1972), New York (Schweiker, et al., 1960; Davis, et al., 1966), Pennsylvania (Stone, 1953), Tennessee (Barr, 1961), Virginia (Douglas, 1964; Holsinger, 1975a), and West Virginia (Davies, 1958, 1965; Medville and Medville, 1971, 1976). Data on unpublished caves are often deposited in the cave files of the National Speleological Society. The locations of caves referred to in Georgia are found on a map published by Holsinger and Peck (1971).

ACKNOWLEDGMENTS.—I am grateful to the many biologists and cavers who assisted with the field work or donated specimens for study. Credits to all those who have helped are given in the "material examined" sections under the various species. I am especially grateful to Roger A. Baroody, David C. Culver, and Stewart B. Peck for their substantial and long-term assistance with the collection of specimens. In addition, D. C. Culver is thanked for his helpful comments during the course of the study. The West Virginia Association for Cave Studies (WVACS) is also thanked for assistance with field work in southern West Virginia.

Many cave owners allowed access to their properties, and their cooperation and interest in our ongoing biospeleological research is greatly appreciated. The managements of Endless and Luray caverns and the superintendents of Cumberland Gap National Historical Park, Rock Creek Park, Shenandoah National Park, and Natural Tunnel State Park are acknowledged for allowing me to collect from caves and springs under their jurisdictions. Gary W. Dickson and James A. Estes assisted with the preparation of the figures, and James F. Matta ran the SPSS Pearson Correlation Subroutine program. J. Laurens Barnard and Thomas E. Bowman arranged for loans of specimens from the Smithsonian Institution and Harold S. Feinberg arranged for a loan from the American Museum of Natural History (AMNH).

This study was supported by a grant from the National Science Foundation (GB-42332). In addition, travel funds for field work during August 1972

were provided by the Department of Invertebrate Zoology at the Smithsonian Institution.

Stygobromus Cope

Stygobromus Cope, 1872:422.
Apocrangonyx Stebbing, 1899:422.
Stygonectes W. P. Hay, 1903:430.
Synpleonia Creaser, 1934:1.

DIAGNOSIS.—Body smooth, uronites free or fused (sometimes only in part), without dorsal spines; head without rostrum, lateral lobe rather narrowly rounded anteriorly; eye absent. Antenna 1 longer than 2 (excepting the aberrant male of one species); 1st peduncular segment stouter and longer than 2nd; primary flagellar segments usually with aesthetascs; accessory flagellum 2-segmented. Antenna 2 of male without calceoli. Upper lip rounded apically, margin not incised. Mandible with well-developed incisor, lacinia mobilis and spine row; molar triturative; palp 3-segmented, with setae. Maxilla 1: inner plate with long, plumose setae apically; outer plate with 7 (rarely 8) mostly serrate spines apically; palp 2-segmented, with stiff setae and often slender spines apically and subapically. Maxilla 2: inner plate broader than outer plate, with oblique row of long, plumose setae on inner margin; both plates with numerous course setae apically. Maxilliped: inner plate with several bladelike spines and stiff setae apically; outer plate with stiff setae on apex and inner margin and sometimes 1 (or rarely 2) bladelike spine near apex; palp 4-segmented. Lower lip with well-developed outer lobes; inner lobes small, vestigial or absent; lateral processes rather short, usually narrowly rounded distally.

Gnathopods: propod 1 larger than, equal to, or smaller than, propod 2; palm of propods with double row of typically distally notched spine teeth; several large rastellate setae often present on posterior margin of segment 5. Pereopods 3 and 4 subequal, except coxal plate of 4 a little larger and with concave posterior margin. Coxal plates 1–4 moderately shallow (in comparison with those of *Crangonyx* and *Synurella,* which are deeper), about as deep as corresponding body segments. Pereopod 7 a little shorter than, equal to, or a little longer than, 6, always longer than 5. Coxal gills moderately small, pedicellate, oblong to subovate, present on pereopods 2–6 and sometimes on 7. Single, median sternal gills often present on pereonites 2–4; simple or bifurcate, paired sternal gills typically on pereonites 6 and 7; 1 pair sternal gills sometimes on pleonite 1. Brood plates somewhat variable in size but usually realtively small (in comparison with *Crangonyx*) and often sublinear.

Posterior corners of pleonal plates usually rounded, sometimes small and distinct, sometimes indistinct, never large or acuminate; posterior margins usually with 1 to several short setae; ventral margins of 2 and 3 typically with a few spines; ventral margin of 1 rarely with spines. Pleopods biramous, subequal in length, each with 2 coupling spines on inner distal margin of peduncle. Uropods 1 and 2 biramous; rami and peduncles bearing spines; uropod 1 usually dimorphic in male (with small distal peduncular process). Uropod 3 uniramous; ramus 1-segmented, shorter than peduncle, sometimes vestigial or absent, if present armed with 1 to several spines. Telson usually as long as, or often longer than, broad, armed apically and occasionally laterally with spines; apical margin subtruncate, convex or with incision seldom extending one-half distance to base.

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

REMARKS ON GENERIC SYNONYMY AND SUBGENERA.—After carefully examining many species I have concluded that the high degree of overlap and intermediacy of characters previously used to separate *Stygobromus, Stygonectes,* and *Apocrangonyx* prevents the unequivocal recognition of three distinct genera. Virtually all of the differences utilized to separate these genera in the past represent varying degrees of morphological variation of single characters often complicated by convergence in different parts of the range. These differences, which were never great to begin with, have tended to blur with time and continued study as more and more species have come to light and interspecific variation has become better documented. In view of the numerous new species described in recent years, the character combinations purporting to differentiate the genera are no longer tenable. In many species it is possible to find character combinations that cut across two or more of the original combinations. Therefore, I suggested recently (Holsinger, 1977:264) "that both *Apocrangonyx* and *Stygonectes* should be synonymized with *Stygobromus,* the latter genus being the

older of the three names proposed." Moreover, in an investigation completely independent of my own, and one based primarily on the literature, Karaman (1974:102) reached a similar conclusion and also suggested merger of the three genera.

The diagnosis for *Stygobromus* given above reflects as much broader concept of the genus than originally proposed by Cope (1872) and is expanded over the more recent diagnoses of the genus by Shoemaker (1942) and Holsinger (1974) to incorporate the morphological variation noted among the included species.

The recognition of a single, presumably monophyletic genus offers an opportunity to make a fresh assessment of *Stygobromus* unbiased by concepts based on artificial differences and *ad hoc* character combinations. In line with this I have tentatively subdivided the genus into three major subgroups along more natural lines that tend to reflect morphological divergence and sexual dimorphism. These subgroups should ultimately be recognized as subgenera, but until careful examination of all of the species in the genus is made I prefer not to give them formal nomenclatural status. The subgeneric groups are tentatively designated and diagnosed by the following character combinations and included species:

Subgeneric Group 1: Propods of gnathopods variable in relative size, propod 1 a little larger than, subequal to, or smaller than, propod 2; pereopods 6 and 7 variable in relative length, pereopod 7 a little shorter than, subequal to, or a little longer than, pereopod 6; mature female larger than mature male; sexual dimorphism never pronounced. Includes species of the *ackerlyi, cumberlandus, emarginatus, ephemerus, flagellatus, gracilipes, hadenoecus, hubbsi, mackini, phreaticus, spinatus* and *spinosus* groups, and *S. baroodyi,* new species, *S. biggersi,* new species, *S. borealis,* new species, *S. exilis* Hubricht, *S. fecundus,* new species, *S. iowae* Hubricht, *S. minutus,* new species, *S. montanensis* Holsinger, *S. mysticus* Holsinger, *S. obscurus* Holsinger, *S. onondagaensis* (Hubricht and Mackin), *S. smithi* Hubricht, S. *stegerorum,* new species, *S. stellmacki* (Holsinger), and *S. vitreus* Cope.

Subgeneric Group 2: Propod of gnathopod 2 about twice the size of propod of gnathopod 1 in mature male, only a little larger in mature female; pereopod 7 a little longer than pereopod 6; mature male larger than mature female; sexual dimorphism pronounced. Includes *S. araeus* (Holsinger), *S. heteropodus* Hubricht, *S. lucifugus* (Hay) (?), *S. nortoni* (Holsinger), *S. subtilis* (Hubricht), and at least two undescribed species from the Interior Low Plateaus region.

Subgeneric Group 3: Propod of gnathopod 1 larger than propod of gnathopod 2 in both sexes; pereopod 7 a little longer than pereopod 6 (excepting one aberrant species known only from the female); mature male larger than mature female; sexual dimorphism pronounced in some species; includes species of the *pizzinii* and *tenuis* groups.

Key to the Species Groups and Ungrouped Species of *Stygobromus* of the Eastern United States

(based on males and females)

1. Propod of gnathopod 1 distinctly larger than propod of gnathopod 2; mature male larger than mature female 2
   Propod of gnathopod 1 only a little larger than, subequal to, or smaller than, propod of gnathopod 2; mature male (where known) usually smaller than mature female (excepting *S. araeus* which is otherwise easily distinguished) 3
2. Palm of gnathopod propod 1 of mature male with prominent distal notch; basis of pereopod 7 of mature male with ventrally produced distoanterior lobe; telson with lateral spines ..... ***pizzinii*** group
   Palm of gnathopod propod 1 of mature male without distal notch; basis of perepod 7 of mature male without ventrally produced distoanterior lobe; telson without lateral spines (except for two species in the Ozark region) ..... ***tenuis*** group
3. Sexual dimorphism pronounced; mature male larger than mature female; propod of gnathopod 2 about twice the size of propod of gnathopod 1 in male, only a little larger in female; palm of gnathopod propod 2 with deep excavation in male ..... ***araeus*** group
   Sexual dimorphism not pronounced; mature female larger than mature male; propod of

gnathopod 2 sometimes larger than propod of gnathopod 1 but never twice as large; palm of gnathopod propod 2 without excavation 4

4. Propod of gnathopod 2, 1/4 to 1/2 times larger than propod of gnathopod 1; pereopod 6 typically a little longer than pereopod 7 (occasionally subequal) 5
   Propod of gnathopod 2 typically subequal in size to propod of gnathopod 1 (but sometimes a little smaller); pereopods 6 and 7 subequal in length (but preopod 6 usually a little longer in the *mackini* group) 8
5. Ramus of uropod 3 vestigial or absent; uropod 1 with 90 or more spines; uropod 2 with 40–45 spines; pereopods 6 and 7 subequal in length ..... ***phreaticus*** group
   Ramus of uropod 3 present; uropod 1 with 40 or fewer spines; uropod 2 with 30 or fewer spines; pereopod 6 a little longer than pereopod 7 6
6. Propod of gnathopod 2, 1/3 to 1/2 times larger than propod of gnathopod 1; coxal plate of pereopod 4 rather shallow, reaching 40–45 percent length of basis ..... ***cumberlandus*** group
   Propod of gnathopod 2 about 1/4 times larger than propod of gnathopod 1; coxal plate of pereopod 4 rather deep, reaching 65–70 percent length of basis 7
7. Apical margin of telson without notch; posterior margin of gnathopod propod 1 about 3/4 length of palm; posterior margin of gnathopod propod 2 nearly as long as palm ..... ***S. biggersi***
   Apical margin of telson with distinct notch; posterior margins of gnathopod propods about 1/3 length of palms ..... ***S. stegerorum***
8. Posterior margin of gnathopod propod 1 with setae 9
   Posterior margin of gnathopod propod 1 without setae 13
9. Segment 5 of gnathopod 1 usually with rastellate setae (except *S. grandis* which is otherwise easily distinguished by large size and large gnathopod propods) 10
   Segment 5 of gnathopod 1 without rastellate setae 11
10. Apical margin of telson with tiny notch; posterior corners of pleonal plates subacute; lateral sternal gills bifurcate ..... ***S. stellmacki***
    Apical margin of telson incised 20–65 percent the distance to base; posterior corners of pleonal plates usually distinct but not subacute; lateral sternal gills simple ..... ***mackini*** group
11. Uropod 3 without ramus ..... ***S. minutus***
    Uropod 3 with ramus 12
12. Gnathopod propods subequal in size; spine teeth of gnathopod propods unnotched; pereopod 7 slightly longer than pereopod 6 ..... ***S. borealis***
    Gnathopod propod 2 a little larger than gnathopod propod 1; spine teeth of gnathopod propods distally notched; pereopod 6 a little longer than pereopod 7 ..... ***S. fecundus***
13. Gnathopod propod 2 slightly larger than gnathopod propod 1; segment 5 of gnathopod 1 with several small rastellate setae ..... ***S. baroodyi***
    Gnathopod propod 2 subequal to, or often a litle smaller than, gnathopod propod 1; segment 5 of gnathopod 1 without rastellate setae 14
14. Telson with lateral spines ..... ***gracilipes*** group
    Telson without lateral spines 15
15. Posterior margins of pleonal plates with 3–11 setae each 16
    Posterior margins of pleonal plates with 1 or 2 (rarely 3) setae each 17
16. Gnathopod propod 1 a little larger than gnathopod propod 2; defining angle of 1st propod distinct, with 2 or 3 long spine teeth on outside; posterior margins of pleonal plates with 3–6 setae each ..... ***spinosus*** group
    Gnathopod propod 1 subequal in size to gnathopod propod 2; defining angle of 1st propod indistinct, with 3–5 long spine teeth on outside; posterior margins of pleonal plates with 3–11 setae each ..... ***spinatus*** group
17. Posterior margins of pleonal plates with 1 seta each in notch formed just above posterior corner; uronites free ..... ***ackerlyi*** group
    Posterior margins of pleonal plates with 1 or 2 (rarely 3) setae each (if single, seta usually inserted well above posterior corner); uronites fused or nearly so 18
18. Ramus of uropod 3 vestigial or absent, ramus or peduncle with 1 apical spine; posterior corners of pleonal plates rounded, indistinct ..... ***ephemerus*** group
    Ramus of uropod 3 always present, armed with 2–5 apical spines; posterior corners of pleonal plates small but distinct, sometimes acute ..... ***emarginatus*** group

The *emarginatus* Group

DIAGNOSIS.—Adult size range small to moderately large (ca. 2.3–14.0 mm). Mature female larger than mature male. Inner lobes of lower lip typically poorly developed or vestigial. Gnathopod 1: propod typically subequal in size to 2nd propod but broader proximally and occasionally a little larger; palm rather long, oblique; defining angle with 2–5 spine teeth of unequal length on outside; posterior margin usually short, without setae; segment 5 without rastellate setae. Gnathopod 2: propod palm proportionately shorter and less oblique than 1st, posterior margin longer, with 2–8 sets setae; segment 5 without rastellate setae. Pereopods 6 and 7 usually subequal in length but 7 sometimes slightly longer. Pereopod 7 without coxal gill. Lateral sternal gills bifurcate or simple. Pleonal plates: posterior margins with 1 seta (or rarely 2 or 3) each, single seta usually inserted well above posterior corner; posterior corners small but usually distinct, sometimes acute. Uronites fused or nearly so. Ramus of uropod 3 with 2–5 apical spines. Telson usually a little longer than broad, sometimes slightly tapered distally; apical margin entire or with small notch.

REMARKS.—The *emarginatus* group is composed of nine species, which occupy parts of the Roanoke, Kanawha, Monongahela, and Potomac river basins in southern and west-central Virginia, eastern West Virginia, and western Maryland. All but one species, which is recorded from a well in the Piedmont, are generally confined to caves in the Appalachian Valley and Plateau region. With the exception of *S. culveri,* a very distinct species, which possibly represents a separate subgroup, the group is quite homogeneous and most species can be distinguished only with difficulty.

Stygobromus stellmacki, recorded from a single cave in central Pennsylvania, was formerly assigned to this group (Holsinger, 1967), but a more critical evaluation of its morphology has led me to remove it as indicated elsewhere in this paper. Moreover, the *gracilipes* group was previously included as a subgroup of the *emarginatus* group (Holsinger, 1967) but is elevated to full group status in this paper. The *emarginatus* group has close morphological affinities with four other species groups in the Appalachian region, including the *ackerlyi, gracilipes, spinosus,* and *ephemerus* groups, all of which are diagnosed below.

Key to the Species of the *emarginatus* Group

(based on females, except ***S. cooperi***)

1. About half of spines on telson elongate, 75 percent length of telson or longer 2
   Spines on telson not elongate, none exceeding more than 50–60 percent length of telson 3
2. Posterior margin of 1st gnathopod propod about ⅔ length of palm; spines on segments 4–6 of pereopods 5–7 elongate ..... ***S. culveri,*** new species
   Posterior margin of 1st gnathopod propod only about ⅓ length of palm; spines on segments 4–6 of pereopods 5–7 not elongate ..... ***S. franzi,*** new species
3. Telson about as long as broad, apical margin without notch ..... ***S. obrutus,*** new species
   Telson longer than broad, apical margin usually with small notch (excepting ***S. mundus*** and occasionally ***S. fergusoni***) 4
4. Lateral sternal gills simple (not bifurcate) 5
   Lateral sternal gills bifurcate 6
5. Posterior margins of pleonal plates with 2 or 3 setae each; basis of pereopod 6 broadly convex (known only from males) ..... ***S. cooperi***
   Posterior margins of pleonal plates with 1 seta each; basis of pereopod 6 slightly expanded proximally but not broadly convex ..... ***S. fergusoni,*** new species
6. Apical margin of telson convex, without notch; posterior margin of 2nd pleonal plate with 3 setae; median sternal gills absent ..... ***S. mundus***
   Apical margin of telson not convex, usually with small notch; posterior margin of 2nd pleonal plate with 1 seta; median sternal gills present 7
7. Uropod 1 with up to 26 spines; palms of gnathopod propods with double row of 6 or 7 spine teeth ..... ***S. hoffmani,*** new species
   Uropod 1 with 35–45 spines; palms of gnathopod propods with double row of 8 or more spine teeth 8

8. Telson with 10–20 (usually 12–16) apical spines; basis of pereopod 7 rather narrow, about twice as long as broad; 2nd gnathopod propod with up to about 38 spine teeth ..... ***S. emarginatus***

Telson with 6–8 apical spines; basis of pereopod 7 broader, more than 50 percent broader than long; 2nd gnathopod propod with up to about 23 spine teeth ..... ***S. morrisoni***

Stygobromus emarginatus (Hubricht)

FIGURES 1, 2

Synpleonia emarginata Hubricht, 1943:707–708, pl. 9 [in part] [type-locality: Organ Cave, Greenbrier Co., West Virginia].
Stygonectes emarginatus (Hubricht).—Holsinger, 1967:23–26, fig. 2; 1969a:32–33.—Culver and Holsinger, 1969–632.—Poulson and White, 1969:975.—Culver, 1970a:949; 1970b: 464; 1971a:173; 1971b:98.—Culver and Poulson, 1971:74.—Holsinger, 1972:59.—Culver, 1973:103.—Culver, Holsinger, and Baroody, 1973:691.—Holsinger, Baroody, and Culver, 1976:23.—Rutherford and Handley, 1976:45.
Stygobromus emarginatus (Hubricht).—Karaman, 1974:110.—Holsinger, 1977:261.

MATERIAL EXAMINED.—MARYLAND. Garrett Co.: John Friends Cave, 2 ♀, 1 ♂ (Holsinger, 1967:23). WEST VIRGINIA. Greenbrier Co.: Benedicts Cave, 1 ♀, WVACS, 18 Jan 1966; Bransfords Cave, 1 ♀, J. R. Holsinger and P. Hightower, 2 Jul 1966; Court Street Cave, 15 ♀, 4 ♂ (Holsinger, 1967:23); dug-out spring near Coffmans Cave, 1 ♀, 1 ♂, S. W. Hetrick, 13 May 1972; Fox Cave, 1 ♀ (Holsinger, 1967:23); Fuells Fruit Cave, 1 ♂, D. C. Culver, 18 Jun 1967; Grapevine Cave, 1 ♀, J. R. Holsinger and J. O. Davis, 28 Aug 1967; The Hole (cave), 1 specimen (D. C. Culver coll.), D. C. Culver and W. W. Biggers, 31 Mar 1967, and 1 ♀, J. M. Rutherford, Jr., 22 Jul 1967; Levisay Cave, 1 specimen (D. C. Culver coll.), D. C. Culver and W. W. Biggers, 29 Mar 1967; Organ Cave (system), 9 collections (26 ♀, 9 ♂, 1 juv.) from 1939–1970 (Holsinger, 1967:23); Wades Caves, 2 ♀, WVACS, 23 Apr 1966; Monroe Co.: Coburn Cave, 1 ♀, J. R. Holsinger and G. W. Frederick, 30 May 1969, and 2 ♀, J. R. Holsinger, 28 Jun 1974; McClung-Zenith Cave, 1 ♂, J. R. Holsinger, R. A. Baroody, and D. J. Newson, 31 Aug 1967; Rock Camp Cave, 1 ♀, 1 ♂, T. C. Barr, Jr. and J. H. Carpenter, 1 Jul 1968; Pendleton Co.: Kenny Simmons Cave, 2 ♀, J. R. Holsinger, 25 Aug 1966; Pocahontas Co.: Linwood Cave, 2 ♀, J. R. Holsinger, 22 Aug 1966; Marthas Cave, 1 ♀, 1 ♂, T. C. Barr, Jr., 28 Jul 1966, and 1 ♀, J. R. Holsinger and D. C. Culver, 14 Jan 1967; Upper Marthas Cave, 1 ♂, D. C. Culver, 21 Nov 1967; Piddling Pit (cave), 1 ♂, J. R. Holsinger, R. A. Baroody, and R. L. Swensson, 30 Sep 1967, and 1 ♂, J. R. Holsinger and D. C. Culver, 12 Aug 1972; Poor Farm Cave, 1 ♀, J. R. Holsinger, 4 May 1968; Randolph Co.: Bazzle Cave, 1 ♀, J. R. Holsinger and D. C. Culver, 21 May 1973; Bowden Cave, 2 ♀, 1 ♂, J. R. Holsinger and D. C. Culver, 22 May 1973; Tucker Co.: Big Springs Cave, 5 ♀, J. R. Holsinger, 24 Aug 1966; Harpers Cave, 1 ♀, A. and B. Norden, Jan 1974.

DIAGNOSIS AND DESCRIPTION.—Corresponding to earlier diagnoses and descriptions by Hubricht

FIGURE 1.—Preserved specimen of *Stygobromus emarginatus* (10.0 mm female) from Bazzle Cave, West Virginia, illustrating general morphological facies of the genus *Stygobromus*. (Photograph by G. W. Dickson)

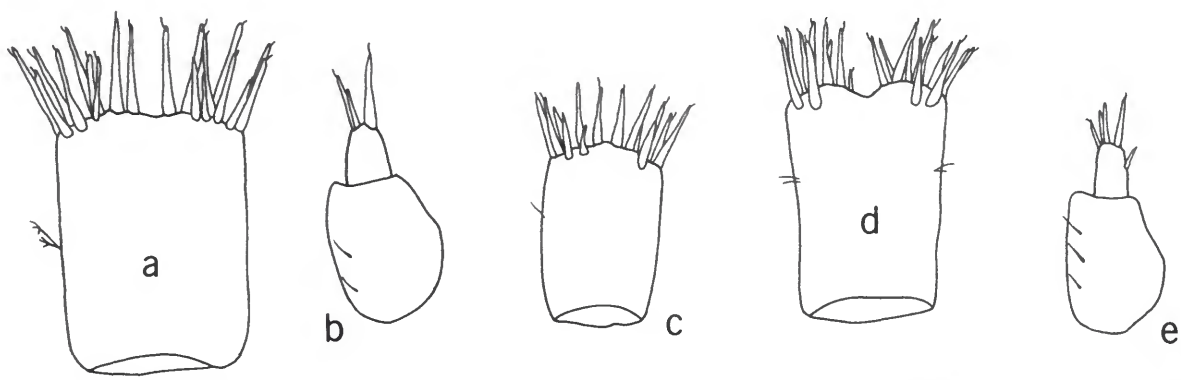

FIGURE 2.—*Stygobromus emarginatus* (Hubricht). Female (12.0 mm), Harper Cave, West Virginia: *a*, telson; *b*, uropod 3. Male (7.0 mm), Piddling Pit Cave, West Virginia: *c*, telson. Female (13.5 mm), Marthas Cave, West Virginia: *d*, telson; *e*, uropod 3.

(1943) and Holsinger (1967) with the following additions and variation: Largest males, 11.2 mm; largest females, 14.0 mm. Antenna 1 with up to 23 primary flagellar segments; antenna 2 with up to 8 flagellar segments. Maxilliped: inner plate with 4 or 5 bladelike spines, 3 plumose spines and 2 naked setae apically and 1 or 2 plumose setae or spines on inner margin distally; outer plate with naked setae on inner margin and apex, 2 plumose setae apically. Defining angle of 2nd gnathopod propod with 1, or rarely 2, long spines on outside; posterior margin with 4–8 sets setae (but usually 5 or 6). Lateral sternal gills bifurcate. Brood plates of sexually mature females rather narrow but somewhat expanded distally. Uronites completely or incompletely fused. Ramus of uropod 3 with typically 3 apical spines but occasionally 2 or 4. Telson somewhat variable in shape (Figure 2), occasionally slightly broader distally than proximally; apical margin usually with slight notch but occasionally without, armed with 10–20 spines but more commonly with 12–16.

DISTRIBUTION AND ECOLOGY.—During the preparation of my 1967 monograph on *Stygonectes*, this species was known only from three caves in Greenbrier Co., West Virginia, and one cave in Garrett Co., Maryland. Since that time the species has been found in numerous caves in eastern West Virginia as indicated. The range of *S. emarginatus*, the third longest of the cave species treated in this paper, extends for a linear distance of 274 km from Monroe County in southeastern West Virginia north-northeast to Garrett County in western Maryland. Except for the localities in Monroe and Pendleton counties, this species is known only from caves developed in the Greenbrier limestone of Mississippian age.

Stygobromus emarginatus is predominately an inhabitant of small, gravel-bottom cave streams, although a few samples have been taken from pools fed by drips and seeps. A single collection was also made from the gravels of a recently excavated spring in Greenbrier County, this being the only noncave locality recorded for this species to date. Samples have been made during all seasons of the year, but females with setose brood plates (size range = 8.5–13.5 mm) have so far been found only during spring and summer. Ovigerous females are known only from an August collection in Court Street Cave in Greenbrier County (Holsinger, 1967:26). Detailed studies on the microhabitat of this species and its interaction with other amphipod species (i.e., *Stygobromus spinatus* Holsinger and *Gammarus minus* Say) and an isopod (*Asellus* sensu lato *holsingeri* Steeves) in caves of the Greenbrier Valley of West Virginia have been published by Culver (1970a).

Stygobromus morrisoni (Holsinger)

FIGURE 3

Stygonectes morrisoni Holsinger, 1967:28–31, fig. 4 [type-locality: Witheros Cave, Bath Co., Virginia]; 1969a:32–34; 1972:59.—Holsinger, Baroody, and Culver, 1976:24.

Stygobromus morrisoni (Holsinger).—Karaman, 1974:114.—Holsinger, 1977:262.

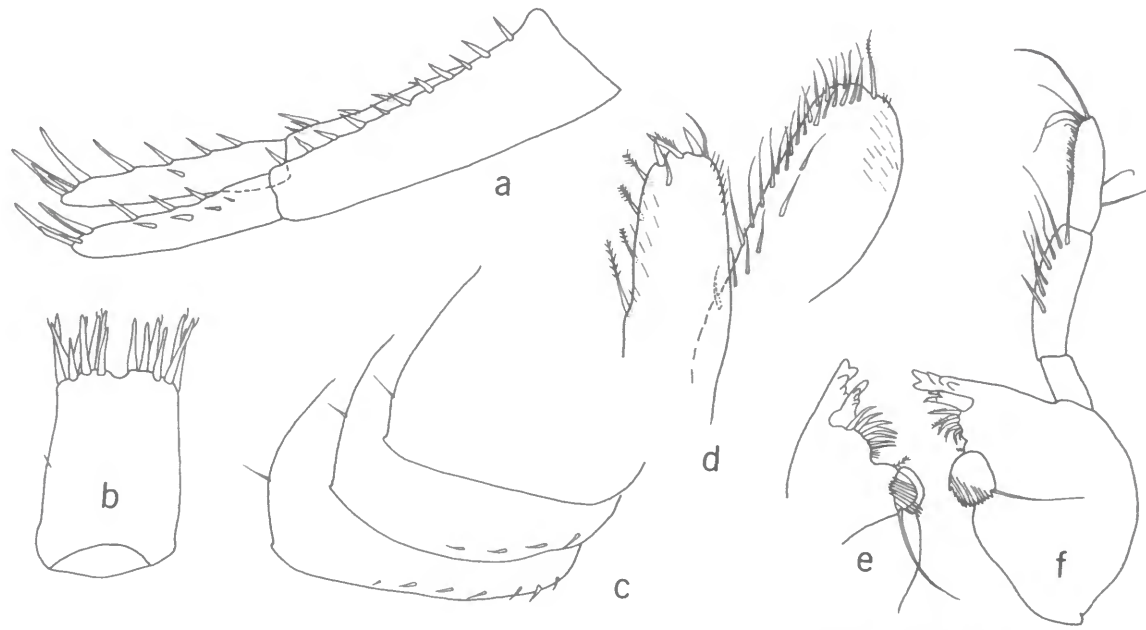

FIGURE 3.—*Stygobromus morrisoni* (Holsinger). Female (5.0 mm), Dyers Cave, West Virginia: *a*, uropod 1. Female (8.0 mm), Kenny Simmons Cave, West Virginia: *b*, telson; *c*, pleonal plates; *d*, inner and outer plates of maxilliped (greatly enlarged); *e*, dentate part of left mandible; *f*, right mandible.

MATERIAL EXAMINED.—VIRGINIA. Bath Co.: Witheros Cave, 7 ♀, 7 ♂ (Holsinger, 1967:28). WEST VIRGINIA. Hardy Co.: Dyers Cave, 1 ♀, J. R. Holsinger, 29 Aug 1966; Pendleton Co.: Kenny Simmons Cave, 1 ♀, J. R. Holsinger, 25 Aug 1966.

DIAGNOSIS AND DESCRIPTION.—Corresponding to the diagnosis and description by Holsinger (1967: 28–31) with the following additions and modifications: Largest male, 6.0 mm; largest female, 8.0 mm. Antenna 1, 50–55 percent length of body; primary flagellum with 15–20 segments. Spine row of mandible with 6 or 7 spines. Maxilla 1: inner plate with 7 or 8 apical, plumose setae; palp with 3 or 4 small spines and 4–6 setae apically. Maxilla 2, inner plate with oblique row of 7–9 plumose setae on inner margin. Maxilliped: inner plate with 2 blade-like spines, 1 plumose spine and 2 or 3 naked setae on apex, few plumose setae or spines on inner margin; outer plate with naked setae on inner margin and apex and 1 apical, plumose seta. Defining angle of gnathopod propod 1 with 3–5 spines on outside and 4–7 on inside. Coxal plate of gnathopod 1 with 4–6 marginal setae. Posterior margin of gnathopod propod 2 with 3 or 4 sets setae. Coxal plate of gnathopod 2 with 5–9 marginal setae; coxal plate of pereopod 3 with 7–11 marginal setae; coxal plate of pereopod 4 with 10–12 marginal setae. Dactyls of pereopods 5–7, 30–40 percent length of corresponding propods. Lateral sternal gills bifurcate. Brood plates of sexually mature females rather narrow but somewhat expanded distally. Uronites completely fused. Uropod 1: inner ramus with 11–13 spines; outer ramus with 10–13 spines; peduncle with 11–19 spines. Uropod 2: inner ramus with 8–11 spines; outer ramus with 7–9 spines; peduncle with 4–6 spines. Uropod 3: ramus with 3–5 apical spines; peduncle with 1 or 2 distolateral spines. Telson with 6–8 apical spines per lobe in female, typically 4 per lobe in male.

VARIATION.—Several structures varied among the population samples as follows: The single female (8.0 mm) from Kenny Simmons Cave had more spines on the defining angle of the 1st gnathopod

propod than females from Witheros (6.0–6.7 mm) or Dyers (5.0 mm) caves. Females from West Virginia had 4 sets of setae on posterior margins of 2nd gnathopod propods as opposed to only 3 sets in the Virginia specimens. The proportionate lengths of pereopod dactyls were less in the two West Virginia samples (30–34 percent in contrast to 40 percent for the Virginia material). Sternal gills were present on the 1st pleonite in females from Witheros and Kenny Simmons caves but absent from the 1st pleonite of the Dyers Cave female. The peduncle of uropod 1 had 16–19 spines in females from West Virginia but only about 11 in females from Virginia. The number of apical spines on the ramus of uropod 3 varied from 3 to 5 and the number of spines on the peduncle from 1 to 2; however, no geographic pattern was discernible for the variation noted in this structure.

DISTRIBUTION AND ECOLOGY.—The range of this species, which is very disjunct, extends from Bath Co., Virginia, north-northeast to Hardy Co., West Virginia, and covers a linear distance of approximately 161 km. Witheros Cave is situated in the upper James River drainage, whereas Kenny Simmons and Dyers caves are in the upper Potomac River drainage. All three caves are developed in Silurian-Devonian limestone, but these strata are not continuous between them. The geographic variation in the several structures noted above is not surprising in view of the long, discontinuous distribution of this species. Whether the northernmost population in Dyers Cave actually represents a distinct subspecies as I have previously implied (Holsinger, 1969a:46; Holsinger, Baroody, and Culver, 1976:24) must await the collection of additional material. Undoubtedly, additional populations of this species remain to be discovered in the large disjunctions between the presently known localities.

Stygobromus morrisoni inhabits a small, gravel-bottom stream in Witheros Cave, where it occurs syntopically with *S. mundus* (Holsinger, 1967:31). In Kenny Simmons Cave a single female of this species was collected along with two specimens of *S. emarginatus* from an old, partly submerged wooden boat in a mud-bottom lake at the rear of the cave. In Dyers Cave a single female was taken from a gravel-and-silt bottom, residual stream pool, which was also occupied by several specimens of *S. allegheniensis*. To date, ovigerous females have been found only in Witheros Cave (Holsinger, 1967:31).

Stygobromus mundus (Holsinger)

Stygonectes mundus Holsinger, 1967:26–28, fig. 3 [type-locality: Witheros Cave, Bath Co., Virginia]; 1969a:32–33, 47; 1972:59.

Stygobromus mundus (Holsinger).—Karaman, 1974:114–115.—Holsinger, 1977:262.

DIAGNOSIS.—A medium-sized cavernicolous species closely related to *S. emarginatus* and *S. morrisoni* but distinguished from the former species as previously noted (Holsinger, 1967) and as follows: Inner plate of maxilliped with fewer spines (generally similar to *S. morrisoni* in this character). Propod of 1st gnathopod with only 2 long spine teeth on outside of defining angle. Posterior margin of 2nd gnathopod propod with only 3 sets setae. Median sternal gills absent. Pleonal plates 1 and 2 with 2 or 3 posterior marginal setae, posterior corners of plate 2 indistinct. Apical margin of telson entire, convex, unnotched. Largest male, 8.0 mm; largest female, 8.2 mm.

DISTRIBUTION.—This species is known only from four specimens (3 females, 1 male) collected from two different localities in west-central Virginia—Witheros Cave in Bath County and a tributary to the Cow Pasture River in Alleghany County (Holsinger, 1967:28). These localities are situated about 24 km apart and both are in the upper James River drainage.

REMARKS.—Although I have pointed out in several papers (Holsinger, 1969a:47; 1972:59) that *S. mundus* was a probable subspecies of *S. emarginatus*, I have now concluded, after critical comparison of pertinent material, that these two species are distinct.

Stygobromus hoffmani, new species

FIGURES 4, 5

Stygonectes species D.—Holsinger, 1969a:32–33.

MATERIAL EXAMINED.—VIRGINIA. Alleghany Co.: Lowmoor Cave, holotype ♀ (USNM 168825), 3 ♀ and 4 ♂ paratypes (JRH), J. R. Holsinger and R. A. Baroody, 18 Jan 1969; McElwee Cave, 53 ♀ paratypes (USNM) and 1 ♀ paratype on slide mounts (JRH), L. Hubricht, 3 Sep 1949.

DIAGNOSIS.—A relatively small cavernicolous species closely allied morphologically with *S. emarginatus, S. morrisoni,* and *S. mundus,* but distinguished from these species by smaller size at sexual

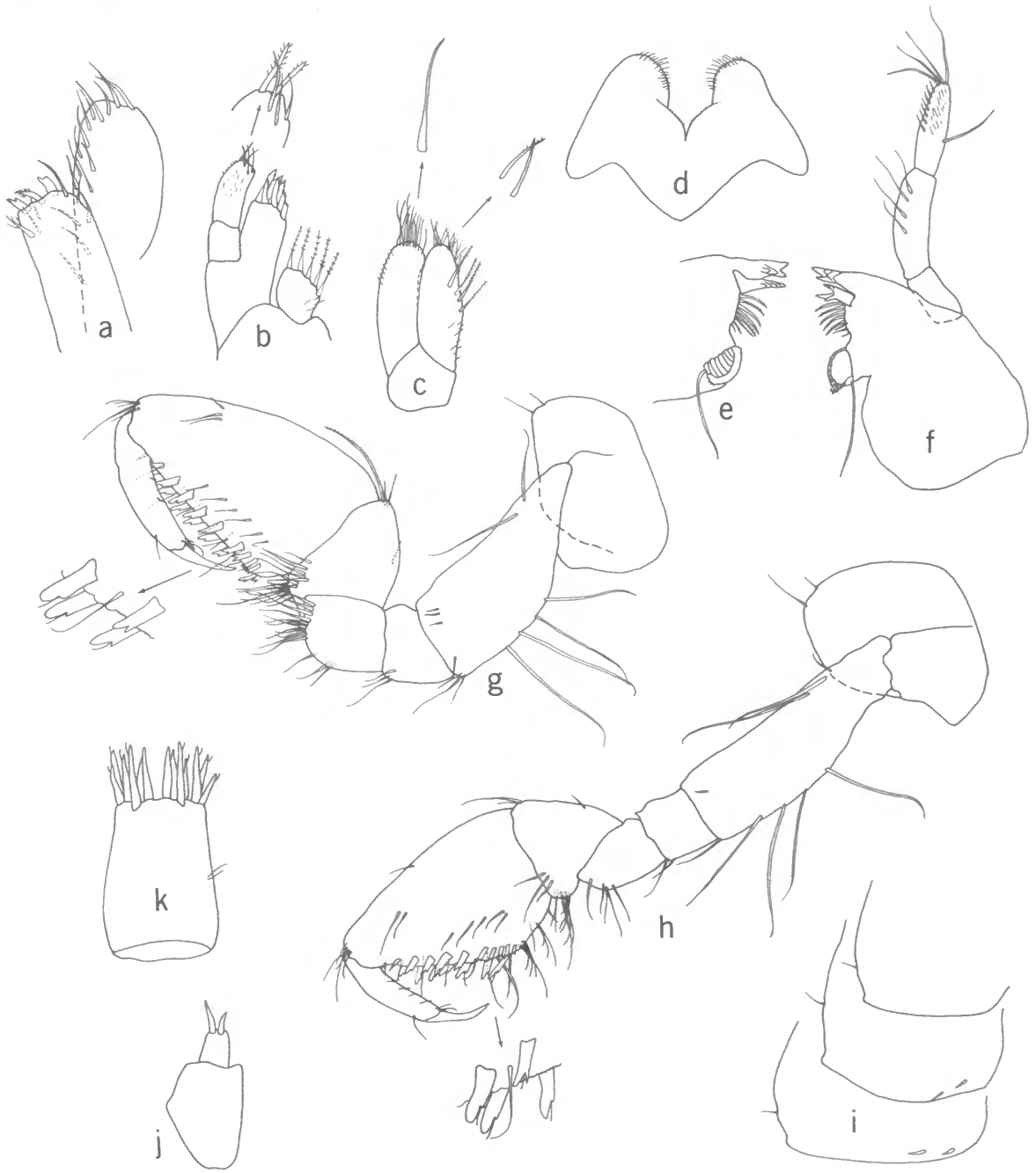

FIGURE 4.—*Stygobromus hoffmani*, new species, female paratype (5.0 mm), McElwee Cave, Virginia: *a*, inner and outer plates of maxilliped; *b*, *c*, maxillae 1, 2 (palp apex of maxilla 1 and apical setae of maxilla 2 enlarged); *d*, lower lip; *e*, dentate part of left mandible; *f*, right mandible; *g*, *h*, gnathopods 1, 2 (palmar spines enlarged); *i*, pleonal plates; *j*, uropod 3, *k*, telson.

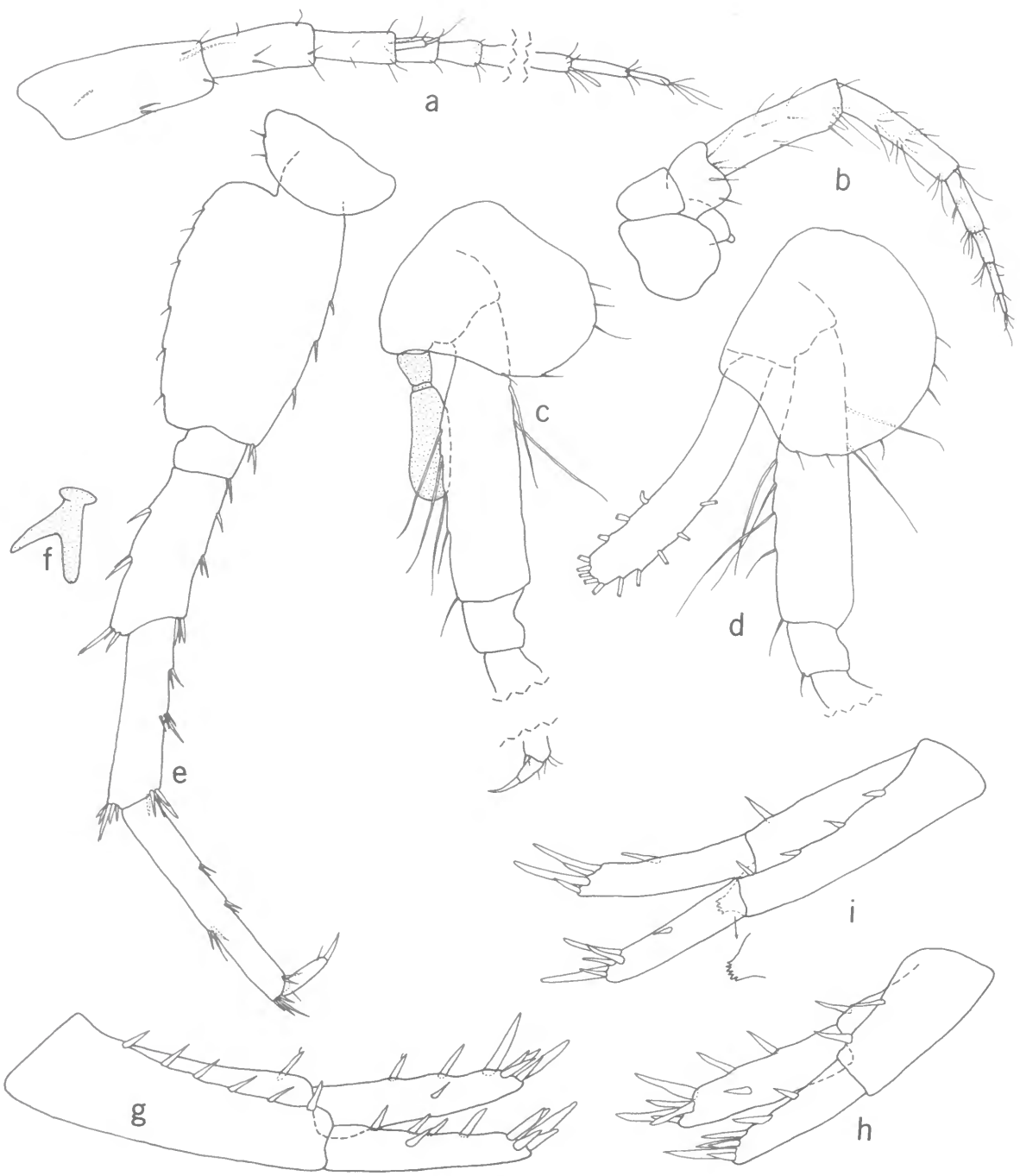

FIGURE 5.—*Stygobromus hoffmani*, new species. Female paratype (5.0 mm), McElwee Cave, Virginia: *a*, *b*, antennae 1, 2; *c*, *d*, pereopods 3, 4 (in part); *e*, pereopod 7; *f*, lateral sternal gill; *g*, *h*, uropods 1, 2. Male paratype (3.0 mm), Lowmoor Cave, Virginia: *i*, uropod 1 (penduncular process enlarged).

maturity, and having fewer flagellar segments of antennae, fewer setae on inner plates of maxillae and on palpal segments 2 and 3 of mandible, fewer spines on palms of gnathopod propods, and fewer spines on uropods 1–3. Further distinguished from *S. emarginatus* by having fewer setae on peduncular segments 4 and 5 of antenna 2 and fewer sets of setae on posterior margin of propod of gnathopod 2. Largest male, 3.0 mm; largest females, 5.5 mm.

FEMALE.—Antenna 1, 40–42 percent length of body, about 40 percent longer than antenna 2; primary flagellum with 12 or 13 segments. Antenna 2, flagellum with 4 or 5 segments. Mandibles subequal; spine row with 7 spines; segment 2 of palp with 4 long setae, segment 3 with 1 long seta on outer margin, row of short setae on inner margin, 4 long setae on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 2 slender, lightly plumose spines and 3 stiff setae on apex. Maxilla 2, inner plate with oblique row of 4 or 5 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines, 2 plumose spines and 3 naked setae; outer plate with row of naked setae on inner margin and apex and 1 apical, plumose seta. Inner lobes of lower lip small.

Propod of gnathopod 1 slightly larger than 2nd propod; palm with double row of 6 spine teeth; defining angle with 3 spine teeth on outside, 3 on inside; inferior medial setae singly inserted, superior medial setae few in number and doubly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, with 2 marginal setae. Propod of gnathopod 2: palm with double row of 6 or 7 spine teeth; defining angle with 1 long spine tooth on outside, 3 shorter ones on inside; inferior medial setae singly inserted, superior medial setae doubly inserted. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, margin of 2 with 3 setae, that of 3 with 5 setae. Coxal plate of pereopod 4 about 40 percent length of basis, slightly broader than long, margin with 7 setae. Pereopods 6 and 7 subequal in length, 40–45 percent length of body, about 28 percent longer than pereopod 5. Bases of pereopods 5–7 slightly convex, distoposterior lobes poorly developed. Dactyls of pereopods 6 and 7, 30–35 percent length of corresponding propods; dactyl of pereoped 5 about 45 percent length of corresponding propod. Three median sternal gills on pereonites 2–4; 2 pairs short, bifurcate lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins convex (but nearly straight in plate 2), with 1 seta each; posterior corners small, subacute to narrowly rounded; ventral margins of plates 2 and 3 with 2 spines each. Uronites completely or incompletely fused. Uropod 1: inner ramus subequal in length to outer ramus, 60–65 percent length of peduncle, armed with 9 spines; outer ramus with 10 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus and peduncle, armed with 8 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: ramus about 40 percent length of peduncle, armed apically with 2 spines. Telson longer than broad, gently tapering distally; apical margin with vestigial notch, armed with 13 or 14 spines.

MALE.—Differing from female as follows: antenna with up to 10 primary flagellar segments. Gnathopod propods with 3 or 4 fewer spine teeth. Uropod 1: inner ramus a little longer than outer ramus, armed with 5 spines; outer ramus with 6 spines; peduncle with 5 spines; apical margin of peduncular process serrate. Uropod 2 with few less spines. Telson with 2 or 3 fewer apical spines.

VARIATION.—The lateral sternal gills were longer and more slender on the specimens from the Lowmoor Cave sample.

TYPE-LOCALITY.—Lowmoor Cave, located 6.4 km southwest of Clifton Forge in Alleghany Co., Virginia, is a large maze cave with 4083 meters of surveyed passage (Holsinger, 1975a:43). The cave has a number of drip pools but no flowing stream.

DISTRIBUTION AND ECOLOGY.—*Stygobromus hoffmani* is known only from two caves which are developed in Upper Silurian limestone and are located about 1.3 km apart on the south side of the Jackson River. Both populations were found in drip pools. The September collection from McElwee Cave contained two ovigerous females (4.0–4.3 mm in length), each of which was carrying three eggs in the brood pouch. Females in the January sample from Lowmoor Cave were sexually immature.

REMARKS.—McElwee Cave, located 8 km southwest of Clifton Forge, Virginia, was completely destroyed by the construction of interstate highway 64 during the early 1960s.

ETYMOLOGY.—It is a pleasure to name this species

in honor of Dr. Richard L. Hoffman, who discovered it in 1949 and who has made substantial contributions to our knowledge of Appalachian invertebrates.

Stygobromus fergusoni, new species

FIGURES 6, 7

Stygobromus species F.—Holsinger, 1969a:30, 44.

MATERIAL EXAMINED.—VIRGINIA. Montgomery Co.: Slussers Chapel Cave, holotype ♀ (USNM 168817), 9 ♀, 1 juv. paratypes (USNM), and 1 ♀ paratype on slide mounts (JRH), J. R. Holsinger and R. E. Whittemore, 21 Apr 1968; Old Mill Cave, 1 ♀ paratype (JRH), L. M. Ferguson, 20 Oct 1969.

DIAGNOSIS.—A medium-sized cavernicolous species closely related to *S. emarginatus* and *S. hoffmani* but distinguished from these species by having pereopod 6 a little longer than 7, broader bases of pereopods 5–7, simple lateral sternal gills, and proportionately shorter ramus of uropod 3. Further distinguished from *S. emarginatus* by the propod of gnathopod 1 which is a little larger than the 2nd and by fewer spine teeth on palms of gnathopod propods. Largest females, 7.0 mm; male unknown.

FEMALE.—Antenna 1, 50–55 percent length of body, 50–60 percent longer than antenna 2; primary flagellum with 19–20 segments. Antenna 2, flagellum with 7 segments. Mandibles subequal; spine row with 7 or 8 spines; segment 2 of palp with 6 setae, segment 3 with 3 long setae on outer margin, row of short setae on inner margin, 4 long setae apically and subapically. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 3 slender spines and 3 stiff setae apically. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: apex of inner plate as shown; outer plate with row of about 16 naked setae on inner margin and apex and 2 apical, plumose setae. Lower lip with small inner lobes.

Propod of gnathopod 1 a little larger than 2nd propod; palm with double row of 7 or 8 spine teeth; defining angle with 3 long spine teeth on outside, 3 or 4 shorter ones on inside; inferior medial setae singly inserted, superior medial setae few in number, mostly doubly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, margin with 4 setae. Gnathopod propod 2: palm with double row of 9 spine teeth, plus 2 additional ones on outside; defining angle with 1 long spine tooth on outside, 3 shorter ones on inside; posterior margin with 4 sets setae; inferior medial setae singly inserted, superior medial setae doubly and triply inserted. Dactyl nail of gnathopod 2 proportionately a little shorter than that of 1st gnathopod. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, with 5 marginal setae each. Coxal plate of pereopod 4 about as broad as long, about 40 percent length of basis, margin with 8 setae. Pereopod 6 a little longer than 7, 45–50 percent length of body, 20–25 percent longer than pereopod 5. Pereopods 5–7: bases broader proximally than distally, distoposterior lobes poorly developed; dactyls 30–35 percent length of corresponding propods. Three median sternal gills on pereonites 2–4; 2 pairs rather long, simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear, not much expanded distally.

Pleonal plates: posterior margins slightly convex, with 1 seta each; posterior corners tiny but usually distinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 6 spines. Uronites completely fused. Uropod 1: inner ramus subequal in length to outer ramus, 60–65 percent length of peduncle, armed with 12 spines; outer ramus with 13 spines; peduncle with 12 spines. Uropod 2: inner ramus longer than outer ramus, slightly shorter than peduncle, armed with 12 spines; outer ramus with 8 spines; peduncle with 7 spines. Uropod 3: ramus very short, only about 1/9 length of peduncle, armed with 2 or 3 apical spines. Telson longer than broad, subrectangular; apical margin usually with very small notch, armed with 18 spines.

TYPE-LOCALITY.—Slussers Chapel Cave, located about 7.3 km north-northeast of Blacksburg in Montgomery Co., Virginia, is a moderately large stream-passage cave developed in Elbrook dolomite of Cambrian age (Holsinger, 1975a:178–179). The type-series was collected from a series of small, seep-fed pools containing bits of decaying wood and troglobitic isopods. *Asellus* (sensu lato) *vandeli* Bresson.

DISTRIBUTION AND ECOLOGY.—At present this species is known only from two caves located about 3.7 km apart in a small karst area drained by the North Fork of the Roanoke River. A single ovigerous female, measuring 6.5 mm and carrying 4 embryos in the brood pouch, was collected from a pool in Old Mill Cave in October. The larger females (6.5–7.0 mm) from the April collection in

FIGURE 6.—*Stygobromus fergusoni*, new species, female paratype (7.0 mm), Slussers Chapel Cave, Virginia: *a*, left mandible; *b*, uropod 3; *c*, *d*, gnathopods 1, 2; *e*, lower lip; *f*, inner plate of maxilliped (greatly enlarged); *g*, pleonal plates; *h*, telson.

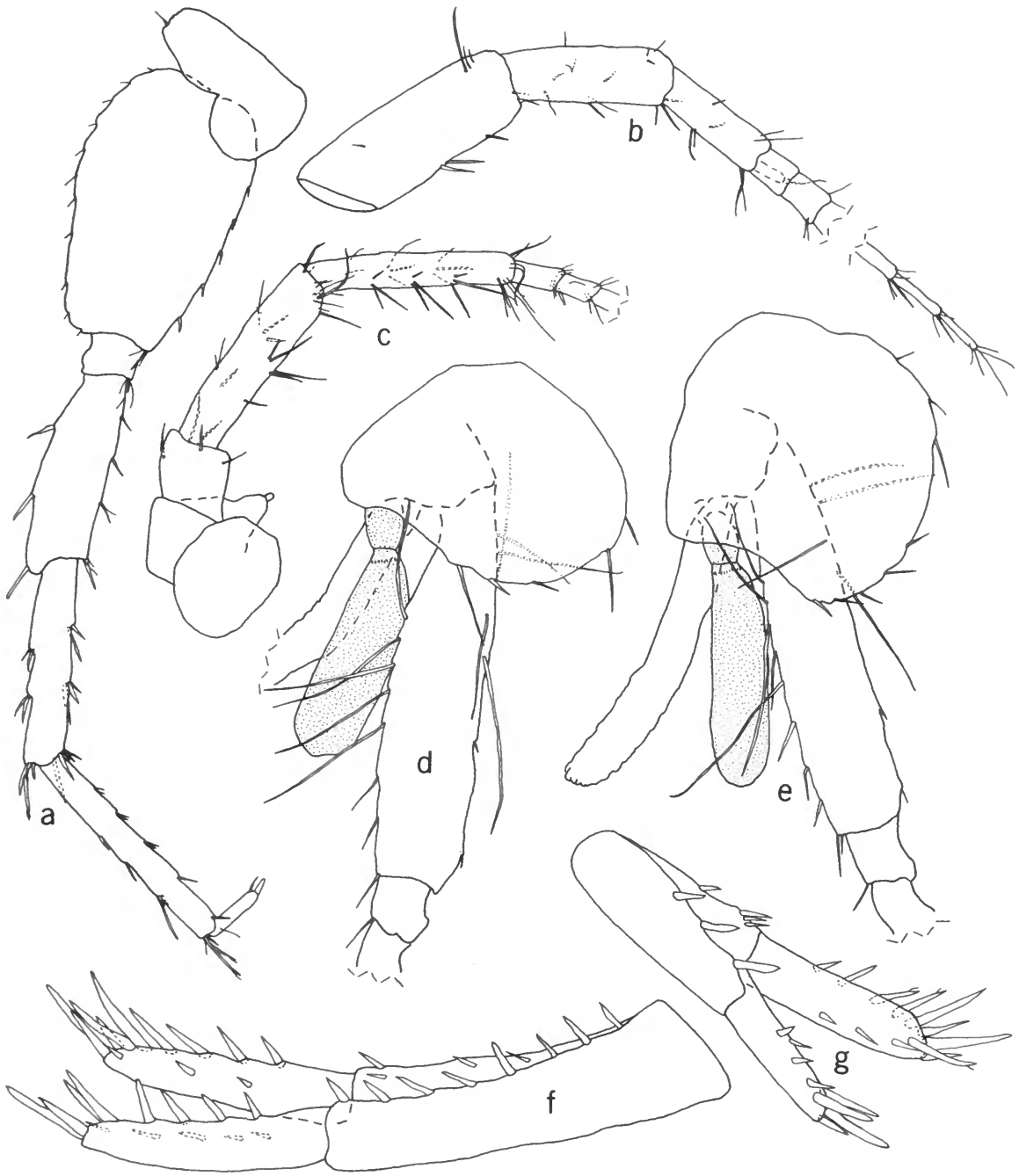

FIGURE 7.—*Stygobromus fergusoni*, new species, female paratype (7.0 mm), Slussers Chapel Cave, Virginia: *a*, pereopod 6; *b*, *c*, antennae 1, 2; *d*, *e*, pereopods 3, 4 (in part); *f*, *g*, uropods 1, 2.

Slussers Chapel Cave had submature brood plates. Males have not been found to date.

REMARKS.—In an earlier paper (Holsinger, 1969a: 44), I indicated that this species was probably closely related to *S. mackini* but, after careful study, it appears only distantly related and has closer affinities with the *emarginatus* group.

ETYMOLOGY.—It is a pleasure to name this species in honor of Lynn M. Ferguson, a biospeleologist who assisted with the collection of this species as well as a number of others.

Stygobromus franzi, new species

FIGURES 8, 9

Stygonectes species.—Holsinger, 1969a:32 [species B].—Franz and Slifer, 1972:26.

MATERIAL EXAMINED.—MARYLAND. Garrett Co.: Crabtree Cave, holotype ♀ (USNM 168821) and 1 ♀ paratype (USNM), A. and B. Norden, 31 Dec 1972; additional ♀ paratypes (in JRH) collected by L. R. Franz as follows: 2 on 2 Jan 1967, 1 in 1969 (?), and 1 on 16 May 1974; Sand Cave, 2 ♀, 1 ♂ paratypes (JRH), L. R. Franz, 1 Mar 1970; Washington Co.: Round Top Mine No. 2, 13 ♀ paratypes (USNM), A. and B. Norden, 4 Mar 1973 and 13 ♀ and 1 ♂ paratypes (JRH), 26 Oct 1974.

DIAGNOSIS.—A relatively small cavernicolous species allied morphologically with *S. emarginatus* but distinguished from that species by smaller size at sexual maturity, and having fewer flagellar segments in antennae, fewer spine teeth on palms of gnathopod propods, fewer sets of setae on posterior margin of gnathopod propod 2, proportionately shorter bases of pereopods 5–7, more spinose uropods 1 and 2, and proportionately longer outer spines on apex of telson. Largest males, 3.5 mm; largest female, 6.9 mm.

FEMALE.—Antenna 1, 50–55 percent length of body, about 50 percent longer than antenna 2; primary flagellum with 14–18 segments. Antenna 2, flagellum with 4 or 5 segments. Mandibles subequal; spine row with 5 spines; segment 2 of palp with 8 long setae, segment 3 with 2 long setae on outer margin, row of shorter setae on inner margin, 4 long setae on apex. Maxilla 1: inner plate with 5 or 6 apical, plumose setae; palp with 2 stiff setae and 2 slender spines apically. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines, 2 pulmose spines and 2 naked setae; outer plate with row of naked setae on inner margin and apex and 2 apical, plumose setae. Inner lobes of lower lip vestigial.

Propod of gnathopod 1 subsequal in size to 2nd propod; palm with double row of 7 spine teeth; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; medial setae mostly singly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, with 4 marginal setae. Gnathopod propod 2: palm with double row of 6 spine teeth; defining angle with 1 long spine tooth on outside, 3 shorter ones on inside; inferior medial setae singly inserted, superior medial setae variable as shown. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, margins with 5 setae each. Coxal plate of pereopod 4 rather shallow, broader than long, margin with 7 setae. Pereopods 6 and 7 subequal in length, 45–50 percent length of body, 20 percent longer than pereopod 5. Pereopods 5–7: bases comparatively short, not much broader proximally than distally, posterior margins nearly straight, distoposterior lobes poorly developed; dactyls 27–31 percent length of corresponding propod. Three long median sternal gills on pereonites 2–4; 2 pairs rather long, bifurcate lateral sternal gills on pereonites 6–7; 1 pair sternal gills on pleonite 1. Brood plates rather narrow but somewhat expanded distally.

Pleonal plates: posterior margins slightly convex, with 1 seta each; posterior corners small, subacute; ventral margins of plates 2 and 3 with up to 3 spines each. Uronites completely fused. Uropod 1: inner ramus equal in length to outer ramus, 60–65 percent length of peduncle, armed with 13 spines; outer ramus with 12 spines; peduncle with 19 spines. Uropod 2: inner ramus a little longer than outer ramus, a little shorter than peduncle, armed with 12 spines; outer ramus with 10 spines; peduncle with 5–7 spines. Uropod 3: ramus ¼ to ⅓ length of peduncle, apex with 3 or 4 (occasionally 2) spines; peduncle sometimes with spinule. Telson a little longer than broad; apical margin entire, armed with 12–16 (usually 12) spines of which several are distinctly longer than the others and up to 75–100 percent length of telson.

MALE.—Differing from female as follows: Gnathopod propods with fewer palmar spines and medial setae. Sternal gills absent from pleonite 1. Ventral margins of pleonal plates 2 and 3 with 1 or 2 fewer

FIGURE 8.—*Stygobromus franzi*, new species. Female paratype (6.9 mm), Crabtree Cave, Maryland: *a*, left mandible; *b*, dentate part of right mandible; *c*, lower lip, *d*, inner and outer plates of maxilliped (greatly enlarged); *e f*, gnathopods 1, 2 (palmar spines of gnathopod 1 enlarged); *g*, *h*, antennae 1, 2; *i*, lateral sternal gill. Male paratype (3.8 mm), Sand Cave, Maryland: *j*, pleonal plates.

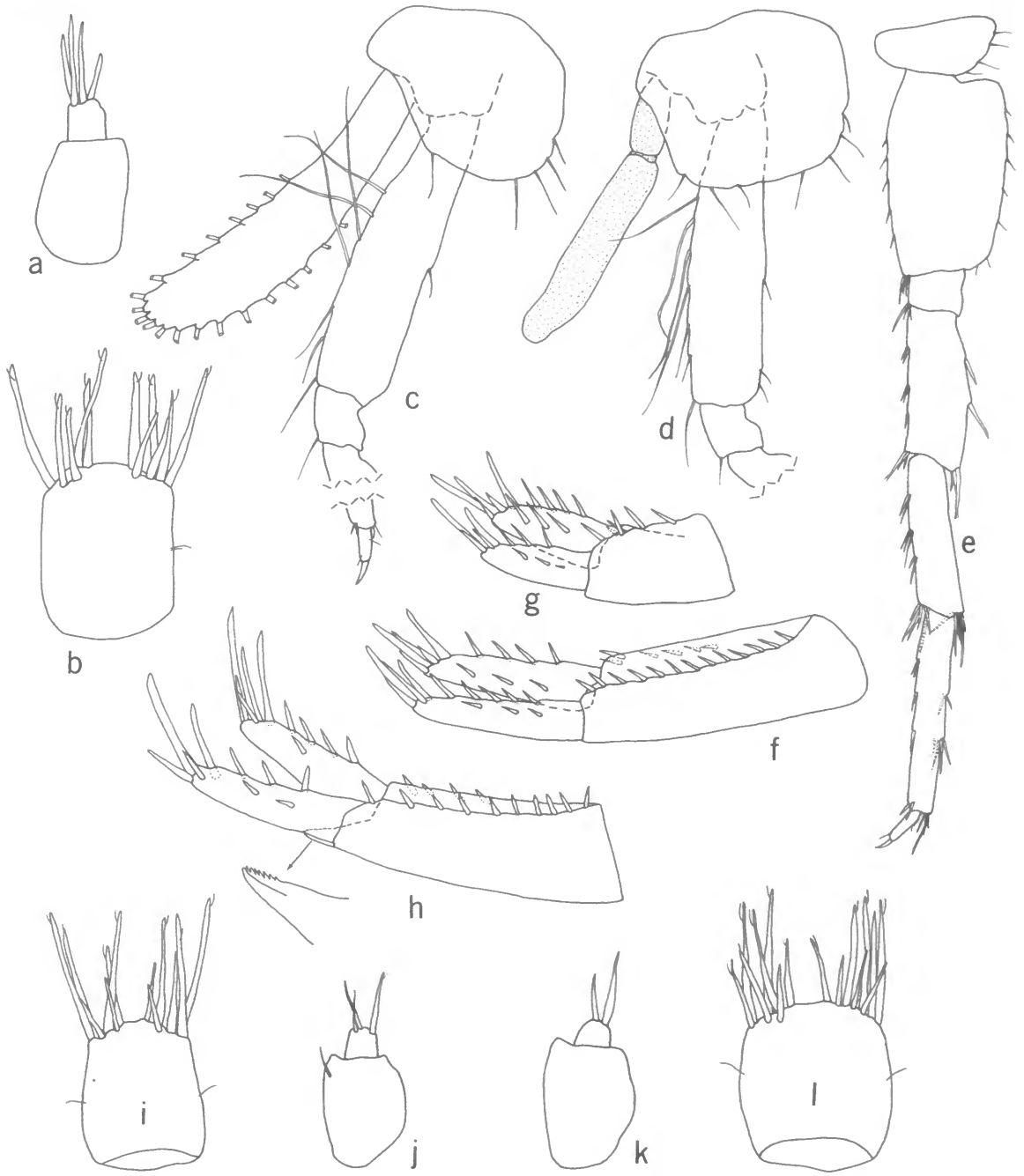

FIGURE 9.—*Stygobromus franzi*, new species. Female paratype (6.9 mm), Crabtree Cave, Maryland: *a*, uropod 3; *b*, telson; *c*, *d*, pereopods 3, 4 (in part); *e*, pereopod 7; *f*, *g*, uropods 1, 2. Male paratype (3.8 mm): *h*, uropod 1 (peduncular process enlarged). Female paratype (5.5 mm), Round Top Mine No. 2, Maryland: *i*, telson; *j*, uropod 3. Female paratype (6.0 mm), Round Top Mine No. 2: *k*, uropod 3; *l*, telson.

spines. Peduncular process of uropod 1 triangular in shape, upper margin serrate toward distal end.

VARIATION.—As shown in Figure 9, the shape of the telson varies both between and within populations. The proportionate length of, and the number of apical spines on, the ramus of uropod 3 is also somewhat variable as noted in the description.

TYPE-LOCALITY.—Crabtree Cave, located 27 km east-northeast of Oakland in Garrett County, is the largest known cave in Maryland, contains 1280 meters of passage and is developed in the Greenbrier limestone (Franz and Slifer, 1971:57–60). Type-specimens have been collected from a small stream and, according to Franz and Slifer (1971:26), also from drip pools.

DISTRIBUTION AND ECOLOGY.—To date this species has been collected from three localities in western Maryland—two caves in Garrett County and one cave-like, limestone mine in Washington County. The range, which is disjunct, covers a linear distance of approximately 105 km and lies within the Potomac River drainage basin. Although the range of *S. franzi* comes to within about 24 km of that of *S. emarginatus,* these two species have never been found in the same cave and their ranges in western Maryland lie within separate drainage systems. *Stygobromus franzi* does, however, occur sympatrically with two other species in the genus—a small, undescribed form in Crabtree Cave (see "*Stygobromus* sp.," elsewhere in this paper) and *S. allegheniensis* in the Round Top mine complex in Washington County.

Stygobromus franzi inhabits both small cave streams and pools. It was found in a tiny stream in Round Top Mine No. 2, in small, seep- or spring-fed pools in Sand Cave and presumably in both a small stream and drip pools in the type-locality. Ovigerous females have not been found to date, but females (measuring 4.2–6.9 mm) with setose brood plates have been taken during fall, winter, and spring.

REMARKS.—On a distribution map showing the ranges of some of the Appalachian species of *Stygonectes* (= *Stygobromus*) (Holsinger, 1969a:33), I inadvertently indicated the Crabtree Cave locality for this species by the letter "A" instead of "B" which it should have been in order to conform with the discussion in the text on page 32. The letters "A" and "B" are reversed on that map.

ETYMOLOGY.—It is a pleasure to name this species in honor of L. Richard Franz, Jr., a biospeleologist who has contributed significantly to our knowledge of the cave fauna of Maryland.

Stygobromus cooperi (Holsinger)

Stygonectes cooperi Holsinger, 1967:31–33, fig. 5 [type-locality: Silers Cave, Berkeley Co., West Virginia]; 1969a:32–33; 1972:59—Holsinger, Baroody, and Culver, 1976:23.
Stygobromus cooperi (Holsinger).—Karaman, 1974:109.—Holsinger, 1977:261.

DIAGNOSIS.—A moderately small cavernicolous species distinguished from other members of the *emarginatus* group by the distinctly convex and somewhat broadly expanded posterior margins of the bases of pereopods 5–7 and by the description of Holsinger (1967). Largest male, 6.0 mm; female unknown.

DISTRIBUTION AND ECOLOGY.—This species is known only from two males collected from a small, mud-bottom pool in Silers Cave, Berkeley Co., West Virginia. The entrance to this cave reportedly was sealed shut by the owner.

Stygobromus obrutus, new species

FIGURES 10, 11

MATERIAL EXAMINED.—VIRGINIA. Pittsylvania Co.: shallow well in woods, Mt. .Cross Rd., 1.6 km northwest of U.S. Rt. 48, W of Danville, holotype ♀ (USNM 168837), 63 ♀, 12 ♂, and 9 juv. paratypes (USNM), L. Hubricht, 4 Dec 1948.

DIAGNOSIS.—A small groundwater species distinguished by small size at sexual maturity, reduced setation of mandibular palp, relatively short antennae, short, simple lateral sternal gills, lightly spined peduncle of uropod 1, and short telson which lacks an apical notch and has relatively short spines. Largest male, 2.5 mm; largest females, 3.6 mm.

