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Systematics of the Subterranean Amphipod Genus *Stygobromus* (Crangonyctidae) in Western North America, With Emphasis on Species of the *Hubbsi* Group

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SYSTEMATICS OF THE SUBTERRANEAN AMPHIPOD GENUS *STYGOBROMUS* (CRANGONYCTIDAE) IN WESTERN NORTH AMERICA, WITH EMPHASIS ON SPECIES OF THE *HUBBSI* GROUP

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ABSTRACT

SYSTEMATICS OF THE SUBTERRANEAN AMPHIPOD GENUS *STYGOBROMUS* (CRANGONYCTIDAE) IN WESTERN NORTH AMERICA, WITH EMPHASIS ON SPECIES OF THE *HUBBSI* GROUP

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This dissertation presents a study of the systematics of the subterranean amphipod genus *Stygobromus* of family Crangonyctidae in western North America. A total of 53 species of *Stygobromus* from western North America (including one species from Wisconsin) are recognized, 28 of which are new to science. All species are described and illustrated using external morphological features. A key to the western North America species of *Stygobromus* is given, as well as a summary of habitats of the species.

Cladistic analyses are conducted using 32 external morphological characters and two categories of outgroup choices: "all-zero" theoretical ancestor and three non-*Stygobromus* species. The consensus trees of unordered/unweighted and ordered/partially weighted are developed. The results of both categories support one monophyletic species cluster, which includes most species in California. Two loose constant congruent species clusters were also recognized in the two category runs: a California-Oregon-Washington species cluster includes *S. imperialis*, *S. rudolphi*, *S. gallawayae*, *S. latus*, *S. grahami*, *S. wengerorum*, *S. harai*, *S. gradyi*, *S. elliotti*, *S. mysticus*, and *S. hubbsi*; a Colorado-Idaho-Montana species cluster includes *S. urospinatus*, *S. fontanalis*, *S. pennaki*, *S. coloradensis*, *S. canadensis*, and *S. idahoensis*. The number of species in each of the two loose constant clusters of the two categories is variable.

The species diversity of *Stygobromus* decreases from east to west in North America, possibly resulting from geologically more recent landforms in western North America. In addition, many habitats presently occupied by western species of *Stygobromus* may not be older than the Pleistocene. Some lava tubes in Oregon and Washington are even more recent. This explanation may also account for close morphological similarity of *hubbsi* group species in western North America.

Dedicated to two of the greatest countries: China and the United States, also to my family and my best friend Sheffan Chan.

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CHAPTER I

INTRODUCTION

Amphipods are the most abundant species of the crustacean superorder Pericarida and are represented by more than 6700 described species (Bousfield 1982). Three (sometimes four) suborders are recognized within the Order Amphipoda, of which suborder Gammaridea with approximately 5700 species is the largest and most diverse taxonomically and ecologically (Barnard and Karaman 1991). Amphipods are primarily aquatic and well represented in faunas of marine, estuarine and freshwater communities throughout the world. Eleven families and nineteen genera of amphipods are represented in the freshwaters of North America.

More species of gammaridean amphipods are represented in subterranean environments than any other major invertebrate group except carabid beetles. In comparison with other crustacean groups that commonly occur in subterranean groundwaters, such as bathynellids, isopods, and decapods, amphipods are probably the most abundant, widespread and taxonomically diverse (Holsinger 1994). Approximately 758 species, or about 13% of all described species in the suborder Gammaridea, inhabit subterranean waters. Approximately 80% of these species occur in limnic or freshwater habitats and 20% in brackish and/or marine waters (Holsinger 1993). The exclusively freshwater family Crangonyctidae occurs in the freshwaters of North America and Euroasia and have never been found in the marine environment. Approximately 82% of crangonyctid species are stygobionts. They are characterized by restriction to subterranean waters and troglomorphisms, including loss of pigment, drastic reduction or loss of eyes, and frequently attenuation of the body and/or certain appendages (especially the antennae).

Stygobiont amphipods are particularly interesting biogeographically because of their limited dispersal ability. The lack of a dispersing larval stage and restriction to groundwater aquifers probably has resulted in considerable geographic isolation and the evolution of many local endemics. Of further interest to evolutionary biologists is the strong probability that many subterranean taxa represent old phylogenetic lineages that have persisted in well-buffered groundwater habitats for long periods of time as relicts (Holsinger 1991, 1994). Crangonyctid amphipods are numerically dominant and highly diverse in the freshwater environments of North America but much less so in similar environments of Eurasia. Three of the six extant crangonyctid genera, *Crangonyx*, *Lyurella*, and *Synurella*, contain both surface and subterranean species; the other three genera, *Bactrurus*, *Stygobromus*, and *Stygonyx* are exclusively subterranean.

The model journal used to format this thesis is *Amphipacifica*.

The present study will be devoted to an ongoing monographic revision of the genus *Stygobromus* that was started in the 1960s by John R. Holsinger. The genus *Stygobromus* of Crangonyctidae is one of the largest genera of freshwater crangonyctid amphipods and is presently composed of 101 described species. Holsinger (1974a 1978) described 17 western species of *Stygobromus* with detailed geographic distributions for each species and assigned 15 species without sternal gills/processes into a species group- the *hubbsi* group. To date, species primarily collected from western North America provide a good opportunity to gain new insight into the systematics of the *hubbsi* group and the genus *Stygobromus*. Meanwhile, some previously described species in the *hubbsi* group need to be redescribed. Complete phylogeny has not been studied. Thus, it is necessary to continue the study of the *hubbsi* group, including its taxonomy, phylogeny and biogeography. On the other hand, because species of *Stygobromus* occur in a wide variety of groundwater habitats (such as wells, springs, subterranean streams, cave pools, and rarely deep lakes), this genus is also important for pollution ecology and environmental monitoring. For example, some species (e.g., *Gammarus spp.*) are used as bioassay organisms and biological indicators of environment quality.

Rapidly expanding human populations and urbanization in many parts of North America and throughout much of the world are contributing to destruction, drastic modification and alteration of groundwater aquifers that have existed for millennia in their natural state. Because many of these aquifers are habitats for subterranean amphipod crustaceans and many of the species that live there are rare endemics, critical information on the systematics and ecology of these potentially threatened or endangered species is essential for the development of protective strategies. At the present time, many species are threatened with extinction before they can be properly studied, or in some cases even recognized. Karst groundwater communities, which are inhabited by more than half of all stygobiont amphipods, are especially vulnerable because surface sinkholes, which are often polluted by dumping of man-made wastes, provide direct conduits into subsurface aquifers. The dominance of amphipods in their size-range in aquatic ecosystems is a primary reason why these organisms are potentially useful as biological indicators and play an important role in environmental impact studies and ecological monitoring.

The study of biodiversity of the *hubbsi* group and *Stygobromus* is also important for biospeleology because all described species are found in caves and related subterranean groundwater habitats or groundwater outlets. The deteriorating environmental scene requires us to describe the invertebrate fauna as soon as possible because some species will go extinct before they are collected and recognized. Unlike vertebrate faunas, invertebrate faunas are easily

neglected by humans. However, they play very important roles in many ecosystems, including influencing of the decomposition rate of organic matter.

Subterranean amphipods (e.g., *Stygobromus* species) make excellent models for the study of speciation, biogeography, regressive evolution, and other aspects of evolutionary biology. They are proving especially valuable to students of biogeography (Holsinger 1991, 1994) and troglobite evolution (Kane and Culver 1991; Culver et al. 1995). Systematic studies of subterranean amphipods have led to hypotheses on vicariance processes. These processes involve stranding of marine amphipods in freshwaters and reliction in subglacial refuge. The vicariance processes also include roles of the preservation of ice-age relicts at higher latitudes in North America and effects of discontinuous karst on geographic isolation. The spatial and temporal relationships between species living in different kinds of groundwater aquifers are also impacted by vicariant events (Stock 1980; Holsinger 1980, 1988; Barr and Holsinger 1985; Ward and Palmer 1994).

Completion of this study, combined with previous work by Holsinger, will further clarify the picture of the phylogeny and biogeography of *Stygobromus*, especially those from subterranean groundwaters in western North America.

REVIEW AND HISTORICAL PERSPECTVIE

The genus *Stygobromus* was originally described by Cope (1872) on the basis of a single species, *S. vitreus*, collected from Mammoth Cave, Kentucky. Several researchers subsequently assigned this species to the genus *Crangonyx*, but Schellenberg (1936) reassigned this species to *Stygobromus* after giving a brief diagnosis of the genus (Holsinger 1974a). Shoemaker (1942a 1942b) published a more complete diagnosis of *Stygobromus* and redescribed *S. vitreus* from topotypes secured from Mammoth Cave. The species *S. hubbsi* was assigned to the genus by Shoemaker, followed by the descriptions of five new species of *Stygobromus* by Hubricht (1943) (Holsinger 1967, 1974, 1978).

Two species previously described and placed in *Crangonyx* by Hubricht and Mackin (1940) were also subsequently assigned to *Stygobromus* by Hubricht (1943). Holsinger (1972) published an illustrated key to the 10 species found in North America, and assigned them to *Stygobromus*. The zoogeography of the Appalachian species was discussed by Holsinger (1969). Holsinger (1974a) also published a revised diagnosis of the genus, accompanied by a redescription of *S. hubbsi* Shoemaker from Oregon and the descriptions of 17 new species from the western United

States. Of the 18 species recorded from the western U.S., 15 were assigned to the *hubbsi* group (Holsinger 1974a). Ward (1977) reported three new species of the *hubbsi* group, *S. coloradensis, S. pennaki, and S. holsingeri.* That was the first record of subterranean amphipods from Colorado. Holsinger (1980) described a new species *S. canadensis* from a cave in British Columbia, Canada. Bousfield and Holsinger (1981) then described *S. secundus n. sp.*, also from Canada. Holsinger and Shaw (1986) described the new species, *S. quatsinensis*, from caves on Vancouver Island, Canada and assigned it to the *hubbsi* group. This species was also discovered recently in southeastern Alaska (Holsinger 1997).

Previous to the study, there are 24 species of *Stygobromus* from western North America; 19 in the *hubbsi* group. Another species, *S. putealis* from a well in Wisconsin, is also assigned to the *hubbsi* group. Appendix 1 is a list of 24 species from western North America plus *S. putealis* from Wisconsin. Of the total 101 described species of *Stygobromus* (Appendix 2), only three species are found outside North America: *S. apscheronia* from a spring near the Caspian Sea (Derzhavin 1945), *S. kazakhstanica* from a spring in Kazakhstan (Kulkina 1992), and *S. pusillus* from Telelzkoye Lake in Siberia (Holsinger 1987a).

Holsinger (1978) published Part 2 of a revision of the genus, including 30 new species from Appalachian and Coastal Plain regions of the eastern United States. Holsinger (1986a) suggested that *Stygobromus* represents a combination of several previously described, but vaguely defined, genera (*Apocrangonyx, Stygonectes* and *Synpleonia*), all of which have been synonymized under the name *Stygobromus* in recent years (Holsinger 1977; Karaman 1974).

OBJECTIVES

1) Taxonomy: description of new species and redescription of previously described species to revise the taxonomy of the *hubbsi* group of *Stygobromus* in western North America based on all available collections and literature.

2) Phylogenetic analysis: utilization of the taxonomic data and other related species to construct a phylogenetic hypothesis of the *hubbsi* group of *Stygobromus*, including character analysis and cladistic analysis using PAUP.

3) Biogeographic analysis: based on the results of phylogenetic analysis, defining patterns of species distribution, relating these patterns to phylogeny and evaluating extrinsic barriers, dispersal limits and other geographic and geological considerations.

MATERIALS AND METHODS

Materials

The specimens for this study came primarily from Holsinger's research collection and those on loan to Holsinger from the United States National Museum of Natural History (USNM). Several other institutions with smaller collections also made their specimens available. Almost all western North America *Stygobromus* collections reported in the literature from North America were examined. There included about 700 collections, each containing about 1- 50 (or more) specimens. Types of all previously described species are deposited in United State National Museum of Natural History under the catalog numbers of the United States National Museum (USNM). All holotypes (except one) and many paratypes of the new species described in this paper will be deposited in the USNM. Under the material examined section for each species, if the deposition of a collection is not indicated for a museum by an abbreviation in parentheses, it is in the Holsinger research collection.

Cave names and locations correspond to those in published or unpublished cave surveys or in other speleological publications. State cave surveys have been published for California (Halliday 1962), Colorado (Parris 1973) and Washington (Halliday 1963). Additional information is available on caves in Oregon (Greeley, 1971), and supplementary information on Washington caves was published in the "Guidebook of the 1972 Convention of the National Speleological Society". A list of museums and their abbreviations included in Materials Examined:

Museum of Southwestern Biology (MSB)

Bernice P. Bishop Museum (BBM)

Canadian Museum of Nature (CMN)

United State National Museum of Natural History (USNM)

John R. Holsinger collections (JRH)

Thomas Burke Memorial Washington State Museum (TBMWSM)

Essig Museum of Entomology, University of California at Berkeley (EME)

Montana Entomology Collection (MTEC).

Methods

All specimens in available collections were examined and where necessary compared with the type specimens. Examinations of specimens emphasized morphological characters (see Table 1) under the dissecting microscope and the compound microscope after the prepared slides were prepared. Routine determination was made with the aid of a dissecting- microscope for some species. However, slides were prepared for accurate identification of most species, as well as for morphological analysis for all species. Prepared slides were examined with the aid of a compound microscope for smaller sized species and for purposes of illustration. Dissecting and slide making techniques were adopted from Holsinger (1967, 1974) and Barnard (1969). Terminology and definitions of external morphological structures followed currently accepted usage (Holsinger 1974, 1978).

The results of the morphological analyses were also used to determine geographic variation, as well as to distinguish individual species, and to establish morphological difference among species. Based on morphological analysis, each species was given a unique morphological diagnosis to establish its specific status. New species were found in both new and old collections. Every collection was determined to species level and either assigned to species already described or, if found to be undescribed, to a new species. A Key to all species was constructed.

In comparison with many arthropods, amphipods are taxonomically difficult because the genitalia are soft finger-like processes that cannot be used for identification. However, every external body part has some diagnostic value and a combination of characters was used to identify species. Although this procedure generally works well, it may also cause some problems as pointed out below. There are two major problems inherent in amphipod taxonomy: the first one is that continuous growth and development through successive instars, and variation in size and proportion of a number of taxonomically important characters in older animals. Another problem is geographic variation. I used sexually mature males and females whenever possible as a basis for morphological analysis, description and illustration.

It is easy to distinguish between mature females and males of species of *Stygobromus*. Mature males have a pair of soft finger-like penies on the ventrum of the 7th pereonite and a distally, minutely serrate peduncular process on uropod 1, which is always small in size. Mature females have brood plates (most with long marginal setae where fully developed). It is sometimes difficult to distinguish immature individuals. I used the following criteria: if a specimen has brood plates (even though sometimes the brood plates are not completely developed), it is considered as a female. All specimens lacking the secondary sex characters

described above are considered juveniles. Characters used in morphological analysis and species identification are currently accepted usage and listed in Table 1.

Description of species was based primarily on the morphological characters of the sexually mature females. The species was given a morphological diagnosis and a comparison with other species in the genus. Each new species was given a detailed description and illustrated drawings according to current acceptance of amphipod taxonomy. The format of description primarily followed Holsinger (1974, 1978). The drawings were made with the aid of a drawing tube mounted on a Leitz compound microscope. The sequence of species descriptions is listed alphabetically. A full lateral view of *S. grahami* is also provided to illustrate the overall facies of the *hubbsi* group.

The phylogenetic relationships of species of *Stygobromus* were studied cladisticaly using the computer software programs PAUP 3.1 (Swoford 1993) and MacClade 3.0 (Madison and Madison 1992). Characters and character states were analyzed and a data matrix was constructed. The data were analyzed by PAUP. One of the purposes of the research is to determine whether the *hubbsi* group is composed of a monophyletic clade in the genus *Stygobromus* and whether other clades exist in western North America. Character polarity was based on the results of character analysis.

Outgroup analysis was used to provide a hypothesis about the relationship of *Stygobromus* to other genera in the family Crangonyctidae. It was based on characters and character states supplied by the literature and augmented by studying specimens. The phylogenetic relationship of genera of Crangonyctidae suggested by Holsinger (1986a, 1993) was used as a starting point. The outgroup was chosen two different kinds: one is "all zero" theoretical ancestor and the other is three closely related genera (*Synurella*, *Crangonyx* and *Bactrurus*) of the family Crangonyctidae.

The determination of the relative plesiomorphy of a series of homologous characters was achieved by the comparison with relevant outgroups established by means of the outgroup analysis. The data matrix of character states was then utilized by computer software programs to construct cladograms. The most parsimonious cladograms (trees) were selected.

A relatively detailed phylogenetic hypothesis for a group of organisms should serve as a basis for inferring its biogeographic history. By combining phylogenetic data with geographic distributions of species, hypotheses about biogeography can be developed. The geographic relationships of the species ranges were tabulated and compared with monophyletic groups found in the cladistic analysis. Interpretation of these results was utilized to explain the origin and

biogeographic patterns of species of *Stygobromus* in western North America. Attempts were made to relate splits of the cladograms to certain vicariant events (e.g. climatic or geologic changes) that might have influenced geographic isolation.

Species of *Stygobromus* are known only as stygobionts in subterranean groundwater habitats. Biogeographic and phylogenetic data are analyzed in attempt to give us a clearer picture of relationships among western species of *Stygobromus*. This thesis aims to answer to several key questions about the biogeography and evolutionary biology of *Stygobromus*:

1) Why are species in *hubbsi* group so closely similar morphologically?
2) Why is the species diversity in western North America significantly less in comparison with that of eastern North America?
3) Are some of the non-*hubbsi* group species in western North America closely related to in-group species even though they possess sternal gills/processes?
4) Is there a relationship between relatively recent climatic and geological changes in western North America and the present distribution patterns of the species in this region?

CHAPTER II

MORPHOLOGICAL CHARACTER ANALYSIS

The following morphological characters are used in species description, identification and character analysis.

Female:

Body length: This is a measurement from the front of the head to the end of the third uronite (excluding antennae, telson and uropod 3). Since intraspecific variation in size occurs between generations and geographical populations, differences in this character are of limited diagnostic value. However, it is important for comparative purposes.

Head: The lateral lobe is slightly concave with a distinct inferior sinus in *Stygobromus* species. Eyes are absent in *Stygobromus* species. The presence or absence of eyes and their shape and size are a very good diagnostic character for distinguishing stygobiont species. But they are also variable in some groups, especially for species with both surface and subterranean populations in *Crangonyx*.

Antenna 1: Peduncular segment 1 is stout and longer than peduncular segment 2. The accessory flagellum is 2-segmented. The number of segments of the flagellum varies between large and small specimens and different populations and hence has little diagnostic value. But it is interesting to note that for most species the range in the number of flagellar segments is 12-28.

Antenna 2: The length and distribution of marginal clusters of setae on peduncle segments 4 and 5 possibly has no diagnostic value for most species because of variation.

Mandibles: The configuration of setae on palpal segment 3 follow the definitions established by Stock (1974) and now widely used in amphipod taxonomy. Zhang (1997) used the presence (or absence) and number of A-setae and B-setae to separate species groups in the genus *Crangonyx*. He recognized three states in *Crangonyx*: several A and several B setae, several A and 1-2 B setae and only 1- 2 A setae. For *Stygobromus*, most species do not have A and C setae. A few species, such as *S. gradyi*, *S. curroae* and *S. interstitialis*, bear one or several B seta on the palp segment 3. This was used as diagnostic character.

Maxilla 1: The number of apical plumose setae on inner plate is a diagnostic character of species. Although the number can vary between specimens, the range of the intraspecific variation was found to be very small: 1-2 less or more setae. The number is greater than 6 in some species and more than 12 in others. The outer plate always has 7 mostly serrate apical spines.

Maxilla 2: The number of plumose setae on the inner margin of inner plate is a very good diagnostic character of species. Like the apical plumose setae of the inner plate of maxilla 1, the intraspecific variation is small. The number is from several in some species to more than 10 in others. In almost all species the plumose setae are in an oblique row.

Maxillipeds: The outer lobe of the maxilliped has one to several bladelike spines, plumose spine/setae or naked setae near the apical or on the inner margin, the number of spines is variable. Inner lobe apical setae and spine shape and number are also variable. The outer lobe is distinctly higher than the inner lobe. The number of setae on the inner margin is highly variable in some species, although it is about 4-8 for most species.

Gnathopods 1 and 2: The shape and size of the propods, number of palmar spine teeth, arrangement of superior and inferior medial setae are very good diagnostic characters of species. Three states are easily recognized: (1) The propods are broader and longer, the palmar margin is strongly oblique and concave, longer than the posterior margin and armed with double row of notched spine teeth, the anterior margin is significantly longer than posterior margin, and most superior medial setae are doubly inserted. Examples are *S. grahami* and *S. harai*; (2) The propod is longer and broader, the palmar margin is oblique, convex and longer than the posterior margin, and armed with notched spine teeth, and the superior medial setae are singly inserted. *S. gradyi*; is an example. (3) The anterior and posterior margin of propod are long and slender. The palmar margin is shorter than the posterior margin and armed with double notched, slender spine teeth. The posterior margin of both propod and carpus are armed with many single inserted setae, for example, *S. mysticus*. The number of spine teeth and their arrangement on the defining angle are diagnostic for species. For most species there is a large strongly notched spine tooth outside the defining angle.

The palmar margin of the propod is oblique, straight, convex or concave. For some species, the posterior margin of the propod bears several groups (3-5) of setae, but the number of groups and setae are variable. The posterior angle bears one long and several short spines.

Pereopods 3-7: The number of setae on the coxal margins is a good character for some species. The shape of the bases and that of the distoposterior margin of the bases of pereopod 5-7 have characteristics for many species. The ratio of width and depth of coxae of pereopods 3 and 4 is also good character. The bases of pereopods 5-7 in some species (e.g., *S. latus* and *S. mysticus*) are greatly expanded, which easily distinguishes them from other species.

Pleonal plates 1-3: The presence or absence of ventral or subventral spines on pleonal plate 1-3 and the number of these spines on a given plate are useful diagnostic characters of species. The distoposterior corner can be produced and acute or not produced and round (although in

some cases the precise condition is very difficult to determine). In some species the corner varies from slightly produced to very produced. The number and arrangement of the setae on the posterior margins are important characteristics for most *Stygobromus* species.

Uropods 1-2: The number of spines on the peduncle and inner and outer rami is a good character. The number of spines on the peduncle and outer ramus of uropod 1 is diagnostic for some species, for example, *S. urospinatus*.

Uropod 3: The ratio of outer ramus length versus peduncle length is diagnostic for some species. The number of spines on the outer ramus is characteristic of some species (e.g., *S. urospinatus*).

Telson: The shape of the telson proportionate length and the number of apical spines are diagnostic for most species. The presence or absence of an apical notch and its relative depth is highly diagnostic even though it is variable in some species, but more constant.

Male:

Body length: When males are mature, they are almost always smaller and slenderer than females. This may be due to the fact that the males do not have brood pauches to carry eggs for development (Zhang 1997). However in some species of *Stygobromus*, males are longer than the longest females in the collection and have almost same body shape.

Gnathopods 1 and 2: The propod 1 is smaller than propod 2. The palmar margin of the propods is armed with a number of notched spines. The sexual dimorphism of gnathopods in size is a valuable diagnostic character for species.

Uropods: Along with comparatively small body size, without calceoli on antenna 2 and proportionately smaller gnathopods, uropod 1 is usually dimorphic in male and bears a small distal peduncular process. Significant interspecific variation is found in the arrangement of shape, and number of spines on the outer ramus. For many species this proved to be a good character for identification.

CHAPTER III
TAXONOMY

FAMILY CRANGONYCTIDAE BOUSFIELD, 1973

Schellenberg (1936) recognized the *Crangonyx* group of the family Gammaridae, which included 15 genera of freshwater amphipods. Following the work of Schellenberg (1936), several workers discussed this group concept and accumulated more knowledge about it (see Holsinger 1967, 1977 for more details). Bousfield (1973) established the family Crangonyctidae to include those genera which had been assigned to the *Crangonyx* group. Holsinger (1977) summarized this family and all genera, including a list of species, distribution and ecology of genera and a key to the genera. Holsinger (1977) recognized 6 genera in the family Crangonyctidae: *Bactrurus*, *Crangonyx*, *Lyurella*, *Palaeogammarus*, *Stygobromus*, and *Synurella*. Subsequently, Bousfield and Holsinger (1989) described the new genus *Stygonyx* and included a new key to the genera of Crangonyctidae.

GENUS *STYGOBROMUS* COPE, 1972

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 of head rather narrowly rounded anteriorly without inferior sinus or rarely narrowly rounded with weak inferior antennal sinus; eyes absent.

Antenna 1 longer than antenna 2 (excepting the aberrant ♂ of one species); First peduncular segment of antenna 1 strouter and longer than second; Antenna 2 of mature male without calceoli. Primary flagellar segments usually with aesthetascs; accessory flagellum 2-segmented. 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 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.

Maxillipeds: outer plate with stiff setae on apex and inner margin and sometimes 1 or 2 bladelike spine near apex; inner plate with several bladellike spines and stiff setae apically; Lower lip with well-developed outer lobes and small, typically indistinct or absent inner lobes.

Gnathopods 1 and 2: propod of second larger than or subequal to first; several long rastellate setae present on posterior margin of propods, segment 5 and segment 4. Palm of propods with double row of typically distally notched spine teeth.

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 6 little longer than 7. Pereopod 7 always longer than 5. Coxal gills moderately small, subovate, present on pereopods 2-6, sometimes on 7.

Single, median sternal gills present on pereonites 2-4; simple paired sternal gills typically on pereonites 6 and 7; one pair of sternal gills sometimes on pleonite 1.

Brood plates of sexually mature female typically rather small and variable in size, and often sublinear in comparison with *Crangonyx* species.

Pleonal plates: distoposterior corners usually rounded,sometimes small and distinct or indistinct, never large or acuminate; posterior margins usually with 1 or several short seta, but sometimes up to 3 setae; ventral margin of 2 and 3 typically with spines; ventral margin of 1 usually without spines, but some species with one or more spines. Pleopods biramous, subequal in length, each with 2 coupling spines on inner distal margin of peduncle.

Uronites free. Uropod 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 laterally and apically.

Telson usually as long as, or often longer than broad; armed apically occasionally laterally with spines; apical margin subtruncate, convex or with incision seldom extending one-half distance to base.

Type-species.-- *Stygobromus vitreus* Cope, 1872 by monotypy.

Distribution and ecology. --The species of *Stygobromus* are exclusively found in freshwater subterranean habitats and are recorded in Eurasia (3 species) and North America (98 species).

Remarks.-- A close ecological and morphological relationship between *Apocrangonyx*, *Stygonectes* and *Stygobromus* was reported by Holsinger (1966, 1967, 1969). As new species were

discovered it was found that certain diagnostic characters of these genera strongly overlapped (Holsinger, 1978). With the accumulation of new information, based on the descriptions of new species, it became apparent that the assignment of many of these species to any one of above three genera was impossible (Holsinger 1977). Karaman (1974) and Holsinger (1976, 1978) suggested that *Apocrangonyx* and *Stygonectes* should be synonymized with *Stygobromus*.

Based on the hypothesized phylogenetic relationship given by Holsinger (1978, 1994), *Stygobromus* has a close relationship with *Bactrurus*, *Synurella* and *Stygonyx*: united by the following 5 synapomorphies: calceoli absent, coxa 1-4 reduced in size (but somewhat variable), posterior corners of pleonal plates 1 and 2 not produced or acuminate, uropod 1 of male typically with peduncular process, and outer ramus of uropod 3 reduced to length of peduncle, or shorter than peduncle, or absent, with few or no lateral spines . *Stygobromus* can be easily separated from *Bactrurus* and *Stygonyx* (a monotypic genus) and other genera of the family Crangonyctidae by the outer ramus of 3rd uropod (Bousfield and Holsinger 1989), which is longer than the peduncle and by the presence of a scale-like inner ramus.

THE *HUBBSI* GROUP

Diagnosis: Posterior margin of gnathopodal propod 1 without setae or rarely with 1 submarginal seta just below defining angle; gnathopodal propod 2 usually much broader proximally (near base), especially in females; sternal gills absent; sternal blisters (small ventral humps) sometimes present on pereonites 2-7 (see Holsinger 1974, 1978 for details).

Remarks: Based on current data, the *hubbsi* group species are very similar morphologically to most of non-*hubbsi* group species in western North America, except that the latter possess sternal gills (see Fig. 19 *S. grahami* for the typical facies of the *hubbsi* group species).