FEMALE.—Antenna 1, 40–43 percent length of body, about 45 percent longer than antenna 2; primary flagellum with 10–12 segments. Antenna 2, flagellum with 3 segments. Mandibles subequal; spine row with 3 spines; segment 2 of palp without setae, segment 3 with 4 short setae on inner margin, 4 long setae on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 4 stiff, apical setae. Maxilla 2, inner plate with oblique row of 6 or 7 plumose setae on inner margin. Maxilliped: apex of inner plate with 2 bladelike spines, 1 plumose spine and 2 naked setae, inner margin with 1

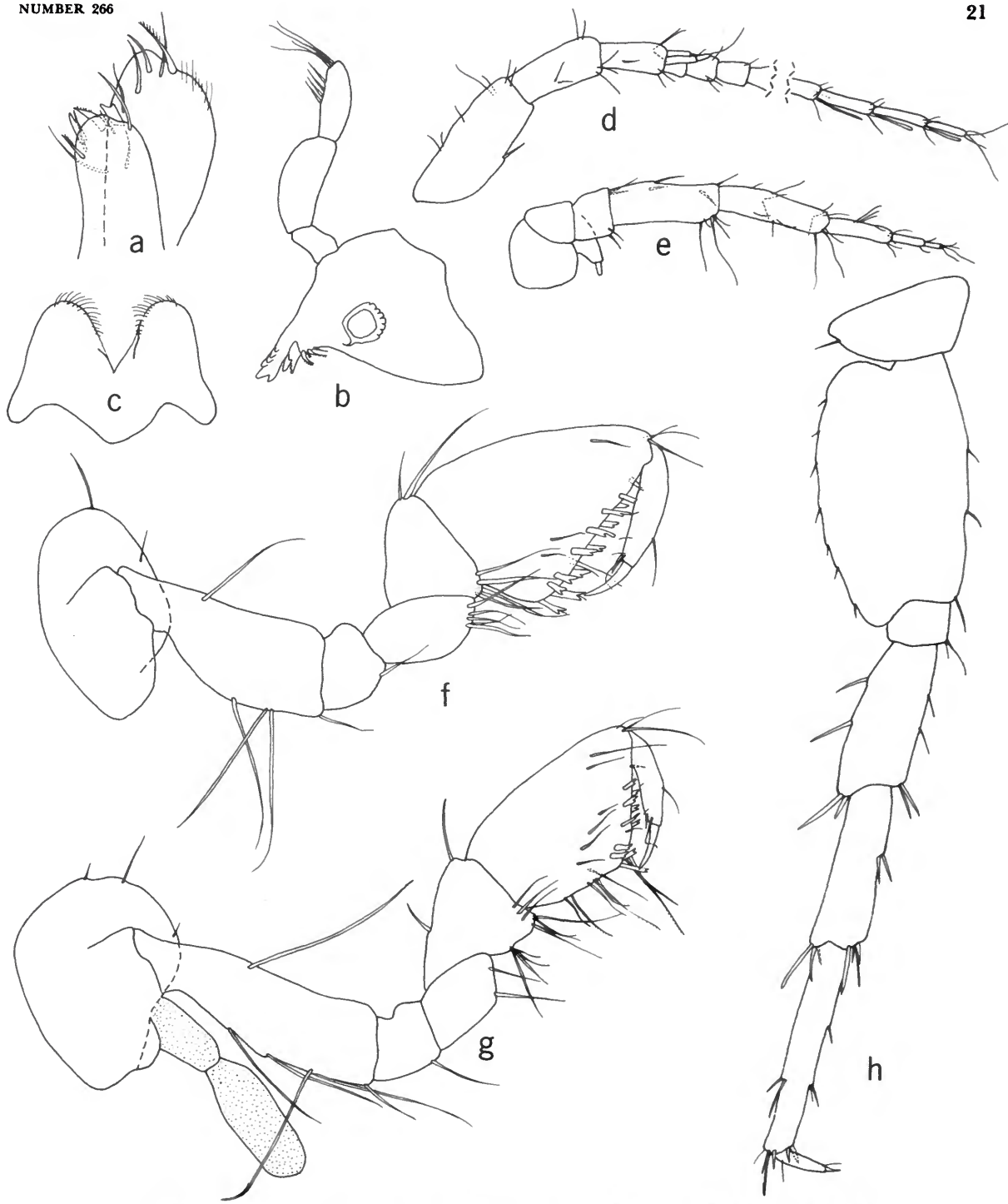

FIGURE 10.—*Stygobromus obrutus*, new species, female paratype (3.6 mm), well west of Danville, Virginia: *a*, inner and outer plates of maxilliped (greatly enlarged); *b*, right mandible; *c*, lower lip; *d*, *e*, antennae 1, 2; *f*, *g*, gnathopods 1, 2; *h*, pereopod 6.

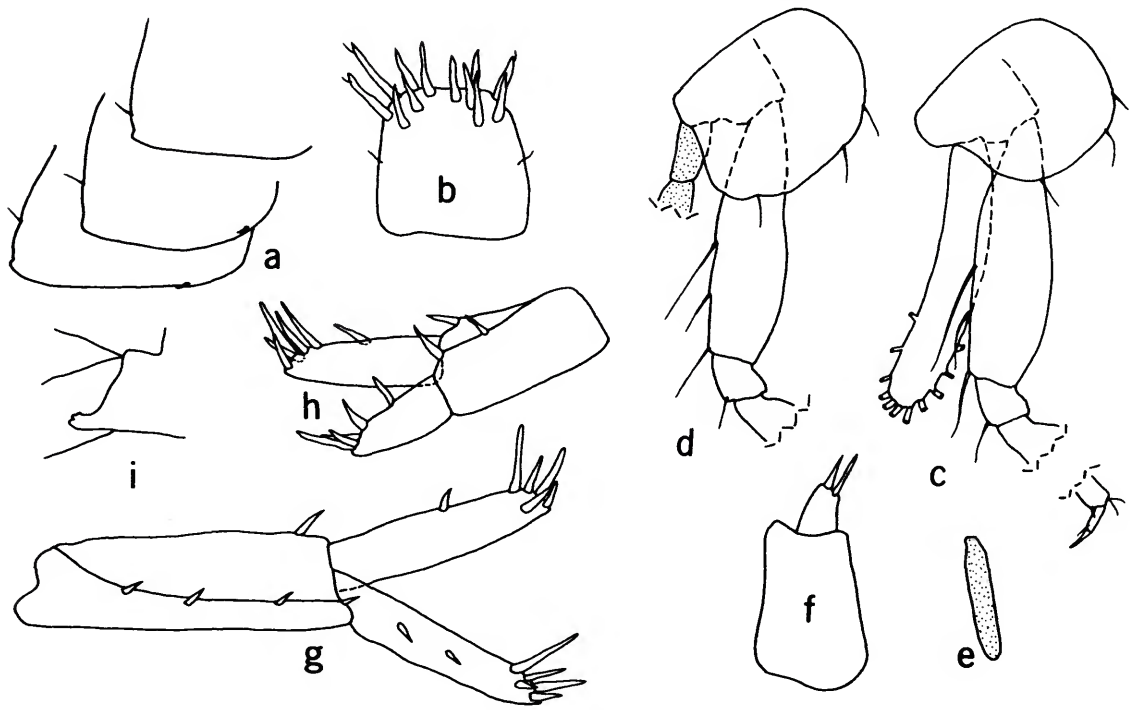

FIGURE 11.—*Stygobromus obrutus*, new species. Female paratype (3.6 mm), well west of Danville, Virginia: *a*, pleonal plates; *b*, telson; *c*, *d*, pereopods 3, 4 (in part); *e*, lateral sternal gill; *f*, uropods 3; *g*, *h*, uropods 1, 2. Male paratype (2.5 mm), well west of Danville: *i*, peduncular process of uropod 1 (medial view).

plumose seta or spine distally; outer plate with few naked setae on inner margin and apex and 1 apical, plumose seta. Lower lip with vestigial inner lobes.

Propod of gnathopod 1 a little larger than 2nd propod; palm armed with double row of 4 or 5 spine teeth; defining angle with 2 long spine teeth on outside, 1 shorter one inside; medial setae few in number, singly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, margin with 2 setae. Gnathopod propod 2: palm with double row of 4 spine teeth; defining angle with 1 long spine tooth on outside, 1 shorter one on inside; posterior margin with 2 sets setae; medial setae few in number, singly inserted. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, margins with 3 setae each. Coxal plate of pereopod 4 broader than long, about 35 percent length of basis, margin with 3 setae. Pereopod 6 subequal in length to pereopod 7, 45–50 percent length of body, about 30 percent longer than pereopod 5. Pereopods 5–7: bases about as broad proximally as distally, posterior margins convex, distoposterior corners distinct and broadly rounded; dactyls of 6 and 7 about 30 percent length of corresponding propods, that of 5 about 37 percent. Three median sternal gills on pereonites 2–4; 2 pairs short, simple lateral sternal gills on pereonites 6 and 7; sternal gill absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins nearly straight, with 1 seta each; posterior corners small, narrowly rounded; ventral margins of plates 2 and 3 with 1 spine each. Uronites completely or incompletely fused. Uropod 1: inner ramus subequal in length to outer ramus, about 70 percent length of peduncle, armed with 5–7 spines; outer ramus with 5–7 spines; peduncle with 5 spines. Uropod 2: inner ramus about 35 percent longer than outer ramus, a little shorter than peduncle, armed with 6 spines; outer

ramus with 5 spines; peduncle with 3 spines. Uropod 3: ramus about 1/3 length of peduncle, armed with 2 apical spines. Telson comparatively short, about as broad as long, gently tapering distally; apical margin entire, armed with 12 relatively short spines.

MALE.—Differing from female slightly as follows: Gnathopod propods proportionately a little smaller. Posterior margin of gnathopod propod 2 with 1 set setae. Peduncular process of uropod 1 small, apex trilobed.

TYPE-LOCALITY.—A shallow well in woods west of Danville, Pittsylvania Co., Virginia. This well is either in early Paleozoic or Precambrian granite gneiss or Triassic sandstone. The locality data given on the collection label were not specific enough to pinpoint the location precisely.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, which is situated in the Roanoke River drainage basin and lies some 75 airline miles southeast of the range of any other species in the *emarginatus* group. In contrast to other species in this group, all of which occur west of the Blue Ridge Mountains in the Applachian Valley and Plateau provinces, *S. obrutus* is found in the Piedmont Province in south-central Virginia.

Five of the females in the type series had setose brood plates and varied in length from 2.7 to 3.6 mm.

ETYMOLOGY.—The epithet *obrutus* is from the Latin, meaning "buried," "covered," or "hidden."

Stygobromus culveri, new species

FIGURES 12, 13

Stygonectes species.—Holsinger, Baroody, and Culver, 1976:24.

MATERIAL EXAMINED.—WEST VIRGINIA. Randolph Co.: Stillhouse Cave, holotype ♀ (USNM 168805), 5 ♀, 1 ♂ paratypes (USNM) and 1 ♀ paratype on slide mounts (JRH), J. R. Holsinger, D. C. Culver, S. B. Peck, and P. J. Starr, 21 Jun 1968.

DIAGNOSIS.—A small, rather aberrant member of the *emarginatus* group easily distinguished by the relatively long setae of the antennae and coxal plates of the gnathopods and pereopods 3 and 4, presence of 3 plumose setae on inner plates of maxillae, proportionately rather long posterior margin of 1st gnathopod propod, and long, slender spines on pereopods 5–7, uropods 1–3, and telson. Largest male, 2.3 mm; largest females, 3.2 mm.

FEMALE.—Antenna 1, 50 percent length of body, about 60 percent longer than antenna 2; primary flagellum with 10–13 segments. Antenna 2: flagellum short, with 3 segments. Mandibles subequal; spine row with 4 spines; segment 2 of palp with 2 long setae, segment 3 with 1 long seta on outer margin, several short setae on inner margin, 4 or 5 long setae on apex. Maxilla 1: inner plate with 3 apical, plumose setae; palp with 5 or 6 stiff setae apically. Maxilla 2, inner plate with oblique row of 3 plumose setae on inner margin. Maxilliped: apex of inner plate with 2 bladelike spines, 1 plumose spine and 2 naked setae, inner margin with 1 plumose spine or seta distally; outer plate with naked setae on inner margin and apex and 1 plumose seta apically. Lower lip with small inner lobes.

Propod of gnathopod 1 subequal in size to 2nd propod; palm with 3 spine teeth; defining angle with 3 long spine teeth on outside, 2 shorter ones on inside; medial setae few, singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, with 2 long marginal setae. Gnathopod propod 2: palm equal in length to posterior margin, armed with double row of 2 spine teeth; defining angle with 1 long spine tooth on outside, shorter one on inside; medial setae few, singly inserted. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, margins with 2 long setae each. Coxal plate of pereopod 4 slightly broader than long, about 40 percent length of basis, margin with 4 long setae. Pereopod 7 slightly longer than 6, 50–55 percent length of body, 30–35 percent longer than pereopod 5. Pereopods 5–7: bases with convex posterior margins and broadly rounded distoposterior lobes; segments 4–6 with long, slender spines; dactyls rather long, 40–45 percent length of corresponding propods. Three long, slender median sternal gills on pereonites 2–4; 2 pairs long, simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins convex, with 1 seta each; posterior corners small, narrowly rounded; ventral margin of plate 3 with 1 spine. Uronites completely fused. Uropod 1: inner ramus subequal in length to outer ramus, 65–70 percent

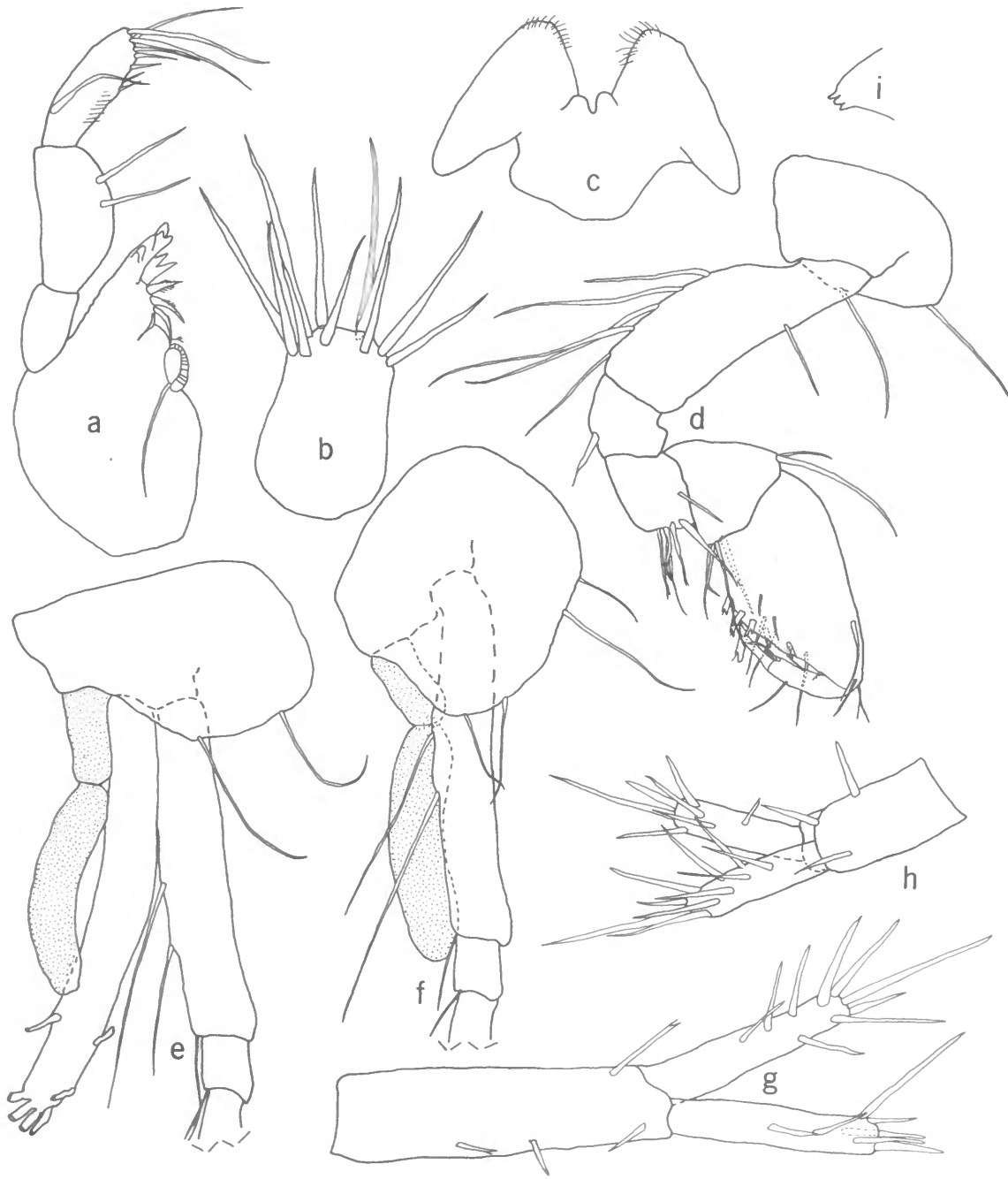

FIGURE 12.—*Stygobromus culveri*, new species. Female paratype (3.0 mm), Stillhouse Cave, West Virginia: *a*, left mandible; *b*, telson, *c*, lower lip; *d*, gnathopod 1; *e*, *f*, pereopods 3, 4 (in part); *g*, *h*, uropods 1, 2. Male paratype (2.3 mm), Stillhouse Cave: *i*, peduncular process of uropod 1.

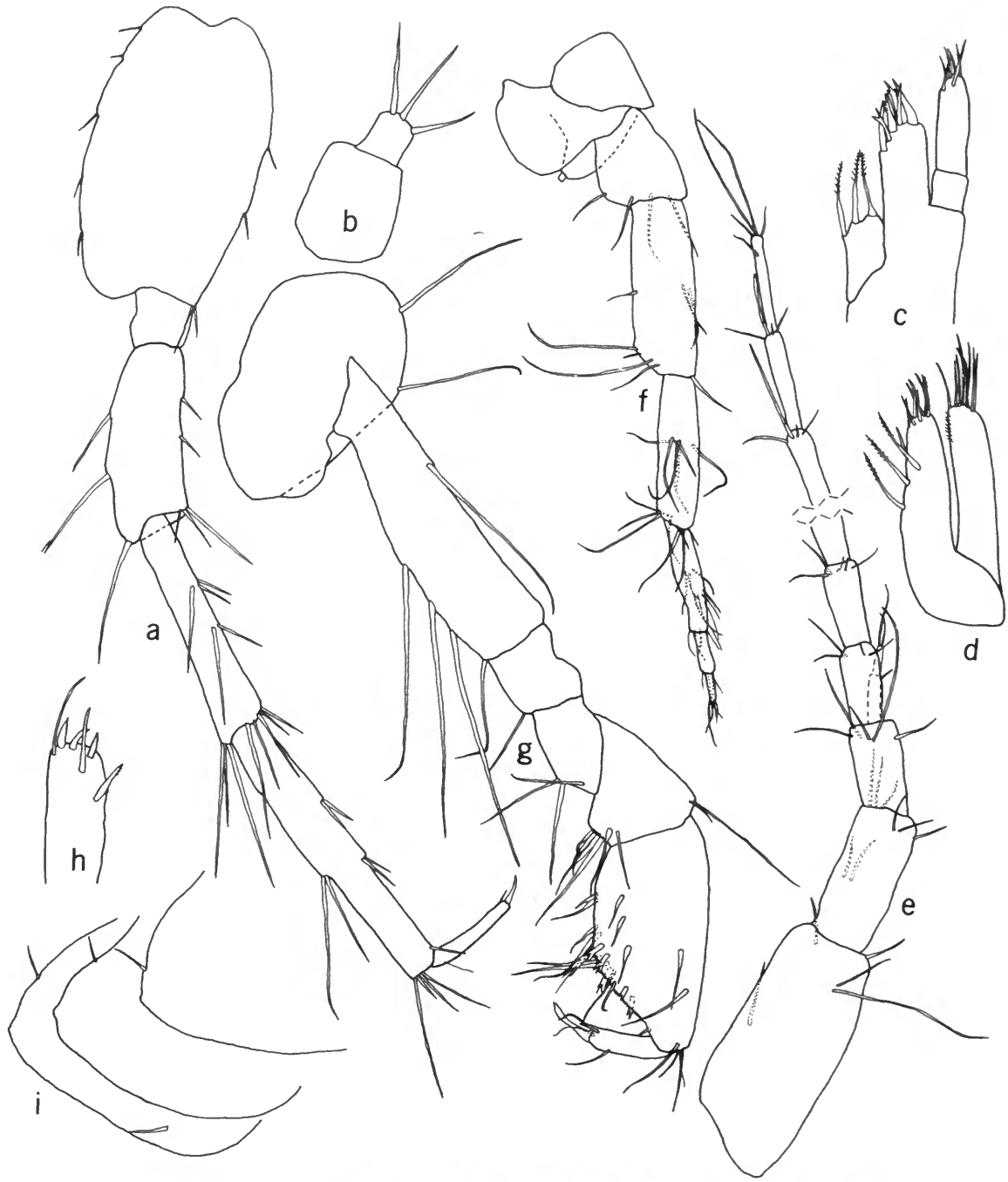

FIGURE 13.—*Stygobromus culveri*, new species. Female paratype (3.0 mm), Stillhouse Cave, West Virginia: *a*, pereopod 7; *b*, uropod 3; *c*, *d*, maxillae 1, 2; *e*, *f*, antennae 1, 2; *g*, gnathopod 2; *h*, inner plate of maxilliped. Male paratype (2.3 mm): *i*, pleonal plates.

length of peduncle, armed with 9 long spines; outer ramus with 7 long spines; peduncle with 4 spines. Uropod 2: inner ramus subequal in length to outer ramus and peduncle, armed with 7 mostly long spines; outer ramus with 10 long spines; peduncle with 3 spines. Uropod 3: ramus nearly 50 percent length of peduncle, with 3 long apical spines. Telson longer than broad, slightly tapering distally; apical margin entire, with 11 or 12 long spines.

MALE.—Differing from female as follows: Uropods 1 and 2 with few less spines. Peduncular process of uropod 1 small, apex trilobed. Ramus of uroped 3 with 2 apical spines. Telson with 6 apical spines.

TYPE-LOCALITY.—Stillhouse Cave (sometimes called Hermit Cave), located approximately 9.7 km west of Spruce Knob near Osceola in Randolph Co., West Virginia. This cave is developed in the Greenbrier limestone and lies just north of the drainage divide between the Greenbrier River (upper Kanawha drainage basin) and Gandy Creek (upper Monongahela drainage basin). The cave was originally described by Davies (1958:315) and more recently by Medville and Medville (1971:157–159).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected from a series of mud-bottom seep and drip pools. Four females, measuring 2.4–3.2 mm, had setose brood plates but none were ovigerous.

ETYMOLOGY.—It is a pleasure to name this species in honor of my distinguished colleague, Dr. David C. Culver, who has contributed significantly to our knowledge of the ecology of aquatic cave crustaceans.

The *ackerlyi* Group

DIAGNOSIS.—Closely allied morphologically with the *emarginatus* group but distinguished from that group as follows: Adult size range, 4.5(?)–8.0 mm. Posterior margins of pleonal plates with 1 seta each in notch formed just above posterior corner. Urosites free, not fused.

REMARKS.—The *ackerlyi* group is composed of two closely related species, which inhabit caves of the Appalachian Valley in Polk and Floyd counties, Georgia, and Calhoun Co., Alabama. The species in this group are distantly removed geographically from species in the *emarginatus* group farther north but are nevertheless closely allied with them morphologically.

Key to the Species of the *ackerlyi* Group

Coxal plate of pereopod 4 less than 50 percent length of corresponding basis; telson only slightly longer than broad ..... ***S. ackerlyi,*** new species

Coxal plate of pereopod 4 more than 50 percent length of corresponding basis; telson 25–30 percent longer than broad ..... ***S. inexpectatus,*** new species

Stygobromus ackerlyi, new species

FIGURES 14, 15

Stygobromus species N.—Holsinger, 1969a:31–32.
Stygobromus species.—Holsinger and Peck, 1971:30 [in part].

MATERIAL EXAMINED.—GEORGIA. Polk Co.: White River Cave, holotype ♀ (USNM 168786) and 9 ♀ paratypes (USNM), E. Ackerly, 29 Dec 1946; additional paratypes collected by Ackerly as follows: 2 ♀ (USNM and slide mounts in JRH), 2 Feb 1945; 2 ♀ (USNM), 11 Aug 1945, 4 ♀ (USNM), 23 Dec 1950; Floyd Co.: Cave Springs Cave, 1 ♀ and several juv. paratypes (JRH), J. R. Holsinger, S. B. Peck, R. A. Baroody, and A. Fiske, 13 Jun 1967.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished from members of the *emarginatus* group, to which it is apparently related, by the characters given above for the *ackerlyi* group. Largest females, 8.0 mm; male unknown.

FEMALE.—Antenna 1, 40–50 percent length of body, 40–50 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2, flagellum with 7 segments. Mandibles subequal; spine row with 4 spines; segment 2 of palp with 8 long setae on inner margin, segment 3 with 2 long setae on outer margin, row of mostly short setae on inner margin, 5 long setae on apex. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 2 slender spines (or stiff setae) and 4 setae apically. Maxilla 2, inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 2 plumose spines and 2 naked setae apically and 2 plumose spines or setae

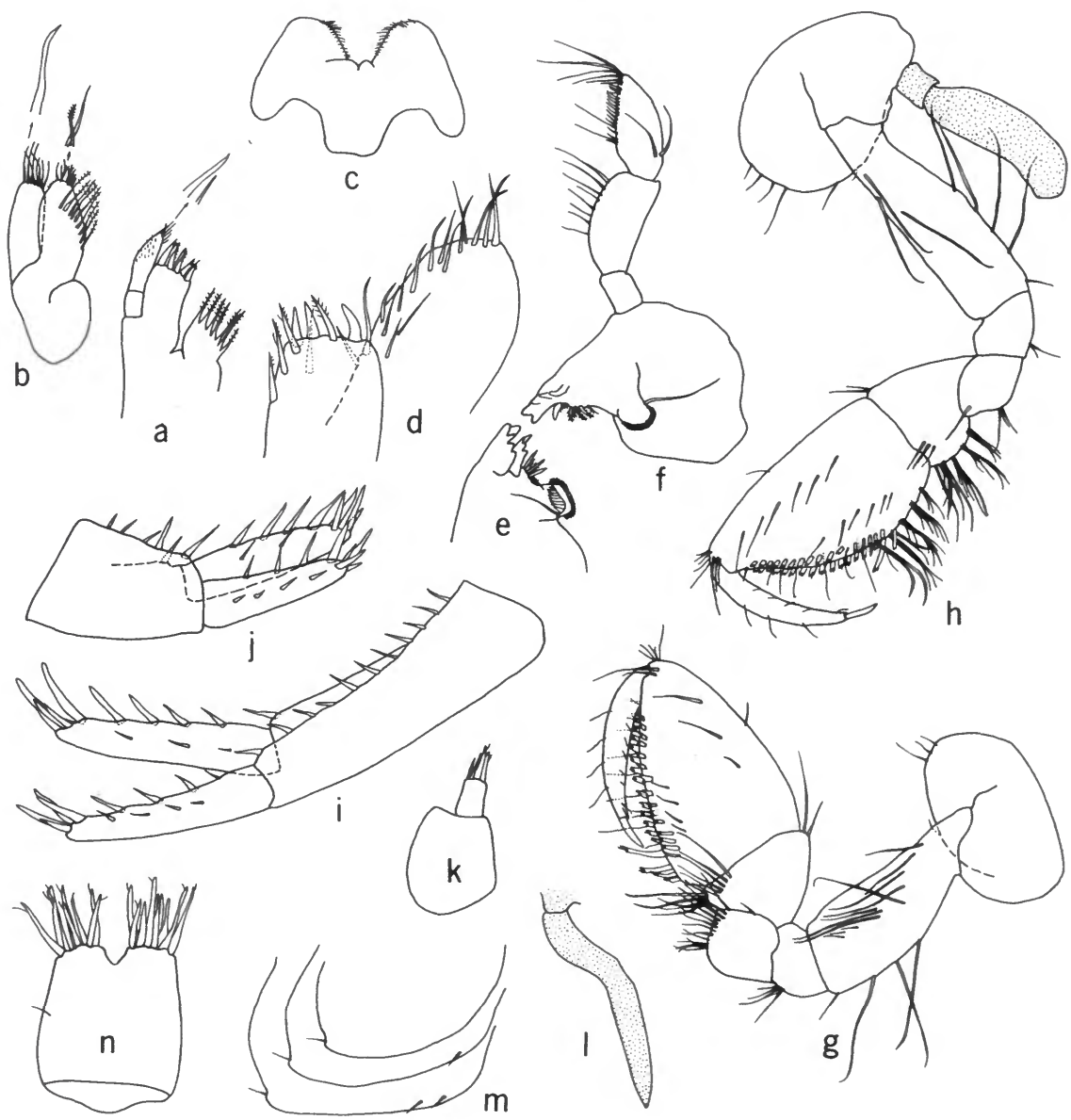

FIGURE 14.—*Stygobromus ackerlyi*, new species. Female paratype (8.0 mm), White River Cave, Georgia: *a*, *b*, maxillae 1, 2 (apical setae and spines enlarged); *c*, lower lip; *d*, inner and outer plates of maxilliped (greatly enlarged); *e*, dentate part of left mandible; *f*, right mandible; *g*, *h*, gnathopods 1, 2; *i*, *j*, *k*, uropods 1, 2, 3; *l*, lateral sternal gill; *m*, pleonal plates. Female paratype (7.0 mm), White River Cave: *n*, telson.

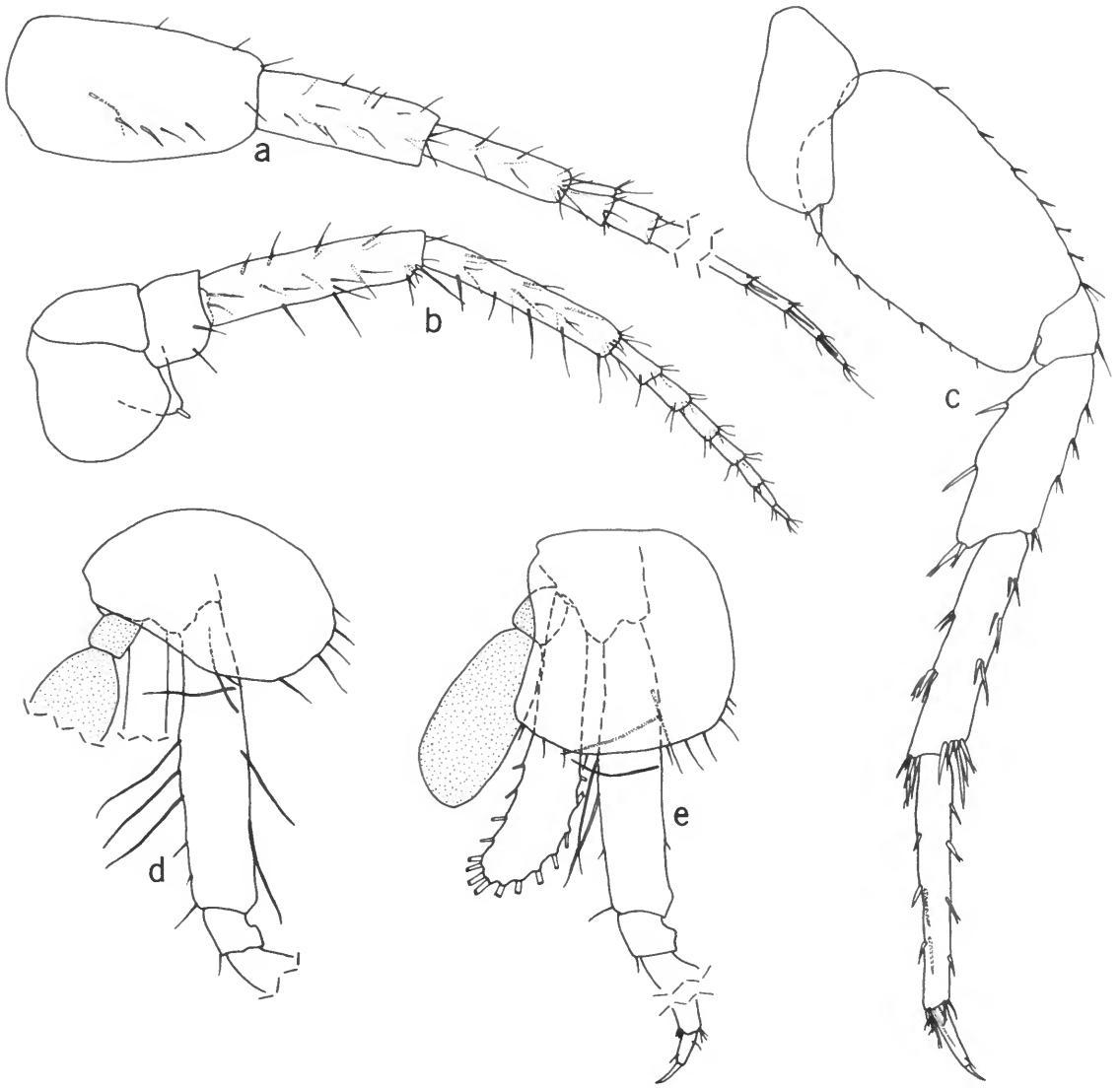

FIGURE 15.—*Stygobromus ackerlyi*, new species, female paratype (8.0 mm), White River Cave, Georgia: *a*, *b*, antennae 1, 2; *c*, pereopod 6; *d*, *e*, pereopods 3, 4 (in part).

on inner margin distally; outer plate with naked setae on inner margin and apex and 1 very lightly plumose seta apically. Lower lip with small inner lobes.

Propod of gnathopod 1 subequal in size to 2nd propod; palm with double row of 13 or 14 spine teeth; defining angle with 4 long spine teeth on outside, none or 1 on inside; medial setae few, mostly singly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, with 4 marginal setae. Gnathopod propod 2: palm with double row of about 15 spine teeth; defining angle with 2 long spine teeth on outside, shorter one on inside; posterior margin

with 3 sets setae; medial setae mostly singly inserted. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 6 setae each. Coxal plate of pereopod 4 about as broad as long, reaching about 40 percent length of basis. Pereopod 6 slightly longer than pereopod 7, 38–45 percent length of body, about 20 percent longer than pereopod 5. Pereopods 5–7: bases a little broader proximally than distally, distoposterior lobes broadly rounded; dactyls about 37 percent length of corresponding propods. Two median sternal gills on pereonites 2 and 3; 2 pairs rather long, simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear but slightly broadening distally.

Pleonal plates: posterior margins moderately convex, with 1 seta each; posterior corners small, narrowly rounded; ventral margin of plate 2 with 1 spine, that of 3 with 2 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 75 percent length of peduncle, armed with 12 spines; outer ramus with 12 spines; peduncle with 12 spines. Uropod 2: inner ramus a little longer than outer ramus, subequal in length to peduncle, armed with 10 spines; outer ramus with 12 spines; peduncle with 6 spines. Uropod 3: ramus about 40 percent length of peduncle, with 4 apical spines. Telson slightly longer than broad, gently tapering distally; apical margin with distinct notch, armed with 16–18 spines.

TYPE-LOCALITY.—White River Cave, located approximately 29 km south-southeast of Rome and 4.8 km northeast of Rockmart in Polk Co., Georgia. The type-locality is developed in Lower Ordovician limestone.

DISTRIBUTION AND ECOLOGY.—This species is recorded from two caves, situated about 34 km apart, in the Coosa River drainage of northwestern Georgia. Type specimens were collected from a small stream in White River Cave and from the underside of rotting boards in a small, gravel-bottom stream in Cave Springs Cave. Females with setose brood plates, ranging in size from 4.8–8.0 mm, have been collected during winter, spring, and summer. The single female from Cave Springs Cave appeared to have just released her young at the time of collection.

ETYMOLOGY.—This species is named in honor of its discoverer, the late Ernest Ackerly.

Stygobromus inexpectatus, new species

FIGURE 16

Stygobromus species.—Holsinger and Peck, 1971:30 [in part].

MATERIAL EXAMINED.—ALABAMA. Calhoun Co.: Meadows Cave, holotype ♀ (USNM 168827), 6 ♀, 1 ♂ and 3 juv. paratypes (JRH), S. B. Peck, L. Guy, and G. McCluskey, 3 Sep 1968.

DIAGNOSIS.—A medium-sized cavernicolous species closely related to *S. ackerlyi* but distinguished from that species by fewer setae on outer margin of gnathopod dactyls, larger coxal plate of pereopod 4 which is about ⅔ length of basis, proportionately broader bases of pereopods 5–7, proportionately larger pleonal plates with more ventral marginal spines, fewer spines on inner ramus but more spines on peduncle of uropod 1, and proportionately longer telson with shallower apical notch. Largest male (immature ?), 4.5 mm; largest female, 7.7 mm.

FEMALE.—Antenna 1, 40–45 percent length of body, 40 percent longer than antenna 2; primary flagellum with 15 segments. Antenna 2, flagellum with 6 segments. Mandible, maxilliped, and lower lip like those of *S. ackerlyi*. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 2 slender spines and 5 setae apically. Maxilla 2, inner plate with oblique row of 7 or 8 plumose setae on inner margin. Gnathopod 1 about like that of *S. ackerlyi* except outer margin of dactyl with 1 seta instead of 4. Gnathopod propod 2: palm with double row of 14 or 15 spine teeth; defining angle with 3 long spine teeth on outside, 5 shorter ones on inside; posterior margin with 3 or 4 sets setae; medial setae mostly singly inserted. Coxal plates of gnathopod 2 and pereopod 3 like those of *S. ackerlyi*. Coxal plate of pereopod 4 rather broad and deep, reaching about ⅔ length of basis, margin with 9 setae. Pereopod 6 subequal in length to pereopod 7, 40–45 percent length of body, 15–20 percent longer than pereopod 5. Pereopods 5–7: bases broader proximally than distally, posterior margins broadly convex, distoposterior lobes broadly rounded; dactyls 34–39 percent length of corresponding propods. Gills and brood plates like those of *S. ackerlyi*.

Pleonal plates: posterior margins of 1 and 3 convex, that of 2 nearly straight, margins with 1 seta each; posterior corners small, 1 and 2 bluntly rounded, 3 more narrowly rounded; ventral margins

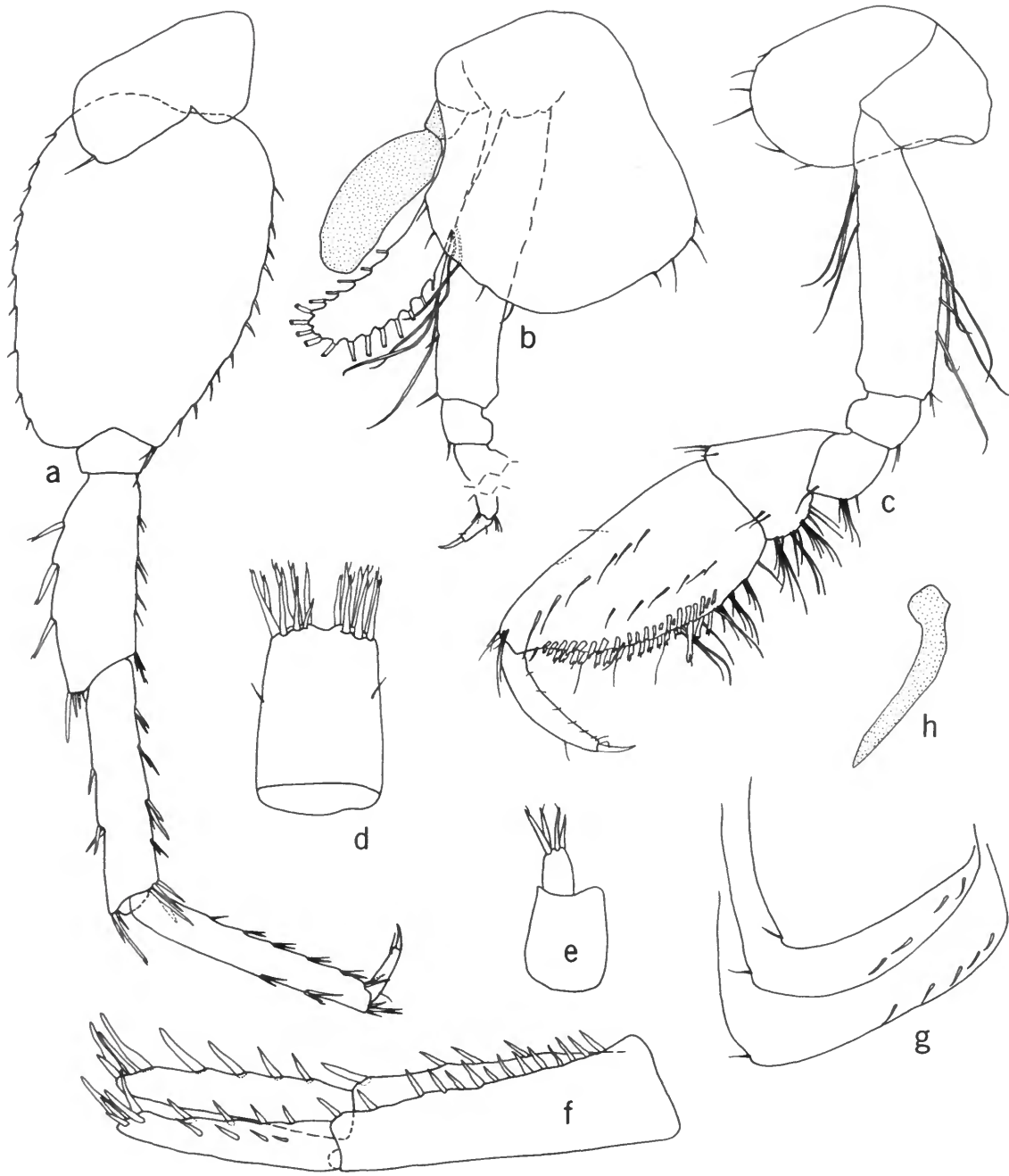

FIGURE 16—*Stygobromus inexpectatus*, new species, female paratype (7.7 mm), Meadows Cave, Alabama: *a*, pereopod 6; *b*, pereopod 4; *c*, gnathopod 2; *d*, telson; *e*, uropod 3; *f*, uropod 1; *g*, pleonal plates; *h*, lateral sternal gill.

of plates 2 and 3 with 4 or 5 spines. Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, 70–75 percent length of peduncle, armed with 8 or 9 spines; outer ramus with 12 or 13 spines; peduncle with 18 or 19 spines. Uropods 2 and 3 about like those of *S. ackerlyi*. Telson 25–30 percent longer than broad, gently tapering distally; apical margin with shallow notch, armed with 16–18 spines.

MALE.—Single specimen in collection apparently immature; differing from female by having few less spines and setae on most appendages. Peduncular process of uropod 1 short, apex trilobed.

TYPE-LOCALITY.—Meadows Cave which, according to S. B. Peck who collected the type series, is located 1.6 km northwest of Weaver in Calhoun Co., Alabama. This is a small cave with several pools but apparently no flowing stream (see map 94 in Tarkington, Varnedoe, and Veitch, 1965; Varnedoe, 1973). Varnedoe (1973:33) indicated that Meadows Cave was developed in the Fort Payne chert (Mississippian age), but on the basis of the Geological Map of Alabama, by Adams, et al. (1926) it would be in Cambrian limestone or dolomite.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, which is located approximately 61 km southwest of Cave Springs Cave (see *S. ackerlyi*, above) in the Coosa River drainage. Only a single female (7.7 mm) in the type series had setose brood plates.

REMARKS.—After more critical study, I have concluded that this species is distinct from *S. ackerlyi* and not conspecific as indicated previously (Holsinger and Peck, 1971:30).

ETYMOLOGY.—The epithet *inexpectus* is from Latin, meaning "unexpected."

The *gracilipes* Group

DIAGNOSIS.—Closely related to the *emarginatus* group but distinguished as follows: Adult size range small to large (ca. 4.3–18.0 mm). Defining angle of gnathopod propod 1 with 4–6 long spine teeth of unequal length on outside. Lateral sternal gills bifurcate. Posterior margins of pleonal plates with 1–6 setae each. Ramus of uropod 3 with 1–4 apical spines. Telson longer than broad, gently tapering distally; apical margin entire; lateral margins with spines.

REMARKS.—The *gracilipes* group is composed of two species, both previously described (Holsinger, 1967), which inhabit caves in the upper James River drainage of west-central Virginia and the Potomac River drainage in northwestern Virginia, northeastern West Virginia, central Maryland and extreme south-central Pennsylavnia.

Key to the Species of the *gracilipes* Group

Ramus of uropod 3 about 20 percent length of peduncle, with 1 apical spine; posterior margins of pleonal plates with 4–6 setae each; defining angle of gnathopod propod 1 with 6 long spine teeth on outside ..... ***S. gracilipes***

Ramus of uropod 3, 25–30 percent length of peduncle, with 3 or 4 apical spines; posterior margins of pleonal plates with 1 seta each; defining angle of gnathopod propod 1 with 4 long spine teeth on outside ..... ***S. conradi***

Stygobromus gracilipes (Holsinger)

Stygonectes gracilipes Holsinger, 1967:36–40, fig. 7 [type-locality: Skyline Caverns, Warren Co., Virginia]; 1969a:32–33; 1972:60.—Holsinger, Baroody, and Culver, 1976:23–24.—Holsinger, 1976:76.

Stygobromus gracilipes (Holsinger).—Karaman, 1974:111–112.—Holsinger, 1977:261.

MATERIAL EXAMINED.—MARYLAND. Washington Co.: Jugtown Cave, 1 ♀, L. R. Franz, Nov 1967 and 1 ♀, 4 Jan 1969. VIRGINIA. Frederick Co.: Ogdens Cave, 1 ♂, J. R. Holsinger, 25 Jan 1969; Rockingham Co.: Deer Hole Cave, 1 ♀, J. R. Holsinger and R. W. Burnette, 9 Mar 1963; Endless Caverns, 1 ♂, 1 juv., J. R. Holsinger, G. W. Dickson, and S. W. Hetrick, 17 Jan 1976; Massanutten Caverns, 1 ♂ (USNM), L. Hubricht, 13 Aug 1939; 3-D Maze Cave, 1 ♂, J. R. Holsinger, 27 Jun 1974. WEST VIRGINIA. Berkeley Co.: Nestle Quarry Cave, 1 ♀, 1 ♂, J. R. Holsinger, 31 Mar 1973.

DIAGNOSIS.—A large cavernicolous species distinguished by proportionately long 6th and 7th pereopods, small, 1-spined ramus of uropod 3, dorsolaterally spinose telson, and by the description of Holsinger (1967). Largest males, 10.5 mm; largest females, 18.0 mm.

DISTRIBUTION AND ECOLOGY.—The range of this species extends from Rockingham Co., Virginia, north-northeast to Franklin Co., Pennsylvania, covering a linear distance of approximately 177 km. To date the specimens have been collected from 11 caves, all of which are situated in the Potomac River drainage and are developed in Cambrian and Ordovician limestones and dolomites.

Despite its comparatively long range, *S. gracilipes* is quite rare in most of the caves in which it occurs. Only in Skyline Caverns, Virginia, where seven collections over a 20-year period yielded 49 specimens, has this species been found in any abundance. *Stygobromus gracilipes* inhabits small streams and pools but has been found more frequently in the latter habitat. Females (10.0–18.0 mm in length) with setose brood plates have been collected during fall, winter, and spring but so far not in summer. One female (11.7 mm) from a January collection in Jugtown Cave, Maryland, was ovigerous and contained nine embryos in the brood pouch.

Stygobromus conradi (Holsinger)

Stygonectes conradi Holsinger, 1967:40–42, fig. 8 [type-locality: Breathing Cave, Bath Co., Virginia]; 1969a:32–33; 1972:60. *Stygobromus conradi* (Holsinger).—Karaman, 1974:109.—Holsinger, 1977:261; 1978.

MATERIAL EXAMINED.—VIRGINIA. Bath Co.: Butler-Sinking Creek Cave, 2 ♂, J. R. Holsinger, L. V. Amundson, and T. Vigour, 2 Nov 1968.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished from *S. gracilipes,* to which it is closely related, by the characters given in the above key and by the description of Holsinger (1967). Largest male (submature?), 4.3 mm; largest female, 8.2 mm.

DISTRIBUTION AND ECOLOGY.—This rare species is known only from two females and two males collected from Breathing and Butler-Sinking Creek caves, respectively. These caves are hydrologically integrated components of an extensive cavern system developed in Upper Silurian and Lower Devonian limestones of the upper James River drainage in northern Bath and southern Highland counties, Virginia (Holsinger, 1975a:23). The two males from Butler-Sinking Creek Cave were collected from under flat rocks in a stream also inhabited by isopods, *Asellus* (sensu lato) *holsingeri,* and snails, *Fontigens orolibas* Hubricht.

The *spinosus* Group

DIAGNOSIS.—Closely related to the *emarginatus* group but distinguished from that group as follows: Adult size range, 3.7–6.0 mm. Propod of gnathopod 1 a little larger than 2nd propod; defining angle with 2 or 3 long spine teeth of unequal length on outside. Lateral sternal gills simple. Posterior margins of pleonal plates with 3 to 6 setae each. Urosites usually free but sometimes partly fused. Telson subquadrate to subrectangular, usually a little longer than broad; apical margin entire, slightly convex.

REMARKS.—The *spinosus* group is composed of three closely allied species which occupy groundwater habitats in the Potomac River drainage of northwestern Virginia and Washington, D. C. Two species inhabit primarily springs and spring-runs in the Blue Ridge Mountains and Piedmont region, whereas the third species inhabits a cave in the Shenandoah Valley.

Key to the Species of the *spinosus* Group

1. Many spines on telson elongate, 90–100 percent length of telson; uropod 3 of male with 4 long apical spines ..... ***S. spinosus***
   Spines on telson not elongate, not exceeding 50–60 percent length of telson; uropod 3 of male with 2 short spines 2
2. Ramus of uropod 3 only about 1/8 length of peduncle; palmar margin of gnathopod propod 1 nearly straight; telson with 16–20 apical spines ..... ***S. kenki,*** new species
   Ramus of uropod 3 about 1/5 length of peduncle; palmar margin of gnathopod propod 1 slightly concave; telson with 10–14 apical spines ..... ***S. pseudospinosus,*** new species

Stygobromus spinosus (Hubricht and Mackin)

FIGURES 17, 18

Crangonyx spinosus Hubricht and Mackin, 1940:203–204, fig. 10 [type-locality: spring near Hawksbill Mountain, Shenandoah National Park, Madison Co., Virginia].

Stygobromus spinosus (Hubricht and Mackin).—Hubricht, 1943:697 [in part].—Barnard, 1958:74 [in part].—Hubricht, 1959:878 [in part].—Nicholas, 1960:129 [in part].—Holsinger, 1963:29 [in part]; 1964:62 [in part]; 1969a:29–30; 1972:72.—Karaman, 1974:119 [in part].—Holsinger, 1977:262.

MATERIAL EXAMINED.—VIRGINIA. Albemarle Co.: spring in Saddle Hollow, 4.8 km W of Crozet, 6 ♀ (USNM), R. L. Hoffman, Mar 1948; Augusta Co.: spring 2.1 km SE of Sawmill Ridge overlook in Shenandoah National Park, 37 ♀, 7 ♂ (USNM), L. Hubricht, 6 Jun 1952; Greene Co.: spring near Pinefield shelter, Shenandoah National Park, 45 ♀, 3 ♂ (USNM), L. Hubricht, 6 June 1952 and 13 ♀, J. R. and C. H. Holsinger, 15 May 1971; Swift Run Gap, Skyline Drive (elev. 762 m), 16 ♀ (USNM), 10 May 1940 (habitat and collector not given on label); Madison Co.: spring near Hawksbill Mt., Shenandoah National Park, 7 ♀, 4 ♂ cotypes (syntypes) (USNM 77808) and 16 additional cotypes (USNM), J. G. Mackin, 20 Jun 1937; Page Co.: 3.2 km S of Big Meadows (elev. 1006 m), Skyline Drive, 7 ♀, 2 ♂ (USNM), 10 May 1940 (habitat and collector not given on label); Rappahannock Co.: spring at Indian Run shelter, Shenandoah National Park, 1 ♀ (USNM), L. Hubricht, 5 Jun 1952; Warren Co.: spring near Browntown Valley overlook, Shenandoah National Park, 8 ♀ (USNM), L. Hubricht, 5 Jun 1952; seep in woods near Blue Mtn., ca. 1.6 km N of Linden, 2 ♀, J. R. Holsinger and T. E. Bowman, 8 Jun 1973.

DIAGNOSIS.—A moderately small groundwater species generally distinguished by the characters given for the *spinosus* group and specifically by the relatively heavily spinose 1st and 2nd uropods of the male and the elongate spines of uropod 3 and telson of both sexes. Largest males, 4.0 mm; largest females, 5.5 mm.

FEMALE.—Antenna 1, 50–55 percent length of body, 45–50 percent longer than antenna 2; primary flagellum with 14–16 segments. Antenna 2, flagellum with 3 or 4 segments. Mandibles subequal; spine row with 3 spines; segment 2 of palp with 1 long seta on inner margin distally, segment 3 with 4 short and 2 long setae on inner margin, 4 long setae on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 3 or 4 slender spines apically. Maxilla 2, inner plate with oblique row of 5 pulmose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 pulmose spine, and 2 naked setae apically, 1 plumose spine subapically; outer plate with few naked setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 a little larger than 2nd propod; palmar margin slightly concave, armed with double row of 4 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; medial setae few, singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, margin with 1 seta. Propod of gnathopod 2: palm with double row of 5 spine teeth; defining angle with 1 long spine tooth on outside, 4 shorter ones on inside; posterior margin with 2 or 3 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 long. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, margins with 1 or 2 setae each. Coxal plate of pereopod 4 rather shallow, broader than long, reaching about ⅓ length of basis; margin with 4 setae. Pereopods 6 and 7 subequal in length, 50–55 percent length of body, 25–30 percent longer than pereopod 5. Pereopods 5–7: bases rather narrow, distoposterior lobes distinct; dactyls 30–35 percent length of corresponding propods. Three median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6–7; 1 pair sternal gills on pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins sinuate distally, with 3 or 4 setae each; posterior corners small, narrowly rounded; ventral margin of plate 2 with 1 spine, that of 3 with 3 spines. Uronites free. Uropod 1: inner ramus a litle longer than outer ramus, 55–60 percent length of peduncle, armed with 13 spines; outer ramus with 8 spines; peduncle with 15 spines. Uropod 2: inner ramus longer than outer ramus, about 85 percent length of peduncle, armed with 11 spines; outer ramus with 6 spines; peduncle with 5 spines. Uropod 3: ramus about 20 percent length of peduncle, with 2 or 3 long, apical spines. Telson subquadrate; apical margin entire, with 23 or 24 mostly long spines, some of which are 90–95 percent length of telson.

MALE.—Differing from female as follows: Palm of gnathopod propod 1 straight to slightly convex, with 2–4 more spine teeth. Coxal plate of pereopod 3 with 3 marginal setae, that of pereopod 4 with 6 marginal setae. Pereopods 5–7 with few more spines. Sternal gills on pleonite 1 smaller. Uropod 1: inner ramus about equal in length to outer ramus, armed with 18 spines; outer ramus with 16 spines; peduncle with 16 spines; peduncular process rather short,

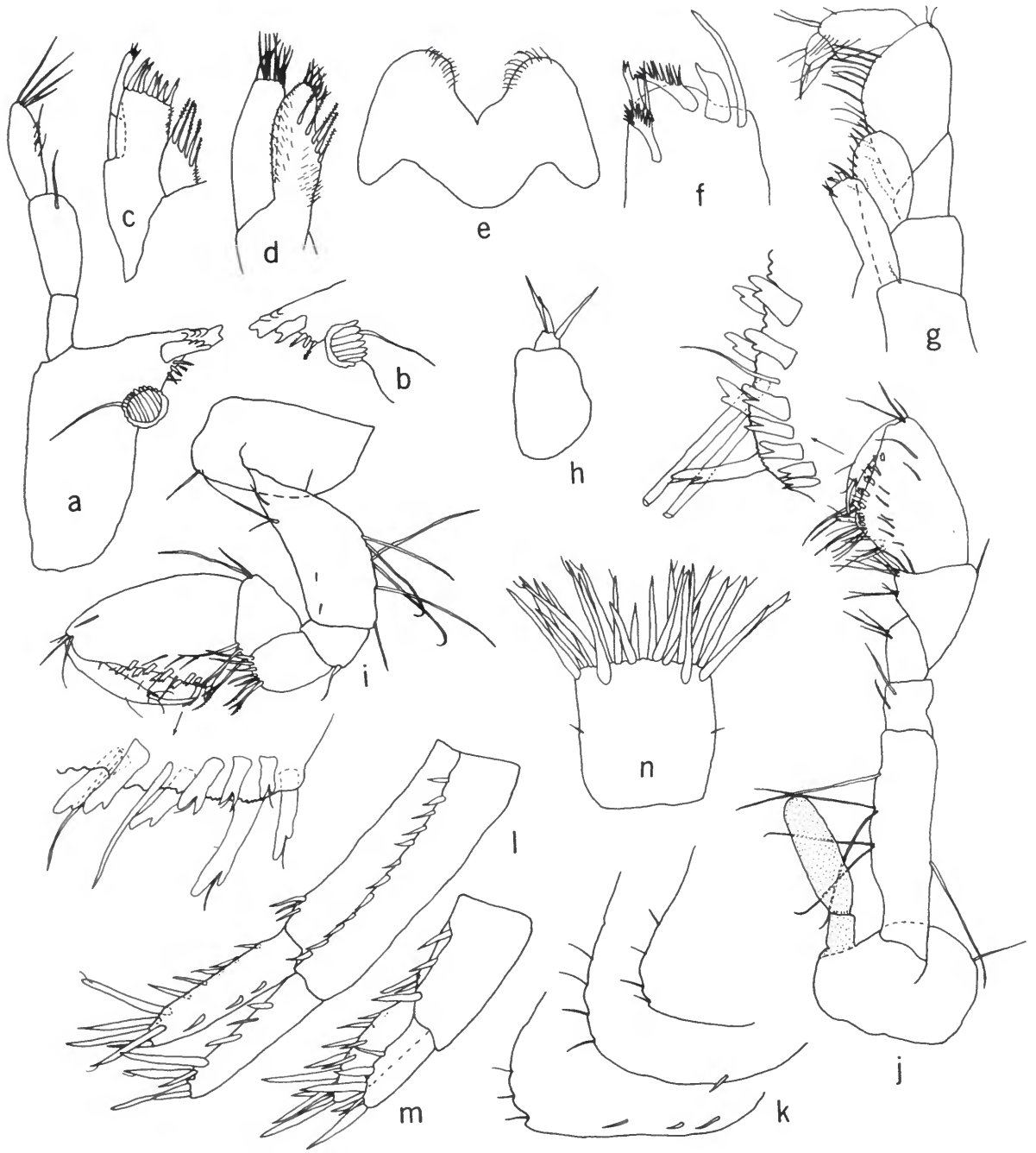

FIGURE 17.—*Stygobromus spinosus* (Hubricht and Mackin), female (5.5 mm), seep near Blue Mt., Virginia: *a*, left mandible *b*, dentate part of right mandible; *c*, *d*, maxillae 1, 2; *e*, lower lip; *f*, apical part of inner plate of maxilliped (greatly enlarged); *g*, maxilliped; *h*, uropod 3; *i*, *j*, gnathopods 1, 2 (part of palms and defining angles enlarged); *k*, pleonal plates; *l*, *m*, uropods 1, 2; *n*, telson.

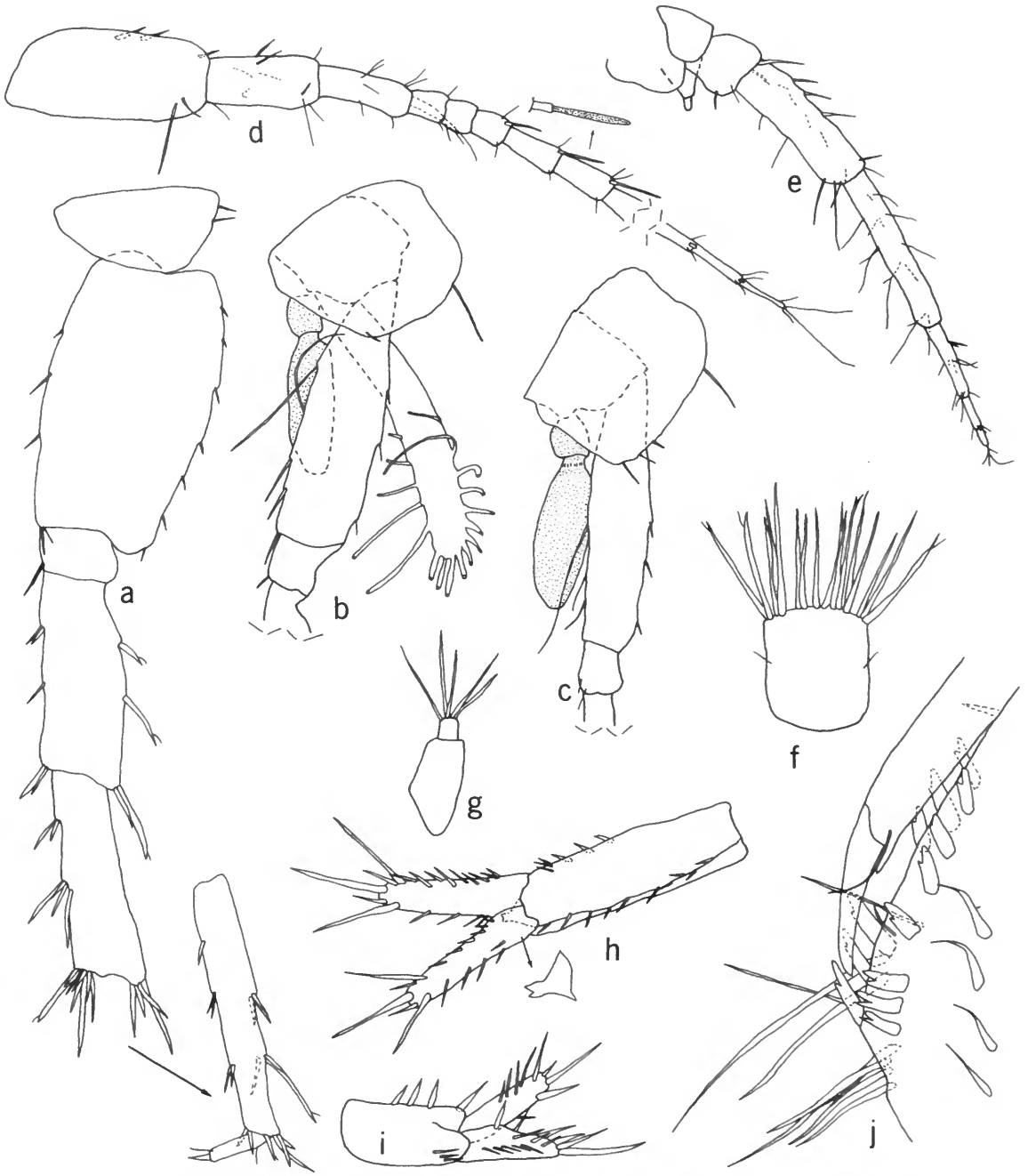

FIGURE 18.—*Stygobromus spinosus* (Hubricht and Mackin). Female (5.5 mm), seep near Blue Mt., Virginia: *a*, pereopod 7 (arrow indicates continuation of appendage); *b*, *c*, pereopods 3, 4 (in part). Male (4.0 mm), spring SE of Sawmill Ridge overlook, Virginia: *d*, *e*, antennae 1, 2 (aesthetasc of antenna 1 enlarged); *f*, telson; *g*, uropod 3; *h*, *i*, uropods 1, 2 (peduncular process of uropod 1 enlarged); *j*, palm of gnathopod propod 2 (greatly enlarged).

apex bilobed. Uropod 2: inner ramus subequal in length to outer ramus, a little shorter than peduncle, armed with 9 spines; outer ramus with 12 spines; peduncle with 7 spines. Uropod 3: ramus about 25 percent length of peduncle, with 4 or 5 long, slender spines. Telson a little longer than broad; apical margin armed with 16–18 long, slender apical spines, many of which are 90–100 percent length of telson.

DISTRIBUTION. AND ECOLOGY.—The range of this species, which is restricted to the Blue Ridge Mountains of northwestern Virginia, extends from Albemarle and Augusta counties north-northeast to Warren County and covers a linear distance of approximately 105 km.

Near Pinefield shelter in Greene County, I collected this species from a fine gravel substrate, under heavy leaf litter and in clumps of aquatic vegetation (moss) in a small spring-run, where it was fairly common and associated with numerous, tiny snails *(Fontigens orolibas),* and a few cyclopoid copepods, ostracods, mayfly and stonefly nymphs and caddis fly cases. It was also observed, but was not as abundant, in two other spring-runs nearby. In Warren County near Blue Mountain, I found the species in the runoff from a seep.

Three ovigerous females (4.3, 4.4, and 5.0 mm) were observed in the June 1952 collection from a spring near Pinefield shelter. The larger female had seven eggs in the brood pouch, but an exact number could not be determined for the other specimens. Females (3.5–5.5 mm) with setose brood plates have been noted in March, May, and June collections but none have been ovigerous.

REMARKS.—Hubricht (1943:697) determined material collected from Luray Caverns in Page Co., Virginia, as *S. spinosus,* but my study of this population has revealed a number of significant differences and I have designated it as a new species described below.

Stygobromus pseudospinosus, new species

FIGURES 19, 20

Stygobromus spinosus (Hubricht and Mackin).—Hubricht, 1943:697 [in part].—Barnard, 1958:74 [in part].—Hubricht, 1959:878 [in part].—Nicholas, 1960:129 [in part].—Holsinger, 1963:29 [in part]; 1964:62 [in part].—Karaman, 1974:119 [in part].

Stygobromus species C.—Holsinger, 1969a:29–30.

MATERIAL EXAMINED.—VIRGINIA. Page Co.: Luray Caverns, holotype ♀ (USNM 168845), 94 ♀ paratypes (USNM), L. Hubricht, 14 Aug 1939; additional paratypes as follows: 2 ♀ (USNM), J. M. Valentine, 6 Aug 1930; 10 ♀ (USNM), J. P. E. Morrison, 2 Mar 1941; 3 ♀ (USNM), J. P. E. Morrison, 15 Feb 1942; 2 ♀, 1 ♂ (JRH), J. R. Holsinger, 15 May 1964.

DIAGNOSIS.—A moderately small cavernicolous species, distinguished from *S. spinosus,* to which it is apparently closely related, by more spine teeth on palms of gnathopods, narrower bases of pereopods 6 and 7, shorter and fewer spines on uropod 3 and telson, proportionately longer telson, and less spinose uropods 1 and 2 (especially in male). Largest male, 4.0 mm; largest females, 7.0 mm.

FEMALE.—Antenna 1, 50–60 percent length of body, 50–60 percent longer than antenna 2; primary flagellum with 13–17 segments. Antenna 2, flagellum with 3 segments. Mouthparts generally similar to those of *S. spinosus* except as noted: Maxilla 1, palp with 7 or 8 setae on apex. Maxilla 2, inner plate with oblique row of 8 or 9 plumose setae on inner margin. Inner plate of maxilliped with 3 bladelike spines, 1 plumose spine and 2 naked setae apically; 2 plumose spines (or setae) subapically on inner margin.

Propod of gnathopod 1 a little larger than 2nd propod; palmar margin slightly concave, armed with double row of 6 spine teeth; defining angle with 3 long spine teeth on outside, 2 shorter ones on inside; medial setae singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, margin with 2 setae. Propod of gnathopod 2: palm with double row of 6 spine teeth; defining angle with 2 long spine teeth on outside, 4 very small ones on inside; medial setae singly inserted; posterior margin with 2 or 3 sets setae. Dactyl nail of gnathopod 2 long. Coxal plates of gnathopod 2 and pereopod 3 slightly longer than broad, margins with 3 setae each. Coxal plate of pereopod 4 about as broad as long, reaching about 1/3 length of basis, margin with 4 setae. Pereopod 7 a little longer than pereopod 6, 40–50 percent length of body, about 30 percent longer than pereopod 5. Bases of pereopods 6 and 7 rather narrow, about as broad proximally as distally; posterior margins slightly convex; distoposterior lobes poorly developed, broadly rounded. Dactyls of pereopods 5–7 about 33 percent length of corresponding propods. Gills and brood plates like those of *S. spinosus.*

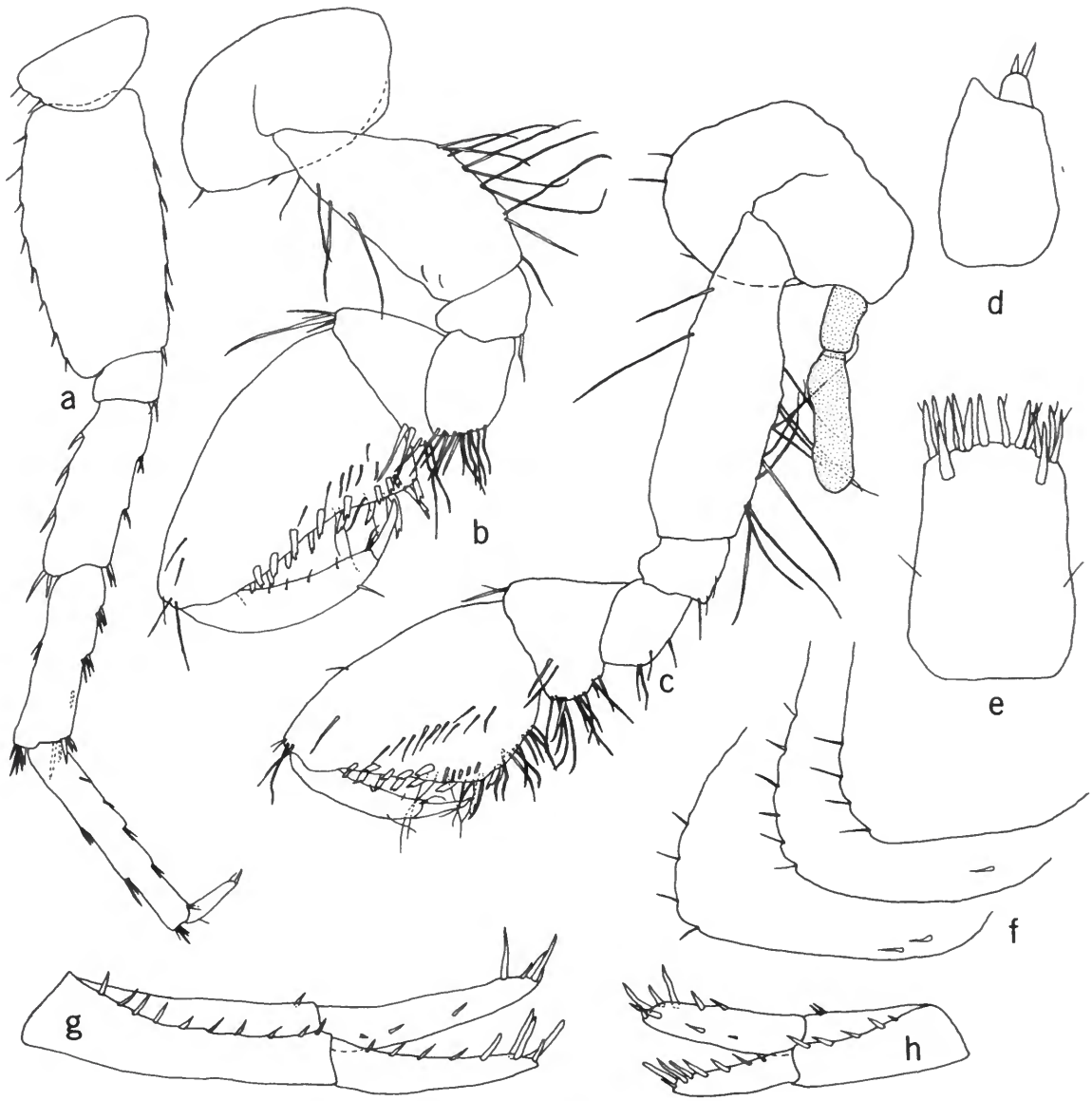

FIGURE 19.—*Stygobromus pseudospinosus*, new species, female paratype (7.0 mm), Luray Caverns, Virginia: *a*, pereopod 7; *b*, *c*, gnathopods 1, 2; *d*, uropod 3; *e*, telson; *f*, pleonal plates; *g*, *h*, uropods 1, 2.

Pleonal plates: posterior margins sinuate distally, those of plates 1 and 3 with 4 setae each, that of plate 2 with 6 setae; posterior corners about like those of *S. spinosus;* ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 75 percent length of peduncle, armed with 8 spines; outer ramus with 10 spines, peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 9 spines; outer ramus with 8 spines; peduncle with 7 spines. Uropod 3: ramus about 20 percent

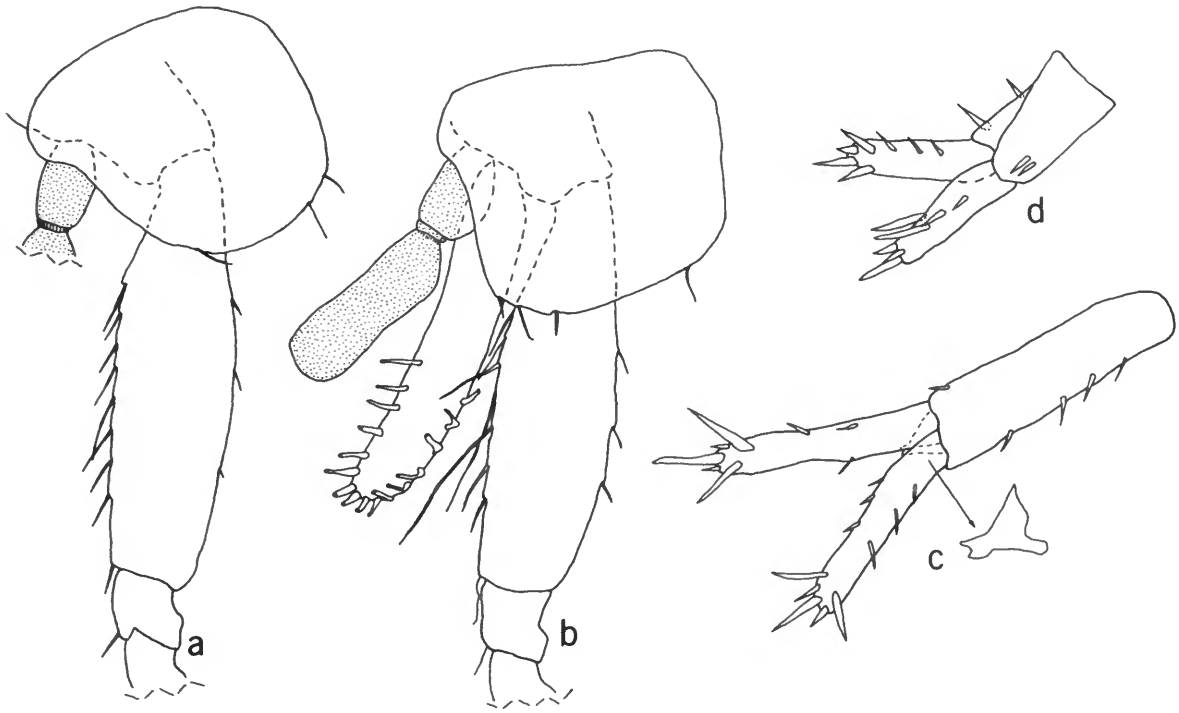

FIGURE 20.—*Stygobromus pseudospinosus*, new species. Female paratype (7.0 mm), Luray Caverns, Virginia: *a*, *b*, pereopods 3, 4 (in part). Male paratype (4.0 mm) Luray Caverns: *c*, *d*, uropods 1, 2 (peduncular process of uropod 1 enlarged).

length of peduncle, with 2 apical spines. Telson longer than broad, gently tapering distally; apical margin entire, armed with 14 spines.

MALE.—Differing from female as follows: Propod of gnathopod 1 with 3 or 4 fewer spine teeth, palm straight. Propod of gnathopod 2 with 10 or 11 spine teeth and fewer setae. Uropod 1: inner ramus subequal in length to outer ramus, about 85 percent length of peduncle, armed with 8 spines; outer ramus with 11 spines; peduncle with 5 spines; peduncular process about like that of *S. spinosus*. Uropod 2: inner ramus subequal in length to outer ramus, a little longer than peduncle, armed with 7 spines; outer ramus with 7 spines; peduncle with 4 spines. Telson with 10 or 11 apical spines.

TYPE-LOCALITY.—Luray Caverns, located just west of Luray in Page Co., Virginia, is a well known commercial cave developed in limestone of the Beekmantown Formation (Lower Ordovician age). The cave contains a number of drip pools but does not have a flowing stream.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected from a series of drip pools on five different occasions between 1930 and 1964. Of the 113 specimens collected, 112 have been females, indicating, as pointed out by Hubricht (1943:697) and Culver and Holsinger (1969), a trend toward parthenogenesis in certain cave species of this genus. Collections are available from winter, spring, and summer, and ovigerous females or females with setose brood plates have been found during all three seasons. Collections made on 14 August 1939 and 2 March 1941 contained seven ovigerous females ranging in size from 4.4 to 6.0 mm ($\bar{X}$ = 5.19). The mean number of eggs per female was 5. One female from the August collection had a newly hatched young (1.4 mm in length) in the brood pouch.

REMARKS.—On 15 May 1964, I made an extensive search in all of the pool areas in Luray Caverns but was able to find only three amphipods in a mud-bottom pool in the Carls Spring area. As indicated

by earlier collections, this species is apparently sporadically abundant at different times and in different pools in the cave.

Although Hubricht (1943:697) relegated material he collected in Luray Caverns to *S. spinosus,* the species from this cave is clearly distinct as indicated by the above description.

Stygobromus kenki, new species

FIGURES 21, 22

MATERIAL EXAMINED.—WASHINGTON, D. C. Spring in Rock Creek Park, SE of North National Capital Parks headquarters, holotype ♀ (USNM 168830), 8 ♀ and 2 ♂ paratypes (JRH), R. Kenk, 5 May 1967; additional paratypes collected by R. Kenk from the same locality as follows: 2 ♀, 1 juv. (JRH), 8 Dec 1966; 6 ♀, 15 juv. (USNM), 11 Jun 1967; 1 ♀, 2 ♂ (USNM), 10 Mar 1967; 5 ♀, 1 juv. (JRH), 26 Mar 1967; 2 ♀, 2 ♂, 1 juv. (JRH), 30 Mar 1967; 1 ♀ (JRH), 6 Dec 1968. Seep in Rock Creek Park, 0.8 km S of park headquarters, 24 ♀ paratypes (JRH), J. R. Holsinger and M. Straskraba, 4 Jul 1967. VIRGINIA. Fairfax Co.: well, 12 m deep, N of Edsall Rd. and just W of Alexandria-Fairfax Co. line, 1 ♂, J. R. Holsinger and W. W. Biggers, 2 Apr 1973.

DIAGNOSIS.—A moderately small groundwater species, closely related to both *S. spinosus* and *S. pseudospinosus,* but distinguished from these species by the palmar margin of gnathopod 1 which is nearly straight and the rudimentary ramus of uropod 3 which is only about 1/8 length of peduncle. Further distinguished from *S. spinosus* by less spinose uropods of the male and shorter telson spines of both sexes; further distinguished from *S. pseudospinosus* by the telson which is proportionately shorter and more spinose. Largest males, 3.7 mm; largest females, 5.5 mm.

FEMALE.—Antenna 1, 40–50 percent length of body, 35–45 percent longer than antenna 2; primary flagellum with 14–16 segments. Antenna 2, flagellum with 3 segments. Mandibles subequal; spine row with 2 or 3 spines; segment 2 of palp with 2 long setae on inner margin, segment 3 with row of short setae on inner margin, 3 long setae apically. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 4 thick setae apically. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine, and 2 naked setae apically, 1 plumose spine (or seta) subapically; outer plate like that of the two previously described species. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 a little larger than 2nd propod; palmar margin nearly straight, armed with double row of 5 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; medial setae few, singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, margin with 2 setae. Propod of gnathopod 2: palm with double row of 3 or 4 spine teeth; defining angle with 1 long spine tooth on outside, 4 shorter ones on inside; posterior margin with 2 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 long. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, margins with 2 setae each. Coxal plate of pereopod 4 rather shallow, broader than long, reaching a little less than 1/3 length of basis. Pereopods 6 and 7 subequal in length, 45–50 percent length of body, 30–35 percent longer than pereopod 5. Bases of pereopods 6 and 7 narrow; posterior margins nearly straight; distoposterior lobes distinct, broadly rounded. Dactyls of pereopods 5–7 about 33 percent length of corresponding propods. Gills and brood plates like those of the two previously described species.

Pleonal plates: posterior margins sinuate distally, with 4 or 5 setae each; posterior corners small, narrowly rounded; ventral margin of plate 2 with 1 spine, that of 3 with 2 spines. Uronites free or sometimes partly fused. Uropod 1: inner ramus equal in length to outer ramus, 55–60 percent length of peduncle, armed with 12 or 13 spines; outer ramus with 9 spines; peduncle with 13 spines. Uropod 2: inner ramus longer than outer ramus, about 80 percent length of peduncle, armed with 10 or 11 spines; outer ramus with 6 spines; peduncle with 5 spines. Uropod 3: ramus very small, only about 1/8 length peduncle, with 2 apical spines. Telson a little longer than broad; apical margin entire, convex, armed with 19 or 20 spines.

MALE.—Differing from female as follows: Propod of gnathopod 1 with 2–4 fewer spine teeth. Propod of gnathopod 2: defining angle with 2 spine teeth on inside; posterior margin with 1 set setae. Uropod 1: inner ramus with 10 spines; outer ramus with 6 spines; peduncle with 7 spines; peduncular process with bilobed apex, the larger lobe being serrulate. Apical margin of telson with 2 or 3 fewer spines.

TYPE-LOCALITY.—Spring southeast of North National Capital Parks headquarters in Rock Creek Park, Washington, D. C. The type series was collected from wet leaf litter at the spring exit;

FIGURE 21.—*Stygobromus kenki*, new species, female paratype (4.6 mm), spring in Rock Creek Park, Washington, D.C.: *a*, inner and outer plates of maxilliped (greatly enlarged); *b*, uropod 3; *c*, lower lip; *d*, dentate part of left mandible; *e*, right mandible; *f*, *g*, gnathopods 1, 2; *h*, pleonal plates; i, telson; *j*, *k*, uropods 1, 2.

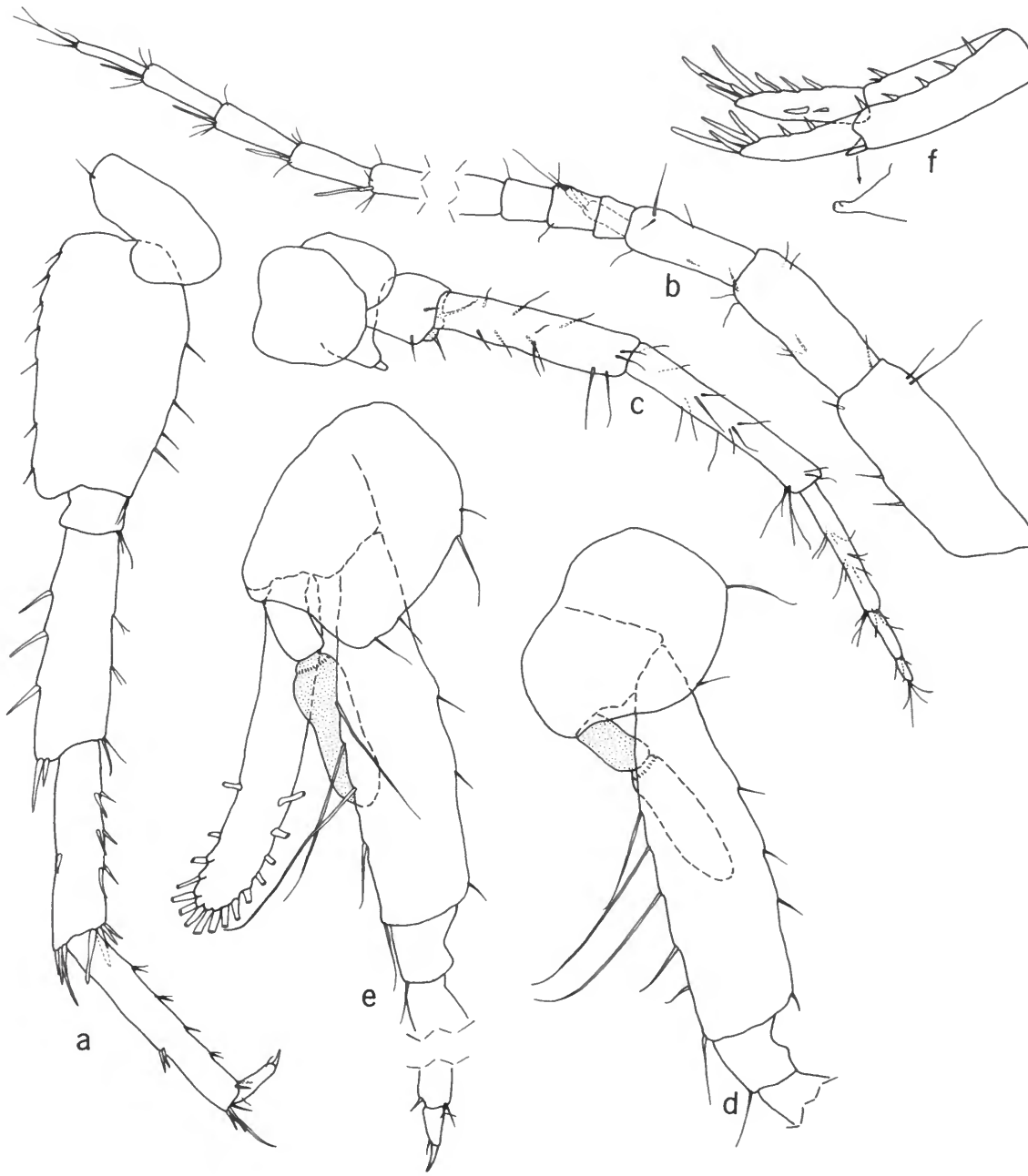

FIGURE 22.—*Stygobromus kenki*, new species. Female paratype (4.6 mm), spring in Rock Creek Park, Washington, D.C.: *a*, pereopod 6; *b*, *c*, antennae 1, 2; *d*, *e*, pereopods 3, 4 (in part). Male paratype (3.3 mm), spring in Rock Creek Park: *f*, uropod 1 (peduncular process enlarged).

the water temperature was 11.3°C (R. Kenk, pers. comm.). This spring, like others in Rock Creek Park, is developed in Precambrian crystalline rocks (granite gneiss?) of the Piedmont Province and is exposed in a ravine cut by Rock Creek or one of its tributaries.

DISTRIBUTION AND ECOLOGY.—*S. kenki* is recorded from a small spring and a spring-like seep in Rock Creek Park and a well in nearby Fairfax Co., Virginia. Rock Creek Park and the well in Virginia are approximately 21 km apart and are further separated by the Potomac River. Both localities in Rock Creek Park have an intermittent flow and sometimes dry up during late summer or early fall. Specimens from both sites were collected from wet leaf litter. Collections are available from winter, spring, and summer, but only females (3.0–5.0 mm) from spring and summer samples had setose brood plates. The collection made on 30 March 1967 contained a single specimen of *S. tenuis potomacus*.

REMARKS.—The single male (2.0 mm) from the well in Virginia was apparently immature and lacked sternal gills on the first pleonite. Although it appears conspecific, I have not made it a paratype. This specimen was collected in a bottle baited with fresh shrimp.

ETYMOLOGY.—It is a pleasure to name this species in honor of its discoverer, my distinguished colleague, Dr. Roman Kenk, who has made numerous contributions to our knowledge of freshwater invertebrates.

The *ephemerus* Group

DIAGNOSIS.—Closely related to the *emarginatus* group but distinguished as follows: Adults small (ca. 1.6–5.8 mm). Gnathopod propod 1 a little larger than, or subequal in size to, 2nd propod; defining angle with 2 long spine teeth of unequal length on outside. Pereopod 7 slightly longer than pereopod 6 but sometimes equal in length. Pleonal plates: posterior margins with 1 seta (rarely 2 or 3) each; posterior corners rounded, usually indistinct. Ramus of uropod 3 tiny or absent; peduncle or ramus of uropod 3 with 1 apical spine. Telson usually short and somewhat variable in shape, often subquadrate, sometimes a little broader than long, sometimes a little longer than broad, usually tapering distally; apical margin entire or occasionally with slight notch.

REMARKS.—The *ephemerus* group is composed of six small, rare, closely related species which inhabit small, mud-bottom pools in caves, where they are frequently found only sporadically. The range of this group covers parts of the Greenbrier and Tygart river drainage basins in eastern West Virginia and parts of the James and New river drainage basins in western Virginia.

Key to the Species of the *ephemerus* Group

1. Uropod 3 with small ramus ..... ***S. redactus,*** new species
   Uropod 3 without ramus 2
2. Distoposterior lobes of bases of pereopods 5–7 broadly expanded; telson about 25 percent longer than broad ..... ***S. nanus,*** new species
   Distoposterior lobes of bases of pereopods 5–7 not broadly expanded, usually poorly developed; telson not much longer than broad, sometimes broader than long 3
3. Propods of gnathopods with 18–20 spine teeth; telson with 12 apical spines ..... ***S. estesi,*** new species
   Propods of gnathopods with 12 or less spine teeth; telson with 10 or less apical spines 4
4. Propods of gnathopods with 10–13 spine teeth ..... ***S. ephemerus***
   Propods of gnathopods with 6–7 spine teeth 5
5. Telson with 9 or 10 spines; propod of gnathopod 1 not much broader proximally than distally ..... ***S. parvus***
   Telson with 6–8 spines; propod of gnathopod 1 distinctly broader proximally than distally ..... ***S. pollostus,*** new species

Stygobromus ephemerus (Holsinger)

Apocrangonyx species C.—Holsinger, 1969a:28.
Apocrangonyx ephemerus Holsinger, 1969b:18–22, figs. 7, 8 [type-locality: Tawneys Cave, Giles Co., Virginia]; 1972:54.
Stygobromous ephemerus (Holsinger).—Karaman, 1974:110.—Holsinger, 1977:261.

MATERIAL EXAMINED.—VIRGINIA. Giles Co.: Tawneys Cave, 1 ♂, G. Marland, Feb 1962; 1 ♂, J. R. Holsinger and E. Bauer, 20 Aug 1965.

DIAGNOSIS.—A moderately small cavernicolous species, but one of the larger members of the *ephemerus* group, distinguished by having about 13 spine teeth on propod of gnathopod 1 and about 10 spine teeth on propod of gnathopod 2, relatively narrow bases of pereopods 5–7, and short, unnotched telson which is about as broad as long. Largest male, 3.4 mm; largest female, 5.0 mm.

DISTRIBUTION AND ECOLOGY.—This species is recorded from Tawneys and Canoe caves, which are situated about 4 km apart in the Sinking Creek Valley of Giles Co., Virginia (Holsinger, 1969b:22). *Stygobromus ephemerus* inhabits mud-bottom, drip, and seep pools in both caves and occurs sympatrically with *S. mackini* in Tawneys Cave. Females (3.5–5.0 mm) with setose brood plates have been collected during summer, fall, and winter but none have been ovigerous.

Stygobromus estesi, new species

FIGURES 23, 24

MATERIAL EXAMINED.—VIRGINIA. Craig Co.: Rufe Caldwells Cave, holotype ♀ (USNM 168813), 3 ♀ paratypes (JRH), J. R. Holsinger, L. M. and B. L. Ferguson, 19 Apr 1975; New Castle Murder Hole (cave), 1 paratype (JRH), J. A. Estes, 1 Mar 1975.

DIAGNOSIS.—A moderately small cavernicolous species, closely related to *S. ephemerus*, but distinguished from that species by having more spine teeth on gnathopod propods, more setae on margins of coxal plates of gnathopod 2 and pereopods 3 and 4 and on posterior margins of pleonal plates 2 and 3, more spines on uropods 1 and 2, and by the apical margin of the telson, which has a shallow notch and 12 spines. Largest female, 5.8 mm; male unknown.

FEMALE.—Antenna 1 about 50 percent length of body, 45–50 percent longer than antenna 2; primary flagellum with 17 or 18 segments. Antenna 2, flagellum with 6 or 7 segments. Mandibles subequal; spine row with 5 or 6 spines; segments 2 of palp with 4 long setae on inner margin, segment 3 with 1 long seta on outer margin, row of short setae on inner margin, 6 setae of unequal length on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 3 slender spines and 4 or 5 setae on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines, 1 plumose spine, and 1 naked seta, subapically with 1 plumose spine (or seta); outer plate with naked setae on inner margin and apex and 2 plumose setae apically. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 a little larger than 2nd propod; palm slightly concave, armed with double row of 6 or 7 spine teeth; defining angle with 2 long spine teeth on outside, 4 shorter ones on inside; medial setae few, singly inserted. Coxal plate of gnathopod 1 longer than broad, with 2 marginal setae. Gnathopod propod 2: palm with double row of about 8 spine teeth; defining angle with 1 long spine tooth on outside, 3 shorter ones on inside; posterior margin 3 or 4 sets setae; medial setae mostly singly inserted. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, margins with 6 or 7 setae each. Coxal plate of pereopod 4 about as broad as long, reaching 35–40 percent length of basis, margin with 8 setae. Pereopods 6 and 7 equal in length, 50 percent length of body, 20 percent longer than pereopod 5. Bases of pereopods 6 and 7 rather narrow, distoposterior lobes small and poorly developed. Dactyls of pereopods 6 and 7, 35–40 percent length of corresponding propods; dactyl of pereopod 5, 30–35 percent length of corresponding propod. Three rather long median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins of plates 1 and 2 weakly convex, with 1–3 setae each, posterior margin of plate 3 strongly convex, with 3 or 4 setae; posterior corners of plates 2 and 3 small and narrowly rounded, that of plate 1 indistinct; ventral margin of plate 2 with 1–3 spines, that of plate 3 with 3 or 4 spines. Uronites fused. Uropod 1: inner ramus slightly shorter than outer ramus, 60 percent length of peduncle, armed with 11 spines; outer ramus with 11 spines; peduncle with 11 spines.

(cave), Virginia: *a*, left mandible; *b*, dentate part of right mandible; *c*, lower lip; *d*, apical part of inner plate of maxilliped (greatly enlarged); *e*, *f*, gnathopods 1, 2; *g*, pleonal plates; *h*, telson; *i*, uropod 3; *j*, lateral sternal gill.

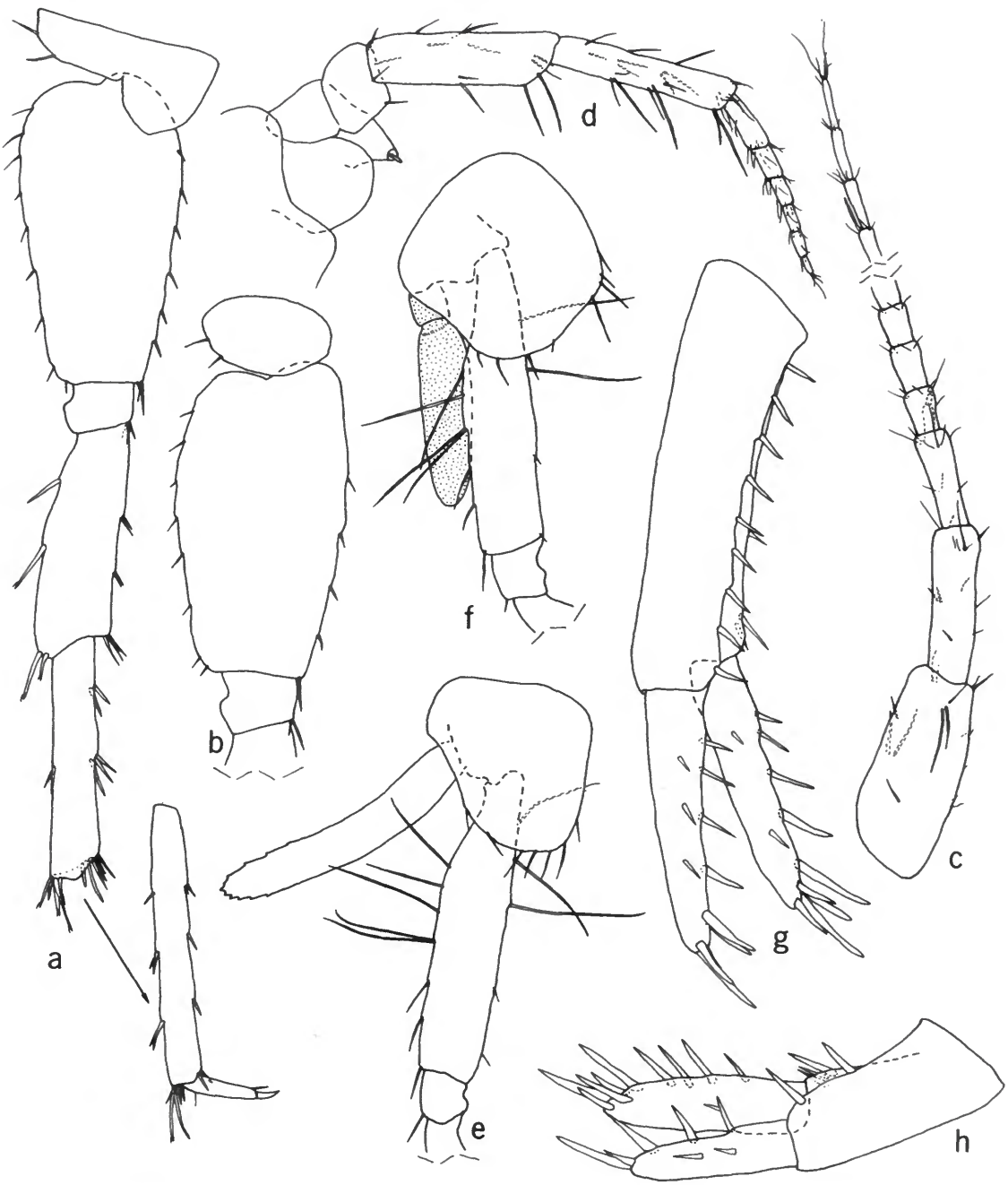

FIGURE 24.—*Stygobromus estesi*, new species, female paratype (5.8 mm), New Castle Murder Hole (cave), Virginia; *a*, pereopod 6 (arrow indicates continuation of appendage); *b*, pereopod 7 (in part); *c*, *d*, antennae 1, 2; *e*, *f*, pereopods 3, 4 (in part); *g*, *h*, uropods 1, 2.

Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 10 spines; outer ramus with 7 spines; peduncle with 5 spines. Uropod 3 lacking ramus, peduncle with 1 apical spine. Telson a little longer than broad; apical margin with shallow notch, armed with 12 spines.

TYPE-LOCALITY.—Rufe Caldwells Cave, located 6.4 km southwest of New Castle in Craig Co., Virginia, is a medium-sized cave (with a small stream) developed in Middle Ordovician limestone.

DISTRIBUTION AND ECOLOGY.—This species is known only from two caves which are located 2.3 km apart near the head of a karsted limestone cove formed between Sinking Creek and Johns Creek mountains. Both caves are situated in the James River drainage basin just east of the limestone interfluve between Sinking Creek (New River drainage) and Meadow Creek (James River drainage). The range of this species is approximately 29 km northeast of the range of *S. ephemerus*. In both caves, *S. estesi* has been collected from mud-bottom pools fed by drips and seeps. Two females (4.5 and 5.5 mm) from the April collection in Rufe Caldwells Cave had setose brood plates. In New Castle Murder Hole, this species occurs sympatrically with *S. interitus*, new species (p. 95), and an undecided form closely related to *S. mackini* (see "*Stygobromus* species").

ETYMOLOGY.—It is a pleasure to name this species in honor of James A. Estes, who first discovered it in New Castle Murder Hole.

Stygobromus parvus (Holsinger)

Apocrangonyx species A.—Holsinger, 1969a:28.

Apocrangonyx parvus Holsinger, 1969b:22–25, fig. 9 [type-locality: Crawford Cave No. 2, Randolph Co., West Virginia]; 1972:54.—Holsinger, Baroody, and Culver, 1976:21.

Stygobromus parvus (Holsinger).—Karaman, 1974:116.—Holsinger, 1977:262.

MATERIAL EXAMINED.—WEST VIRGINIA. Pocahontas Co.: Piddling Pit Cave, 2 ♀, 2 ♂, J. R. Holsinger and D. C. Culver, 12 Aug 1972.

DIAGNOSIS.—A small cavernicolous species, closely allied morphologically with *S. ephemerus*, but distinguished from that species by the diagnosis of Holsinger (1969b:22) and in the above key. Largest males, 2.6 mm; largest female, 3.0 mm.

DESCRIPTION.—Corresponding to the description by Holsinger (1969b:22–25) with the following additions and modifications: Antenna 1, 50–60 percent length of body. Propod of gnathopod 1 a little larger than 2nd propod. Pereopods 6 and 7 sometimes about equal in length, 50–60 percent length of body, 30–35 percent longer than pereopod 5. Uronites fused.

DISTRIBUTION AND ECOLOGY.—This species is recorded from three caves in eastern West Virginia: Piddling Pit and Cassell caves, which are developed along the eastern flanks of Cloverlick and Back Allegheny mountains, respectively, in the upper Greenbrier River drainage; and Crawford Cave No. 2, which is west of Cheat Mountain in the upper Tygart River drainage (upper Monongahela basin). *Stygobromus parvus* has been collected from mud-bottom, drip, and seep pools in all three caves. Several females (2.5–3.0 mm) from August collections in Piddling Pit and Crawford No. 2 caves had setose brood plates. In Piddling Pit, this species occurs sympatrically with both *S. emarginatus* and *S. nanus*, new species, but these species have not been found together in the same place within the cave.

REMARKS.—I indicated earlier (Holsinger, 1972: 54) that the single specimen from the Windy Cave entrance section of Cassell Cave might represent another species, but I have now concluded that it is *S. parvus* (see also Holsinger, Baroody, and Culver, 1976:21).

Stygobromus pollostus, new species

FIGURES 25, 26

Apocrangonyx sp.—Culver, 1973:103.—Holsinger, Baroody, and Culver, 1976:22.

MATERIAL EXAMINED.—WEST VIRGINIA. Greenbrier Co.: Arbuckles Cave, holotype ♀ (USNM 168842), 1 ♀ paratype (slide mounts in JRH) and 1 ♂ paratype (USNM), D. C. Culver and R. A. Baroody, Oct 1970; Parlor Cave, 3 ♀ paratypes (JRH), J. R. Holsinger, R. A. Baroody, and H. DuChene, 27 Apr 1969; Monroe Co.: Haynes Cave, 4 ♀ paratypes (1 in JRH, 3 in USNM), 1 ♂ paratype (USNM), J. R. Holsinger, D. C. Culver, and R. A. Baroody, 6 Apr 1971; Pocahontas Co.: Snedegars Cave, 1 ♂, 2 juv. paratypes (JRH), D. C. Culver, and R. A. Baroody, 3 Jul 1972.

DIAGNOSIS.—A small cavernicolous species distinguished from *S. parvus*, to which it is very closely related, by the gnathopod propods, which

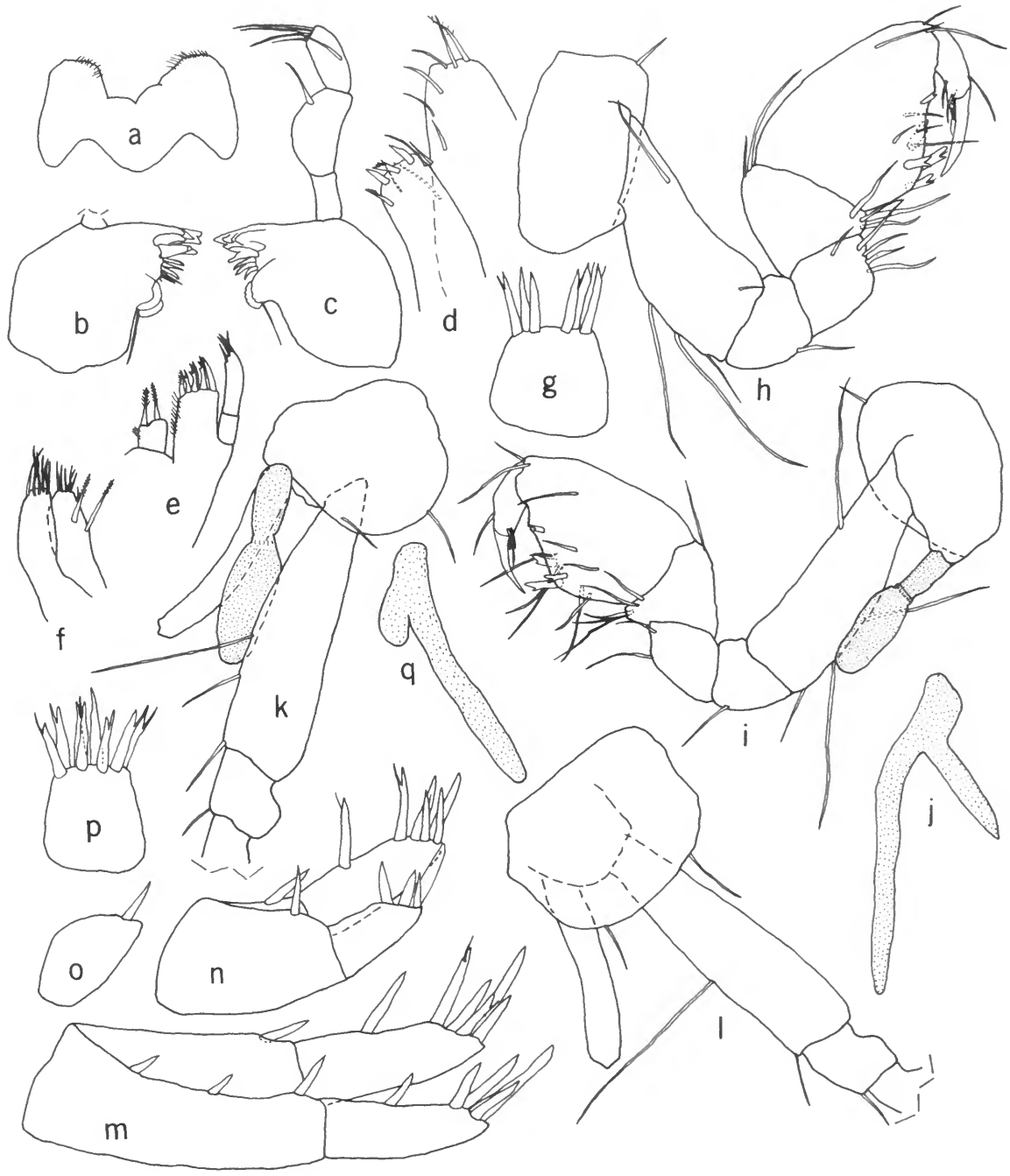

FIGURE 25.—*Stygobromus pollostus*, new species. Female paratype (2.5 mm), Arbuckles Cave, West Virginia: *a*, lower lip: *b*, left mandible (in part); *c*, right mandible; *d*, inner and outer plates of maxilliped (enlarged × 2 size of other mouth parts); *e*, *f*, maxillae 1, 2; *g*, telson; *h*, *i*, gnathopods 1, 2; *j*, lateral sternal gill; *k*, *l*, pereopods 3, 4 (in part); *m*, *n*, uropods 1, 2. Male paratype (2.0 mm), Arbuckles Cave: *o*, uropod 3; *p*, telson. Female paratype (2.3 mm), Haynes Cave, West Virginia: *q*, lateral sternal gill.

FIGURE 26.—*Stygobromus pollostus*, new species. Female paratype (2.5 mm), Arbuckles Cave, West Virginia: *a*, *b*, antennae 1, 2; *c*, pereopod 7. Male paratype (2.3 mm), Snedegars Cave, West Virginia: *d*, pereopod 7 (arrow indicates continuation of appendage); *e*, pleonal plates; *f*, uropod 1 (peduncular process enlarged). Male paratype (2.0 mm), Parlor Cave, West Virginia: *g*, *h*, gnathopods 1, 2.

are proportionately broader proximally, the telson, which tapers distally and has fewer spines, and by smaller size at sexual maturity. Largest male, 2.3 mm; largest females, 2.5 mm.

FEMALE.—Antenna 1, 40–50 percent length of body, 40–50 percent longer than antenna 2; flagellum with 7–9 segments. Antenna, 2, flagellum with 3 segments. Mandibles subequal; spine row with 3 spines; segments 2 of palp with 1 long seta on inner margin distally, segment 3 with 1 long seta on outer margin, 4 long setae apically. Maxilla 1: inner plate with 2 apical, plumose setae; palp with 4 setae apically. Maxilla 2, inner plate with oblique row of 2 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine and 1 naked seta apically, 1 plumose spine (or seta) and 1 naked seta subapically; outer plate with few setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip small but distinct.

Propod of gnathopod 1 a little larger than 2nd propod; palm armed with 2 spine teeth; defining angle with 2 or 3 long spine teeth on outside, 1 or 2 shorter ones on inside; medial setae few, singly inserted. Dactyl nail of gnathopod 1 elongate, nearly 50 percent as long, or sometimes more than 50 percent longer than, dactyl. Coxal plate of gnathopod 1 longer than broad, with 1 marginal seta. Gnathopod propod 2: palm with 2 spine teeth; defining angle with 1 or 2 long spine teeth on outside, 1 or 2 shorter ones on inside: posterior margin with 1 or 2 setae; medial setae few, singly inserted. Dactyl nail of gnathopod 2 elongate like that of 1st gnathopod. Coxal plates of gnathopod 2 and pereopod 3 about as broad as long, with 1 or 2 marginal setae each. Coxal plate of pereopod 4 shallow, broader than long, reaching about 20 percent length of basis, margin with 2 setae. Pereopod 7 a little longer than pereopod 6, 35–40 percent length of body (occasionally up to 50 percent), 30–35 percent longer than pereopod 5. Pereopods 5–7: bases relatively narrow, with few marginal setae and spines, posterior margins nearly straight, distoposterior lobes poorly developed; dactyls long, 40–50 percent length of corresponding propods. Three median sternal gills on pereonites 2–4; 2 pairs lateral sternal gills on pereonites 6 and 7, sometimes simple, sometimes bifurcate but with branches of unequal length; sternal gills absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates: posterior margins weakly convex, with 1 relatively long seta each; posterior corners indistinct, broadly rounded; ventral margin of plate 3 with 1 spine. Uronites fused. Uropod 1: inner ramus a little longer than outer ramus, about 65 percent length of peduncle, armed with 6 spines; outer ramus with 5 or 6 spines; peduncle with 4–6 spines. Uropod 2: inner ramus longer than outer ramus, about 80 percent length of peduncle, armed with 6 spines; outer ramus with 4 or 5 spines; peduncle with 2 or 3 spines. Uropod 3: ramus lacking; peduncle with 1 apical spine. Telson a little broader than long, gently tapering distally; apical margin entire, armed with 6 spines.

MALE.—Differing only slightly from female as follows: Peduncular process of uropod 1 very short, apical margin serrate. Telson about as broad as long, apical margin with 6–8 spines.

VARIATION.—Specimens from Arbuckles Cave (middle of the range) and Haynes Cave (southern end of the range) had bifurcate lateral sternal gills, whereas those from Snedegars Cave (northern end of the range) and Parlor Cave (near middle of the range) had simple lateral sternal gills. There was also some slight but insignificant variation in the arrangement of spine teeth on the gnathopod in different populations.

TYPE-LOCALITY.—Arbuckles Cave, located 7.9 km north-northeast of the center of Lewisburg in Greenbrier Co., West Virginia, is a small, mostly dry cave with intermittent drip pools. It is developed in the Greenbrier limestone.

DISTRIBUTION AND ECOLOGY.—This species is recorded from four caves in the Greenbrier Valley of West Virginia. The range covers a linear distance of 40 km and is separated from that of *S. parvus* by a distance of about 48 km. *Stygobromus pollostus* is found in tiny, usually intermittent, drip pools, where it occurs only sporadically. Females (2.0–2.3 mm) with setose brood plates have been observed in April collections from Parlor and Haynes caves.

REMARKS.—Although *S. pollostus* is very closely allied morphologically with *S. parvus*, I have recognized it as specifically distinct, pending further attempts to locate and analyze populations between the presently known ranges of these two species.

ETYMOLOGY.—The epithet *pollostus* is from the Greek *pollostos*, meaning the "smallest" or the "least."

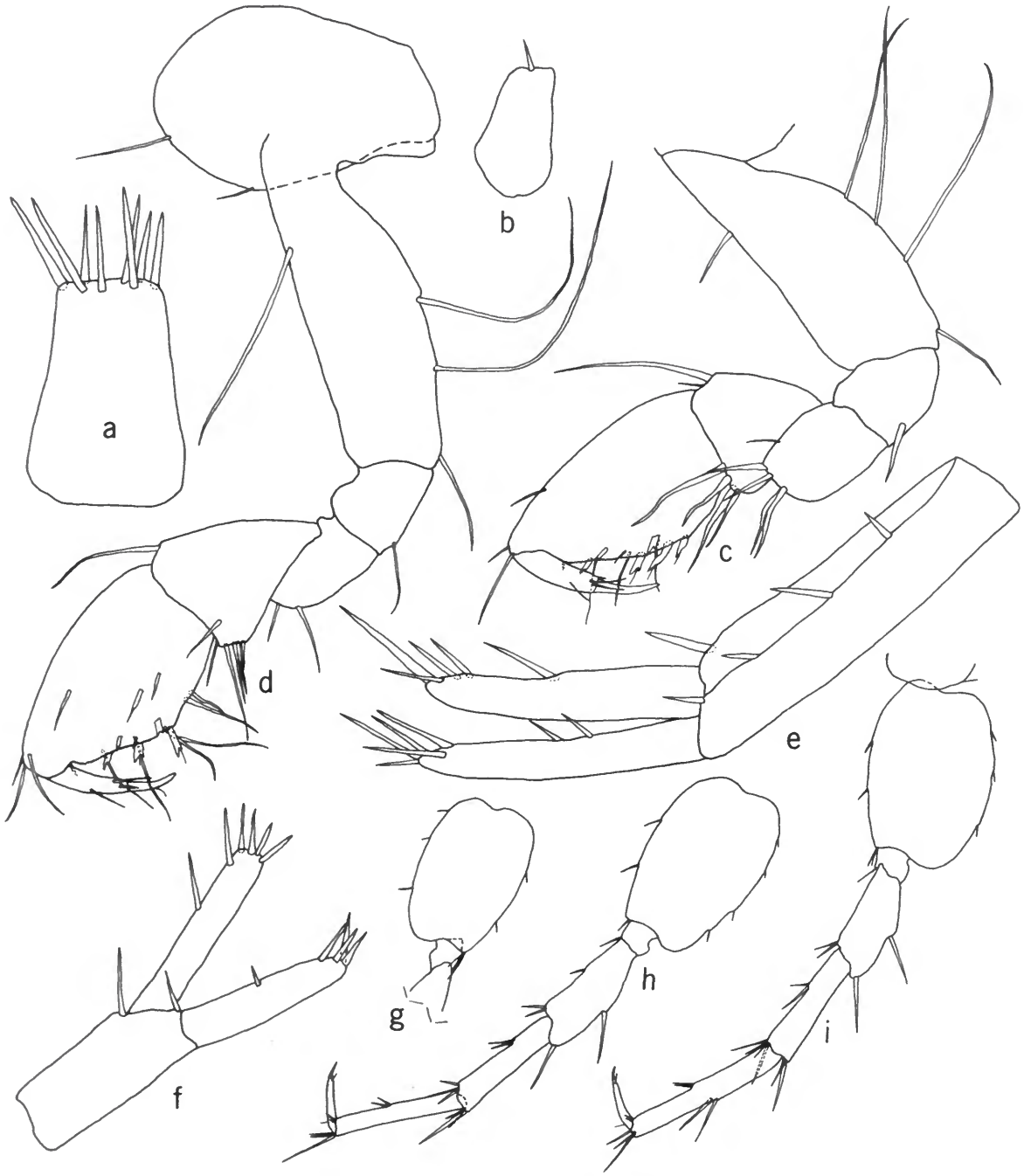

FIGURE 27.—*Stygobromus nanus*, new species, female paratype (2.2 mm), Piddling Pit Cave, West Virginia: *a*, telson; *b*, uropod 3; *c*, *d*, gnathopods 1, 2; *e*, *f*, uropods 1, 2; *g*, pereopod 5 (in part); *h*, *i*, pereopods 6, 7 (note: pereopods drawn to much smaller scale than other appendages).

Stygobromus nanus, new species

FIGURE 27

Apocrangonyx species B.—Holsinger, 1969a:28.
Apocrangonyx sp.—Holsinger, Baroody, and Culver, 1976:22.

MATERIAL EXAMINED.—WEST VIRGINIA. Pocahontas Co.: Piddling Pit Cave, holotype ♀ (USNM 168835), 1 ♀ paratype (slide mount in JRH), 1 ♂ paratype (USNM), J. R. Holsinger, R. A. Baroody, and R. L. Swensson, 30 Sep 1967.

DIAGNOSIS.—A very small cavernicolous species, closely related to *S. parvus* and *S. pollostus*, but distinguished from these species by the bases of pereopods 5–7 which are broader and have well-developed distoposterior lobes and the telson which is proportionately longer (up to 25 percent longer than broad). Further distinguished from *S. parvus* by having simple lateral sternal gills and from *S. pollostus* by proportionately narrower gnathopod propods. Largest male, 1.6 mm; largest female, 2.2 mm.

FEMALE.—Antenna 1 about 45 percent length of body, about 40 percent longer than antenna 2; primary flagellum with 7–9 segments. Antenna 2, flagellum with 3 segments. Mouthparts like those of *S. pollostus* except inner lobes of lower lip vestigial. Propod of gnathopod 1 subequal in size to 2nd propod; palm with double row of 2 spine teeth; defining angle with 2 spine teeth on outside; medial setae absent. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, with 1 marginal seta. Gnathopod propod 2: palm with 3 spine teeth; defining angle with 1 long spine tooth on outside, smaller one on inside; posterior margin with 1 set setae; medial setae few, singly inserted. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, with 2 marginal setae each. Coxal plate of pereopod 4 like that of *S. pollostus*. Pereopod 7 a little longer than pereopod 6, about 50 percent length of body, 25–30 percent longer than pereopod 5. Pereopods 5–7: bases comparatively broad, posterior margins convex, distoposterior lobes distinct and broadly rounded; dactyls relatively long, 45–50 percent length of corresponding propods. Three median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates sublinear, not expanded distally.

Pleonal plates like those of *S. pollostus*. Uronites fused. Uropod 1: inner ramus subequal in length to outer ramus, 65–70 percent length of peduncle, armed with 5 spines; outer ramus with 7 spines; peduncle with 5 spines. Uropod 2: inner ramus a little longer than outer ramus, subequal in length to peduncle, armed with 6 spines; outer ramus with 5 spines; peduncle with 2 spines. Uropod 3 lacking ramus, peduncle with 1 apical spine. Telson about 25 percent longer than broad, taptering distally; apical margin entire, with 8 spines.

MALE.—About like female. Peduncular process of uropod 1 small, apex serrate.

TYPE-LOCALITY.—Piddling Pit Cave, located 4.8 km west of Cloverlick on the eastern flank of Cloverlick Mountain in Pocahontas Co., West Virginia, is a fairly extensive cave with several small streams and pools. The cave is developed in the Greenbrier limestone and is in the upper Greenbrier River drainage.

DISTRIBUTION AND ECOLOGY.—This rare species is known only from its type-locality, where it was collected from two mud-bottom pools fed by drips and seeps. As pointed out above, two other species of *Stygobromus (S. emarginatus* and *S. parvus)* also inhabit this cave, but on two visits to the cave none of these species has been found together in the same place. The two female paratypes (2.0 and 2.2 mm) had setose brood plates but were not ovigerous.

ETYMOLOGY.—The epithet *nanus* is from Latin, meaning a "dwarf."

Stygobromus redactus, new species

FIGURE 28, 29

Stygobromus species G.—Holsinger, 1969a:30.
Stygobromus n. sp. 1.—Culver, Holsinger, and Baroody, 1973: 691.
Stygobromus sp.—Holsinger, Baroody, and Culver, 1976:23.

MATERIAL EXAMINED.— WEST VIRGINIA. Monroe Co.: Patton Cave, holotype ♀ (USNM 168851), 1 ♀, 1 ♂, 1 juv. paratypes (USNM) and 1 ♂ paratype (slide mounts in JRH), J. R. Holsinger, 11 May 1966.

DIAGNOSIS.—A very small cavernicolous species distinguished from other members of the *ephemerus* group by the proportionately small gnathopod propods which have reduced numbers of spines and setae, possession of small ramus on uropod 3, and proportionately short telson which is broader than long. Largest males, 2.0 mm; largest female, 2.0 mm.

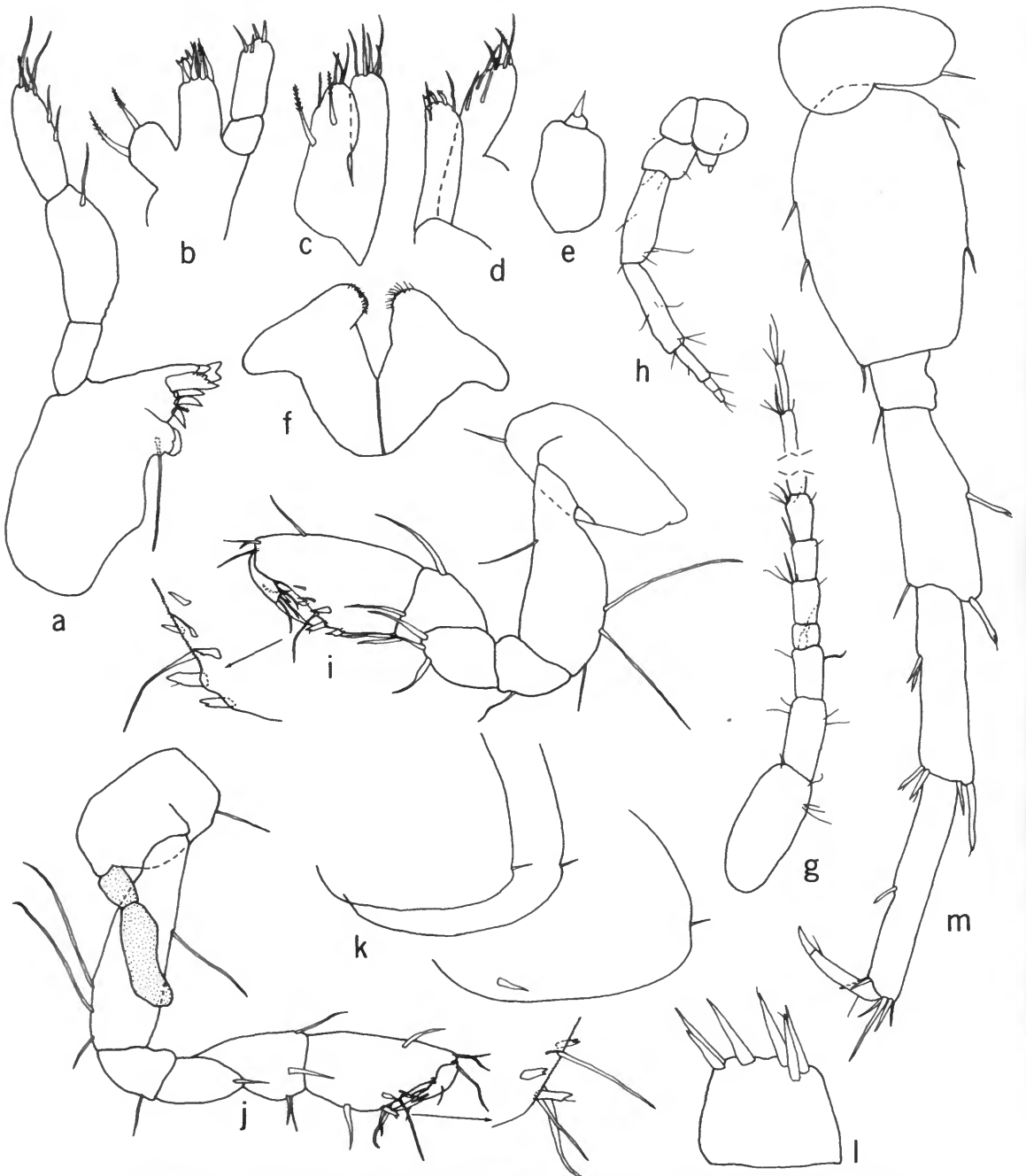

FIGURE 28.—*Stygobromus redactus*, new species, male paratype (2.0 mm), Patton Cave, West Virginia: *a*, left mandible; *b*, *c*, maxillae 1, 2; *d*, inner and outer plates of maxilliped; *e*, uropod 3; *f*, lower lip; *g*, *h*, antenna 1, 2; *i*, *j*, gnathopods 1, 2 (palmar spines enlarged); *k*, pleonal plates; *l*, telson; *m*, pereopod 6.

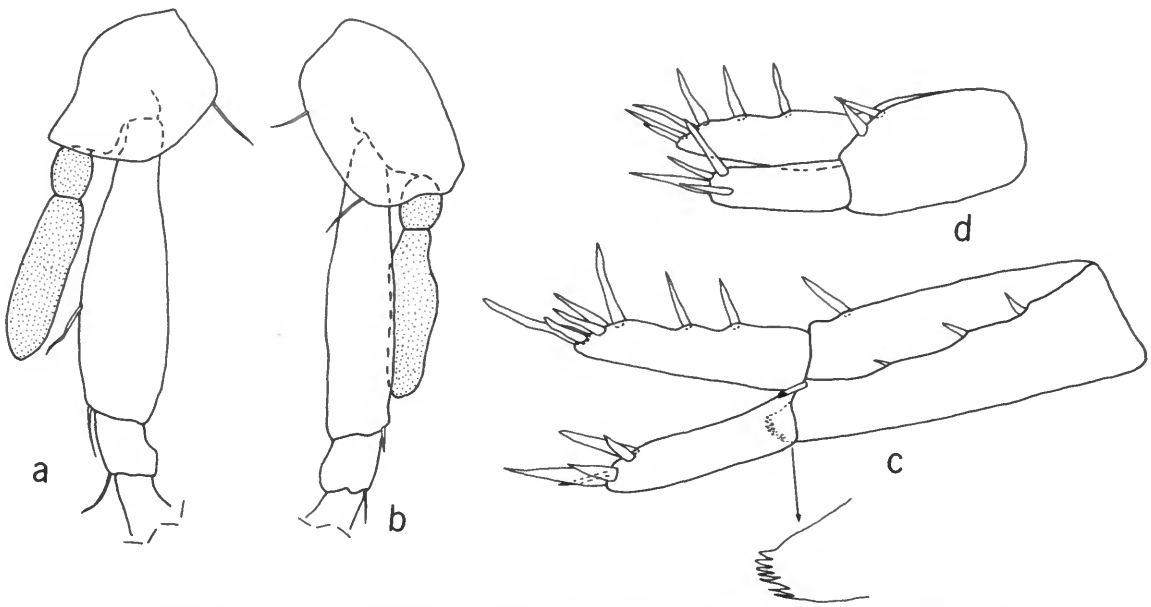

FIGURE 29.—*Stygobromus redactus*, new species, male paratype (2.0 mm), Patton Cave, West Virginia: *a*, *b*, pereopods 2, 4, (in part); *c*, *d*, uropods 1, 2 (peduncular process of uropod 1 enlarged).

MALE.—Antenna 1, 45–50 percent length of body, 40–50 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2, flagellum with 4 or 5 segments. Mandibles subequal; spine row with 3 spines; segment 2 of palp with 1 long seta on inner margin distally, segment 3 with coarse setae on inner margin and 4 setae (2 long, 2 short) apically. Maxilla 1: inner plate with 2 apical, plumose setae; palp with 4 thick setae apically. Maxilla 2, inner plate with oblique row of 2 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 2 plumose spines, and 1 naked seta apically, 1 naked seta and 1 plumose spine (or seta) subapically; outer plate with few naked setae apically and subapically, 1 plumose seta on apex. Inner lobes of lower lip lacking.

Propod of gnathopod 1 a little larger than 2nd propod; palm with 2 spine teeth; defining angle with 2 spine teeth on outside, 1 on inside; medial setae absent. Dactyl nail of gnathopod 1 nearly 50 percent length of dactyl. Coxal plate of gnathopod 1 longer than broad, margin with 1 seta. Gnathopod propod 2; palm with 1 spine tooth; defining angle with 1 spine tooth on outside, 1 on inside; posterior margin with 1 thick seta; medial setae reduced to 1. Dactyl nail of gnathopod 2 long. Coxal plates of gnathopod 2 and pereopod 3 shallow, broader than long, margins with 1 seta each. Coxal plate of pereopod 4 shallow, broader than long, reaching about 25 percent length of basis, margin with 2 setae. Pereopods 6 and 7 subequal in length, about 50 percent length of body, 25–30 percent longer than pereopod 5. Pereopods 5–7; posterior margins of bases weakly convex, distoposterior lobes poorly developed; dactyls relatively long, about 45 percent length of corresponding propods. Three long sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1.

Pleonal plates: posterior margins weakly convex, with 1 seta each; posterior corners indistinct, broadly rounded; ventral margin of plate 3 with 1 spine. Uronites partly fused, suture visible between 1 and 2. Uropod 1: inner ramus longer than outer ramus, 60–65 percent length of peduncle, armed with 7 spines; outer ramus with 5 spines; peduncle with 5 spines; peduncular process short, apex broad and serrate. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 6 spines; outer ramus with 4 spines; peduncle with 2 spines. Uropod 3: ramus short, about 1/6 length of peduncle, with 1 apical

spine. Telson short, broader than long, gently tapering distally; apical margin entire or with very tiny notch, armed with 6 spines.

FEMALE.—About like male. Brood plates sublinear, not expanded distally.

TYPE-LOCALITY.—Patton Cave, located 2.4 km southeast of Gap Mills in Monroe Co., West Virginia, is a moderately large cave developed in Middle Ordovician limestone. The cave opens in a narrow karst valley formed just west of Peters Mountains and is situated in the Greenbrier River drainage.

DISTRIBUTION AND ECOLOGY.—This rare species is known only from its type-locality, where it was collected from a small, mud-bottom pool fed by seepage. Amphipods were observed burrowing in the soft mud substrate of the pool. The largest female (2.0 mm) in the type series had setose brood plates.

REMARKS.—A return visit to this cave on 28 June 1974, approximately eight years after the type series was collected, failed to yield additional specimens, even though a number of mud-bottom pools were searched extensively.

ETYMOLOGY.—The epithet *redactus* is from the Latin, meaning reduced or edited.

The *spinatus* Group

DIAGNOSIS.—Adult size range, 4.0–7.5 mm. Mature female larger than mature male. Inner lobes of lower lip vestigial or absent. Gnathopod 1: propod a little larger than 2nd propod and broader proximally; palm rather long, oblique; defining angle indistinct, continuous with posterior margin, with 3–5 long spine teeth on outside; posterior margin short, without setae; segment 5 without rastellate setae. Gnathopod 2: propod palm proportionately shorter and less oblique than 1st, posterior margin longer, with 3 or 4 sets setae; segment 5 without rastellate setae. Pereopods 6 and 7 subequal in length. Pereopod 7 without coxal gill. Lateral sternal gills simple or bifurcate. Pleonal plates: posterior margins with 3–11 setae each; posterior corners small or indistinct, not acute. Uronites free to partly fused. Ramus of uropod 3 with 3 or 4 apical spines. Telson usually slightly longer than broad; apical margin convex, entire or rarely with slight notch.

REMARKS.—This group, which I first recognized in 1967, is composed of a single species that occupies caves in the New-Greenbrier River drainage of southeastern West Virginia. *Stygobromus spinatus* is rather closely allied morphologically with the *emarginatus* group but differs in a number of significant ways as indicated in the diagnosis.

Stygobromus spinatus (Holsinger)

FIGURES 30, 31, 32

Stygonectes spinatus Holsinger, 1967:43–46, fig. 9 [type-locality: Court Street Cave, Greenbrier Co., West Virginia]; 1969a:32–33.—Culver and Holsinger, 1969:632.—Poulson and White, 1969:975.—Culver, 1970a:949; 1970b:464; 1971a:173; 1971b:98.—Culver and Poulson, 1971:74.—Holsinger, 1972:60.—Culver, 1973:103.—Culver, Holsinger, and Baroody, 1973:691.—Holsinger, Baroody, and Culver, 1976: 24.—Rutherford and Handley, 1976:45.

Stygobromus spinatus (Holsinger).—Karaman, 1974:118–119.—Holsinger, 1977:262.

Stygobromus n. sp. 2.—Culver, Holsinger, and Baroody, 1973: 691.

Stygobromus sp.—Holsinger, Baroody, and Culver, 1976:23.

MATERIAL EXAMINED.—WEST VIRGINIA. Greenbrier Co.: Allisons Cave, 3 ♀, D. C. Culver, 4 Aug 1973; Benedicts Cave, 1 ♀, WVACS, 5 Mar 1966, 1 ♀, J. R. Holsinger, 20 Aug 1966, and 1 ♀, D. C. Culver, 10 Aug 1967; Bone-Norman Cave, 1 ♀, WVACS, 18 Jun 1966; Bransfords Cave, 1 ♀, 1 ♂, 1 juv., J. R. Holsinger and P. Hightower 2 Jul 1966; Buckeye Creek Cave, 1 ♀, D. C. Culver and R. A. Baroody, 14 Oct 1970; Court Street Cave, 11 ♀, 2 ♂ (D. C. Culver coll.), D. C. Culver, 14 Aug 1967; dug-out spring near Coffmans Cave, 3 ♀, S. W. Hetrick, 13 May 1972; Fox Cave, 3 ♀, 2 ♂, 1 juv. (Holsinger, 1967:43); General Davis Cave, 4 ♀, 1 ♂, D. C. Culver and R. A. Baroody, 11 Oct 1970 and 2 ♀, 1 ♂, J. R. Holsinger, S. W. Hetrick and G. W. Dickson, 27 Sep 1974; Grapevine Cave, 3 ♀, 3 ♂, J. R. Holsinger and J. O. Davis, 28 Aug 1967; The Hole (cave), 2 specimens (D. C. Culver coll.), D. C. Culver, 31 Mar 1967; Jewel Cave, 1 ♀, 1 ♂, J. R. Holsinger, 16 Sep 1967 and 8 ♀, 1 ♂, D. C. Culver and R. A. Baroody, 11 Oct 1970; Levisay Cave, 6 specimens (D. C. Culver coll.), D. C. Culver and W. W. Biggers, 29 Mar 1967, and 3 ♀, D. C. Culver, 21 Jun 1967; McClungs Cave, 1 ♀ (USNM), T. C. Barr, Jr., 10 Aug 1958, and 9 ♀, J. R. Holsinger and D. C. Culver, 22 Jun 1968; Organ Cave, 1 ♀ (USNM), T. C. Barr, Jr., Aug 1958; Piercys Mill Cave, 5 ♀, D. C. Culver and R. A. Baroody, 10 Oct 1970; Pollock Cave, 5 ♀, J. R. Holsinger, D. C. Culver, and S. W. Hetrick, 10 Feb 1973; Pollock Saltpetre Cave, 1 ♀, J. R. Holsinger, D. C. Culver and S. W. Hetrick, 10 Feb 1973; Sinks-of-the-Run Cave, 3 ♀, J. R. Holsinger, S. W. Hetrick, and G. W. Dickson, 28 Sep 1974; Stove Cave, 1 ♀, 1 juv., D. C. Culver and R. A. Baroody, 12 Oct 1970; Windy Mouth Cave, 1 ♀, S. W. Hetrick, 26 Jul 1975; Monroe Co.: Coburn Cave, 1 ♀, J. R. Holsinger and G. W. Frederick, 30 May 1969; Greenville Saltpetre Cave, 1 ♀, 2 ♂, J. R. Holsinger, D. C. Culver, and R. A. Baroody,

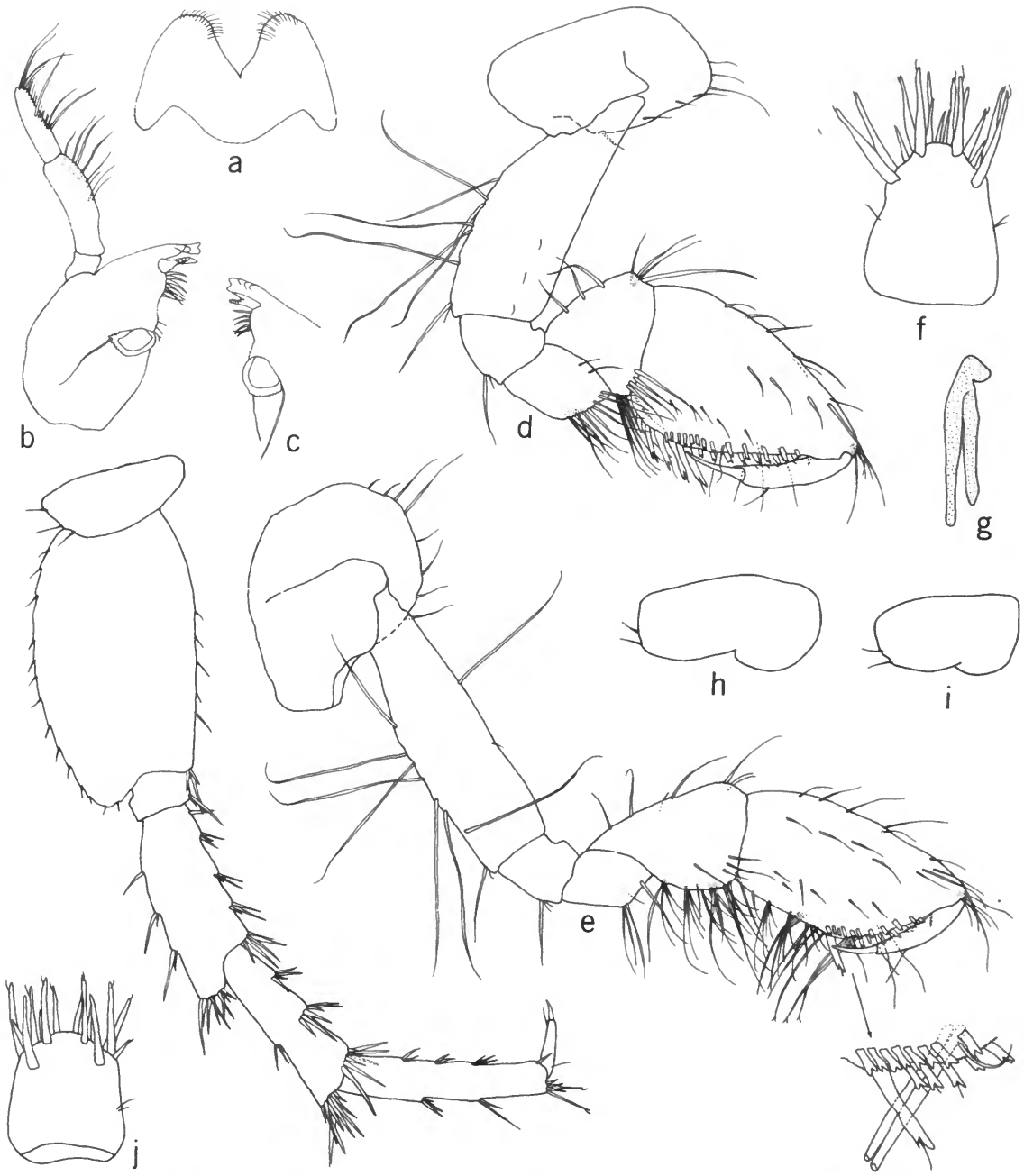

FIGURE 30.—*Stygobromus spinatus* (Holsinger). Female (6.0 mm), Benedicts Cave, West Virginia: *a*, lower lip; *b*, left mandible; *c*, dentate part of right mandible; *d*, *e*, gnathopods 1, 2 (part of palm and defining angle of gnathopod 2 enlarged); *f*, telson; *g*, lateral sternal gill; *h*, *i*, coxal plates of pereopods 5, 6. Male (4.0 mm), Benedicts Cave: *j*, telson.

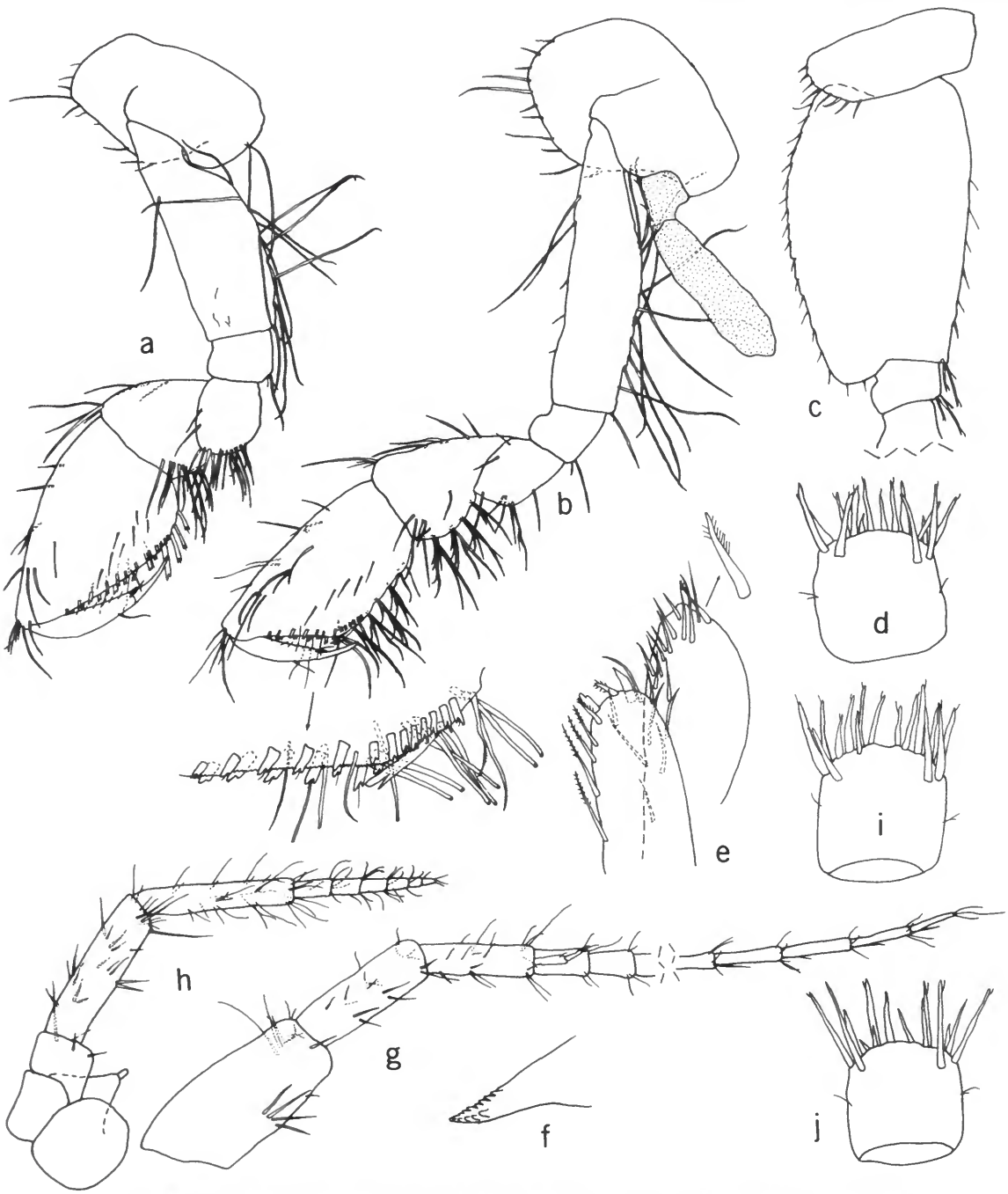

FIGURE 31.—*Stygobromus spinatus* (Holsinger). Female (7.0 mm), General Davis Cave, West Virginia: *a, b,* gnathopods 1, 2 (part of palm and defining angle of gnathopod 2 enlarged); *c,* pereopod 7 (in part); *d,* telson; *e,* inner and outer plates of maxilliped (greatly enlarged). Male (5.5 mm), General Davis Cave: *f,* peduncular process of uropod 1. Female (6.0 mm), Benedicts Cave, West Virginia: *g, h,* antennae 1, 2. Female (7.0 mm), Salmon Cave, West Virginia: *i,* telson. Female (4.8 mm), Laurel Creek Cave, West Virginia: *j,* telson.