A KEY TO SPECIES OF *STYGOBROMUS* IN WESTERN NORTH AMERICA, INCLUDING *S. PUTEALIS* FROM IN WISCONSIN

1. Sternal gills present on pereonites 4-5 or 6-7.....2
   Sternal gills absent from pereonites 4-5 and 6-7.....3
2. Gnathopod propod 1 slightly larger than 2nd; bases of pereopods 5-7 narrow, not expanded proximally.....*S. obscurus*
   Gnathopod propod 2 larger than 1st; bases of pereopods 5-7 broader proximally than

distally 47

3. Coxal plate of pereopod 4 more than half length of segment 2; bases of pereopods 5-7 broadly expanded, distoposterior lobes large; telson deep and 2 times longer than broad.....*S. mysticus*

   Coxal plate of pereopod 4 less than half length of segment 2; bases of pereopods 5-7 not broadly expanded, distoposterior lobes small or lacking; telson depth not 2 times longer than broad.....4

4. Inner plate of maxilla 1 with 10-16 apical, plumose setae; inner plate of maxilla 2 with oblique row of 13-15 plumose setae on inner margin; inner plate of maxilliped with 8-13 apical spines.....5

   Inner plate of maxilla 1 with 6-9 apical, plumose setae; inner plate of maxilla 2 with oblique row of 6-10 plumose setae on inner margin; inner plate of maxilliped with 4-8 apical spines.....8

5. Gnathopodal propod 2 of mature ♀ only little larger than propod 1, palm with double row of 5 spine teeth.....6

   Gnathopodal propod 2 of mature ♀ nearly twice (or more) the size of propod 1, palm with double row of 9-13 spine teeth.....*S. gradyi*

6. Palms of gnathopd propods of mature females with double row of 13 spine teeth, ventral margin of pleonal plate 1 with spines, ventral margin of plate 3 with 7 spines.....*S. wengerorum*

   Palms of gnathopd propods of mature females with double row of 10 or less spine teeth; ventral margin of pleonal plate 1 without spines, ventral margin of plate 3 with 4-5 spines 7

7. Inner marginal spines of posterior angle of gnathopodal propod 1 of mature ♀ mostly forked; gnathopodal propod 2 of mature ♂ proportionately smaller than ♀; coxal plate of pereopod 4 extending about 1/2 length of segment 2.....*S grahami*

   Inner marginal spines of posterior angle of gnathopodal propod 1 of mature ♀ mostly unforked; gnathopodal propod 2 of mature ♂ proportionately larger than ♀; coxal plate of pereopod 4 extending about 1/3 length of segment 2 .....*S. harai*

8. Length of sexually mature ♀ not exceeding 5.0 mm (excepting *S. arizonensis*); bases of pereopods 5-7 often not much broader proximally tan distally; peduncle of uropod 2 of mature ♀ with more than 3 spines (excepting *S. sierrensis*); ramus of uropod 3 with 2 or 3 apicalspines; apical margin of telson with small notch.....9

Length of sexually mature ♀ often exceeding 5.0 mm (excepting *S. arizonensis*); bases of pereopods 5-7 often not much broader proximally tan distally; peduncle of uropod 2 of mature ♀ with more than 3 spines (excepting *S. sierrensis*); ramus of uropod 3 with 3 or more apical spines (excepting *S. arizonensis*); apical margin of telson usually emarginated.....10

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

Inner plate of maxilliped with 4 apical spines; gnathopodal propod 2 of ♂ about 1/4 longer than 1st propod; ramus of uropod 3 with 3 or more apical spines.....*S. mackenziei*

10. Posterior margins of bases of pereopods 5-7 convex midmarginally, distoposterior lobes lacking; ramus of uropod 3 with 2 apical spines; apical margin of telson incised 1/4 the distance to base.....*S. arizonensis*

Posterior margins of bases of pereopods 5-7 not convex midmarginally, distoposterior lobes lacking or not; ramus of uropod 3 with 3 or more apical spines; apical margin of telson usually shallow notch, but not exceeding 1/4 the distance to base.....11

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

Bases of pereopods 5-7 not much broader than distally; posterior margins nearly straight or irregular but not convex, distoposterior lobes small but not distinct.....13

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

Palm of gnathopodal propod 2 concave with double row of 12spine teeth; pleonal plates with small, rounder posterior corners; telson with 12-14 apical spines.....*S. lacicolous*

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

Uropods 1 and 2 not heavily spined, uropod 1 usually with less 52 spines, uropod 2 with less 27 spines; apical spines of telson usually subequal in length

.....14

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

Outer plate of maxilla 1 with 7 serrate spines apically; inner margin of palpal segment 2 of maxilliped not elongate and heavily setose; posterior margins of bases of pereopods 5-7 typically straight or near so; sexually mature female reaching 7.0 mm in length.....15

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

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

16. Pleonal plates 2 and 3 with 2 ventral spines each; ramus of uropod 3 about 1/4 length of peduncle; apical margin of telson with very slight emargination.....*S. sierrensis*

Pleonal plates 2 and 3 with at least 4 ventral spines each; ramus of uropod 3 about 1/3 length of peduncle; apical margin of telson with small but distinct notch.....17

17. Gnathopdal propod 2 of mature female up to 1/3 larger than 1st propod, palm with double row of 11 or 12 spines teeth.....*S. hubbsi*

Gnathopdal propod 2 of mature female only a little larger than 1st propod, palm with double row of 7 or 8 spines teeth.....18

18. Palms of gnathopodal propod 1 and 2 straight; coxal plates of pereopods 3 and 4 deeper than broad 19

Palms of gnathopodal propod 1 and 2 less straight or convex medially; coxal plates of pereopods 3 broader than deep.....20

19. Pleonal plates 1-3 with 24 or more spines on corner margin.....*S. urospinatus*, new species

Pleonal plates 1-3 with fewer (< 24) spines on corner margin.....*S. holsingeri*

20. Few teeth (< 14) on palmar margin of gnathopodal propods 1 and 2; 4 apical plumose setae on inner plate of maxilla 1; largest mature ♀ and ♂ size not exceeding 4.5 mm in length.....21

More teeth (14 or more) on palmar margin of gnathopodal propods 1 and 2; 5 or more apical plumose setae on inner plate of maxilla 1; largest mature ♀ and ♂ size exceeding 5.0 mm in length.....22

21 Uropods 1 and 2 with short spines (< 30% of rami) on rami ..... *S. coloradensis*

Uropods 1 and 2 with very long spines (> 40% of rami) on rami ..... *S. pennaki*

22. Posterior margins of bases of pereopods 5-7 convex but lacking distoposterior lobes; 4 or more apical spines on inner plate of maxilliped.....23

Posterior margins of bases of pereopods 5-7 not convex but distoposterior lobes developed; less than 4 apical spines on inner plate of maxilliped.....24

23. Posterior margins of pleonal plates 3 with 4 setae..... *S. fontanalis*, new species

Posterior margins of pleonal plates 2 and 3 with 3 setae..... *S. cherylae*, new species

24. Antenna 1 twice as long as antenna 2; maxilla 1-2 with more setae on inner plate; coxal plates 3-4 broader than deep.....25

Antenna 1 not twice as long as antenna 2; maxilla 1-2 with fewer setae on inner plate; coxal plates 3-4 not broader than deep.....26

25. Pereopod 6 with poorly developed distoposterior lobe 27

Pereopod 6 with distoposterior lobe 28

26. Pleonal plates 1-3 lacking spines on ventral margin and few spines on posterior corner..... ..... *S. utahensis*, new species

Pleonal plates 1-3 with more spines on ventral margin and posterior corner..... ..... *S. limbus*, new species

27. Pleonal plate 2 and 3 with 6-7 spines on posterior margins..... *S. boultoni*, new species

Pleonal plate 2 and 3 one spines on posterior margins.....29

28.Coxal plate 3 and 4 broader than deep..... *S. lanensis*, new species

Coxal plate 3 and 4 deeper than broad or subequal.....30

29.Propod palm of gnathopod 2 concave; telson with very shallow notch or lacking 31

Propod palm of gnathopod 2 not concave; telson with notch 32

30.Propods of gnathopods 1 and 2 with proportionately long posterior margin ..... *S. saltuaris*, new species

Propods of gnathopods 1 and 2 with proportionately short posterior margin..... *S. wahkeenensis*, new species

31. Uropod 1 and 2 with long, stout spines on rami and peduncle.....33

Uropod 1 and 2 without long, stout spines on rami and peduncle.....34

32. Ramus of uropod 3 small; maxilla 2 with fewer setae on inner plate..... *S. interstitialis*, new species

Ramus of uropod 3 proportionately large; maxilla 2 with more setae on inner plate.....*S. blinni*, new species

33. Gnathopod 2 posterior margin about ½ length of palm.....35

Gnathopod 2 posterior margin about 1/3 length of palm.....36

34. Bases of pereopods 4-7 narrow and proportionately longer .....*S. latus*, new species

Bases of pereopods 4-7 very broad and proportionately longer than its remaining segments..... .....*S. duplus*, new species

35. Palmer margins of propods of gnathopods 1 and 2 with 28 or more teeth..*S. rallus*, new species

Palmer margins of propods of gnathopods 1 and 2 with 20 or fewer teeth.....37

36. Pleonal plates 2 and 3 with 4 ventral spines.....*S. rudolphi*, new species

Pleonal plates 2 and 3 with 5 or more ventral spines.....38

37. Uropod 1 with proportionately short peduncle.....39

Uropod 1 with proportionately long peduncle 40

38. Palmar margin of gnathopod 2 straight or slightly concave.....*S. gallawayae*, new species

Palmar margin of gnathopod 2 convex.....*S. hyporheicus*, new species

39. Telson with long apical spines.....*S. interstitialis*, new species

Telson with short apical spines.....41

40. Coxal plate of pereopods 3 and 4 deeper than broad .....*S. imperialis*, new species

Coxal plate of pereopods 3 and 4 slightly deeper than broad 42

41. Pleonal plate 2 with 1-2 ventral spines.....43

Pleonal plate 2 with 3 or more ventral spines.....44

42. Pleonal plate 1 with 1 ventral spine.....*S. cowani*, new species

Pleonal plate 1 with 3 ventral spines .....*S. trinus*, new species

43. Uropod 2 with relatively longer peduncle; telson apical margin with tiny notch..... .....*S. herbsti*, new species

Uropod 2 with relatively shorter peduncle; telson apical margin with distinct notch 45

44. Telson lacking notch or indistinct.....*S. myersae*, new species

Telson with tiny notch but distinct.....46

45. Maxillae and maxillipeds with 9 or more setae on inner plates.....*S. putealis*

Maxillae and maxillipeds with 7 or fewer setae on inner plates.....*S. jemezensis*, new species

46. Telson with about 10 apical spines.....*S. quatsinensis*

Telson notch with only 6 apical spines.....*S. tahoensis*

47. Gnathopod 1 posterior margin about 1/4 length of palm.....*S. glacialis*, new species

Gnathopod 1 posterior margin 1/3 length of palm.....49

48. Pleonal plate 3 with 2 ventral margin spines.....*S. simplex*, new species

Pleonal plate 3 with 1 ventral margin spines.....50

49. Uropods 1-2 with long and thick spines on rami.....*S. curroae*, new species

Uropods 1-2 with short spines on rami.....51

50. Telson notch indistinct .....*S. idahoensis*, new species

Telson notch distinct.....*S. montanensis*

51. Pereopod 6 posterior lobes distinct. .....*S. secundus*

Pereopod 6 posterior lobes indistinct 52

52. Bases of pereopods 6 - 7 with 2-3 spines on posterior margin.....*S. wardi*, new species

Bases of pereopods 6 - 7 with 4 or more spines on posterior margin.....*S. canadensis*

Stygobromus arizonensis Holsinger, 1974

Stygobromus arizonensis Holsinger, 1974: 47-49, figs. 28-29 [type-locality: small cave on Flying "H" Ranch near Fort Huachuca, Cochise Co., Arizona].

Material examined. ARIZONA. Cochise Co.: Mine Cave, south of Sierra Vista, 2 ♀, R. B. Pape, 17 Sept. 1994; Santa Cruz Co.: bog springs, Madera Canyon, 2 ♂, 1 juv., W. D. Sheppard, 3 June 1993.

Diagnosis. A relatively small to medium-sized cavernicolous species, distinguished by the diagnosis and description of Holsinger (1974). Largest ♀ 7.0 mm; largest ♂ 5.0 mm.

Distribution and ecology. This species is recorded from 4 localities (2 caves, 1 mine and 1 spring) in southeastern Arizona. Mine Cave is a cave that was broken into by miners and is located on the opposite side of Huachuca Mountains from the type-locality cave on Flying "H" Ranch (R. B. Pape, pers. comm.). The specimens from this cave were collected from a pool approximately 1.8 m deep and 61 m from the entrance. Bog spring is a spring/seep located approximately 48 km NNW of Fort Huachuca.

Stygobromus blinni, new species

(Figs. 1-2)

Material examined. ARIZONA. Coconino Co.: Roaring Springs Cave, HOLOTYPE ♀ (USNM), 2 ♀ paratypes, D. Blinn, 28 Sept. 1994.

Diagnosis. A medium-sized cavernicolous species, closely related to *S. arizonensis* in

gnathopods and *S. holsingeri* in uropod 2, but distinguished from the 2 species by the following: maxilla 2 with fewer setae on inner plate; maxilliped with bladelike spines on outer plate (unlike *S. holsingeri*); coxal plate 4 broader than deep; bases of pereopods 5-7 narrow and with more setae on the margin; uropod 1 with more long and stout spines on rami and peduncle; uropod 2 with more long and stout spines on rami; uropod 3 ramus smaller; telson notched slightly. Largest ♀, 6.0 mm, male unknown.

Female. Antenna 1: 67 percent length of body, 25 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 6 rather long setae on inner margin; palp segment 3 bearing 1 long B seta, 5 C setae, few D setae, 4 E setae, lacking A setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 5 apical, plumose setae; palp with 7 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, and 2 naked setae apically, and 2 plumose spines on inner margin; outer plate with setae on inner margin and apex, and 1 lightly plumose spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and little longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; superior medial setae 3; 2 inferior medial setae; dactyl nail rather long; coxa rather narrow, deeper than broad, margin with 3 setae.

Gnathopod 2: propod oblique, deeper than broad; palm straight and armed with 17 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of setae near defining angle; 8 - 9 superior medial setae, doubly inserted; 4 singly-inserted inferior medial setae; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 6 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 33 percent length of basis,

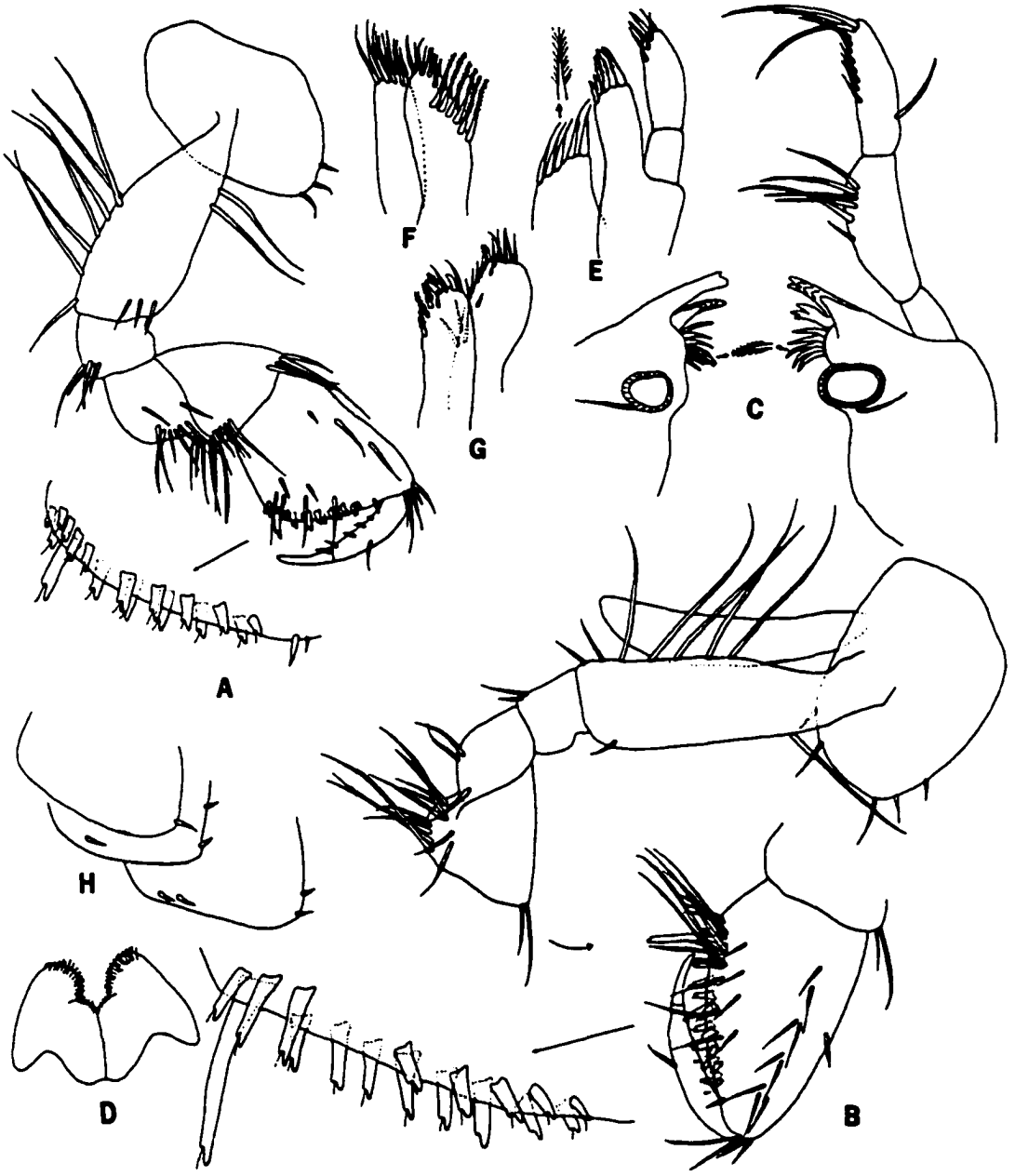

Fig. 1. ***Stygobromus blinni*****, new species, female paratype (5.8 mm), Roaring Springs Cave, Cocaning County, Arizona: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged); H, pleonal plates.**

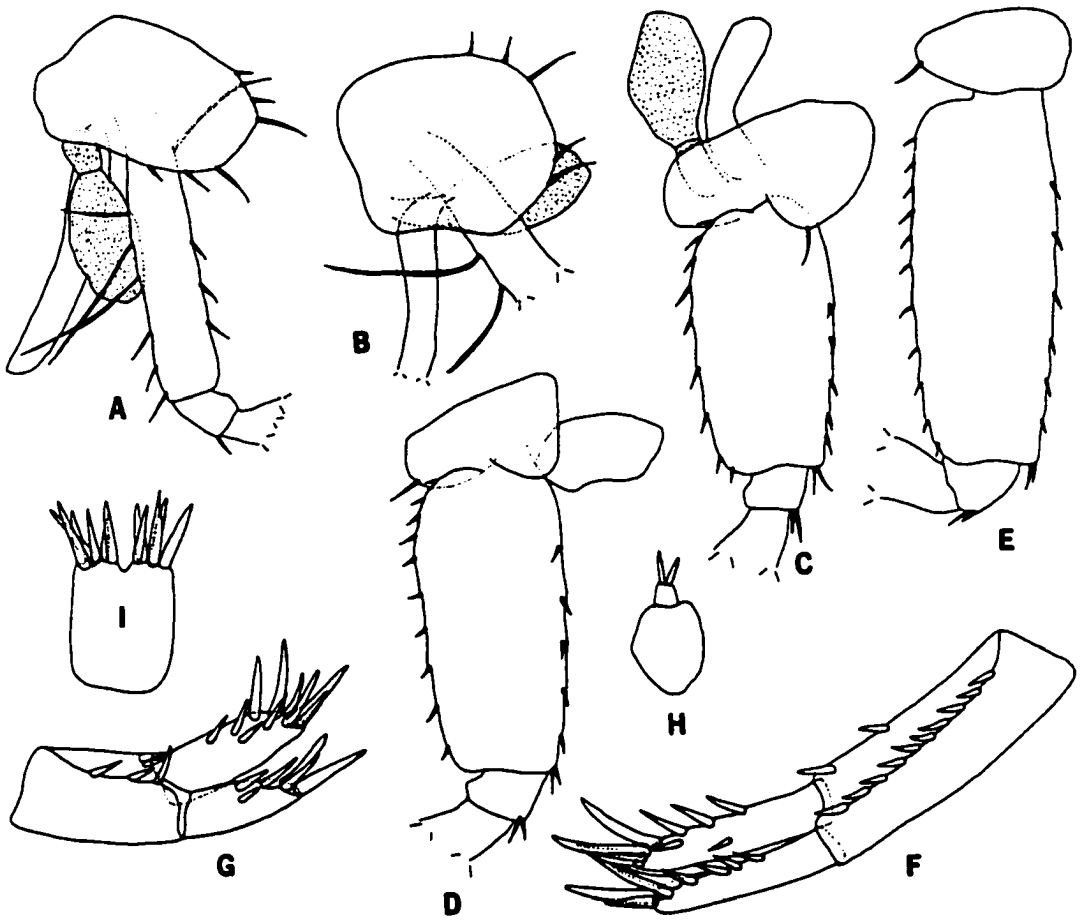

Fig. 2. ***Stygobromus blinni*****, new species, female paratype (5.8 mm), Roaring Springs Cave, Cocaning County, Arizona: A, B, C, pereopods 3, 4, 5 (in part); D, E, pereopods 6, 7 (in part); F, G, H, uropods 1, 2, 3; I, telson.**

margin with 5 setae.

Pereopod 6 little longer than pereopod 7, about 80 percent length of body, 15 percent longer than pereopod 5.

Pereopods 5-7: bases as broad proximally as distally; posterior margins slightly convex; distoposterior lobes weakly developed, that of 7 indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 45 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 2 setae near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 8-9 spines; outer ramus with 8-9 spines; peduncle with 12 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 10 spines; outer ramus with 6 spines; peduncle with 4 spines.

Uropod 3: peduncle usually lacking small setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, apical margin with small median notch between spine clusters, bearing 10-11 relatively long spines.

Type locality. Roaring Spring Cave, on the north rim of the Grand Canyon, near Bright Angel Trail and Bright Angel Creek, Coconino County, Arizona.

Distribution and ecology. This species is only known from its type-locality (Fig. 93, 95). It was collected from a slow-moving stream with a fine sediment/gravel substrate, about 1.6 km inside the cave (Dean Blinn, pers. comm.).

Etymology. It is pleasure to name this species for its collector, Dr. Dean Blinn.

Stygobromus boultoni, new species

(Figs. 3-4)

Material examined. ARIZONA. Maricopa Co.: PVC well no. 1 at Sycamore Creek, HOLOTYPE ♀ (USNM), 4 ♀ paratypes, 3 juvs., A. Boulton, 12 Mar, 1990; PVC well no. 1, 2 juvs., A. Boulton, 2 Mar, 1990; PVC well no. 3 on Sycamore Creek, 1 ♀, A. Boulton, 2 Mar, 1990.

Diagnosis. A small-sized goundwater species, closely related to *S. arizonensis* but distinguished as follows: palms of gnathopod 1 and 2 oblique and with fewer teeth; maxilla 2 with fewer setae; posterior margin of gnathopods 1 and 2 longer; coxal plates 3 deeper; base of pepeopods 6 and 7 more narrow and with fewer spines on posterior margin; telson with longer apical spines; distoposterior lobes of pereopod 6 well developed; uropods 1-2 with more long and thick spines on rami; pleonal plates 2 and 3 with more spines on posterior margin. Largest ♀ 4.0 mm, ♂ unkown.

Female. Antenna 1: 54 percent length of body, 43 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4-5 plumose spines; palp segment 2 with row of 3 rather long setae on inner margin; palp segment 3 with 4 C setae, 5 E setae, lacking A, B and D setae.

Inner lobes of lower lip vestigial.

Maxilla 1: inner plate with 4 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 4 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 2 plumose spines, and 3 naked setae apically, and without plumose spines on inner margin; outer plate with 3 setae on inner margin and 4 setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and 2 times longer than posterior margin, armed with 11 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; fewer superior medial setae; lacking inferior medial, dactyl nail long; coxa broader than deep; margin with 2 setae.

Gnathopod 2: propod subrectangular, deeper than broad; palm armed with 9 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin 50 percent of palm in length, with 1 set of setae; 3 superior medial setae, singly inserted; few inferior medial setae; coxa broader than deep, margin with 2 or 3 setae.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae.

Pereopod 4: coxal plate about as broad as deep, reaching about 30 percent length of basis, margin with 2 setae.

Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 30 percent longer than pereopod 5.

Fig. 3 . *Stygobromus boultoni*, new species, female paratype (3.7 mm), well No. 1, Sycanare Creek, Maricopa County, Arizona: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged); H, pleonal plates.

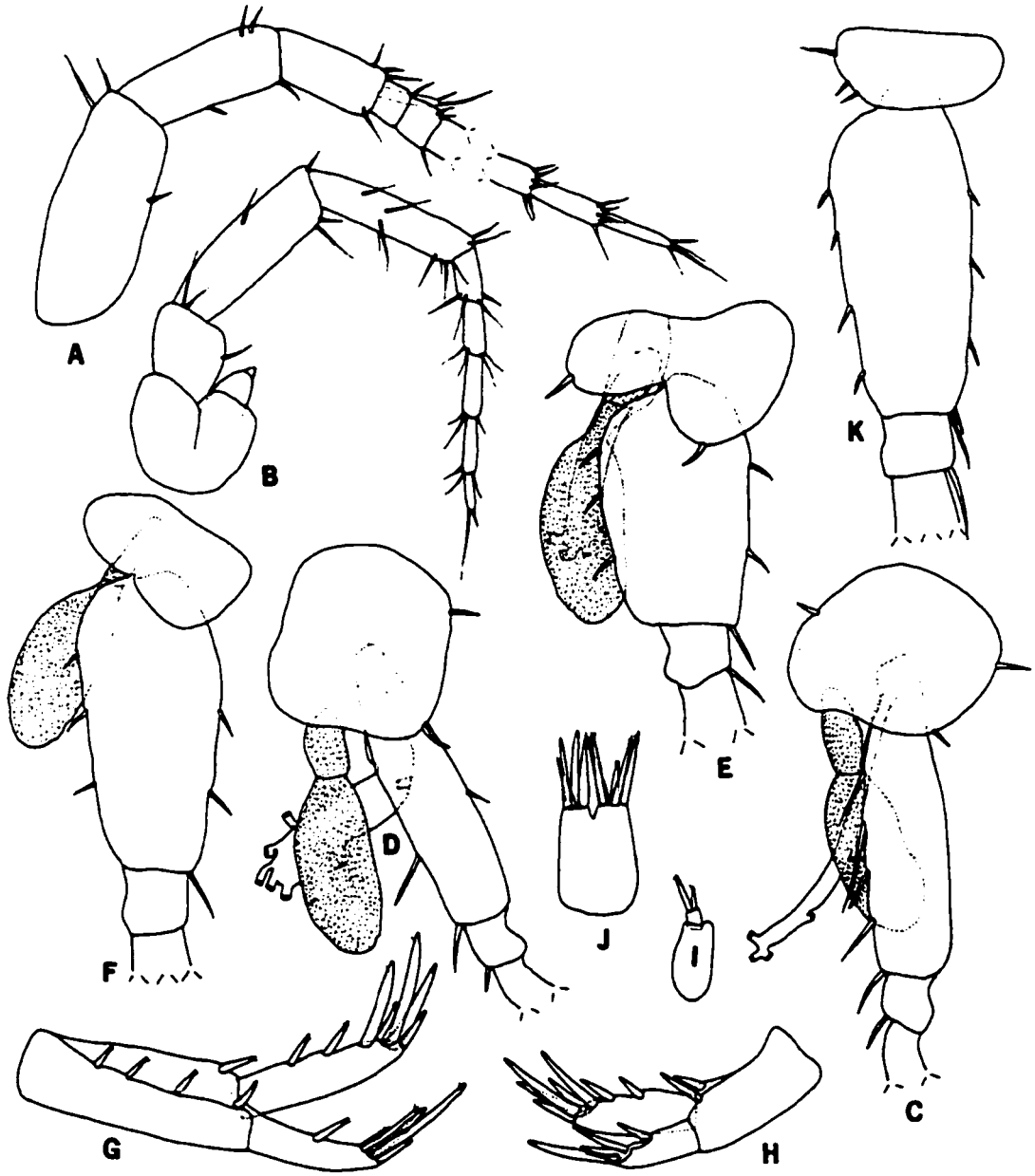

Fig. 4. ***Stygobromus boultoni*****, new species, female paratype (3.7 mm), well No. 1, Sycanare Creek, Maricopa County, Arizona: A, B, antennae 1, 2; C, D, E pereopods 3, 4, 5; F, pereopod 6; G, H, I, uropods 1, 2, 3; J, telson; K, pereopod 7.**

Pereopods 5-7: bases little broader proximally than distally; posterior margins nearly straight; distoposterior lobes not developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 typically 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates little narrowing distally.

Pleonal plates: posterior margin of plate 1 and 2 convex, each with 3 spines near distoposterior corner, that of 3 less convex, with 5 setae near distoposterior corner; distoposterior corners of plate 2 and 3 rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 8 spines; outer ramus with 6 spines; peduncle with 5 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 2 spines.

Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson longer than broad, gently tapered distally; apical margin with small median notch between spine clusters, bearing 9 relatively long spines.

Type locality. PVC well no. 1, Sycamore Creek, approximately approximately 32 km northeast of Phoenix, Maricopa County, Arizona (Figs. 93, 95).

Distribution and ecology. This species is known only from PVC wells drilled into substrate of Sycamore Creek, 32 km northeast of Phoenix, Arizona. According to Dr. Andrew Boulton (pers. comm.), the material was collected during a study of interstitial fauna utilizing phreatic pumping through PVC wells from a depth of approximately 180 cm.

Etymology. This species is named in honor of its collector, Dr. Andrew Boulton.

Stygobromus cherylae, new species

(Figs. 5-7)

Material examined. CALIFORNIA. Sonoma Co.: spring box, just east of Macama Creek Bridge, approximately 19.5 km east of Geyserville, HOLOTYPE ♀ (USNM), and 60 paratypes (EME and JRH), C. B. Barr and W. B. Shepard, 21 Feb. 2000; spring box and feeder pipe in the same location, 1 ♂, 1 juv., C. B. Barr, 5-7 Oct 1995; feeder pipe at spring box, 19.5 km east of Geyserville, 1 ♀, 2 juvs., 26-28 Apr. 1996; pipe at unnamed spring on hillside, 19.5 km east of Geyserville, 4 ♀, 33 juvs., 26-28 Apr. 1996.

Diagnosis. A medium-sized groundwater species, probably closely related to the *S. grahami* species complex farther to the east, but characterized by smaller males at sexually maturity. Further distinguished from *S. grahami* by having fewer setae on inner plates of maxillae and maxilliped; nearly straight to slightly convex palms of propods of gnathopods 1 and 2; coxal plates 1 and 2 proportionately smaller; pleonal plates 2 and 3 with fewer ventral spines; apical margin of telson with tiny notch. Largest ♀, 7.5 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 60 percent length of body, 24 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 5-6 plumose spines; palp segment 2 with 6 long setae on inner margin, 2 on outer margin; palp segment 3 with 5 C setae, about 10 D setae and 5 E setae, lacking both A and B setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 8 apical plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 2 plumose spine, and 2 naked setae apically, and 2 coarse plumose setae on inner margin; outer plate with setae on inner margin and apex, and 1 bladelike spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm slightly convex or straight and approximately 2 times longer than posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4 doubly inserted superior medial setae; 4 or 5 inferior medial setae; dactyl nail short; coxa approximately 2 times broader than deep, margin with 3 setae.

Gnathopod 2: propod deeper than broad; palm convex medially and armed with 21-22 spine teeth in double row; defining angle with 1 long spine tooth on outside, 1 shorter spine tooth on inside; posterior margin about 25 percent of length palm, with 2 sets of doubly or triply inserted setae; 9- 10 doubly inserted superior medial setae; 4 or 5 singly inserted inferior medial setae; dactyl nail shorter; coxa broader than deep, margin with 4 setae.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae.

Pereopod 4: coxal plate about as broad as deep, reaching about 33 percent length of basis, margin with 4 setae.

Pereopod 6, slightly longer than pereopod 7, about 57 percent length of body, 33 percent longer than pereopod 5.

Pereopods 5-7: bases as broad proximally as distally; posterior margins variably convex;

distoposterior lobes moderatedly well developed, anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 30 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 3 convex, with 1 setule near distoposterior corner, that of plates 1 and 2 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plates 2 and 3 each bearing 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 10 spines; outer ramus with 11 spines; peduncle with 12 spines.

Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 10 spines; outer ramus with 7 spines; peduncle with 3 spines.

Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 3-4 apical spines.

Telson longer than broad, apical margin with tiny median notch between spine clusters, bearing 14-16 relatively long spines.

Male. Differing from female in a number of characters as follows: sexually mature specimens approximately 3.0 mm shorter; antenna 1 with longer esthetascs, and presence of peduncular process on uropod 1, which is approximately 20-25 percent length of outer ramus. Gnathopod propods smaller, palm of propod 2 longer than posterior margin, with fewer teeth on palmar margin. Uropod 2: inner ramus with 9-11 spines, peduncle with 3-5 spines. Telson with 13-15 apical spines.

Type locality. The type-material was collected from the water of an unnamed spring located on a hillside just east of Macamba Creek Bridge, beside Highway 128, approximately 19.5 km east of Geyserville, in Sonoma County, California. According to C. B. Barr (pers. comm.), who collected most of the specimens, some of the water from the spring is diverted at the spring head into a feeder pipe that carries water downhill to a spring box. Specimens were obtained from both the feeder pipe (by netting) and spring box. The large 21 February collection was made by picking through roots and debris in the upper spring box.