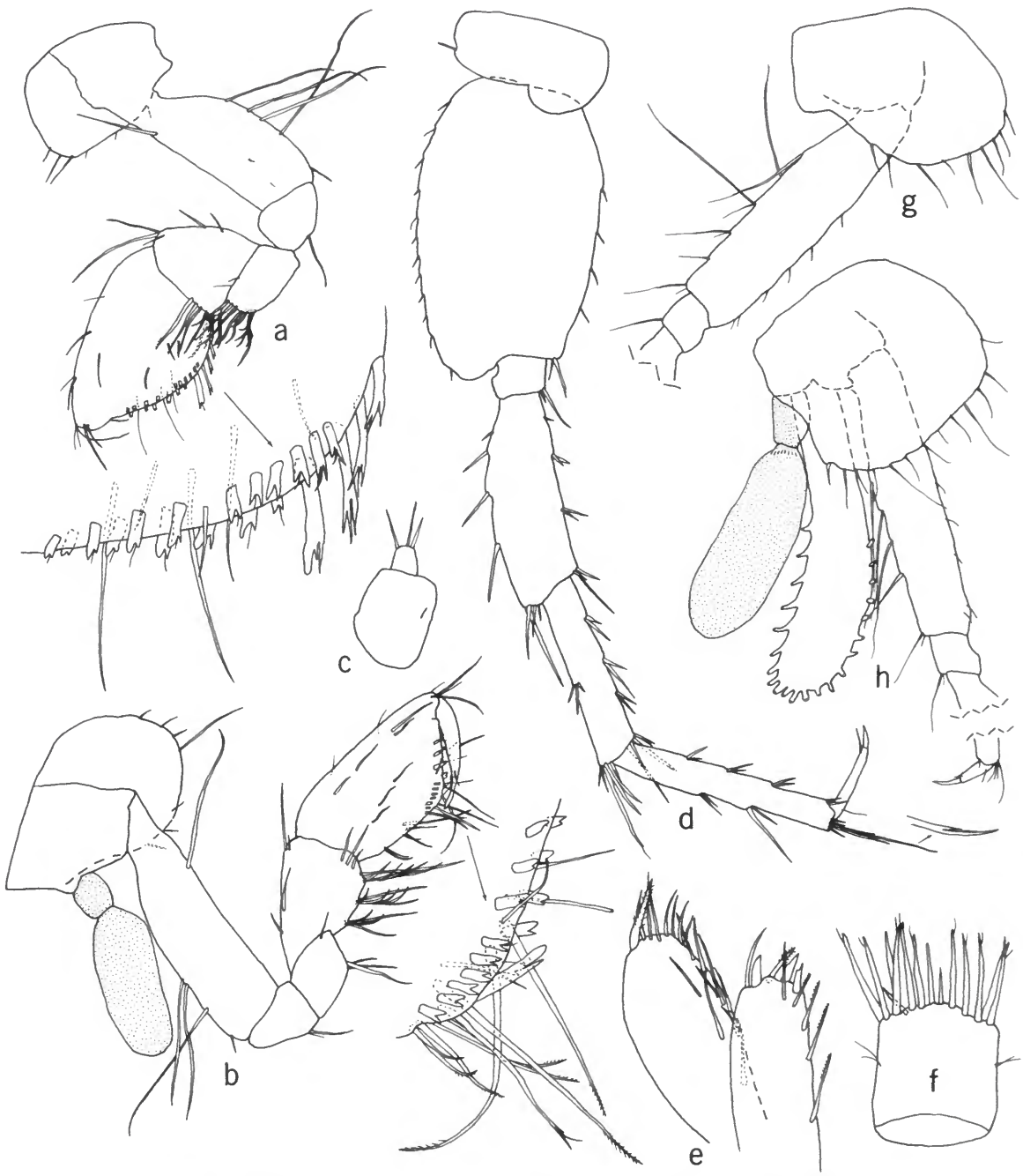

FIGURE 32.—*Stygobromus spinatus* (Holsinger). Female (4.2 mm), Coburn Cave, West Virginia: *a, b,* gnathopods 1, 2 (part of palms and defining angles enlarged); *c,* uropod 3; *d,* pereopod 6; *e,* inner and outer plates of maxilliped (greatly enlarged); *f,* telson. Female (6.0 mm), Benedicts Cave, West Virginia: *g, h,* pereopods 3, 4 (in part).

5 Apr 1971; Hunt Cave, 3 ♀, 1 ♂, D. C. Culver and R. A. Baroody, 14 Oct 1970; Indian Draft Cave, 1 ♀, D. C. Culver and R. A. Baroody, 13 Oct 1970; Laurel Creek Cave, 1 ♀, D. C. Culver and R. A. Baroody, 13 Oct 1970; Pocahontas Co.: Blue Springs Cave, 1 ♀, D. C. Culver, 22 Nov 1967; Martha Cave, 1 ♀, T. C. Barr, Jr., 28 Jul 1966, and 1 ♀, J. R. Holsinger and D. C. Culver, 14 Jan 1967; Salmon Cave, 1 ♀, J. R. Holsinger, 3 Jul 1966, and 1 ♂, 17 Sep 1967; Upper Marthas Cave, 1 ♂, D. C. Culver, 15 Aug 1967 and 1 ♂, 21 Nov 1967.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished by the plumose spine on apex of outer plate of maxilliped, long spine teeth on indistinct defining angle and distal part of posterior margin of gnathopod propod 1, 2 or 3 long, slender spines on distal end of segment 6 of pereopods 5 and 6, setose posterior margins of pleonal plates, and relatively short telson. Largest males, 5.5 mm; largest female, 7.5 mm.

FEMALE.—Antenna 1, 50–75 (usually about 60) percent length of body, 40–60 percent longer than antenna 2; primary flagellum with 15–21 segments. Antenna 2, flagellum with 5–7 segments. Mandibles subequal; spine row with 5–7 spines; segment 2 of palp with row of long setae on inner margin, segment 3 with row of short setae and few long setae on inner margin, 3–5 long setae on apex. Maxilla 1: inner plate with 5–7 apical, plumose setae; palp with 3–5 setae and 2 or 3 slender spines apically. Maxilla 2, inner plate with oblique row of 5–8 plumose setae on inner margin. Maxilliped: inner plate with 2–4 bladelike spines, 2 or 3 plumose spines and 1 or 2 naked setae apically, row of plumose setae (or spines) on inner margin; outer with numerous naked setae on inner margin and apex and 1 plumose spine apically. Inner lobes of lower lip vestigial or absent.

Propod of gnathopod 1 a little larger than 2nd propod; palm long, oblique, armed with double row of 6–8 spine teeth; defining angle usually indistinct, with 3–5 long spine teeth on outside extending onto distal part of posterior margin, 3–6 smaller spine teeth on inside; medial setae singly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, margin with 6–10 setae. Gnathopod propod 2: palm relatively short, armed with double row of 5–9 spine teeth; defining angle with 1 long spine tooth on outside, 2–5 smaller ones on inside; posterior margin relatively long, with 3 or 4 (usually 3) sets setae; inferior medial setae singly inserted, superior medial setae singly, doubly, and triply inserted. Coxal plate of gnathopod 2 a little longer than broad, margin with 7–11 setae. Coxal plate of pereopod 3 longer than broad, margin with 2 or 3 slender spines and 6–9 setae. Coxal plate of pereopod 4 a little broader than long, reaching about 35–40 percent length of basis, margin with 11–18 setae. Pereopods 6 and 7 usually about equal in length (pereopod 6 occasionally slightly longer), 45–60 percent length of body, 15–25 percent longer than pereopod 5. Segment 6 of pereopods 5 and 6 with 2 or 3 long, slender spines on distal end. Pereopods 5–7; posterior margins of bases convex, distoposterior lobes well developed, broadly rounded; coxal plates of 5 and 6 with 1 or 2 setae each on posterior margins, that of 7 with variable number of setae (ca. 3–8); dactyl of 5 about 35–40 percent length of corresponding propod, dactyl of 6, 37–45 percent length of corresponding propod, dactyl of 7, 33–43 percent length of corresponding propod. Three median sternal gills on pereonites 2–4; 2 pairs simple or bifurcate lateral sternal gills on pereonites 6 and 7; 1 pair small sternal gills on pleonite 1. Brood plates relatively narrow but slightly expanded distally.

Pleonal plates generally corresponding to previous descriptions by Holsinger (1967:45) with the following additions and modifications: posterior margin of plate 1 with 3–9 (usually 6–9) setae, that of plate 2 with 5–9 setae, that of plate 3 with 7–11 setae; ventral margin of plate 1 with 0–3 (usually 2 or 3) spines, that of plate 2 with 2–5 spines, that of plate 3 with 4 or 5 spines. Uronites usually free, sometimes partly fused. Uropods generally corresponding to previous description by Holsinger (1967:45) with the following additions: Uropod 1: inner ramus with 9–12 spines; outer ramus with 10–14 spines; peduncle with 10–17 spines. Uropod 2: inner ramus with 6–13 (usually 9–13) spines; outer ramus with 6–9 spines; peduncle with 3–7 (usually 5–7) spines. Uropod 3, ramus with 3 or 4 (usually 4) apical spines. Telson proportionately rather short, somewhat variable in shape throughout range but usually slightly longer than broad; apical margin convex, usually entire (rarely with tiny notch), armed with 13–18 spines.

MALE.—Differing only slightly from female as follows: Sternal gills absent from pleonite 1. Peduncular process of uropod 1 triangular, distally serrate.

VARIATION.—As noted in the above description there is considerable morphological variation throughout the range of this species. Variation in numbers of spines and setae was especially evident on the gnathopod propods, coxal plates, pleonal plates, uropods 1 and 2, and to some extent on the mouthparts and telson. The length and number of flagellar segments of the antennae also varied, as did the presence of either simple or bifurcate lateral sternal gills and the shape of the apical margin of the telson.

As might be expected, much of this variation was observed in populations found in peripheral or isolated parts of the range. Populations from near the middle of the range tended to be more numerous, larger, and more homogeneous in structure. Populations in the Pollock caves west of Muddy Creek Mountain on the western margin of the range, populations in the isolated exposure of Greenbrier limestone in the vicinity of Greenville in western Monroe County (i.e., Greenville Saltpetre, Indian Draft, and Laurel Creek caves) at the southwestern end of the range, and the population in Coburn Cave in the valley just west of Peters Mountain at the extreme southeastern end of the range differed from other populations in having simple lateral sternal gills. However, specimens from Piercys Mill Cave, which is also west of Muddy Creek Mountain and 8.9 km north-northeast of the Pollock caves, had bifurcate lateral sternal gills. Elsewhere in the range, with the exception of one female (out of three sampled) from Sinks-of-the-Run Cave in Greenbrier County which had one pair of simple and one pair of unequally bifurcate lateral sternal gills, all other populations examined had two pairs of bifurcate lateral sternal gills.

Both Sinks-of-the-Run Cave and nearby General Davis Cave are isolated hydrologically from most of the other *spinatus* caves farther north and east in Greenbrier County (Jones, 1973, map 1), and specimens from these caves differed in a number of ways from those near the middle of the range (cf., Figures 30*d,e*, 31*a–c* of the gnathopods and basis of pereopod 7 of specimens from General Davis and Benedicts caves). In several specimens from populations north of Droop Mountain at the northern end of the range in Pocahontas County (i.e., Marthas and Salmon caves), the apical margin of the telson had a tiny notch (Figure 31*i*). Elsewhere in the range the telson was not notched.

DISTRIBUTION AND ECOLOGY.—The range of this species, which is largely within the Greenbrier Valley, extends from southern Monroe County north-northeast to central Pocahontas County, covering a linear distance of approximately 108 km. All populations but the one recorded from Coburn Cave in Monroe County have been found in caves (and one spring) developed in the Greenbrier limestone. Coburn Cave is developed in Lower Ordovician limestone which crops out in a narrow strike belt just west of Peters Mountain and east of the St. Clair fault. In addition to the cave populations, this species was collected once from a recently excavated spring in Greenbrier County.

Stygobromous spinatus inhabits both small, gravel-bottom streams and pools but appears to be more abundant in the former habitat. This species sometimes occurs with *S. emarginatus* in the same cave streams but, as demonstrated by Culver (1970a), these two species tend to avoid each other and to occupy different parts of the substrate when found together.

In a short paper on sex ratios in cave amphipods, Culver and Holsinger (1969) pointed out a possible trend toward parthenogenesis in the population of *S. spinatus* from Court Street Cave. Six samples from this cave taken periodically during all four seasons of the year contained 67 females and eight males. Of the 143 specimens examined from all parts of the range during the present study, 124 were females and 19 were males, thus giving a sex ratio generally similar to that found in the Court Street Cave population. An aberrant sex ratio in favor of females is not restricted to *S. spinatus,* however, but appears to be the rule in nearly all of the cavernicolous species of *Stygobromus* (see also "Distribution and Ecology" under *S. pseudospinosus*).

Sexually mature females (i.e., either ovigerous or with setose brood plates) have been found during all four seasons of the year and ranged in size from 4.0 to 7.5 mm. Juveniles have been found in samples taken during spring, summer, and fall. The clutch size of 13 ovigerous females, ranging in size from 4.3 to 6.0 mm ($\overline{X}$ = 5.38, SD = 1.52, CV = 0.19), is summarized as follows: N = 13, range = 2–11 eggs or embryos, $\overline{X}$ = 5.15, SD = 2.85, CV = 0.55.

REMARKS.—Because of the large amount of new material accumulated during the last 10 years and the fact that my previous description of *S. spinatus*

(Holsinger, 1967) was based on specimens in mostly poor shape from only two caves, I found it necessary to critically reexamine this species and to prepare the redescription given above. After more careful study the specimen from Coburn Cave, listed earlier as an undescribed species by Culver, Holsinger, and Baroody (1973:691) and Holsinger, Baroody, and Culver (1976:23), has proven to be conspecific with *S. spinatus*.

The *mackini* Group

DIAGNOSIS.—Adult size range small to large (ca. 2.8–19.0 mm). Mature female larger than mature male. Inner lobes of lower lip small to vestigial. Gnathopod 1: propod generally subequal in size to 2nd propod but usually broader proximally; palm rather long, oblique; defining angle with 2–4 long spine teeth of unequal length on outside; posterior margin short, with a few setae; segment 5 usually with rastellate setae. Gnathopod 2: 2nd propod palm proportionately shorter than 1st propod palm, posterior margin longer, with 2–5 sets setae; segment 5 usually with rastellate setae. Pereopod 6 usually a little longer than 7. Coxal gill often present on pereopod 7. Lateral sternal gills simple. Pleonal plates: posterior margins with 1 to several setae each; posterior corners tiny but usually distinct. Uronites usually free. Uropod 3 with 1–5 apical spines; ramus sometimes vestigial or absent. Telson as long as, or longer than, broad, apical margin incised (cleft) from 20 to 65 percent the distance to base.

REMARKS.—The *mackini* group is at present composed of nine species, although one or two provisionally recognized species from caves in eastern Kentucky may be assigned to the group after further study. On the basis of the species treated in this paper, the group is distributed from northwestern Georgia and northeastern Alabama northeastward through the Appalachians of eastern Tennessee, western North Carolina and southwestern Virginia to southeastern West Virginia. The group range covers a linear distance of approximately 644 km and spans parts of several major drainage basins. Except for one species recorded from seeps in the Black Mountains of North Carolina, members of this group occupy caves (and occasionally springs) developed in limestone areas of the Appalachian Plateau, Appalachian Valley, and Blue Ridge provinces.

At least three, and possibly four, lines of evolutionary divergence, corresponding to the subgroups established below, have been noted. The *mackini* subgroup is composed of four very closely related species or semi-species, of which three can be distinguished only with some difficulty. Closely allied to members of the *mackini* subgroup is *S. leensis* which, principally because of the absence of the ramus of uropod 3, has been placed in a separate, monotypic subgroup. The *sparsus* subgroup, composed of three species with unmistakable affinity with the *mackini-leensis* ensemble, occupies a rather compact geographic area in the mountainous region of extreme eastern Tennessee and western North Carolina. Finally, the monotypic *grandis* subgroup, while retaining certain affinity with species in the other subgroups, also displays a number of unique morphological characters and is only tentatively assigned to the *mackini* group pending further study.

Key to the Species of the *mackini* Group

(based on females except *S. barryi* and *S. sparsus*)

1. Telson incised more than 50 percent the distance to base; palms of gnathopod propods armed with double row of 23 or more spine teeth; dactyl nail of gnathopods reduced to tiny stub (*grandis* subgroup) ..... ***S. grandis***, new species
   Telson incised less than 50 percent the distance to base; palms of gnathopod propods with no more than 12 spine teeth in double row; dactyl nail of gnathopods normal, not reduced (*mackini*, *leensis*, and *sparsus* subgroups) 2
2. Uropod 3 without ramus 3
   Uropod 3 with ramus 4
3. Apical spines of telson not more than 50 percent length of telson; uropod 1 of male with distinct peduncular process ..... ***S. leensis***, new species
   Apical spines of telson more than 50 percent length of telson, some up to 85 percent the length; uropod 1 of male without distinct peduncular process (based on mature male) ..... ***S. sparsus***, new species

4. Lateral sternal gills absent ..... ***S. carolinensis,*** new species
   Lateral sternal gills present 5
5. Ramus of uropod 3 reduced to only about 1/12 length of peduncle, armed with 1 apical spine (based on mature male) ..... ***S. barryi,*** new species
   Ramus of uropod 3 proportionately longer, 25–50 percent length of peduncle, armed with 2–4 spines 6
6. Peduncle of uropod 3 with 1 or more distal spines; ramus of uropod 3, 35–50 percent length of peduncle ..... ***S. mackini***
   Peduncle of uropod 3 without distal spines; ramus of uropod 3, 25–33 percent length of peduncle 7
7. Ramus of uropod 3 with 4 apical spines; pleonal plates 1 and 2 with 1 seta each; bases of pereopods 6 and 7 relatively broad ..... ***S. abditus,*** new species
   Ramus of uropod 3 with 2 or 3 apical spines; pleonal plates 1 and 2 with more than 1 seta each; bases of pereopods 6 and 7 relatively narrow 8
8. Coxal plate of pereopod 4 a little broader than long, reaching about 45 percent length of basis; telson with 10–12 apical spines ..... ***S. finleyi,*** new species
   Coxal plate of pereopod 4 about as broad as long, reaching about 55 percent length of basis; telson with 12–16 apical spines ..... ***S. dicksoni,*** new species

The *mackini* Subgroup

DIAGNOSIS.—Adults small to moderately large (ca. 3.5–10.0 mm). Peduncle of uropod 3 often with spines or spinules. Telson longer than broad, apical margin incised from 20 to 45 percent the distance to base.

Stygobromus mackini Hubricht

FIGURES 33, 34, 35

Stygobromus mackini Hubricht, 1943:695–697, pl. 3 [type-locality: Sikes Cave, 7.2 km N of Lebanon, Russell Co., Virginia].—Pennak, 1953:443, fig. 276G.—Barnard, 1958:74.—Hubricht, 1959:878.—Nicholas, 1960:128–129.—Barr, 1961:32.—Holsinger, 1963:29; 1964:62.—Poulson and White, 1969:973.—Holsinger, 1969a:30–32.—Holsinger and Peck, 1971:30.—Holsinger, 1972:71.—Culver, 1973:103.—Culver, Holsinger, and Baroody, 1973:691.—Karaman, 1974:114.—Holsinger, Baroody, and Culver, 1976:23.—Estes and Holsinger, 1976:487.—Holsinger, 1977:262.

MATERIAL EXAMINED.—TENNESSEE. Anderson Co.: Offutts Cave, 9 ♀, 2 ♂, J. A. Payne, 11 Jul 1965; Grainger Co.: Indian Cave, 1 ♀ (USNM), L. Hubricht, 8 Aug 1939; Hancock Co.: Cantwell Valley Cave, 1 ♀, J. R. Holsinger and C. W. Maus, 28 Oct 1966; Hawkins Co.: Sensabaugh Saltpetre Cave, 4 ♀, 2 ♂, J. R. Holsinger, 15 Apr 1967; Roane Co.: Berry Cave, 1 ♂, R. M. Norton, 15 Jul 1964; Union Co.: Oaks Cave, 3 ♀, R. M. Norton, 17 Jul 1965; Ridenour Pit Cave, 1 ♀, R. M. Norton, 2 Jul 1967. VIRGINIA. Bland Co.: Hamilton Cave, 2 ♀ (USNM), T. C. Barr, Jr., 6 Jun 1958, and 1 ♀, 2 ♂, 1 juv., J. R. Holsinger 10 May 1965; Repass Saltpetre Cave 11 ♀, 10 ♂ (5 specimens in Museo Civico Di Storia Naturale, Verona), J. R. Holsinger, 10 May 1965; Giles Co.: Ballards Cave, 2 ♀, J. R. Holsinger and L. M. Ferguson, 29 Jun 1974; spring at Bear Cliff near Mt. Lake, 3 ♀, 5 ♂ (USNM), H. H. Hobbs, Jr., 25 Jun 1947; Starnes Cave, 1 ♀, J. R. Holsinger and S. W. Hetrick, 19 May 1974; Tawneys Cave, 1 ♀, J. R. Holsinger and E. Bauer, 20 Aug 1965; Russell Co.: Banners Corner Cave, 1 ♀, 1 ♂, D. C. Culver and P. J. Starr, 18 Aug 1967; Bundys Cave No. 2, 1 ♀, 1 juv., J. R. Holsinger, 9 May 1965; Burns Cave, 1 ♀, J. R. Holsinger, 13 Apr 1968; Grays Cave, 2 ♀, J. R. Holsinger, 6 Apr 1968; Jessie Cave, 3 ♀, 1 ♂, J. R. Holsinger, 9 May 1965; Johnson Cave, 4 ♀, 1 juv., J. R. Holsinger, S. S. Taylor, and J. M. Beck, III, 11 May 1968; Munsey Cave, several specimens (D. C. Culver coll.), J. R. Holsinger and D. C. Culver, 29 Aug 1971; Porgie Bundys Cave, 4 ♀, 1 ♂, J. R. Holsinger and D. C. Culver, 16 Aug 1972; Sikes Cave, 5 ♀, 1 ♂ cotypes (syntypes) (USNM 79324) and 3 ♀, 2 ♂ cotypes (USNM), L. Hubricht, 26 Aug 1939; Smiths Drop Cave, 2 ♀, 1 ♂, 1 juv., J. R. Holsinger and D. C. Culver, 29 Jul 1974; Scott Co.: Blair-Collins Cave, 5 ♀, J. R. Holsinger and S. S. Taylor, 6 Nov 1966; Blowing Hole Cave, 1 ♀, J. R. Holsinger, 22 Apr 1962; Deep Spring Cave, 1 ♀, J. R. Holsinger, S. S. Taylor and J. M. Beck, III, 11 May 1968; Flannery Cave, 6 ♀, 2 ♂, J. R. Holsinger and S. B. Peck, 1 Aug 1964; Grigsby Cave, 7 ♀, J. R. Holsinger and C Rippey, 18 Jul 1965; Hill Cave, 3 ♀, J. R. Holsinger and J. Tichenor, 3 Aug 1967; Jack Cave, 1 ♀, 4 ♂, J. R. Holsinger, 10 Jun 1966; Jackson Cave, 1 ♀, 1 ♂, J. R. Holsinger, 13 Nov 1966; Kerns Smoke-Hole Cave, 2 ♀, 2 ♂, J. R. Holsinger, 19 Aug 1969; McDavids Cave, 1 ♀, J. R. Holsinger and D. C. Culver, 3 Aug 1974; McNew Cave, 1 ♀, 3 ♂, J. R. Holsinger, 18 Jul 1976; Moccasin Valley Cave, 10 ♀, 2 ♂, J. R. Holsinger, 25 Aug 1969; Natural Tunnel Cavern, 1 ♂, J. R. Holsinger and J. A. Estes, 22 Nov 1976; Pond Cave, 7 ♀, 1 ♂, J. R. Holsinger and S. S. Taylor, 5 Nov 1966; Spurlock Cave, 1 ♂, J. R. Holsinger, 25 Nov 1966; Taylor Cave No. 1, 1 ♀, J. R. Holsinger, 6 May 1967; Winding Stair Cave, 9 ♀, 1 ♂, 1 juv., J. R. Holsinger and G. Powers, 12 Aug 1969; Wolfe Cave, 1 ♀, J. R. Holsinger, G. and A. Powers, 14 Aug 1969; Smyth Co.: Buchanan Saltpetre Cave, 2 ♀, 1 ♂, J. R. Holsinger, 13 Apr 1963, and 2 ♀, 2 ♂, G. Marland, Jul 1964; McMullin Cave, 1 juv. (?), J. R. Holsinger and P. M. Hauer, 17 Jul 1969; Tilson Saltpetre Cave, 1 ♀, 1 ♂, J. R. Holsinger, and D. C. Culver, 15 Aug 1972; Tazewell Co.: Cauliflower

FIGURE 33.—*Stygobromus mackini* Hubricht, female syntype (8.7 mm), Sikes Cave, Virginia: *a*, lower lip; *b*, dentate part of left mandible; *c*, right mandible; *d*, inner and outer plates of maxilliped (greatly enlarged); *e*, *f*, maxillae 1, 2 (apical setae enlarged); *g*, uropod 3; *h*, *i*, gnathopods 1, 2 (palmar spines and rastellate setae enlarged); *j*, *k*, uropods 1, 2; *l*, pleonal plates; *m*, telson.

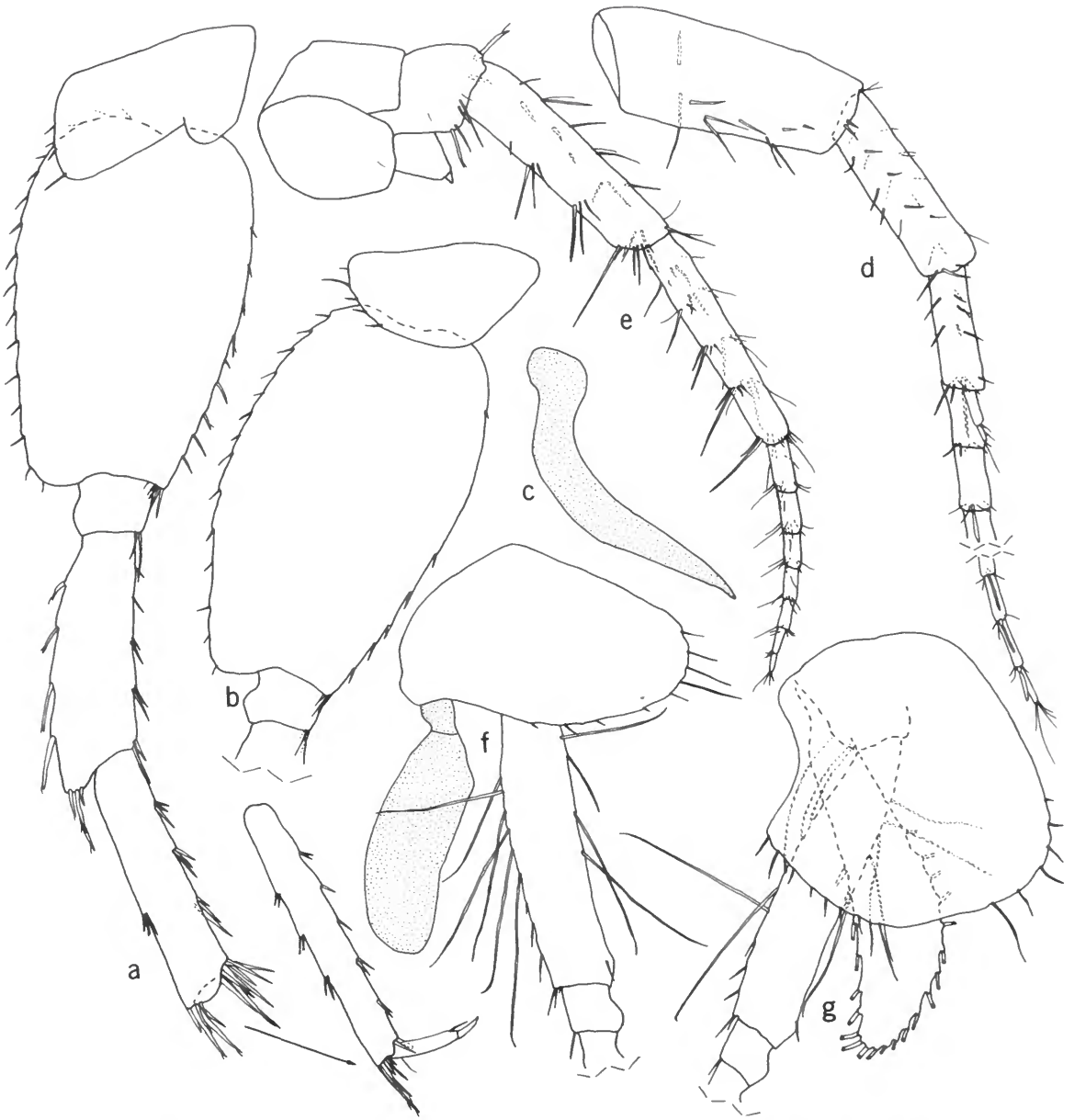

FIGURE 34.—*Stygobromus mackini* Hubricht, female syntype (8.7 mm), Sikes Cave, Virginia: *a*, pereopod 6 (continuation of appendages indicated by arrow); *b*, pereopod 7 (in part); *c*, lateral sternal gill; *d*, *e*, antennae 1, 2; *f*, *g*, pereopods 3, 4 (in part).

Cave, 1 ♀, J. R. Holsinger, S. W. Hetrick, and J. Tichenor, 29 Apr 1972; Chimney Rock Cave, 5 ♀, 1 ♂ (USNM), L. Hubricht, 25 Aug 1939; Crocketts Cave, 1 ♀, J. R. Holsinger and G. W. Dickson, 10 Apr 1974; Fallen Rock Cave, 1 ♀, J. R. Holsinger, 9 Nov 1968, and 8 ♀, J. R. Holsinger, G. D. Corbett, G. W. Dickson, and S. W. Hetrick, 13 Oct 1973; Glenwood Church Cave, 4 ♀, 1 ♂, J. R. Holsinger, R. M. Norton, and R. Schultetus, 28 May 1966; Hugh Young Cave, 3 ♀, J. R. Holsinger, R. M. Norton, and R. Schultetus, 28 May 1966, and 2 ♀, J. R. Holsinger and D. C. Culver,

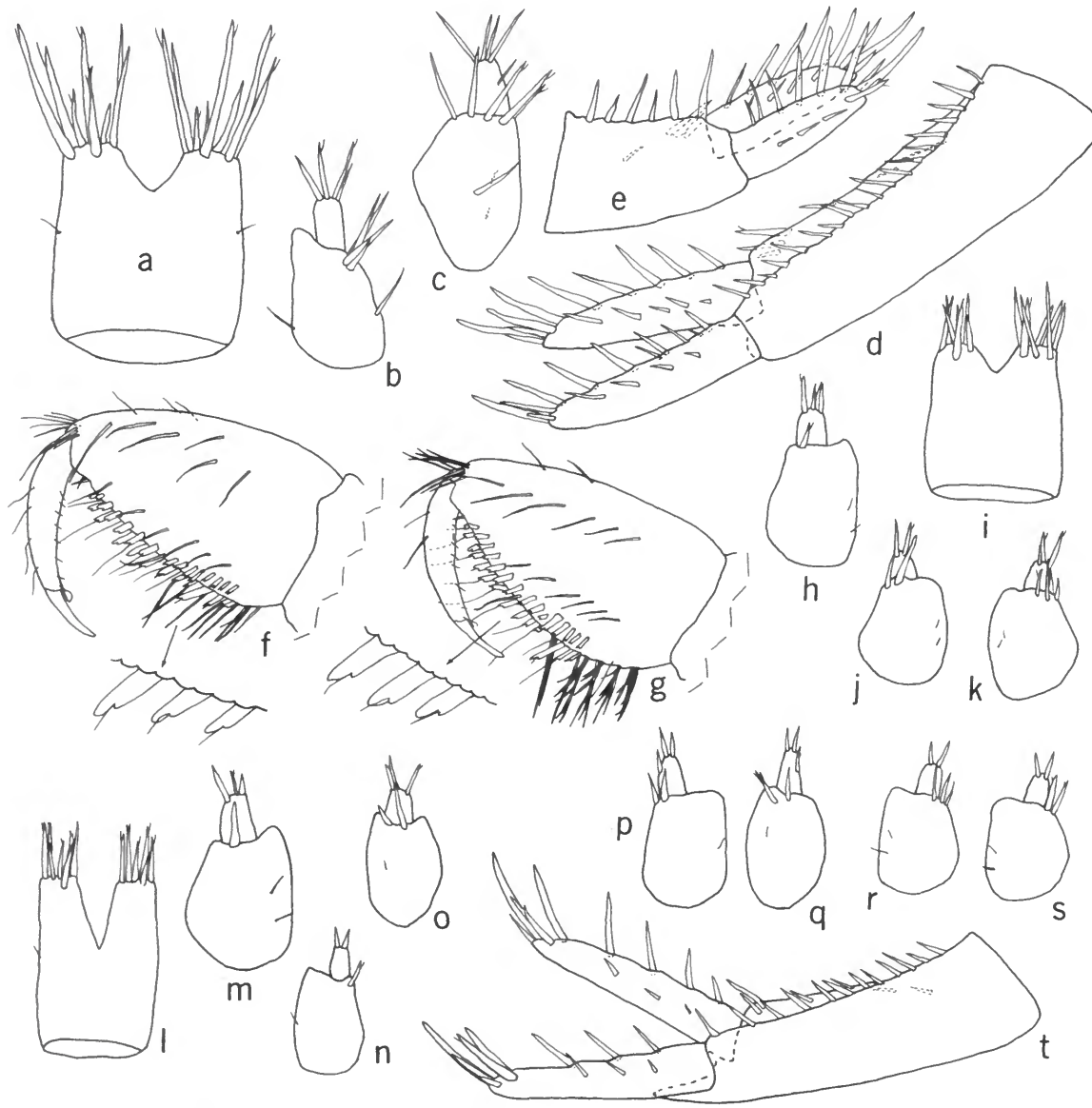

FIGURE 35.—*Stygobromus mackini* Hubricht. Female (7.2 mm), Tilson Saltpetre Cave, Virginia: *a*, telson; *b*, *c*, 3rd uropods; *d*, *e*, uropods 1, 2. Female (8.0 mm), Oaks Cave, Tennessee: *f*, *g*, gnathopods 1, 2 (palmar spines enlarged); *h*, uropod 3. Female (8.0 mm), Fallen Rock Cave, Virginia: *i*, telson; *j*, *k*, 3rd uropods. Male (7.5 mm), Offutts Cave, Tennessee: *l*, telson. Female (8.5 mm), Blair-Collins Cave, Virginia: *m*, uropod 3. Female (6.5 mm), Repass Saltpetre Cave, Virginia: *n*, uropod 3. Female (6.5 mm), Big Springs Cave, West Virginia: *o*, uropod 3. Female (7.2 mm), Sensabaugh Saltpetre Cave, Tennessee: *p*, *q*, 3rd uropods. Female (7.0 mm), Cross Road Cave, West Virginia: *r*, *s*, 3rd uropods. Male syntype (7.0 mm), Sikes Cave, Virginia: *t*, uropod 1. (Note: all 3rd uropods to same scale except *b*, *c*.)

30 Apr 1972; Lost Mill Cave No. 1, 1 ♀, J. R. Holsinger, 28 May 1966; Steeles Cave, 4 ♀, J. R. Holsinger and D. C. Culver, 15 Aug 1972; Ward Cove Cave, 8 ♀, 2 ♂, J. R. Holsinger, R. M. Norton, and R. Schultetus, 29 May 1966; Washington Co.: covered spring 1.6 km NW of Court House in Abingdon, 3 ♀, R. M. Norton, 30 Jul 1964; Singleton Cave, 1 ♀, J. R. Holsinger and C. B. Moore, 9 Dec 1967; Wise Co.: Wildcat Saltpetre Cave, 1 ♀, J. R. Holsinger, G. W. Dickson, and T. C. Kane, 27 Nov 1975. WEST VIRGINIA. Mercer Co.: Beacon Cave, 1 ♀, J. R. Holsinger, 12 May 1966; Big Springs Cave, 5 ♀, 3 ♂, J. R. Holsinger, D. C. Culver, and P. J. Starr, 20 Aug 1967; Panther Cave, 1 ♀, G. Park, 29 Oct 1972, and 2 ♀, 27 Dec 1972; Thompson School Cave, 1 ♀, J. R. Holsinger, 12 May 1966; Monroe Co.: Cross Road Cave, 1 ♀, J. R. Holsinger, 1 Sep 1967; Greenville Saltpetre Cave, 1 ♂, J. R. Holsinger, D. C. Culver, and R. A. Baroody, 5 Apr 1971.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished by the gnathopod propods which are subequal in size, the 1st gnathopod propod which has a long, oblique palm and short posterior margin with few setae, the peduncle of uropod 3 which has 1–6 rather conspicuous distal spines, and the distinct apical notch (incision) of the telson. Largest males, 7.5 mm; largest female, 10.0 mm.

FEMALE.—Antenna 1, 38–65 percent length of body, 28–64 percent longer than antenna 2; primary flagellum with 14–23 segments. Antenna 2, flagellum with 5–7 segments. Mandibles subequal; spine row with 5 spines; segment 2 of palp with row of rather long setae on inner margin, segment 3 with 3 long setae on outer margin, proximally long and distally short setae on inner margin, and 3 or 4 long setae on apex. Maxilla 1: inner plate with 6–9 apical, plumose setae; palp with 5–8 setae and 2 or 3 slender spines apically and subapically. Maxilla 2, inner plate with oblique row of 6–10 plumose setae on inner margin. Maxilliped: inner plate with 3 or 4 bladelike spines, 1 or 2 plumose spines and 2 naked setae apically, and 3 plumose spines (or coarse setae?) on inner margin distally; outer plate with numerous naked setae on inner margin and apex and 1 or 2 lightly plumose setae apically. Inner lobes of lower lip vestigial.

Propod of gnathopod 1 subequal in size to 2nd propod; palm armed with double row of 7–12 spine teeth; defining angle with 2–4 (usually 3 or 4) long spine teeth on outside, 2–4 shorter ones on inside; posterior margin with 3–8 setae; medial setae mostly singly inserted. Dactyl nail of gnathopod 1 moderately long. Coxal plate of gnathopod 1 longer than broad, margin with 4–6 setae. Gnathopod propod 2: palm with double row of 7–12 spine teeth; defining angle with 2 or 3 spine teeth of unequal length on outside, 2–4 short spine teeth on inside; posterior margin with 3–5 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Coxal plate of gnathopod 2 longer than broad, margin with 5–9 (usually 7) setae. Coxal plate of pereopod 3 longer than broad, margin with 5–11 (usually 9–11) setae. Coxal plate of pereopod 4 relatively broad and deep, about as broad as long, reaching approximately 55–60 percent length of basis; margin with 6–17 (usually 10–14) setae. Pereopod 6 little longer than pereopod 7, 40–60 percent length of body, 10–30 percent longer than pereopod 5. Bases of pereopods 5–7: posterior margin of 7 usually more convex than in 5 and 6; distoposterior lobes distinct, broadly rounded; anterior and posterior margins with variable number of spines and setae, respectively. Dactyls of pereopods 6 and 7, 35–37 percent length of corresponding propods; dactyl of pereopod 5 about 30 percent length of corresponding propod. Coxal gill present on pereopod 7. Three median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates somewhat expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 3–6 setae, that of plate 2 nearly straight, with 5 or 6 setae, that of plate 3 slightly sinuate, with 4–6 setae; posterior corners small, bluntly rounded; ventral margin of plate 2 with 3–5 spines, that of plate 3 with 4–6 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 60–65 percent length of peduncle, armed with 9–15 spines; outer ramus with 8–15 spines; peduncle with 10–27 (usually 13–24) spines. Uropod 2: inner ramus a little longer than outer ramus, a little shorter than peduncle, armed with 8–12 spines; outer ramus with 7–13 spines; peduncle with 4–10 (usually 5–7) spines. Uropod 3: peduncle with 1–6 (usually 1–3) distal spines; ramus 35–50 percent length of peduncle, with 2–5 (usually 2–4) apical spines. Telson longer than broad, gently tapered distally; apical margin incised 20–45 (usually 20–33) percent the distance to base, armed with 10–16 (usually 11–15) spines.

MALE.—Differing only slightly from female as follows: Coxal gill sometimes absent from pereopod

7. Peduncular process of uropod 1 about 25 percent length of outer ramus, narrowing distally, apex usually weakly serrate.

VARIATION.—As indicated in the description there is considerable morphological variation in meristic characters (i.e., numbers of setae and spines) in this species. Variation was also noted in the length and number of flagellar segments of the antennae and in the depth of incision of the telson. In view of the wide range of this species and its occurrence in several different drainage basins and in many geologically isolated valleys, this variation is not surprising. With the exception of a few populations possibly isolated geographically from the main part of the range, much of the meristic variation does not appear to have a geographic pattern. In some instances, variation in meristic characters was noted among specimens in the same population, especially between males and females. In other instances, meristic characters appeared to vary between populations and can be attributed in part to the different sizes at which animals in different populations reach sexual maturity (e.g., females from 4.5 to 10.0 mm and males from about 4.5 to 7.5 mm). Larger specimens of the same species frequently have more spines and setae on a given structure than smaller ones (see also Holsinger, 1967:149). With one exception, all specimens examined had from 1 to 3 distal spines on the peduncle of uropod 3. A sexually mature female (7.2 mm long with setose brood plates) from Tilson Saltpetre Cave in Smyth Co., Virginia, differed in having 5 and 6 spines, respectively, on the peduncles of uropod 3 and a few more spines on uropods 1 and 2 and the telson. Because of the limited sample size from this cave, it is difficult to assess the significance of this variation. However, Tilson Saltpetre Cave does not appear to be any more isolated geographically (or geologically) than many other caves that contain populations of *S. mackini.*

The variation in the depth of the incision of the telson, like the meristic characters, did not correspond to a geographic pattern. The depth of the notch of the telson varied between 20 and 33 percent in most populations examined critically, and in only two populations from different parts of the range did it exceed 33 percent.

The variation in only one character examined—the ratio of the length of antenna 1 to body length—appeared to have a geographic correlation. As indicated by the data in Table 1, populations from caves in Mercer Co., West Virginia, which are isolated in a valley just north of East River Mountain, differ from populations elsewhere in the range by having longer first antennae. The ratio of the length of antenna 1 to body length in most populations examined outside of Mercer County generally fell between 0.40 and 0.55, and the samples analyzed in Table 1 from Repass Saltpetre Cave (New River drainage), Moccasin Valley Cave (Holston River drainage), and Offutts Cave (Clinch River drainage) appear typical in this respect. Al-

TABLE 1.—Comparison of the means[1] of the ratio of length of antenna 1 to length of body in four populations of *Stygobromus mackini*

Locality	Sample size	Body length (mm)		Length of antenna 1/length of body			
		Range	$\bar{X}$	Range	$\bar{X}$	SD	C.V.
Three caves in Mercer Co., West Va. (data pooled)	12	4.5–7.0	5.38	0.47–0.65	0.57	0.05	0.10
Repass Saltpetre Cave, Bland Co., Va.	16	4.0–6.5	5.13	0.40–0.50	0.45	0.03	0.07
Moccasin Valley Cave, Scott Co., Va.	10	4.9–8.0	5.73	0.40–0.50	0.47	0.03	0.07
Offutts Cave, Anderson Co., Tenn.	10	5.0–8.5	7.30	0.40–0.51	0.45	0.03	0.07

[1]Statistical significance by two-tailed t-test between antenna 1/body length ratios in different populations:
Mercer Co. vs. Repass Saltpetre Cave ($p < .001$)
Mercer Co. vs. Moccasin Valley Cave ($p < .001$)
Mercer Co. vs. Offutts Cave ($p < .001$)
Repass Saltpetre Cave vs. Moccasin Valley Cave ($p > .10$) (not significant)
Repass Saltpetre Cave vs. Offuts Cave ($p > .10$) (not significant)
Moccasin Valley Cave vs. Offuts Cave ($p > .10$) (not significant)

though the ratios obtained from the Mercer County samples varied to some extent (between 0.47 and 0.65), the mean, as indicated by the t-tests in Table 1, was significantly higher than in the three other populations compared.

DISTRIBUTION AND ECOLOGY.—The range of this species, the second largest of the cave species treated in this paper, extends from Roane Co., Tennessee, in the Tennessee River drainage basin north-northeastward to Monroe Co., West Virginia, in the New River drainage basin and covers a linear distance of 403 km. Populations appear to be more common in caves near the middle of the range in limestone valleys drained by the Clinch River (upper Tennessee River drainage) in southwestern Virginia. In Russell, Scott, and Tazewell counties, Virginia, more than 80 percent of the caves examined with superficially suitable habitats contained populations of *S. mackini*. Elsewhere, populations are found in limestone valleys drained by the Holston River (upper Tennessee River drainage) and the New River (upper Kanawha River drainage), and a single population is recorded from the Powell River Valley (upper Tennessee River drainage) in Wise Co., Virginia. With the exception of two spring localities, all other populations have been sampled from caves, many of which are developed in Ordovician limestones.

Stygobromus mackini is primarily an inhabitant of small, mud-bottom drip and seep pools, although a few populations have been found in small streams with gravel or mud substrates. Out of 62 samples, 49 have come from pools, 11 from streams and 2 from surface springs (Table 2). As is the case with many other species of the genus, females are far more abundant in collections than males. Of the 244 specimens examined during this study, 184, or 75 percent, were females. Sexually mature females (with setose brood plates), ranging in size from 4.5 to 8.7 mm, have been recorded from all seasons of the year. Ovigerous females have been found during the months of May, July, and August. Juveniles have been found in samples from the same months. The clutch size of seven ovigerous females, ranging in size from 4.5 to 8.0 mm ($\overline{X}$ = 6.80, SD = 1.24, C.V. = 0.18) is summarized as follows: N = 7, range = 1–12 eggs or embryos, $\overline{X}$ = 6.43, SD = 3.78, C.V. = 0.59. Newly hatched young are approximately 1.7 mm in length.

REMARKS—Although I indicated earlier (Holsinger, 1969a:44–45) that *S. mackini* occurred in Craig Co., Virginia (upper James River drainage), a re-examination of the material from this county (a single specimen from New Castle Murder Hole Cave) has led me to conclude that, while this specimen is closely allied with *S. mackini*, it represents a distinct species but one that cannot be described pending collection of additional specimens (see "*Stygobromus* spp.").

Hubricht (1943:697) designated Sikes Cave (7.2 km north of Lebanon, Russell Co., Virginia) as the type-locality for this species. I have made several attempts to locate this cave but have so far failed. In the general vicinity of Hubricht's Sikes Cave, however, I was able to find a small, dry cave in a limestone bluff just south of the Clinch River which the owner referred to as "Sykes Cave" (Holsinger, 1975a:259). This cave contained no water and, according to L. Hubricht (in litt.), was not the same cave which he designated as the type-locality.

Stygobromus abditus, new species

FIGURES 36, 37

MATERIAL EXAMINED.—VIRGINIA. Pulaski Co.: James Cave, holotype ♀ (USNM 168785) and 1 ♀ paratype (JRH), J. R. Holsinger, L. M. and B. L. Ferguson, 16 Oct 1971.

DIAGNOSIS.—A medium-sized cavernicolous species closely allied morphologically with *S. mackini*, but distinguished from that species by proportionately broader bases of pereopods 5–7, having 1 seta each on posterior margins of pleonal plates, and lacking distal spines on peduncle of uropod 3. Largest female, 6.0 mm; male unknown.

FEMALE.—Antenna 1, 50 percent length of body, 40 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2, flagellum with 6 segments. Mouthparts corresponding closely to those described for *S. mackini* but differing slightly as follows: Spine row of mandible with 3 or 4 spines; segments 2 and 3 of palp with few less setae. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 5 stiff setae and 2 slender spines apically. Maxilla 2, inner plate wtih oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 4 bladelike spines, 1 plumose spine and 3 or 4 naked setae apically, and 2 plu-

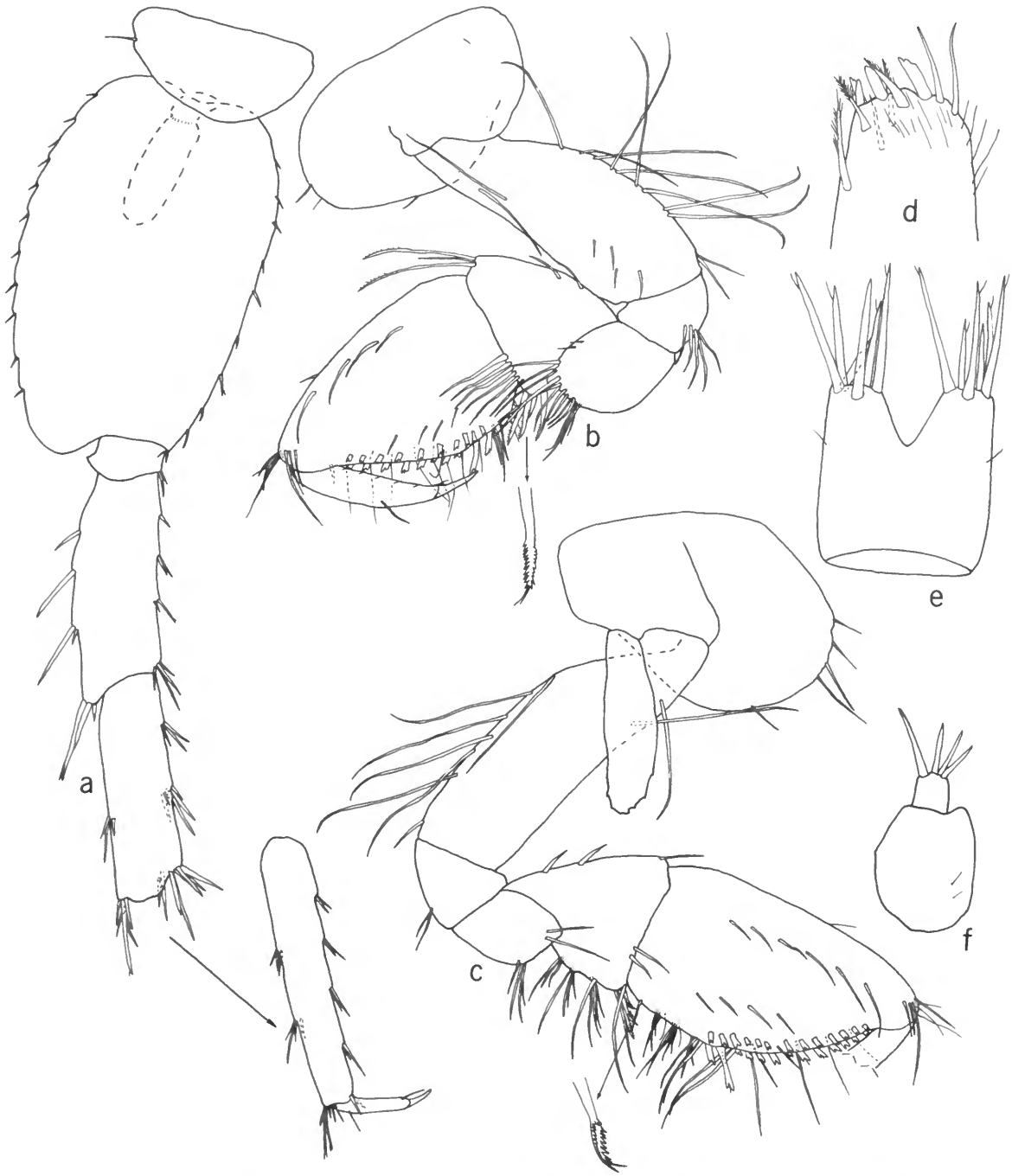

FIGURE 36.—*Stygobromus abditus*, new species, female paratype (6.0 mm), James Cave, Virginia: *a*, pereopod 6 (arrow indicates continuation of appendage); *b*, *c*, gnathopods 1, 2 (rastellate setae enlarged); *d*, apical part of inner plate of maxilliped (greatly enlarged); *e*, telson, *f*, uropod 3.

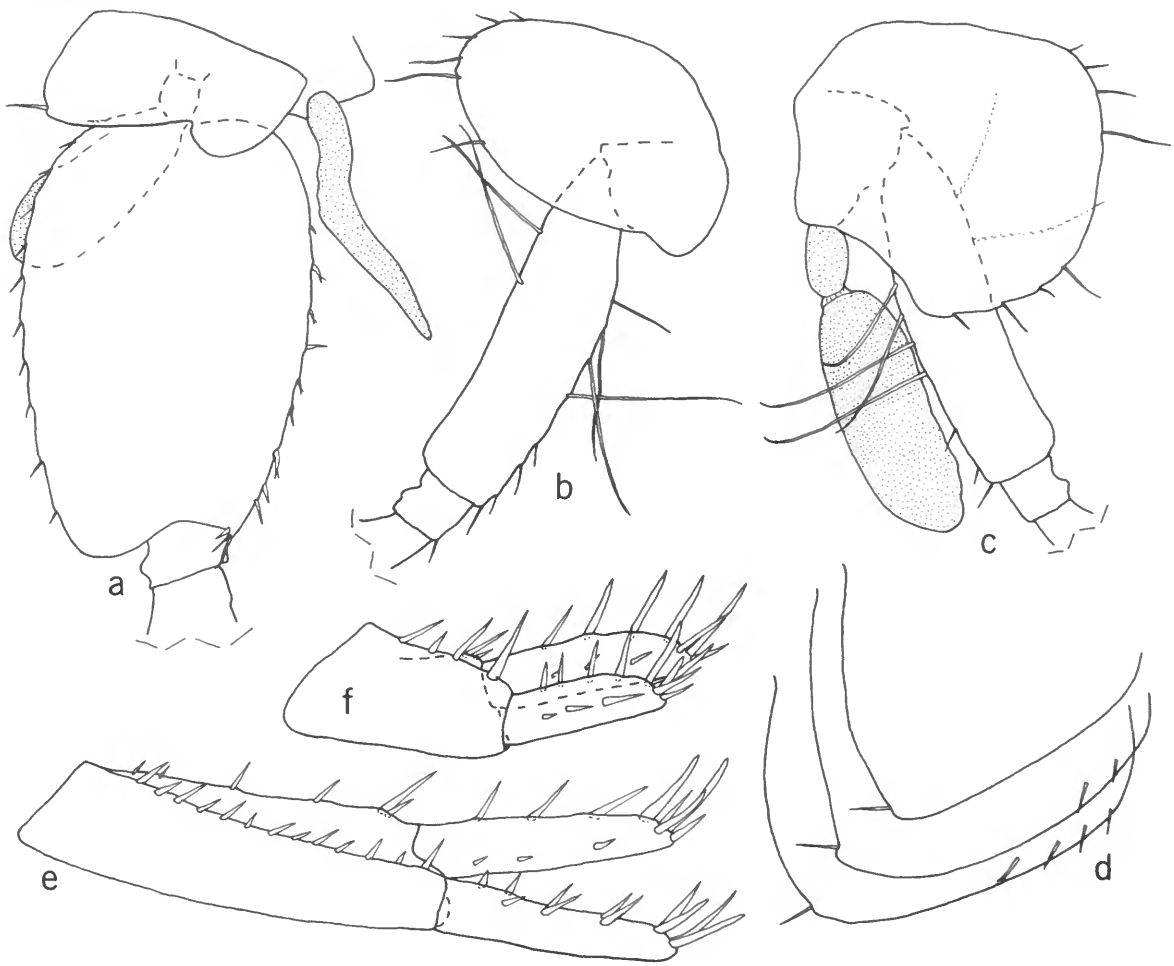

FIGURE 37.—*Stygobromus abditus*, new species, female paratype (6.0 mm); James Cave, Virginia: *a*, pereopod 7 (in part) with lateral sternal gill; *b*, *c*, pereopods 3, 4, (in part); *d*, pleonal plates; *e*, *f*, uropods 1, 2.

mose spines (or coarse setae ?) on inner margin distally; outer plate with naked setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 subequal in size to 2nd propod; palm armed with double row of 7 spine teeth; defining angle with 2 long spine teeth on outside, 3 shorter ones on inside; posterior margin with 6 setae; medial setae mostly singly inserted. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm with double row of 11 spine teeth; defining angle with 2 spine teeth of unequal length on outside, 2 shorter ones on inside; posterior margin with 4 sets setae; medial setae mostly singly inserted. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 5 or 6 setae each. Coxal plate of pereopod 4 about as broad as long, reaching approximately 55 percent length of basis; margin with 8 setae. Pereopod 6 a little longer than pereopod 7, 50–55 percent length of body, 20 percent longer than pereopod 5. Bases of pereopods 5–7 rather broad; posterior margins convex; distoposterior lobes distinct, broadly rounded. Dactyls of pereo-

pods 5–7, 36–42 percent length of corresponding propods. Coxal gill present on pereopod 7. Three median sternal gills on pereonites 2–4; 2 pairs simple, lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates not setose in specimens at hand but apparently like those of *S. mackini*.

Pleonal plates: posterior margins of plates 1 and 3 convex, that of plate 2 nearly straight, all margins with 1 seta each; posterior corners small, bluntly rounded; ventral margin of plate 2 with 2 spines; that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 60 percent length of peduncle, armed with 11 or 12 spines; outer ramus with 11 spines; peduncle with 18 or 19 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 10 or 11 spines; outer ramus with 12 spines; peduncle with 6 spines. Uropod 3: ramus about ⅓ length of peduncle, armed with 4 apical spines. Telson a little longer than broad; apical margin incised about 33 percent the distance to base, armed with 12 spines.

TYPE-LOCALITY.—James Cave, located approximately 4.3 km northwest of Radford in Pulaski Co., Virginia, is a large, stream-passage cave developed in limestone and dolomite of the Conococheague Formation (Upper Cambrian age) (Holsinger, 1975a:190).

DISTRIBUTION AND ECOLOGY.—This species is known only from two specimens (both females) collected from under gravels in the stream in James Cave, where it was associated with the troglobitic isopod *Asellus* (sensu lato) *henroti* Bresson. Both specimens lacked setose brood plates but appeared to be submature. The single locality for *S. abditus* is situated only about 19 km south of two localities for *S. mackini* (two caves in Giles Co., Virginia) but is extrinsically isolated from them by several prominent ridges of clastic sediments.

ETYMOLOGY.—The epithet *abditus* is from Latin, meaning "hidden" or "concealed."

Stygobromus dicksoni, new species

FIGURES 38, 39

Stygobromus sp.—Holsinger, 1969a:32.—Holsinger and Peck, 1971:30.

MATERIAL EXAMINED.—ALABAMA. Jackson Co.: Sauta Cave, holotype ♀ (USNM 168809), 12 ♀ and 3 ♂ paratypes (JRH), J. R. Holsinger, S. B. Peck, and R. M. Norton, 17 Mar 1964; Horseskull Cave, 4 ♀ paratypes (JRH), S. B. Peck and A. Fiske, 5 Aug 1967; Indian Rocks Cave, 6 ♀ paratypes (JRH), S. B. Peck and A. Fiske, 7 Aug 1967; Out Cave, 5 ♀ paratypes (USNM), S. B. Peck and A. Fiske, 13 Aug 1967; Sheldons Cave, 1 ♀ paratype (JRH), S. B. Peck, 25 Jan 1967; Madison Co.: Varnedoe Cave, 1 ♀ paratype (JRH), E. Steenburn, 17 Dec 1972; Marshall Co.: Cathedral Caverns (all collections by S. B. Peck), 1 ♀ paratype (USNM), 3 Aug 1965, 1 ♀ paratype (JRH), 12 Aug 1965, 3 ♀, 1 ♂ paratypes (USNM), 17 Aug 1965, 1 ♀, 5 juv. paratypes (JRH), 1 Sept. 1965. GEORGIA. Chatooga Co.: Blowing Spring Cave, 1 ♀, 2 ♂ paratypes (JRH), J. R. Holsinger, S. B. Peck, R. A. Baroody, and A. Fiske, 11 Jun 1967; Dade Co.: Byers Cave, 15 ♀, 2 ♂ paratypes (JRH), J. R. Holsinger, S. B. Peck, and A. Fiske, 18 Jun 1967; Howards Waterfall Cave, 3 ♀ paratypes (JRH), J. R. Holsinger, S. B. Peck, and R. M. Norton 15 Mar 1964; Rustys Cave, 1 ♂ paratype (JRH), A. Iles, 23 Sep 1967; Walker Co.: Pettijohn Cave, 1 ♂ paratype (JRH), J. R. Holsinger, S. B. Peck, R. A. Baroody, and A. Fiske, 10 Jun 1967.

DIAGNOSIS.—A relatively small to medium-sized cavernicolous species, very closely allied with *S. mackini*, but distinguished from that species by reaching sexual maturity at a smaller size, lacking distal spines on peduncle of uropod 3, proportionately shorter ramus of uropod 3, and longer peduncular process of uropod 1 of the male which is about 60 percent length of outer ramus. Largest male, 3.8 mm; largest female, 6.7 mm.

FEMALE.—Antenna 1, 38–42 percent length of body, 30–40 percent longer than antenna 2; primary flagellum with 14 or 15 segments. Antenna 2, flagellum with 5 or 6 segments. Mandibles subequal; spine row with 4 spines; segment 2 of palp with row of 5 setae (3 long, 2 short) on inner margin, segment 3 with 1 or 2 long setae on outer margin, 1 long seta and row of short setae on inner margin, and 3 long setae on apex. Maxilla 1: inner plate with 5 or 6 apical, plumose setae; palp with 2 or 3 slender spines and 4 or 5 thick setae apically. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 1 plumose spine, and 1 naked seta apically, and 1 plumose spine (or coarse seta?) and 1 naked seta subapically; outer plate with row of naked setae on inner margin and apex and usually 1 plumose seta apically. Inner lobes of lower lip small.

Propod of gnathopod 1 subequal in size to 2nd propod; palm armed with double row of 7 or 8 spine teeth; defining angle with 3 or 4 long spine

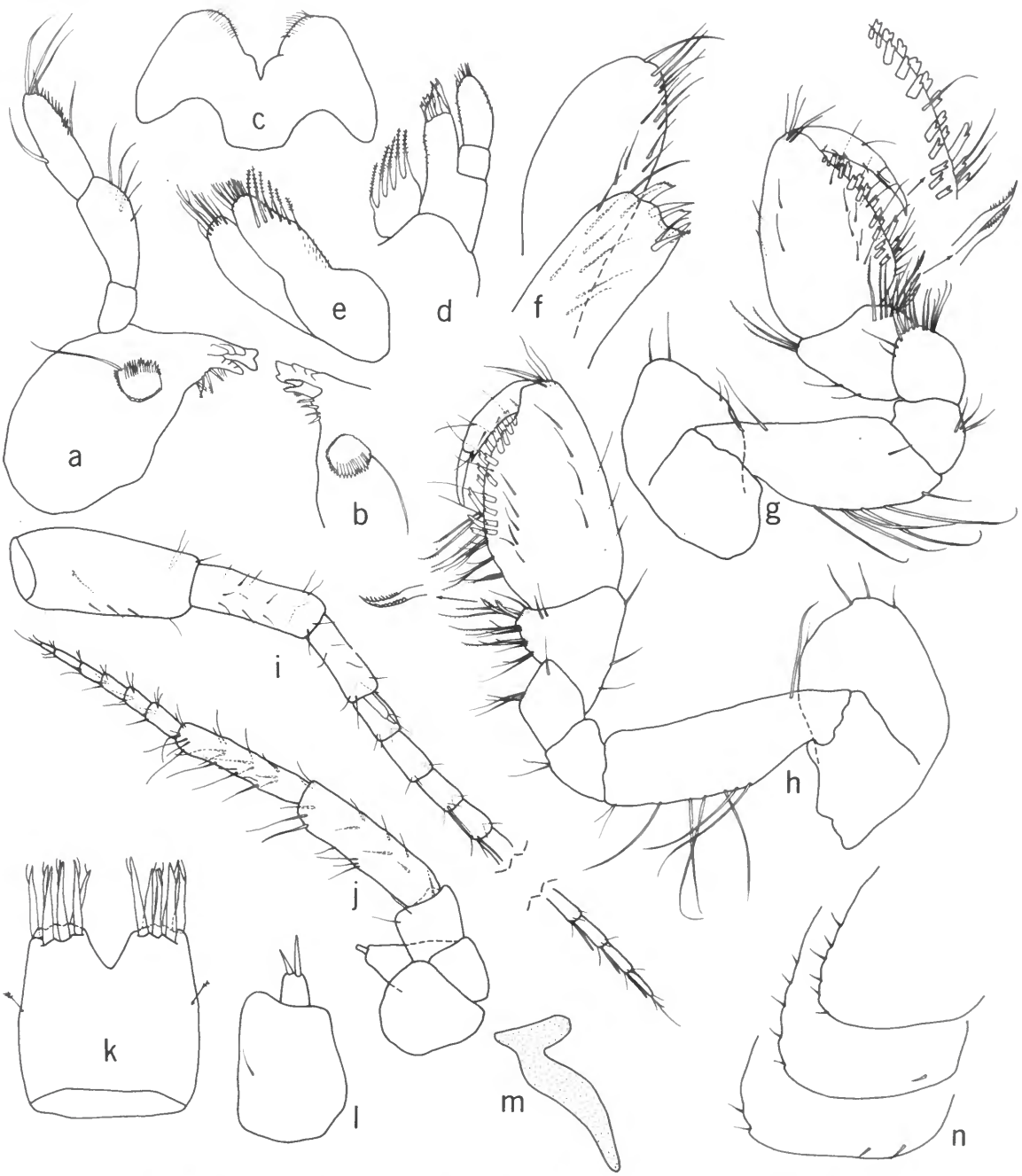

FIGURE 38.—*Stygobromus dicksoni*, new species, female paratype (5.0 mm), Byers Cave, Georgia: *a*, left mandible; *b*, dentate part of right mandible; *c*, lower lip; *d*, *e*, maxillae 1, 2; *f*, inner and outer plates of maxilliped (greatly enlarged); *g*, *h*, gnathopods 1, 2 (part of palm, defining angle, and rastellate seta of gnathopod 1 enlarged; rastellate seta of gnathopod 2 enlarged); *i*, *j*, antennae 1, 2; *k*, telson; *l*, uropod 3; *m*, lateral sternal gill from pereonite 7; *n*, pleonal plates.

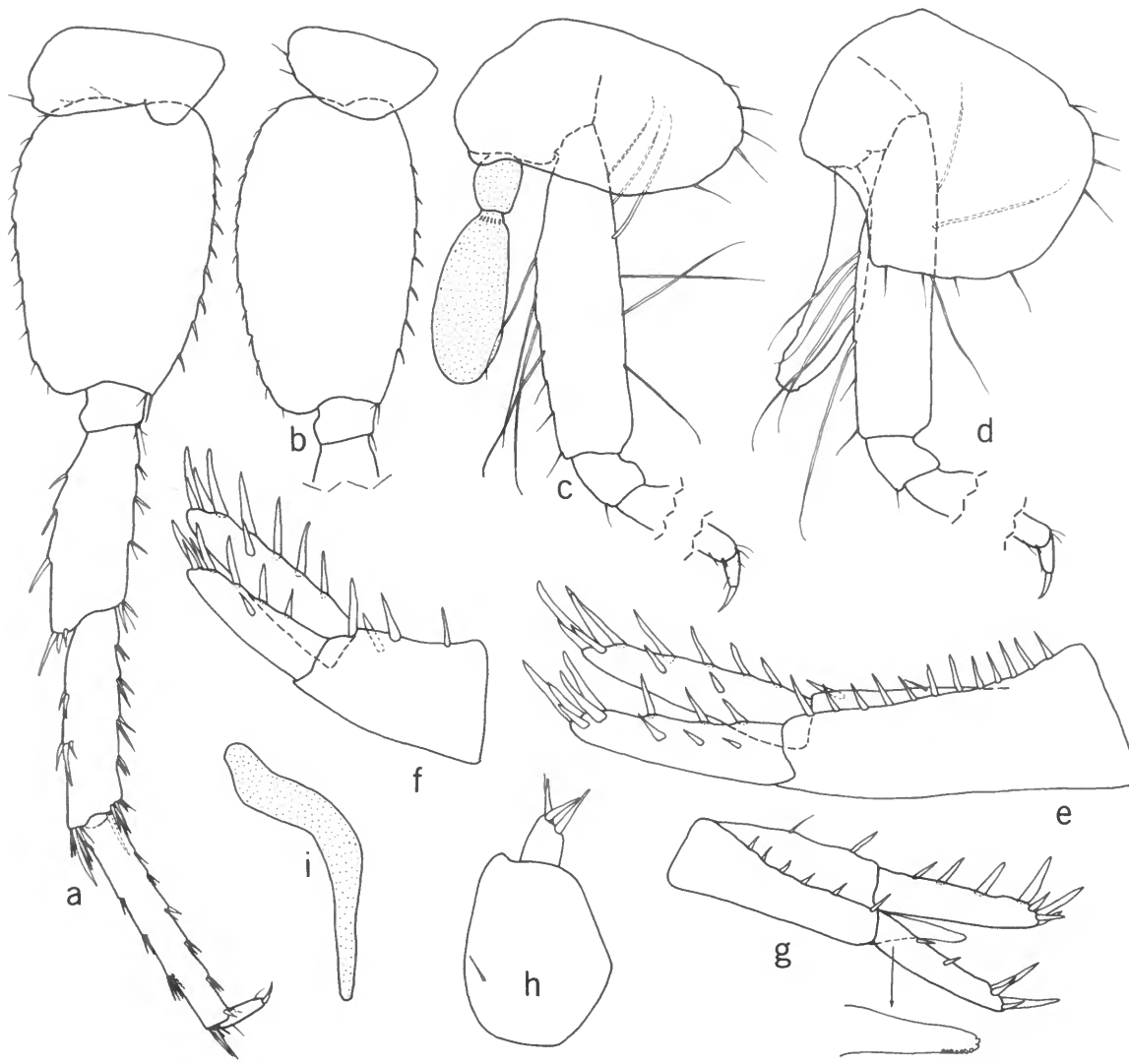

FIGURE 39.—*Stygobromus dicksoni*, new species. Female paratype (5.0 mm), Byers Cave, Georgia: *a*, pereopod 6; *b*, pereopod 7 (in part); *c*, *d*, pereopods 3, 4 (in part); *e*, *f*, uropods 1, 2. Male paratype (3.3 mm), Byers Cave: *g*, uropod 1 (same scale as *e* and *f*; peduncular process enlarged). Female paratype (6.0 mm), Sauta Cave, Alabama: *h*, uropod 3; *i*, lateral sternal gill from pereonite 7 (same scale as Figure 38*m*).

teeth on outside, 2 or 3 shorter ones on inside; posterior margin with 3 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 rather long. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm with double row of 7 or 8 spine teeth; defining angle with 3 long spine teeth on outside, 2 or 3 shorter ones on inside; posterior margin with 3 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 rather long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 4 or 5 setae each. Coxal plate of pereopod 4

relatively broad and deep, nearly as broad as long, reaching about 55 percent length of basis; margin with 8 setae. Pereopod 7 slightly longer than pereopod 6, 40–45 percent length of body, 15–30 percent longer than pereopod 5. Bases of pereopods 5–7 about like those of *S. mackini;* dactyls of pereopods 6 and 7, 30–35 percent length of corresponding propods, that of pereopod 5, 35–40 percent length of corresponding propod. Coxal gill present or absent on pereopod 7. Two median sternal gills usually present on pereonites 2 and 3; 2 pairs simple, lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates somewhat expanded distally (similar to those of *S. mackini).*

Pleonal plates: posterior margins slightly sinuate, plates 1 and 2 with 5 or 6 setae each, plate 3 with 1 or 2 setae; posterior corners of plates 2 and 3 small and rounded, that of plate 1 indistinct; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 70 percent length of peduncle, armed with 10–12 spines; outer ramus with 9–11 spines; peduncle with 12–13 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 9–11 spines; outer ramus with 6 or 7 spines; peduncle with 4 or 5 spines. Uropod 3: ramus about 25 percent length of peduncle, armed with 2 or 3 apical spines. Telson a little longer than broad; apical margin incised about 25 percent the distance to base, with 12–16 spines.

MALE.—Differing from female as follows: Flagellum of antenna 1 with 10 or 11 segments. Gnathopod propods with few less spines and setae. Coxal gill absent from pereopod 7. Uropod 1: inner ramus with 8–11 spines; outer ramus with 7–9 spines; peduncle with 7–9 spines; peduncular process elongate and narrowing distally, reaching about 60 percent length of outer ramus, weakly serrate distally. Uropod 2: inner ramus with 7–9 spines; outer ramus with 7 spines; peduncle with 3 or 4 spines. Apical margin of telson armed with 12 spines.

VARIATION.—The specimens from caves in Chatooga and Walker counties, Georgia, lacked median sternal gills, but these structures were present in all other populations examined. The presence or absence of a coxal gill on pereopod 7 of the female was also variable throughout the range—specimens from Byers Cave in Dade Co., Georgia, and Cathedral Caverns in Marshall Co., Alabama, lacked this structure. Three out of four females from Horseskull Cave in Jackson Co., Alabama, also lacked a coxal gill on pereopod 7, whereas the other female in the sample possessed a coxal gill on only one of the two seventh pereopods. All other females examined possessed a coxal gill on both seventh pereopods.

TYPE-LOCALITY.—Sauta Cave, located 11.3 km southwest of Scottsboro in Jackson Co., Alabama, is a large, stream-passage cave developed in the Bangor limestone of Mississippian age. The type series was collected from mud-bottom, rimstone pools in the "Great Lakes" section of the cave. The pools contained pieces of rotting wood and are located on an upper level of the cave well above the stream.

DISTRIBUTION AND ECOLOGY.—The range of this species is contained within the Cumberland Plateau and occupies a part of the Tennessee River drainage basin in northeastern Alabama and northwestern Georgia and a part of the Coosa River drainage (upper Alabama River basin) in northwestern Georgia. The range, which covers a linear distance of approximately 108 km from east to west, extends from southeastern Madison County and northern Marshall County northeast through Jackson County in Alabama and then south-southeast from Dade County through western Walker County to northwestern Chatooga County in Georgia. The northernmost record for this species (Horseskull Cave in Jackson County) is situated about 150 km southwest of the southernmost record for *S. mackini* (Berry Cave, Roane Co., Tennessee).

All collections made to date have been from drip and seep pools in caves developed in Mississippian limestones. Although collections are available from all seasons of the year, ovigerous females have not been found. However, females (size range, 3.8–6.7 mm) with setose brood plates have been collected during spring, summer, and fall, and the September collection from Cathedral Caverns contained five newly hatched young.

ETYMOLOGY.—It is a pleasure to name this species in honor of Gary W. Dickson, who has materially assisted with the collection and study of cavernicolous amphipods.

Stygobromus finleyi, new species

FIGURES 40, 41

Stygobromus sp.—Holsinger, 1969a:31–32.

MATERIAL EXAMINED.—TENNESSEE. Claiborne Co.: English Cave, holotype ♀ (USNM 168819), 2 ♀ and 1 ♂ paratypes (USNM), T. C. Barr, Jr., 16 May 1957; additional paratypes from English Cave in JRH as follows: 5 ♀, 2 ♂, J. R. Holsinger and C. Rippy, 17 Jul 1965; 2 ♀, 3 ♂, 3 juv., J. R. Holsinger and D. C. Culver, 10 Aug 1973.

DIAGNOSIS.—A relatively small cavernicolous species very closely allied with *S. dicksoni* and *S. mackini* but distinguished from the latter species by reaching sexual maturity at smaller size, fewer setae on margins of coxal plates 1–4 (especially plates 2 and 3), proportionately smaller 4th coxal plate which reaches only about 45 percent length of basis, fewer setae on posterior margins of pleonal plates 2 and 3, longer peduncular process of uropod 1 of male which is 55–60 percent length of outer ramus, absence of distal spines on peduncle of uropod 3, and proportionately shorter ramus of uropod 3. Distinguished from *S. dicksoni* by fewer setae on margins of coxal plates 3 and 4 and proportionately smaller coxal plate of pereopod 4. Largest male, 3.5 mm; largest female, 4.8 mm.

FEMALE.—Antenna 1, 40–50 percent length of body, 40 percent longer than antenna 2; primary flagellum with 11 or 12 segments. Antenna 2, flagellum with 5 segments. Mouthparts closely similar to those of *S. mackini* and *S. dicksoni*. Mandibles subequal; spine row with 4 or 5 spines; segment 2 of palp with row of rather long setae on inner margin, segment 3 with 2 long setae on outer margin, 2 long setae and row of short setae on inner margin, and 3 or 4 long setae on apex. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 2 slender spines and 3 stiff setae apically. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 2 blade-like spines, 2 plumose spines and 2 or 3 naked setae apically; outer plate with naked setae on inner margin and apex and 1 lightly plumose seta apically. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 subequal in size to 2nd propod; palm armed with double row of 7 spine teeth; defining angle with 4 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 5 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopod propod 2: palm with double row of 7 or 8 spine teeth; defining angle with 3 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 3 sets setae; medial setae single inserted. Dactyl nail of gnathopod 2 moderately long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, with 3 or 4 marginal setae each. Coxal plate of pereopod 4 a little broader than long, reaching about 45 percent length of basis, margin with 3 setae. Pereopod 6 slightly longer than pereopod 7, about 45 percent length of body, 25–30 percent longer than pereopod 5. Pereopods 5–7: bases about like those of *S. mackini;* dactyls 35–40 percent length of corresponding propods. Coxal gill present on pereopod 7. Two or 3 median sternal gills on pereonites 2–4; 2 pairs simple, lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates somewhat expanded distally (similar to those of *S. mackini*).

Pleonal plates: posterior margins convex, plate 1 with 3 setae, plate 2 with 4 setae, plate 3 with 1 seta; posterior corners small, bluntly rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 60 percent length of peduncle, armed with 11 spines; outer ramus with 10 spines; peduncle with 19 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 9 spines; outer ramus with 8 spines; peduncle with 4 spines. Uropod 3: ramus about 25 percent length of peduncle, with 2 apical spines. Telson slightly longer than broad; apical margin incised about 25 percent the distance to base, armed with 11 or 12 spines.

MALE.—Differing only slightly from female as follows: Gnathopod propods with few less spine teeth. Coxal gill absent from pereopod 7. Uropod 1: inner ramus with 9 spines; outer ramus with 9 or 10 spines; peduncle with 10 spines; peduncular process elongate and narrowing distally like that of *S. dicksoni,* reaching 55–60 percent length of outer ramus, weakly serrate distally. Uropod 2 with few less spines. Ramus of uropod 3 with 1 apical spine. Telson armed with 10 apical spines.

TYPE-LOCALITY.—English Cave, located 5 km southeast of Harrogate on the south side of the Powell River in Claiborne Co., Tennessee, is a relatively large, well known cave developed in Copper

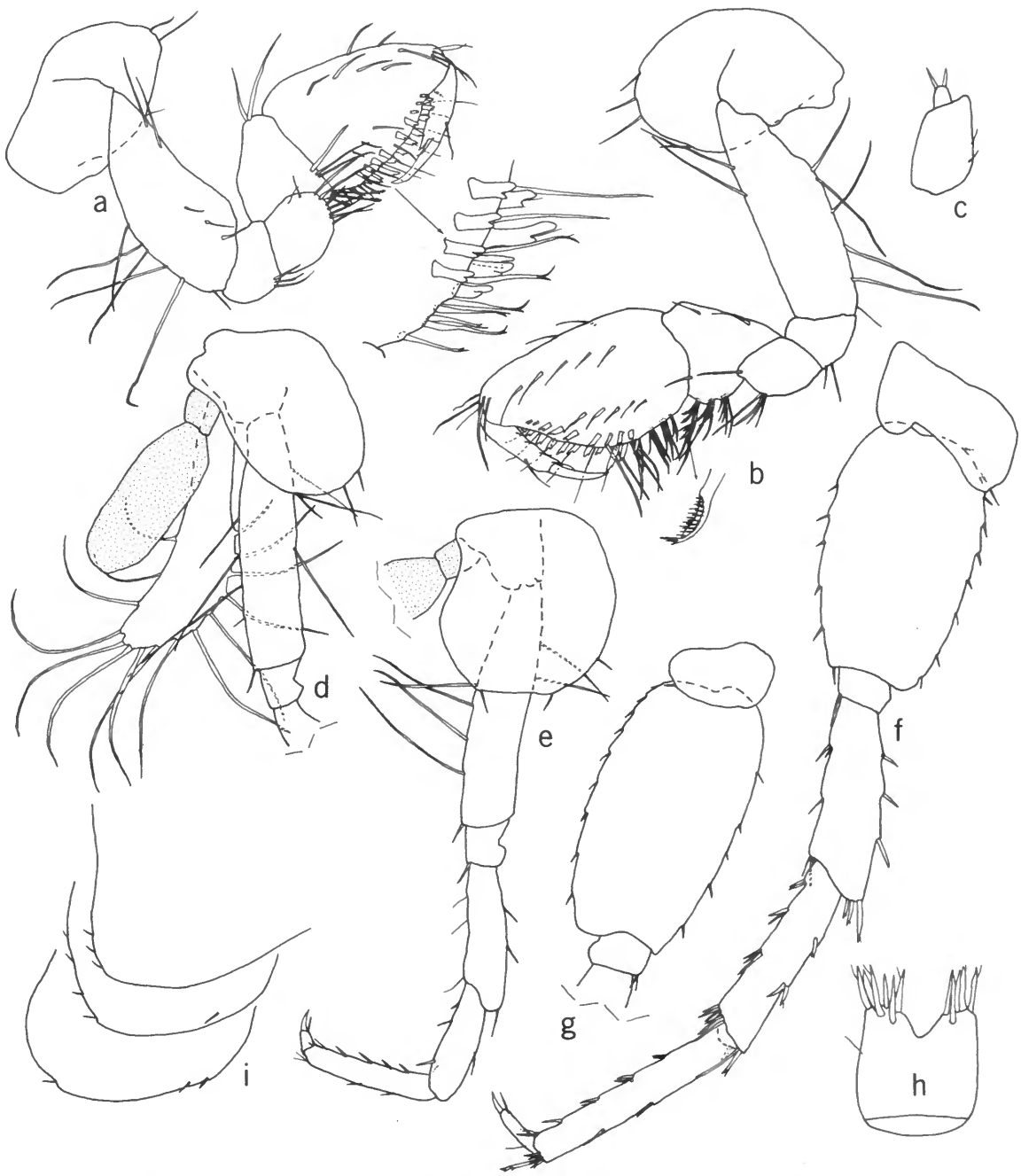

FIGURE 40.—*Stygobromus finleyi*, new species, female paratype (4.8 mm), English Cave, Tennessee: *a*, *b*, gnathopods 1, 2 (defining angle and posterior margin of propod 1 enlarged; rastellate seta of gnathopod 2 enlarged); *c*, uropod 3; *d*, pereopod 3 (in part); *e*, pereopod 4; *f*, pereopod 6; *g*, pereopod 7 (in part); *h*, telson; *i*, pleonal plates.

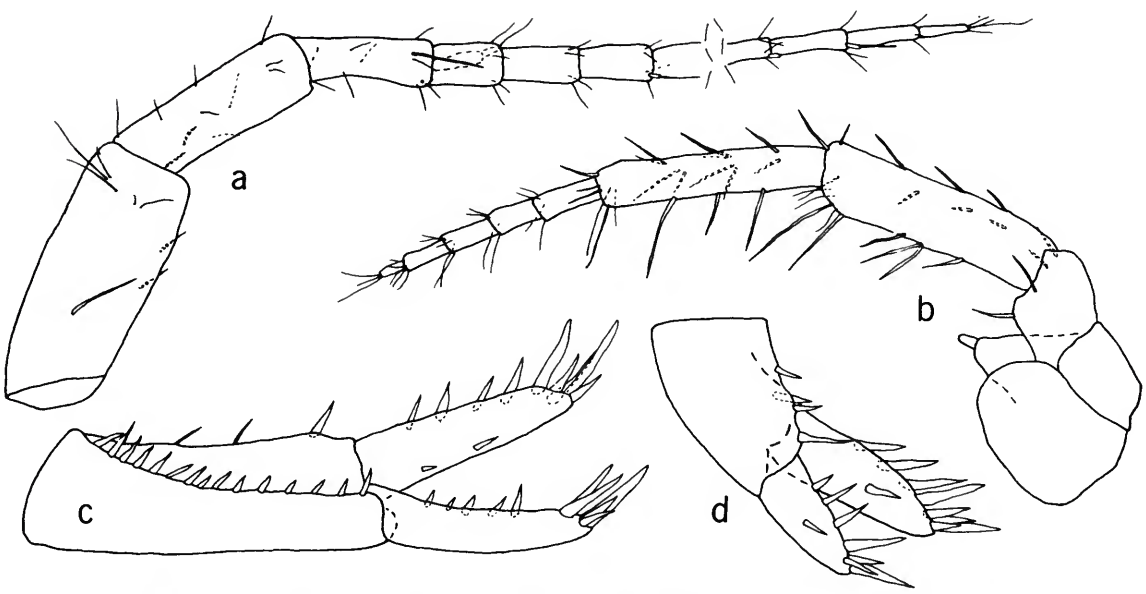

FIGURE 41.—*Stygobromus finleyi*, new species, female paratype (4.8 mm), English Cave, Tennessee: *a, b*, antennae 1, 2; *c, d*, uropods 1, 2.

Ridge dolomite of Cambrian age. On two different occasions (July 1965 and August 1973) I collected *S. finleyi* from very shallow seep and/or drip pools, where it was associated with the troglobitic isopod *Asellus* (sensu lato) *recurvatus* Steeves. Other pools located nearby, which were deeper and had mud-bottoms, contained the troglobitic amphipod *Crangonyx antennatus* Packard but not *S. finleyi*.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it appears to be fairly common in a series of shallow pools. Two ovigerous females (4.0 and 4.5 mm) were in the May 1957 collection and one ovigerous female (4.5 mm) was obtained in the July 1965 collection. Two were carrying newly hatched young (most had been released prior to collection) and the other had a single embryo. The newly hatched young measured 1.2–1.5 mm in length. Two other females with setose brood plates, measuring 4.5 and 4.8 mm, were observed in the May 1957 and August 1973 collections, respectively.

REMARKS.—In a previous paper (Holsinger, 1969a: 32), I indicated that the population of *Stygobromus* in English Cave might possibly represent an intergradation between *S. mackini* and *S. leensis* which is recorded from three caves in Lee Co., Virginia. After careful study, I have concluded that both the population in English Cave and those in nearby Lee County are distinct species and not subspecies of *S. mackini*.

ETYMOLOGY.—It is a pleasure to name this species in honor of Donald L. Finley, who has been of substantial assistance in the location of caves and the collection of troglobitic amphipods in southwestern Virginia and eastern Tennessee.

The *leensis* Subgroup

DIAGNOSIS.—Adults small (ca. 2.8–3.7 mm). Pereopod 7 without coxal gill. Posterior margins of pleonal plates with 1 seta each. Uropod 3 without ramus, peduncle with 1 apical spine. Telson about as broad as long.

Stygobromus leensis, new species

FIGURES 42, 43

Stygobromus sp.—Holsinger, 1969a:31.
Stygobromus n. sp.—Culver, 1973:103.

MATERIAL EXAMINED.—VIRGINIA. Lee Co.: Litton Cave No. 1, holotype ♀ (USNM 168833) and 1 ♀ paratype (JRH), J. R.

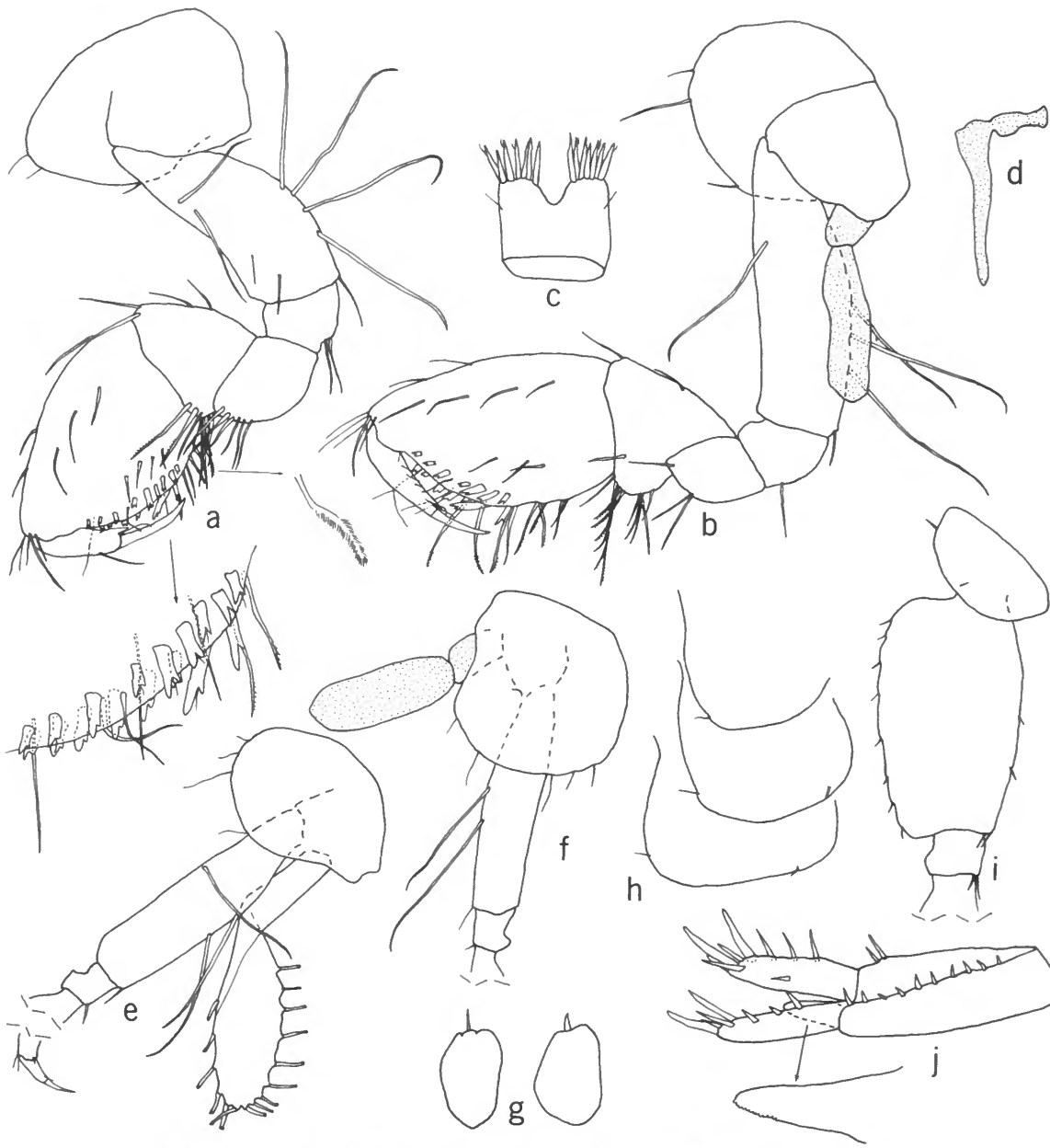

FIGURE 42.—*Stygobromus leensis,* new species, female paratype (3.7 mm), Litton Cave No. 1, Virginia: *a, b,* gnathopods 1, 2 (part of palm, defining angle, and rastellate seta of gnathopod 1 enlarged); *c,* telson; *d,* lateral sternal gill; *e, f,* pereopods 3, 4 (in part); *g,* 3rd uropods; *h,* pleonal plates; *i,* pereopod 7 (in part). Male paratype (2.8 mm), Gallohan Cave No. 2, Virginia; *j,* uropod 1 (peduncular process enlarged).

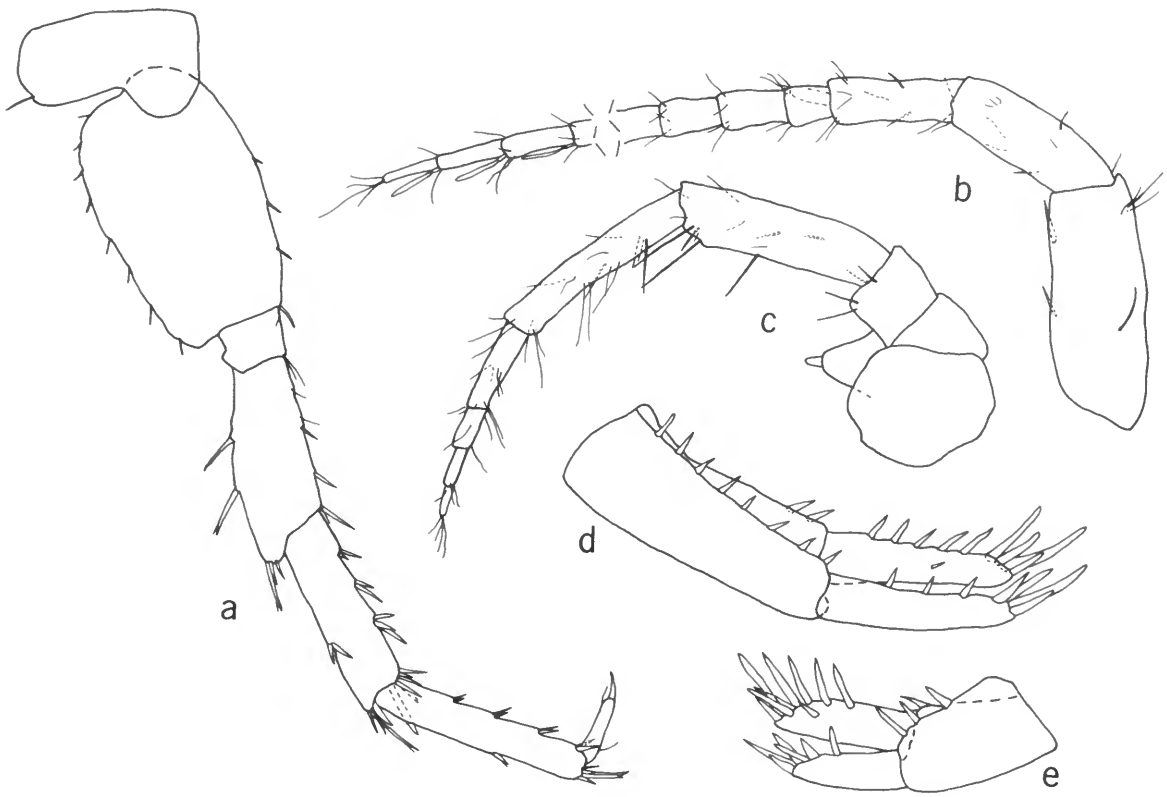

FIGURE 43.—*Stygobromus leensis,* new species, female paratype (3.7 mm), Litton Cave No. 1, Virginia: *a,* pereopod 6; *b, c,* antennae 1, 2; *d, e,* uropods 1, 2.

Holsinger and D. L. Finley, 17 Aug 1965; Gallohan Cave No. 2, 1 ♂ paratype (JRH), J. R. Holsinger and D. L. Finley, 16 Aug 1965; Skull Cave, 2 ♀ paratypes (JRH), J. R. Holsinger, G. W. Dickson, and T C. Kane, 27 Nov 1975.

DIAGNOSIS.—A small cavernicolous species distinguished from members of the *mackini* subgroup by the characters given for the *leensis* subgroup and by fewer spine teeth on the gnathopod propods. Largest male, 2.8 mm; largest female, 3.7 mm.

FEMALE.—Antenna 1 about 45 percent length of body, about 40 percent longer than antenna 2; primary flagellum with 10–12 segments. Antenna 2, flagellum with 4 segments. Mandibles subequal; spine row with 2 or 3 spines; segment 2 of palp with 3 long setae on inner margin, segment 3 with 1 long seta on outer margin, 1 long seta and row of short setae on inner margin, and 3 or 4 long setae apically. Maxilla 1: inner plate with 4 apical, plumose setae; palp with 2 slender spines and 3 stiff setae apically. Maxilla 2, inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate with 2 or 3 bladelike spines, 2 plumose spines and 2 or 3 naked setae apically; outer plate with naked setae on inner margin and apex and 1 lightly plumose seta apically. Inner lobes of lower lip small.

Propod of gnathopod 1 a little broader and a little shorter than 2nd propod; palm slightly convex, armed with double row of 5 or 6 spine teeth; defining angle with 2 long spine teeth on outside, 4 shorter ones on inside; posterior margin with 4 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 long. Coxal plate of gnathopod 1 longer than broad, with 3 marginal setae. Gnathopod propod 2: palm slightly convex, armed with double row of 5 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 2 sets setae; medial setae

singly inserted. Dactyl nail of gnathopod 2 moderately long. Coxal plates of gnathopod 2 and pereopod 3 a little longer than broad, margins with 3 or 4 setae each. Coxal plate of pereopod 4 about as broad as long, reaching 35–40 percent length of basis, margin with 5 setae. Pereopod 6 a little longer than pereopod 7, about 45 percent length of body, 10–15 percent longer than pereopod 5. Bases of pereopods 5–7: posterior margins nearly straight to slightly convex; distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 6 and 7, 48–50 percent length of corresponding propods; dactyl of pereopod 5, 43 percent length of corresponding propod. Coxal gill absent from pereopod 7. Two median sternal gills on pereonites 2 and 3; 2 pairs simple, lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates somewhat expanded distally (similar to those of *S. mackini*).

Pleonal plates: posterior margins of plates 1 and 3 convex, that of plate 2 nearly straight, margins with 1 seta each; ventral margins of plates 2 and 3 with 1 spine each. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 65 percent length of peduncle, armed with 10 spines; outer ramus with 7 spines; peduncle with 10 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 9 spines; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3: ramus absent; peduncle with 1 apical spine. Telson about as long as broad; apical margin incised about 25 percent the distance to base, armed with 14 spines.

MALE.—Differing slightly from female as follows: Gnathopods with few less spines and setae. Uropod 1: inner ramus with 9 spines; outer ramus with 7 spines; peduncle with 12 spines; peduncular process elongate and narrowing distally (very similar to those of *S. dicksoni* and *S. finleyi*). Uropod 2 with 1 less spine each on inner and outer rami. Apical margin of telson with 12 spines.

TYPE-LOCALITY.—Litton Cave No. 1, located 10 km east of Jonesville in Lee Co., Virginia, is a medium-sized cave developed in Middle Ordovician limestone. The cave contains several deep pools of water on the lower level and a series of shallow, mud-bottom drip and seep pools on the upper level. The type-material was collected from the shallow pools.

DISTRIBUTION AND ECOLOGY.—This rare species is recorded from three caves in the Powell Valley of south-central Lee Co., Virginia, where it is known only from five specimens collected over a 10-year period. The range, which covers a linear distance of approximately 21 km, is dissected by the Powell River. All three cave localities are developed in Middle Ordovician limestones. *Stygobromus leensis* has been collected from shallow, drip and seep pools, and in Gallohan No. 2 and Litton No. 1 caves it was associated with the more common troglobitic amphipod *Crangonyx antennatus*. Two females with setose brood plates, measuring 3.5 and 3.7 mm, were observed in the August 1965 collection from the type-locality. The two females collected from Skull Cave in November 1975 were 2.3 and 2.6 mm in length and were presumably immature.

REMARKS.—After more critical study, I have concluded that this form is a distinct species and not a "probable subspecies of *S. mackini*" as indicated in an earlier paper (Holsinger, 1969a:31–32).

ETYMOLOGY.—The specific name refers to the occurrence of this species in Lee County.

The *sparsus* Subgroup

DIAGNOSIS.—Adults small to medium-sized (ca. 4.3–6.0 mm). Gnathopod propod 1 slightly smaller than 2nd propod. Pereopod 7 a little longer than pereopod 6 in one species (*S. sparsus*). Sternal gills absent in one species (*S. carolinensis*). Posterior margins of pleonal plates with 1 seta each; posterior corners sometimes rounded and indistinct. Uronites free or only partly fused. Ramus of uropod 3 vestigial or absent, ramus or peduncle with 1 apical spine. Telson about as long as broad.

Stygobromus sparsus, new species

FIGURES 44, 45

Apocrangonyx sp. D.—Holsinger, 1969a:28–29.

MATERIAL EXAMINED.—TENNESSEE. Blount Co.: Gregorys Cave, holotype ♂ partly on slide mounts (USNM 168853), 1 ♂ and 1 ♀ paratype (USNM), L. Hubricht, 9 Aug 1939.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished from other species of the *sparsus* subgroup by proportionately longer pereopod 7 which is longer than pereopod 6, smaller distoposterior

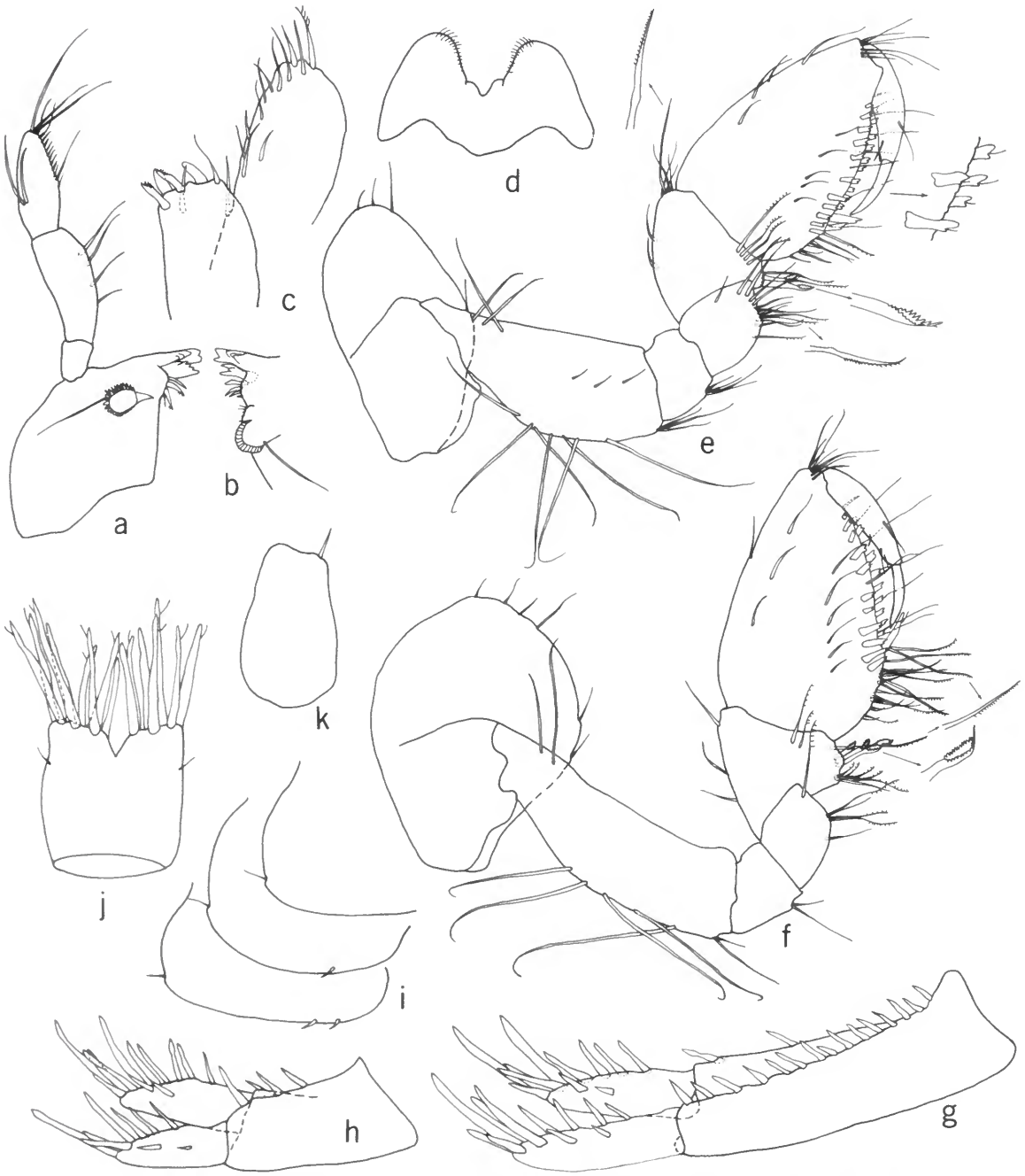

FIGURE 44.—*Stygobromus sparsus*, new species, male holotype (6.0 mm), Gregorys Cave, Tennessee: *a*, left mandible; *b*, dentate part of right mandible; *c*, inner and outer plates of maxilliped (greatly enlarged); *d*, lower lip; *e*, *f*, gnathopods 1, 2 (palmer spines and setae of gnathopod 1 enlarged; setae of gnathopod 2 enlarged); *g*, *h*, uropods 1, 2; *i*, pleonal plates; *j*, telson; *k*, uropod 3.

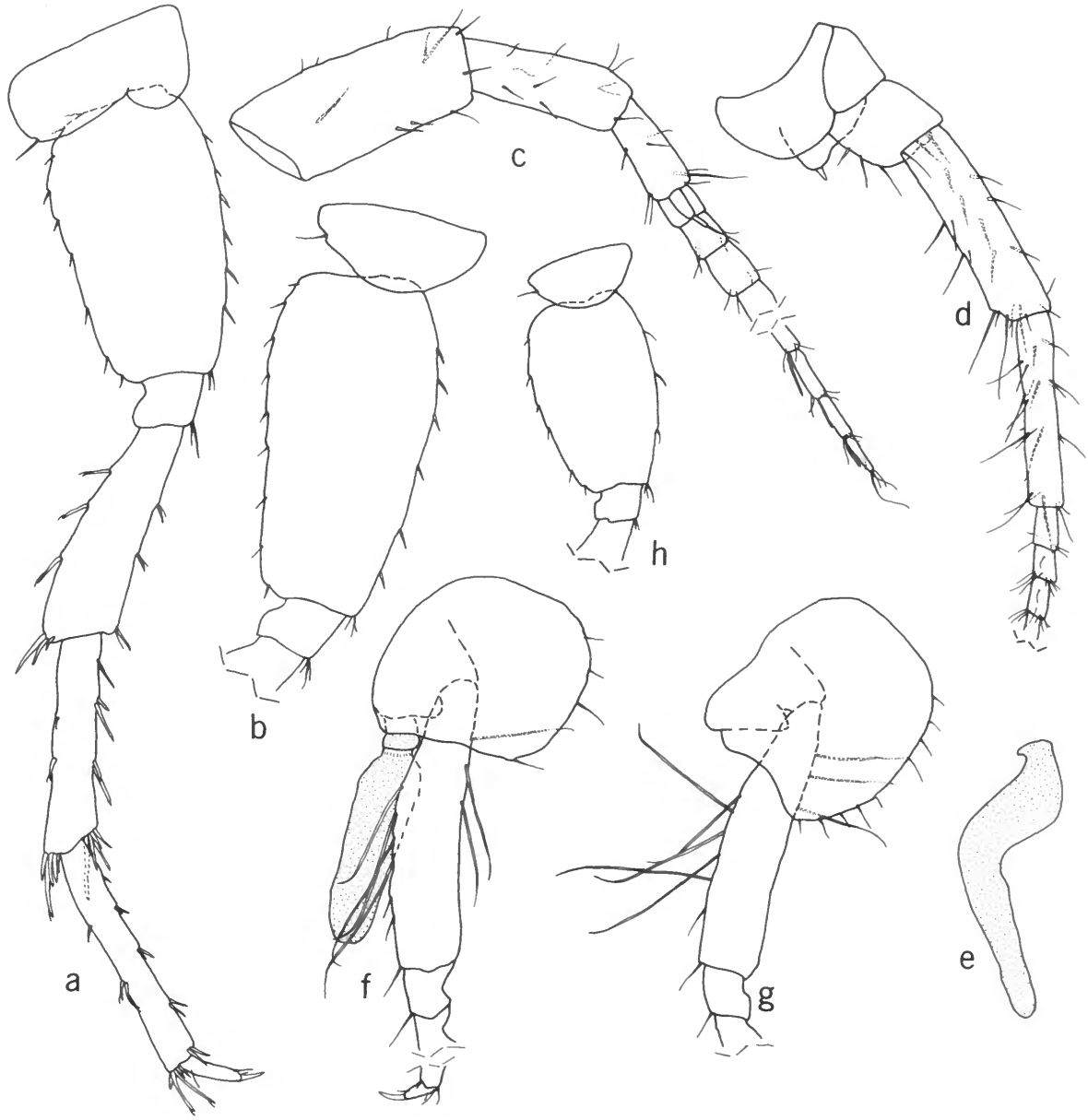

FIGURE 45.—*Stygobromus sparsus*, new species, male holotype (6.0 mm), Gregorys Cave, Tennessee: *a*, pereopod 6; *b*, pereopod 7 (in part); *c*, *d*, antennae 1, 2; *e*, lateral sternal gill; *f*, *g*, pereopods 3, 4 (in part). Female paratype (4.7 mm), Gregorys Cave: *h*, pereopod 7 (in part) (to same scale as *a* and *b*).

lobes of bases of pereopods 6 and 7, lack of distinct peduncular process of uropod 1 in male, absence of ramus of uropod 3, and proportionately longer apical spines of telson. Largest males, 6.0 mm; largest female (immature), 4.7 mm.

MALE.—Antenna 1, 55 percent length of body, 40 percent longer than antenna 2; primary flagellum with 18 or 19 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal; spine row with 3 spines; segment 2 of palp with 4 long setae on outer margin, segment 3 with 2 long setae on outer margin, 1 long seta and row of short setae on inner margin, and 4 long setae of unequal length apically. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 2 slender spines and 3 stiff setae apically. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 2 plumose spines and 2 naked setae apically; outer plate with naked setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip small.

Propod of gnathopod 1 slightly smaller than 2nd propod; palm armed with double row of 8 or 9 spine teeth; defining angle with 2 long spine teeth on outside, 3 shorter ones on inside; posterior margin with 7 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 moderately long. Coxal plate of gnathopod longer than broad, margin with 4 setae. Gnathopod propod 2: palm with double row of 9 or 10 spine teeth; defining angle with 1 long spine tooth on outside, 2 or 3 shorter ones on inside; posterior margin with about 5 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Coxal plate of gnathopod 2 a little longer than broad, margin with 6 setae. Coxal plate of pereopod 3 slightly longer than broad, margin with 4 setae. Coxal plate of pereopod 4 slightly broader than long, reaching about 40 percent length of basis, margin with 9 setae. Pereopod 7 longer than pereopod 6 (25 percent longer in 2 specimens examined), 70 percent length of body, 45 percent longer than pereopod 5. Bases of pereopod 6 and 7 narrowing slightly distally; distoposterior lobes poorly developed. Dactyls of pereopods 5–7 about 30 percent length of corresponding propods. Coxal gill absent from pereopod 7. Median sternal and pleonite sternal gills absent; 2 pairs large, simple, lateral sternal gills on pereonites 6 and 7.

Pleonal plates: posterior margins convex, with 1 seta each; posterior corners of plates 1 and 2 rounded and indistinct, that of plate 3 small and distinct; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus a little longer than outer ramus, about 45 percent length of peduncle, armed with 11 spines; outer ramus with 11 spines; peduncle with 17 spines; peduncular process vestigial or absent. Uropod 2: inner ramus a little longer than outer ramus, 65–70 percent length of peduncle, armed with 12 spines; outer ramus with 10 spines; peduncle with 4 spines. Uropod 3 lacking ramus; peduncle with 1 apical spine. Telson slightly longer than broad; apical margin with distinct notch, armed with 14–16 spines.

FEMALE.—Single specimen in collection immature but differing from male as follows: Primary flagellum of antenna 1 with 14 segments; flagellum of antenna 2 with 5 segments. Gnathopods with fewer setae and spines. Pereopod 7 only slightly longer than pereopod 6; basis proportionately shorter and broader, posterior margin convex. Coxal gill present on pereopod 7. Brood plates small and not setose. Uropods 1 and 2 with few less spines.

TYPE-LOCALITY.—Gregorys Cave, located in Great Smoky Mountain National Park in Blount Co., Tennessee, is a small cave developed in dolomite of the Knox group (Lower Ordovician age). The cave is located in Cades Cove, which is a widow in the Great Smoky Mountain thrust sheet (Barr, 1961:74). The area is drained to the west by tributaries of the Tennessee River. Gregorys Cave contains a number of rimstone pools fed by ceiling drips but does not have a flowing stream.

DISTRIBUTION AND ECOLOGY.—This species is known only from a drip pool in its type-locality, where it appears to be extremely rare.

REMARKS.—Four trips to Gregorys Cave by biologists over the last 33 years have resulted in the collection of 127 specimens of *S. fecundus* (new species described below) and only three of *S. sparsus*. The latter species was collected once by Hubricht in 1939, and subsequent visits to the cave have resulted only in the collection of *S. fecundus*. Of the three specimens in the type-series, only the two males appeared to be mature.

ETYMOLOGY.—The epithet *sparsus* is from Latin, meaning "few," "rare," or "scattered."

Stygobromus barryi, new species

FIGURES 46, 47

MATERIAL EXAMINED.—TENNESSEE. Unicoi Co.: Blankenship Cave, holotype ♂ partly on slide mounts (USNM 168794) and 2 ♀ paratypes (JRH), L. M. and B. L. Ferguson, 8 Jul 1972.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished from *S. sparsus,* with which it is apparently closed allied, by the presence of a distinct peduncular process on uropod 1 of the male and a tiny ramus on uropod 3 (of mature male). Largest male, 5.5 mm; largest females (immature), 3.0 mm.

MALE.—Antenna 1, 45–50 percent length of body, 40–45 percent longer than antenna 2; primary flagellum with 15 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal; spine row with 5 spines; segment 2 of palp with row of long setae on inner margin, segment 3 with 1 long seta on outer margin, 1 long seta and row of short setae on inner margin, and 4 or 5 long setae apically. Maxilla 1: inner plate with 9 apical, plumose setae; palp with 2 slender spines and 4 stiff setae apically. Maxilla 2, inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 2 plumose spines and 1 naked seta apically, and 1 or 2 plumose spines (or coarse setae?) and 1 naked seta subapically; outer plate with naked setae on inner margin and apex and sometimes 1 very lightly plumose seta on apex. Inner lobes of lower lip small.

Propod of gnathopod 1 a little smaller than 2nd propod; palm with double row of 9 spine teeth; defining angle with 3 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 3 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 rather short. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm slightly convex, armed with double row of 12 spine teeth; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; posterior margin with 2 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 rather short. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 4 setae each. Coxal plate of pereopod 4 as broad as long, reaching about 45 percent length of basis, margin with 6 setae. Pereopod 6 a little longer than pereopod 7, 50–55 percent length of body, about 30 percent longer than pereopod 5. Bases of pereopods 6 and 7 narrowing somewhat distally, distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 5–7, 30–35 percent length of corresponding propods. Coxal gill absent from pereopod 7. Median and pleonite sternal gills absent; 2 pairs rather long, simple lateral sternal gills on pereonites 6 and 7.

Pleonal plates: posterior margins convex, with 1 seta each; posterior corners of plates 1 and 3 indistinct, bluntly rounded, that of plate 2 small and distinct; ventral margins of plates 2 and 3 with 3 spines each. Uronites partly fused. Uropod 1: inner ramus longer than outer ramus, about 65 percent length of peduncle, armed with 10 spines; outer ramus with 10 spines; peduncle with 13 spines; peduncular process about 30 percent length of outer ramus, tapering distally, apex weakly serrate. Uropod 2: inner ramus longer than outer ramus, slightly shorter than peduncle, armed with 11 spines; outer ramus with 9 spines; peduncle with 6 or 7 spines. Uropod 3: ramus tiny, only about $\frac{1}{12}$ length of peduncle, armed with 1 apical spine. Telson about as broad as long; apical margin incised about 25 percent the distance to base, armed with 16–18 spines.

FEMALE.—Two specimens in collection immature but differing from male as follows: Antennae, gnathopods, pereopods, and telson having fewer setae and spines overall. Three long, median sternal gills on pereonites 2–4. Ramus absent from uropod 3. Brood plates small and narrow, not setose.

TYPE-LOCALITY.—Blankenship Cave, located 3.2 km northeast of Erwin in Unicoi Co., Tennessee, is a small cave developed in Lower Cambrian dolomite of the Shady or Rome formation. The cave is essentially dry except for a stream trickle in the rear (Barr, 1961:445).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected from under rocks in a stream trickle with a clay substrate. Blankenship Cave lies approximately 145 km northeast of Gregorys Cave (type-locality of *S. sparsus)* and is in the Nolichucky River drainage (upper Tennessee River basin).

REMARKS.—Of the three specimens in the type-series, only a single male was mature and was utilized as the basis of the above description.

ETYMOLOGY.—It is a pleasure to name this species in honor of Barry L. Ferguson, who assisted with the collection of the type-material.

FIGURE 46.—*Stygobromus barryi*, new species, male holotype (5.5 mm), Blankenship Cave, Tennessee: *a*, left mandible; *b*, lower lip; *c*, uropod 3; *d*, inner and outer plates of maxilliped (greatly enlarged); *e*, telson; *f*, lateral sternal gill; *g*, pereopod 6; *h*, *i*, gnathopods 1, 2 (setae of gnathopod 1 enlarged); *j*, *k*, uropods 1, 2 (peduncular process of uropod 1 enlarged).

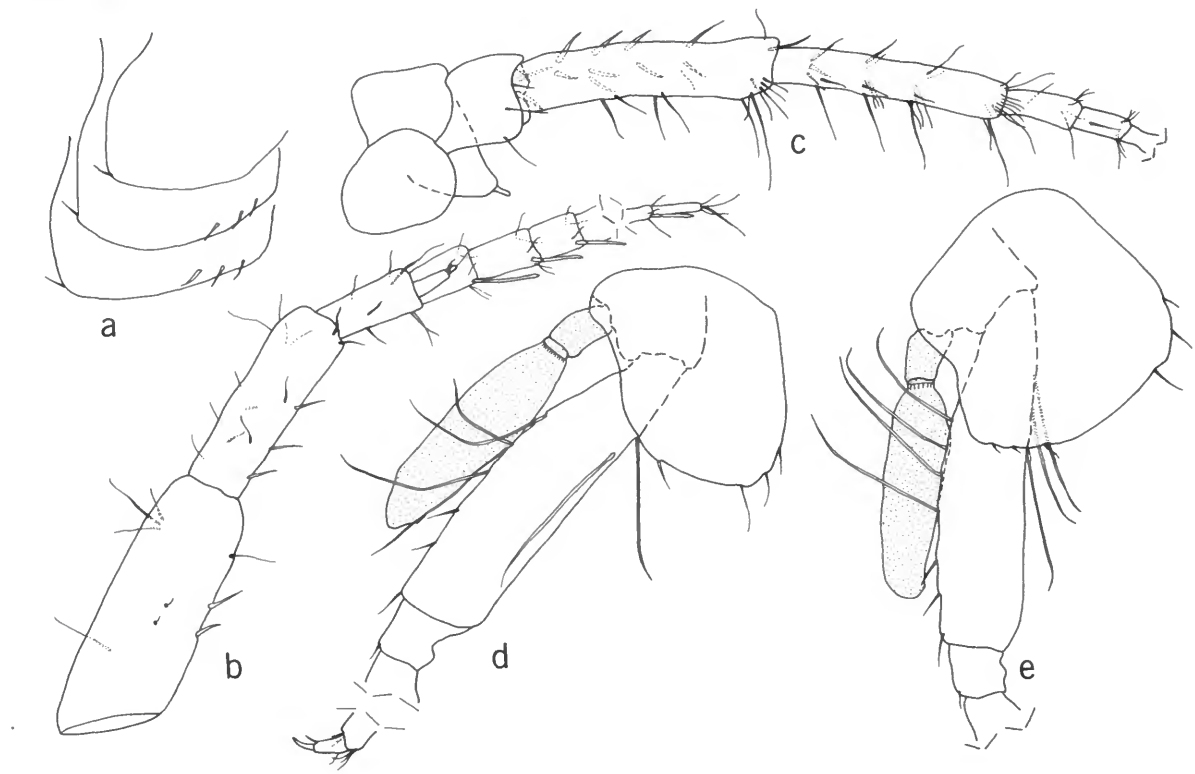

FIGURE 47.—*Stygobromus barryi*, new species, male holotype (5.5 mm), Blankenship Cave, Tennessee: *a*, pleonal plates; *b*, *c*, antennae 1, 2; *d*, *e*, pereopods 3, 4 (in part).

Stygobromus carolinensis, new species

FIGURES 48, 49

MATERIAL EXAMINED.—NORTH CAROLINA. Yancey Co.: seeps on W side of state route 128, 2.4 km N of Blue Ridge Parkway, holotype ♀ (USNM 168803), 17 ♀ and 3 ♂ paratypes (USNM), 34 ♀ and 5 ♂ paratypes (JRH), L. Hubricht, 15 Sep 1971.

DIAGNOSIS.—A relatively small to medium-sized groundwater species distinguished from other members of the *sparsus* subgroup by the absence of sternal gills. Further distinguished from *S. sparsus* by the presence of a tiny ramus on uropod 3. Largest male, 4.3 mm; largest female, 5.5 mm.

FEMALE.—Antenna 1, 40–45 percent length of body, 40–45 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2, flagellum with 4–6 segments. Mandibles subequal; spine row with 4 or 5 spines; segment 2 of palp with about 5 setae of unequal length on inner margin, segment 3 with 1 long seta on outer margin, 1 long seta and row of short setae on inner margin, and 3 long setae apically. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 2 slender spines and 3 stiff setae apically. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 2 baldelike spines, 1 plumose spine and 2 naked setae apically; outer plate with naked setae on inner margin and apex and 1 lightly plumose seta on apex. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 slightly smaller than 2nd propod; palm armed with double row of 6 or 7 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 3 setae; medial setae singly inserted. Dactyl nail of gnathopod 1 moderately long. Coxal plate of gnathopod 1 about as broad as long, margin with 2 setae. Gnathopod propod 2: palm armed with

FIGURE 48.—*Stygobromus carolinensis,* new species. Female paratype (5.0 mm), seeps, Yancey Co., North Carolina: *a,* left mandible; *b,* dentate part of right mandible; *c,* inner and outer plates of maxilliped (greatly enlarged); *d, e,* gnathopods 1, 2; *f,* pleonal plates. Male paratype (4.3 mm), seeps, Yancey County: *g,* uropod 3; *h,* uropod 1 (peduncular process enlarged).

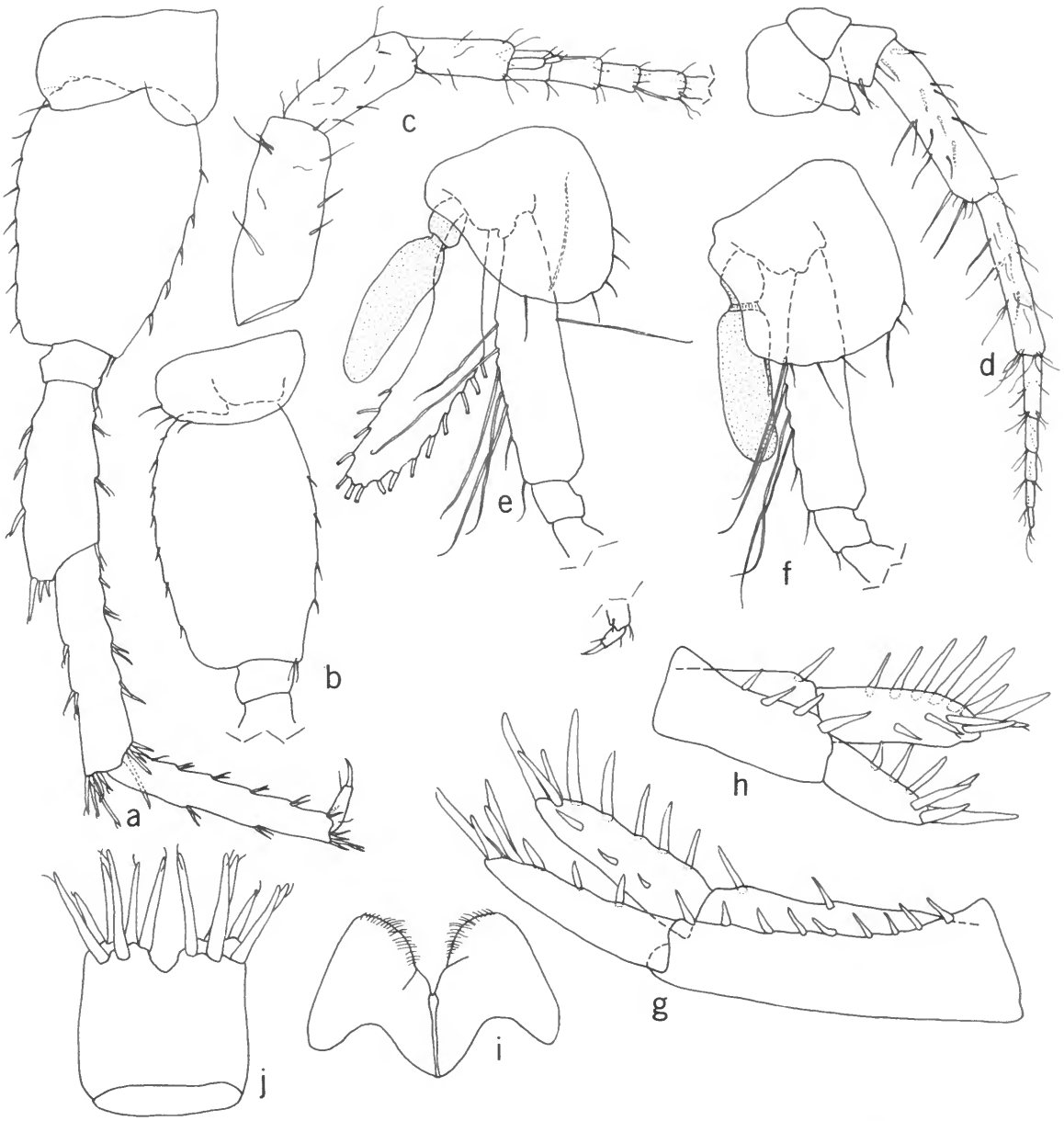

FIGURE 49.—*Stygobromus carolinensis*, new species, female paratype (5.0 mm), seeps, Yancey Co., North Carolina: *a*, pereopod 6; *b*, pereopod 7 (in part); *c*, *d*, antennae 1, 2; *e*, *f*, pereopods 3, 4; *g*, *h*, uropods 1, 2; *i*, lower lip; *j*, telson.

double row of 6 or 7 spine teeth; defining angle with 1 long spine tooth on outside, 3 shorter ones on inside; posterior margin with 3 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Segment 5 of gnathopod 2 without rastellate setae. Coxal plate of gnathopod 2 about as broad as long, margin with 3 setae. Coxal plate of pereopod 3 a little longer than broad, margin with 5 setae. Coxal plate of pereopod 4 a little longer than broad, reaching about 45 percent length of basis, margin with 7 setae. Pereopod 6 a little longer than pereopod 7, 45 percent length of body, about 20 percent longer than pereopod 5. Bases of pereopod 6 and 7 narrowing somewhat distally, distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 5–7, 32–37 percent length of corresponding propods. Coxal gill absent from pereopod 7. Sternal gills absent. Brood plates relatively narrow but somewhat expanded distally.

Pleonal plates: posterior margins of plates 1 and 3 convex, that of plate 2 nearly straight, margins with 1 seta each; posterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 55 percent length of peduncle, armed with 11 spines; outer ramus with 7 spines; peduncle with 11–13 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 12 spines; outer ramus with 6 or 7 spines; peduncle with 4 or 5 spines. Uropod 3: ramus tiny, only about $\frac{1}{10}$ length of peduncle, with 1 apical spine. Telson about as broad as long; apical margin incised about 25 percent the distance to base, armed with 12 spines.

MALE.—Differing only slightly from female as follows: Gnathopods with few less setae and spines. Uropod 1: inner ramus with 10 spines; peduncle with 8 spines; peduncular process similar that described for *S. barryi*. Uropod 2: inner ramus with 10 spines; peduncle with 3 spines. Telson with 12 to 16 apical spines.

TYPE-LOCALITY.—The type-series was obtained from groundwater seeps on the west side of North Carolina Route 128, 2.4 km north of the Blue Ridge Parkway in Mt. Mitchell State Park (Yancey Co., North Carolina). This locality, approximately 2.4 km southwest of the summit of Mt. Mitchell, is underlain by metamorphic rocks of Precambrian age and is drained to the north and west by tributaries of the Nolichucky River (upper Tennessee River drainage basin).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality. Its range is situated approximately 26 airline miles (42 km) south of the range of *S. barryi* and in the same drainage basin. Of the 52 females in the type-series, 11 had setose brood plates and ranged in length from 4.0 to 5.0 mm.

ETYMOLOGY.—The specific name refers to the occurrence of this species in the state of North Carolina.

The *grandis* Subgroup

DIAGNOSIS.—Adults large (ca. 12.0–19.0 mm). Gnathopod propods proportionately larger than in other species of the *mackini* group. First gnathopod propod subtriangular, slightly larger than 2nd propod; segment 5 without rastellate setae. Dactyl nails of gnathopods reduced. Posterior margins of pleonal plates with 1 seta each. Telson incised 65 percent the distance to base.

Stygobromus grandis, new species

FIGURES 50, 51

Stygobromus sp.—Holsinger, 1969a:31–32.—Holsinger and Peck, 1971:30.

MATERIAL EXAMINED.—GEORGIA. Chatooga Co.: Parker Cave, holotype ♀ (USNM 168824), 1 ♀ and 1 ♂ paratype (JRH), S. B. Peck and A. Fiske, 20 Jun 1967; 2 ♀ paratypes (JRH), J. R. Holsinger, S. B. Peck, R. A. Baroody and A. Fiske, 12 Jun 1967.

DIAGNOSIS.—A large, rather unusual cavernicolous species distinguished from other members of the *mackini* group by the characters given for the *grandis* subgroup. Largest male, 12.0 mm; largest females, 19.0 mm.

FEMALE.—Antenna 1, 50 percent length of body, 40 percent longer than antenna 2; primary flagellum with 26–30 segments. Antenna 2, flagellum with 8–10 segments. Mandibles subequal; spine row with 7 spines; segment 2 of palp with row of setae of unequal length on inner margin, segment 3 with 2 long setae on outer margin, row of rather short setae (of unequal length) on inner margin, and 6 long setae apically. Maxilla 1: inner plate with 10 apical, plumose setae; palp with about 12 stiff setae apically

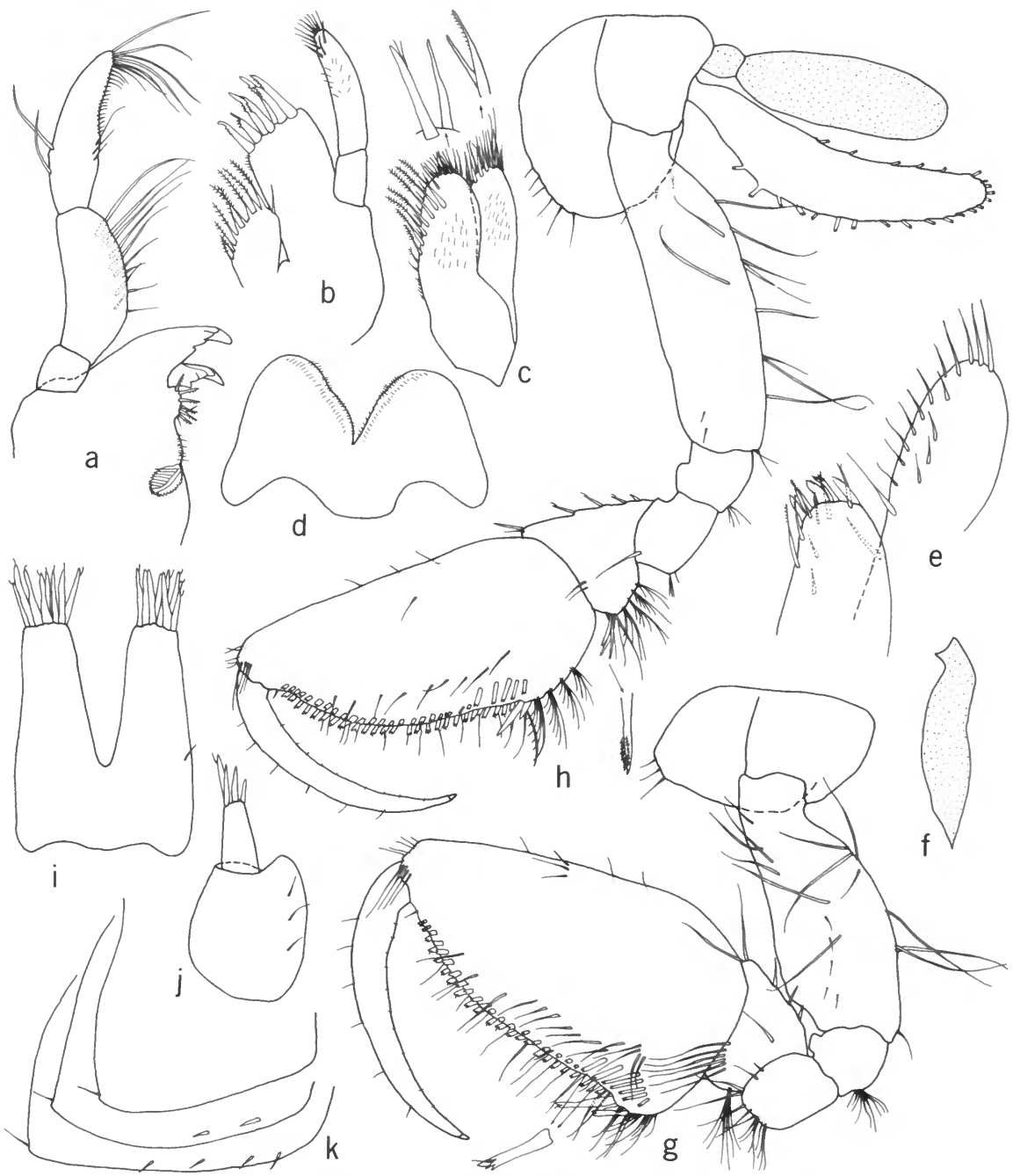

FIGURE 50.—*Stygobromus grandis*, new species, female paratype (18.0 mm), Parker Cave, Georgia: *a*, left mandible; *b*, *c*, maxillae 1, 2 (apical setae of maxilla 2 enlarged); *d*, lower lip; *e*, inner and outer plates of maxilliped (greatly enlarged); *f*, lateral sternal gill; *g*, *h*, gnathopods 1, 2 (trifid spines of gnathopod 1 enlarged; rastellate seta of gnathopod 2 enlarged); *i*, telson, *j*, uropod 3; *k*, pleonal plates.

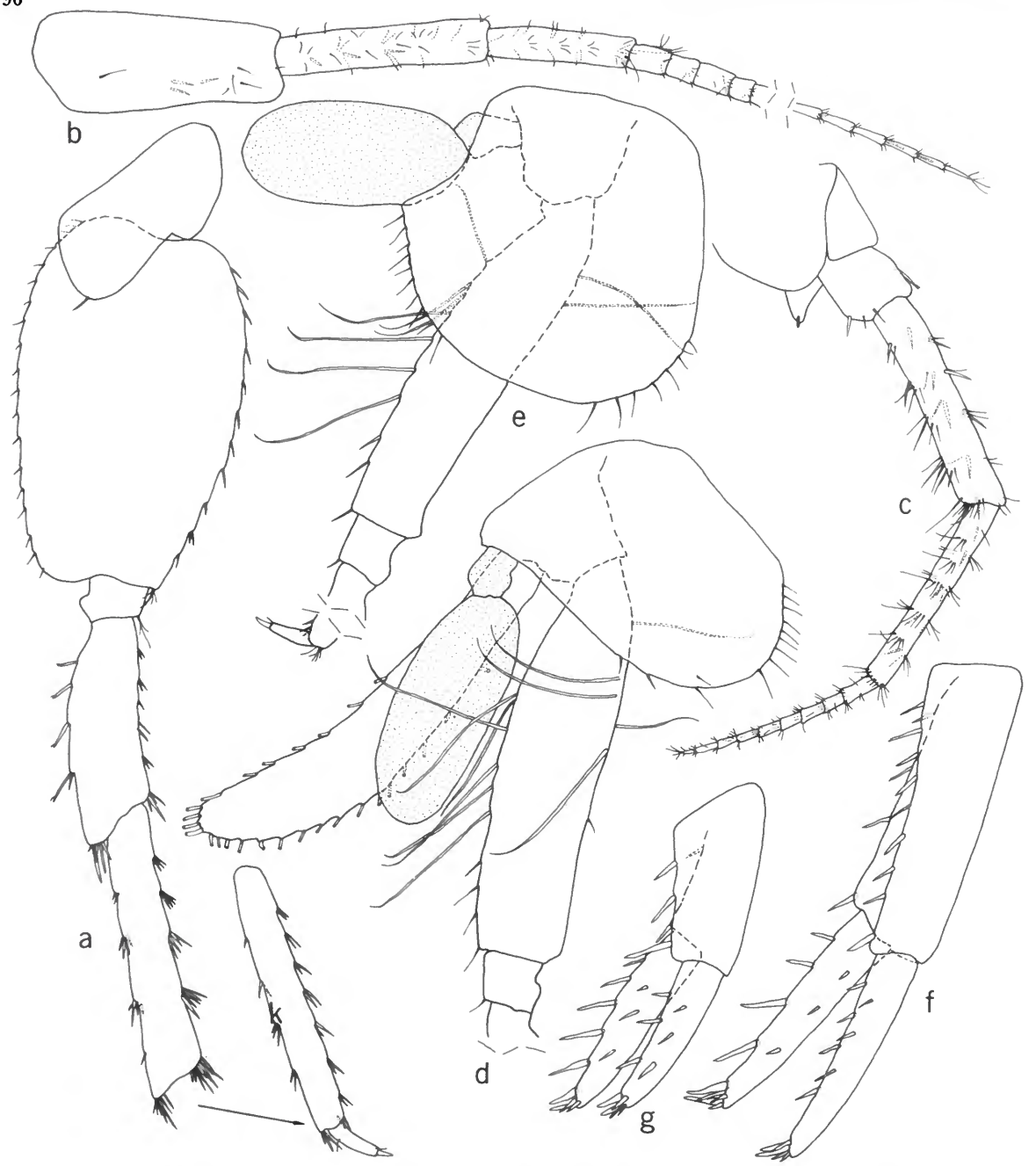

FIGURE 51.—*Stygobromus grandis*, new species, female paratype (18.0 mm), Parker Cave, Georgia: *a*, pereopod 6 (arrow indicates continuation of appendage); *b*, *c*, antennae 1, 2; *d*, *e*, pereopods 3, 4 (in part); *f*, *g*, uropods 1, 2.

and subapically. Maxilla 2, inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 4 or 5 bladelike spines, 2 plumose spines and 2 or 3 naked setae apically, and 2 plumose spines (or coarse setae?) on inner margin distally; outer plate with naked setae on inner margin and apex. Inner lobes of lower lip vestigial.

Propod of gnathopod 1 a little larger than 2nd propod; palm long, oblique, slightly convex distally, armed with double row of about 23 spine teeth (a few spines on inside near defining angle sometimes trifid and longer than remainder); defining angle with 2 long and 1 short spine teeth on outside, 4 slender spine teeth on inside; posterior margin with cluster of setae on distal 1/3 near defining angle; inferior medial setae singly inserted, superior medial setae reduced to about 2. Dactyl nail of gnathopod 1 very short. Coxal plate of gnathopod 1 proportionately small in comparison with size of propod, longer than broad, margin with 3 setae. Gnathopod propod 2: palm long, oblique, slightly convex distally, armed with double row of 26 or 27 spine teeth, about 5 on inside near defining angle being longer than remainder; defining angle with 1 long and 1 short spine tooth on outside, none on inside; posterior margin with 4 sets setae; inferior medial setae singly inserted, superior medial setae reduced to 1. Dactyl nail of gnathopod 2 very short. Coxal plate of gnathopod 2 proportionately small in comparison with size of propod, longer than broad, margin with 7 setae and 2 spines. Coxal plate of pereopod 3 longer than broad, margin with 10 setae and 2 spines. Coxal plate of pereopod 4 broad and relatively deep, about as broad as long, reaching a little more than 50 percent length of basis, margin with 17 setae. Pereopod 6 a little longer than pereopod 7, 50 percent length of body, 25–30 percent longer than pereopod 5. Bases of pereopods 5–7 with convex posterior margins and broadly rounded distoposterior lobes. Dactyls of pereopods 6 and 7 relatively short, 26–27 percent length of corresponding propods; dactyl of pereopod 5 proportionately longer, about 38 percent length of corresponding propod. Coxal gill present on pereopod 7. Median and pleonite sternal gills absent; 2 pairs rather long, simple lateral sternal gills on pereonites 6 and 7. Brood plates relatively narrow but somewhat expanded distally.

Pleonal plates: posterior margins of plates 1 and 3 slightly convex, that of plate 2 nearly straight, margins with 1 seta each; posterior corners small, distinct, bluntly rounded; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 75 percent length of peduncle, armed with 12 spines; outer ramus with 12 spines; peduncle with 13 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 12 spines; outer ramus with 11 spines; peduncle with 5 spines. Uropod 3: ramus comparatively long, 45–50 percent length of peduncle, armed with 3 or 4 apical spines; peduncle with 3 stiff setae or spinules laterally. Telson longer than broad; apical margin incised 65 percent the distance to base, armed with 14–18 spines.

MALE.—Differing from female as follows: Antenna 1, 60 percent length of body. Antennae with few less flagellar segments. Propod of gnathopod 1 with few less spine teeth on palm. Uropods 1 and 2 with few less spines on rami: peduncular process of uropod 1 absent.

TYPE-LOCALITY.—Parker Cave, located approximately 17.7 km southeast of Lafayette in Chatooga Co., Georgia, is a small cave developed in the Fort Payne limestone of Mississippian age. The cave is located in the Appalachian Valley and in the Coosa River drainage.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected on two occasions from a relatively deep, mud-bottom pool fed by groundwater seepage. On a visit to the cave on 12 June 1967, two females were obtained from this pool which, at that time, was about 1 meter deep. On a return visit eight days later three more specimens (two females and one male) were found in the same pool which, in the interim, had receded to about 0.3 meter in depth. Amphipods presumably gain access to this pool by migration through fissures saturated with groundwater. Of the four females in the type-series, only one 18.0 mm specimen had setose brood plates.