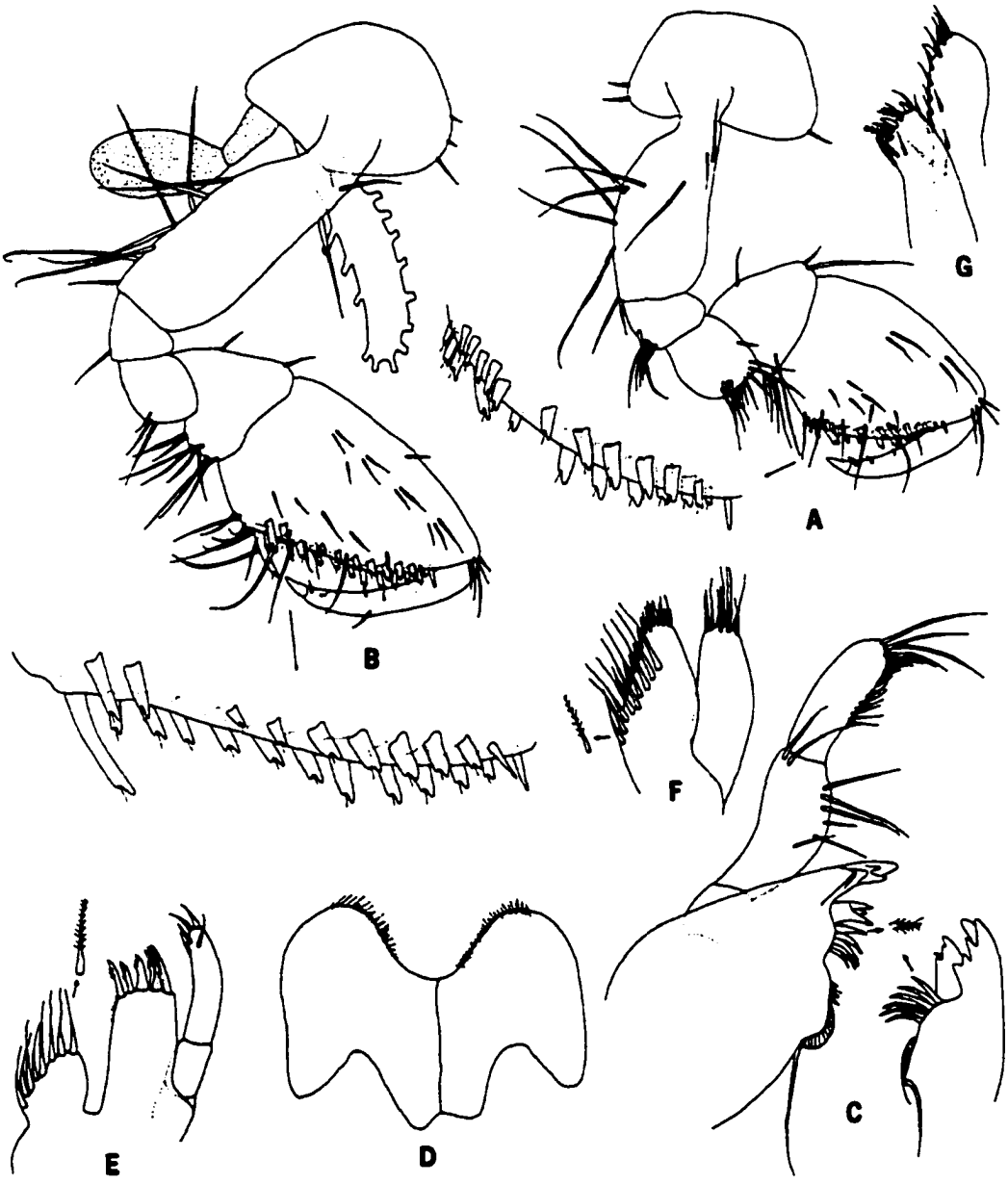

Fig. 5. ***Stygobromus cherylae*****, new species, female paratype (7.0 mm), unnamed spring, Sonoma County, California: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

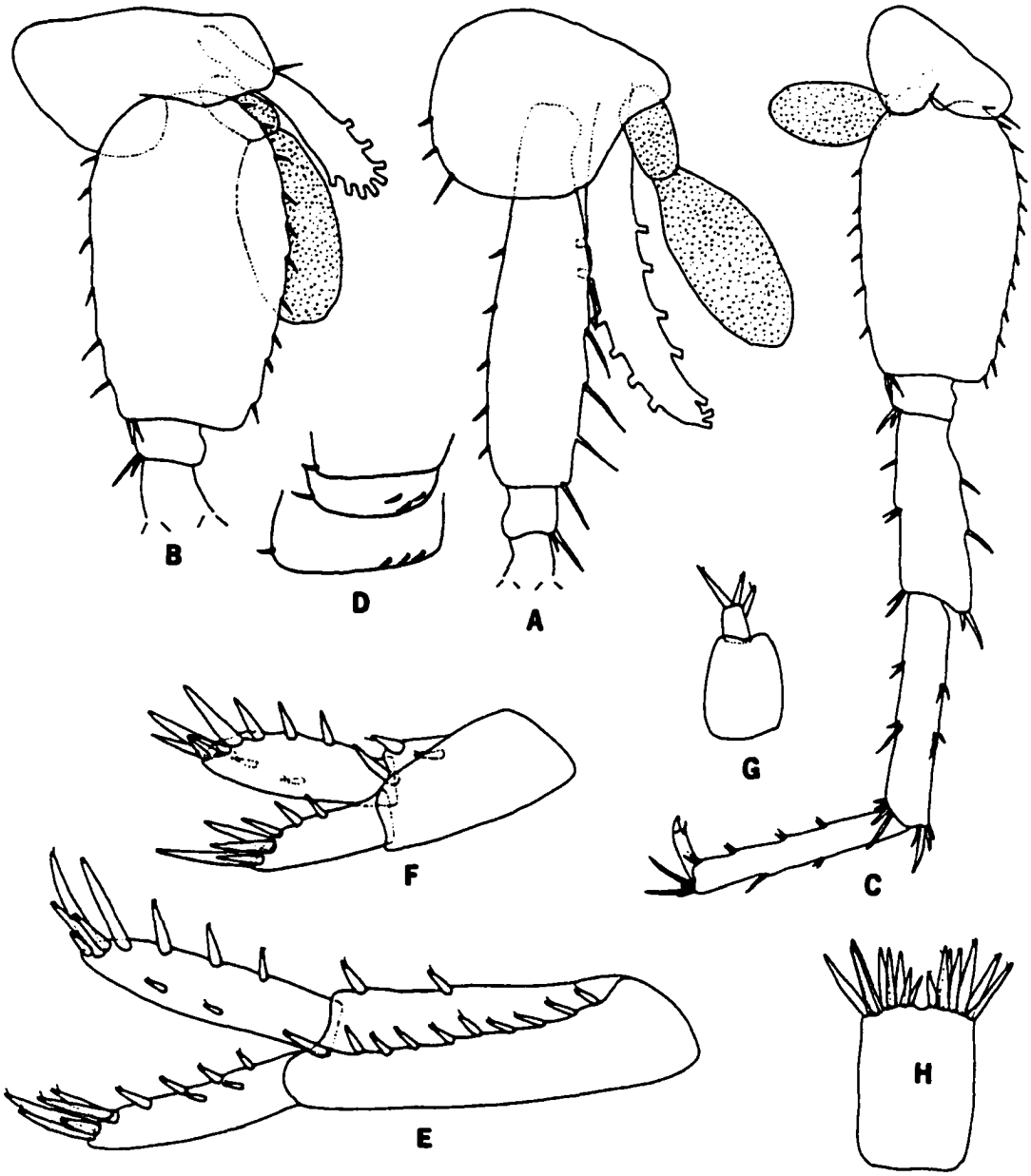

Fig. 6. ***Stygobromus cherylae*****, new species, female paratype (7.0 mm), unnamed spring, Sonoma County, California: A, B, pereopods 3, 5; C, pereopod 6; D, pleonal plates; E, F, G, uropods 1, 2, 3; H, telson.**

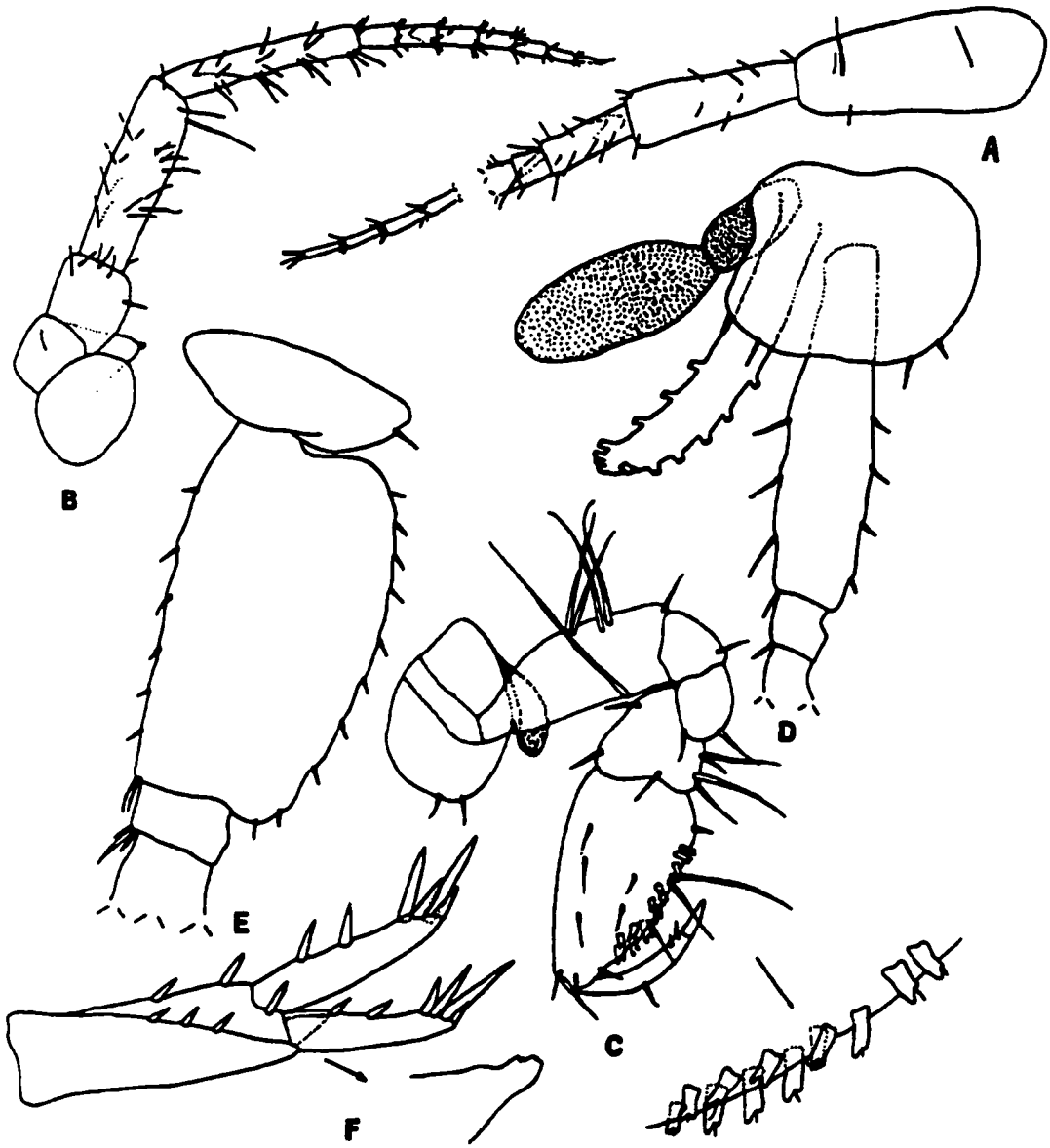

Fig. 7 . *Stygobromus cherylae*, new species, female paratype (7.0 mm), spring, Sonoma County, California: A, B, antennae 1, 2; D, E, pereopods 4, 7; Male paratype (4.5 mm), C, gnathopod 2 (palm enlarged); F, uropod 1.

Distribution and ecology. This species is only known from its type-locality (Figs. 9395).

Etymology. It is a pleasure to name this species for Cheryl B. Barr in recognition of her collections of amphipods from springs in western North America and for supplying our study with useful data on habitats and collecting techniques.

Remarks. A second, smaller (undescribed) species of *Stygobromus*, occurs with *S. cherylae* in the type-locality, but was not detected until the collection of 21 February 2000 was examined. The second species, which is distinguished by significantly smaller size at sexual maturity, proportionately shorter appendages, broader bases of pereopods 6 and 7, and fewer spines on the uropods and telson, will be described in a subsequent paper.

Stygobromus coloradensis Ward, 1977

Stygobromus coloradensis Ward, 1977: 452-456, figs. 1-2 [type-locality: hyporheic in North Fork of the South Platte River, Jefferson Co., Colorado].

Material examined. COLORADO. Jefferson Co.: hyporheic in North Fork of South Platte River, by S. P. Canton as follows: upstream of confluence with mainstream, 1 ♀, 4 Apr. 1984; 0.48 km W of S. Platte, 17 ♀, 26 Mar. 1985 and 3 ♀, 5 Apr. 1985; 0.8 km W of S. Platte, 17 ♀, 5 apr. 1985; just below jct. with N. Fork, S. Platte, 1 ♀, 5 Apr. 1985; 100 m downstream from jct. with N. Fork, 2 ♀, 5 Apr. 1985; upstream from Dam Rock, 7 ♀, 9 Apr. 1985; behind S. Platte Hotel, 17 ♀, 1 ♂, 9 apr. 1985; just upstream from jct. with N. fork, 2 ♀, 9 Apr. 1985; near gaging station in S. Platte, 25 femlae, 9 Apr. 1985; S. Platte, 2 ♀, 9 Apr. 1985.

Diagnosis. A very small hyporheic species, distinguished by possession of 4 apical plumose setae on inner plate of maxilla 1; oblique row of 4 plumose setae on margin of inner plate of maxilla 2; gnathopodal propods small and robust, palmar margins slightly oblique and distinctly serrated, few teeth on palmar margin; uropod 3 with one short and one longer spine. Largest ♀, 3.3 mm; largest ♂, 3.0 mm.

Distribution and ecology. This species is known from hyporheic habitats in the North Fork of South Platte River, Jefferson Co., Colorado (see Pennak and Ward, 1986 and Figs. 93, 97). In most collections made in March, April and November 1985, this species was found together with *S. pennaki*.

Stygobromus cowani, new species

(Figs. 8-9)

Material examined. CALIFORNIA. Napa Co.: roadside pipe from unnamed spring, Soda Canyon Road, ca. 6.4 km E of Yountville, HOLOTYPE ♀ (USNM), 1 ♂ (in poor shape), 1 juv., C. B. Barr, 23 Feb. 1991.

Diagnosis. A small groundwater species closely related to *S. gradyi* but distinguished as follows: maxilla 1 with 8-9 setae on inner plate; maxilla 2 and maxilliped with fewer setae on inner plate; lower lip without inner lobes; palm of propod of gnathopod 2 slightly concave; coxal plate of pereopods 3 and 4 deeper than broad; and ventral margin of pleonal plate 2 with fewer spines. Largest ♀, 4.6 mm; ♂ ca. 3.5 mm.

Female. Antenna 1: 52 percent length of body, 76 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6-8 plumose spines; palp segment 2 with 5 long setae on inner margin; palp segment 3 with 5-6 C setae, 5 D setae, and 5 E setae, lacking both A and B setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 9 apical plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin.

Maxilliped: inner plate with 3 blade-like spines, 3 plumose spines and 1 naked seta apically on inner margin; outer plate with setae on inner margin and 10-12 lightly plumose setae on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm straight or slightly concave medially, little longer than posterior margin, armed with 16 spine teeth in double row; defining angle with 3 spine teeth on outside, 4 shorter ones on inside; posterior margin not bearing setae; 3 singly inserted superior medial setae; 4 singly inserted inferior medial setae; dactyl nail short; coxa about as broad as deep, margin with 3 setae.

Gnathopod 2: propod longer than broad; palm straight or very weakly concave, and armed with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with 1 set of triply inserted setae; 5-6 singly inserted superior medial setae; 4 singly inserted inferior medial setae; coxa little deeper than broad, margin with 3 setae.

Pereopod 3: coxal plate about as deep as broad, margin with 3 setae.

Pereopod 4: coxal plate relatively broad, broader than deep, reaching about 40 percent length

of basis, margin with 5 setae.

Pereopod 6 little longer than pereopod 7, about 44 percent length of body, 11 percent longer than pereopod 5 in length.

Pereopods 5-7: bases broader proximally than distally; posterior margins convex but more strongly convex in pereopod 7; distoposterior lobes relatively well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 typically 33 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates sublinear, slightly broader distally.

Pleonal plates: posterior margin of plate 1 weakly convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, with 7 spines, about 75 percent length of peduncle; outer ramus with 7 spines; peduncle with 7 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 6 spines; outer ramus with 4 spines; peduncle with 2 spines.

Uropod 3: peduncle narrow, lacking small setae; ramus also narrow, approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad; apical margin with tiny median notch between spine clusters, with 11-12 relatively long spines.

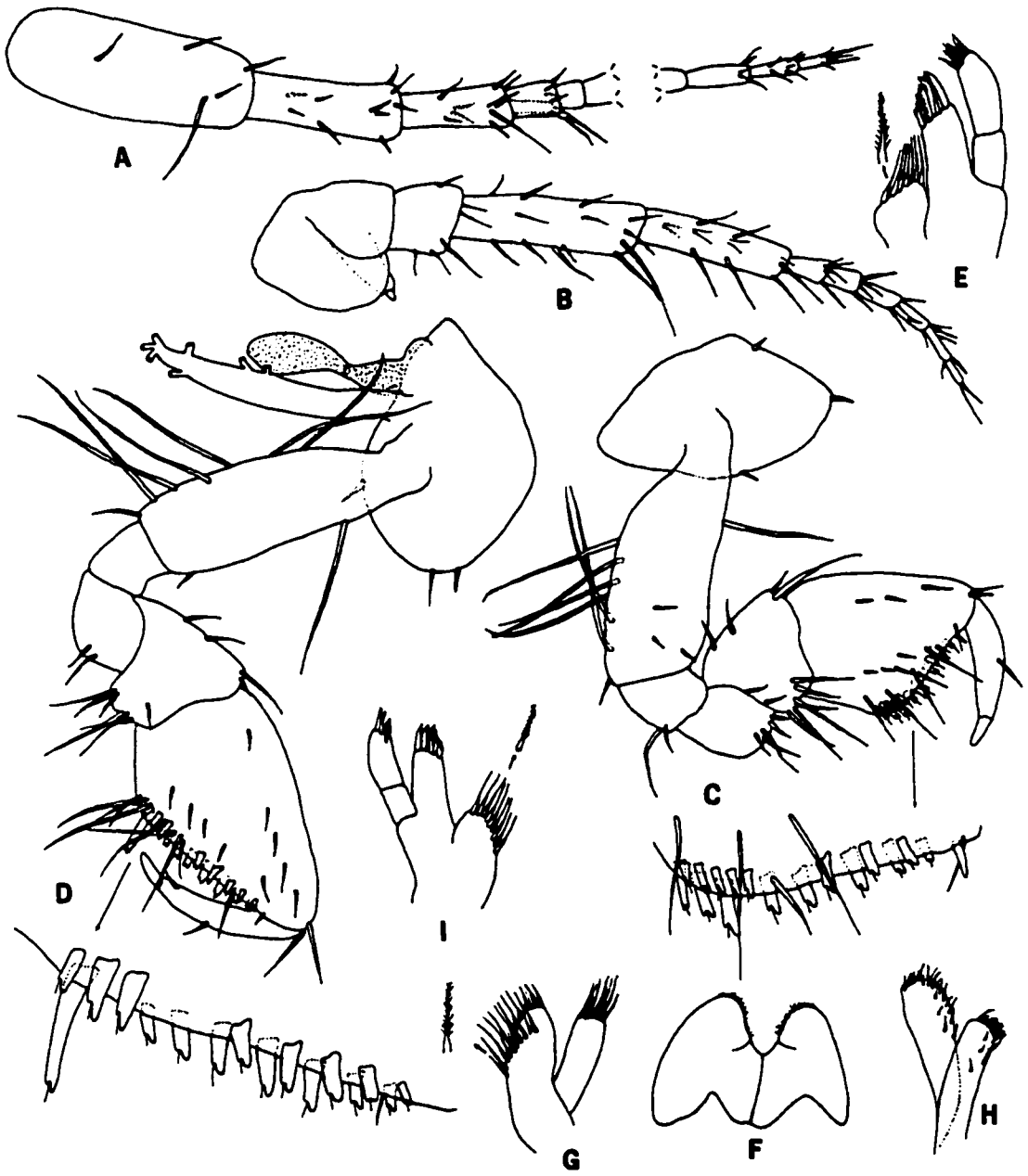

Fig. 8. ***Stygobromus cowani*****, new species, female holotype (4.6 mm), roadside pine from unnamed spring, Napa County, California: A, B, antennae 1, 2; C, D, gnathopods 1, 2 (palms enlarged); E, I, maxilla 1(apical setae enlarged); F, lower lip; G, maxilla 2; H, inner and outer plates of maxilliped (enlarged).**

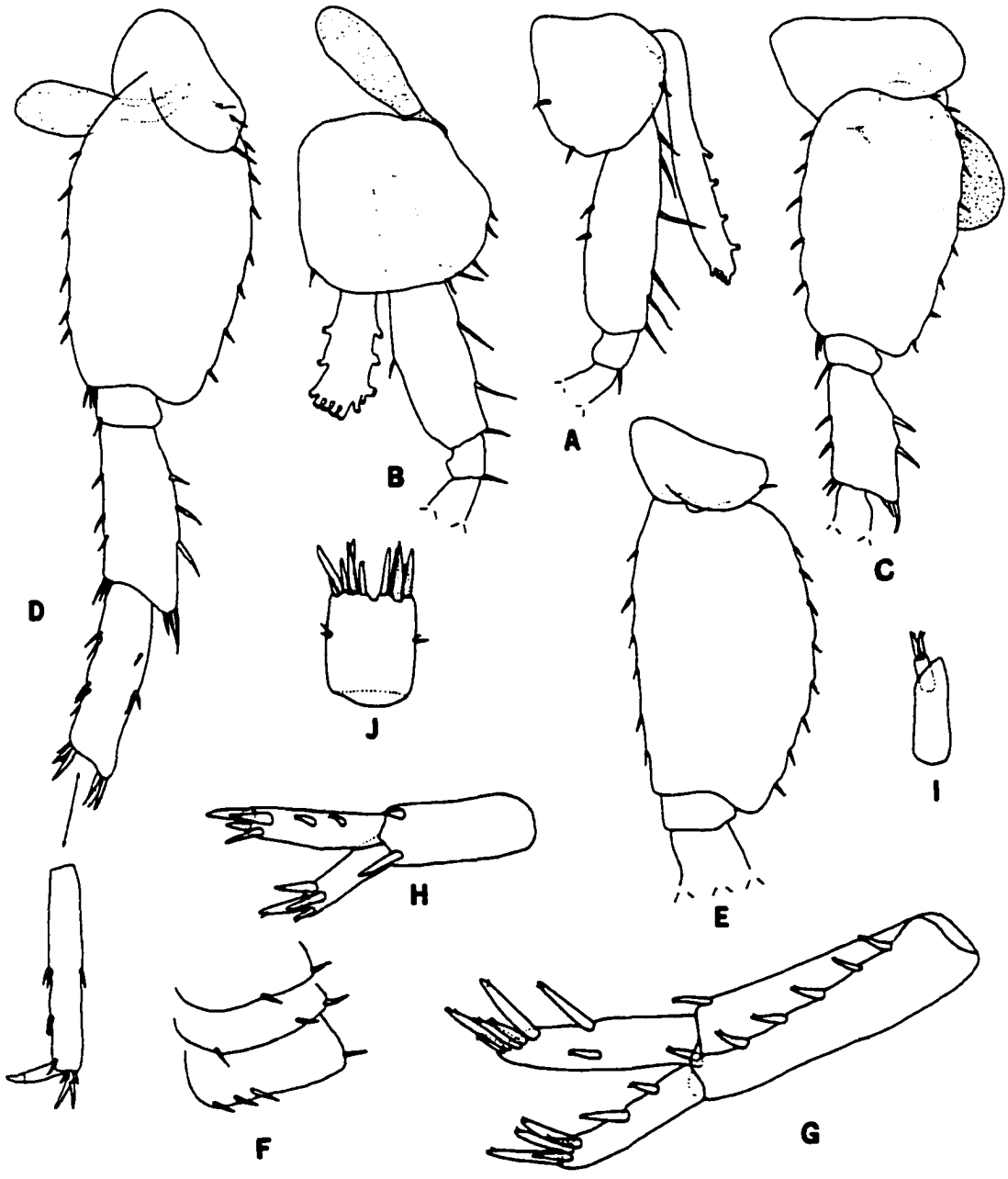

Fig. 9. *Stygobromus cowani*, new species, female holotype (4.6 mm), roadside pine from unnamed spring, Napa County, California: A, B, C, pereopods 3, 4, 5 (in part); D, pereopod 6; E, pereopod 7 (in part); F, pleonal plates; G, H, I, uropods 1, 2, 3; J, telson.

Type-locality. Roadside pipe extending from an unnamed spring on Soda Canyon Road, approximately 6.4 km north of junction with Silverado Trail and about 6.4 km east of Yountville, Napa County, California (Figs. 93, 95).

Distribution and ecology. This species is only known from its type-locality. The type material is in poor shape. The male specimen is covered by fungi and can not be measured accurately or dissected.

Etymology. This species is named for David Cowan, in recognition of his able assistance with the collection of amphipods from subterranean waters in California.

Stygobromus duplus, new species

(Figs. 10-12)

Material examined. WASHINGTON. Spokane Co.: well No. 7 in Spokane Valley, HOLOTYPE ♀ on slide mounts(USNM), L. A. Fuste, 21 Apr. 1981; well No. 5 in Spokane Valley, 1 ♂, L. A. Fusts, 25 Feb. 1981.

Diagnosis. A medium-sized groundwater species, related to *S. mysticus* and *S. latus* in structure of the gnathopods, but distinguished from those species as follows: gnathopod 2 with shorter posterior margin; bases of pereopods 5-7 much narrower and proportionately longer than other segments; distoposterior lobes of pereopod 5-7 poorly developed or absent; uropods 1 and 2 with more spines on rami and peduncles; telson proportionately broader with long spines. Largest (and only known) ♀ 5.4 mm; largest (and only known) ♂, 5.0 mm.

Female. Antenna 1: 70 percent length of body, 90 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 7 rather long setae on inner margin; palp segment 3 bearing 2 B setae, 7 D setae, and 3 E setae, lacking A and C setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 8 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, and 3 naked setae apically, and 3 coarse setae on inner margin; outer plate with numerous setae along inner margin and 5 setae on or near apex.

Gnathopod 1: propod shorter than propod of gnathopod 2; palm slightly convex and about 35 percent longer than posterior margin, armed with 12 spine teeth in double row; defining angle with 2

spine teeth on outside, but no shorter ones on inside; posterior margin with 2 setae; 6 superior medial setae, in unevern row; few inferior medial setae; dactyl nail rather long and slender; coxa deeper than broad, margin with 2 setae.

Gnathopod 2: propod subtriangular, almost 2 times longer than broad; palm armed with 15-16 spine teeth in double row; defining angle with 1 long and 2 shorter teeth on outside, no spine teeth on inside; posterior margin rather short, only about 50 percent length of palm, with 3 sets of mostly doubly inserted setae; 4 superior medial setae; 6 inferior medial setae; coxa about as deep as broad, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 5 setae.

Pereopod 4: coxal plate deeper than broad, reaching about 35 percent length of basis, margin with 5 setae.

Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 25 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than distally; posterior margins convex proximally, but not greatly expanded; distoposterior lobes poorly developed or vestigial; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 not greatly elongate, that of pereopod 6 approximately 33 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner and 4 spines on ventral margin, that of 2 and 3 also convex, each with 2 setae near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 2 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 11 spines; outer ramus with 8 spines; peduncle with 11 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 5 spines.