ETYMOLOGY.—The epithet *grandis* is from Latin, meaning "large," "great," or "magnificent."

The *cumberlandus* Group

DIAGNOSIS.—Adults relatively small. Mature female larger than mature male. Inner lobes of lower lip small to vestigial. Propod of gnathopod 1 smaller

than 2nd propod; palm only about ½ length of propod; defining angle with several long spine teeth on outside, some of which may be serrate on distal half; posterior margin subequal in length to palm, with row of mostly singly inserted setae. Segment 5 of gnathopod 1 usually with rastellate setae. Propod of gnathopod 2: palm rather long and oblique; posterior margin rather short, with 2–4 sets setae. Segment 5 of gnathopod 2 without rastellate setae. Pereopod 6 a little longer than pereopod 7. Pereopod 7 without coxal gill. Lateral sternal gills simple. Pleonal plates: posterior margins with 1 to several setae each; posterior corners small to indistinct. Uronites free. Ramus of uropod 3 with 2 or 3 apical spines. Telson subquadrate, apical margin with small notch.

REMARKS.—As defined at present, the *cumberlandus* group is composed of two rather closely allied species, which occupy caves and groundwater habitats in west-central and southwestern Virginia. One rare species is known from a single cave in the headwarters of the James River in Craig County, and the other is recorded from three caves and one well in the upper Tennessee River basin in Lee, Scott, and Wise counties. *Stygobromus vitreus* (Shoemaker, 1942; Holsinger, 1972) and several closely allied species from the Interior Low Plateau region of central Kentucky, central Tennessee, and northern Alabama are apparently closely related to the two species from the Virginia Appalachians and will probably be assigned to the *cumberlandus* group after further study.

Key to the Species of the *cumberlandus* Group

(based on mature and submature females)

Posterior margins of pleonal plates with 1 seta each; ramus of uropod 3 with 3 apical spines; apical margin of telson with 10–12 spines ..... ***S. cumberlandus,*** new species

Posterior margins of pleonal plates with 3 or 4 setae each; ramus of uropod 3 with 2 apical spines; apical margin of telson with 8 spines ..... ***S. interitus,*** new species

Stygobromus cumberlandus, new species

FIGURES 52, 53

Stygobromus spp. I & J.—Holsinger, 1969a:31.

MATERIAL EXAMINED.—VIRGINIA. Wise Co.: Wildcat Saltpetre Cave, holotype ♀ (USNM 168807), 2 ♀ and 1 ♂ paratypes (USNM), 5 ♀ and 2 ♂ paratypes (JRH), J. R. Holsinger, G. W. Dickson, and T. C. Kane, 27 Nov 1975; Lee Co.: Baileys Cave, 1 ♀ paratype (JRH), J. R. Holsinger, R. A. Baroody, and P. L. Broughton, 29 Nov 1969; Cliff Cave, 1 ♀, 1 ♂ paratypes (JRH), R. M. Norton, D. C. Finley, and R. Schultetus, 24 Nov 1966, and 1 ♀ paratype (JRH), J. R. Holsinger and D. C. Culver, 29 Nov 1974; Scott Co.: hand-dug well 1 km ENE of Duffield, 1 ♀ paratype (JRH), J. R. Holsinger and S. O. Pinkerton, 8 Apr 1967.

DIAGNOSIS.—A relatively small cavernicolous and groundwater species distinguished generally by the characters diagnostic for the *cumberlandus* group and specifically by the small lobes of lower lip, posterior margins of pleonal plates which have 1 seta each, and ramus of uropod 3 which has 3 apical spines. Largest male, 3.3 mm; largest female, 4.5 mm.

FEMALE.—Antenna 1, 40–50 percent length of body, 30–45 percent longer than antenna 2; primary flagellum with 10–12 segments. Antenna 2, flagellum with 4 or 5 segments. Mandibles subequal; spine row with 4 or 5 spines; segment 2 of palp with several long setae on distal half of inner margin, segment 3 with 1 long seta on outer margin, row of moderately long setae on inner margin, and 4 long setae on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 5 stiff setae on apex. Maxilla 2, inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine and 1 naked seta apically, 1 naked seta and 2 plumose spines (or coarse setae?) subapically; outer plate with naked setae on inner margin and apex, and 1 plumose seta apically. Inner lobes of lower lip small.

Propod of gnathopod 1 about ⅔ size of 2nd propod; palm slightly convex, armed with double row of 3–5 spine teeth; defining angle with 2 or 3 spine teeth of unequal length on outside (1 or 2 of which are partly serrate), 2 or 3 serrate spine teeth

FIGURE 52.—*Stygobromus cumberlandus*, new species, female paratype (4.1 mm), well at Duffield, Virginia: *a*, left mandible; *b*, dentate part of right mandible; *c*, lower lip; *d*, *e*, maxillae 1, 2; *f*, inner and outer plates of maxilliped (greatly enlarged); *g*, uropod 3; *h*, *i*, antennae 1, 2; *j*, *k*, gnathopods 1, 2 (palm, defining angle, and rastellate seta of gnathopod 1 enlarged); *l*, telson; *m*, pleonal plates; *n*, *o*, uropods 1, 2.

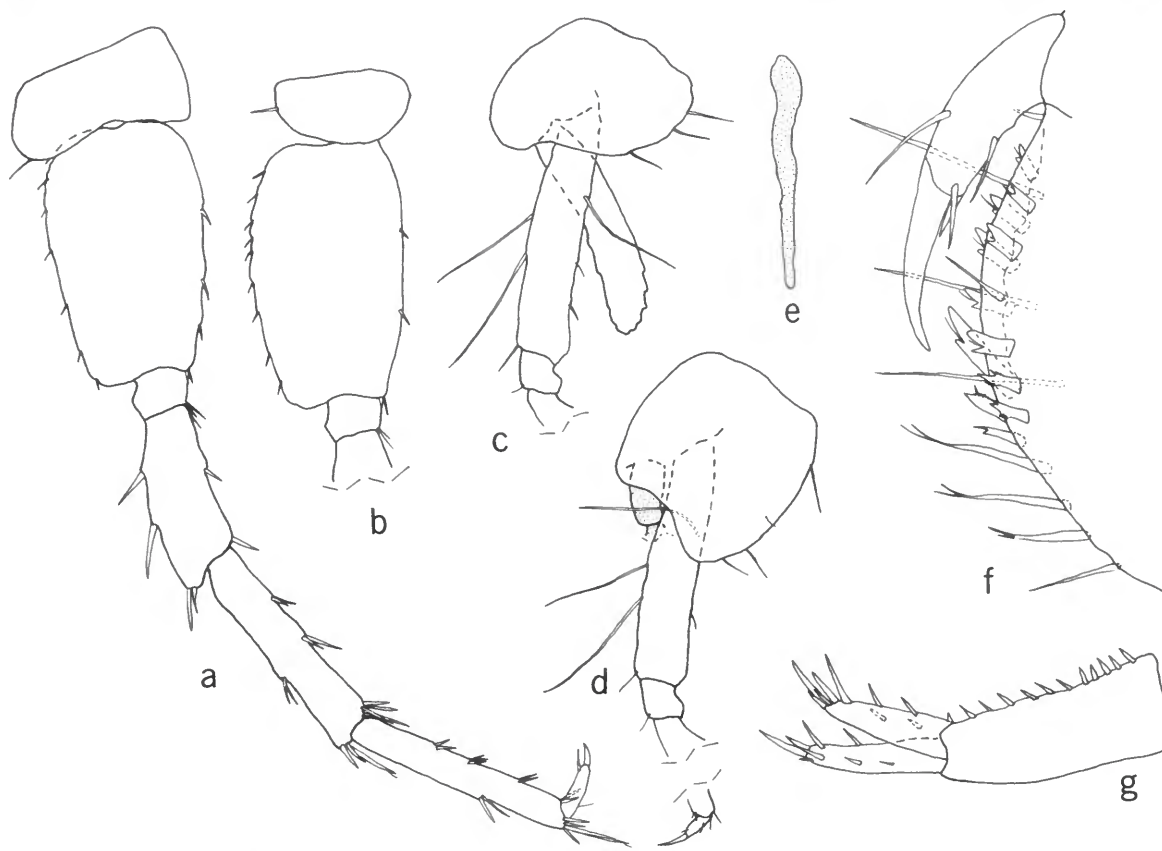

FIGURE 53.—*Stygobromus cumberlandus*, new species. Female paratype (4.1 mm), well at Duffield, Virginia: *a*, pereopod 6; *b*, pereopod 7 (in part); *c*, *d*, pereopods 3, 4 (in part). Female paratype (4.5 mm), Wildcat Saltpetre Cave, Virginia: *e*, lateral sternal gill from pereonite 6. Female paratype (3.1 mm), Cliff Cave, Virginia: *f*, enlarged palm region of gnathopod propod 1 (same scale as Figure 52*j*). Female paratype (3.5 mm), Baileys Cave, Virginia: *g*, uropod 1.

on inside; posterior margin with row of 4–6 mostly singly inserted setae; medial setae few in number, singly inserted. Dactyl nail of gnathopod 1 long. Segment 5 of gnathopod 1 with 1 rastellate seta. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm long, straight, armed with 6–8 spine teeth on outside and 4 or 5 on inside (in unequal double row); defining angle with 2 long spine teeth on outside, shorter one on inside; posterior margin with 2 or 3 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 3 seate each. Coxal plate of pereopod 4 about as broad as long, reaching about 50 percent length of basis, margin with 3 or 4 setae. Pereopod 6 a little longer than pereopod 7, 50–55 percent length of body, 30–35 percent longer than pereopod 5. Bases of pereopods 5–7 relatively narrow, distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 5–7, 30–40 percent length of corresponding propods. Coxal gill absent from pereopod 7. One, 2 or 3 (usually 2 or 3) median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates slightly expanded distally.

Pleonal plates: posterior margins convex, with 1 seta each; posterior corners indistinct; broadly rounded; ventral margin of plate 3 with 1 spine. Uronites free. Uropod 1: inner ramus subequal in

length to outer ramus, 55–60 percent length of peduncle, armed with 7–9 spines; outer ramus with 8 or 9 spines; peduncle with 9–12 spines. Uropod 2: inner ramus a little longer than outer ramus, shorter than peduncle, armed with 8 or 9 spines; outer ramus with 7 or 8 spines; peduncle with 4 or 5 spines. Uropod 3: ramus about 1/3 length of peduncle, with 3 apical spines. Telson about as long as broad; apical margin with small notch, armed with 10–12 spines.

MALE.—Nearly identical to female. Peduncular process of uropod 1 absent.

VARIATION.—Considering the relatively long, disjunct range and presumably extrinsically isolated populations of this species, surprisingly little variation was noted. There was slight variation in the number of median sternal gills: the female from the well at Duffield had only 1 such gill, whereas females from other populations had 2 or 3. The structure of the spine teeth on the palmar margin of gnathopod 1 also varied slightly as indicated in Figures 52*j* and 53*f*.

TYPE-LOCALITY.—Wildcat Saltpetre Cave, located 2.7 km southeast of Big Stone Gap in Wise Co., Virginia, is a medium-sized cave developed in Hancock limestone of Silurian age. The cave contains a small stream and several active drip pools. The type-series was collected from two different pools, one with small rocks and silt on the bottom and the other with a soft mud bottom. The latter pool also contained one specimen of *S. mackini*. The cave stream is inhabited by the amphipod *Crangonyx antennatus*, but *Stygobromus* has not been found there to date.

DISTRIBUTION AND ECOLOGY.—The broken range of this species extends from the Clinch River drainage in western Scott Co., Virginia, north and northwest to the Powell River drainage of southwestern Wise and northeastern Lee counties, Virginia, and then west-southwest to extreme western Lee County. The range crosses the Powell Mountain between Scott and Lee counties, and a major disjunction of approximately 72 km separates the populations in northeastern Lee, southwestern Wise, and western Scott counties from the population in western Lee County.

Stygobromus cumberlandus has been collected from drip pools in three caves in Lee and Wise counties and from a hand-dug well (about 4 meters deep) in Scott County. The latter is excavated in Upper Devonian shale (or overlying mantle), whereas the caves are developed in Paleozoic limestones. The well in Scott County is also inhabited by a large population of the flatworm *Planaria occulta* (Kenk, 1969:556). Females, measuring 3.5–4.5 mm, have been collected only during November.

ETYMOLOGY.—The specific name refers to the occurrence of this species in the vicinity of the eastern margin of the Cumberland Plateau in southwestern Virginia.

Stygobromus interitus, new species

FIGURES 54, 55

Stygobromus sp. H.—Holsinger, 1969a:31.

MATERIAL EXAMINED.—VIRGINIA. Craig Co.: New Castle Murder Hole (cave), holotpye ♀ partly on slide mounts (USNM 168828) and 1 ♀ paratype (USNM), H. W. Jackson, 31 Oct 1943.

DIAGNOSIS.—A relatively small cavernicolous species distinguished from *S. cumberlandus*, with which it is apparently closely allied morphologically, by proximally broader propod of gnathopod 1, lacking serrate spine teeth at defining angle of 1st gnathopod propod, shorter coxal plate of pereopod 4 which reaches only about 40 percent length of basis, more than 1 seta each on posterior margins of pleonal plates, 2 apical spines on ramus of uropod 3, and 8 apical spines on telson. Largest female, 4.2 mm; male unknown.

FEMALE.—Antenna 1, 40 percent length of body, 40–45 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2, flagellum with 4 or 5 segments. Mandibles subequal; spine row with 3 or 4 spines; segment 2 of palp with about 5 setae on inner margin, segment 3 with 1 long seta on outer margin, row of 2 long and several shorter setae on inner margin, and 4 long setae on apex. Maxilla 1: inner plate with 5 apical, plumose setae; palp with 2 slender spines and 4 setae apically. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine and 1 or 2 naked setae apically, 3 plumose spines (or coarse setae?) subapically; outer plate with naked setae on inner margin and apex, and 1 plumose seta apically. Inner lobes of lower lip small.

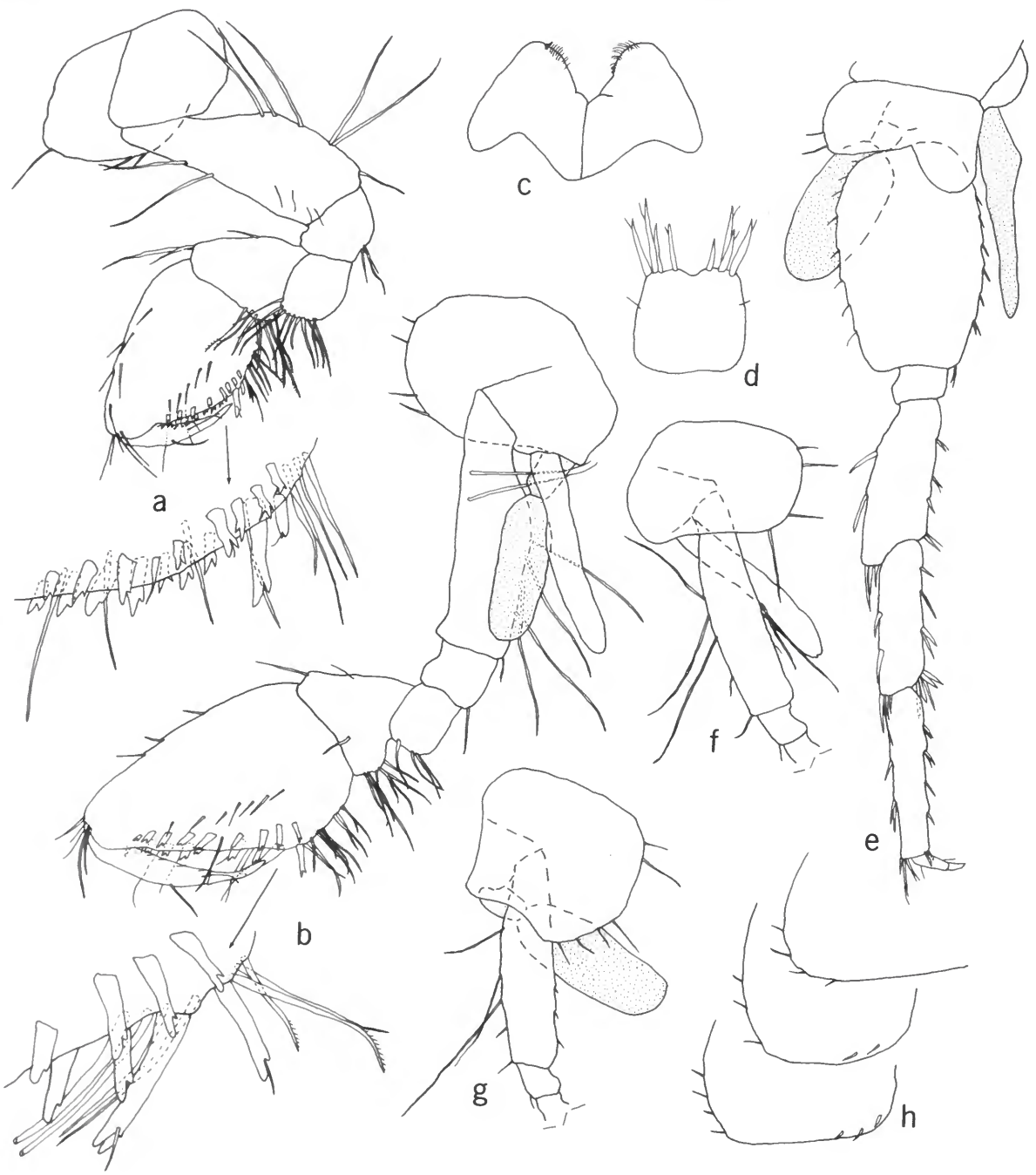

FIGURE 54.—*Stygobromus interitus*, new species, female holotype (4.2 mm), New Castle Murder Hole (cave), Virginia: *a*, *b*, gnathopods 1, 2 (part of palms and defining angles enlarged); *c*, lower lip; *d*, telson; *e*, pereopod 6 with lateral sternal gill; *f*, *g*, pereopods 3, 4 (in part); *h*, pleonal plates.

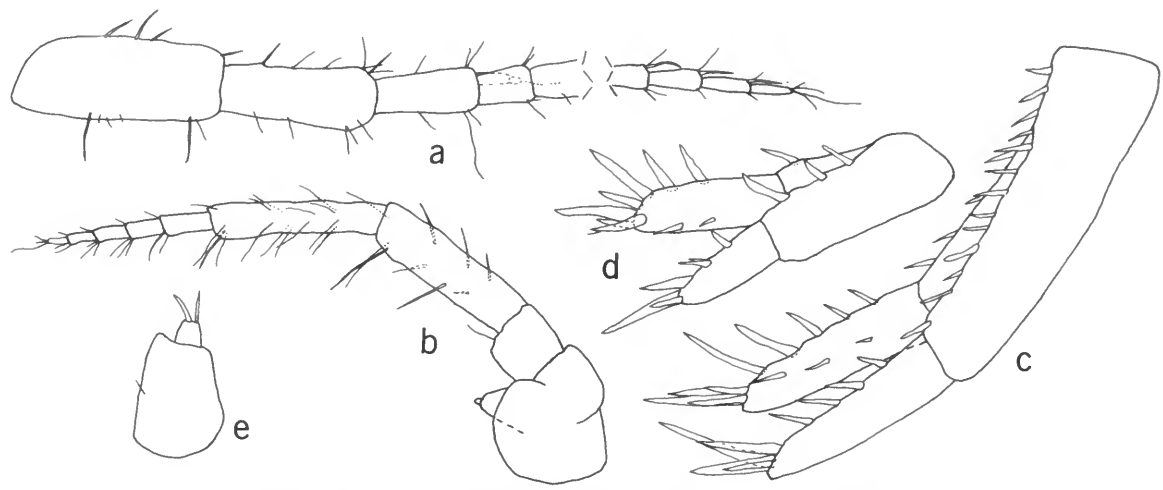

FIGURE 55.—*Stygobromus interitus*, new species, female holotype (4.2 mm), New Castle Murder Hole (cave), Virginia: *a*, *b*, antennae 1, 2; *c*, *d*, *e*, uropods 1, 2, 3.

Propod of gnathopod 1 between ½ and ⅔ the size of 2nd propod; palm slightly convex, armed with partly unequal double row of about 6 or 7 spine teeth; defining angle with 2 spine teeth of unequal length on outside, 2 shorter trifid spine teeth on inside; posterior margin with row of about 8 mostly singly inserted setae; medial setae singly inserted. Dactyl nail of gnathopod 1 moderately long. Segment 5 of gnathopod 1 with 2 small rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm long, nearly straight, armed with double row of 7 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 3 sets setae; inferior medial setae singly inserted, superior medial setae absent. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 4 setae each. Coxal plate of pereopod 4 about as broad as long, reaching about 40 percent length of basis, margin with 6 setae. Pereopod 6 a little longer than pereopod 7, 40–45 percent length of body, 30–35 percent longer than pereopod 5. Bases of pereopods 5–7 nearly straight to slightly convex; distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 6 and 7 about 35 percent length of corresponding propods; that of pereopod 5 about 30 percent length of propod. Coxal gill absent from pereopod 7. Three long median sternal gills on pereonites 2–4; 2 pairs simple, lateral sternal gills on pereonites 6 and 7; 1 pair sternal gills on pleonite 1. Brood plates not fully mature in specimens examined but apparently not much expanded distally.

Pleonal plates: posterior margins convex, with 3 or 4 setae each; posterior corners of plates 1 and 2 indistinct, that of plate 3 small but distinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus equal in length to outer ramus, about 55 percent length of peduncle, armed with 12 spines; outer ramus with 8 spines; peduncle with 17 spines. Uropod 2: inner ramus longer and thicker than outer ramus, shorter than peduncle, armed with 9 spines; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3: ramus about ¼ length of peduncle, with 2 apical spines. Telson about as broad as long; apical margin with slight notch, armed with 8 spines.

TYPE-LOCALITY.—New Castle Murder Hole, located 4.8 km southwest of New Castle in Craig Co., Virginia, is a large, deep cave developed in Middle Ordovician limestone. The cave lies just east of a limestone drainage divide between the New and James river watersheds (see "Distribution and Ecology" under *S. estesi*).

DISTRIBUTION AND ECOLOGY.—This rare species is known only on the basis of two females collected in October 1943. Although the habitat was not

specified on the collection label, presumably, given the make-up of the cave, the specimens were taken from a pool. Neither female had setose brood plates but the holotype appeared to be at least submature.

REMARKS.—The collection containing this species also had one specimen of an undescribed form closely allied with *S. mackini* (see *"Stygobromus* spp." below). James A. Estes visited New Castle Murder Hole in March 1975 with the goal of finding additional specimens of both *S. interitus* and the undescribed form related to *S. mackini.* Neither of these species were found, however, but a third species was discovered (i.e., *S. estesi*) and is being described in this paper.

ETYMOLOGY.—The epithet *interitus* is from Latin, meaning "perished," "lost," or "destroyed."

The *phreaticus* Group

DIAGNOSIS.—Mature female slightly larger than mature male. Inner lobes of lower lip vestigial. Propod of gnathopod 1 distinctly smaller than propod of gnathopod 2; palm ¼ to ⅓ longer than posterior margin; defining angle with several long spine teeth on outside; posterior margin with row of mostly singly inserted setae. Segment 5 of gnathopod 1 with rastellate setae. Gnathopod 2: propod palm long, oblique; posterior margin shorter than palm, with 4 sets setae; segment 5 with or without rastellate setae. Pereopods 6 and 7 subequal in length. Pereopod 7 without coxal gill. Lateral sternal gills simple. Pleonal plates; posterior margins with 3 or 4 setae each; posterior corners small, distinct, typically subacute. Uronites free to partly fused. Uropod 3: ramus vestigial or absent; ramus or peduncle with 1 or 2 apical spines. Telson a little broader than long; apical margin with small, distinct notch.

REMARKS.—The *phreaticus* group is based on a single, rather unique species recorded from two wells in the northern Virginia suburbs of Washington, D. C.

Stygobromus phreaticus, new species

FIGURES 56, 57

MATERIAL EXAMINED.—VIRGINIA. Fairfax Co.: well at Vienna, holotype ♂ (USNM 168839), 11 ♀, 3 ♂, and 2 juv. paratypes (USNM), W. S. Abbott, 27 Dec 1921; Alexandria, well water, 12 ♀ paratypes (USNM), R. M. Lynch, Dec 1948.

DIAGNOSIS.—A unique, medium-sized groundwater species easily distinguished by the characters given for the *phreaticus* group and by heavily spinose uropods 1 and 2. Largest male, 6.8 mm; largest female, 7.0 mm.

MALE.—Antenna 1, 45–50 percent length of body, 40–45 percent longer than antenna 2; primary flagellum with 14–20 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal; spine row with 2 or 3 spines; segment 2 of palp with row of setae of unequal length on inner margin, segment 3 with 2 long setae on outer margin, row of short setae on distal half of inner margin, and 4 long setae on apex. Maxilla 1: inner plate with 7–11 apical, plumose setae; setae; palp with 2 slender spines apically and 4 or 5 stiff setae subapically. Maxilla 2, inner plate with oblique row of 7–10 plumose setae on inner margin. Maxilliped: inner plate with 2 blade-like spines, 2 plumose spines and 1 naked seta apically, 1 naked and 2 plumose spines (or coarse setae?) subapically; outer plate with row of naked setae on inner margin and apex and 1 or 2 plumose setae apically. Inner lobes of lower lip vestigial.

Propod of gnathopod 1 about ⅔ size of 2nd propod; palm weakly convex, armed with double row of 9 or 10 spine teeth; defining angle poorly delimited, with 3 long spine teeth on outside, 4 shorter ones on inside; posterior margin with row of mostly singly inserted setae; medial setae singly inserted. Dactyl nail of gnathopod 1 moderately long. Coxal plate of gnathopod 1 longer than broad, margin with 3 setae. Gnathopod propod 2: palm rather long, nearly straight, armed with double row of 10 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin with 4 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 relatively short. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 5 or 6 setae each. Coxal plate of pereopod 4 a little longer than broad, reaching 45–50 percent length of basis, margin with 9 setae. Pereopods 6 and 7 about equal in length, 40–45 percent length of body, 15–20 percent longer than pereopod 5. Pereopods 5–7; posterior margins of bases weakly convex, distoposterior lobes distinct, bluntly rounded; segments 5 and 6 rather heavily spinose on anterior margins; dactyls, 25–30 percent length of corresponding propods. Coxal gill absent from pereopod 7. Median and pleonite sternal

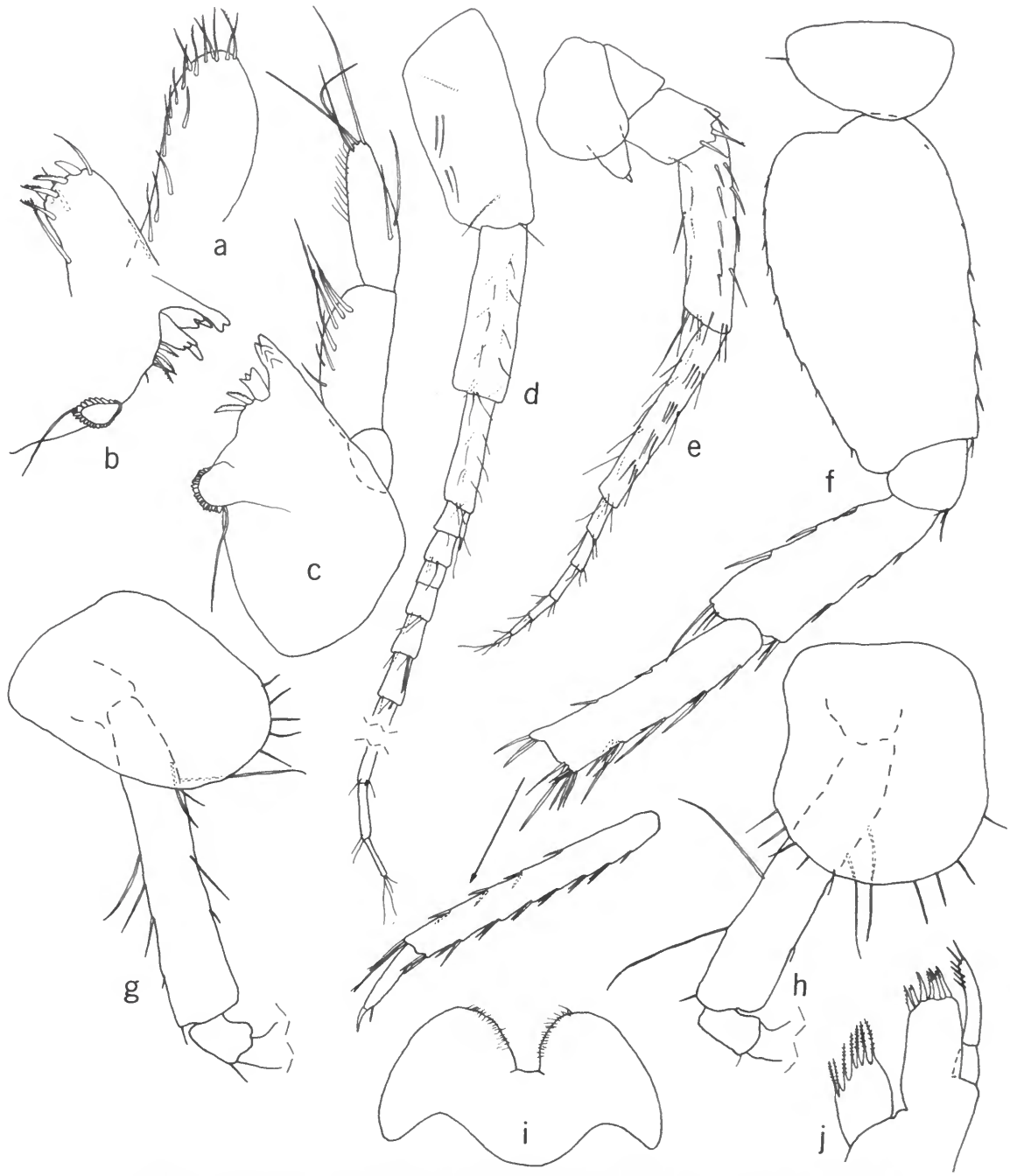

FIGURE 56.—*Stygobromus phreaticus*, new species. Female paratype (6.7 mm), well at Vienna, Virginia: *a*, inner and outer plates of maxilliped (greatly enlarged); *b*, dentate part of left mandible; *c*, *right* mandible; *d*, *e*, antennae 1, 2; *f*, pereopod 7 (arrow indicates continuation of appendage); *g*, *h*, pereopods 3, 4 (in part). Male paratype (6.7 mm), well at Vienna: *i*, lower lip; *j*, maxilla 1.

gills absent; 2 pairs small, simple lateral sternal gills on pereonites 6 and 7.

Pleonal plates: posterior margins weakly convex, with 3 or 4 setae each; posterior corners small, distinct, usually subacute; ventral margin of plate 2 with 1–3 spines, that of plate 3 with 2 or 3 spines. Uronites free to partly fused but discernible suture between 1 and 2. Uropod 1: inner ramus a little longer than outer ramus, about 60 percent length of peduncle, armed with 25 spines; outer ramus

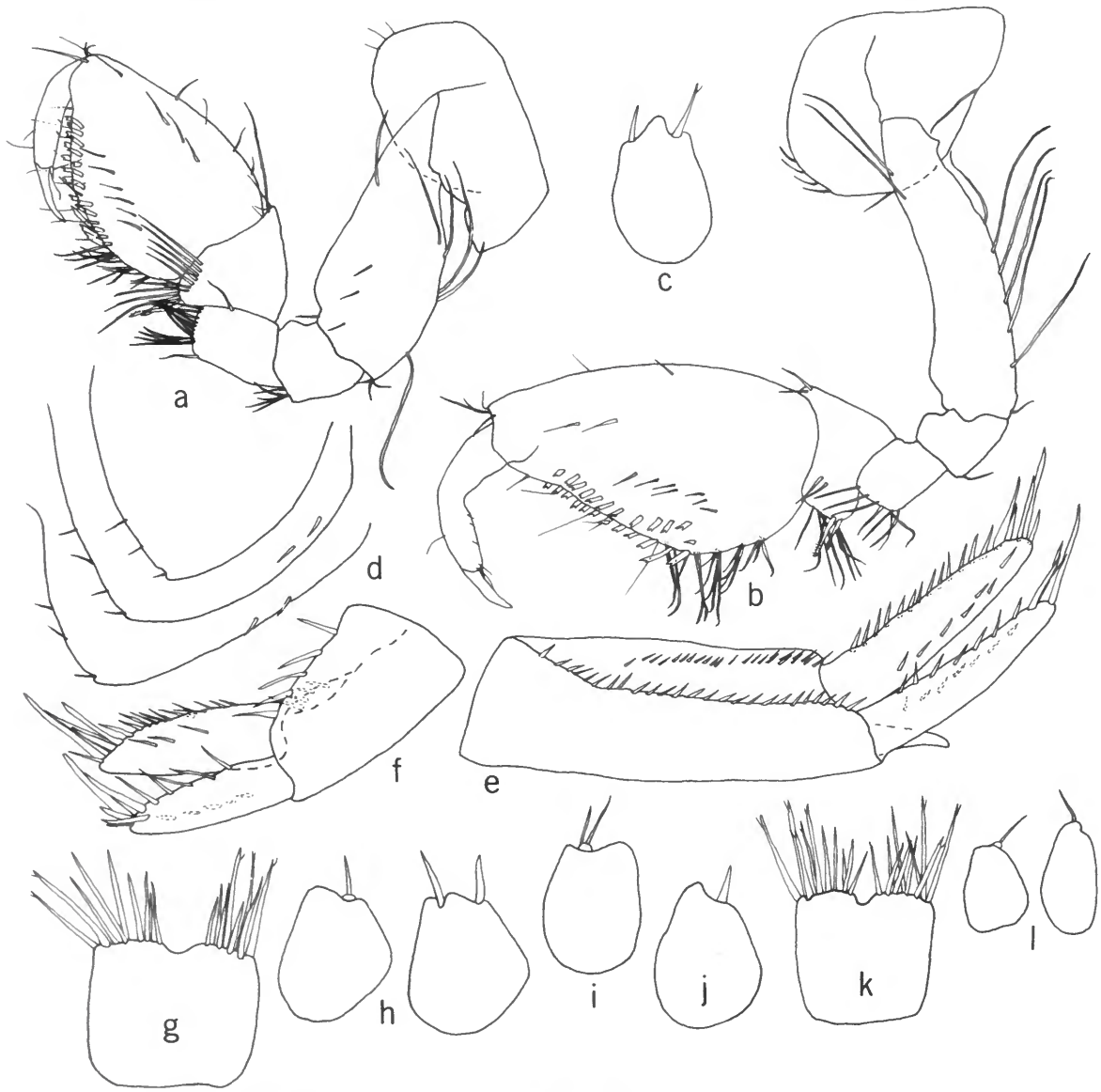

FIGURE 57.—*Stygobromus phreaticus*, new species. Male paratype (6.7 mm), well at Vienna, Virginia: *a*, *b*, gnathopods 1, 2; *c*, uropod 3; *d*, pleonal plates; *e*, *f*, uropods 1, 2. Female paratype (7.0 mm), well at Vienna: *g*, telson; *h*, 3rd uropods. Another female paratype (7.0 mm) from well at Vienna: *i*, uropod 3. Male paratype (6.5 mm), well at Vienna: *j*, uropod 3. Female paratype (5.5 mm), well water at Alexandria, Virginia: *k*, telson; *l*, 3rd uropods.

with 17 spines; peduncle with 49–50 spines; peduncular process rather long, 30–35 percent length of outer ramus, slightly curved distally. Uropod 2: inner ramus longer and thicker than outer ramus, a little shorter than peduncle, armed with 20 spines; outer ramus with 15 spines; peduncle with 9 spines. Uropod 3: ramus variable, sometimes absent, sometimes vestigial, when present armed with 1, or rarely 2, apical spines; peduncle with 1 or 2 apical spines when ramus absent. Telson a little broader than long; apical margin with shallow notch, armed with 14–20 (usually 16–18) spines of unequal length.

FEMALE.—Differing only slightly from male as follows: Propod of gnathopod 2 proportionately a little smaller, with 2 or 3 more spine teeth. Segment 5 of gnathopod 2 without rastellate setae. Brood plates sublinear, only slightly expanded distally.

VARIATION.—The specimens from Alexandria differed slightly from those from Vienna by having 2 more setae on the inner plate of maxilla 1, 1 or 2 more setae on the inner margin of the inner plate of maxilla 2, proportionately smaller 3rd uropod, and 2 to 4 more apical spines on the telson. The most variable structure, however, both within and between populations and even on the same specimen in some cases, was uropod 3. In some specimens from both localities the ramus was vestigal, whereas in others it was absent. In one female from Vienna, one 3rd uropod lacked a ramus but had 2 apical spines on the peduncle, while the other 3rd uropod had a vestigial ramus with one apical spine. The variation of this structure is shown in Figure 57.

TYPE-LOCALITY.—A well at Vienna in Fairfax Co., Virginia. Because of the lack of additional information on the label in the collection, it is impossible to pinpoint the location of this well. In view of the early collection date (Dec. 1921), the well was probably of the shallow, hand-dug variety. In recent years, due to the rapid urbanization around Vienna, many of the old hand-dug wells in the area have been abandoned and either filled in or completely destroyed and it will probably be impossible to ever locate the original site of this collection.

DISTRIBUTION AND ECOLOGY.—This species is known from two collections made 27 years apart from single wells in Vienna and Alexandria, Virginia. The locality given on the label in the collection from Alexandria simply read "well-water, Alexandria, Virginia"; thus this well, like the one at Vienna, cannot be specifically pinpointed. Vienna and Alexandria are situated approximately 16 km apart and both are drained by tributaries of the nearby Potomac River. The city of Alexandria is underlain principally by Coastal Plain sediments of Cretaceous age, in contrast to Vienna and vicinity which is underlain by metamorphosed sedimentary rocks and Greenstone volcanics (lower Paleozoic or Precambrian in age) of the Piedmont Province.

Three females in the December collection from Alexandria had setose brood plates and ranged in length from 4.5 to 5.0 mm. None of the females from Vienna (December collection) had setose brood plates, although some were 6.0–7.0 mm in length.

ETYMOLOGY.—The epithet *phreaticus* is derived from the Greek word *phreatos,* meaning "well" or "reservoir."

The *araeus* Group

DIAGNOSIS.—Adults, 3.5–7.0 mm in length. Mature male larger than mature female; sexual dimorphism pronounced. Inner lobes of lower lip small but well developed. Gnathopod 1: propod palm and posterior margin about equal in length, the latter with row of singly inserted setae; segment 5 with small rastellate setae. Propod of gnathopod 2 sexually dimorphic, about twice size of 1st propod in male, only a little larger in female; palm of male with deep excavation; posterior margin about equal in length to palm, with row of distally split setae. Segment 5 of gnathopod 2 with small rastellate setae. Pereopod 7 a little longer than pereopod 6, without coxal gill. Lateral sternal gills bifurcate. Pleonal plates: posterior margins with 2–5 setae each; posterior corners typically well developed but larger and more acute in female. Uronites fused. Uropod 1 sexually dimorphic; elongate and with long, slender spines on peduncle in male; not elongate and with short spines on peduncle in female. Uropod 3: ramus vestigial or absent; ramus or peduncle with 1 apical spine. Telson sexually dimorphic: that of male about 50 percent longer than broad, apical margin entire and slightly convex; that of female not much longer than broad, apical margin with tiny notch.

REMARKS.—This group is based on a single, highly unusual species which occupies groundwater habitats on the Coastal Plain of southeastern Virginia. The unique character combination of this monotypic group clearly distinguishes it from any other in the genus.

Stygobromus araeus (Holsinger)

Apocrangonyx araeus Holsinger, 1969b:13–18, figs. 5,6 [type-locality: seep, 1.6 km N of Crittenden, Nansemond Co., Virginia]: 1972:54.

Stygobromus araeus (Holsinger).—Karaman, 1974:107.—Holsinger, 1977:261.

MATERIAL EXAMINED.—VIRGINIA. Nansemond Co.: Sören Spring, 9.7 km SSW of Suffolk, 1 ♂, D. Gaultney, 19 Mar 1975; New Kent Co.: seep and small, seep-fed stream in Crump Swamp, 24 km E of Richmond, 1 ♀, 1 ♂, J. R. Holsinger, 19 Mar 1972, and 12 ♀, 9 ♂, J. R. Holsinger, 23 Apr 1972.

DIAGNOSIS.—A medium-sized groundwater species distinguished by the characters of the *araeus* group and by the earlier diagnosis and description of Holsinger (1969b). Largest male, 6.9 mm; largest female, 5.5 mm.

DISTRIBUTION AND ECOLOGY.—*S. araeus* occupies groundwater seeps, small springs and small, seep-fed streams emerging from loosely consolidated and unconsolidated Coastal Plain sediments (upper Miocene and Pliocene–Pleistocene in age) in southeastern Virginia. The range extends from South Norfolk (now a part of the City of Chesapeake) and Nansemond County (now included within the political boundaries of Suffolk) for approximately 97 km north to Mathews County and approximately 118 km northwest to New Kent County. The locality in New Kent County, discovered in 1972, extended the previously known range (Holsinger, 1969b:18, 1972:54) of this species 72.4 km to the west.

Collections of this species have been made only during the winter and spring, and samples from the months of February, March, and April contained ovigerous females ranging in size from 3.4 to 5.5 mm (Holsinger, 1969b:18, for a summary of clutch size from previous samples). In Crump Swamp, New Kent County, this species was collected twice (March and April 1972) from submerged leaf litter and decaying vegetation at the exit of a seep and from a small, intermittent seep-fed stream. This habitat was also occupied by an epigean amphipod, *Crangonyx shoemakeri* (Hubricht and Mackin), and an epigean isopod of the genus *Asellus* (sensu lato). On a third visit to this site in July 1972, the seep and stream were nearly dry and no amphipods were found. The single male from Sören Spring in Nansemond County was taken from substrate debris in a small stream just beyond the spring resurgence which emerges from underground through a pipe (J. F. Matta, Old Dominion University, pers. comm.). The March collection from Crump Swamp contained one ovigerous female (3.5 mm) with eight embryos in the brood pouch; the April collection contained two larviparous females (3.5–4.5 mm), each of which had a few newly hatched young remaining in the brood pouch.

The *pizzinii* Group

REMARKS.—A detailed diagnosis and discussion of the geographic distribution of this group were published previously by Holsinger (1967) and little new data have accumulated since then. Briefly, this group is composed of two rather closely allied species which inhabit a variety of groundwater habitats on the Coastal Plain of southeastern Virginia and eastern North Carolina and in the Piedmont region of northern Virginia, Washington, D.C., central Maryland, and southeastern Pennsylvania. A key to the species was also provided in Holsinger (1967:47). This group is easily distinguished from the *tenuis* group, with which it has some morphological affinity, by the sexually dimorphic characters of the mature male (viz., propod palm of gnathopod 1 with distal excavation, broad 4th segment of pereopods 5 and 6 and basis of pereopod 7 with prominent distoanterior lobe which extends ventrally beyond segment 3).

Stygobromus pizzinii (Shoemaker)

Synpleonia pizzinii Shoemaker, 1938:137–142 [in part] [type-locality: Wetzels Springs, Glover Archbold Parkway, Washington, D. C.].

Stygonectes pizzinii (Shoemaker).—Holsinger, 1967:47–52, fig. 10; 1969a:43.—Culver and Holsinger, 1969:632.—Holsinger, 1972:60–61; 1976:75.

Stygobromus pizzinii (Shoemaker).—Karaman, 1974:117.—Holsinger, 1977:262.

MATERIAL EXAMINED.—PENNSYLVANIA. Lancaster Co.: Refton

Cave, 3 ♀, 3 ♂ (AMNH 9157) and 69 specimens (USNM), L. Hubricht, 19 Aug 1939, and 2 ♀, 1 ♂, A. and B. Norden, 4 Jan 1973; Montgomery Co.: Brooks Evans Creek at Pottstown, 1 ♂, D. C. Stefan, 20 Feb 1973; wells at road site on Schuylkill River, Pottstown, 5 ♀, D. C. Stefan, 20 Feb 1973. WASHINGTON, D. C. Georgetown: Wetzels Spring in Glover Archbold Parkway, 1 ♂ (M. Straskraba coll.), J. R. Holsinger and M. Straskraba, 4 Jul 1967, and 2 ♀ (USNM), T. E. Bowman, 6 Oct 1969.

DIAGNOSIS.—This species is distinguished by the characters given in previous descriptions by Shoemaker (1938:137–139, 1942:27–29) and Holsinger (1967:48–51). Largest males, 18.7 mm; largest females, 15.7 mm.

DISTRIBUTION AND ECOLOGY.—*S. pizzinii* inhabits a number of different kinds of groundwater biotopes, including seeps, small springs, small spring- and seep-fed streams, mines, wells, and caves, and is distributed from Fairfax Co., Virginia, northeastward through central Maryland to Chester and Montgomery counties in southeastern Pennsylvania. The range, covering a linear distance of approximately 201 km, is restricted to the Piedmont and occupies parts of the Potomac, Susquehanna, and Delaware river drainage basins.

REMARKS.—Additional information on the distribution and ecology of this species was given by Holsinger (1967:51–52, 1972:60–61). The recently discovered populations of this species in Montgomery Co., Pennsylvania, extends its previously known range 27.3 km to the north and across the Schuylkill River.

Stygobromus indentatus (Holsinger)

Stygonectes indentatus Holsinger, 1967:52–55, fig. 11 [type-locality: outlet of drain, 4.8 km NW of Suffolk, Nansemond Co., Virginia]; 1969b:26.—Culver and Holsinger, 1969:632.—Holsinger, 1972:61.

Stygobromus indentatus (Holsinger).—Karaman, 1974:113.—Holsinger, 1977:262.

MATERIAL EXAMINED.—NORTH CAROLINA. Nash Co.: shallow well at Bailey, 1 ♀, donated by R. S. Fox, collected 24 Mar 1974. VIRGINIA. Isle of Wight Co.: seep, 3.2 km SE of Bartlett, 1 ♀, L. Hubricht, 2 Apr 1944.

DIAGNOSIS.—This species is distinguished by the diagnosis and description of Holsinger (1967:53–55). Largest males, 9.7 mm; largest females, 8.2 mm.

DISTRIBUTION AND ECOLOGY.—The range of *S. indentatus* extends from Isle of Wight and Nansemond counties in the Tidewater area of southeastern Virginia southwestward to Nash Co., North Carolina, and covers a linear distance of 193 km. A large disjunction, probably due to the lack of collecting, occurs in the range between the Virginia and North Carolina localities. This species is recorded from one seep and two drain outlets in Virginia and a shallow well in North Carolina, all habitats being developed in Coastal Plain sediments of Miocene age. The female from the seep in Isle of Wight County was collected along with 15 specimens of *S. araeus*. Additional information on the ecology of this species was given by Holsinger (1967, 1972).

REMARKS.—The single specimen from Nash County, a female (7.2 mm long) with setose brood plates, was missing the telson (broken off and lost) but otherwise appeared conspecific with *S. indentatus*. The discovery of this species in North Carolina extends its previously known range for 177 km to the southwest and across parts of several drainage basins.

The *tenuis* Group

REMARKS.—A detailed diagnosis, discussion of the geographic distribution, and key to the species of this group were published by Holsinger (1967:55–58). The *tenuis* group is composed of 14 species, of which only three occur in the geographic area covered in this paper. The range of the group, the broadest of any in the genus, extends from central New York and Connecticut southward through Pennsylvania and Maryland to Virginia and West Virginia, and then again from eastern Alabama westward and northwestward across Mississippi, Arkansas, and Missouri to eastern Kansas, and southwestward through Oklahoma to central Texas. Species in this group inhabit a variety of groundwater habitats, including seeps, small springs, small spring- and seep-fed streams, wells and caves, and many are very closely allied morphologically.

Stygobromus tenuis tenuis (Smith)

Crangonyx tenuis Smith, 1874:656–657 [type-locality: wells at Middletown, Middlesex Co., Connecticut].

Stygonectes tenuis tenuis (Smith).—Holsinger, 1967:58–62, fig. 12.—Culver and Holsinger, 1969:632.—Holsinger, 1972:61.

Stygobromus tenuis tenuis (Smith).—Karaman, 1974:119–120.—Holsinger, 1977:262.

MATERIAL EXAMINED.—MARYLAND. Baltimore Co.: spring-fed stream at Carroll Rd. in Phoenix, 2 ♂, A. and B. Norden, 18 Apr 1976.

DIAGNOSIS.—This subspecies is distinguished by the diagnosis and description given earlier by Holsinger (1967:58–62). Largest males, 12.00 mm; largest females, 9.7 mm.

DISTRIBUTION AND ECOLOGY.—A discussion of the distribution and general ecology of *S. t. tenuis* are found in Holsinger (1967, 1972). Briefly, the subspecies occupies shallow groundwater habitats (e.g., wells, seeps, and small springs) and ranges from the New England Province in central Connecticut and southeastern New York south-southwestward to the Coastal Plain and Piedmont of eastern Maryland. A large disjunction in the range occurs between New York and Maryland.

REMARKS.—Prior to its recent discovery in Baltimore Co., Maryland, this subspecies was believed to be confined to areas east of the Chesapeake Bay and the Susquehanna River (see Holsinger, 1967, map on p. 45). The collection of *S. t. tenuis* from the locality in Baltimore County extends its range west of the Susquehanna River and brings it to within about 40 km of the nearest known records of *S. t. potomacus* (discussed below). The fact that this collection consisted of only two immature males leaves open the possibility that it may represent an intergrading population. A larger series from this site, consisting of sexually mature specimens of both sexes, is necessary for clarification.

Stygobromus tenuis potomacus (Holsinger)

Stygonectes tenuis potomacus Holsinger, 1967:62–65, fig. 13 [type-locality: bog in Burleith Woods, Glover Archbold Parkway, Washington, D. C.].—Culver and Poulson, 1971: 74.—Holsinger, 1972:61; 1976:75.

Stygobromus tenuis potomacus (Holsinger).—Karaman, 1974: 120.—Holsinger, 1977:262.

MATERIAL EXAMINED.—MARYLAND. Frederick Co.: spring near water supply ponds, Camp Mar-Lu-Ridge near Jefferson, 4 ♀, 1 ♂ (USNM), T. E. Bowman, 30 May 1967; Howard Co.: seep near Sucker Branch, just NW of Ellicott City, 4 ♀, 3 ♂, A. and B. Norden, 14 Mar 1976; Montgomery Co.: Limekiln Branch, ca. 0.8 km N of Great Falls, 1 ♂, R. Kenk, 7 May 1969. VIRGINIA. Alexandria: seep just W of Hamlet West Apts., 4 ♀, 2 juv., J. R. and C. H. Holsinger, 25 Jun 1972; seep in ravine just E of Beauregard St., 5 ♀, 3 ♂, J. R. Holsinger, 3 May 1973; Fairfax Co.: shallow well just N of Edsall Rd. and just W of Alexandria-Fairfax Co. line, 7 adults, 1 juv., R. Kenk and W. W. Biggers, 17 May 1971; seep in woods near previous locality, 2 ♀, 1 ♂, 1 juv., J. R. Holsinger, 17 Mar 1973; tiny spring or seep, ca. 3.2 km ESE of Fairfax, 1 ♂, J. R. Holsinger, W. W. Biggers, and C. Hybner, 13 Jul 1967; seep in Lake Accotink Pk., 9 ♀, 5 ♂, 1 juv., J. R. Holsinger, 7 Apr 1973; bog near Scott Run, 1.2 km from Leesburg North Pike, 1 juv., A. Pizzini, 19 Mar 1939; seep just E of Scott Run, 36 ♀, 23 ♂, 6 juv. (30 specimens in M. Straskraba coll.), J. R. Holsinger and M. Straskraba, 4 Jul 1967; small spring near Scott Run, 2 ♂, J. R. Holsinger and M. Straskraba, 4 Jul 1967. WASHINGTON, D. C. Rock Creek Park: small spring SE of Park headquarters, 1 ♂, R. Kenk, 30 Mar 1967.

DIAGNOSIS.—This subspecies is distinguished from *S. t. tenuis* by the absence of a coxal gill on pereopod 7 in both sexes and the absence of sternal gills on pleonite 1 of the male. Largest males, 16.5 mm; largest females, 9.5 mm.

DISTRIBUTION AND ECOLOGY.—The range of this subspecies extends from south-central Pennsylvania (Adams-Franklin County area) southward through central Maryland to the vicinity of Richmond, Virginia (see Holsinger, 1967:65, for further details). *Stygobromus t. potomacus* is a common inhabitant of shallow groundwater habitats in the greater metropolitan area of Washington, D.C., where it is frequently found in wet leaf litter in woodland seeps and bogs during wetter periods of the year. Most of these seeps are intermittent and dry up during late summer and early fall. Data on the clutch size in this subspecies, based on material examined prior to the present study, were summarized previously by Holsinger (1967:65). In the recently examined material two ovigerous females were noted: a specimen, 8.0 mm long, in the May 1973 sample from Alexandria contained eight eggs in the brood pouch and a specimen, 6.5 mm long, in the April 1973 sample from Accotink Park (Fairfax County) had six embryos in the pouch. Females, 5.3–9.5 mm in length, with setose brood plates were observed in spring and summer collections and juveniles were also found in collections made during this time of the year.

REMARKS.—Despite the loss of many of its habitats to urbanization, *S. t. potomacus* remains the most common groundwater amphipod in the Piedmont and Coastal Plain of the Middle Atlantic region. Although rarely found with other subterranean amphipods, this subspecies has occasionally been taken syntopically with *S. pizzinii, S. hayi,* and *S. kenki* in Maryland and Washington, D.C. It is also sometimes associated with the epigean (but

groundwater-related) amphipod *Crangonyx shoemakeri* and the semi-epigean isopod *Asellus* (sensu lato) *kenki* Bowman.

In my 1967 paper on *Stygonectes,* I stated (p. 65) that "*S. t. potomacus* occurs southeast of the Susquehanna River and east of the Chesapeake Bay. . . ." This was a typographic error and should read "southwest of the Susquehanna River and west of the Chesapeake Bay. . . ."

Stygobromus allegheniensis (Holsinger)

FIGURE 58

Stygonectes allegheniensis Holsinger, 1967:66–71, fig. 15 [type-locality: spring at Ilion, Herkimer Co., New York]; 1969a: 32–33.—Culver and Holsinger, 1969:632.—Holsinger, 1972: 61–62; 1976:75.

Stygonectes sp. A.—Holsinger, 1969a:32–33 [species A and B inadvertently reversed on distribution map, p. 33].

Stygonectes sp.—Holsinger, Baroody, and Culver, 1976:24.

Stygobromus allegheniensis (Holsinger).—Karaman, 1974:106–107.—Holsinger, 1977:261.

MATERIAL EXAMINED.—MARYLAND. Washington Co.: Round Top mines near Hancock, 1 ♂, D. S. Lee and A. Norden, Jan 1970, and 2 ♀, L. R. Franz, 27 Nov 1971; unnamed tributary of Potomac River at Ernstville, 2 ♀, A. and B. Norden, 26 Mar 1976. NEW YORK. Albany Co.: Ward-Gregory Cave (listed as two separate caves by Holsinger, 1967:66), 3 ♀, S. B. Peck, 9 Oct 1966; Onesquethaw Cave, 28 ♀, 20 ♂, S. B. Peck, 9 Oct 1966; Skull Cave, 2 ♀, 1 juv., D. P. Beiter, 3 Nov 1966; Jefferson Co.: Glen Park Labyrinth Cave, 4 ♀, 7 ♂, 1 juv., S. B. Peck, 15 Oct 1966; Montgomery Co.: Mitchells Cave, 1 ♀, 3 ♂, R. M. Norton, 6 Dec 1969; Orange Co.: Graham Mt Cave, 5 ♀, 1 ♂, S. B. Peck, 11 Nov 1966; Schoharie Co.: Gage Caverns, 2 ♂, S. B. Peck, 2 Oct 1966; McFails Cave, 1 ♂, S. B Peck, 30 Oct 1966, 1 ♂ D. P. Beiter, 12 Nov 1966, and 9 ♀, 1 ♂, R. M. Norton, 21 Oct 1967; Schoharie Caverns, 1 ♀, S. B. Peck, 1 Oct 1966; Sullivan Co.: Surprise Cave, 2 ♀, 3 ♂, S. B. Peck, 11 Nov 1966, and 1 ♂, R. D. O'Leary, Nov 1967. PENNSYLVANIA. Berks Co.: Schofer Cave, 1 ♂, R. M. Norton, 1970; Centre Co.: Millers Cave, 2 ♀, J. A. Stellmack, 4 Sep 1966. WEST VIRGINIA. Hardy Co.: Dyers Cave, 7 ♀, J. R. Holsinger, 29 Aug 1966.

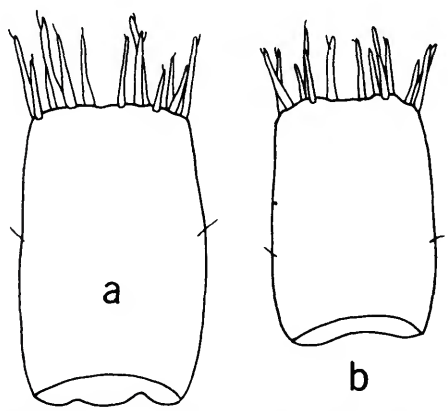

FIGURE 58.—*Stygobromus allegheniensis* (Holsinger). Male (11.0 mm), Round Top mines, Maryland: *a,* telson. Female (9.0 mm), Dyers Cave, West Virginia: *b,* telson. (Both drawn to same scale.)

DIAGNOSIS.—This species, which is closely allied with *S. tenuis,* is distinguished by the diagnosis and description given by Holsinger (1967). Largest males, 13.5 mm; largest females, 13.0 mm.

VARIATION.—Population samples from Round Top mines in Washington Co., Maryland, and Dyers Cave in Hardy Co., West Virginia, both situated on the extreme southern end of the range, differ slightly from specimens elsewhere in the structure of the telson (Figure 58). In both sexes the apical margin has a very tiny notch or break in the spine row, and in the male the outermost spines are not deflected laterally and lack inner distal tines (cf., fig. 15*m,w,* in Holsinger, 1967). Considering the variation observed in the telson of other species in the genus, the differences in the Maryland and West Virginia specimens are minor and do not appear to warrant recognition of these populations as a separate taxon.

As pointed out previously (Holsinger, 1967:69), I have been unable to find significant morphological variation in this species, despite its wide range. Undoubtedly, subtle differences exist among populations throughout the range but the general lack of large samples has so far prevented a quantitative analysis of variation. Whether *S. allegheniensis* is in fact a complex of sibling species, semi-species, or simply subspecies can be answered only by future, detailed study, employing perhaps both multivariate analysis and electrophoresis.

DISTRIBUTION AND ECOLOGY.—The range of this species, one of the broadest of any in the genus, extends from central and eastern New York southward through Pennsylvania to western Maryland and northeastern West Virginia and covers a linear distance of approximately 596 km from north to south. *Stygobromus allegheniensis* occupies a variety of

groundwater habitats, including cave pools and streams, wells, mines, seeps, small springs, and spring- or seep-fed streams, and is found in parts of the Allegheny Plateau, Valley and Ridge, and Piedmont provinces. The species is apparently rather common in caves developed in the glaciated Appalachian Plateau region of New York and, in addition to established localities, there are unconfirmed sight records from Howe Cavern and Bently and Spider caves in Schoharie County. One locality in New York, Glen Park Labyrinth Cave, is actually situated west of the Plateau region in the Eastern Lake Section of the Central Lowland Province. Additional information on distribution can be found in Holsinger (1967:69–71).

The following data, based on recently examined material, supplements the information given earlier on clutch size by Holsinger (1967:70–71). Collections are now available from all months of the year, and ovigerous females have been observed during the period extending from March to November. Fourteen ovigerous and/or larviparous females, of which 10 appeared to have all eggs or embryos intact in the brood pouches, were noted in collections from the months of August to November. The clutch size of these 10 females, ranging in size from 6.5–8.5 mm ($\overline{X}$ = 7.49, SD = 1.46, CV = 0.19) is summarized as follows: N = 10, range = 1–10 eggs or embryos, $\overline{X}$ = 5.0, SD = 3.33, CV = 0.67. Females (5.5–9.0 mm in length) with setose brood plates (but not ovigerous) and juveniles (ca. 1.9 mm in length) were also noted in collections from October and November.

Stygobromus hayi (Hubricht and Mackin)

Synpleonia hayi Hubricht and Mackin, 1940:205, fig. 11 [type-locality: small spring, S end of the National Zoological Park, Washington, D. C.].

Stygonectes hayi (Hubricht and Mackin).—Holsinger, 1967: 71–74, fig. 17; 1972:62; 1976:76.

Stygobromus hayi (Hubricht and Mackin).—Karaman, 1974: 112.—Holsinger, 1977:262.

REMARKS.—This species, which is closely allied with both *S. tenuis* and *S. allegheniensis,* is known only from its type-locality. A diagnosis and redescription are found in Holsinger (1967). I have attempted to locate the type-locality and collect additional specimens of this poorly known species but have so far been unsuccessful.

Species Unassigned to Groups

The seven species treated below have not been assigned to species groups pending further study. Two of them, *S. baroodyi* and *S. stellmacki,* probably have affinities with the *emarginatus* group and its allies but are excluded from this group for reasons given below. *Stygobromus borealis,* from a glaciated area in the Northeast, is unique and may constitute a monotypic group. *Stygobromus biggersi* and *S. stegerorum,* both from caves in the upper Potomac River drainage, are probably related to each other but neither is closely allied with any other species in the Appalachians. On the other hand, *S. fecundus,* from a single cave in eastern Tennessee, is closely allied with several species farther west in the Interior Low Plateau region. Finally, *S. minutus,* a tiny, enigmatic species from a single cave in northwestern Georgia, is possibly related to members of the *ephemerus* group.

Stygobromus stellmacki (Holsinger)

Stygonectes stellmacki Holsinger, 1967:33–36, fig. 6 [type-locality: Millers Cave, near Rockspring, Centre Co., Pennsylvania]; Holsinger, 1969a:32–33; Holsinger, 1972:60; 1976: 76.

Stygobromus stellmacki (Holsinger).—Karaman, 1974:119.—Holsinger, 1977:262.

MATERIAL EXAMINED.—PENNSYLVANIA. Centre Co.: Millers Cave, 2 ♀ topotypes, J. A. Stellmack, 4 Sep 1966.

DIAGNOSIS.—A relatively large cavernicolous species corresponding to the diagnosis and description by Holsinger (1967). Largest male, 14.2 mm; largest female, 16.5 mm.

FEMALE.—Since the original description, which was based on a single male, the following characters have been noted for the female: Antenna 1, 55–62 percent length of body, 50–55 percent longer than antenna 2; primary flagellum with 25–26 segments. Flagellum of antenna 2 with 8–10 segments. Gnathopod 1: propod a little larger than 2nd propod; segment 5 with 2 rastellate setae. Gnathopod 2: propod with 3 or 4 sets setae on posterior margin; segment 5 with 2–5 rastellate setae. Coxal gill on pereopod 7. Three, rather small median sternal gills on pereonites 2–4; 2 pairs bifurcate lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Ramus of uropod 3 with 4 apical spines.

Apical margin of telson with or without small notch, armed with 16 spines.

DISTRIBUTION AND ECOLOGY.—This rare species is known only from its type-locality, where three specimens (one male and two females) have been collected from a wide, shallow mud-bottom pool on an upper level of the cave. A small stream in the lower level is inhabited by *S. allegheniensis* (Holsinger, 1967:36). The two females in the September 1966 collection did not have setose brood plates but otherwise appeared mature.

REMARKS.—The presence of setae on the posterior margin of the first gnathopod propod and rastellate setae on segment 5 of both gnathopods, the presence of a coxal gill on pereopod 7, and the absence of a peduncular process on uropod 1 of the male exclude this species from the *emarginatus* group to which I had originally assigned it in 1967.

Stygobromus baroodyi, new species

FIGURES 59, 60

Stygobromus sp. E.—Holsinger, 1969a:29–31.

MATERIAL EXAMINED.—VIRGINIA. Rockbridge Co.: Bathers Cave, holotype ♀ (USNM 168791), 20 ♀ and 4 juv. paratypes (USNM), 1 ♀ paratype on slide mounts (JRH), J. R. Holsinger, R. A. Baroody, R. M. Norton, and R. W. Burnette, 17 Apr 1965; Billy Williams Cave, 1 ♂ paratype (JRH), J. R. Holsinger and J. E. Cooper, 27 May 1961, and 6 ♀ paratypes (JRH), J. R. Holsinger, R. W. Burnette and R. M. Norton, 17 Apr 1965; Buck Hill Cave, 2 ♀ paratypes (JRH), T. C. Barr, Jr., 2 Jan 1959; cave between Lexington and Buena Vista (probably Bell Cave), 5 ♀ paratypes (USNM), J. A. Fowler, 31 Oct 1943; Grahams Cave, 1 ♀ paratype (JRH), J. Tichenor, Dec 1970; Showalters Cave, 1 ♀, 1 juv. paratypes (JRH), R. M. Norton, 17 Apr 1965, and 2 ♀, 3 ♂ paratypes (JRH), J. R. Holsinger, J. H. Carpenter and T. G. Marsh, 13 July 1969.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished by rather long, nonsetose posterior margin and slightly concave palm of gnathopod propod 1, small rastellate setae on segment 5 of gnathopods, small, often acute posterior corners of pleonal plates, and relatively short, unnotched telson. Largest males, 7.0 mm; largest female, 11.9 mm.

FEMALE.—Antenna 1, 50–60 percent length of body, 50 percent longer than antenna 2; primary flagellum with up to 32 segment. Antenna 2, flagellum with up to 9 segments. Mandibles subequal; spine row with 9 spines; segment 2 of palp with row of rather long setae on inner margin, segment 3 with 1 long seta on outer margin, row of short setae on inner margin and 4 long setae on apex. Maxilla 1: inner plate with 9 apical, plumose setae; palp with 2 spines and 5 setae apically and subapically. Maxilla 2, inner plate with oblique row of 8 or 9 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike (often serrate) spines, 2 plumose spines and 2 naked setae apically, 3 plumose spines (or coarse setae?) on inner margin distally; outer plate with naked setae on inner margin and apex, and 2 or 3 spines (or thick setae) and 1 plumose seta apically. Inner lobes of lower lip small to vestigial.

Propod of gnathopod 1 slightly smaller than 2nd propod; palm slightly concave, armed with double row of 9 spine teeth; defining angle with 5 spine teeth on outside, 5 spine teeth on inside; posterior margin about 50 percent length of palm, without setae; medial setae singly and doubly inserted. Dactyl nail of gnathopod 1 relatively short. Segment 5 of gnathopod 1 with several small, poorly developed rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 4 setae. Gnathopod propod 2: palm oblique, margin nearly straight, armed with double row of 11 or 12 spine teeth; defining angle with 1 long spine tooth on outside, 1 short spine tooth on inside; posterior margin with 4 sets setae; inferior medial setae singly inserted, superior medial setae singly, doubly, and triply inserted. Dactyl nail of gnathopod 2 relatively short. Segment 5 of gnathopod 2 with several very small, poorly developed rastellate setae. Coxal plate of gnathopod 2 longer than broad, margin with 1 or 2 small spines and 4 or 5 setae. Coxal plate of pereopod 3 longer than broad, margin with 3 short spines and 6 setae. Coxal plate of pereopod 4 about as broad as long, reaching about 45 percent length of basis, margin with 10 setae. Pereopod 7 usually a little longer than, but occasionally about equal to, pereopod 6, 45–55 percent length of body, 20–30 percent longer than pereopod 5. Bases of pereopods 5–7 a little broader proximally than distally, distoposterior lobes distinct, bluntly rounded. Dactyls of pereopods 6 and 7 about 25 percent length of corresponding propods; dactyl of pereopod 5 about 33 percent length of corresponding propods. Coxal gill present on pereopd 7. Three median sternal gills on pereonites 2–4; 2 pairs

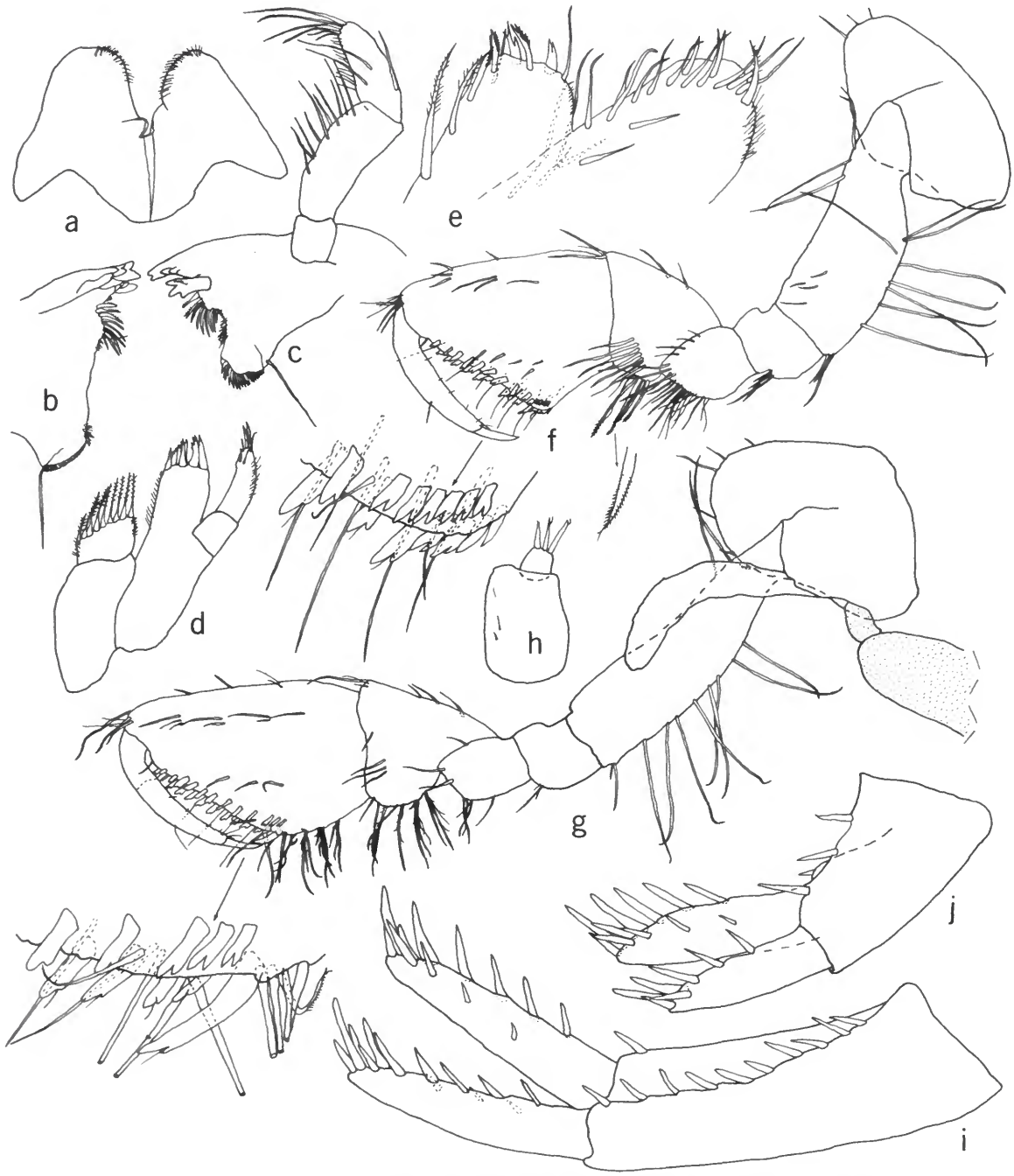

FIGURE 59.—*Stygobromus baroodyi*, new species, female paratype (10.0 mm), Bathers Cave, Virginia: *a*, lower lip; *b*, dentate part of left mandible; *c*, right mandible; *d*, maxilla 1; *e*, inner and outer plates of maxilliped (greatly enlarged); *f*, *g*, gnathopods 1, 2 (part of palms and defining angles enlarged); *h*, uropod 3; *i*, *j*, uropods 1, 2.

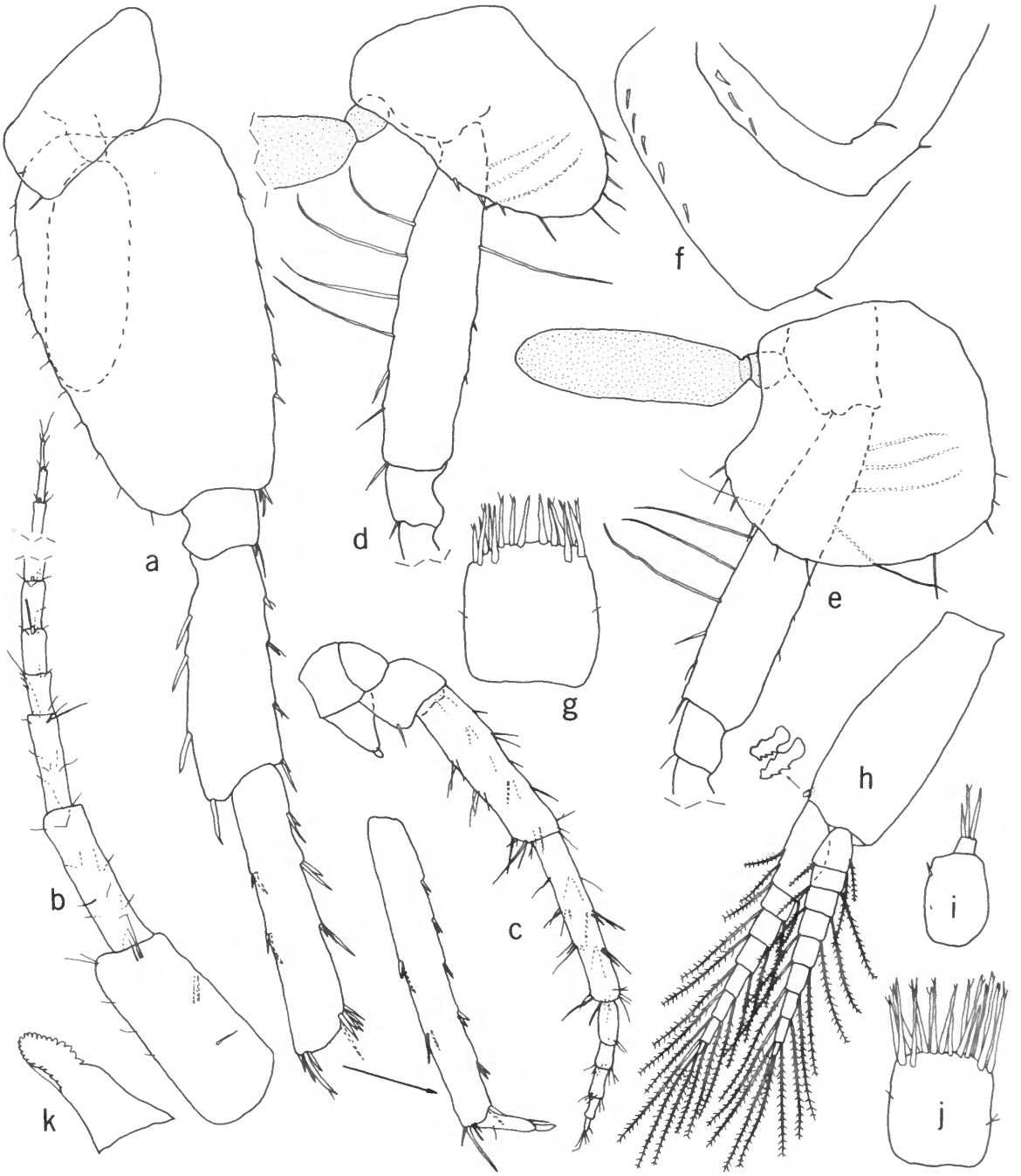

FIGURE 60.—*Stygobromus baroodyi*, new species. Female paratype (10.0 mm), Bathers Cave, Virginia: *a*, pereopod 6 (arrow indicates continuation of appendage); *b*, *c*, antennae 1, 2; *d*, *e*, pereopods 3, 4 (in part); *f*, pleonal plates; *g*, telson; *h*, pleopod 3 (coupling spines enlarged). Male paratype (7.0 mm), Showalters Cave, Virginia: *i*, uropod 3; *j*, telson; *k*, peduncular process of uropod 1.

bifurcate lateral sternal gills on pereonites 6 and 7; 1 pair sternal gills on pleonite 1. Brood plates relatively narrow but somewhat expanded distally.

Pleonal plates: posterior margins slightly convex, each with 1 setae inserted well above posterior corner; posterior corners small, subacute to acute; ventral margin of plate 1 with 5 spines, that of plate 2 with 3 spines. Uronites free. Uropod 1: inner ramus equal in length to outer ramus, about 60 percent length of peduncle, armed with 12 spines; outer ramus with 13 spines; peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 11 spines; outer ramus with 8 spines; peduncle with 4 spines. Uropod 3: ramus about 30 percent length of peduncle, with 3 rather short apical spines. Telson about as broad as long; apical margin entire but with small break in spine row, armed with 14–16 moderately short spines.

MALE.—Differing from female as follows: Propod of gnathopod 2 with 3 or 4 more spine teeth. Peduncular process of uropod 1 rounded apically, margin of distal half serrate. Uropod 3: ramus, 20–25 percent length of peduncle, with 3 rather long apical spines; peduncle with 1 small spine distolaterally. Telson slightly longer than broad; apical margin entire, armed with 16 spines, most of which are relatively long.

TYPE-LOCALITY.—Bathers Cave, located 3.2 km north of Lexington in Rockbridge Co., Virginia, is a medium-sized cave developed in Middle Ordovician limestone. In this cave, amphipods are fairly abundant in a series of small, mud-bottom stream pools about 91 m from the entrance.

DISTRIBUTION AND ECOLOGY.—The range of this species, which as presently known is limited to Rockbridge County, lies within the James River drainage basin and covers a linear distance of about 42 km. *Stygobromus baroodyi* is commonly associated with small, slow-flowing cave streams with mud or silt bottoms. It has also been taken from mud-bottom drip and seep pools. Females with setose brood plates, ranging in size from 7.5–11.9 mm, have been collected during all seasons of the years.

REMARKS.—This species undoubtedly has some affinity with members of the *emarginatus* group but has not been assigned there because of the following character differences: short spine teeth on outside of the defining angle of gnathopod propod 1, second gnathopod propod slightly larger than first, presence of rastellate setae on segment 5 of the gnathopods, presence of a coxal gill on pereopod 7, and unfused uronites.

ETYMOLOGY.—It is a pleasure to name this species in honor of Roger A. Baroody, a speleologist who has substantially assisted in the location of Appalachian caves and in the collection of subterranean amphipods.

Stygobromus borealis, new species

FIGURES 61, 62

Stygobromus sp.—Bell, 1971:41, fig. 81.

MATERIAL EXAMINED.—VERMONT. Rutland Co.: Morris Cave, holotype ♀ (USNM 168800), 17 ♀ and 6 ♂ paratypes (JRH), S. B. Peck, 20 May 1968; additional paratypes from Morris Cave as follows: 6 ♀ (USNM), S. B. Peck, 23 Apr 1967; 25 ♀, 2 ♂ (USNM), S. B. Peck and W. A. Shear, 18 Oct 1968; 6 ♀ (JRH), R. M. Norton, 14 Feb 1970; 2 ♀ (JRH), G. Bilyard, 1970 (?). NEW YORK. Rensselaer Co.: springhouse, 1.6 km S of Berlin, 1 ♀ paratype (JRH), S. B. Peck, 11 May 1969.

DIAGNOSIS.—A relatively small groundwater and cavernicolous species distinguished by absence of setae on palp segment 2 of mandible, reduced number of setae on inner plates of maxillae 1 and 2, unnotched spine teeth of gnathopod propods, shallow coxal plates of pereopods 3 and 4, narrow bases of pereopods 5–7, and narrow, 1-spined ramus of uropod 3. Largest males, 3.0 mm; largest females, 4.0 mm.

FEMALE.—Antenna 1, 50–60 percent length of body, 45–50 percent longer than antenna 2; primary flagellum with 9–12 segments. Antenna 2, flagellum with 3 segments. Mandibles subequal; spine row with 2 or 3 spines; segment 2 of palp without setae, segment 3 with 1 long seta on outer margin, row of moderately short setae on distal half of inner margin, 4 or 5 long setae on apex. Maxilla 1: inner plate with 2 apical, plumose setae; palp with 3 stiff setae and 1 slender spine (or stiff seta?) apically. Maxilla 2, inner plate with oblique row of 2 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine and 1 naked seta apically, 1 naked and 1 plumose seta subapically; outer plate with naked setae on inner margin and apex, and 1 plumose seta apically. Inner lobes of lower lip small to vestigial.

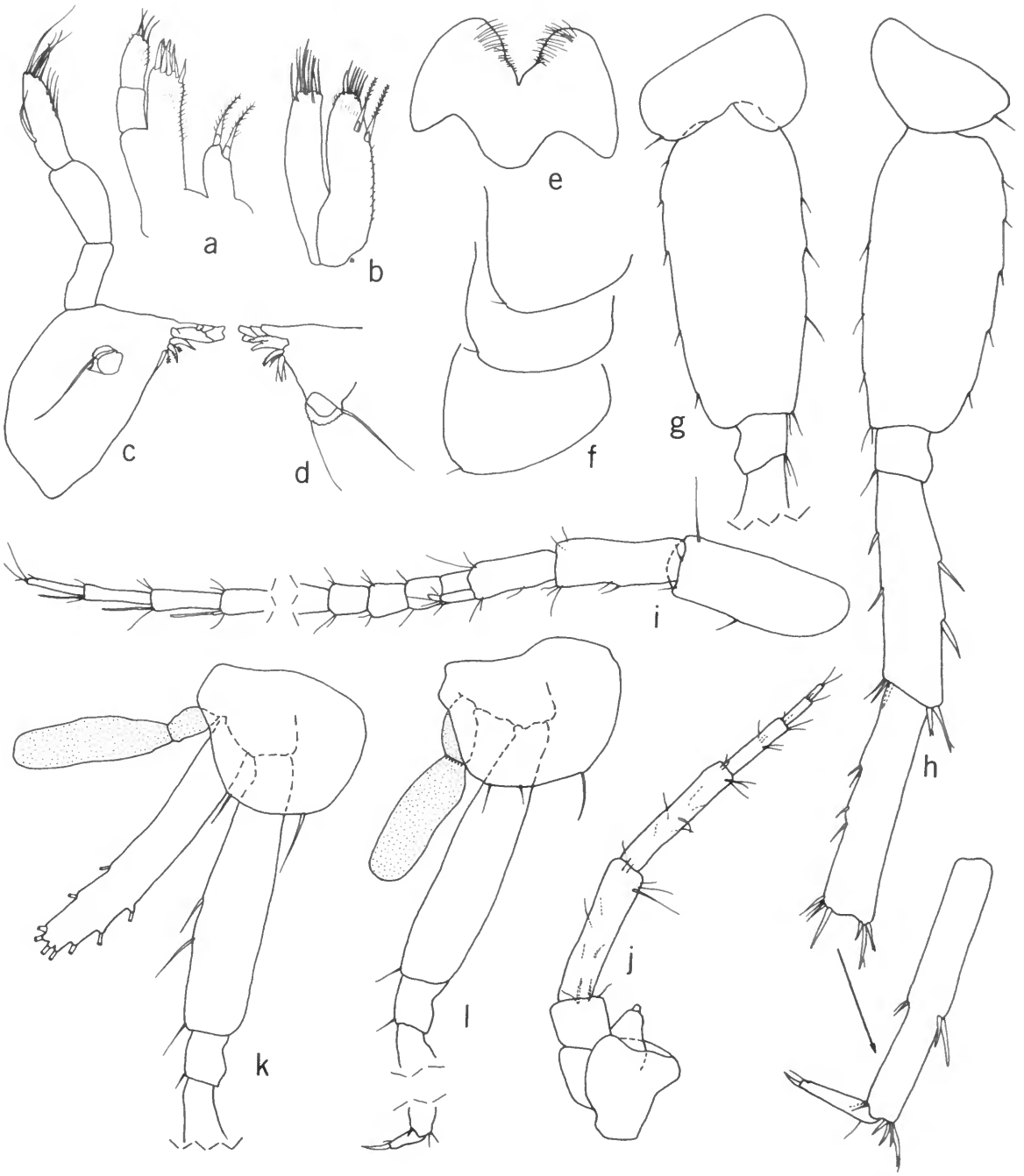

FIGURE 61.—*Stygobromus borealis*, new species, female paratype (4.0 mm), Morris Cave, Vermont: *a*, *b*, maxillae 1, 2; *c*, left mandible; *d*, dentate part of right mandible; *e*, lower lip; *f*, pleonal plates; *g*, pereopod 6 (in part); *h*, pereopod 7 (arrow indicates continuation of appendage); *i*, *j*, antennae 1, 2; *k*, *l*, pereopods 3, 4 (in part).

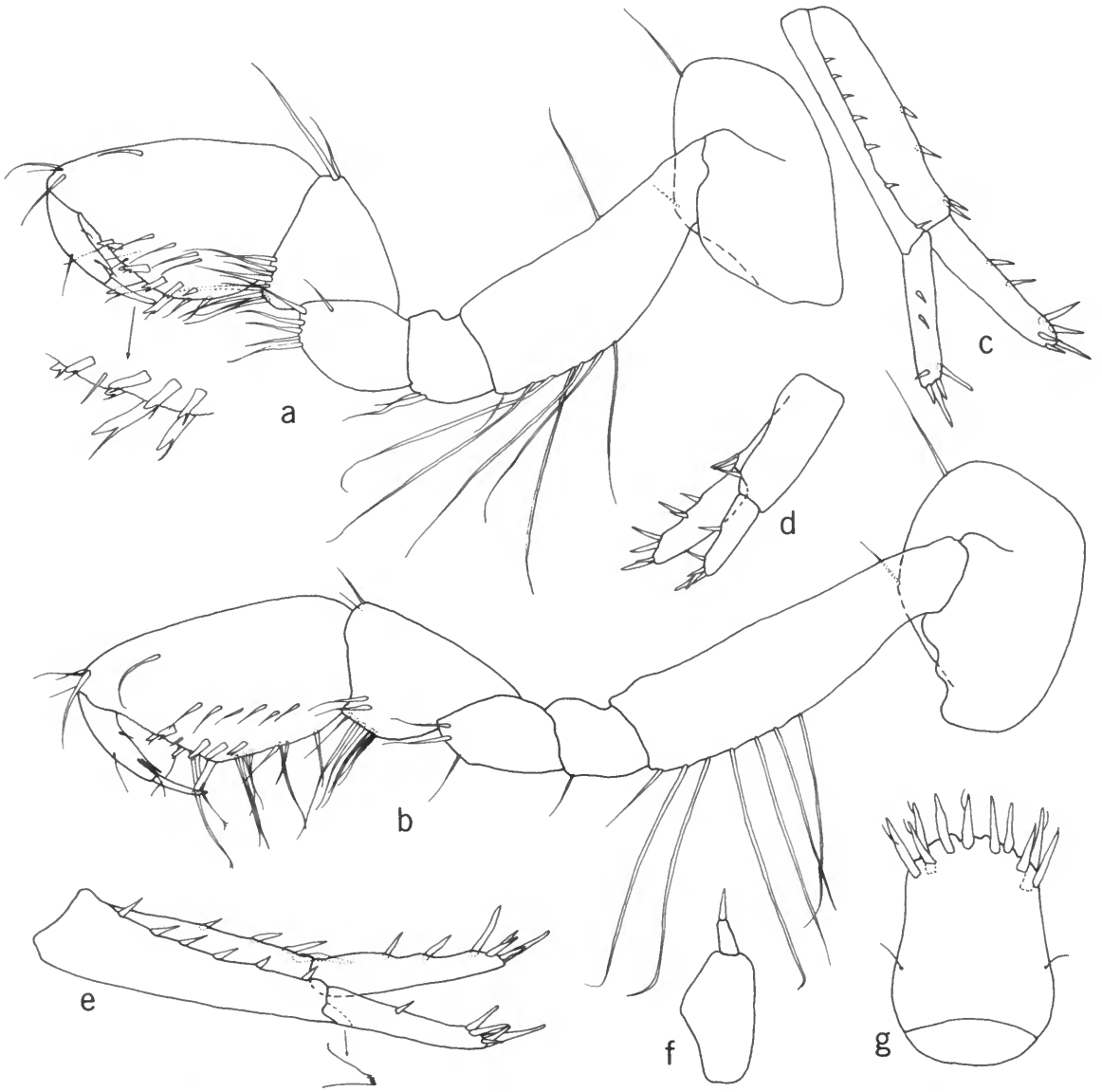

FIGURE 62.—*Stygobromus borealis*, new species. Female paratype (4.0 mm), Morris Cave, Vermont: *a*, *b*, gnathopods 1, 2 (palm and defining angle of gnathopod 1 enlarged); *c*, *d*, uropods 1, 2. Male paratype (3.0 mm), Morris Cave: *e*, uropod 1 (peduncular process enlarged); *f*, uropod 3; *g*, telson.

Propod of gnathopod 1 subequal in size to 2nd propod but broader proximally; palm armed with double row of 3 unnotched spine teeth; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; posterior margin about ⅔ length of palm, with 2 thick setae; inferior medial setae rather long, singly inserted, superior medial setae reduced in number, singly inserted. Dactyl nail of gnathopod 1 moderately long. Segment 5 of gnathopod 1 without rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 2 setae. Gnathopod propod 2: palm rather short, straight,

armed with double row of 2 unnotched spine teeth; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; posterior margin longer than palm, with 3 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Segment 5 of gnathopod 2 without rastellate setae. Coxal plates of gnathopod 2 and pereopod 3 shallow, about as broad as long, margins with 2 long setae each. Coxal plate of perepod 4 shallow, broader than long, reaching only about 30 percent length of basis, margin with 3 setae. Pereopod 7 slightly longer than pereopod 6, 45–50 percent length of body, about 25 percent longer than pereopod 5. Pereopods 5–7: bases narrow, distoposterior lobes poorly developed; dactyls, 39–42 percent length of corresponding propods. Coxal gills absent from pereopod 7. Three median sternal gills on pereonites 2–4; 2 pairs simple, moderately long lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates narrow, not expanded distally.

Pleonal plates: Posterior margins convex, with 1 seta each; posterior corners small to nearly indistinct; ventral margins without spines. Uronites sometimes partly fused, sometimes completely fused. Uropod 1: inner ramus a little longer than outer ramus, about 60 percent length of peduncle, armed with 7 spines; outer ramus with 7 spines; peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 7 spines; outer ramus with 5 spines; peduncle with 3 spines. Uropod 3: ramus narrow, about 30 percent length of peduncle, armed with 1 rather large spine. Telson longer than broad, gently tapering distally; apical margin convex, sinuate, armed with 9 or 10 spines.

MALE.—Differing from female in structure of uropods 1 and 2 as follows: Uropod 1: inner ramus with 7 spines; outer ramus with 6 spines; peduncle with 10 spines; peduncular process subtriangular, apex serrate. Inner ramus of uropod 2 with 8–9 spines.

TYPE-LOCALITY.—Morris Cave, located just south of Danby in Rutland Co., Vermont, is a small cave in a restricted band of marble with a deep pool of water in the rear. The pool, which is inhabited by *S. borealis,* has a silt and/or sand bottom and slopes down at an angle of approximately 45 degrees to a depth probably exceeding 9 meters (S. B. Peck, in litt.). According to Peck, the pool is probably in contact with phreatic water in the marble bedrock.

DISTRIBUTION AND ECOLOGY.—This species is recorded from two localities, Morris Cave in Vermont and a spring in Rensselaer Co., New York, both of which are located in the Taconic Mountains (New England Province) and lie about 81 km apart. The Vermont locality is in the Lake Champlain drainage basin, whereas the New York locality is in the Hudson River drainage. Collections are available from winter, spring, and fall, and females (2.8–4.0 mm in length) with setose brood plates have been observed during all three seasons.

REMARKS.—*Stygobromus borealis* is the seventh species of the genus to be found north of the southern limits of Pleistocene glaciation and its distribution is of zoogeographic interest. This species may be distantly related to members of the *spinosus* group of northern Virginia, but its affinities are, at best, unclear. The absence of distal notches in the palmar margin spines is unique for species of *Stygobromus* and obscures any relationship with other species that might exist.

Bell (1971:41) mentioned the occurrence of *Stygobromus* sp. from Dorset Cave in southern Vermont. This cave is presumably the same as Morris Cave (D. G. Smith, University of Massachusetts, in litt.), and the species referred to is undoubtedly the one described above.

ETYMOLOGY.—The epithet *borealis* is from Latin, meaning "northern."

Stygobromus biggersi, new species

FIGURES 63, 64

Stygobromus sp. B.—Holsinger, 1969a:29–30.

Stygobromus sp.—Franz and Slifer, 1971:26.—Holsinger, Baroody, and Culver, 1976:23.—Holsinger, 1976:76.

MATERIAL EXAMINED.—VIRGINIA. Frederick Co.: Ogdens Cave, holotype ♀ (USNM 168795), 25 ♀, 3 ♂ paratypes (USNM) and 1 ♀, and 1 ♂ paratypes (JRH), J. R. Holsinger, 25 Jan 1969; 2 ♀, 1 ♂ paratypes (USNM), A. Wicker, fall, 1968. Additional paratypes as follows: MARYLAND. Washington Co.: Dam No. 4 Cave, 1 ♀ (JRH), L. R. Franz, 3 Dec 1965; Hogmaw Cave, 2 ♀ (JRH), L. R. Franz, 13 May 1967, and 2 ♀ (JRH), 10 Aug 1967. PENNSYLVANIA. Franklin Co.: Needy Cave, 2 ♀ (USNM), R. Bray, 22 Feb 1940, and 2 ♀ (USNM), 7 Apr 1940. WEST VIRGINIA. Jefferson Co.: Ditmer Cave, 2 ♀ (JRH), D. J. Newson, 21 Jun 1967.

DIAGNOSIS.—A medium-sized cavernicolous spe-

FIGURE 63.—*Stygobromus biggersi*, new species, female paratype (6.0 mm), Ogdens Cave, Virginia: *a*, *b*, maxillae 1, 2 (setae enlarged); *c*, inner plate of maxilliped (greatly enlarged); *d*, lower lip; *e*, *f*, gnathopods 1, 2 (palms and defining angles enlarged); *g*, pleonal plates; *h*, uropod 3, *i*, uropod 1.

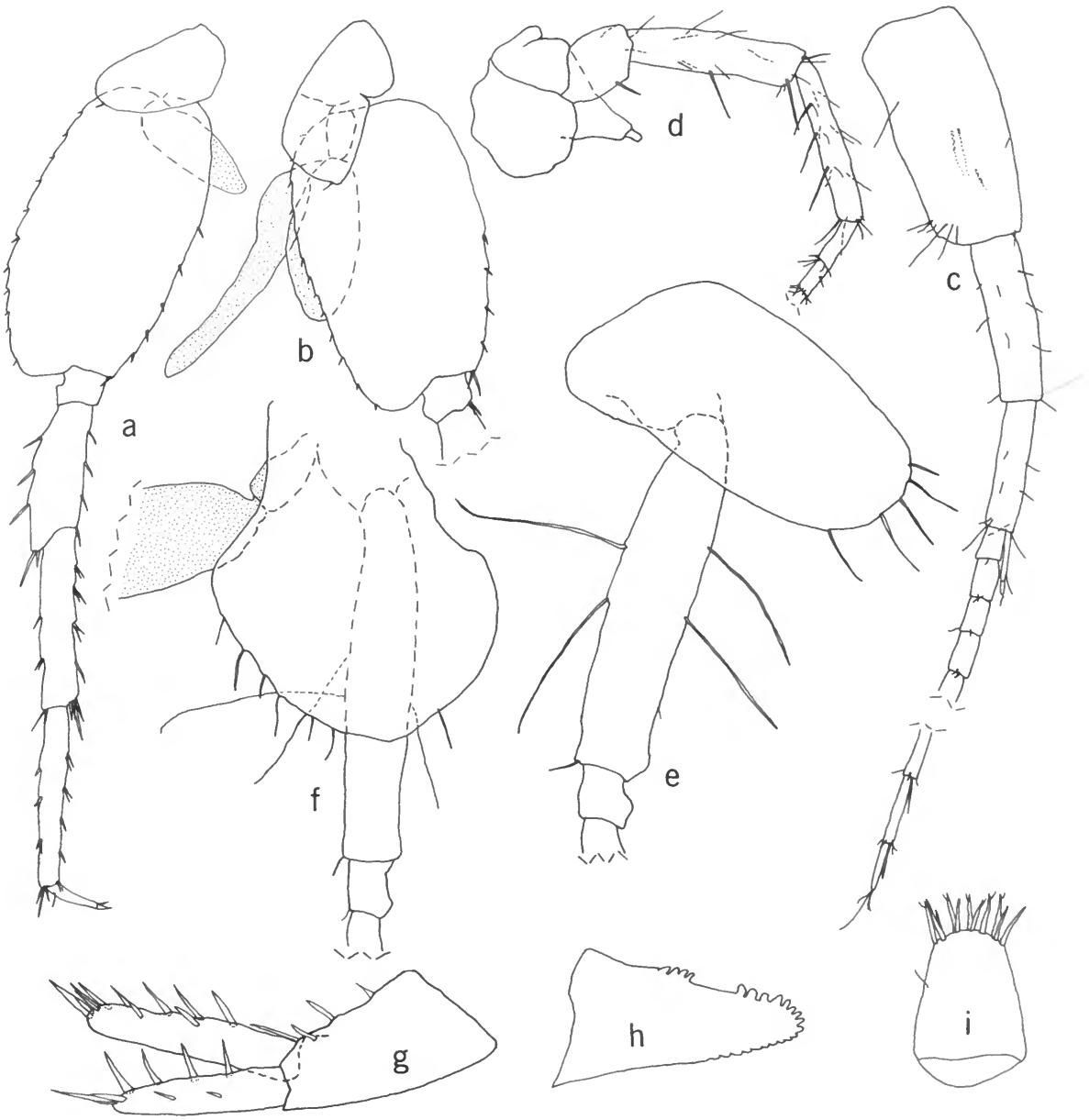

FIGURE 64.—*Stygobromus biggersi*, new species. Female paratype (6.0 mm); Ogdens Cave, Virginia: *a*, pereopod 7; *b*, pereopod 6 (in part) with lateral sternal gill; *c*, *d*, antennae 1, 2; *e*, *f*, pereopods 3, 4 (in part). Male paratype (5.6 mm), Ogdens Cave: *g*, uropod 2; *h*, peduncular process of uropod 1 (greatly enlarged); *i*, telson.

cies distinguished by relatively deep coxal plates of gnathopod 2 and pereopods 3 and 4, broad distoposterior lobe of basis of pereopod 7, distinct and bluntly rounded posterior corners of pleonal plates, and unnotched apical margin of telson. Largest male, 5.6 mm; largest female, 7.0 mm.

FEMALE.—Antenna 1, 50–60 percent length of body, about 50 percent longer than antenna 2; primary flagellum with 13–17 segments. Antenna 2, flagellum with 5 or 6 segments. Mandibles subequal; spine row with 4 or 5 spines; segment 2 of palp with long setae on inner margin, segment 3 with 2 long setae on outer margin, 2 long setae and row of short setae on inner margin, 4 or 5 long setae on apex. Maxilla 1: inner plate with 10 or 11 apical, plumose setae; palp with 6 slender spines and 3 or 4 setae apically and subapically. Maxilla 2, inner plate with oblique row of 11 plumose setae on inner margin. Maxilliped: inner plate with 4 bladelike spines, 3 plumose spines and 2 naked setae apically and subapically, 3 plumose spines (or coarse setae?) on inner margin distally; outer plate with naked setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip absent.

Propod of gnathopod 1 about 25 percent smaller than 2nd propod; palm slightly convex, armed with double row of 7 or 8 spine teeth; defining angle with 3 long spine teeth of unequal length on outside, 3 or 4 shorter ones on inside; posterior margin with row of about 7 mostly singly inserted setae; medial setae few in number, singly inserted. Dactyl nail of gnathopod 1 relatively short. Segment 5 of gnathopod 1 with 3 rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 3 long setae. Gnathopod propod 2: palm slightly convex, armed with double row of 9 or 10 spine teeth; defining angle with 1 long and 2 short spine teeth on outside, 3 short spine teeth on inside; posterior margin with 3 sets setae; medial setae singly inserted. Segment 5 of gnathopod 2 without rastellate setae. Coxal plates of gnathopod 2 and pereopod 3 rather deep, longer than broad, margins with 5 or 6 setae each. Coxal plate of pereopod 4 relatively broad and deep, about as broad as long, reaching about 65 percent length of basis, margin with 7 setae. Pereopod 6 a little longer than pereopod 7, 40–55 percent length of body, 15–25 percent longer than pereopod 5. Pereopods 5–7: basis of 7 broader distally than proximally, bases of 5 and 6 a little broader proximally, distoposterior lobes distinct, broadly rounded; dactyls about 33 percent length of corresponding propods. Coxal gill present on pereopod 7. One median sternal gill on pereonite 2; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates rather narrow but somewhat expanded distally.

Pleonal plates: posterior margins of 1 and 3 slightly convex, that of 2 nearly straight, margins with 1 seta each; posterior corners distinct, bluntly rounded; ventral margins of plates 2 and 3 with 2 spines each. Uronites free. Uropod 1: inner ramus a little longer than outer ramus, about 75 percent length of peduncle, armed with 12 spines; outer ramus with 8 spines; peduncle with 13 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, armed with 11 spines; outer ramus with 9 spines; peduncle with 4 spines. Uropod 3: ramus about 40 percent length of peduncle, with 3 or 4 apical spines. Telson longer than broad, narrowing distally; apical margin entire, slightly convex, with 11 or 12 spines.

MALE.—Differing slightly from female as follows: Gnathopod propods with 2 or 3 more spine teeth. Coxal gill absent from pereopod 7. Peduncular process of uropod 1 subtriangular, distally serrate.

TYPE-LOCALITY.—Ogdens Cave, located 4 km west-northwest of Middletown in Frederick Co., Virginia, is a medium-sized cave developed in Beekmantown limestone of lower Ordovician age. The cave contains a small stream and a series of mud-bottom pools fed by drips and seepage and has a moderately rich, troglobitic aquatic fauna consisting of two amphipods (*S. gracilipes* and *S. biggersi*), an isopod (*Asellus* senu lato *pricei*) and a snail (*Fontigens* sp.). *Stygobromus biggersi* is usually fairly abundant in one or more of the pools but has not been found in the stream.

DISTRIBUTION AND ECOLOGY.—The range of this species, which is restricted to a part of the Potomac River drainage basin, extends from Ogdens Cave in northwestern Virginia for approximately 97 km north-northeastward through northeastern West Virginia and central Maryland to Needy Cave in south-central Pennsylvania. The range coincides in part with that of *S. gracilipes,* and the two species are sometimes found in the same cave. *Stygobromus biggersi* is predominately an inhabitant of cave pools and is often associated with the isopod

Asellus (sensu lato) *pricei* (Levi). Females (4.9–7.0 mm) with setose brood plates have been collected during all seasons of the year.

ETYMOLOGY.—It is a pleasure to name this species in honor of William W. Biggers, who has accompanied me on many cave trips and has assisted with the collection of subterranean amphipods.

Stygobromus stegerorum, new species

FIGURES 65, 66

Stygobromus sp. D.—Holsinger, 1969a:29–30.

MATERIAL EXAMINED.—VIRGINIA. Augusta Co.: Madisons Saltpetre Cave, holotype ♂ (USNM 168855), 2 ♂ paratypes (USNM), 1 ♀ and 1 ♂ paratypes (JRH), J. R. Holsinger and R. W. Burnette, 24 Aug 1964; 1 ♀ paratype (JRH), R. M. Norton, Sep 1970; 1 ♀ paratype (USNM), J. A. Estes and G. W. Dickson, 19 Mar 1975; Stegers Fissure, 1 ♀ paratype (JRH), J. R. Holsinger, S. W. Hetrick, and J. A. Estes, 8 Jun 1974.

DIAGNOSIS.—A medium-sized cavernicolous species distinguished by long, slender antennae, pereopods, and uropods 1 and 2, long, narrow coxal plate of pereopod 3, large, deep coxal plate of pereopod 4, and relatively long telson which is nearly 50 percent broader proximally than distally and has distinct apical notch. Largest males, 5.5 mm; largest female, 6.8 mm.

MALE.—Antenna 1, 70–90 percent length of body, 35–40 percent longer than antenna 2; primary flagellum with 20–21 segments. Antenna 2, flagellum with 5 segments. Mandibles subequal; spine row with 5 spines; segment 2 of palp with 4 long and 2 short setae on inner margin, segment 3 with 1 long seta on outer margin, 1 long seta and row of short setae on inner margin, 4 long setae on apex. Maxilla 1: inner plate with 9 apical, plumose setae; palp with 2 slender spines and 4 stiff setae apically. Maxilla 2, inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 2 plumose setae and 1 naked seta apically, 1 bladelike spine, 2 naked setae and row of 4 plumose setae subapically; outer plate with naked setae on inner margin and apex, and 1 plumose seta apically. Inner lobes of lower lip absent.

Propod of gnathopod 1 shorter than 2nd propod; palm oblique, margin straight, armed with unequal double row of 16 or 17 spine teeth; defining angle without long spine teeth on outside; posterior margin with 2 setae; medial setae few in number, singly inserted. Dactyl nail of gnathopod 1 relatively long. Segment 5 of gnathopod 1 with 1 rastellate seta. Coxal plate of gnathopod 1 longer than broad, margin with 5 or 6 setae. Gnathopod propod 2: palm long, oblique, slightly convex, armed with double row of about 13 spine teeth; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; medial setae singly inserted. Dactyl nail of gnathopod 2 relatively long. Segment 5 of gnathopod 2 without rastellate setae. Coxal plate of gnathopod 2 rather deep, longer than broad, margin with 4 or 5 setae. Coxal plate of pereopod 3 long and rather narrow, reaching about 60 percent length of basis, margin with 6 setae. Coxal plate of pereopod 4 broad and deep, reaching about 70 percent length of basis, margin with 9–11 setae. Pereopod 6 a little longer than pereopod 7, about 60 percent length of body, about 10 percent longer than pereopod 5. Pereopods 5–7: bases broader proximally than distally, distoposterior lobes relatively small; dactyls of 6 and 7 about 33 percent length of corresponding propods, that of 5 about 37 percent length of corresponding propod. Coxal gill absent from pereopod 7. Three median sternal gills on pereonites 2–4, 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1.

Pleonal plates: posterior margins of 1 and 2 nearly straight, that of 3 slightly convex, margins with 1 seta each; posterior corners distinct, bluntly rounded; ventral margin of plate 3 with 1 spine. Uronites free. Uropod 1: inner ramus a little longer than outer ramus, about 85 percent length of peduncle, armed with 15 spines; outer ramus with 14 spines; peduncle with 11 spines; peduncular process comparatively short, outer margin rugose. Uropod 2: inner ramus broader and longer than outer ramus, longer than peduncle, armed with 15 spines; outer ramus with 13 spines; peduncle with 2 spines. Uropod 3: ramus about 1/3 length of peduncle, with 2 or 3 apical spines; peduncle with 1 distal spine. Telson longer than broad, tapering distally; apical margin incised about 20 percent the distance to base, armed with 8–10 spines.

FEMALE.—Differing only slightly from male as follows: Propod of gnathopod 1 with few less spine teeth; segment 5 of gnathopod 1 with 3 rastellate setae. Propod of gnathopod 2 with few more spine

FIGURE 65.—*Stygobromus stegerorum*, new species, male paratype (5.5 mm), Madison Saltpetre Cave, Virginia: *a*, inner plate of maxilliped (greatly enlarged); *b*, dentate part of left mandible; *c*, right mandible; *d*, *e*, gnathopods 1, 2 (palm, defining angle, and rastellate seta of gnathopod 1 enlarged; part of palm and defining angle of gnathopod 2 enlarged); *f*, telson; *g*, pleonal plates, *h*, *i*, uropods 1, 2 (peduncular process of uropod 1 enlarged).

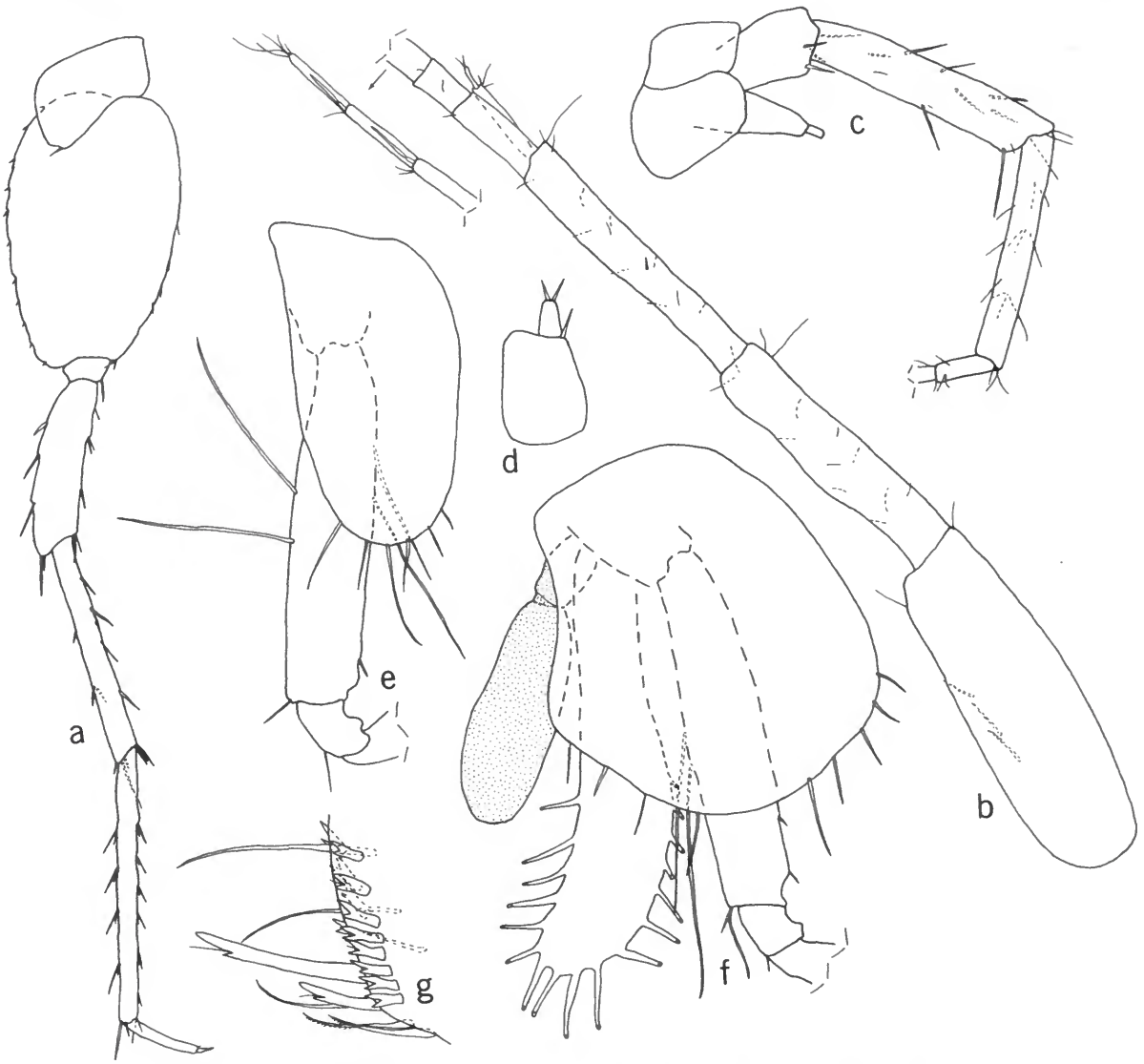

FIGURE 66.—*Stygobromus stegerorum*, new species. Male paratype (5.5 mm); Madison Saltpetre Cave, Virginia: *a*, pereopod 6; *b*, *c*, antennae 1, 2; *d*, uropod 3. Female paratype (6.8 mm), Stegers Fissure, Virginia: *e*, *f*, pereopods 3, 4 (in part); *g*, defining angle region of gnathopod propod 1 (greatly enlarged).

teeth. Brood plates relatively narrow but somewhat expanded distally.

TYPE-LOCALITY.—Madison Saltpetre Cave, located in Augusta Co., Virginia, is developed in Cave Hill which lies just west of Grottoes and just west of South River (upper Potomac River drainage). The cave is comparatively small and is developed in limestone or dolomite of the Cambrian-aged Conococheague Formation. Two deep lakes of phreatic water occur on the lower level, both of which are occupied by *S. stegerorum* and the troglobitic cirolanid isopod *Antrolana lira* Bowman.

DISTRIBUTION AND ECOLOGY.—Outside of the type-locality, this species has been collected from a deep

pool of phreatic water at the bottom of Stegers Fissure which is a 4.5-meter-deep vertical crevice situated about 152 meters north of Madison Saltpetre Cave. The water in this fissure, which is probably continuous through subterranean crevices with that in the deep lakes in Madison Saltpetre Cave, is also inhabited by cirolanid isopods. Two females, measuring 6.0 and 6.8 mm in length and collected in March and June, respectively, had setose brood plates.

ETYMOLOGY.—It is a pleasure to name this species in honor of Mr. and Mrs. Lyall O. Steger, the owners of Madisons Saltpetre Cave, who have generously offered their cooperation in allowing us to study the interesting fauna of their cave.

Stygobromus fecundus, new species

FIGURES 67, 68

Stygobromus exilis Hubricht, 1943:697–699, pl. 4 [in part].—Barr, 1961:32 [in part].
Stygobromus sp. K.—Holsinger, 1969a:31.

MATERIAL EXAMINED.—TENNESSEE. Blount Co.: Gregorys Cave, holotype ♀ (USNM 168814), 10 ♀ and 4 ♂ paratypes (JRH), J. R. Holsinger, S. B. Peck, and R. M. Norton, 16 Mar 1964. Additional paratypes from Gregorys Cave as follows: 25 ♀, 4 ♂ (USNM 79326), 63 ♀, 12 ♂ (USNM), L. Hubricht, 9 Aug 1939; 6 ♀ (JRH), S. B. Peck, 5 Aug 1965; 1 ♀, 1 ♂ (JRH), L. M. and B. L. Ferguson, 12 Jun 1972.

DIAGNOSIS.—A moderately small cavernicolous species distinguished by relatively long posterior margins of gnathopod propods, 2-spined ramus of uropod 3, and slightly notched apical margin of telson. Largest males, 3.5 mm; largest females, 4.0 mm.

FEMALE.—Antenna 1, 45 percent length of body, 50–55 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2, flagellum with 3 segments. Mandibles subequal; spin row with 2 or 3 spines; segment 2 of palp with 1 long seta on inner margin, segment 3 with 1 long seta on outer margin, row of short setae on distal half of inner margin and 3 long setae on apex. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 4 stiff setae apically. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines and 1 naked seta apically, 1 bladelike spine and 1 plumose seta subapically; outer plate with naked setae on inner margin and apex and 1 lightly plumose seta apically. Inner lobes of lower lip absent.

Propod of gnathopod 1 a little smaller than 2nd propod; palm relatively short, slightly convex, armed with double row of about 5 spine teeth; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin rather long, nearly as long as palm, with 5 singly inserted setae; medial setae singly inserted. Dactyl nail of gnathopod 1 moderately long. Segment 5 of gnathopod 1 without rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 1 seta. Gnathopod propod 2: palm rather short, slightly convex, armed with 6 spine teeth on outside, 3 on inside; defining angle with 2 long spine teeth on outside, 2 shorter ones on inside; posterior margin rather long, nearly as long as palm, with 4 or 5 sets setae; medial setae singly inserted. Dactyl nail of gnathopod 2 moderately long. Segment 5 of gnathopod 2 without rastellate setae. Coxal plates of gnathopod 2 and pereopod 3 longer than broad, margins with 2 setae each. Coxal plate of pereopod 4 about as broad as long, reaching about 45 percent length of basis, margin with 3 setae. Pereopod 6 a little longer than pereopod 7, 45 percent length of body, 15–20 percent longer than pereopod 5. Pereopods 5–7: distoposterior lobes of bases well developed, broadly rounded; dactyl of 5 about 40 percent length of corresponding propod, dactyls of 6 and 7 about 33 percent length of corresponding propods. Coxal gill absent from pereopod 7. Two or 3 median sternal gills on pereonites 2–4; 2 pairs simple lateral sternal gills on pereonites 6 and 7; sternal gills absent from pleonite 1. Brood plates narrow, not expanded distally.

Pleonal plates: posterior margins of 1 and 3 slightly convex, that of 2 nearly straight, margins with 1 seta each; posterior corner of plate 1 distinct, bluntly rounded, those of plates 2 and 3 indistinct, broadly rounded; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus subequal in length to outer ramus, about 55 percent length of peduncle, armed with 9 spines; outer ramus with 7 spines; peduncle with 7 or 8 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 11 spines; outer ramus with 6 or 7 spines; peduncle with 5 spines. Uropod 3: ramus about 30 percent length of peduncle, armed with 2 apical spines. Telson a little longer than broad,

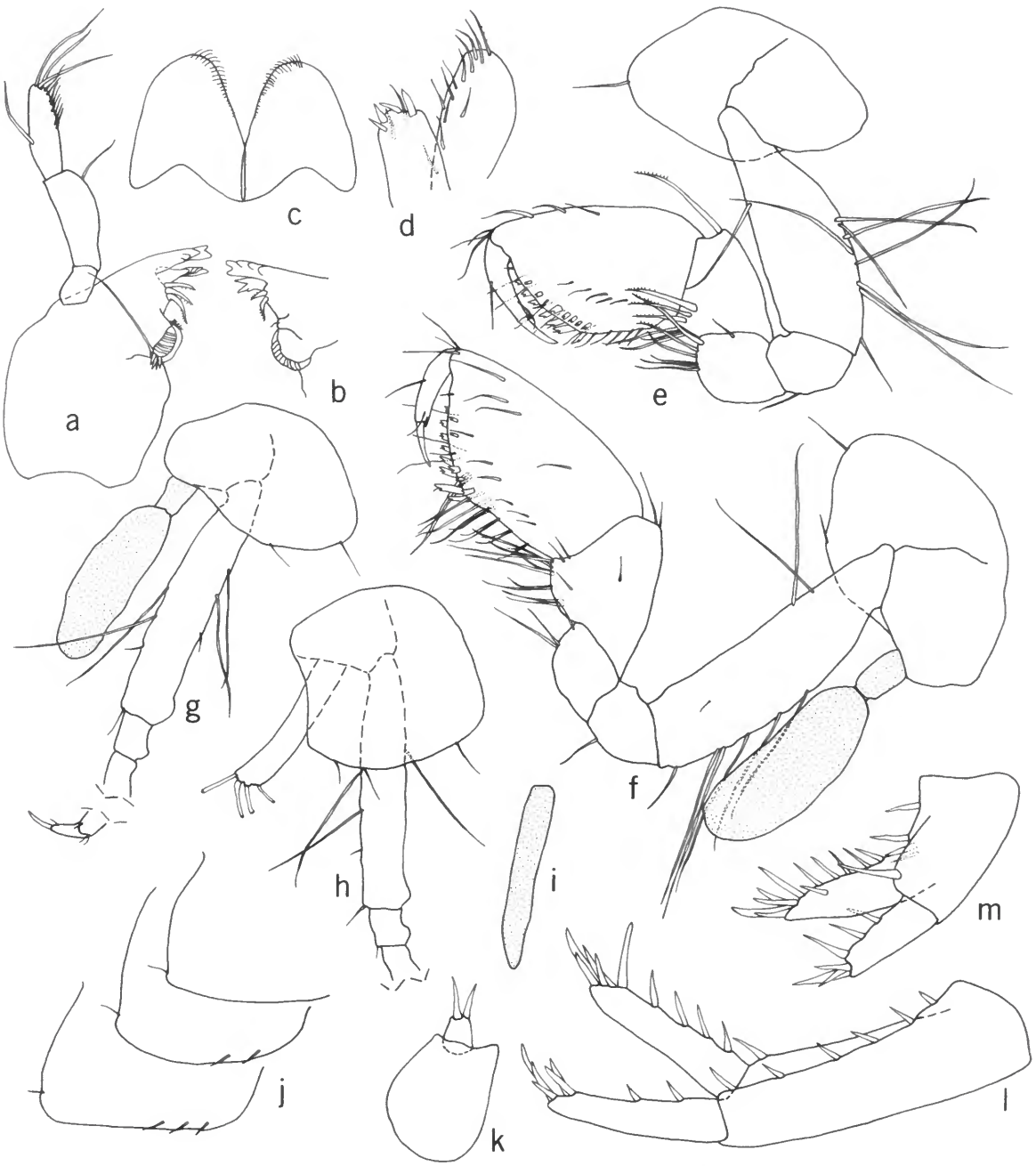

FIGURE 67.—*Stygobromus fecundus*, new species, female paratype (4.0 mm), Gregorys Cave, Tennessee: *a*, left mandible; *b*, dentate part of right mandible; *c*, lower lip; *d*, inner and outer plates of maxilliped (enlarged); *e*, *f*, gnathopods 1, 2; *g*, *h*, pereopods 3, 4 (in part); *i*, lateral sternal gill; *j*, pleonal plates; *k*, uropod 3; *l*, *m*, uropods 1, 2.

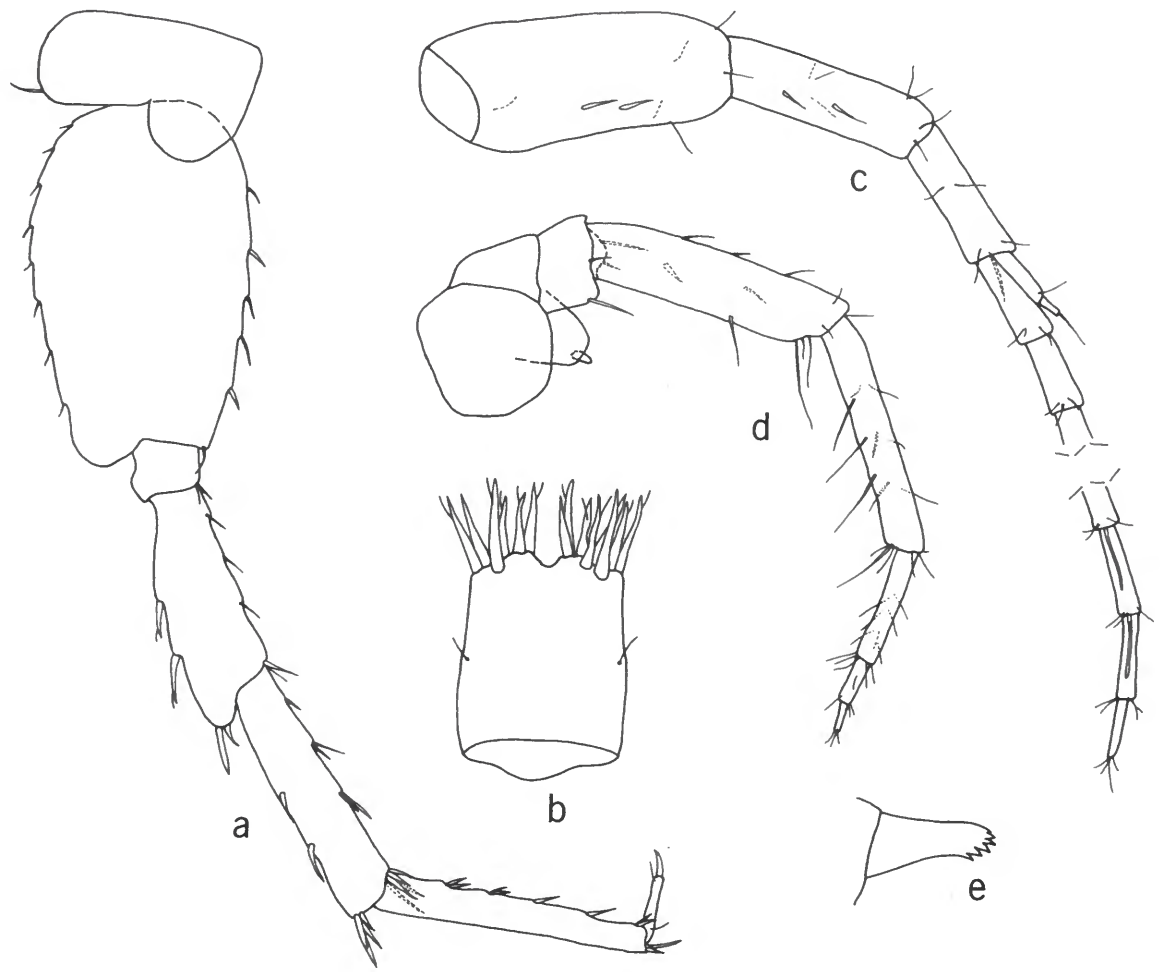

FIGURE 68.—*Stygobromus fecundus*, new species. Female paratype (4.0 mm), Gregorys Cave, Tennessee: *a*, pereopod 6; *b*, telson; *c*, *d*, antennae 1, 2. Male paratype (3.3 mm), Gregorys Cave: *e*, peduncular process of uropod 1.

slightly broader proximally than distally; apical margin with small notch, armed with 12–14 spines.

MALE.—Differing slightly from female as follows: Gnathopod propods proportionately a little broader, armed with 2 or 3 more spine teeth; posterior margin of gnathopod propod 2 with few less setae. Peduncular process of uropod 1 about 25 percent length of outer ramus, apex serrate.

TYPE-LOCALITY.—Gregorys Cave, located in Great Smoky Mountain National Park in Blount Co., Tennessee, is also the type-locality for *S. sparsus* (see p. 82 for further descriptive details on the type-locality).

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it is common is a series of rimstone pools fed by ceiling drips. Collections have been made during March, June, and August and those from March and August contained females (3.5–4.0 mm in length) with setose brood plates. The August 1939 collection had three ovigerous females (3.5–4.0 mm), two brooding one egg each and one brooding two eggs.

Both *S. sparsus* and *S. fecundus* have been collected from pools in Gregorys Cave, but only the latter has been found with regularity (on four separate visits to the cave over the last 33 years) and is by far the most abundant of the two species (127 out of 130 specimens collected to date) in the cave.

REMARKS.—*Stygobromus fecundus* is closely related to *S. exilis* Hubricht and its allies from farther west in caves of the Interior Low Plateau region of south-central Kentucky, central Tennessee and northern Alabama. Hubricht (1943:699) assigned the Gregorys Cave population (material described as *S. fecundus* above) to *S. exilis,* but my examination has revealed slight but consistent differences and this, coupled with the extreme geographic isolation of the population in the mountains of eastern Tennessee, has led me to recognize it as a distinct species. A thorough analysis, however, of the *exilis* complex (now in preparation) is necessary to ascertain the precise relationship of these species.

Hubricht (1943:699) also indicated that his series of over 100 specimens collected from Gregorys Cave in 1939 contained only females. My examination of this series, however, revealed 88 females and 16 males.

ETYMOLOGY.—The epithet *fecund*us is from Latin, meaning "abundant" or "plentiful."

Stygobromus minutus, new species

FIGURES 69, 70

MATERIAL EXAMINED.—GEORGIA. Walker Co.: Pettijohn Cave, holotype ♀ (USNM 168834), 2 ♀ paratypes (JRH), J. R. Holsinger, S. B. Peck, R. A. Baroody, and A. Fiske, 10 Jun 1967.

DIAGNOSIS.—A small cavernicolous species distinguished by small size at sexual maturity, relatively short 1st antenna, shallow coxal plates, proportionately long dactyls of pereopods 5–7, absence of ramus on uropod 3, and subquadrate telson which has comparatively few and heavy spines and small apical notch. Largest female, 2.3 mm; male unknown.

FEMALE.—Antenna 1 about 33 percent length of body, 45–50 percent longer than antenna 2; primary flagellum with 8 segments. Antenna 2, flagellum with 3 segments. Mandibles subequel; spine row with 3 spines; segment 2 of palp with 1 long seta on inner margin, segment 3 with 2 long setae on outer margin, few short setae on distal half of inner margin and 4 long setae on apex. Maxilla 1: inner plate with 3 apical, plumose setae; palp with 4 stiff setae apically. Maxilla 2, inner plate with oblique row of 3 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine and naked setae apically, 3 plumose spines (or coarse setae?) subapically; outer plate with naked setae on inner margin and apex and 1 plumose seta apically. Inner lobes of lower lip vestigial or absent.

Propod of gnathopod 1 subequal in size to 2nd propod; palm with 2 spine teeth on outside, 1 on inside; defining angle with 2 spine teeth of unequal length on outside; posterior margin with 1 seta; medial setae singly inserted. Dactyl nail of gnathopod 1 long. Segment 5 of gnathopod 1 without rastellate setae. Coxal plate of gnathopod 1 longer than broad, margin with 2 setae. Gnathopod propod 2: palm slightly convex, with 2 spine teeth on outside; defining angle with 1 long spine tooth on outside, shorter one on inside; posterior margin rather long, a little longer than palm, with 1 set setae; medial setae rather long, singly inserted. Dactyl nail of gnathopod 2 moderately long. Segment 5 of gnathopod 2 without rastellate setae. Coxal plates of gnathopod 2 and pereopod 3 about as long as broad, margins with 2 setae each. Coxal plate of pereopod 4 about as broad as long, reaching about 35 percent length of basis, margin with 2 long setae. Pereopod 7 slightly longer than pereopod 6, 37 percent length of body, about 25 percent longer than pereopod 5. Pereopods 5–7: bases comparatively short and broad, distoposterior lobes small, distinct, bluntly rounded; dactyls relatively long, 55–60 percent length of corresponding propods. Coxal gill absent from pereopod 7. Three median sternal gills on pereonites 2–4, 2 pairs long, slender, simple lateral sternal gills on pereonites 6 and 7; 1 pair sternal gills on pleonite 1. Brood plates small and narrow.

Pleonal plates: posterior margins of 1 and 3 convex, that of 2 nearly straight, margins with 1 seta each; posterior corners indistinct, broadly rounded; ventral margins of plates 2 and 3 with 1 spine each. Uronites partly fused. Uropod 1: inner ramus subequal in length to outer ramus, about 60 percent length of peduncle, armed with 7 spines;

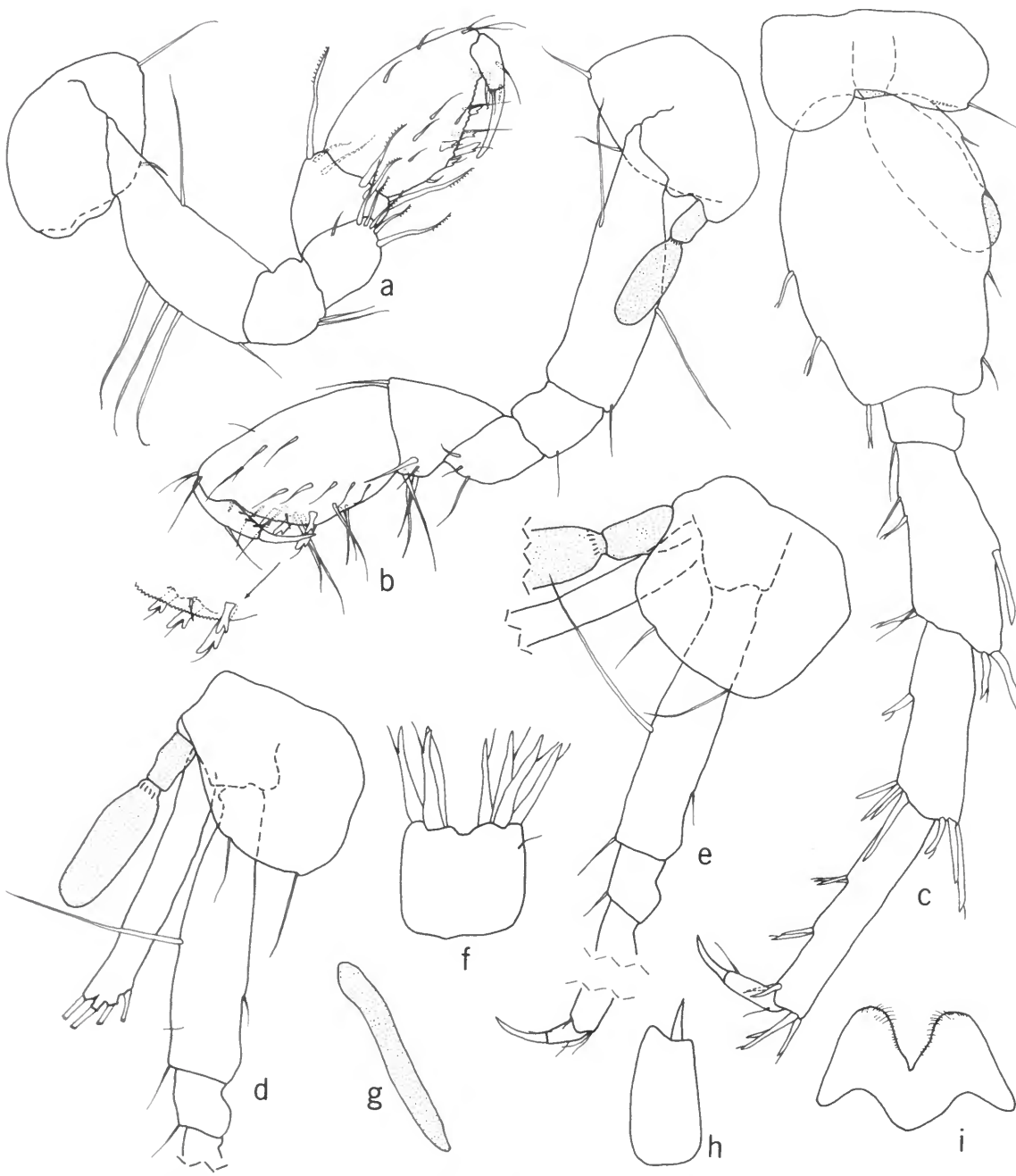

FIGURE 69.—*Stygobromus minutus*, new species, female paratype (2.3 mm), Pettijohn Cave, Georgia: *a*, *b*, gnathopods 1, 2 (palm and defining angle of gnathopod 2 enlarged); *c*, pereopod 6; *d*, *e*, pereopods 3, 4 (in part); *f*, telson; *g*, lateral sternal gill; *h*, uropod 3; *i*, lower lip.

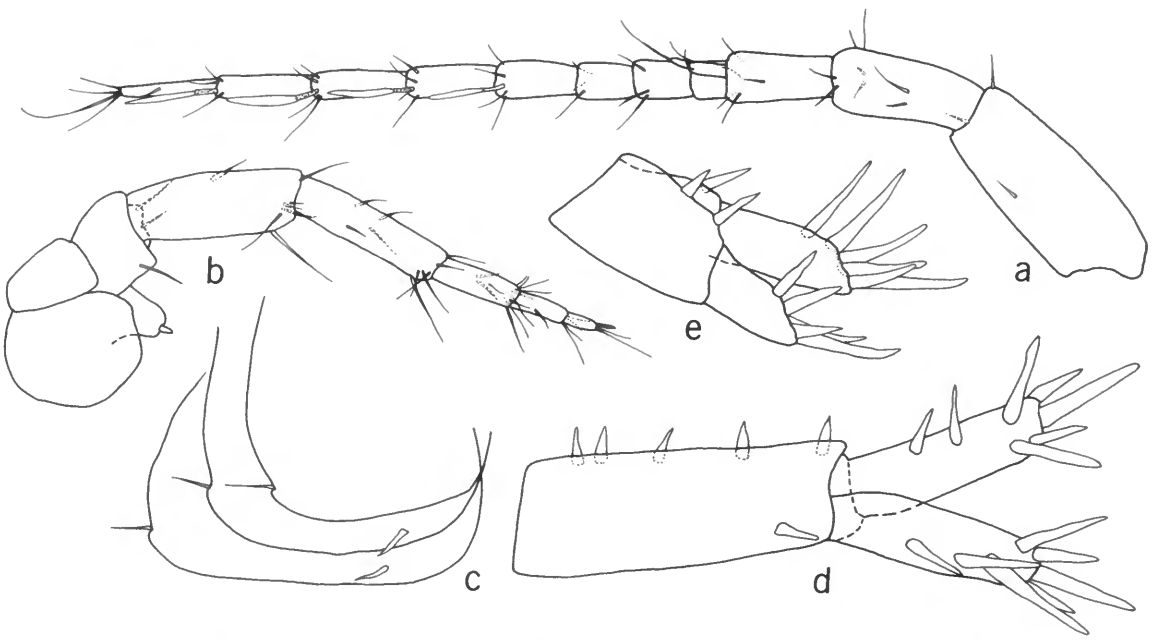

FIGURE 70.—*Stygobromus minutus*, new species, female paratype (2.3 mm), Pettijohn Cave, Georgia: *a*, *b*, antennae 1, 2; *c*, pleonal plates; *d*, *e*, uropods 1, 2.

outer ramus with 7 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, a little shorter than peduncle, armed with 6 spines; outer ramus with 5 spines; peduncle with 3 spines. Uropod 3: ramus absent; peduncle with 1 apical spine. Telson subquadrate; apical margin with small notch, armed with 7 or 8 long spines.

TYPE-LOCALITY.—Pettijohn Cave, located 8 km southwest of Lafayette in Walker Co., Georgia, is a large cave developed in Mississippian limestone along the eastern flank of Pigeon Mountain. The cave is in the upper Coosa River drainage.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where it was collected from a series of two mud-bottom seep/drip pools. A single specimen of *S. dicksoni* was also taken from one of these pools. Of the three females in the type-series, the largest was 2.3 mm in length and had setose brood plates.

REMARKS.—*Stygobromus minutus* appears to be allied morphologically with members of the *ephemerus* group some 515 km to the northeast, but because of its large geographic separation I have not assigned it to this group.

ETYMOLOGY.—The epithet *minutus* is from Latin, meaning "little" or "small."

Stygobromus species

The following six populations are provisionally recognized as distinct species but have not been described for lack of mature specimens or adequate material:

1. A single, immature female (8.0 mm in length), with part of antenna 1 broken off, collected from a well at French Creek, Upshur Co., West Virginia, by F. E. Brooks. This species apparently belongs to the *emarginatus* group.

2. A single, immature female (5.0 mm in length) collected from a spring in a pasture at milepost 6 on the Blue Ridge Parkway, Augusta Co., Virginia, by L. Hubricht (6 June 1952). This species is possibly a member of the *spinosus* group.

3. A single, immature female (7.0 mm in length) collected from New Castle Murder Hole (cave), Craig Co., Virginia, by H. W. Jackson (31 October 1943). This species is closely related to *S. mackini* but differs in having 1 seta each on the posterior

margins of the pleonal plates and a more deeply incised telson (cleft 50 percent the distance to base).

4. A single, mature female (3.0 mm in length), with pereopods 6 and 7 broken off, collected from a small, mud-bottom stream in Crabtree Cave, Garrett Co., Maryland, by L. R. Franz (22 October 1966). Group affinity has not been determined.

5. A single, immature female (4.0 mm in length) collected from a seep below Mt. Lyn Lowry (= Jones Knob) in the Plott Balsam Mountains, Jackson Co., North Carolina, by L. Hubricht (26 May 1958). Group affinity has not been determined.

6. A single, immature female (3.0 mm in length) collected from a seep 1.6 km northeast of Adairsville, Bartow Co., Georgia, by J. R. Holsinger (12 June 1967). Group affinity has not been determined.

Zoogeographical and Ecological Considerations

Origin of Freshwater Stygobromids

Considering the newly expanded concept of *Stygobromus* to include both *Stygonectes* and *Apocrangonyx* and the accumulation of new taxonomic and distributional data on the family Crangonyctidae, my earlier theory for the origin of the genus *Stygobromus* must be signficantly modified to accommodate a larger group with a far broader geographic distribution. In previous papers (Holsinger, 1966:119, 1967:125–130, 1969a:34–39, 1969b:25–27, 1974:58–59), I suggested that species of *Stygobromus,* which were then treated under three separate genera, might have been derived from marine or brackish water ancestors during periods of extensive marine embayments on the North American continent in the Late Cretaceous and throughout parts of the Tertiary. In two recent papers (Holsinger, 1974:59, 1977), however, I also pointed out that the genus or its ancestral stock conceivably could have been in the freshwaters of North America even before the Cretaceous and thus be of greater freshwater antiquity than originally supposed. Two related lines of reasoning now lead me to believe that ancestral stygobromid amphipods were probably established in the freshwater environment prior to the Cretaceous.

1. Unlike several other groups of predominantly subterranean and interstitial amphipods, such as the hadziids (sensu lato), bogidiellids, salentinellids, and ingolfiellids, in which the freshwater forms have obvious marine or brackish water ancestors, the crangonyctids are exclusively freshwater and have no apparent relationship with any marine forms. Furthermore, there are no known groups of marine amphipods that could have been ancestral to, or even related to, ancestors of freshwater crangonyctids. These facts would tend to indicate a very old freshwater lineage for the family. If marine ancestors of freshwater crangonyctids existed in the past they are undoubtedly long since extinct. Bousfield (1958:56) has also alluded to the possible presence of the *Crangonyx* group in North America fresh waters during the Mesozoic.

The presence of three species of *Stygobromus* in areas close to the Chesapeake Bay, which were covered by shallow marine waters several times during the Tertiary, and of several other species that occur close to the old Eocene shoreline of Mississippian embayment in the southern United States previously persuaded me in part to postulate a relatively recent derivation of these species from marine or brackish water ancestors. In retrospect this seems like circular reasoning, since it can be argued just as easily that these species originated farther inland and migrated to these areas following recession of marine waters. I had also previously regarded the Coastal Plain species (i.e., members of the *tenuis* and *pizzinii* groups) as being less specialized morphologically than species farther inland and therefore probably phylogenetically closer to putative ancestral forms (Holsinger, 1967:125–126). Viewed cladistically and within the context of a more broadly expanded generic diagnosis, I can no longer find a legitimate reason for assuming the Coastal Plain species to be less specialized or more ancestral than other species in the genus.