Fig. 10. ***Stygobromus duplus*****, new species, female holotype (5.4 mm), well no. 7 in Spokane Valley, Spokane County, Washington: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, E, maxilla 1, 2 (apical setae enlarged); F, inner and outer plates of maxilliped (enlarged).**

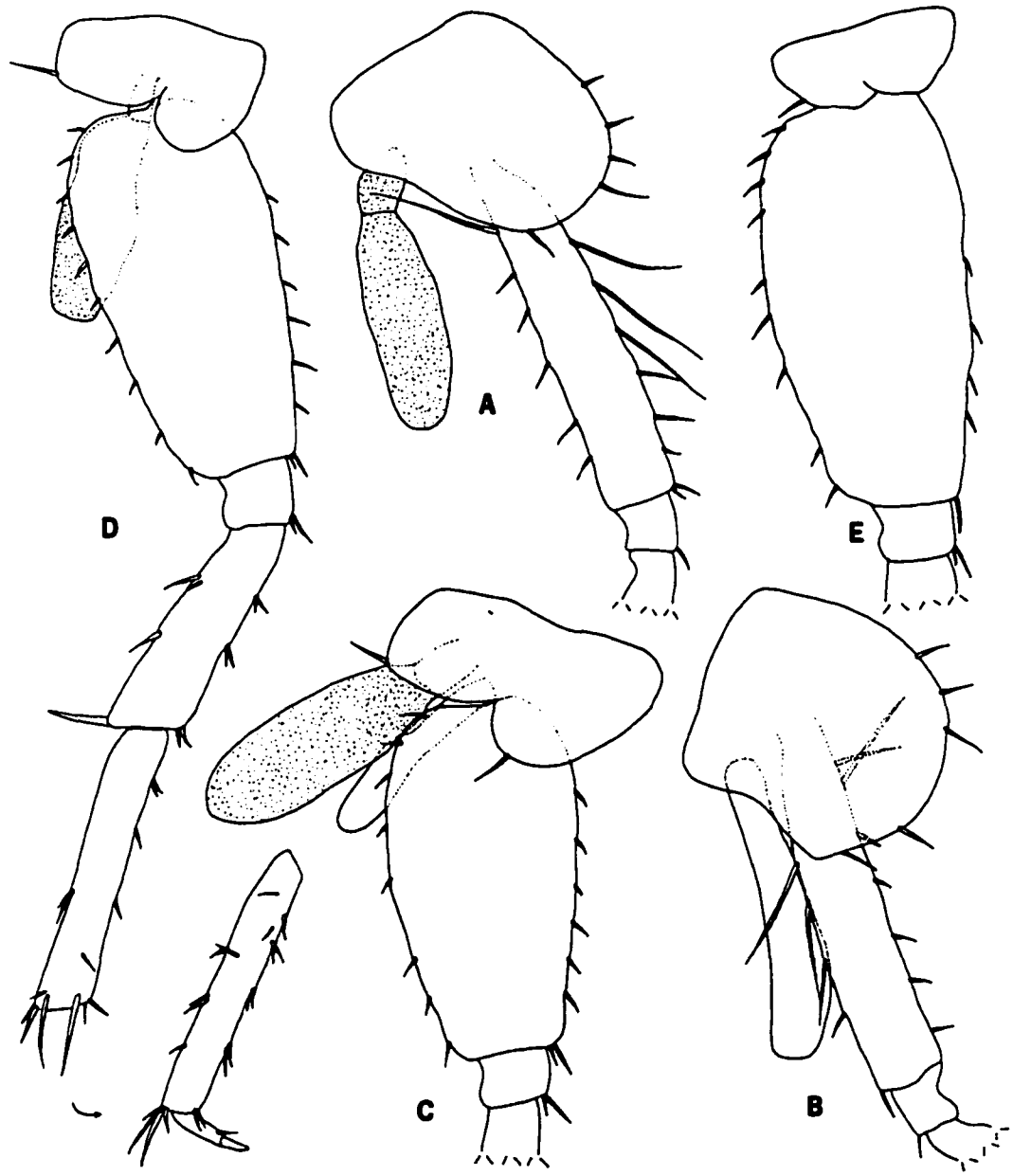

Fig. 11. ***Stygobromus duplus*****, new species, female holotype (5.4 mm), well no. 7 in Spokane Valley, Spokane County, Washington: A, B, C, pereopods 3, 4, 5; D, E, pereopods 6, 7.**

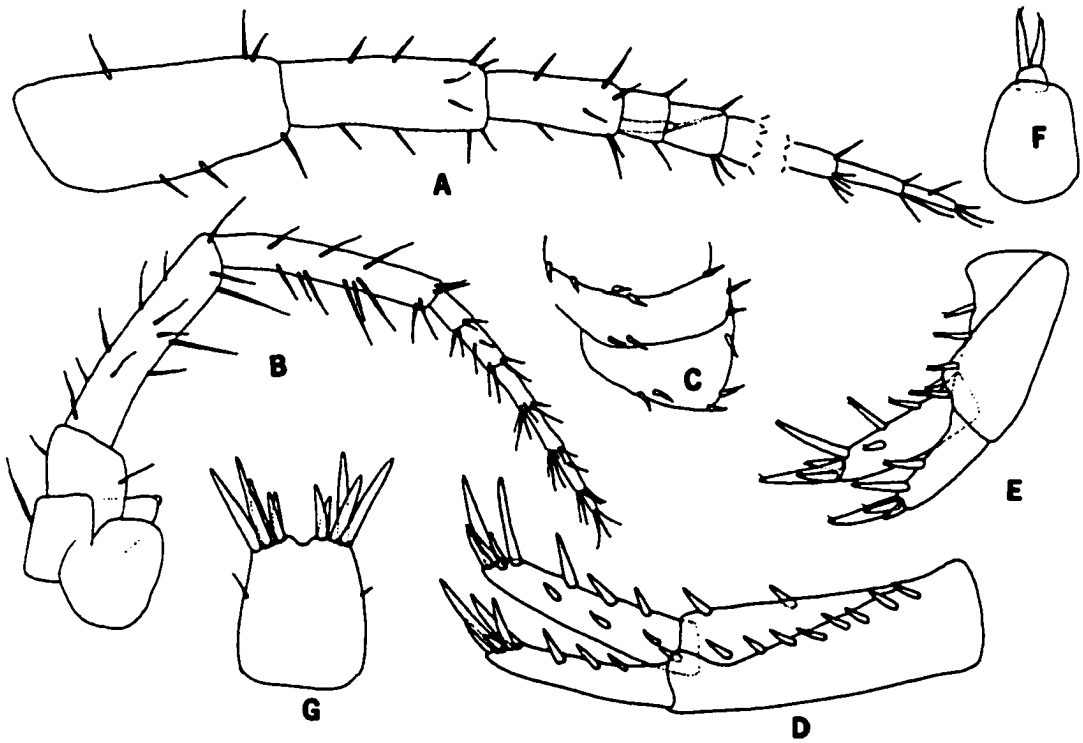

Fig. 12. ***Stygobromus duplus*****, new species, female holotype (5.4 mm), well # 7 in Spokane Valley, Spokane County, Washington: A, B, antennae 1, 2; C, pleonal plates; D, E, F, uropods 1, 2, 3; G, telson.**

Uropod 3: ramus short and only approximately 25 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with tiny median notch between spine clusters, bearing 10-11 mostly longish spines.

Type locality. well no. 7 in the Spokane Valley near Millwood, Spokane County, Washington.

Distribution and ecology. To date this species is known only from two specimens from two test wells in the Spokane Valley near Millwood, Spokane County, Washington (Figs. 93, 96).

Etymology. The epithet *duplus* is from the Latin, meaning "double or 2 times," which refers to the 2 sets of setae on the posterior margin of the propod of gnathopod 2.

Remarks: The single male specimen was lost in handling after initial examination.

Stygobromus elliotti Holsinger, 1974

Stygobromus elliotti Holsinger, 1974: 16-20, figs. 8-9 [type-locality: Deadhorse Cave, Skamania Co., Washington].

Material examined. WASHINGTON. Skamania Co.: Deadhorse Cave, 1 ♀ (TBMWSM), R. L. Crawford, 8-9 Oct. 1977; Little Red River Cave (lava tube), 1 ♀, 1 ♂ and 1 ♂ juv., R. L. Crawford and C. M. Serger, Oct. 1983.

Diagnosis. A medium-sized cavernicolous species apparently distinguished from other species of the *hubbsi* group by the long and heavily setose palpal segment 2 of maxilliped; broadly rounded outer lobes and short lateral processed of lower lip; proportionately uneven posterior margins of the bases of pereopods 5-7. Largest ♀ 9.5 mm; largest ♂, 7.0 mm.

Distribution and ecology. This species is recorded from small streams in three lava caves in Skamania Co., Washington, two of which (Readhorse Cave and Upper Falls Creek Cave system) are also inhabited by the stygobiont isopod *Salmasellus howarthi*(see Holsinger 1974; Lewis 2001).

Stygobromus fontinalis, new species

(Figs. 13-15)

Stygobromus sp. B: -- Ward and Holsinger, 1981: 64-67.

Material examined. COLORADO. Rio Blanco Co.: spring, ca. 32 km northwest of Rio Blanco, HOLOTYPE ♀ (USNM), 2 ♂ and 1 ♀paratypes, J. V. Ward, 19 May 1977; 5 ♂, 5 ♀, J. V. Ward, 20 May 1977; spring at mouth of Stewart Gulch, ca. 32 km north-northwest of Rio Blanco, 1 ♀, J. V. Ward, 2 Nov. 1979.

Diagnosis. A medium-sized groundwater species, closely related to *S. holsingeri* in gnathopods and uropods 1-2, but distinguished from the species above as follows: maxilliped with 3 bladelike apical spines on inner plate; gnathopods with more teeth on palmar margin of propods; palmar margin of gnathopod 1 straight or slightly convex; maxillae 1 and 2 with more setae on inner plate; telson proportionately longer. Largest ♀, 7.5 mm; largest ♂, 6.5 mm.

Female. Antenna 1: 60 percent length of body, 57 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 8 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 13 D setae, 3 E setae, lacking both A and C setae.

Inner lobes of lower lip vestigial.

Maxilla 1: inner plate with 9 apical, plumose setae; palp with 8 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin.

Maxilliped: inner plate with 3 bladelike spines, 5 plumose spines, 2 naked setae apically, and 4 plumose setae on inner margin; outer plate with setae on inner margin and face, and on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm slightly convex and about 30 percent longer than posterior margin in length, armed with 27-28 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 2 superior medial setae; about 6 singly inserted inferior medial setae; dactyl nail rather short; coxa much broader than deep, margin with 3 setae.

Gnathopod 2: propod longer than broad; palm slightly concave and armed with 21 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 cluster of setae; 9 superior medial setae,

Fig. 13. ***Stygobromus fontinalis*****, new species, female paratype (7.5 mm), unnamed spring about 32 km NW of Rio Blanco, Rio Blanco County, Colorado: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged); H, pleonal plates.**

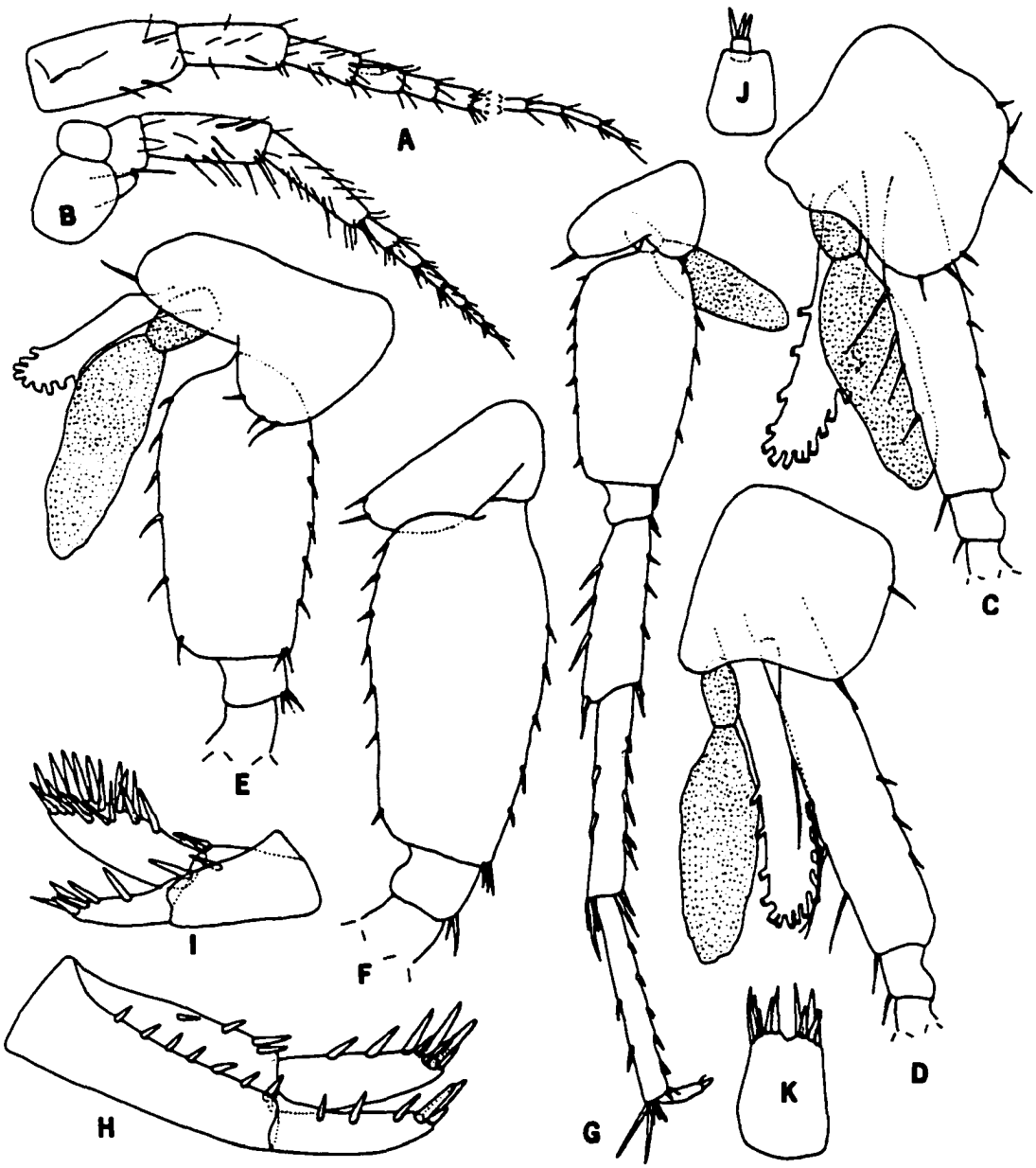

Fig. 14. ***Stygobromus fontinalis*****, new species, female paratype (7.5 mm), unnamed spring, about 32 km NW of Rio Blanco, Rio Blanco County, Colorado: A, B, antennae 1, 2; C, D, E, pereopods 4, 3, 5; F, G, pereopods 7,6; H, I, J, uropods 1, 2, 3; K, telson.**

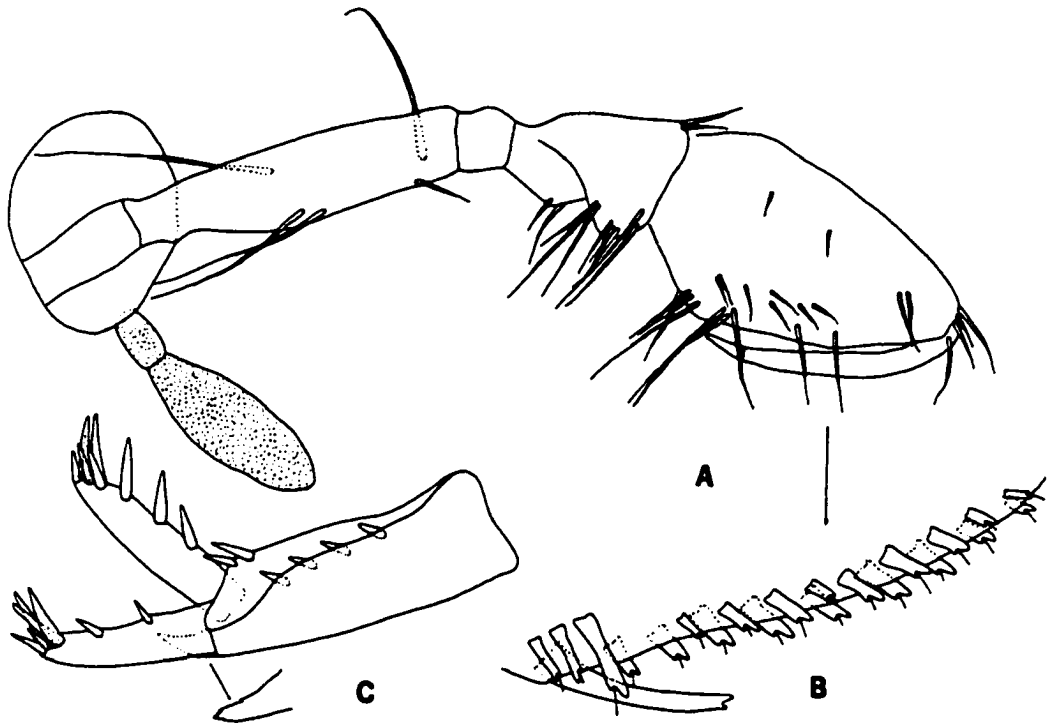

Fig. 15. ***Stygobromus fontinalis*****, new species, Male paratype (6.0 mm), unnamed spring, about 32 km NW of Rio Blanco, Rio Blanco County, Colorado: A, B, gnathopod 2, enlarged palm; C, uropod 1.**

most doubly inserted; about 4 singly inserted inferior medial setae; coxa broader than deep, margin with 2 setae.

Pereopod 3: coxal plate deep, about as broad as deep, margin with 2 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 30 percent length of basis, margin with 6 setae.

Pereopod 6 little longer than pereopod 7, about 67 percent length of body, 50 percent longer than pereopod 5.

Pereopods 5-7: bases of about as broad proximally as distally; posterior margins convex; distoposterior lobes developed but not prominent; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 1 with 1 setule near distoposterior corner, those of 2 and 3 weakly convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 67 percent length of peduncle, with 8 spines; outer ramus with 8 spines; peduncle with 11 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, heavily spined, with 19 spines, many toward distal end; outer ramus with 6 spines; peduncle with 4 spines.

Uropod 3: peduncle without setae; ramus approximately 33 percent length of peduncle, with 3 apical spines.

Telson little longer than broad, gently tapered distally; apex with tiny median notch between spine clusters, bearing 11-12 relatively long spines.

Male. Differing from female as follows: Gnathopod propods broader, palm of propod 2 with more teeth on margin. Uropod 1: peduncular process 20 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 8 spines; peduncle with 6 spines. Uropod 2: inner ramus with 24 spines, peduncle with 4 spines. Telson with 12 apical spines.

Type locality. A spring, ca. 32 km northwest of Rio Blanco, Rio Blanco County, Colorado.

Distribution and ecology. The species is recorded from its type-locality and a spring at the mouth of Stewart Gulch, both in Rio Blanco County, Colorado (Figs. 93, 97). The salinity of the type-locality springs was about 1,000 mg/l at the time of collection, 19 and 20 May, 1977 (Ward and

Holsinger, 1981).

Etymology. The epithet *fontinalis* is from the Latin, meaning "a spring," with refererence to the spring habitat of the species.

Stygobromus gallawayae, new species

(Figs. 16-18)

Material examined. CALIFORNIA. Butte Co.: an unnamed spring on Rock Creek, Chico, HOLOTYPE ♀ (USNM), 2 ♂paratypes, 6 juvs., J. Gallaway, 28 July 1997; 1 ♀, 1 fragment, J. Gallaway, 15 Oct 1996.

Diagnosis. A medium size stygobiont species closely related to *S. grahami* but distinguished from that species as follows: gnathopod 2 with straight or slightly concave palmar margin; pleonal plates 2 and 3 with more spines on ventral margin; uropod 1 with proportionately longer peduncle and with fewer spines; peduncle of uropod 2 with 2 spines; peduncle of uropod 3 with 1-3 spines and proportionately long and broad; telson only slightly notched. Largest ♀, 6.0 mm; largest ♂, 5.0 mm.

Female. Antenna 1: 63 percent length of body, about 70 percent longer than antenna 2; primary flagellum with 15 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 9 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 with 8 D setae, 7 E setae, lacking A, B and C setae.

Inner lobes of lower lip small.

Maxilla 1: inner plate with 11 apical, plumose setae; palp with 8 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin.

Maxilliped: inner plate with 3 bladelike spines, 4 plumose spines, 2 naked setae apically, and 5 plumose spines on inner margin; outer plate with setae on inner margin and 3 bladelike spines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm about 2 times longer than posterior margin, armed with 20 spine teeth in double row; defining angle with 2 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; 2 superior medial setae; 4-6 inferior medial setae; dactyl nail short; coxa approximately 60 percent broader than deep, margin with 4 setae.

Gnathopod 2: propod subrectangular, palm slightly concave medially and armed with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 33 percent length of palm, with 2 sets of triply inserted setae; 8 superior medial setae, doubly inserted; 4-5 inferior medial setae, 3 long medial setae; coxa broad as

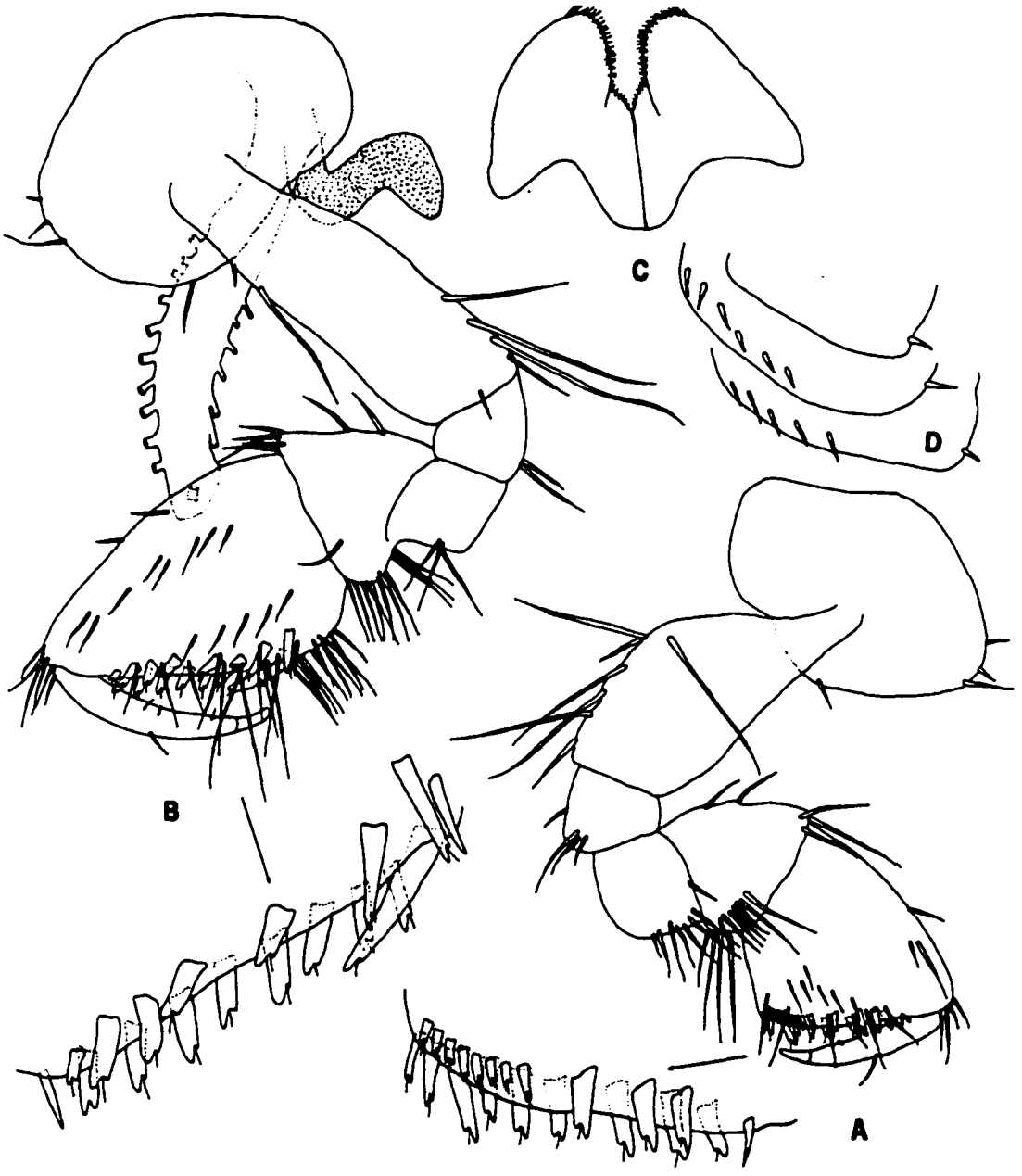

Fig. 16. ***Stygobromus gallawayae*****, new species, female paratype (6.0 mm), unnamed spring on Rock Creek, Butte County, California: A, B, gnathopods 1, 2 (palms enlarged); C, lower lip; D, pleonal plates.**

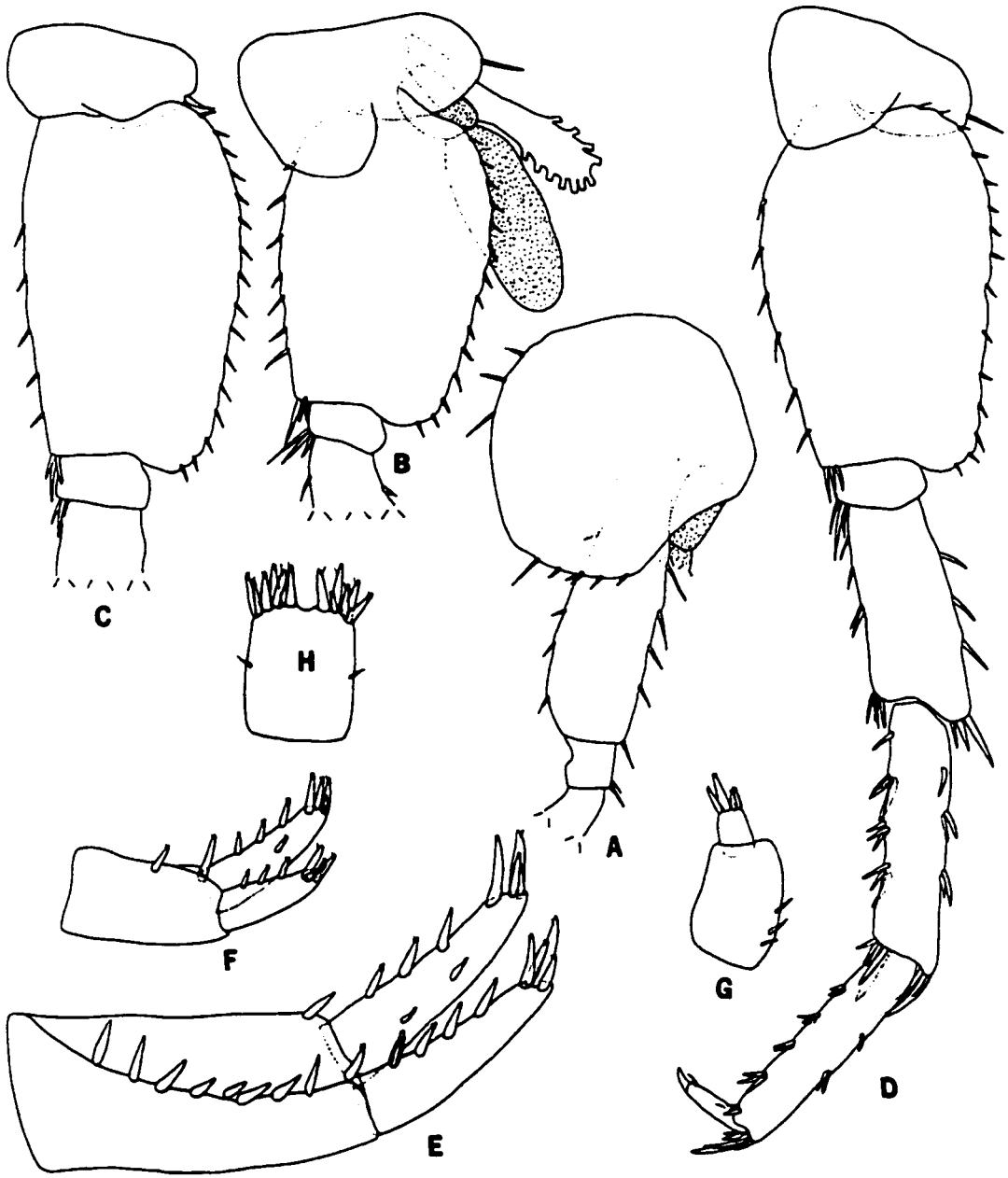

Fig. 17. ***Stygobromus gallawayae,*** **new species, female paratype (5.0 mm), unnamed spring on Rock Creek, Butte County, California: A, B, pereopods 4, 5; C, D, pereopods 7, 6; E, F, G, uropods 1, 2, 3; H, telson.**

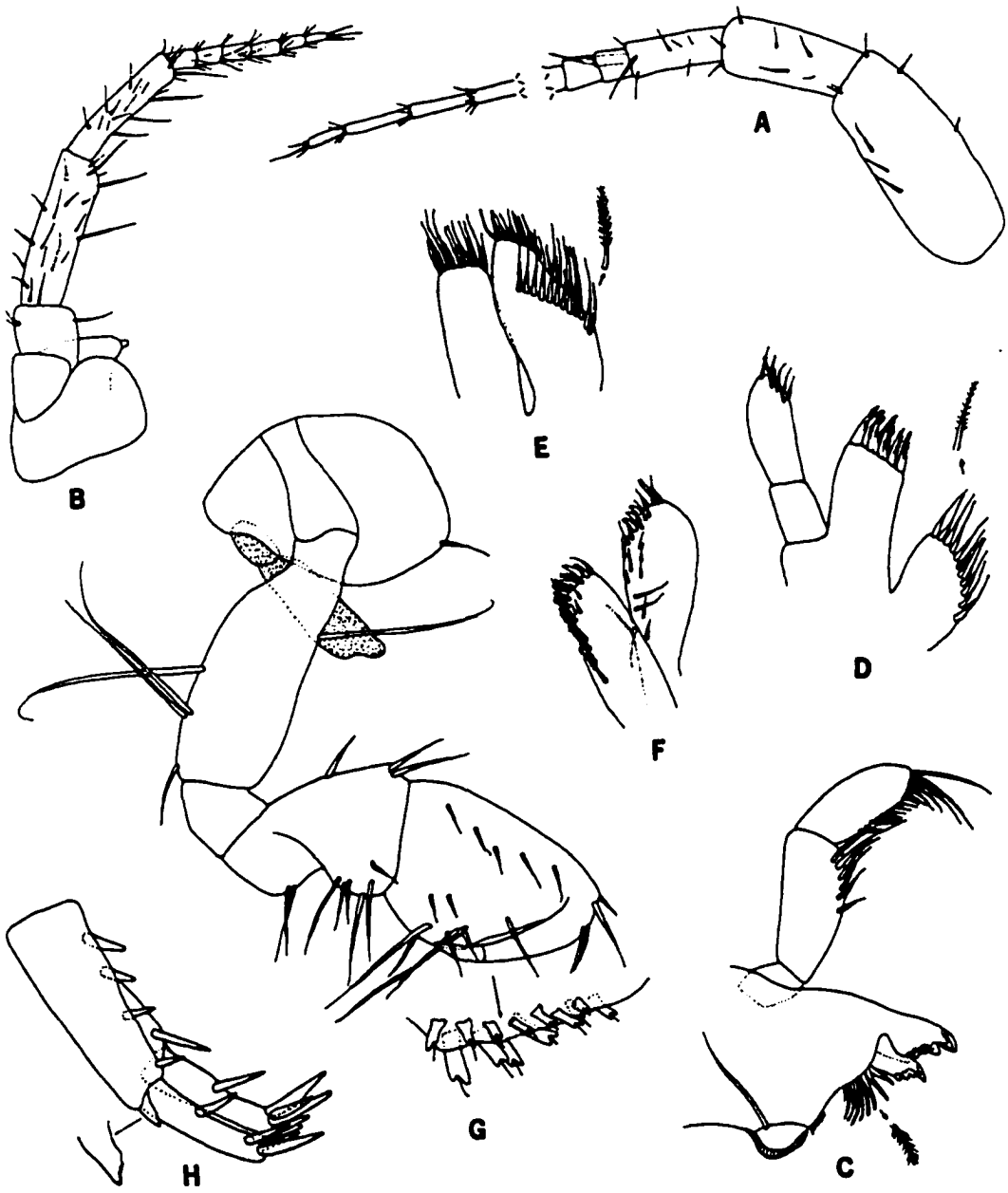

Fig. 18. ***Stygobromus gallawayae*****, new species, female paratype (6.0 mm), unnamed spring on Rock Creek, Butte County, California: A, B, antennae 1, 2; C, left mandible; D, E, maxilla 1, 2 (apical setae enlarged); F, inner and outer plates of maxilliped (enlarged); Male paratype (4.8mm), G, gnathopod 2; H, uropod 1.**

deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 50 percent length of basis, margin with 8 setae.

Pereopod 6 little longer than pereopod 7, about 67 percent length of body, about 33 percent longer than pereopod 5.

Pereopods 5-7: bases almost as broader proximally as distally; posterior margins slightly convex; distoposterior lobes well developed; anterior and posterior margins withvariable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with short spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 6 spines, that of plate 3 with 5 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 9 spines; outer ramus with 8 spines; peduncle with 10 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 2 spines.

Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 4 apical spines.

Telson longer than broad; apical margin typically with tiny median notch between spine clusters, bearing 12 relatively long spines.