2. The fact that the three largest genera of the six presently included in the family Crangonyctidae have a Holarctic distribution may possibly indicate that they had colonized freshwater habitats on the old Laurasian landmass prior to continental breakup and drifting in the Jurassic. *Crangonyx* occurs in both Europe (as far east as the Ural Mountains) and North America; *Synurella* occurs in North America, Europe and Asia; and, outside of North America, *Stygobromus* is apparently represented in Asia by one poorly known species in Teletzkoye Lake (Siberia) (Holsinger, 1974:1, 1977) and possibly one species (presently assigned to *Synurella*) from a spring on the west coast of the

Caspian Sea (Holsinger, 1977). Moreover, in view of the fact that large areas of Siberia have not been explored for aquatic crustaceans (Bowman and Holmquist, 1975:68), the chances of finding additional species of *Stygobromus* in remote subterranean habitats there cannot be ruled out.

Further evidence of the freshwater antiquity of the crangonyctids is based on the opinions of Barnard (1976), Bousfield (1977), and myself that the northern hemisphere crangonyctids are allied at the superfamily level with a Gondwanaland group of strictly freshwater amphipod genera living in Australia, New Zealand, South Africa, the Falkland Islands, and possibly Madagascar. These genera, like those of the Holarctić crangonyctids, cannot be traced to marine or brackish water ancestors and presumably also have an ancient freshwater ancestry.

In summary, a parsimonious interpretation of the evidence, albeit quite limited, tends to rule out a recent origin of *Stygobromus* from marine ancestors and, on the contrary, points to a very old freshwater lineage dating back at least to the Mesozoic and possibly earlier.

Habitat Diversity

Species of *Stygobromus* have exploited a wide variety of groundwater habitats in the eastern United States. Outside of this region two species of the genus have been described from depths generally exceeding 600 m in Lake Tahoe (California and Nevada) (Holsinger, 1974:40–47), one species has been recorded from a deep lake in Siberia, U.S.S.R. (Holsinger, 1974:1), and J. V. Ward of Colorado State University (in litt.) has recently discovered two undescribed species from a hyporheic habitat (saturated spaces between gravels beneath and to the sides of stream beds) in a mountain river in north-central Colorado. The latter discovery marks the first record known to me of North American subterranean amphipods from the hyporheic medium, but it is not surprising in view of the lack of attention given this important subterranean biotope by American biologists. The hyporheic medium has been extensively investigated in Europe, where it has yielded a rich and significant interstitial fauna (Delamare-Deboutteville, 1960; Vandel, 1965; Husmann, 1971; Bou, 1974).

In an attempt to gain further insight into ecology and dispersal, I have compiled general descriptive data on the different groundwater biotopes inhabited by species of *Stygobromus* in the eastern United States. A good working knowledge of the habitat is indispensable to undesrtanding the potential dispersal ability of subterranean amphipods. Much of this information is based on personal observation; other information has come from colleagues who have assisted with the field work. Species have been collected from basically four different places: (1) caves, (2) wells, (3) surface seeps, bogs, small springs, and their associated runoff, and (4) surface streams. In Table 2, I have enumerated the records for each species from different kinds of habitats. Cave waters have been subdivided to more clearly reflect the specific kinds of habitats represented. The general seep-bog-spring macrohabitat has been divided into two categories, but this division is not always clear-cut as indicated below. In rare instances a few species have been collected from mines and the outlets of surface drains constructed under fields in low-lying areas where the water table is near the surface. For the sake of simplicity, these unusual habitats have been included under other categories in Table 2 as noted. Larger surface streams are undoubtedly atypical habitats for groundwater amphipods but the few occurrences recorded from them, which are believed to be accidental, have been included in the compilation.

Thirty-eight of the 48 species treated in this paper are predominantly cavernicolous and only seven of them have been found in groundwater habitats outside of caves per se. Except for one species (the highly vagile, wide-ranging *S. allegheniensis*), which is commonly found outside of caves, the other six have been collected from noncave habitats only rarely. The questionable spring records for *S. emarginatus* and *S. spinatus* are based on a collection from a tiny, subsurface stream which was exposed at about 3 meters beneath the ground during excavation for spring water (S. W. Hetrick, Old Dominion University, pers. comm.). This artificially excavated spring is in the same immediate area as several cave populations of both species.

Among the 10 remaining species, nine occur outside of karst areas and are strictly noncavernicolous. The range of the tenth species, *S. pizzinii*, is largely in a noncavernous region, but where it ex-

TABLE 2.—Records of species of *Stygobromus* from different kinds of habitats in the Appalachian and Coastal Plain regions of the eastern United States

Species (by groups)	Caves[1]			Wells	Bogs and seeps[2]	Springs or spring-runs	Surface streams (accidental)
	Streams	Drip/seep pools	Phreatic lakes				
emarginatus group							
S. emarginatus	18	5	1	-	-	1(?)	-
S. morrisoni	2	-	1	-	-	-	-
S. mundus	1	-	-	-	-	-	1
S. hoffmani	-	2	-	-	-	-	-
S. fergusoni	-	2	-	-	-	-	-
S. franzi	2	2	-	-	-	-	-
S. cooperi	-	1	-	-	-	-	-
S. obrutus	-	-	-	1	-	-	-
S. culveri	-	1	-	-	-	-	-
ackerlyi group							
S. ackerlyi	2	-	-	-	-	-	-
S. inexpectatus	-	1(?)	-	-	-	-	-
gracilipes group							
S. gracilipes	4	7	-	-	-	-	-
S. conradi	2	-	-	-	-	-	-
spinosus group							
S. spinosus	-	-	-	-	-	8	-
S. pseudospinosus	-	1	-	-	-	-	-
S. kenki	-	-	-	1	-	2	-
ephemerus group							
S. ephemerus	-	2	-	-	-	-	-
S. estesi	-	2	-	-	-	-	-
S. parvus	-	3	-	-	-	-	-
S. pollostus	-	4	-	-	-	-	-
S. nanus	-	1	-	-	-	-	-
S. redactus	-	1	-	-	-	-	-
spinatus group							
S. spinatus	16	13	-	-	-	1(?)	-
mackini group							
S. mackini	11	49	-	-	-	2	-
S. abditus	1	-	-	-	-	-	-
S. dicksoni	-	9	-	-	-	-	-
S. finleyi	-	1	-	-	-	-	-
S. leensis	-	3	-	-	-	-	-
S. sparsus	-	1	-	-	-	-	-
S. barryi	1	-	-	-	-	-	-
S. carolinensis	-	-	-	-	1	-	-
S. grandis	-	1	-	-	-	-	-
cumberlandus group							
S. cumberlandus	-	3	-	1	-	-	-
S. interitus	-	1(?)	-	-	-	-	-
phraeticus group							
S. phreaticus	-	-	-	2	-	-	-
araeus group							
S. araeus	-	-	-	-	3	5	-
pizzinii group							
S. pizzinii	-	1(?)	1	4	2	4	1
S. identatus	-	-	-	1	3	-	-
tenuis group							
S. tenuis s. lat.	-	-	-	9	20	16	7
S. allegheniensis	7+2(?)	12	1(?)	6	2	9	2
S. hayi	-	-	-	-	-	1	-
ungrouped species							
S. stellmacki	-	1	-	-	-	-	-
S. baroodyi	4	1	-	-	-	-	-
S. borealis	-	-	1	-	-	-	-
S. biggersi	1(?)	3	-	-	-	-	-
S. stegerorum	-	-	2	-	-	-	-
S. fecundus	-	1	-	-	-	-	-
S. minutus	-	1	-	-	-	-	-

[1]Includes one-record each for S. allegheniensis, S. franzi, and S. pizzinii from mines in limestone areas.
[2]Includes two drain outlets for one species, S. indentatus.

tends into an area of limestone bedrock (i.e., Lancaster Co., Pennsylvania), the species has been found in one cave and one mine.

Aquatic cave habitats usually consist of streams, drip/seep pools, and phreatic pools. Cave streams vary greatly in size but species of *Stygobromus* are usually found in smaller streams (up to 2 m wide and 10–15 cm deep) where the substrate is small rocks and gravels or mud and silt. Some streams are only tiny trickles fed by seeps or overflow from pools and are thus intermediate between true streams and ponds. Cave pools are generally fed by ceiling drips or lateral seepage from wall crevices and may have mud, gravel or bedrock substrates. The majority of amphipods, however, are found in the mud-bottom, ceiling drip variety, where conditions for burrowing (see Holsinger and Dickson, 1977) and available nutrients from organically enriched mud (Dickson and Kirk, 1976) are satisfied. Phreatic pools, which are deeper and much less common than drip/seep pools, are found where cave passages or mine shafts intersect the groundwater table. Species of *Stygobromus* are rarely encountered in phreatic pools, although one species, *S. stegerorum*, is found there exclusively and, outside of a spring record, *S. borealis* is known only from this kind of habitat.

As indicated by the data in Table 2, approximately 63 percent of the records of *Stygobromus* from caves are from drip/seep pools and approximately 21 species are known only from this habitat. Nine species appear to be primarily stream dwellers but only four or five have been collected enough times to be accurately classified according to habitat. Two of these species, *S. emarginatus* and *S. spinatus,* have been studied in detail by Culver (1970a) and he has concluded that they are adapted to the rock-gravel substrate of small streams but that each species occupies a separate microhabitat according to substrate depth and rock or gravel size. Both species, however, also occur in drip pools but only *S. spinatus* occurs there with any frequency or in substantial numbers. Several predominantly pool-dwelling species are also found in streams but are encountered in pools much more frequently. For example, *S. gracilipes* and *S. mackini,* occur in streams occasionally but stream populations are small and sporadic, indicating that this is probably not the preferred habitat of the species.

Wells have not been as thoroughly investigated as some of the other habitats enumerated in Table 2, but 25 out of 334 (7.5 percent) of the collections of *Stygobromus* have come from them. Although wells do not constitute a natural habitat, they nevertheless provide an important means of access to perched or permanent groundwaters (phreatic waters) beneath the surface. The amphipod fauna of wells is that which inhabits reservoirs or sheets of phreatic water. In the present study, eight species have been found in wells and two of these are known only from them. Wells generally tap phreatic water at varying depths, depending on the groundwater hydrology in a given area. On the Coastal Plain and along the eastern margin of the Piedmont, wells are often quite shallow and some reach groundwater at depths of a few meters. Further inland wells are usually much deeper. About one-half of the wells represented in the collections are the shallow, hand-dug type, the others being deeper and thus more difficult to sample and observe. In my own experience with well sampling, which is quite limited, I have found them to be unpredictable places for finding amphipods and usually difficult to adequately sample. Many of the well records cited in this paper are based on museum specimens and not on my own field work.

Of particular significance in the distribution of *Stygobromus* are those species found in groundwater habitats at the surface. These "epigean" habitats are typically in the form of: (1) seeps or bogs where groundwater oozes to the surface from the underlying mantle or bedrock and frequently forms tiny streams of rivulets which flow through leaf litter and/or vegetation; and (2) small springs which are usually larger, more permanent, and may have faster runoff than seeps but are otherwise similar. A distinction between these two habitats is not always easy to make because there are sometimes intermediate situations, e.g., a large seep might be called a small spring, a small spring a large seep, etc.

Meštrov (1962) proposed the term *"biotope hypotelminorhéique"* for a type of groundwater habitat similar to the one described under (1), and to a lesser extent under (2), above. The hypotelminorheic habitat (see also Vandel, 1965:11) was first recognized by Meštrov from a mountainous area in eastern Croatia (Yugoslavia) and from the central Pyrénées in southern France. In the hypotelminorheic habitat both Meštrov (1962) and Bouillon

(1964) found a number of organisms, including the amphipod *Niphargus* and the isopod *Stenasellus,* which are also cavernicolous. Both workers suggested that this habitat appeared to be primary for some species of *Niphargus* and that the cave populations, which are often smaller, are probably replenished periodically by mirgrants from shallow groundwaters above caves.

Among species of *Stygobromus* in the eastern United States, 13 have been recorded from groundwater outlets at the surface and three of these are known only from this kind of habitat. The other 10 species are also known from caves and/or wells and three are primarily cavernicoles. Surface seeps and small springs (mostly hypotelminorheic habitats) with *Stygobromus* appears to be much more common in the Coastal Plain, the Piedmont and parts of the Blue Ridge Mountains, where groundwater tables are often close to the surface, than in the karst areas of the Appalachians, where groundwater tables are frequently much deeper. In most karst areas, springs are typically large, permanent resurgences of underground streams (i.e., karst springs), frequently inhabited by the epigean form (form III, see Holsinger and Culver, 1970:3) of the amphipod *Gammarus minus* and epigean species of the asellid isopod *Lirceus.* I have rarely found hypotelminorheic habitats in limestone areas of the Appalachians.

On the Coastal Plain and in the eastern Piedmont near Washington, D.C., and east of Richmond, Virginia, I have made a number of pertinent observations and collections of *Stygobromus* (viz., *S. tenuis* and *S. araeus*) during the last 10 years. Most of the sites visited were hypotelminorheic habitats situated in small wooded areas. Amphipods were found in dead leaves or fine sediment submerged in the water. Many of these habitats are temporary and dry up completely during the summer or fall. Some, however, remain viable in wet years and amphipods have been taken in several of them during all seasons of the year. In the Blue Ridge Mountains of Virginia and on the flanks of ridges in east-central Pennsylvania, I have collected *S. spinosus* and *S. allegheniensis,* respectively, from similar habitats except that in some cases the outlets were larger and appeared to have year-around flow.

Although I suggested in an earlier paper (Holsinger, 1967:10) that those species of *Stygobromus* found almost exclusively in seeps and small springs occurred at the surface mainly because of flooding or periodic fluctuation of the groundwater table, my recent observations indicate that some populations apparently live more or less permanently in the "epigean" waters of the hypotelminorheic medium and probably burrow into damp sediments or leaf litter during dry weather to escape desiccation. Other populations probably occupy both phreatic and hypotelminorheic habitats and presumably migrate between the two under certain conditions which are as yet poorly understood. Outside of caves, very little is really known about groundwater ecosystems in North America and future research is badly needed.

Stygobromus tenuis is the only species of the genus that has been collected from a surface stream (excluding tiny streams fed by seeps and small springs) more than twice. As already pointed out, larger surface streams are undoubtedly an atypical habitat for species of *Stygobromus,* and the few existing records have probably resulted from specimens having been washed out of hypotelminorheic or cave habitats during flooding or, possibly, having been flushed out of hyporheic habitats beneath stream beds. *Stygobromus tenuis* is very common in shallow groundwater habitats in parts of its range, and its occasional occurrence in surface streams is not surprising.

Geographic Distribution and Dispersal

The distribution of species of *Stygobromus* in the eastern United States is shown in Figures 71–77. Although species ranges are quite variable in extent, they appear to fit one of three basic patterns: (1) Localized distribution in which ranges are moderately to highly insular and species are known only from one or several neighboring localities within a radius of 16–24 km. Included here are 32 species, of which 18 are recorded from single localities, 9 from two localities and the remainder from three to six localities. (2) Distribution restricted to a single major drainage system. This pattern includes four species, of which only one has a range barely exceeding 161 km. (3) Distribution covers parts of two or more major drainage systems. Included here are 12 species, of which six have ranges exceeding 161 km.

Ranges undoubtedly have been influenced to a large degree by physical barriers to dispersal (Hol-

singer, 1967, 1969a, 1969b), but ecological factors, some of which are discussed below, are also believed to be important in determining dispersal potential and the extent of range. The different range sizes suggest that some species are probably better dispersers than others, but two problems should be kept in mind when analyzing dispersal potential based on range size: (1) owing to the cryptic nature of the fauna, complete ranges of many species are probably not yet known; and (2) some species may be "morphologic" rather than "genetic" inasmuch as all populations in the range of a species may appear generally similar morphologically but may not be capable of interbreeding.

I have already shown elsewhere (Holsinger, 1969a: 42–43, 1975b) that at least one species of cavernicolous amphipod, *Crangonyx antennatus,* is apparently able to disperse between caves by utilizing

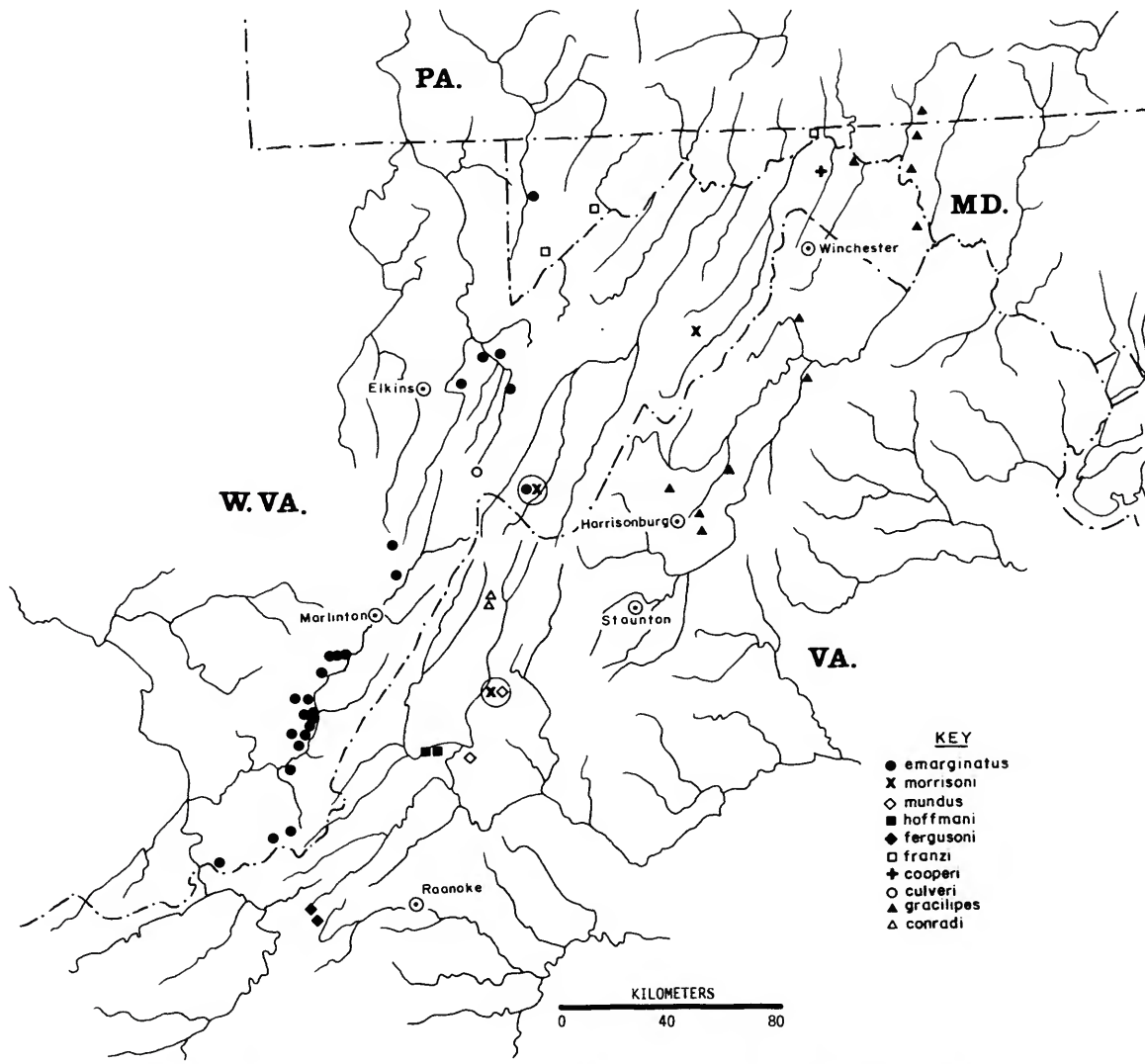

FIGURE 71.—Distribution of *Stygobromus* in the eastern United States: species of the *emarginatus* group (except *S. obrutus,* see Figure 77) and *gracilipes* group. (Two symbols in a circle indicate two species from the same locality.)

shallow groundwater habitats. On two different occasions amphipods of this species were caught in plastic buckets as they passed into a cave through ceiling drips, and it was assumed from these observations that amphipods inhabit a zone saturated with groundwater above the cave and pass downward into dry passages by migration and/or accident. Further evidence of this mode of dispersal and cave entry comes from an observation made on a large population of *S. mackini* in two wooden troughs on the upper, comparatively dry level of a cave in Bland Co., Virginia (Holsinger, 1969a:42). The troughs, which are presumably relics from a saltpetre mining operation in the middle 1800s, are situated below ceiling drips, which is their only source of water. The only way amphipods could have gained access to the troughs would have been via dripping water, which is fed either by vadose circulation or from a perched water table above the cave. A number of other caves in the Appalachians also contain old wooden troughs and buckets populated by subterranean amphipods. In none of these cases has the habitat above the cave been observed directly but it is assumed to be in the form of saturated crevices and joints in the bedrock or saturated interstices in the overlying mantle. The

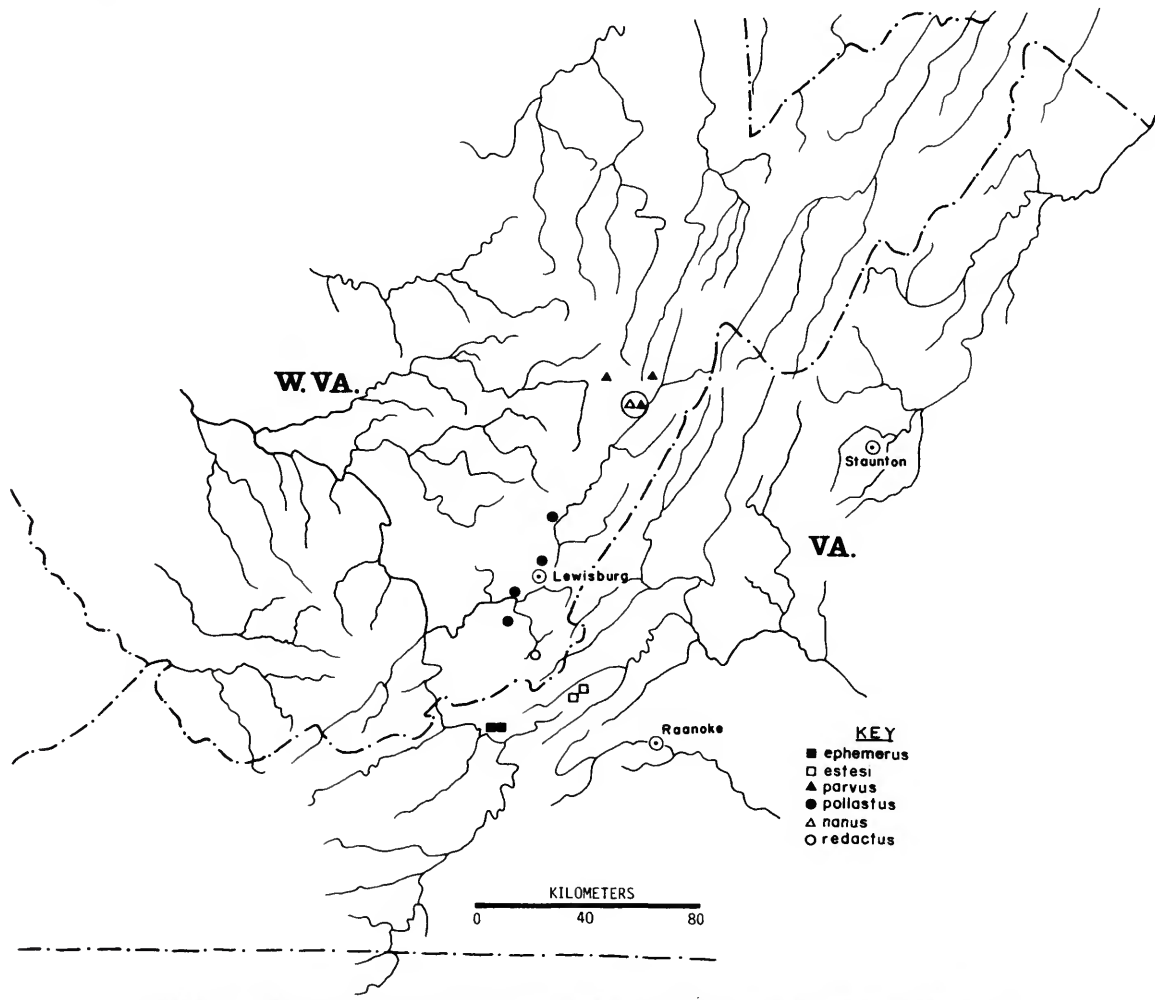

FIGURE 72.—Distribution of *Stygobromus* in the eastern United States: species of the *ephemerus* group. (Two symbols in a circle indicate two species from the same locality.)

fact that both *S. mackini* and *C. antennatus* have been found in small springs and seeps at the surface is further evidence that they are able to populate shallow groundwaters and thus potentially migrate through this zone. I have termed this theoretical means of movement of small, subterranean crustaceans through shallow groundwaters "interstitial dispersal" and have discussed it in some detail in previous papers on amphipods (Holsinger, 1967, 1969a), isopods (Steeves and Holsinger, 1968; Holsinger and Steeves, 1971), and West Virginia cave invertebrates (Holsinger, Baroody, and Culver, 1976). A similar mode of dispersal for species of *Stygobromus* living in the noncavernous Piedmont and Costal Plain regions has also been suggested (Holsinger, 1967:129).

As indicated in Table 2, more than 50 percent of the cave species of *Stygobromus* in the eastern United States are known only from pools. But, despite the fact that the majority of cave species occur in this habitat and that some individuals apparently secrete themselves in the muddy substrate, cave pool populations, with some exceptions, are generally small and often sporadic. This is especially true of the typically tiny species of the *ephemerus* group, smaller species of the *cumber-*

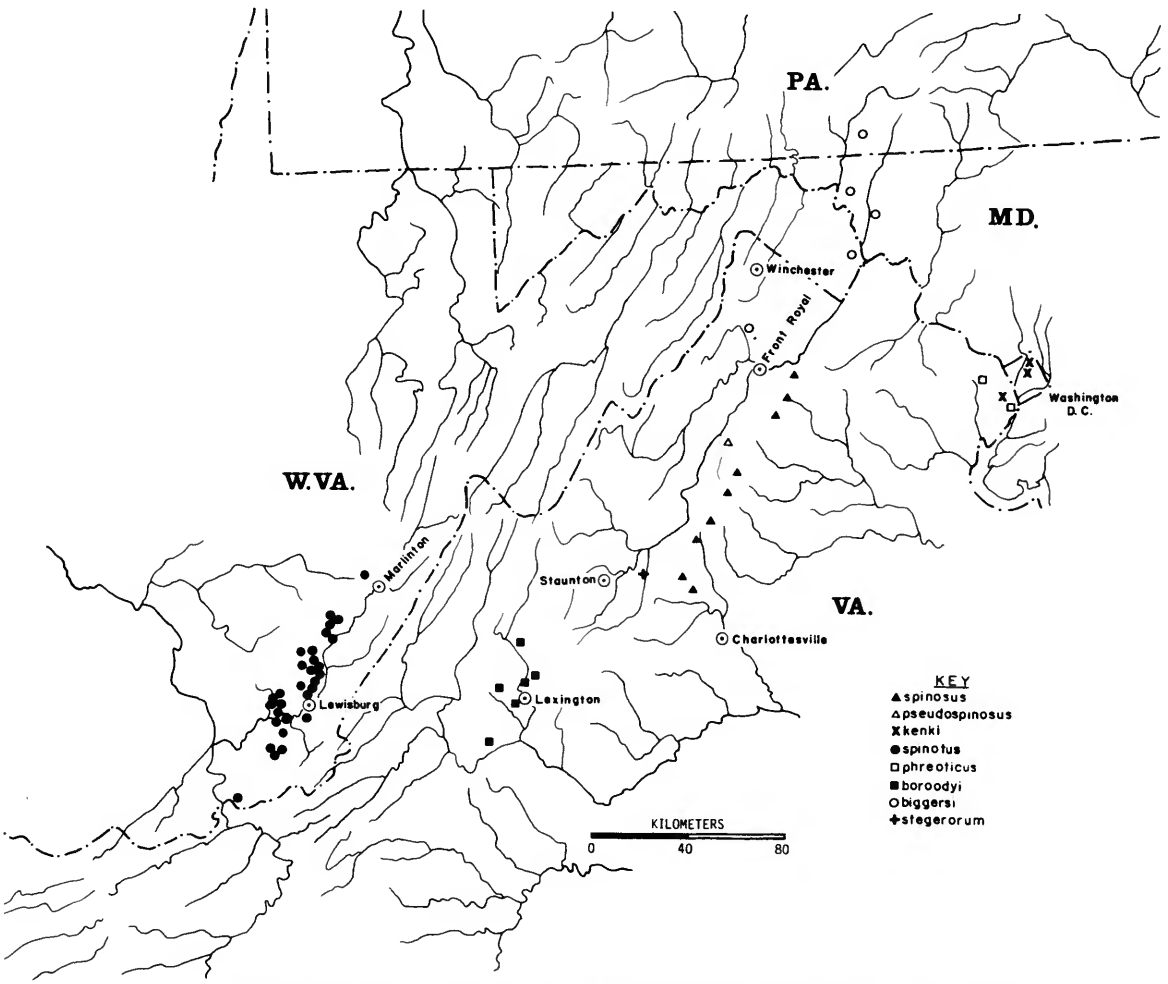

FIGURE 73.—Distribution of *Stygobromus* in the eastern United States: species of the *spinosus*, *spinatus*, and *phreaticus* groups, and *S. baroodyi*, *S. biggersi*, and *S. stegerorum*.

landus, emarginatus, and *mackini* groups, and also *S. minutus* and *S. pseudospinosus.* Two larger species, *S. grandis* and *S. stellmacki,* are similarly known only from a few rare specimens in pools.

Based on the small size and sporadic nature of many cave pool populations, the evidence for interstitial dispersal and the fact that a number of cave species are also found in groundwater habitats outside of caves, I have concluded that cave pools for many species of *Stygobromus* are probably marginal habitats that are populated at random as amphipods pass into caves via ceiling drips and seepage. Apparently few species of *Stygobromus,* then, are strictly obligatory cavernicoles (i.e., troglobites), but many are, broadly speaking, phreatobites, which potentially colonize a number of different kinds of groundwater habitats within their respective ranges.

If my assumption is correct, caves were originally and are continuing to be invaded and colonized by a pervasive, phreatobitic amphipod fauna that enters caves from the surrounding groundwater. However, some species, like *S. emarginatus* and *S. spinatus,* which appear to be permanent members of the cave stream fauna, and *S. mackini,* which is common and widespread in cave pools and also occurs in streams, are probably more firmly entrenched in caves and might have been there longer than many of the seemingly ephemeral species that appear in pools occasionally and in small numbers.

In nonkarst areas species of *Stygobromus* inhabit

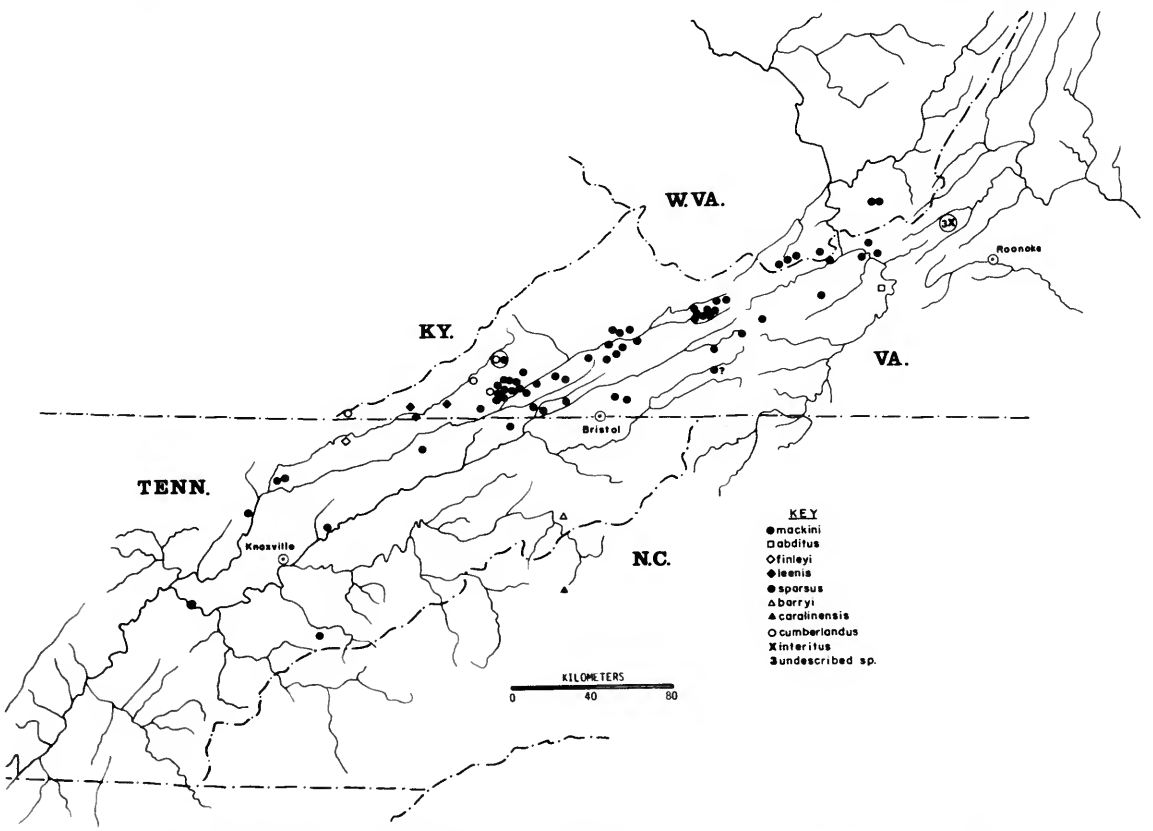

FIGURE 74.—Distribution of *Stygobromus* in the eastern United States: species of the *mackini* group (in part, see Figure 75) and *cumberlandus* group. (Question mark indicates a questionable record for *S. mackini;* an undescribed species from New Castle Murder Hole (cave) is indicated by number 3 (see text); two symbols in a circle indicate two species from the same locality.)

both phreatic water (as evidenced by their presence in wells) and surface groundwater of the hypotelminorheic. The presence of some of the same species in both biotopes indicates that dispersal occurs between the two zones, presumably in a manner analogous to that in cave regions.

Another indicator of dispersal potential in subterranean amphipods may be niche breadth and mobility as reflected by species size. Poulson and White (1969:973) suggested that the ability of troglobities to move between caves depends mainly on their size and that small species attain wide geographic distribution because they can move through stream gravels, soil, and various interstitial media outside of caves. According to this hypothesis, smaller cavernicolous species would have wider ranges than larger species. This generalization is too broad, however, and Barr and Holsinger (1971:115) have suggested that mobility and niche breadth are also significant factors in troglobite dispersal. Contrary to the suggestion of Poulson and White (1969:973), the larger species in a number of troglobitic and/or phreatobitic groups, such as beetles and amphipods, for example, fre-

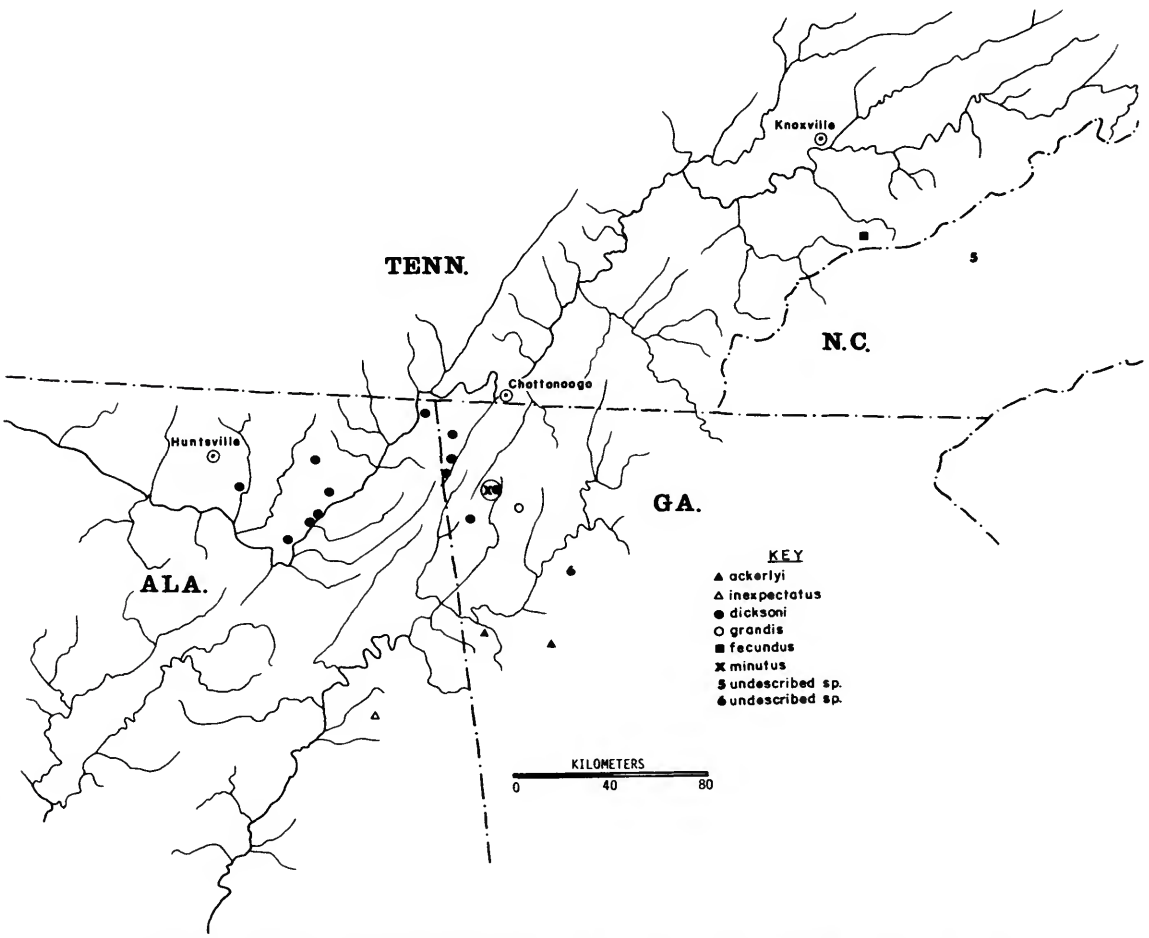

FIGURE 75.—Distribution of *Stygobromus* in the eastern United States: species of the *ackerlyi* group and *mackini* group (in part, see Figure 74), and *S. fecundus* and *S. minutus*. (Undescribed species from seeps in North Carolina and Georgia are indicated by numbers 5 and 6, respectively—see text; two symbols in a circle indicate two species from the same locality.)

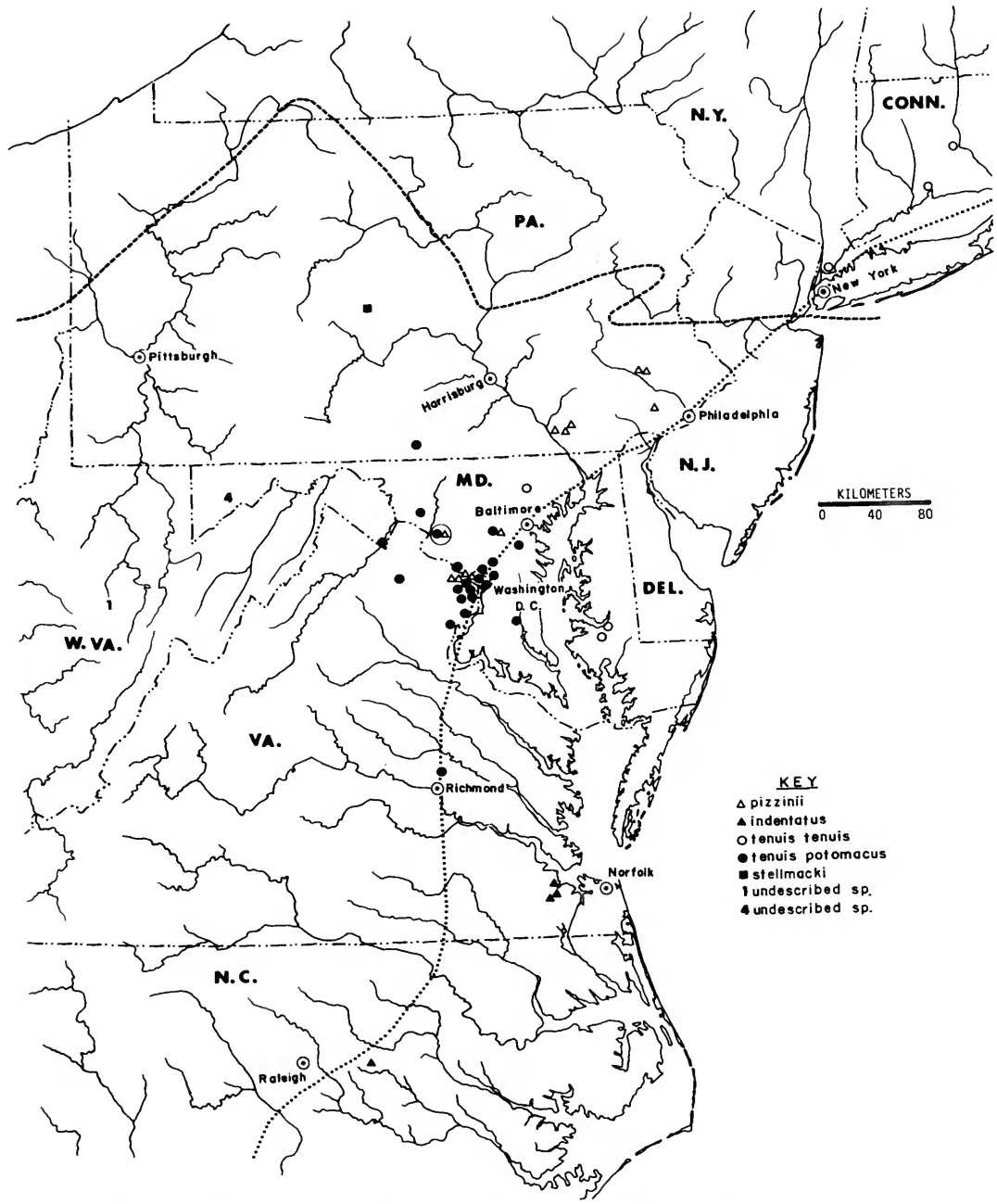

FIGURE 76.—Distribution of *Stygobromus* in the eastern United States: species of the *pizzinii* group and *tenuis* group (in part, see Figure 77) and *S. stellmacki*. (Undescribed species from a well in West Virginia and a cave in Maryland are indicated by numbers 1 and 4, respectively (see text). Not all locality records for *S. t. potomacus* in the Washington, D.C. area are shown. Two symbols in a circle indicate two species from the same locality. The dashed line indicates the approximate southern extent of glaciation during the Pleistocene. The dotted line marks the approximate boundary between the Coastal Plain to the east and the Appalachian region to the west.)

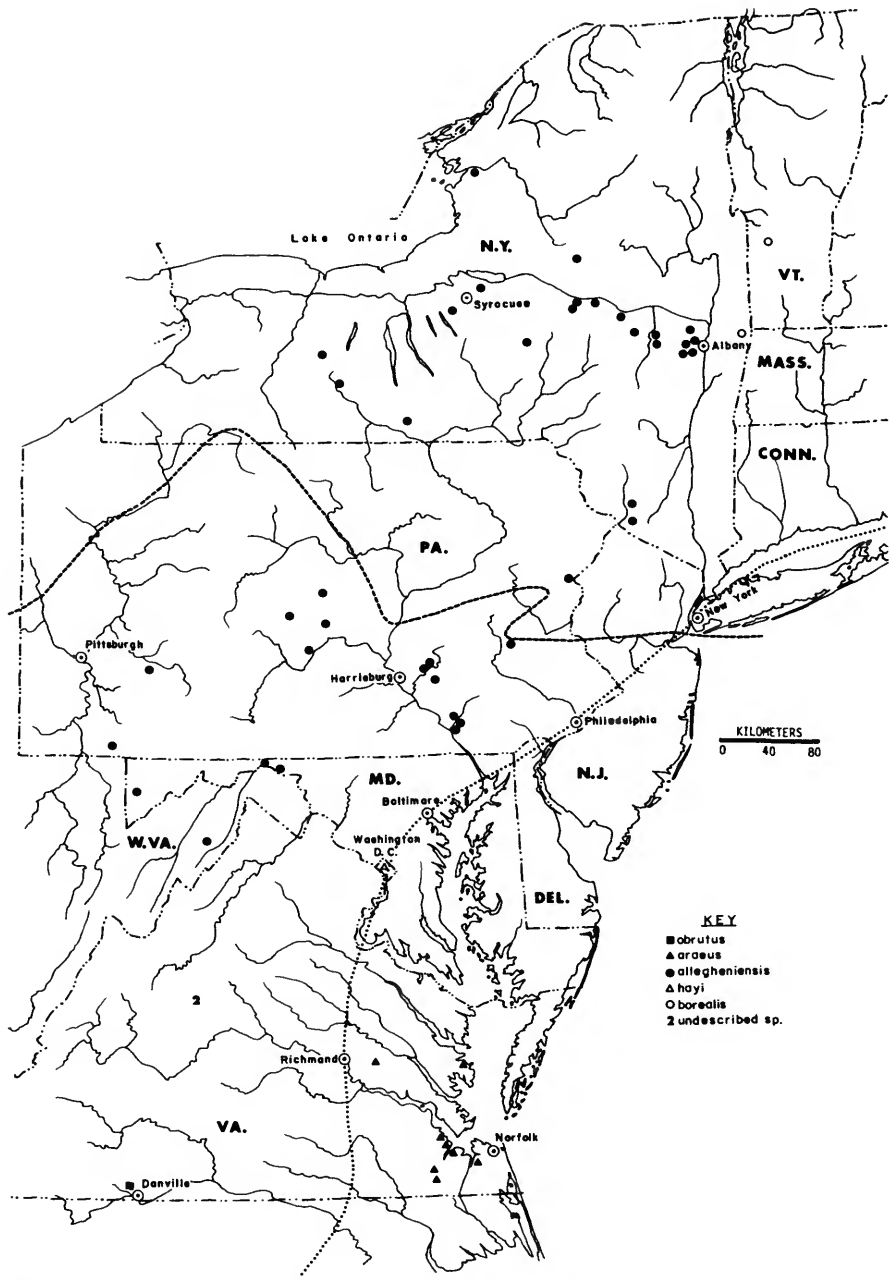

FIGURE 77.—Distribution of *Stygobromus* in the eastern United States: species of the *araeus* group and *tenuis* group (in part, see Figure 76), and *S. obrutus* (*emarginatus* group) and *S. borealis*. (An undescribed species from a spring in Virginia is indicated by number 2—see text. The dashed line indicates the approximate southern extent of glaciation during the Pleistocene. The dotted line marks the approximate boundary between the Coastal Plain to the east and the Appalachian region to the west.)

quently have wider ranges than the smaller species (Barr and Holsinger, 1971:115).

With some exceptions, the larger species of *Stygobromus* appear to have the widest ranges. In order to demonstrate this quantitatively, a comparison of maximum body length with range size was made for the 48 species in the eastern United States and the results are given in Table 3. A significant correlation between species size and range size was found in three categories of comparison: among all species, among cavernicolous species, and among noncavernicolous species. These correlations are even greater if the square roots of range size are used. By utilizing square roots the variance in range size is reduced and the relationship becomes more linear. Although none of the correlation coefficients is particularly high, all are significant and indicate that range size increases with species size.

Since larger size alone would probably not facilitate dispersal, another causal relationship must be sought. As pointed out above, Barr and Holsinger (1971) have already suggested that niche breadth and mobility are significant factors in subterranean dispersal, and it appears likely that these factors affect the ranges of species of *Stygobromus*. Habitat diversity is generally greater for larger species of both cavernicolous and noncavernicolous forms (Table 2). Among the 15 larger cave species (length 7.0 mm or longer), 8 are found in both pools and streams and 4 of these have also been collected outside of caves, 5 are found only in pools, and 2 only in streams. Among the 23 smaller cave species (less than 7.0 mm in length), 20 are known only from pools, 2 only from streams, and 1 from both pools and streams. Among the noncavernicolous species, the five larger ones occupy a greater variety of habitats than the five smaller ones. Three of the larger species are found in two or more different kinds of habitats, whereas only two of the smaller species are found in more than one kind of habitat.

From these observations it appears that larger species tend to occupy a greater range of habitats, therefore suggesting a relationship between greater niche breadth and mobility and larger size. The adaptive flexibility which allows many of the larger cave species to select both streams and pools would increase their chances for dispersal and would ultimately lead to wide ranges. Similarly, greater adaptive flexibility in larger noncave species would also enhance dispersal and thus result in wider ranges. Smaller species, both cavernicolous and noncavernicolous, may be more narrowly adapted and consequently more restricted in habitat selection and dispersal potential.

Co-occurrence of Species

In Table 4 I have given the records for co-occurrence among species of *Stygobromus* in the the eastern United States. Twenty-six species have been collected together either from the same habitat (syntopy) or from different habitats in the same cave. Fifteen cases of syntopy involving species pairs have been noted, but only five of these are

TABLE 3.—Comparison of maximum size[1] with range size[2] of species of *Stygobromus* from the Appalachian and Coastal Plain regions of the eastern United States using Pearson product-moment correlation coefficients

Variable pairs	No. of species	r	P
All species	48	1.3118	<.015
All species (square root of ranges)	48	0.4382	<.001
Cavernicolous species	38	0.2836	<.042
Cavernicolous species (square root of ranges)	38	0.3619	<.013
Non-cavernicolous species	10	0.6068	<.031
Non-cavernicolous species (square root of ranges)	10	0.6992	<.012

[1]Length in millimeters of largest adults in each species.
[2]Calculated in square kilometers. The ranges of one-locality endemics were arbitrarily set at 2.56 square kilometers or 1 square mile.

TABLE 4.—Co-occurrence of species of *Stygobromus* from the Appalachian and Coastal Plain regions of the eastern United States (x = record of two species from the same cave but not together in the same collection from the same habitat; xx = record of two species in the same collection from the same habitat)

Species	emarginatus	morrisoni	mundus	franzi	gracilipes	kenki	ephemerus	estesi	parvus	nanus	spinatus	mackini	dicksoni	sparsus	cumberlandus	interitus	araeus	pizzinii	indentatus	tenuis	allegheniensis	hayi	stellmacki	biggersi	fecundus	minutus
emarginatus		xx							x	x	xx										xx					
morrisoni	xx		xx																		xx					
mundus		xx																								
franzi																					x					
gracilipes																								xx		
kenki																				xx						
ephemerus												xx														
estesi																x										
parvus	x									x																
nanus	x								x																	
spinatus	xx											xx														
mackini							xx				xx				xx											
dicksoni																										xx
sparsus																									xx	
cumberlandus												xx														
interitus								x																		
araeus																			xx							
pizzinii																				xx						
indentatus																	xx									
tenuis						xx												xx				xx				
allegheniensis	xx	xx		x																			x			
hayi																				xx						
stellmacki																					x					
biggersi					xx																					
fecundus														xx												
minutus													xx													

based on more than one collection from a given site and it is difficult to determine whether these associations are permanent or occur at random. In most cases of syntopy one species was usually found to be much more abundant than the other. Of the five cases of syntopy based on multiple collections, only the species pair *S. emarginatus–S. spinatus* from caves in the Greenbrier Valley of West Virginia has been analyzed in depth (see Culver, 1970a, and elsewhere in this paper). The other four are summarized as follows: *S. emarginatus* was taken with *S. allegheniensis* twice in four collections from John Friends Cave in Maryland; *S. mackini* was taken with *S. ephemerus* once in four collections from Tawneys Cave in Virginia; *S. sparsus* was taken with *S. fecundus* once in four collections from Gregorys Cave in Tennessee; and *S. tenuis* was taken with *S. kenki* once in seven collections from a small spring in Washington, D. C.

In most cases where the ranges of two species coincide they have been found together in the same cave or same habitat at least once. Several exceptions have been noted, however. The range of *S. pollostus* overlaps parts of the ranges of both *S. emarginatus* and *S. spinatus* in the Greenbrier Valley, but *S. pollostus* has never been found in the same cave with either of the other species. The ranges of five species coincidè in the greater Washington, D. C., area but syntopy is uncommon and habitat exclusion appears rigorous. In this area, *S. tenuis* has been found only once with *S. hayi* and once with *S. kenki.*

With the exception of several species pairs which have broadly overlapping ranges (e.g., *S. emarginatus–S. spinatus, S. biggersi–S. gracilipes, S. araeus–S. indentatus,* and *S. pizzinii–S. tenuis*), most cases of co-occurrence have been noted near the periphery of two otherwise allopatric ranges or where a wide-ranging species is distributed through an area containing a local endemic.

Within species groups, allopatric ranges are the rule and only a few exceptions involving syntopy or sympatry between morphologically closely allied species have been noted. In the *emarginatus* group, *S. emarginatus* has been taken together with *S. morrisoni* in one cave on the outer periphery of the range of the former, and *S. morrisoni,* in turn, has been taken together with *S. mundus* in a single cave where the ranges of the two species meet in Bath Co., Virginia. In the *ephemerus* group, *S. parvus* and *S. nanus* have been collected from the same cave but at different times in different places. In the *tenuis* group, *S. tenuis* has been taken together once with *S. hayi* from a small spring in Washington, D. C., but the latter outnumbered the former 21 to 1.

Based on the above observations, I have concluded that only a few species of *Stygobromus* occur together on a regular basis and those that do are almost always morphologically distinct enough to be placed in separate groups. Further studies are needed, however, to determine the interactions of syntopic species. With the exception of one case involving possible hybridization between *S. tenuis* and *S. hayi* in the Washington, D. C., area (Holsinger, 1967:74–75), there is no other evidence of interbreeding between species where ranges are sympatric or where species occur syntopically. By inference it appears that speciation in *Stygobromus* has been allopatric and that most contact between species has been established since reproductive isolating mechanisms were perfected.

Glacial Relicts

One final zoogeographic problem involves subterranean amphipods that range north of the southern limits of Pleistocene glaciation. Seven species of *Stygobromus* and two species of *Bactrurus* occur in glaciated areas of North America. *Stygobromus allegheniensis, S. borealis,* and *S. tenuis* occur in the northeastern United States; *S. iowae* and *S. putealis* are found on the periphery of the Driftless Area in northeastern Iowa, extreme northwestern Illinois and eastern Wisconsin; and *S. lucifugus* and *S. subtilis* occur in western Illinois. Since the last four species occur outside of the region covered in this paper, their zoogeography will be treated in Part III of the current generic revision.

As shown in Figure 77, more than 50 percent of the range of *S. allegheniensis* extends north of the glacial boundary, whereas, in contrast, only a small segment of the range of *S. tenuis* occupies a glaciated region (Figure 76). *Stygobromus borealis,* on the other hand, is known only from localities far north of glacial limits (Figure 77). I suggested previously (Holsinger, 1967:155) that *S. allegheniensis* either has migrated north into glaciated areas since

the late Pleistocene or was already living in glaciated areas before the Pleistocene and was able to survive glaciation by retreating into deep groundwater refugia under the ice.

Stygobromous allegheniensis and *S. tenuis* are very closely allied morphologically and are presumably sister species; they are in turn closely related to other species of the *tenuis* group that occur in the southern United States. Considering that both species have obvious morphological affinity with southern relatives and that their ranges also cover areas to the south of glaciation (Figure 76, 77), a northward migration following retreat of the Wisconsin glacier is a possibility that cannot be ruled out and is the one that I had tended to favor in the past (Holsinger, 1967:155, 1976:84). However, the distance involved in postglacial dispersal would have been tremendous, especially for *S. allegheniensis,* and the migration of small, cryptic subterranean amphipods from some hypothetical place in southern Pennsylvania to the vicinity of Lake Ontario in the span of some 10,000 to 15,000 years may be stretching credence. It seems more probable, at least for *S. allegheniensis,* that relict populations survived in glaciated areas by remaining protected in groundwater refugia during the Pleistocene. The probability that *S. borealis* survived glaciation in a deep groundwater refugium is even greater. This species is unique morphologically and is apparently not closely related to any other in the genus. There is at present no zoogeographic evidence to suggest that *S. borealis* (or its precursor) has undergone extensive postglacial dispersal.

Since troglobitic organisms are generally absent from glaciated regions in the northern hemisphere, most workers have assumed that any cave faunas that might have existed at northern latitudes prior to the Pleistocene were subsequently exterminated by the effects of glaciation (Vandel, 1965:275–276). Most terrestrial troglobites in the temperate climate of the northern hemisphere, however, are believed to have evolved under the influence of fluctuating climates in areas to the south of glaciation during the Pleistocene (Vandel, 1965:468–469; Barr, 1968: 84). On the other hand, small, aquatic crustaceans like amphipods and isopods have probably been in the hypogean environment much longer than terrestrial forms, and their invasion of subterranean waters for the most part is probably unrelated to the climatic vicissitudes of the Pleistocene.

Subterranean amphipods were probably established in groundwater habitats long before the Pleistocene, and their occurrence in the northern United States and possibly Canada, as well as in northern Europe, during the Tertiary appears likely. While it is undoubtedly true that many of these hypothetical species would have been extirpated by glaciation, some might have survived in subglacial refugia. There is some indirect evidence to support the contention that certain species of small, subterranean crustaceans might have survived under glacial conditions. R. S. Spencer of Old Dominion University (pers. comm.) has informed me that groundwater under glaciers would probably remain unfrozen at varying depths depending on the thickness of the ice. Ginet (1960) has demonstrated experimentally that the adults of certain species of *Niphargus* can survive at a temperature depression of −0.5° C and maintain normal activity at 1° C. Juveniles, however, need a temperature of at least 4° C for development. Bowman and Holmquist (1975) have presented a rather convincing argument that some epigean species of *Asellus* might have survived glacial conditions in Siberia during the Pleistocene. Finally, Skalski (1976:225), on the basis of a zoogeographic study of the groundwater fauna in Poland, has stated that certain species of *Niphargus* and the interstitial polychaete *Troglochaetus* may be glacial relicts in parts of the Carpathian and Sudetes mountains.

Literature Cited

Adams, G. I., C. Butts, L. W. Stephenson, and W. Cooke
1926. Geology of Alabama. *Geological Survey of Alabama Special Report,* 14: 312 pages.

Barnard, J. L.
1958. Index to the Families, Genera, and Species of the Gammaridean Amphipoda (Crustacea). *Occasional Papers of the Allan Hancock Foundation,* 19:1–145.
1976. Affinities of *Paraniphargus lelouparum* Monod, a Blind Anchialine Amphipod (Crustacea) from the Galapagos Islands. *Proceedings of the Biological Society of Washington,* 89:421–432.

Barr, T. C.
1961. Caves of Tennessee. *Bulletin of the Tennessee Department of Conservation and Commerce, Division of Geology,* 64:1–597, 1 plate.
1968. Cave Ecology and the Evolution of Troglobites. *Evolutionary Biology,* 2:35–102.

Barr, T. C., and J. R. Holsinger
1971. Biogeography of Troglobites. *National Speleological Society Bulletin,* 33:115–118.

Bell, R. T.
1971. *Handbook of the Malacostraca of Vermont.* 65 pages, 84 figures. Published privately by author.

Bou, Claude
1974. Recherches sur les Eaux Souterraines—25—Les Méthodes de Récolte dans les Eaux Souterraines Interstitielles. *Annales de Spéléologie,* 29:611–619.

Bousfield, E. L.
1958. Fresh-Water Amphipod Crustaceans of Glaciated North America. *Canadian Field-Naturalist,* 72:55–113.
1973. *Shallow-Water Gammaridean Amphipoda of New England.* xii + 312 pages. Ithaca: Cornell University Press.
1977. A New Look at the Systematics of Gammaroidean Amphipods of the World. Proceedings of the 3rd International Colloquium on *Gammarus* and *Niphargus,* Schlitz, West Germany, 1975. *Crustaceana* (supplement), 4:282–316.

Bouillon, Michel
1964. Contribution à L'Étude Écologique des Amphipodes du Genre *Niphargus* dans les Pyrénées Centrales. *Annales de Spéléologie,* 19(3):537–551.

Bowman, T. E., and C. Holmquist
1975. *Asellus (Asellus) Alaskensis,* n. sp., the First Alaskan *Asellus,* with Remarks on Its Asian Affinities (Crustacea: Isopoda: Asellidae). *Proceedings of the Biological Society of Washington,* 88(7):59–72.

Cope, E. D.
1872. On the Wyandotte Cave and Its Fauna. *American Naturalist,* 6:406–422.

Creaser, E. P.
1934. A New Genus and Species of Blind Amphipod with Notes on Parallel Evolution in Certain Amphipod Genera. *Occasional Papers of the University of Michigan Museum of Zoology,* 282:105, 1 plate.

Culver, D. C.
1970a. Analysis of Simple Cave Communities: Niche Separation and Species Packing. *Ecology,* 51:949–958.
1970b. Analysis of Simple Cave Communities, 1: Caves as Islands. *Evolution,* 24:463–474.
1971a. Analysis of Simple Cave Communities, III: Control of Abundance. *American Midland Naturalist,* 85: 173–187.
1971b. Caves as Archipelagoes. *National Speleological Society Bulletin,* 33:97–100.
1973. Competition in Spatially Heterogeneous Systems: An Analysis of Simple Cave Communities. *Ecology,* 54:102–110.

Culver, D. C., and J. R Holsinger
1969. Preliminary Observations on Sex Ratios in the Subterranean Amphipod Genus *Stygonectes* (Gammaridae). *American Midland Naturalist,* 82:631–633.

Culver, D. C., J. R. Holsinger, and R. A. Baroody
1973. Toward a Predictive Cave Biogeography: The Greenbrier Valley as a Case Study. *Evolution,* 27:689–695.

Culver, D. C., and T. L. Poulson
1971. Oxygen Consumption and Activity in Closely Related Amphipod Populations from Cave and Surface Habitats. *American Midland Naturalist,* 85: 74–84.

Davies, W. E.
1958. Caverns of West Virginia. *West Virginia Geological and Economic Survey,* 19(A):1–330
1965. Caverns of West Virginia (Supplement). *West Virginia Geological and Economic Survey,* 19(A):1–72.

Davis, H., P. Hauer, D. Hartline, and M. Sease, editors
1966 *Caves of Schoharie County, New York.* 123 pages. Published privately by the Boston Grotto of the National Speleological Society [mimeographed].

Delamare-Debouteville, Claude
1960. *Biologie des Eaux Souterraines Littorales et Continentales.* 740 pages, 1 plate. Paris: Hermann.

Dickson, G. W, and P. W. Kirk, Jr.
1976. Distribution of Heterotrophic Microorganisms in Relation to Detritivores in Virginia Caves (with Supplemental Bibliography on Cave Mycology and Microbiology). *In* B. Parker and others, editors, *The Distributional History of the Biota of the Southern Appalachians, Part IV: Algae and Fungi.* (Research Division Monograph 1.) Blacksburg: Virginia Polytechnic Institute and State University.

Douglas, H. H.
1964. *Caves of Virginia.* iii + 761 pages. Falls Church, Virginia: Econ-Print

Estes, J. A., and J. R. Holsinger
1976. A Second Troglobitic Species of the Genus *Lirceus* (Isopoda, Asellidae) from Southwestern Virginia. *Proceedings of the Biological Society of Washington,* 89:481–490.

Franz, L. R., and D. Slifer
1971. Caves of Maryland. *Maryland Geological Survey Educational Series,* 3: 120 pages.

Ginet, René
1960. Écologie, Éthologie et Biologie de *Niphargus. Annales de Spéléologie,* 15:127-237, 4 plates.

Hay, W. P.
1903. Observations on the Crustacean Fauna of Nickajack Cave, Tennessee and Vicinity. *Proceedings of the United States National Museum,* 25(1292):417–439.

Holsinger, J. R.
1963. Annotated Checklist of the Macroscopic Troglobites of Virginia with Notes on Their Geographic Distribution. *National Speleological Society Bulletin,* 25:23–36.
1964. The Biology of Virginia Caves. Pages 57–74 *in* H. H. Douglas, *Caves of Virginia.* Falls Church, Virginia: Econ-Print.
1966. Subterranean Amphipods of the Genus *Stygonectes* (Gammaridae) from Texas. *American Midland Naturalist,* 76:100–124.
1967. Systematics, Speciation, and Distribution of the Subterranean Amphipod Genus *Stygonectes* (Gammaridae). *Bulletin of the United States National Museum,* 259: 176 pages, 36 figures.
1969a. Biogeography of the Freshwater Amphipod Crustaceans (Gammaridae) of the Central and Southern Appalachians. Pages 19–50 *in* P. C. Holt, editor, *The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates.* (Research Division Monograph 1.) Blacksburg: Virginia Polytechnic Institute and State University.
1969b. The Systematics of the North American Subterranean Amphipod Genus *Apocrangonyx* (Gammaridae), with Remarks on Ecology and Zoogeography. *American Midland Naturalist,* 81:1–28, figures 1–10.
1972. The Freshwater Amphipod Crustaceans (Gammaridae) of North America. In *Biota of Freshwater Ecosystems. United States Environmental Protection Agency Identification Manual,* 5: 89 pages.
1974. Systematics of the Subterranean Amphipod Genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States. *Smithsonian Contributions to Zoology,* 160: 63 pages.
1975a. Descriptions of Virginia Caves. *Bulletin of the Virginia Division of Mineral Resources,* 85:1–450, 7 plates.
1975b. Observation on the Dispersal of the Cavernicolous Amphipod Crustacean *Crangonyx antennatus* (Gammaridae). *Association of Southeastern Biologists Bulletin,* 22:58 [abstract].
1976. The Cave Fauna of Pennsylvania. Pages 72–87 *in* W. B. White, editor, Geology and Biology of Pennsylvania Caves. *Pennsylvania Geological Survey General Geology Report,* 4th series, 66: 103 pages.
1977. A Review of the Systematics of the Holarctic Amphipod Family Crangonyctidae. Proceedings of the 3rd International Colloquium on *Gammarus* and *Niphargus,* Schlitz, West Germany, 1975. *Crustaceana* (supplement), 4:244–281.
1978. A Preliminary Report on the Cave Fauna of Burnsville Cove, Virginia. *National Speleological Society Bulletin* [in press].

Holsinger, J. R., R. A. Baroody, and D. C. Culver
1976. The Invertebrate Cave Fauna of West Virginia. *Bulletin of the West Virginia Speleological Survey,* 7:1–82.

Holsinger, J. R., and D. C. Culver
1970. Morphological Variation in *Gammarus minus* Say (Amphipoda, Gammaridae), with Emphasis on Subterranean Forms. *Postilla,* 146:1–24.

Holsinger, J. R., and G. W. Dickson
1977. Burrowing as a Means of Survival in the Troglobitic Amphipod Crustacean *Crangonyx antennatus* Packard (Crangonyctidae). *Hydrobiologia,* 54:195–199.

Holsinger, J. R., and S. B. Peck
1971. The Invertebrate Cave Fauna of Georgia. *National Speleological Society Bulletin,* 33:23–44.

Holsinger, J. R., and H. R. Steeves III
1971. A New Species of Subterranean Isopod Crustacean (Asellidae) from the Central Appalachians, with Remarks on the Distribution of Other Isopods of the Region. *Proceedings of the Biological Society of Washington,* 84:189–200.

Hubricht, Leslie
1943. Studies on the Nearctic Freshwater Amphipoda, III: Notes on the Freshwater Amphipoda of Eastern United States with Description of Ten New Species. *American Midland Naturalist,* 29:683–712, plates 1–10.
1959. Malacostraca (Amphipoda). Pages 876–878 *in* W. T. Edmondson, editor, *Freshwater Biology.* 2nd edition. New York: Wiley & Sons, Inc.

Hubricht, Leslie, and J. G. Mackin
1940. Description of Nine New Species of Fresh-Water Amphipod Crustaceans with Notes and New Localities for Other Species. *American Midland Naturalist,* 23:187–218, 11 figures.

Husmann, Siegfried
1971. Ecological Studies on Freshwater Meiobenthon in Layers of Sand and Gravel. Pages 161–169 *in* N. C. Hulings, editor, Proceedings of the First International Conference on Meiofauna. *Smithsonian Contributions to Zoology,* 76: 205 pages.

Jones, W. K.
1973. Hydrology of Limestone Karst in Greenbrier County, West Virginia. *West Virginia Geological and Economic Survey Bulletin,* 36:1–49, 2 maps.

Karaman, G. S.
1974. 59. Contribution to the Knowledge of the Amphipoda: Revision of the Genus *Stygobromus* Cope 1872 (Fam. Gammaridae) from North America. *Glasnik Republickog Zavoda Za Zaštitu Prirode I Prirodnjačkog Muzeja Titogradu*, 7:97–125.

Kenk, Roman
1969. Freshwater Triclads (Turbellaria) of North America, I: The Genus *Planaria*. *Proceedings of the Biological Society of Washington*, 82:539–558.

Medville, D. M., and H. E. Medville
1971. Caves of Randolph County. *Bulletin of the West Virginia Speleological Survey*, 1:1–218.
1976. Caves and Karst Hydrology in Northern Pocahontas County. *Bulletin of the West Virginia Speleological Survey*, 6:1–174.

Meštrov, Milan
1962. Un nouveau milieu aquatique souterrain: Le Biotope hypotelminorhéique. *Comptes Rendus*, 254:2677–2679.

Nicholas, Brother G.
1960. Checklist of Macroscopic Troglobitic Organisms of the United States. *American Midland Naturalist*, 64:123–160.

Pennak, R. W.
1953. *Fresh-Water Invertebrates of the United States*. ix + 769 pages, 470 figures. New York: Ronald Press Company.

Poulson, T. L., and W. B. White
1969. The Cave Environment. *Science*, 165(3897):971–981.

Rutherford, J. M., and R. H. Handley
1976. The Greenbrier Caverns. *National Speleological Society Bulletin*, 38:41–52.

Schellenberg, A.
1936. Die Amphipodengattungen um *Crangonyx*, ihre Verbreitung und ihre Arten. *Mitteilungen aus dem Zoologischen Museum in Berlin*, 22:31–43.

Schweiker, R., R. Anderson, P. Van Note, and R. Jurgens
1960. Caves of Albany County, New York. *Northeastern Regional Organization of the National Speleological Society Publication*, 8:48 pages [mimeographed].

Shoemaker, C. R.
1938. A New Species of Fresh-Water Amphipod of the Genus *Synpleonia*, with Remarks on Related Genera. *Proceedings of the Biological Society of Washington*, 51:137–142.
1942. Notes on Some American Fresh-Water Amphipod Crustaceans and Descriptions of a New Genus and Two New Species. *Smithsonian Miscellaneous Collections*, 101:1–31.

Skalski, A. W.
1970. Groundwater Inhabitants in Poland. *International Journal of Speleology*, 8:217–228.

Smith, S. I.
1874. The Crustacea of the Fresh Waters of the United States. Pages 637–665 *in* Part 2 of *Report of the United States Fish Commission, 1872 and 1873*.

Stebbing, T. R. R.
1899. Amphipoda from the Copenhagen Museum and Other Sources, Part II. *Transactions of the Linnean Society of London*, series 7 (Zoology), 2:395–432, plates 30–35.

Steeves, H. R., III, and J. R. Holsinger
1968. Biology of Three New Species of Troglobitic Asellids from Tennessee. *American Midland Naturalist*, 80:75–83.

Stone, R. W.
1953. Caves of Pennsylvania. *National Speleological Society Bulletin*, 15:1–143.

Tarkington, T. W., W. W. Varnedoe, Jr., and J. D. Veitch
1965. *Alabama Caves*. 380 pages. Huntsville Grotto, National Speleological Society.

Vandel, A.
1965. *Biospeleology*. xxiv + 254 pages. New York: Pergamon Press.

Varnedoe, W. W., Jr.
1973. *Alabama Caves and Caverns*. 1140 pages, Published privately by author.

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