Male. Differing from female as follows: Gnathopod propods smaller, palm of propod 2 longer in relation to posterior margin and with fewer teeth on margin. Uropod 1: peduncular process 33 percent length of outer ramus, norrowing sharp distally, upper margin minutely serrate; inner ramus with 5-6 spines; peduncle with 5 spines. Uropod 2: inner ramus with 6-7 spines, peduncle with 3 spines. Telson with 13-14 short apical spines.

Type locality. An unnamed spring on Rock Creek, approximately 20.8 km north of Chico, Butte County, California.

Distribution and ecology. This species is only known from its type-locality, a spring next to Rock Creek in Butte Co., California (Figs. 93, 95). The temperature of the spring was about 20°C (J. Gallaway, pers. comm.).

Etymology. This species is named in honor of its collector, Ms. Jody Gallaway, who is thanked for collecting this material and allowing us to study it.

Stygobromus grahami Holsinger, 1974

(Figs. 19-22)

Stygobromus grahami Holsinger, 1974: 20-22, figs. 10-11 [type-locality: Cave of the Catacombs, Calaveras Co., California].

Material examined. CALIFORNIA. Amador Co.: Fern Frond Cave, 1 ♂, 6 ♀, D. C. Rudolph, S. Winterath, E. van Ingen and D. Cowan, 15 Apr. 1979; Masonic Cave, 3 ♀ (BBM), F. G. Howarth, 17 Oct. 1988; Calaveras Co.: Cave City Cave (= California Caverns), M. Demarest, 5 ♂, 22 Mar. 1996 and 31 specimens (♀, ♂, and juvs.), 2 Apr. 1996; Shaws Cave, 5 ♀, D. C Rudolph, S. Winterath and E. van Ingen, 17 Apr. 1979.

Diagnosis. A medium-sized cavernicolous species differing from other species of the *hubbsi* group by 15 or 16 plumose setae on apex of inner plate of maxilla 2; 12 or 13 apical spines on inner plate of maxilliped; row of forked spine teeth on the inside margin of the posterior angle of gnathopodal propod 1; deep coxal plates of gnathopod 2 and pereopod 3 and 4; more spines on ventral margins of pleonal plates 2 and 3 (except *S. hubbsi*). Largest ♀ 9.0 mm, largest ♂ 5.0 mm.

Distribution and ecology. This species is recorded from eight caves in Amador and Calaveras cos., California (Figs. 93, 95). It has been collected together with *S. gradyi* in Fern Frond (small stream) and Masonic caves in Amador County and Masonic caves.

Remarks. This species is rather "typical of the *hubbsi* group species and therefore serves a useful reference paint for comparison of other species (see also "Methods and Materials").

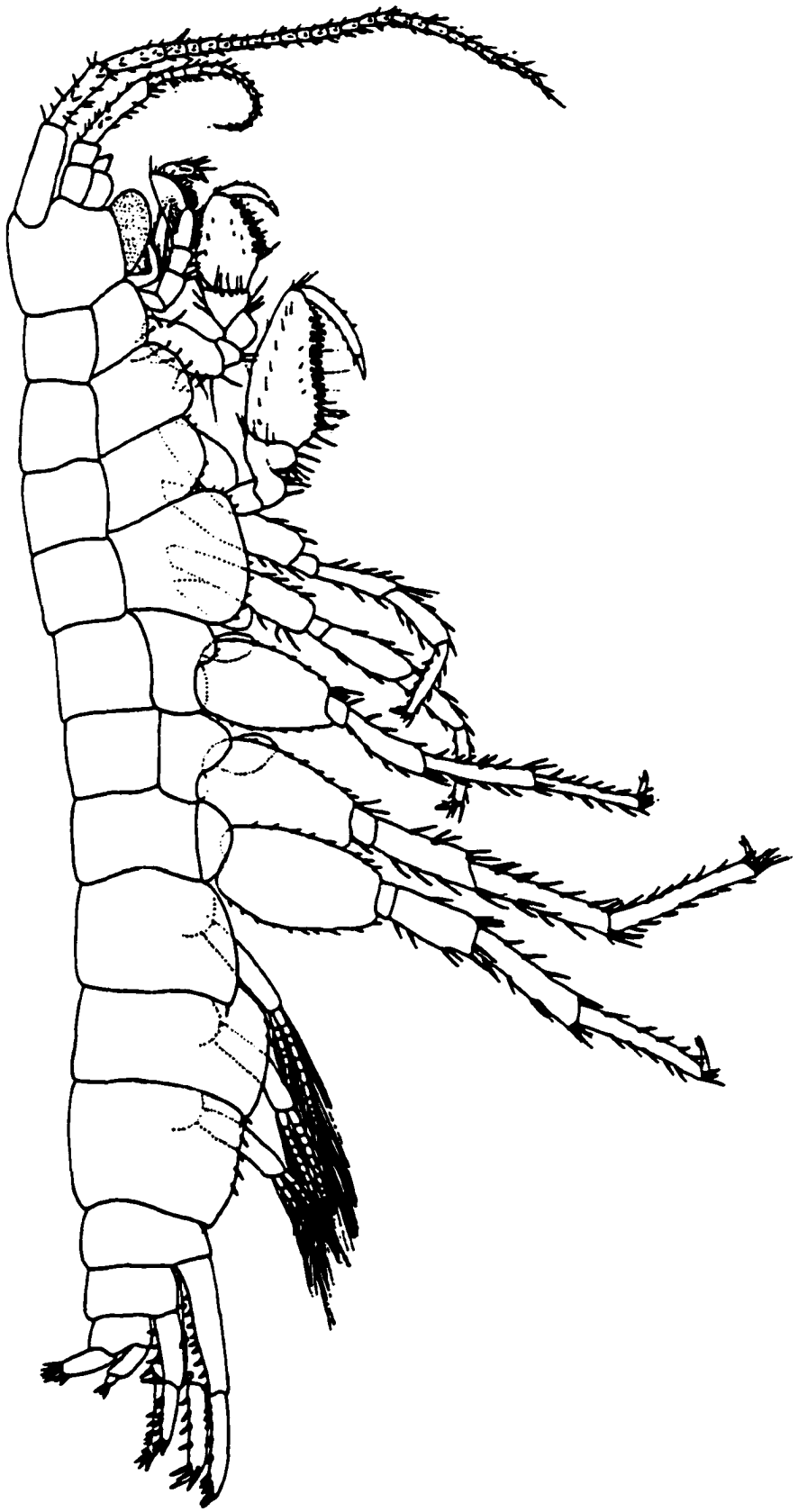

Fig. 19. *Stygobromus grahami* Holsinger, 1974. Female (9.0 mm), Cave City Cave, Calaveras, County, California.

Fig. 20 . *Stygobromus grahami* Holsinger, female (6.7 mm), Fern Frond Cave, Amador County, California: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).

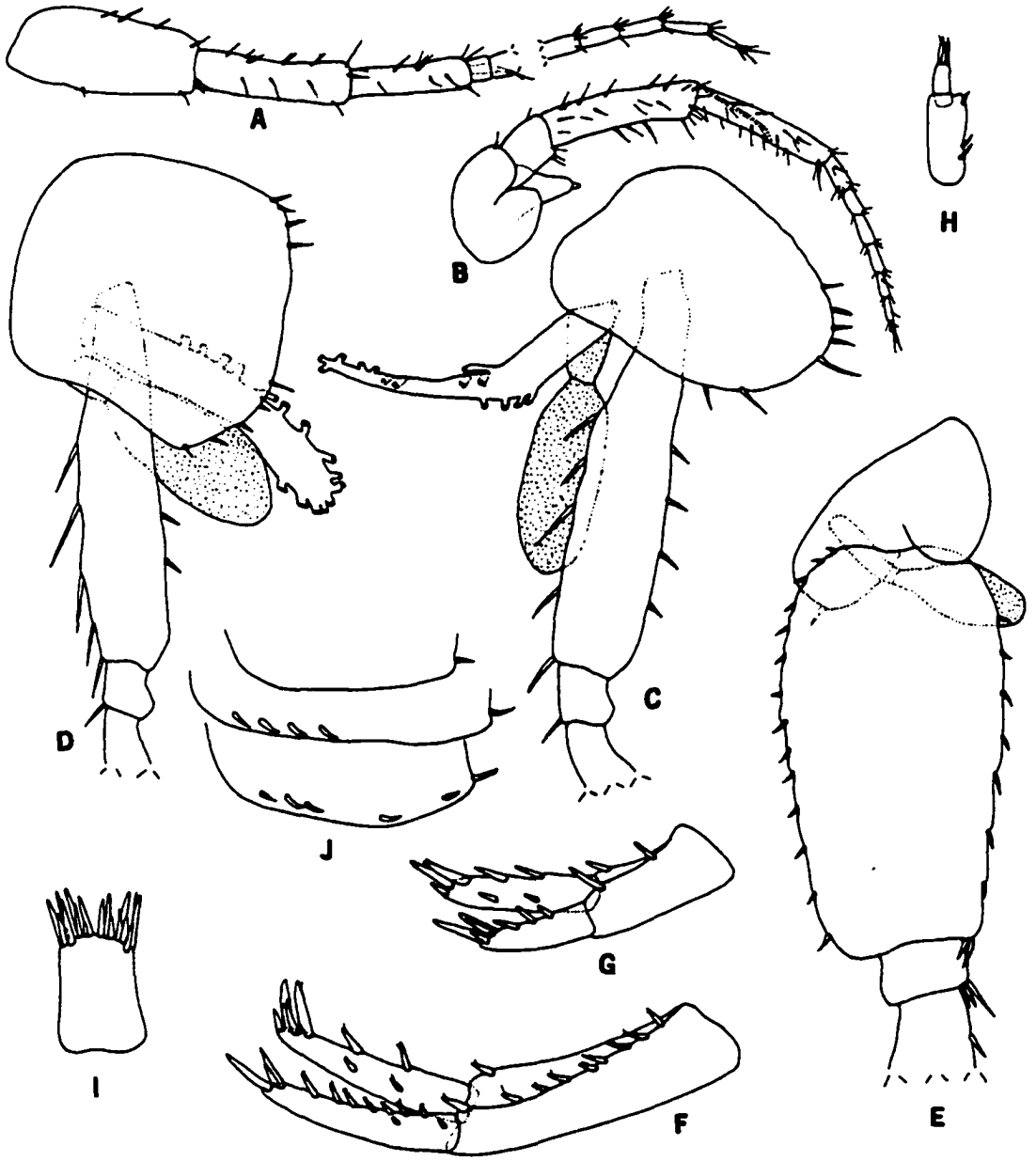

Fig. 21. ***Stygobromus grahami*** **Holsinger, female (6.7 mm), Fern Frond Cave, Amador County, California: A, B, antenna 1, 2; C, D, E, pereopod 3, 4, 5; F, G, H, uropod 1, 2, 3; I, telson; J, pleonal plates.**

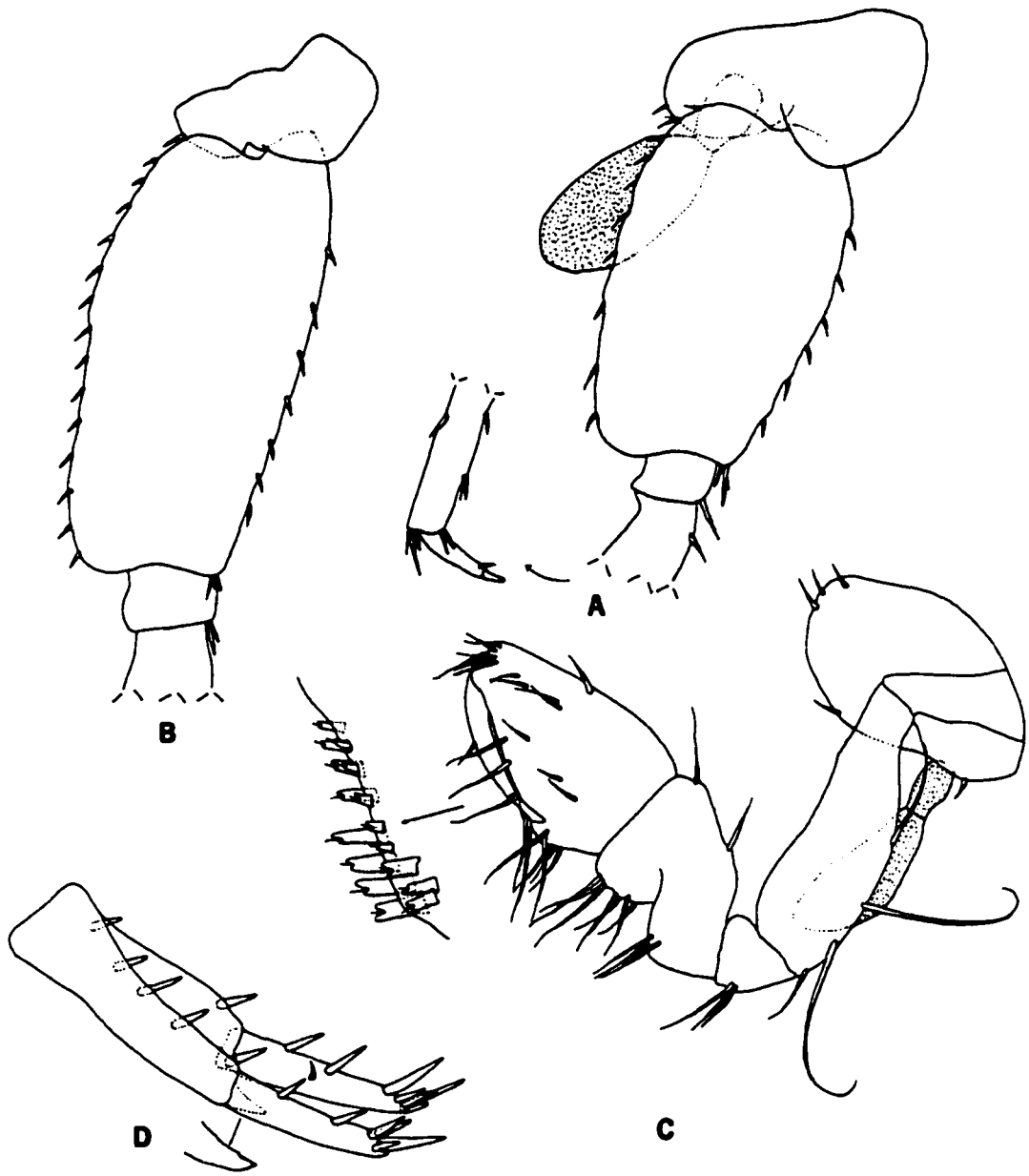

Fig. 22. ***Stygobromus grahami*** **Holsinger, female (6.7 mm), Fern Frond Cave, Amador County, California: A, B, pereopod 6, 7; Male (5.5 mm), C, gnathopod 2; D, uropod 1.**

Stygobromus gradyi Holsinger, 1974

(Figs. 23-26)

Stygobromus gradyi Holsinger, 1974: 23-26, figs. 12-13 [type-locality: Crystal Palace Cave, Tuolumne Co., California].

Material examined. CALIFORNIA. Amador Co.: Fern Frond Cave, 7 ♀, 6 ♂, D. C. Rudolph, S. Winterath, E. van Ingen and D. Cowan, 15 Apr. 1979; unnamed spring, Masonic Cave, 1 ♀, Lulubell Cave, 1 ♀, F. G. Howarth, 17 Oct. 1987; Tuolumne Co.: small unnamed spring, ca. 14.8 km southeast of Angels Camp, 1 ♀, D. Cowan, 19 Nov. 1978.

Diagnosis. A medium-sized cavernicolous species closely related to *S. grahami* but differing from that species by smaller size at sexual maturity; lacking inner lobes on lower lip; proportionately smaller gnathopodal propod 2 of ♀, with shorter and slightly convex palm; 4 spines on ventral margins of pleonal plates 2 and 3; distally serrate peduncular process of male uropod 1. Largest ♀, 7.0 mm; largest ♂, 4.5 mm.

Distribution and ecology. This species is recorded from a small, unnamed springs and four caves in Amador and Tuolumne cos., California (Figs. 93, 95).

Remarks. This species is very similar morphologically to *S. grahami* and *S. harai*. Therefore, it is illustrated as reference to those species.

Fig. 23. ***Stygobromus gradyi*** **Holsinger, female (5.0 mm), Fern Frond Cave, Amador County, California: A, B, antenna 1, 2; C, D, gnathopods 1, 2 (palms enlarged); E, right mandible and dentate part of left mandible; F, lower lip; G, H, maxilla 1, 2 (apical setae enlarged); I, inner and outer plates of maxilliped (enlarged).**

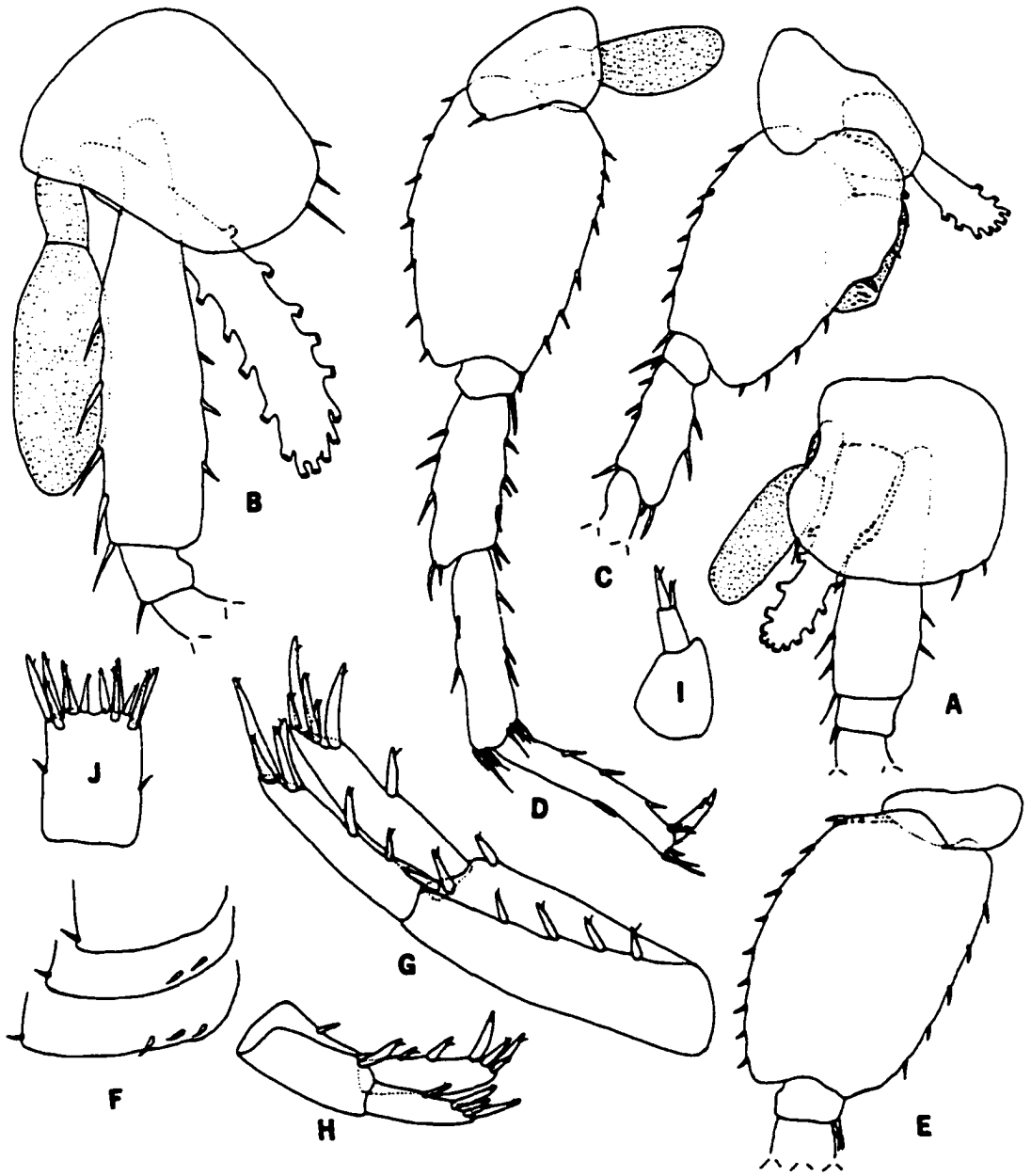

Fig. 24. ***Stygobromus gradyi*** **Holsinger, female (5.0 mm), Fern Frond Cave, Amador County, California: A, B, C, pereopod 3, 4, 5 (in part); D, pereopod 6; E, pereopod 7 (in part); F, pleonal plates; G, H, I, uropod 1, 2, 3; J, telson.**

Stygobromus harai Holsinger, 1974

(Figs. 25-27)

Stygobromus harai Holsinger, 1974: 26-29, figs. 14-15 [type-locality: Pinnacle Point Cave, Tuolumne Co., California].

Material examined. CALIFORNIA. Tuolumne Co.: Windeler Cave, near Vellecito, 1 ♀, B.. Ehr, 21 Feb. 1976; 1 ♀, 2 ♂, W. R. Elliott, 14 Jan. 1978; unnamed spring, 15 km southeast of Sonora, 15 ♀, D. C. Rudolph, S. Winterath and D. Cowan, 19 Feb. 1979.

Diagnosis. A medium-sized cavernicolous species, closely similar to *S. gradyi* and *S. grahami* but differing from these 2 species as follows: fewer apical spines on inner plate of maxilliped; inner margin of posterior angle of gnathopodal propod 1 with mostly unforked spine teeth; gnathopodal propod 2 of male proportionately a little larger than propod 2 of female; coxal plates of gnathopod 2 and pereopods 3 and 4 not as deep; ramus of uropod 3 with 3 apical spines; and proportionately longer telson about one-third deeper than broad. Largest ♀, 7.5 mm; largest ♂, 7.0 mm.

Distribution and ecology. This species is recorded form two caves, one mine tunnel and a spring, all in Tuolumne Co., California (Figs. 93, 95). It was collected from a pool in Windeler Cave and from beneath rocks and organic debris in the unnamed spring. The spring sample contained 1 ovigerous frmale (6.0 mm) with 8 embryos in the brood pouch.

Remarks. This species is very similar morphologically to*S. grahami* and *S. gradyi*. It was illustrated here as a reference to those species.

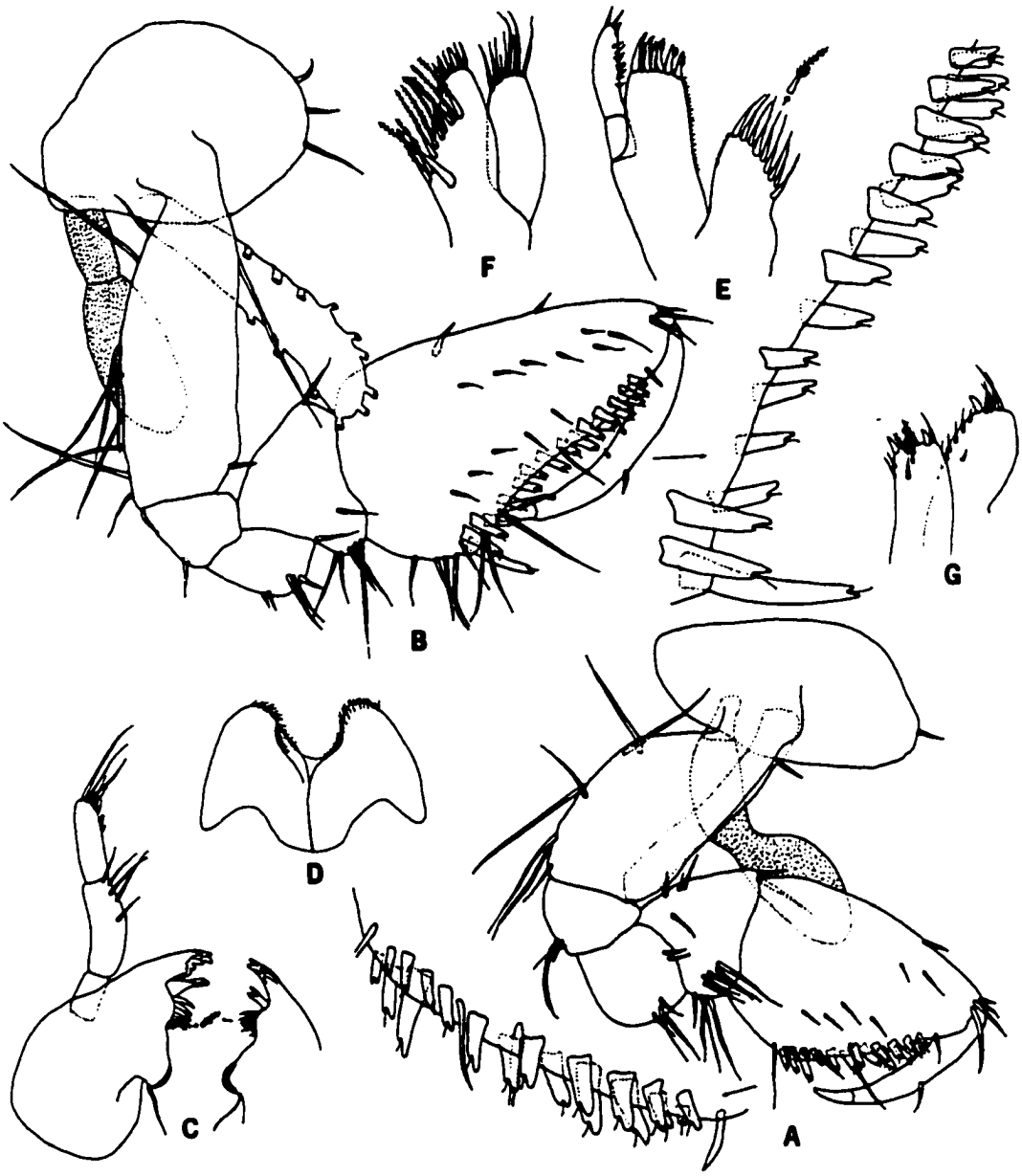

Fig. 25. ***Stygobromus, harai*****, female (6.0 mm), unnamed spring, Tuolumne County, California: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

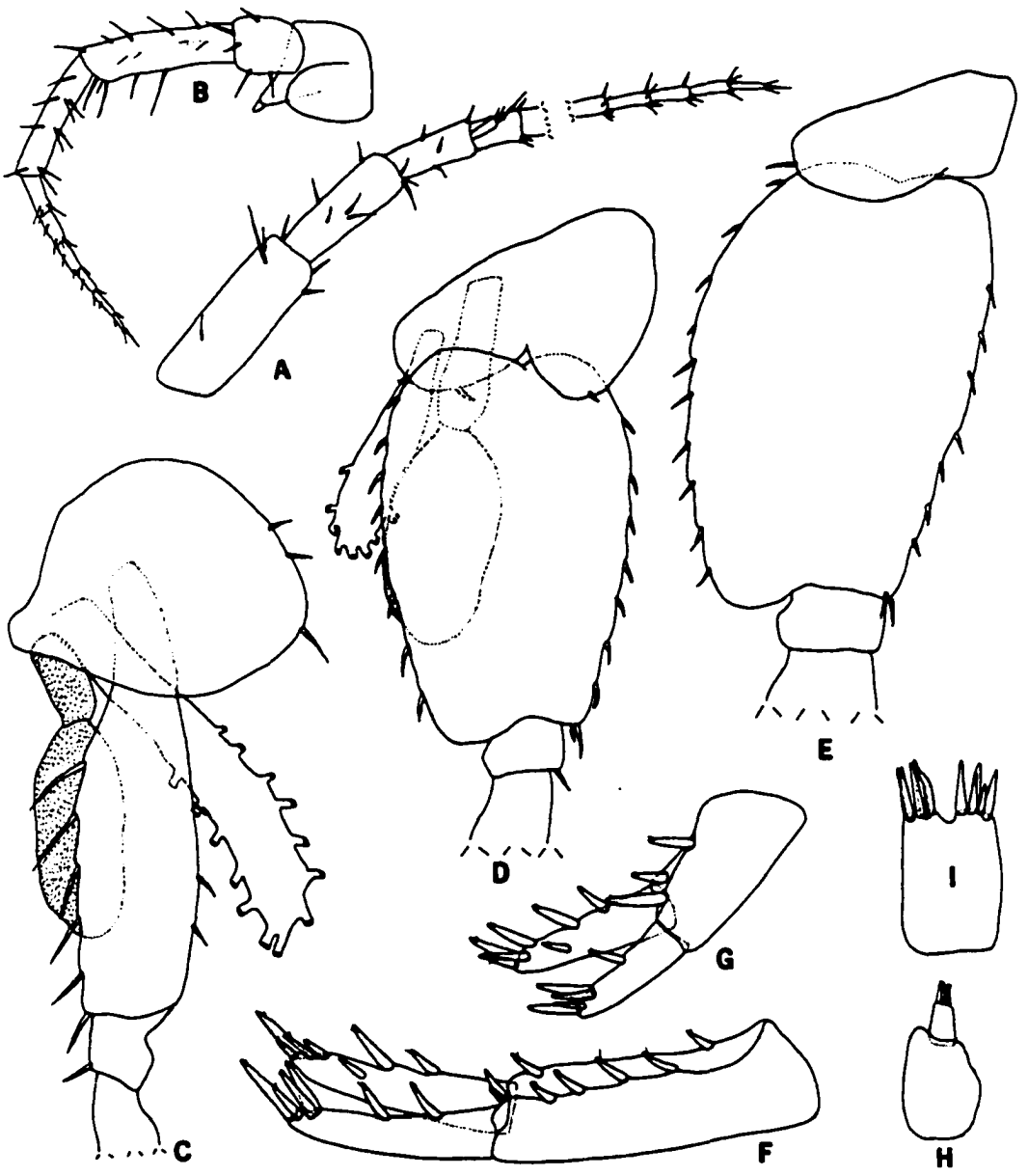

Fig. 26. ***Stygobromus harai*** **Holsinger, female (6.0 mm), unnamed spring, Tuolumne County, California: A, B, antenna 1, 2; C, D, E, pereopod 3, 5, 7; F, G, H, uropod 1, 2, 3; I, telson.**

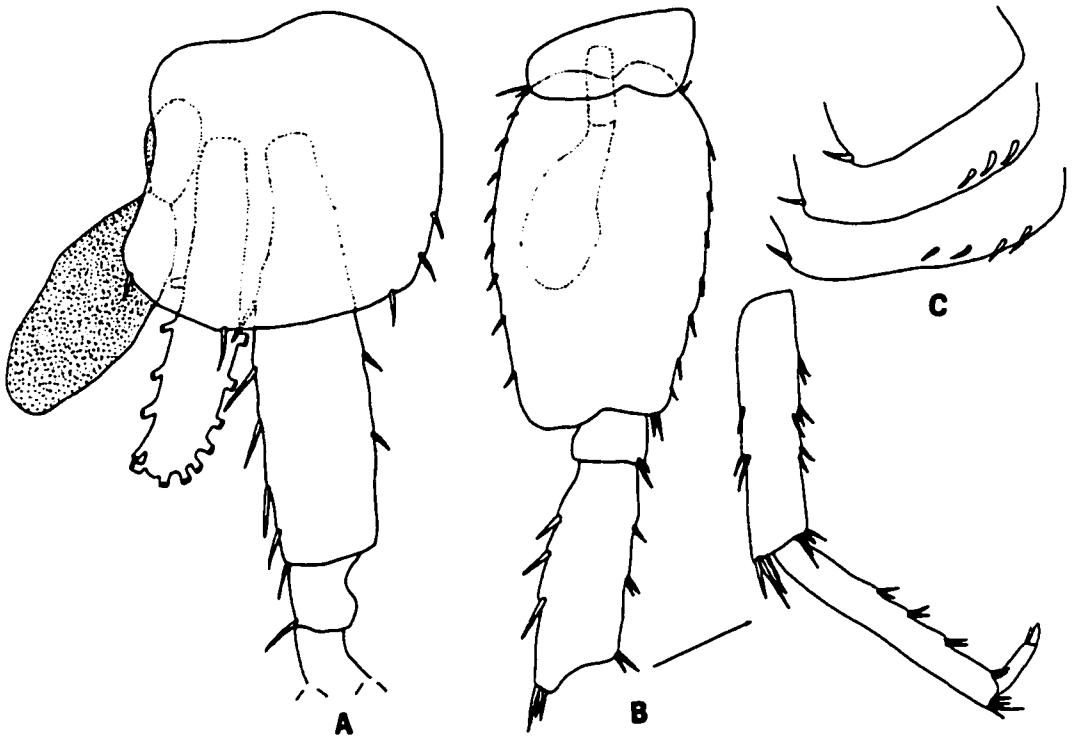

Fig. 27. ***Stygobromus harai*** **Holsinger, female (6.0 mm), unnamed spring, Tuolumne County, California: A, B, pereopod 4, 6; C, pleonal plates.**

Stygobromus herbsti, new species

(Figs. 28-30)

Material examined. NEVADA. Elko Co.: Ruby Lake National Wildlife Refuge, spring No. 121, HOLOTYPE ♀ (USNM), 9 ♂ and 6 ♀ paratypes (2 partly on slide mounts), D. B. Herbst, 10 June 1997; spring No. 229, 2 ♀, D. B. Herbst, 10 June 1997; spring No. 129, 13 ♂, 5 ♀, 1 juv., D. B. Herbst, 9 June 1997, spring No.103, 5 ♀, 1 ♂, D. B. Herbst, summer 1997; White Pine Co.: Ruby Lake National Wildlife Refuge, spring No. 208, 1 ♂, 18 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 191, 4 ♂, 17 ♀, 16 juvs., D. B. Herbst, 13 Sept. 1997, spring No. 180, 4 ♂, 15 ♀, 12 juvs, D. B. Herbst, 12 Sept. 1997; spring No. 223, 5 ♂, 2 ♀, 9 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 217, 22 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 219, 3 ♂, 1 ♀, 26 juvs, D. B. Herbst, 14 Sept. 1997.

Diagnosis. A medium-sized species, closely similar to *S. grahami* and *S. gradyi*, but distinguished from those 2 species as follows: maxilla 1 and maxilliped with fewer setae on inner plate; palms of gnathopod 1 and 2 with more spines; coxal plate of gnathopod 2 broader than deep; lacking distoposterior lobes of pereopod 6 or poorly developed; pleonal plate 2 with fewer ventral spines; uropod 3 with relatively longer peduncle; and telson apical margin with very tiny notch. Largest ♀, 8.5 mm; largest ♂ 6.0 mm.

Female. Antenna 1: 50 percent length of body, 30 percent longer than antenna 2; primary flagellum with 17 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with 10 rather long setae on inner margin; palp segment 3 with 12 D setae, 6 E setae, lacking A, B and C setae.

Inner lobes of lower lip small to vestigial.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 10 stiff setae or slender spines apically.

Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 3 naked setae apically and 2 plumose spines on inner margin; outer plate with setae on inner margin and apex and 5 or 6 small serrate spines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm slightly convex and about 60 percent longer than posterior margin, armed with 24 spine teeth in double row; defining angle with 3 pine teeth on outside, 2 shorter ones on inside; posterior margin with 2 setae; 3 superior medial setae; 10 inferior medial setae; dactyl nail long; coxa about 33 percent deeper than broad, margin with 4 setae.

Gnathopod 2: propod little longer than broad, palm slightly concave medially and armed with

Fig. 28. ***Stygobromus herbsti*****, new species, female paratype (8.5 mm), Spring No. 121, Elko County, Nevada: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

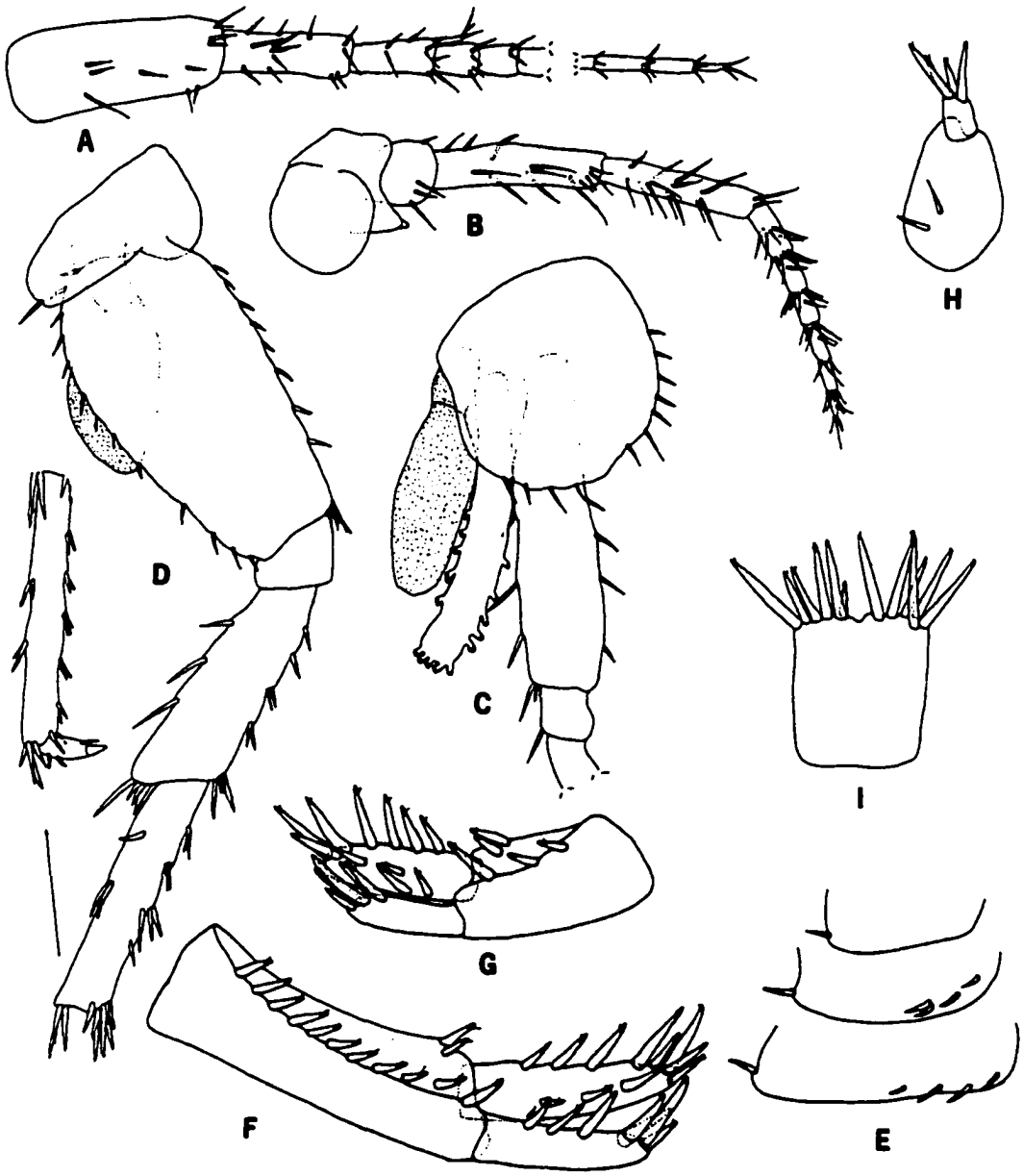

Fig. 29. ***Stygobromus herbsti*****, new species, female paratype (8.5 mm), Spring No. 121, Elko County, Nevada: A, B, antennae 1, 2; C, pereopod 4; D, pereopod 6; E, pleonal plates; F, G, H, uropods 1, 2, 3; I, telson.**

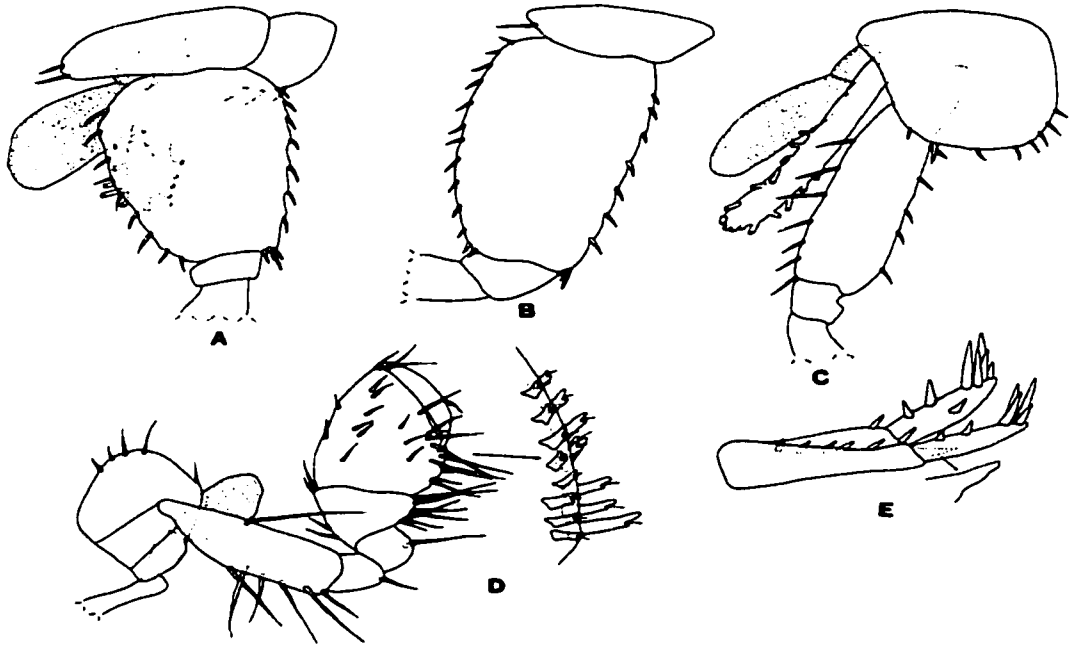

Fig. 30. ***Stygobromus herbsti*****, new species, female paratype (8.5 mm), Spring No. 121, Elko County, Nevada: A, B, pereopods 5, 7; C, pereopod 3. Male paratype (5.5 mm), D, gnathopod 2; E, uropod 1.**

26 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with row of setae; 14 mostly double-inserted superior medial setae; about 12 singly inserted inferior medial setae; coxa broader than deep, margin with 10 setae.

Pereopod 3: coxal plate deeper than broad, margin with 8 setae.

Pereopod 4: coxal plate relatively broad and deep, about as deep as broad, reaching about 33 percent length of basis, margin with 11 setae.

Pereopod 6 little longer than pereopod 7, about 53 percent length of body, 13 percent longer than pereopod 5.

Pereopods 5-7: bases rather narrow, broader proximally than distally; posterior margins slightly convex, distoposterior lobes indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically 30 percent length of corresponding propod.

Coxal gills present on pereopods 2-6.

Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plates 2 and 3 with 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 65 percent length of peduncle, with 12 spines; outer ramus with 7 spines; peduncle with 13 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 11 spines; outer ramus with 5 spines; peduncle with 5 spines.

Uropod 3: peduncle usually bearing 2 small setae; ramus approximately 30 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, apical margin entire or with tiny median notch between spine clusters, usually bearing 12 spines, some relatively long.

Male. Differing from female as follows: Gnathopod propods narrow; palm of propod 2 shorter in comparison with posterior margin. Uropod 1: peduncular process approximately 33 percent length of outer ramus, bluntly rounded distally, lower margin minutely serrate; inner ramus with 8 -9 spines; peduncle with 7-8 spines. Uropod 2: inner ramus with 12-14 spines, peduncle with 10-13 spines. Telson with 10-12 apical spines.

Type locality. Spring No. 121, Ruby Lake National Wildlife Refuge, Elko County, Nevada.

Distribution and ecology. This species is recorded from a series of springs in the Ruby Lake National Wildlife Refuge, Elko and White Pine cos., Nevada (Figs. 93, 95).

Etymology. The species is named in honor of its collector, Dr. David B. Herbst.

Stygobromus holsingeri Ward, 1977

Stygobromus holsingeri Ward, 1977: 461-465, figs. 6-8 [type-locality: small unnamed spring/seep, 3.2 km W. of Ft. Collins, Larimer Co., Colorado]. -- Ward and Holsinger, 1981: 64-65.

Material examined. COLORADO. Larimer Co.: several habitat types associated with interrupted stream drainage near Horsetooth Reservoir, W of Ft. Collins, approximately 240 specimens, J. V. Ward, May 1976 - Jan. 1978 (most in 1977) as follows (number of collections in parentheses): Devils Gulch (1); Redstone site 1-5 (12); Redstone LS (2); Redstone NB (5); Redstone SB (3); Soldier Canyon (7).

Diagnosis. A medium-sized groundwater species, apparently related to *S. arizonensis* but distinguished by inner plate of maxilliped with plumose setae extending partway down inner margin, gnathopodal propod 1 with more oblique palm; 1 or 2 fewer teeth on palmar margin; distoposterior lobes of pereopod 6 and 7 better developed; telson shorter with a shallower notch and more spines on apical lobes (see Ward, 1977; Ward and Holsinger, 1981 for details). Largest ♀ 5.7 mm; largest ♂ 5.4 mm.

Distribution and ecology. This species is recorded form seeps, springs and interrupted stream drainage in the vicinity of Horsetooth Reservoir in Larimer Co., Colorado (Figs. 93, 97, see Ward and Holsinger, 1981 for further details).

Stygobromus hubbsi Shoemaker, 1942

Stygobromus hubbsi Shoemaker, 1942b: 1-6, figs. 1-2 [type-locality: Malheur Cave, Harney Co., Oregon]. --- Hubricht, 1959:878. ---Nicholas, 1960:128. ---Bousfield, 1961: 2-3. ---Holsinger, 1972: 68-69, fig. 26f. --- Holsinger, 1974: 6-8, fig. 1.

Diagnosis. Corresponding to the redescription by Holsinger (1974). A medium-sized cavernicolous species, closely allied morphologically with species of *Stygobromus* from east-central California (especially *S. grahami*, *S. harai*, and *S. wengerorum*) but distinguished by having fewer plumose setae on inner plates on maxillae 1 and 2; fewer apical spines on inner plate of maxilliped; and fewer apical spines on apical margin of telson. Largest ♀, 6.5 mm; largest ♂, 5.5 mm.

Distribution and ecology. This species is known only from a lake in the type-locality, Malheur Cave, Harney Co., Oregon (Figs. 93, 96). According to John Markham (pers. comm.), who is involved with a recent research project in the cave, amphipods are attracted to baited traps left in the cave lake. A recent map and description of Malhens Cave was given by Hill (2000).

Stygobromus hyporheicus, new species

(Figs. 31-33)

Material examined. CALIFORNIA. Marin Co.: gravel-bed of intermittent stream, Cronan Creek, HOLOTYPE ♀ (USNM), 3 ♀ paratypes, 2 juvs., R. Leach, 15 July 1997.

Diagnosis. A medium-sized interstitial species, related to *S. grahami* and *S. wengerorum* but distinguished from those as follows: maxillae 1 and 2 with fewer setae on inner plates; palms of gnathopod 1 and 2 convex or straight, and with more spine rows; coxal plates 3 and 4 broader than deep; pleonal plates 2 and 3 with fewer ventral margin spines, but with more posteriormargin spines; uropods 1-3 with more spines on peduncles and rami; telson 2 times deeper than broad. Largest ♀, 7.0 mm; ♂ unkown.

Female. Antenna 1: 70 percent length of body, 78 percent longer than antenna 2; primary flagellum with 21 segments. Antenna 2: flagellum with 7 segments.

Mandibles: spine row with 7-8 plumose spines; palp segment 2 with row of 11 setae on inner margin, segment 3 bearing 3-4 C setae, approximately 8 D setae, 3 E setae, lacking A and B setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 8 apical plumose setae; palp with 7 stiff setae or slender spines apically or subapically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 9 plumose spines, 2 naked setae apically and 1 plumose seta on inner margin; outer plate with few setae, 1 bladelike spine, and 8-9 lightly plumose setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm convex and about 67 percent longer than posterior margin, armed with 35 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae; 3-4 inferior medial setae; dactyl nail short; coxa broader than deep, margin with 3 setae.

Gnathopod 2: propod deeper than broad; palm convex and armed with 34 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin approximately 30 percent length of palm, with 2-3 sets of doubly inserted

setae; 6 doubled inserted superior medial setae; 3 inferior medial setae, 2 medial setae; coxa slightly

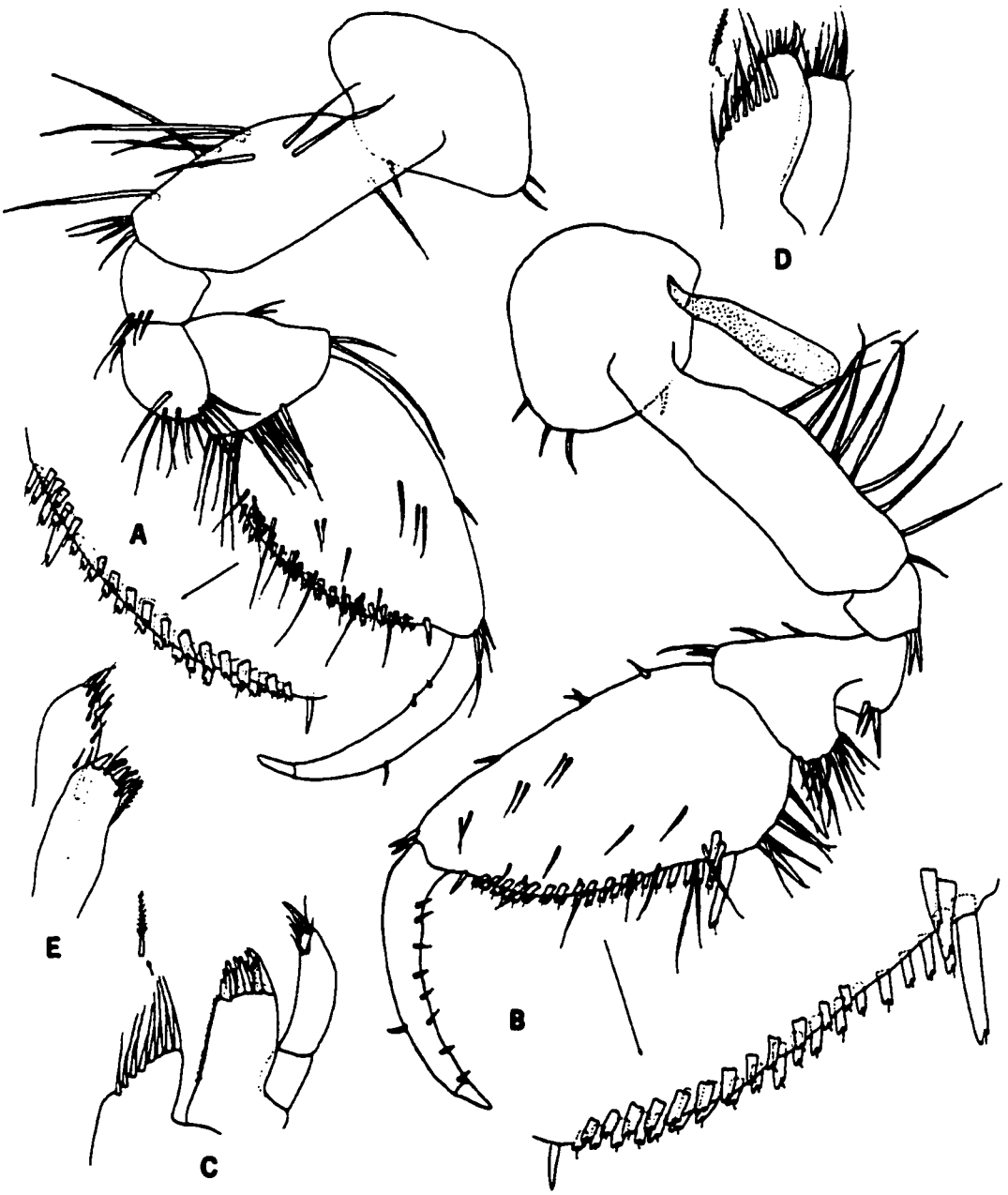

Fig. 31. *Stygobromus hyporheicus*, new species, female paratype (7.0 mm), Cronan Creek, Marin County, California: A, B, gnathopods 1, 2 (palms enlarged); C, D, maxilla 1, 2 (apical setae enlarged); E, inner and outer plates of maxilliped (enlarged).

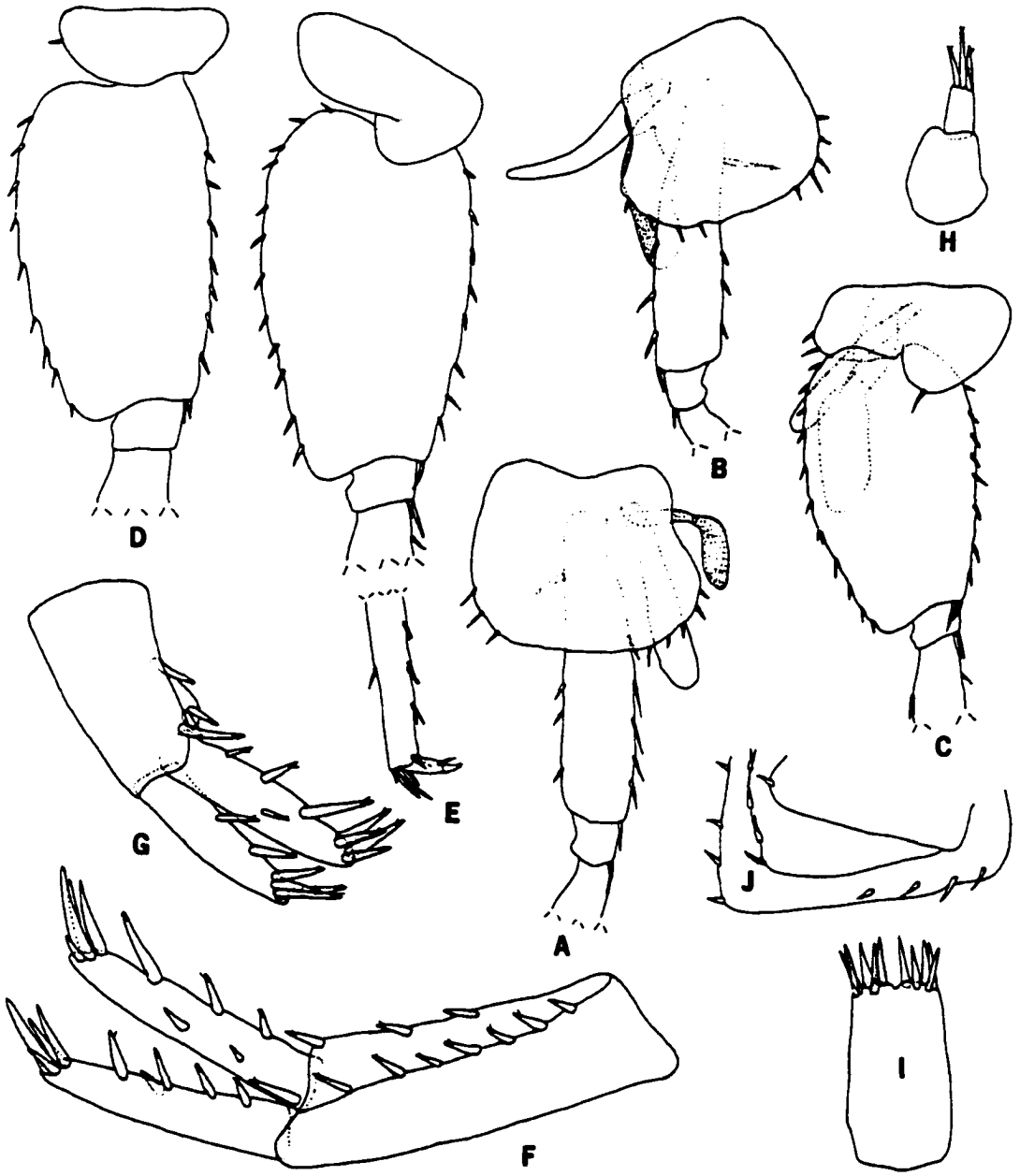

Fig. 32. ***Stygobromus hyporheicus*****, new species, female paratype (7.0 mm), Cronan Creek, Marin County, California: A, B, pereopods 4, 3; C, D, E, pereopod 5, 6, 7; F, G, H, uropods 1, 2, 3; I, telson; J, pleonal plates.**

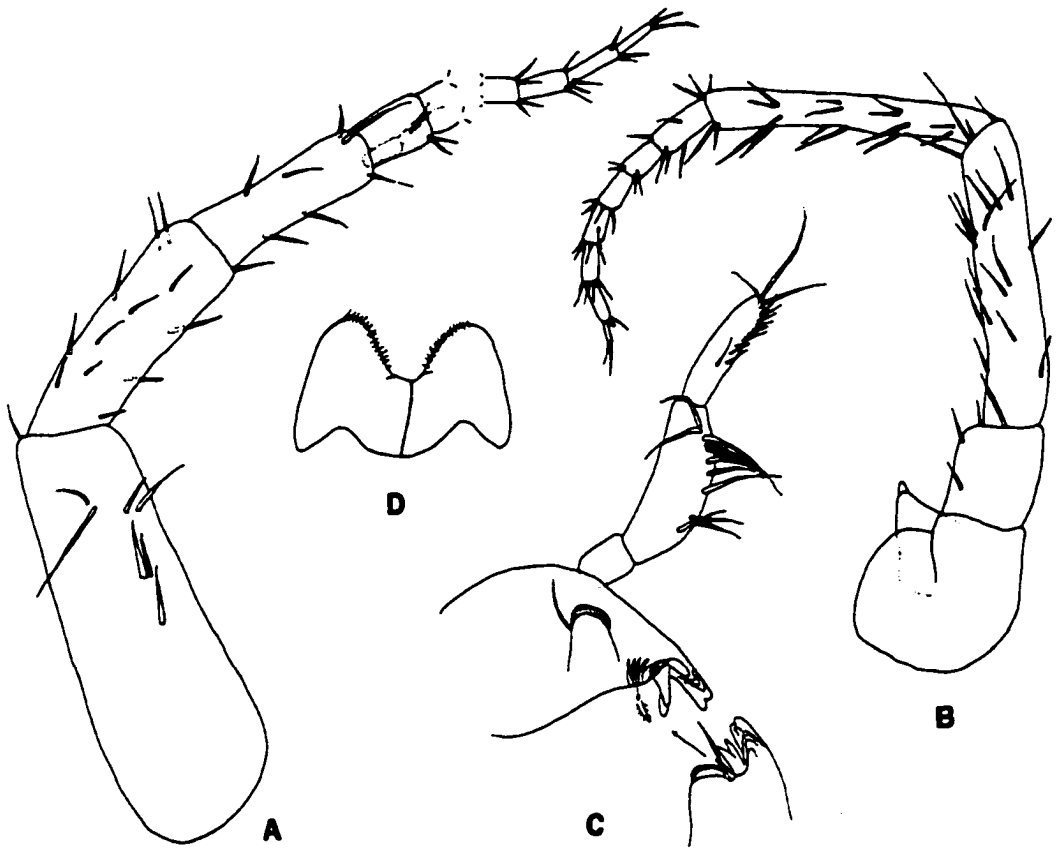

Fig. 33. *Stygobromus hyporheicus*, new species, female paratype (7.0 mm), Cronan Creek , Marin County, California: A, B, antennae 1, 2; C, left mandible and a tentate part of right mandible; D, lower lip.

broader than deep, margin with 4 setae.

Pereopod 3: coxal plate broader than deep, margin with 8-9 setae.

Pereopod 4: coxal plate broader than deep, reaching approximately 50 percent length of basis, margin with 8-9 setae.

Pereopod 6 slightly longer than pereopod 7, about 70 percent length of body, 30 percent longer than pereopod 5.

Pereopods 5-7: bases broader proximally than distallyly; posterior margins convex proximately; distoposterior lobes developed; anterior and posterior margins with variable numberof spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively elongate, that of pereopod 6 approximately 33 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 2 convex, with 4 setae, that of 1 and 3 less convex, plate 1 with 1 setule near distoposterior corner, plate 3 with 4 setules; distoposterior corners rounded; ventral margin of plates 1 and 2 without spines, that of plate 3 with 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 9-10 spines; outer ramus with 9 spines; peduncle with 10 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 3 spines.

Uropod 3: peduncle without setae; ramus approximately 33 percent length of peduncle, with 4 or 5 apical spines.

Telson much longer than broad, apical margin with small median notch between spine clusters, with 9-10 relatively long spines.

Type locality. Gravel-bedded intermittent stream, Cronan Creek, in Golden Gate National Recreational Area, Marin Co., California.

Distribution and ecology. This species is known from the hyporheic zone of a gravel-bedded intermittent stream, Cronan Creek, in Golden Gate National Recreational Area, which is adjacent to Point Reyes National Seashore (Figs. 93, 95). The specimens were collected from a depth of 40 cm. The water temperature was 16 ^{o}C.

Etymology. The epithet *hyporheicus* is from the Latin, meaning "hyporheic," in reference to the habitat of this species.

Stygobromus imperialis, new species

(Figs. 34-36)

Material examined. CALIFORNIA. Santa Cruz Co.: Empire Cave, HOLOTYPE ♀ (USNM) on slide mounts, D. C. Rudolph, D. Cowan and B. van Ingen, 22 Apr. 1979.

Diagnosis. A relatively large cavernicolous species closely similar to *S. grahami* but distinguished as follows: palp segment 2 of mandible with 6 rather long setae on inner margin; maxillae 1 and 2 with more setae on inner plates; posterior margin of propod of gnathopod 2 with 1-3 setae; coxal plate of pereopods 3 and 4 deeper and with more setae; more spines on ventral margins of pleonal plates 2 and 3; uropod 3 with fewer apical spines. Largest ♀, 9.2 mm, ♂ unknown.

Female. Antenna 1: about 58 percent length of body, 70 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal, spine row with 8-9 plumose spines; palp segment 2 with 6 rather long setae on inner margin; palp segment 3 with 4-5 C, 13 D and 4 E setae, lacking both A and B setae.

Inner lobes of lower lip small to vestigial.

Maxilla 1: inner plate with 13 apical plumose setae; palp with 9 stiff setae apically or subapically. Maxilla 2: inner plate with oblique row of 14 plumose setae on inner margin.

Maxilliped: inner plate with 3 bladelike spines, 2 plumose spines, and 3 naked setae apically/subapically, 3 plumose spines on inner margin; outer plate with setae on inner margin; 7 setae and 1 bladelike spine on or near apex.

Gnathopod 1 propod smaller than that of gnathopod 2; palm 2 times longer than posterior margin, armed with 30 spine teeth in double row; defining angle with 4 spine teeth on outside, 6 shorter ones on inside; posterior margin without setae; 8 superior medial setae, 5 inferior medial setae; dactyl nail rather shorter; coxa about 33 percent deeper than broad, margin with 3 setae.

Gnathopod 2 propod subrectangular, longer than broad; palm concave, armed with 25 - 26 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 3 long spine teeth on inside; posterior margin about 1/3 length of palm, with few setae; 8 superior medial setae, 9 inferior medial setae; dactyl nail shorter; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 9 setae.

Pereopod 4: coxal plate relatively broad and deep, subquadrate, reaching about 45 percent length of basis, margin with 9 setae.

Pereopod 6 little longer than pereopod 7, about 65 percent length of body, 20 percent longer than pereopod 5.

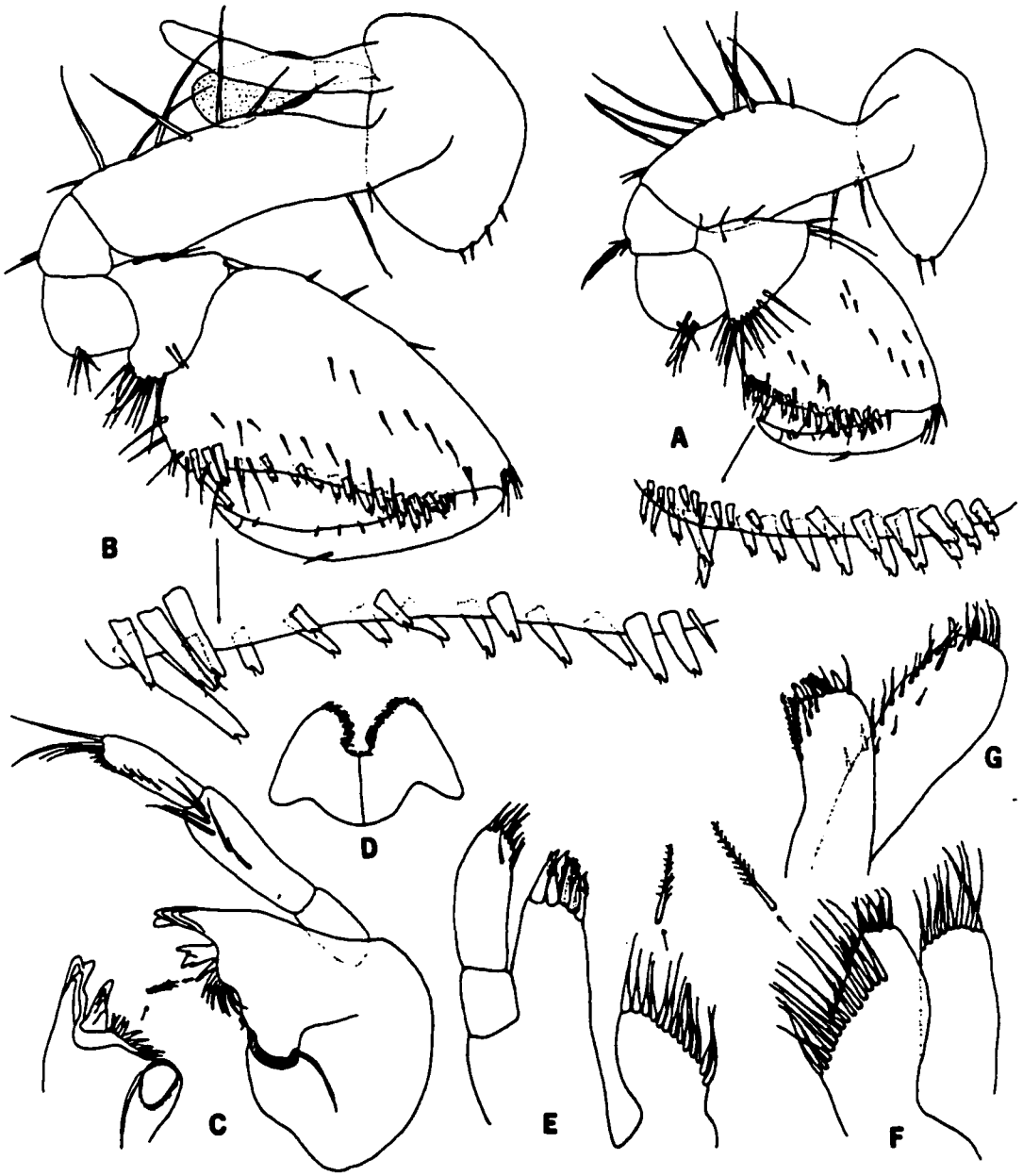

Fig. 34. ***Stygobromus imperialis*****, new species, female paratype (9.2 mm), Empire Cave, Santa Cruz County, California: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

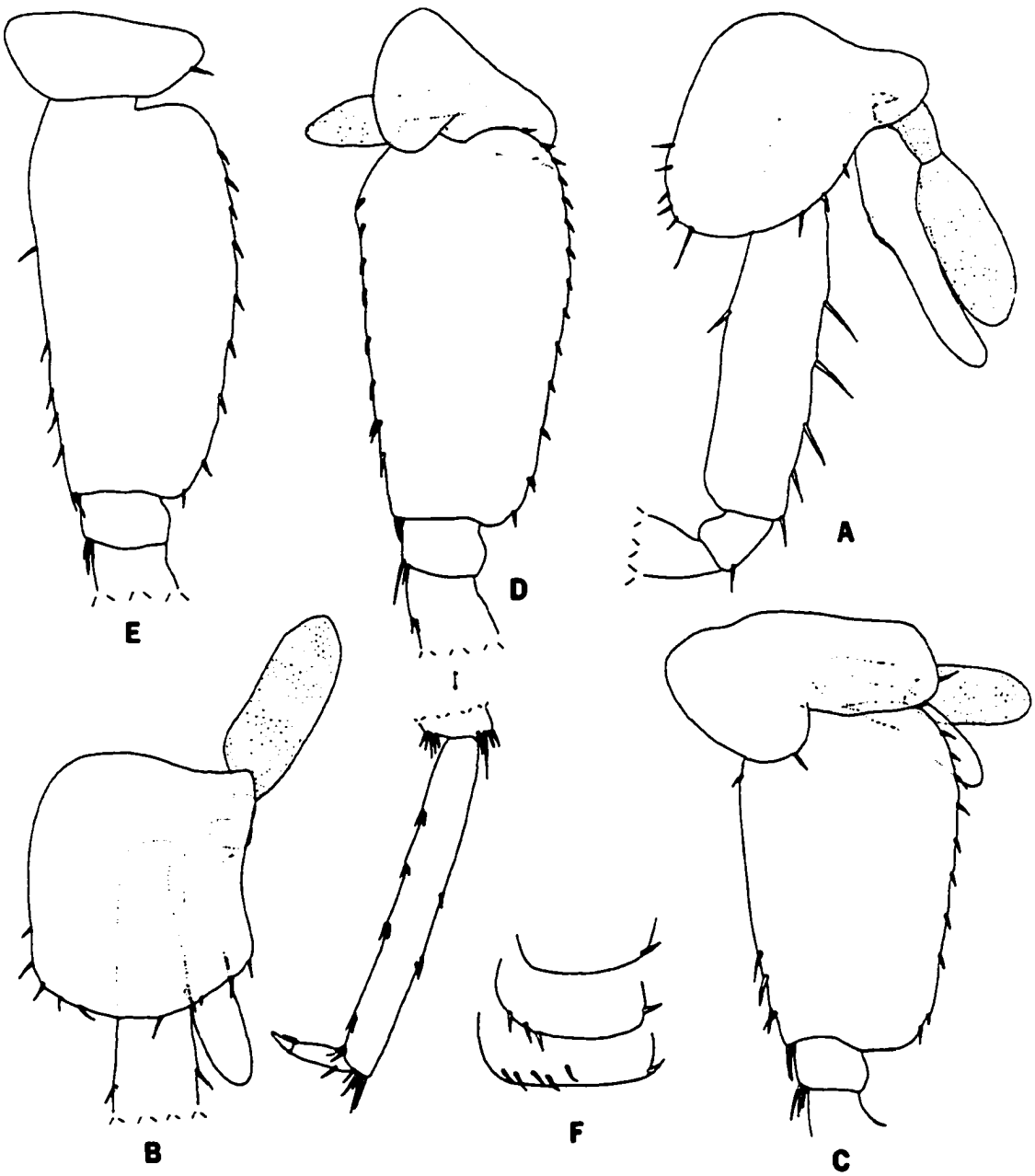

Fig. 35. ***Stygobromus imperialis*****, new species, female paratype (9.2 mm), Empire Cave, Santa Cruz County, California: A, B, C, pereopods 3, 4, 5 (in part); D, E, pereopods 6, 7 (in part); F, pleonal plates.**

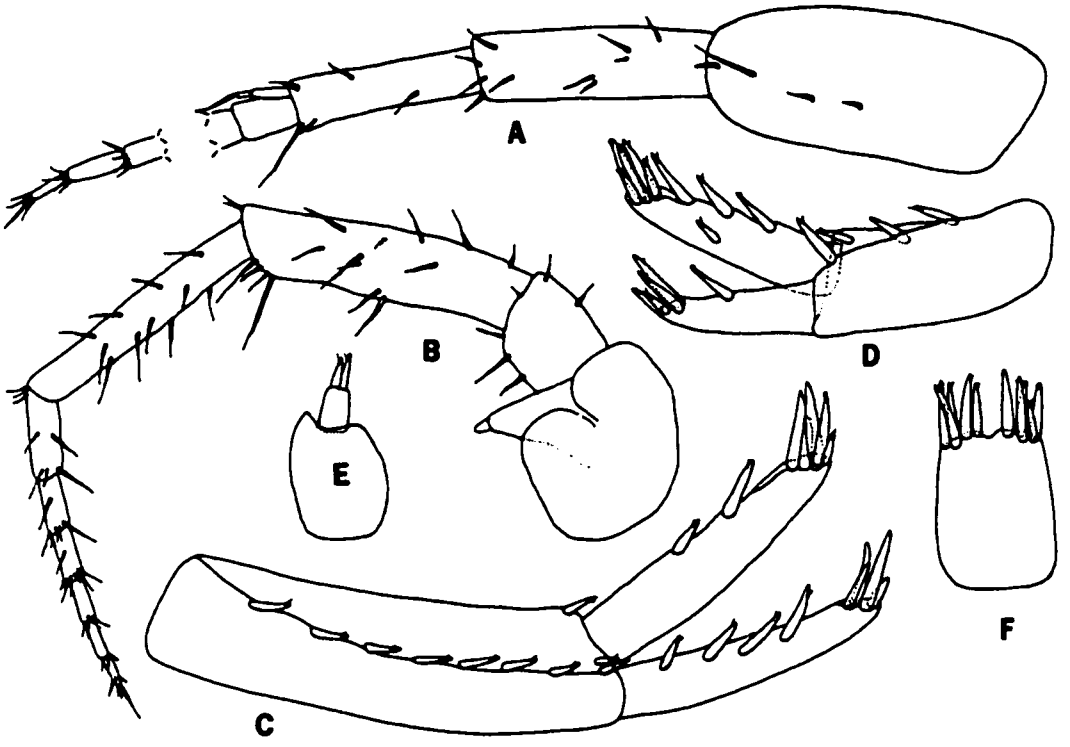

Fig. 36. ***Stygobromus imperialis*****, new species, female paratype (9.2 mm), Empire Cave, Santa Cruz County, California: A, B, antennae 1, 2; C, D, E, uropods 1, 2, 3; F, telson.**

Pereopods 5-7: bases broader proximally than distallyly; posterior margins convex (but not greatly expanded); distoposterior lobes moderately well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively shorter, that of pereopod 6 typically 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta near distoposterior corner, that of 2 and 3 less convex, each with 1 seta near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 3 spines, that of plate 3 with 5 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 60 percent length of peduncle, with 7 spines; outer ramus with 9 spines; peduncle with 10 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 9 spines; outer ramus with 5 spines; peduncle with 4 spines.

Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally, apical margin with tiny median notch between spine clusters, bearing about 10 relatively long spines.

Type locality. Empire Cave, Santa Cruz County, California (Figs. 93, 95). This species was collected from a cave pool up to 1 m in depth (D. C. Ruldolph, pers. comm.). It was taken together with 5 specimens of *Stygobromus mackenziei.*

Distribution and ecology. The species is known only from a single female specimen.

Etymology. The epithet *imperialis* is from the Latin, meaning "imperial," in reference to the type-locality, Empire Cave.

Stygobromus interstitialis, new species

(Figs. 37-39)

Material examined. COLORADO. El Paso Co.: hyporheic of Monument Creek, below Palmer Lake, HOLOTYPE ♀ (USNM), 2 ♂ and 2 ♀ paratypes, J. V. Ward, 5 Oct 1980; Monument Creek, ca. 30 km N of Colorado Springs, 1 ♂, J. V. Ward, 27 July 1979; Monument Creek in Colorado Springs, 1 ♀, S. P. Canton, 4 Nov. 1987.

Diagnosis. A small groundwater species, closely related to *S. coloradensis* but distinguished as follows: maxillae 1 and 2 with more setae on inner plates; posterior margin of palm of propod 2

shorter; pleonal plate 3 lacking ventral spines; uropods 1-2 with more long and thick spines on rami; uropod 3 with very short ramus; telson with longer apical spines and slight notch between spine clusters. Largest ♀, 3.6 mm; largest ♂, 3.0 mm.

Female. Antenna 1: 50 percent length of body, 55 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 5 segments.

Mandibles: spine row with 4-5 plumose spines; palp segment 2 with row of 3 setae on inner margin; palp segment 3 bearing 1 B seta, 4 C setae, and 4 E setae, lacking both A and D setae.

Inner lobes of lower lip vestigial/absent.

Maxilla 1: inner plate with 6 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 2 plumose spines, 1 naked seta apically, and 3 plumose spines on inner margin; outer plate with short setae on inner margin, 3 lightly plumose setae and 1 small bladelike spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm slightly concave medially, approximately 2 times longer than posterior margin, armed with 10 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4-5 singly inserted medial setae, dactyl nail rather long; coxa about 25 percent broader than deep, margin with 1 seta.

Gnathopod 2: propod longer than broad; palm straight and armed with 9 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of triply inserted setae; 2 superior medial setae, 2 singly inserted inferior medial setae; dactyl nail relatively short; coxa little broader than deep, margin with 1 seta.

Pereopod 3: coxal plate about as broad as deep, margin with 1 seta.

Pereopod 4: coxal plate about as broad as deep, reaching about 25 percent length of basis, margin with 1 seta.

Pereopod 6 little longer than pereopod 7, about 50 percent length of body, 36 percent longer than pereopod 5.

Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes poorly developed; anterior and posterior margins with variable but few number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 30 percent length of corresponding propod.

Fig. 37. ***Stygobromus interstitialis*****, new species, female paratype (3.6 mm), Monument Creek, El Paso County, Colorado: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

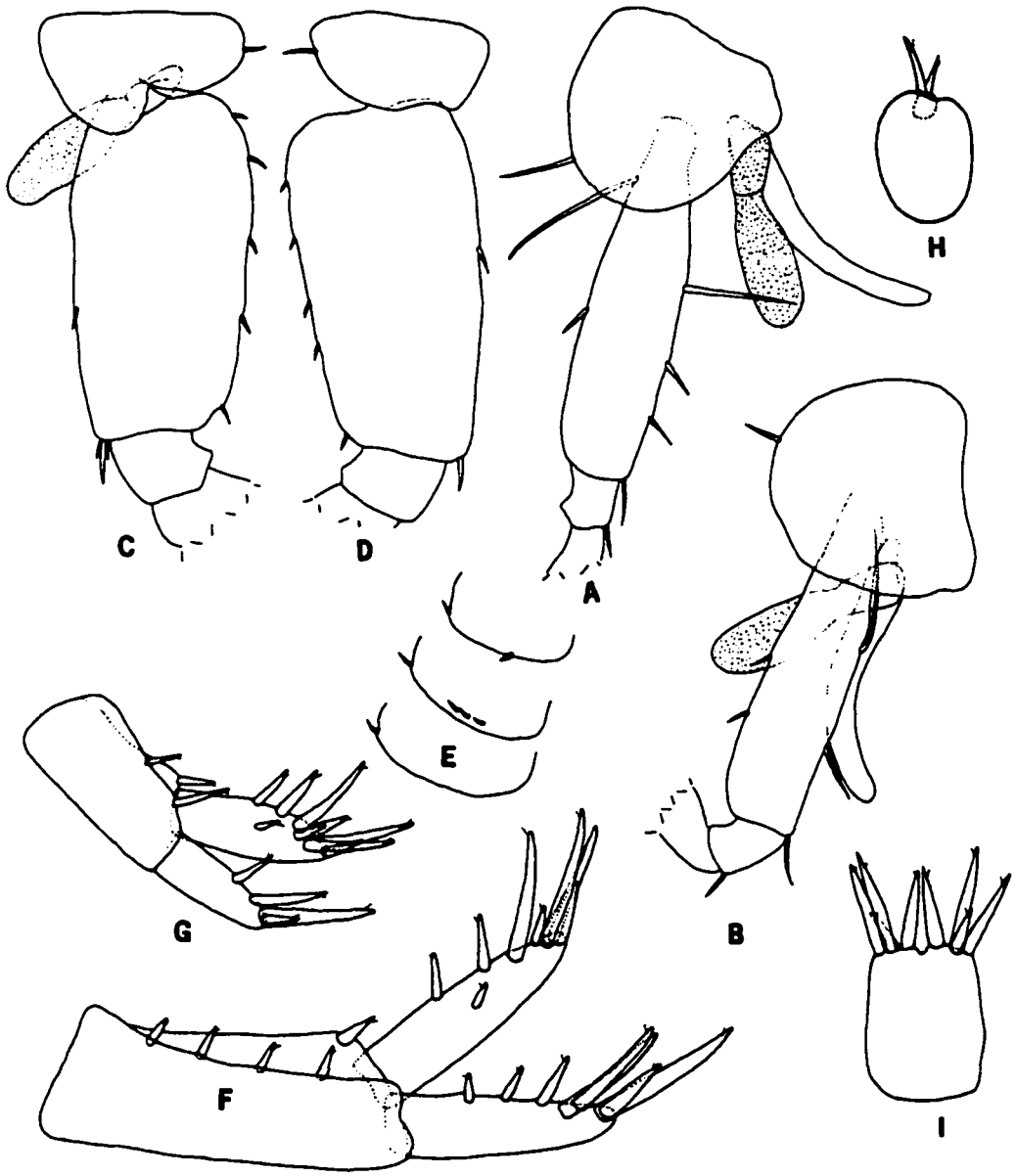

Fig. 38. ***Stygobromus interstitialis*****, new species, female paratype (3.6 mm), Monument Creek, El Paso County, Colorado: A, B, pereopods 3, 4; C, D, pereopods 5, 7; E, pleonal plates (from top to bottom, plates 3, 2 and 1); F, G, H, uropods 1, 2, 3; I, telson.**

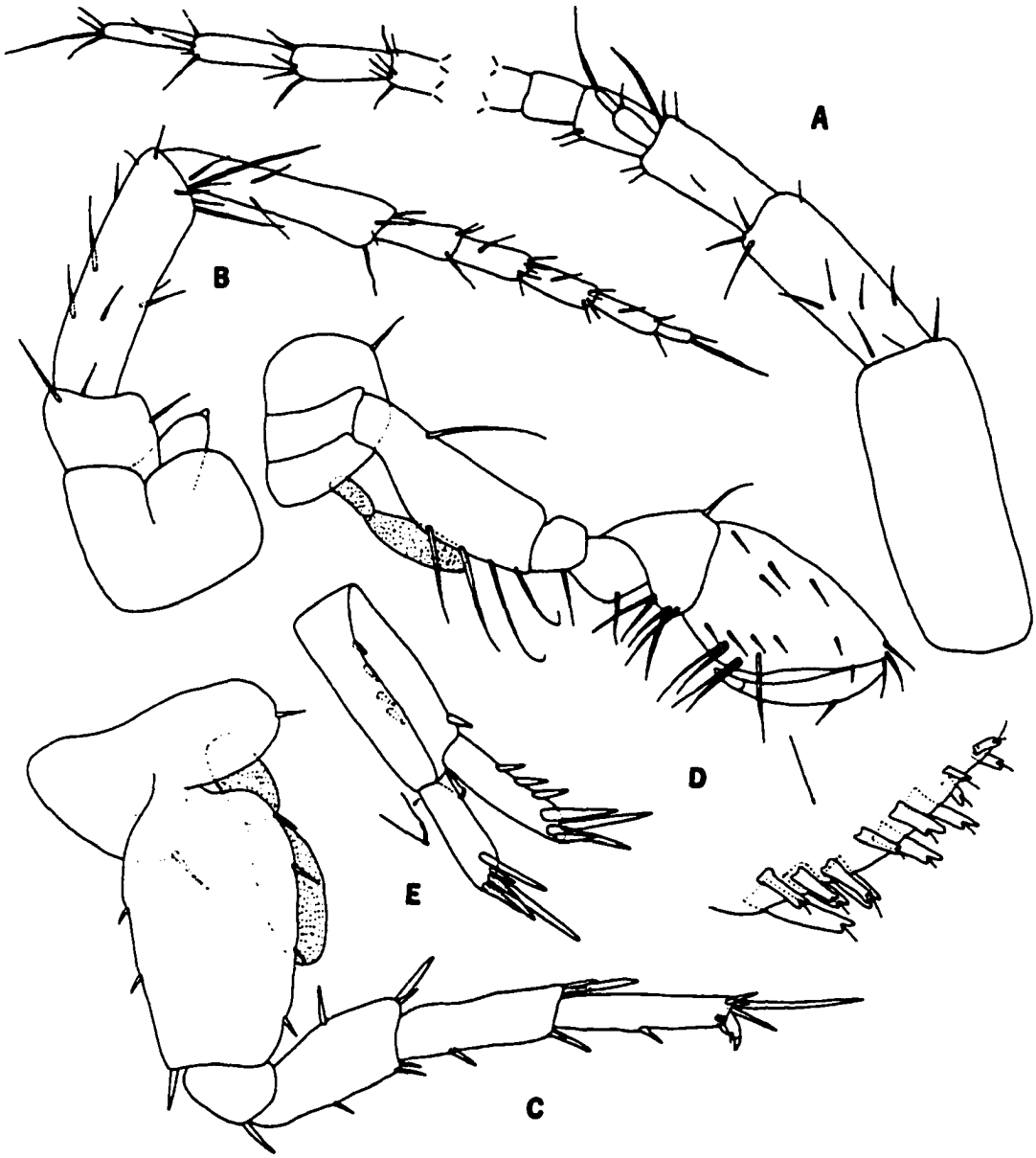

Fig. 39. ***Stygobromus interstitialis*****, new species, female paratype (3.6 mm), Monument Creek, El Paso County, Colorado: A, B, antennae 1, 2; C, pereopod 6; Male paratype (3.0 mm), D, gnathopod 2 (enlarged palm); E, uropod 1.**

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates slightly narrowing distally, but not setose (fully mature) in material examined.

Pleonal plates: posterior margins of plate 1 - 2 weakly convex, each with 1 setule near distoposterior corner; distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 1 with 1 spine, that of plate 2 with 3 spines.

Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 75 percent length of peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 5 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 9 spines; outer ramus with 4 spines; peduncle with 3 spines.

Uropod 3: peduncle not bearing setae; ramus tiny, approximately 20 percent length of peduncle, with 2 apical spines.

Telson longer than broad, apical margin with tiny median notch between spine clusters, bearing approximately 8 relatively long spines.

Male. Differing from female as follows: Gnathopod propods smaller and narrower, palm of propod 2 longer in comparison to posterior margin, with more teeth on palmar margin. Uropod 1: peduncular process 30 percent length of outer ramus, sharp by pointed distally, inner ramus with 7 spines; outer ramus with 5 distal spines; peduncle with 5-6 spines. Uropod 2: inner ramus with 9-10 spines, peduncle with 3-4 spines. Telson with 9 apical spines.

Type locality. Interstitial (hyporheic) habitat in deep gravel alluvium, Mountain Creek below Palmer Lake, El Paso County, Colorado.

Distribution and ecology. This species is recorded from hyporheic habitats in the deep gravel alluvium of Mounument Creek at three different sites (see "material examined" section), El Paso Co., Colorado (Figs. 93, 97).

Etymology. The epithet *interstitialis* is from the Latin, meaning "interstitial," in reference to the habitat of this species.

Stygobromus jemezensis, new species

(Figs. 40-42)

Material examined. NEW MEXICO. Sandoval Co.: well at Bland, HOLOTYPE ♀ (MSB), 1 ♀ and 1 ♂ paratypes, B. Wilson, 29 Aug. 1994.

Diagnosis. A medium-sized groundwater species, closely related to *S. arizonensis* in structure of gnathopods but distinguished from that species as follows: propod of gnathopod 1 with more teeth on palmar margin; pereopod 6 with distinct distoposterior lobe; posterior margins of

pleonal plates with 1 setule; uropod 1-2 with more spines on rami (similar to *S. holsingeri*); uropod 3 with proportionately broad peduncle; telson with short spines and slight apical notch. Largest ♀, 7.0 mm; largest ♂ 4.5 mm.

Female. Antenna 1: 52 percent length of body, 57 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 7 plumose spines; palp segment 2 with row of 8 rather long setae on inner margin; palp segment 3 with 10 D and 5 E setae, lacking A, B and C setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 10 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 2 naked setae on or near apical margin, 3 plumose setae on inner margin; outer plate with numerous short setae on inner margin and 1 bladelike spine and several setae on or near apex.

Gnathopod 1: propod slightly shorter than propod of gnathopod 2; palm straight or slightly concave, about half length of posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; superior medial setae 4, doubly inserted; 2-5 inferior medial setae; dactyl nail rather long; coxa deeper than broad, margin with 3 setae.

Gnathopod 2: propod subrectangular, longer than broad; palm armed with 19-20 spine teeth in double row; defining angle with 1 very long spine tooth on outside, 1 shorter spine tooth on inside; posterior margin about 33 percent length of palm, with 2 setae; 9 superior medial setae, doubly or tripled inserted; 5 or 6, singly inserted inferior medial setae; coxa deeper than broad, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 5 long setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 45 percent length of basis, margin with 8 setae.

Pereopod 6 little longer than pereopod 7, about 66 percent length of body, 30 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than distallyly; posterior margins convex; distoposterior lobes distinct but not prominent; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically 33 percent length of corresponding propod.

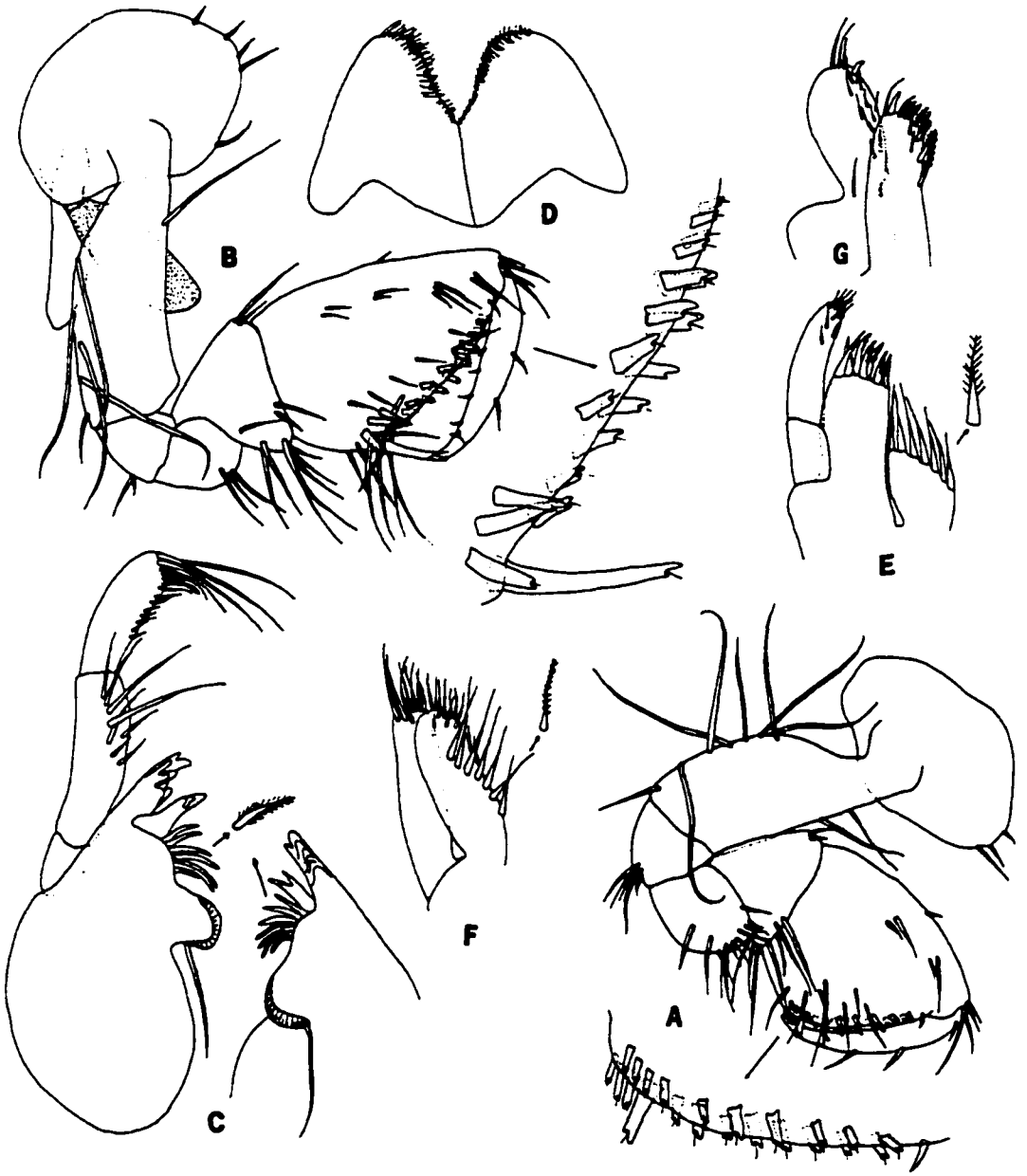

Fig. 40. ***Stygobromus jemezensis*****, new species, female paratype (6.5 mm), well from Bland, Sandovol County, New Mexico: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

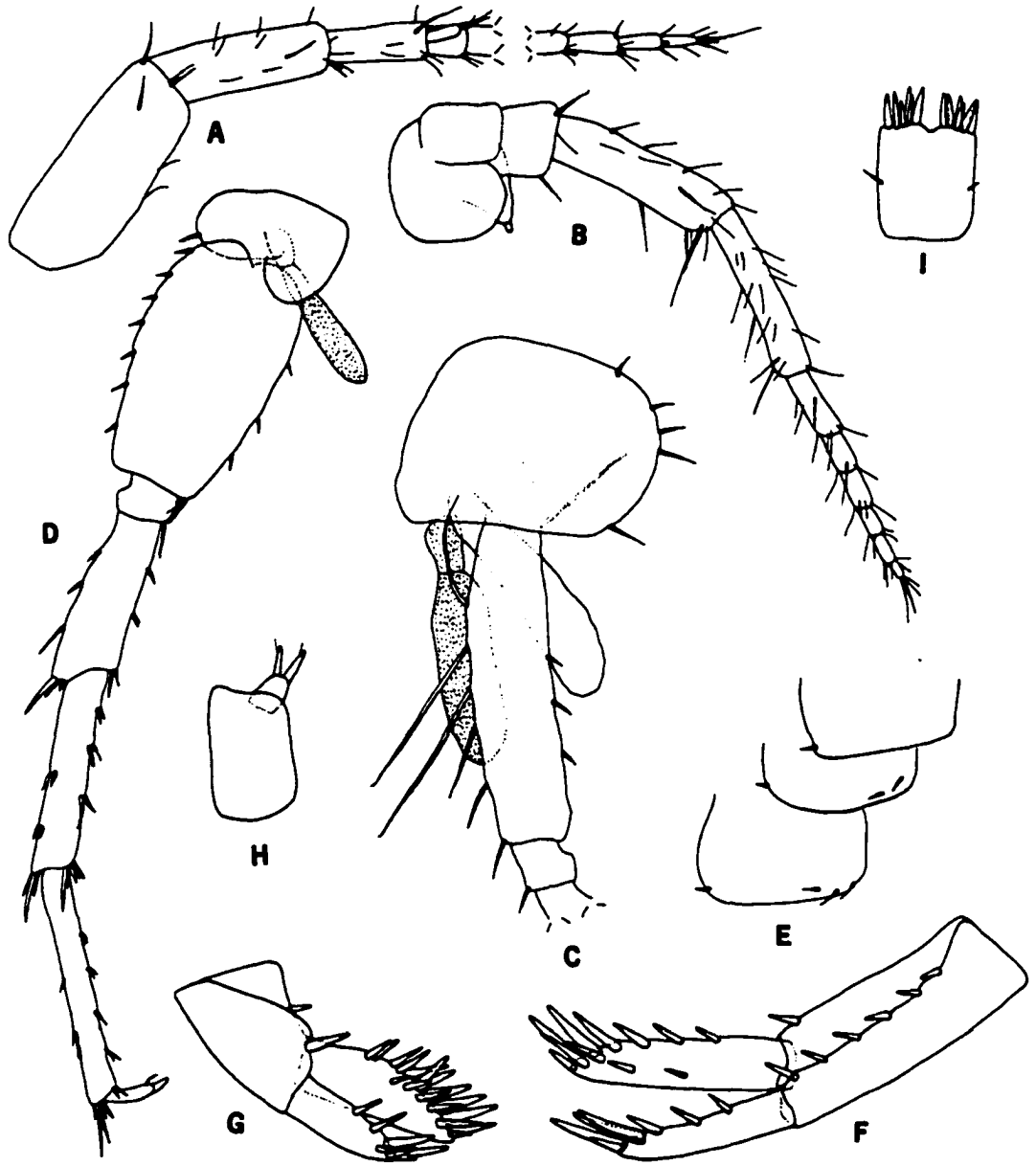

Fig. 41. ***Stygobromus jemezensis*****, new species, female paratype (6.5 mm), well from Bland, Sandovol County, New Mexico: A, B, antennae 1, 2; C, pereopod 3; D, pereopod 6; E, pleonal plates; F, G, H, uropods 1, 2, 3; I, telson.**

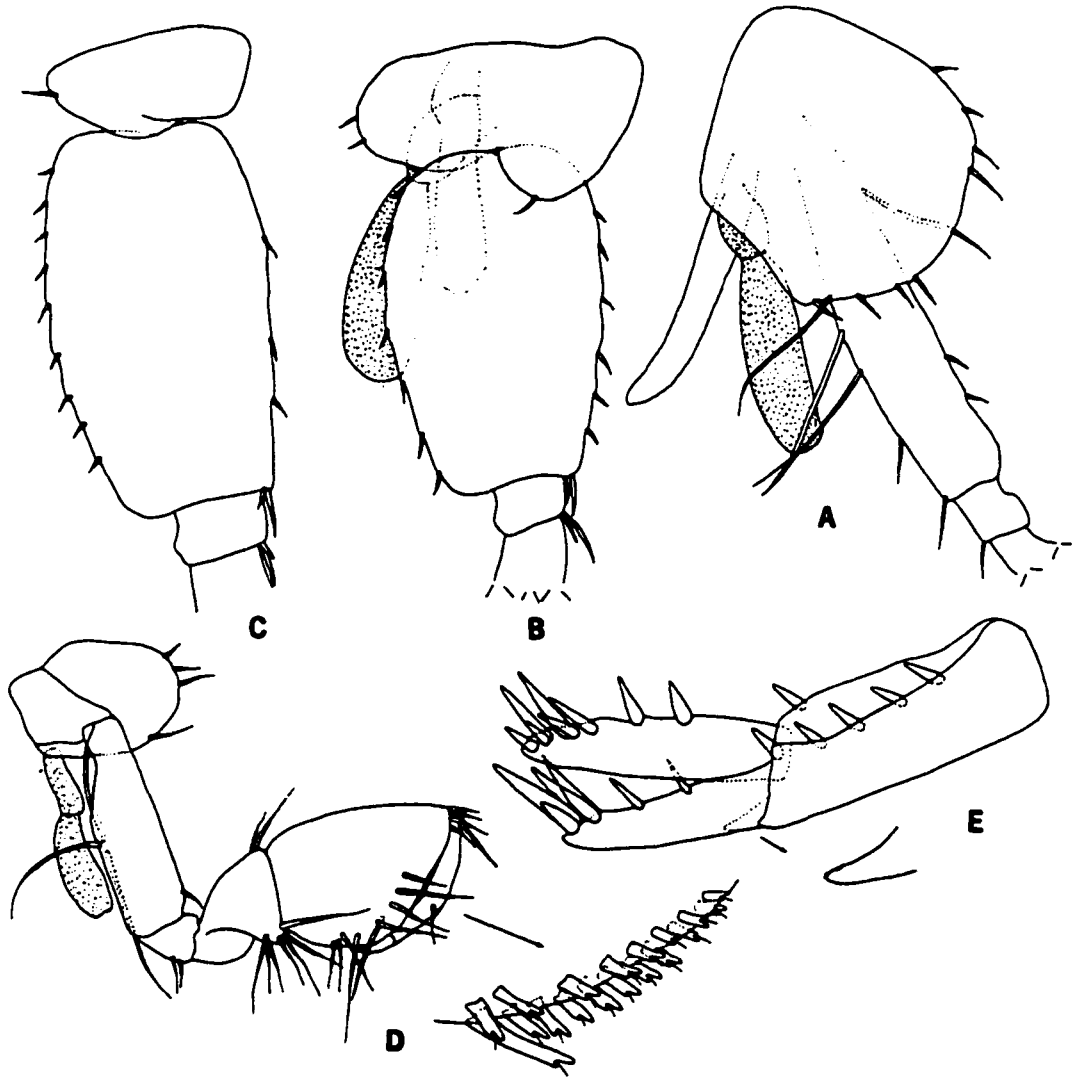

Fig. 42. ***Stygobromus jemezensis*****, new species, Female paratype (6.5 mm), well from Bland, Sandovol County, New Mexico: A, B, C, pereopods 4, 5, 7; Male paratype (4.2 mm), D, gnathopod 2 (enlarged palm); E, uropod 1.**

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates narrowing distally.

Pleonal plates: posterior margins of plate 1 and 3 convex, each with 1 setule near distoposterior corner, that of 2 less convex, with 1 setule near distoposterior corner; distoposterior corners rounded and distinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 90 percent length of peduncle, with 10 spines; outer ramus with 7 spines; peduncle with 7 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 17 relatively long spines; outer ramus with 7 long spines; peduncle with 2 spines.

Uropod 3: peduncle without setae or spines; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad; apical margin with tiny median notch between spine clusters, bearing 12 relatively short spines.

Male. Differing from female as follows: Gnathopod propods smaller, palm of propod 2 longer in relation to posterior margin and with more teeth on palmar margin. Uropod 1: peduncular process present and reaching about 25 percent length of outer ramus, bluntly rounded distally, upper margin slightly serrate; inner ramus with 8 spines; peduncle with 6 spines. Uropod 2: inner ramus with 16 spines, peduncle with 3-4 spines. Telson with 15 short apical spines.

Type locality. An unnamed well at Bland, Sandoval County. New Mexico.

Distribution and ecology. The species is known from its type-locality, where it was collected from a deep water well in the Jemez Mountains of New Mexico (Figs. 93, 97).

Etymology. The species is named for the location of the type-locality in the Jemez Mountains.

Stygobromus lacicolus Holsinger, 1974

Stygobromus lacicolus Holsinger, 1974: 44-47, figs. 26-27 [type-locality: Lake Tahoe at Cave Rock, Douglas Co., Nevada].

Diagnosis. A medium-sized, deep-lake dwelling, stygomorphic species, that occurs sympatrically with *S. tahoensis* but is distinguished from that species by longer palms and more spines on gnathopodal propods; deeper coxal plates of pereopods 3 and 4, broader bases of pereopods 5-7; fewer spines on uropods 1 and 2; longer ramus of uropod 3. Largest ♀, 6.0 mm; largest ♂, 5.5 mm.

Distribution and ecology. This species is only known from samples taken from Lake Tahoe (Figs. 93, 95). It is recorded from various sites in Lake Tohoe in El Darado and Placer cos., California and Douglas Co., Nevada (see Holsinger, 1974).

Stygobromus lanensis, new species

(Figs. 43-45)

Material examined. OREGON. Lane Co.: phreatic water habitat near Blue River Reservoir, HOLOTYPE ♀ (USNM), S. Wondzell, 3 July1991; hyporheic/seep area, Trail Creek, Willamette National Forest, 1 ♀ and 1 ♂ paratypes, 1 juv. (CMN), G. W. Courtney, 22 May 1987.

Diagnosis. A medium-sized groundwater species, apparently related to *S. arizonensis* but distinguished as follows: posterior margin of gnathopod 1 shorter; distoposterior lobes of pereopod 6 distinct; pleonal plate 3 with 1 setule on posterior margin and 2 spines on ventral margin; uropods 1-2 with more long spines on rami and peduncles; telson with more apical spines and only slight apical notch. Largest ♀, 9.0 mm; largest ♂ (?) 5.0 mm.

Female. Antenna 1: 56 percent length of body, 80 percent longer than antenna 2; primary flagellum with 20 segments. Antenna 2: flagellum with 6 segments.

Mandibles: spine row with 6-7 plumose spines; palp segment 2 with row of 10 setae on inner margin; palp segment 3 bearing 2 B setae, 9 D setae, and 5 E setae, lacking A and C setae.

Inner lobes of lower lip vestigial.

Maxilla 1: inner plate with 6 apical, plumose setae; palp with 5 stiff setae apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, and 2 naked setae apically, lacking plumose spines or coarse setae on inner margin; outer plate with few setae on inner margin and 4 setae and 1 bladelike spine on or near apex.

Gnathopod 1: propod slightly shorter than that of gnathopod 2; palm slightly convex and approximately 3 times longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 1 spine tooth on outside, 1 shorter one on inside; posterior margin lacking setae; 1-2 superior medial setae and 3 inferior medial setae; dactyl nail short, all singly inserted; coxa about 2 times broader than deep, margin with 4 setae.

Gnathopod 2: propod deeper than broad; palm convex medially and armed with 21-22 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with 3 sets of setae; 5 superior medial setae, doubly inserted; 4 inferior medial setae; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate about as deep as broad, margin with 4 setae.

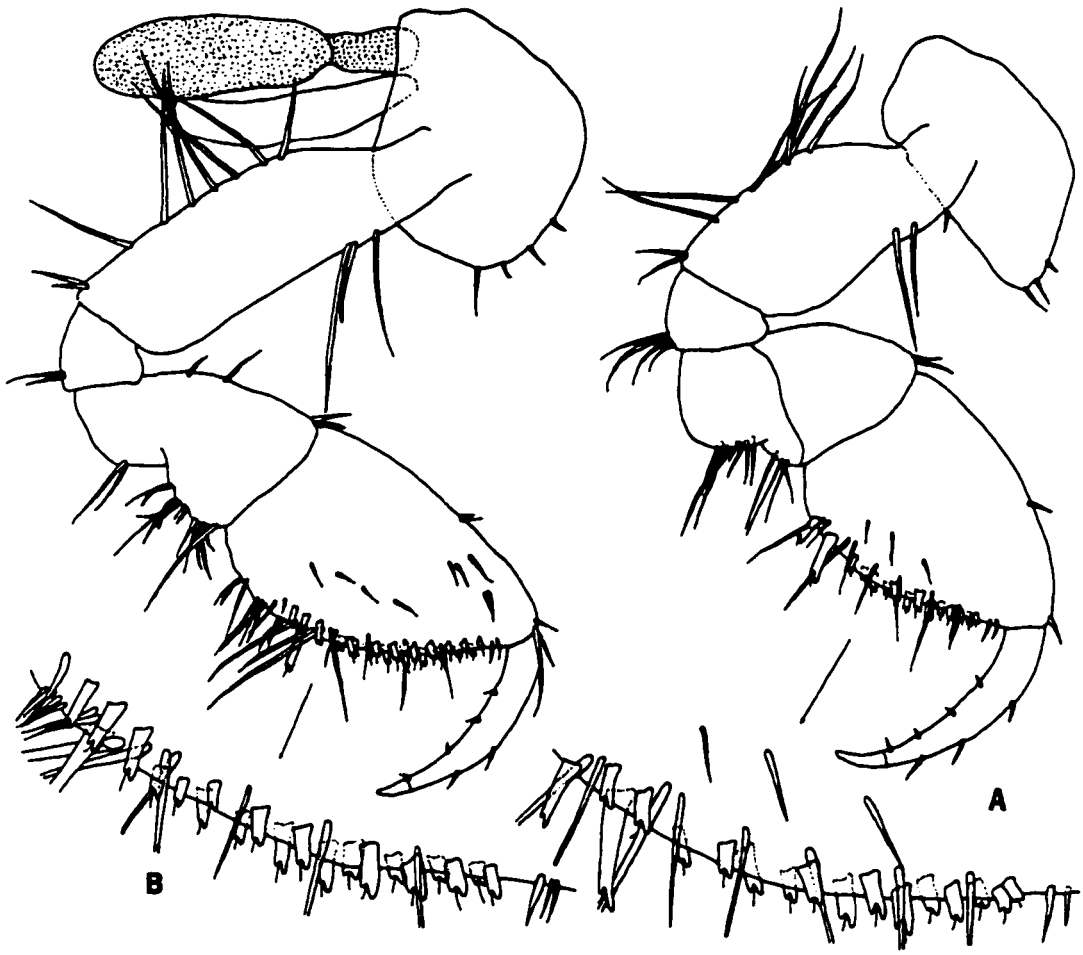

Fig. 43. *Stygobromus lanensis*, new species, female paratype (9.0 mm), pumped from phreatic water near Blue River Reservoir, Lane County, Oregon: A, B, gnathopods 1, 2 (palms enlarged).

Fig. 44. ***Stygobromus lanensis*****, new species, female paratype (9.0 mm), pumped from phreatic water near Blue River Reservoir, Lane County, Oregon: A, B, antennae 1, 2; C, left mandible and dentate part of right mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, right maxilliped; H, I, J, uropods 1, 2, 3; K, pleonal plates.**

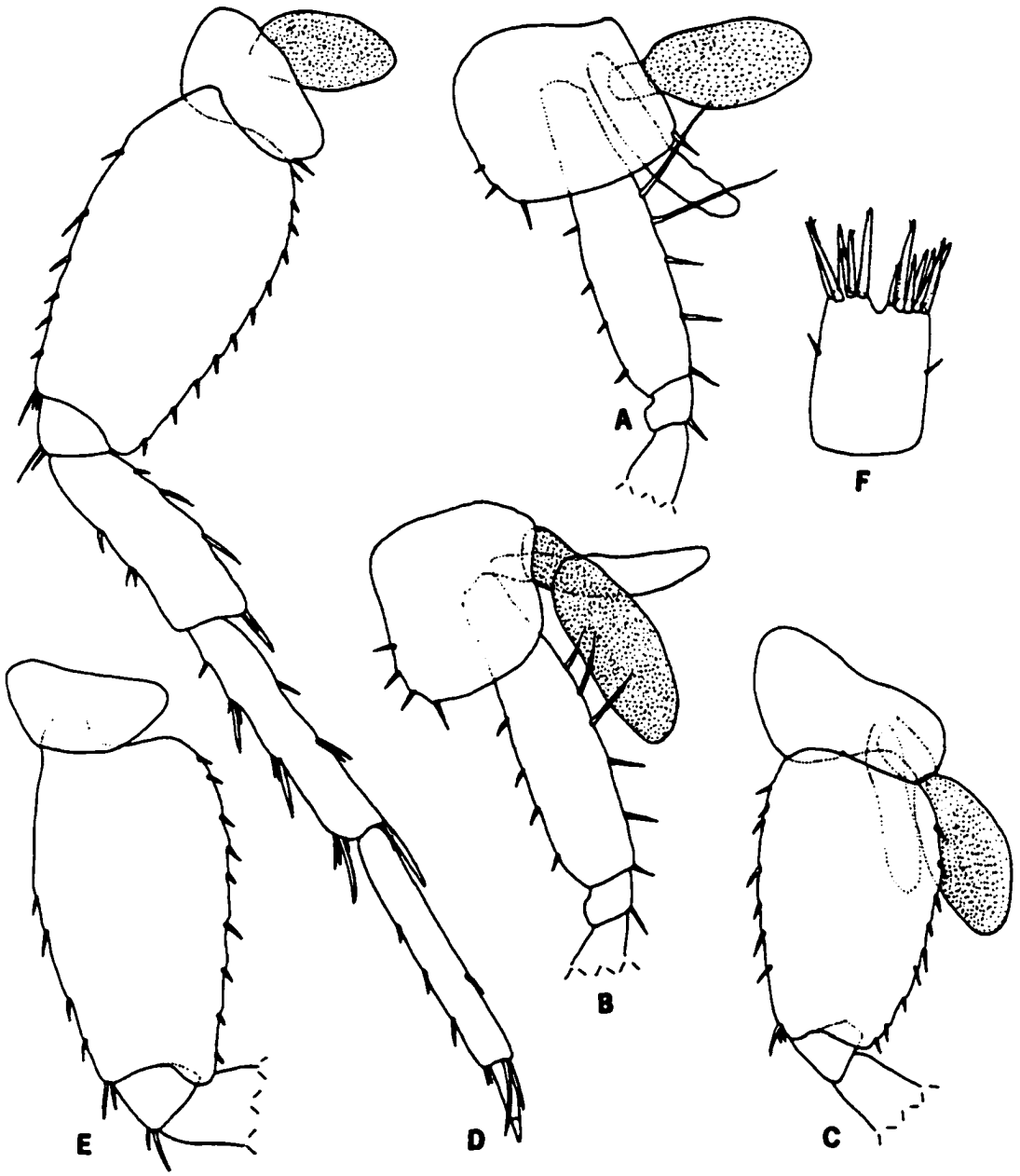

Fig. 45. ***Stygobromus lanensis*****, new species, female paratype (9.0 mm), pumped from phreatic water near Blue River Reservoir, Lane County, Oregon: A, B, pereopods 4, 3; C, pereopod 5; D, pereopod 6; E, 7; F, telson.**

Pereopod 4: coxal plate little deeper than broad, reaching about 35 percent length of basis, margin with 4 setae.

Pereopod 6 little longer than pereopod 7, about 60 percent length of body, 50 percent longer than pereopod 5.

Pereopods 5-7: bases broader proximally than distally; posterior margins nearly straight; distoposterior lobes poorly developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 not particularly elongate, that of pereopod 6 about 30 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margins of plates 1-3 convex, each with 1 setule near distoposterior corner, distoposterior corners rounded and indistinct; ventral margins of plates 1, 2 and 3 each with 2 spines.

Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 80 percent length of peduncle, with 10-11 spines; outer ramus with 10 spines; peduncle with 16 spines.

Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 4 spines.

Uropod 3: peduncle usually bearing 1 small setae; ramus approximately 45 percent length of peduncle, with 4 apical spines.

Telson subrectangular, longer than broad; apical margin with tiny median notch between spine clusters, bearing 12-13 relatively long spines.

Type locality. phreatic water habitat at H. J. Experimental Forest near Blue RiverReservoir, Lane County, Oregon.

Distribution and ecology. This species is only known from its type-locality (Figs. 93, 96), where it was discovered by pumping from a cabble/gravel fill at a depth of 50-100 cm.

Etymology. This species is named for Lane County, Oregon.

Stygobromus latus, new species

(Figs. 46-48)

Material examined. WASHINGTON. Spokane Co.: Millers Spring No. 1, HOLOTYPE ♀ (USNM), 5 ♂ and 2 ♀ paratypes, I. Mohammad, 5 Dec. 1992; Millers Spring No. 2, 3 ♀, I. Mohammad, 5 Dec. 1992; Whitman Co.: Rock Lake Spring, 1 ♂, 3 ♀, I. Mohammad, 2 July 1992.

Diagnosis. A medium-sized stygobiont species, similar to *S. mysticus* of uropod 3 and broad

bases of pereopods 3-7, but distinguished as follows: gnathopods 1 and 2 with more teeth on palmar margin; bases of pereopods 4-7 much broader and proportionately longer than rest segments; uropod 2 with more spines on inner ramus; telson lacking notch, proportionately deep and with more apical spines. Largest ♀, 7.5 mm; largest ♂, 6.0 mm.

Female. Antenna 1: 70 percent length of body, 50 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 5-9 plumose spines; palp segment 2 with row of 4 long setae on inner margin; palp segment 3 bearing 2 A setae, 1 B seta, 2-3 C setae, row of few D setae, and 4 E setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 10 apical, plumose setae; palp with 3 stiff setae or slender spines apically or subapically. Maxilla 2: inner plate with oblique row of 11 plumose setae on inner margin.

Maxilliped: inner plate with 3 bladelike spines, 3 plumose spines, and 1 naked seta apically/subapically, and 1 plumose setae on inner margin; outer plate with fewer setae on inner margin and 3 lightly plumose setae on or near apex.

Gnathopod 1 propod smaller than that of gnathopod 2; palm subequal in length to posterior margin, armed with 15 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; few inferior medial setae; dactyl nail rather short; coxa broader than deep, margin with 2 setae, one of them longer.

Gnathopod 2 propod subrectangular, longer than broad; palm little convex and armed with 13-14 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin subequal to palm in length, with 2 sets of triply inserted setae; few medial setae; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate much deeper than broad, margin with 5 long setae.

Pereopod 4: coxal plate large, broad and deep, reaching about 60-65 percent length of basis, margin with 7 setae.

Pereopod 6 basis very broad and deep, little longer than pereopod 7, about 46 percent length of body, 15 percent longer than pereopod 5.

Pereopods 5-7: bases very broad; posterior margins convex and greatly expanded, expecially that of 7; distoposterior lobes well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively short, that of pereopod 6 about 20 percent length of corresponding propod.

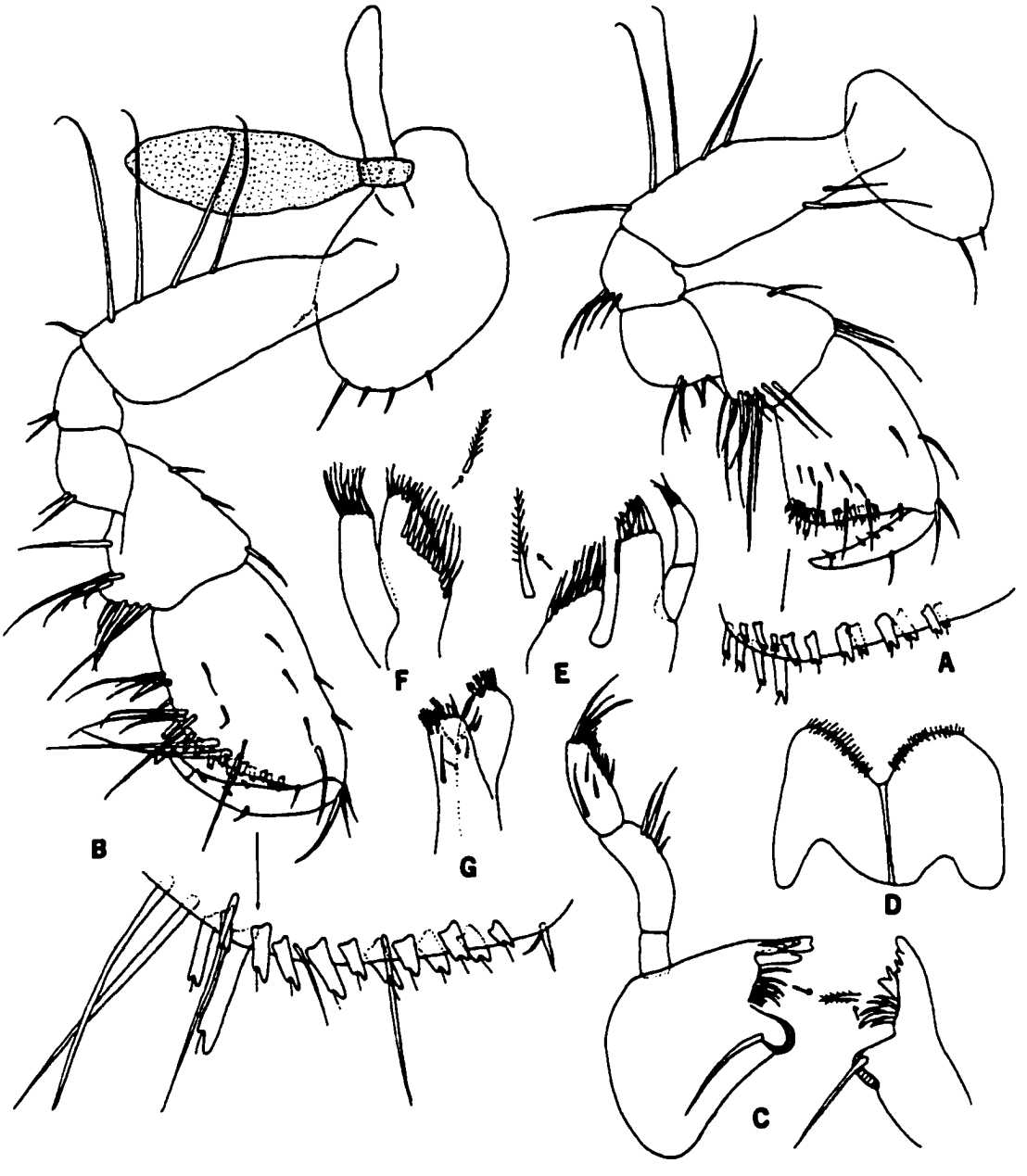

Fig. 46. ***Stygobromus latus*****, new species, female paratype (5.6 mm), Millers Spring No. 1, Spokane County, Washington: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

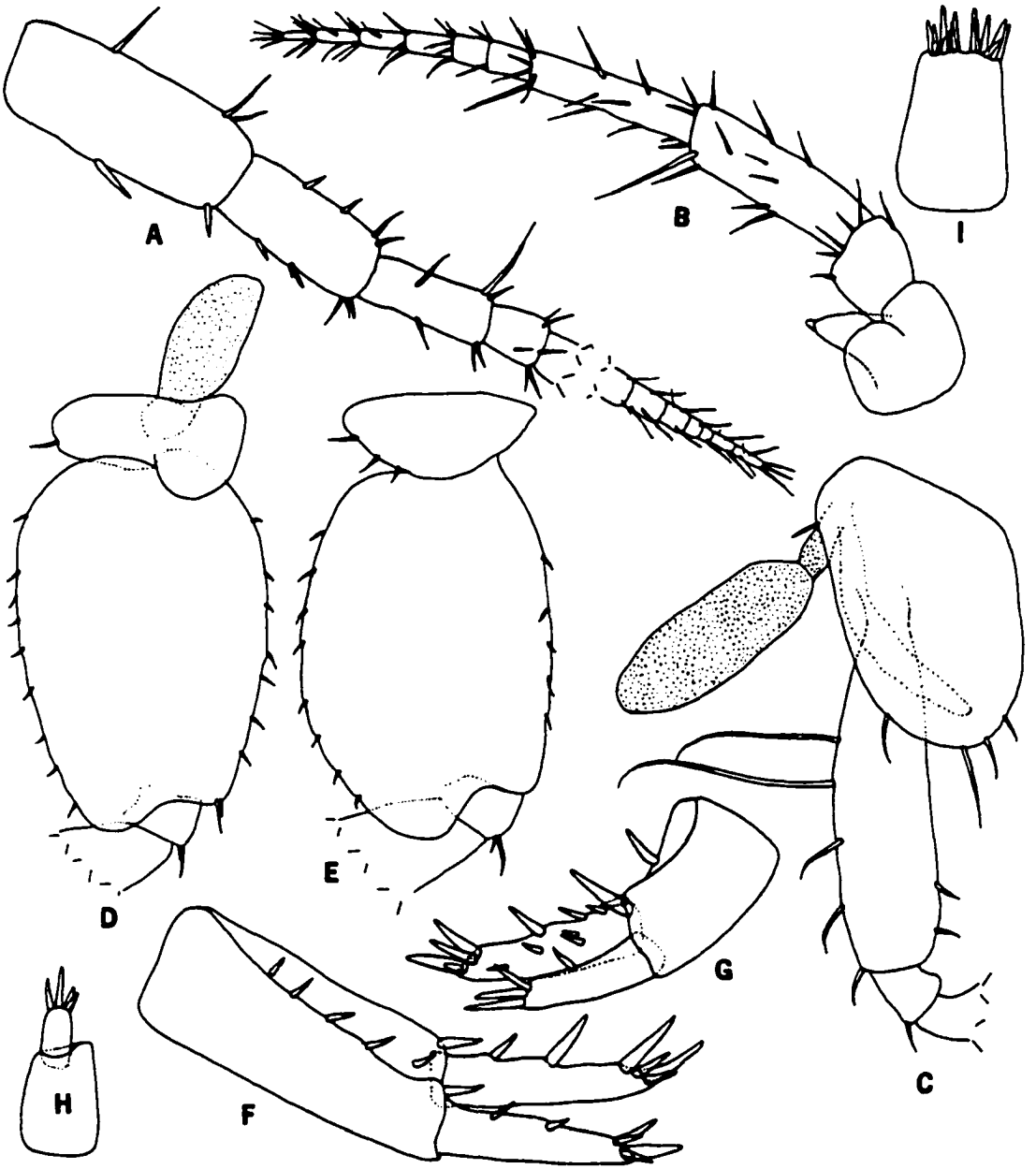

Fig. 47. ***Stygobromus latus*****, new species, female paratype (5.6 mm), Millers Spring No. 1, Spokane County, Washington: A, B, antennae 1, 2; C, pereopod 3; D, E, pereopods 5, 7 (in part); F, G, H, uropods 1, 2, 3; I, telson.**

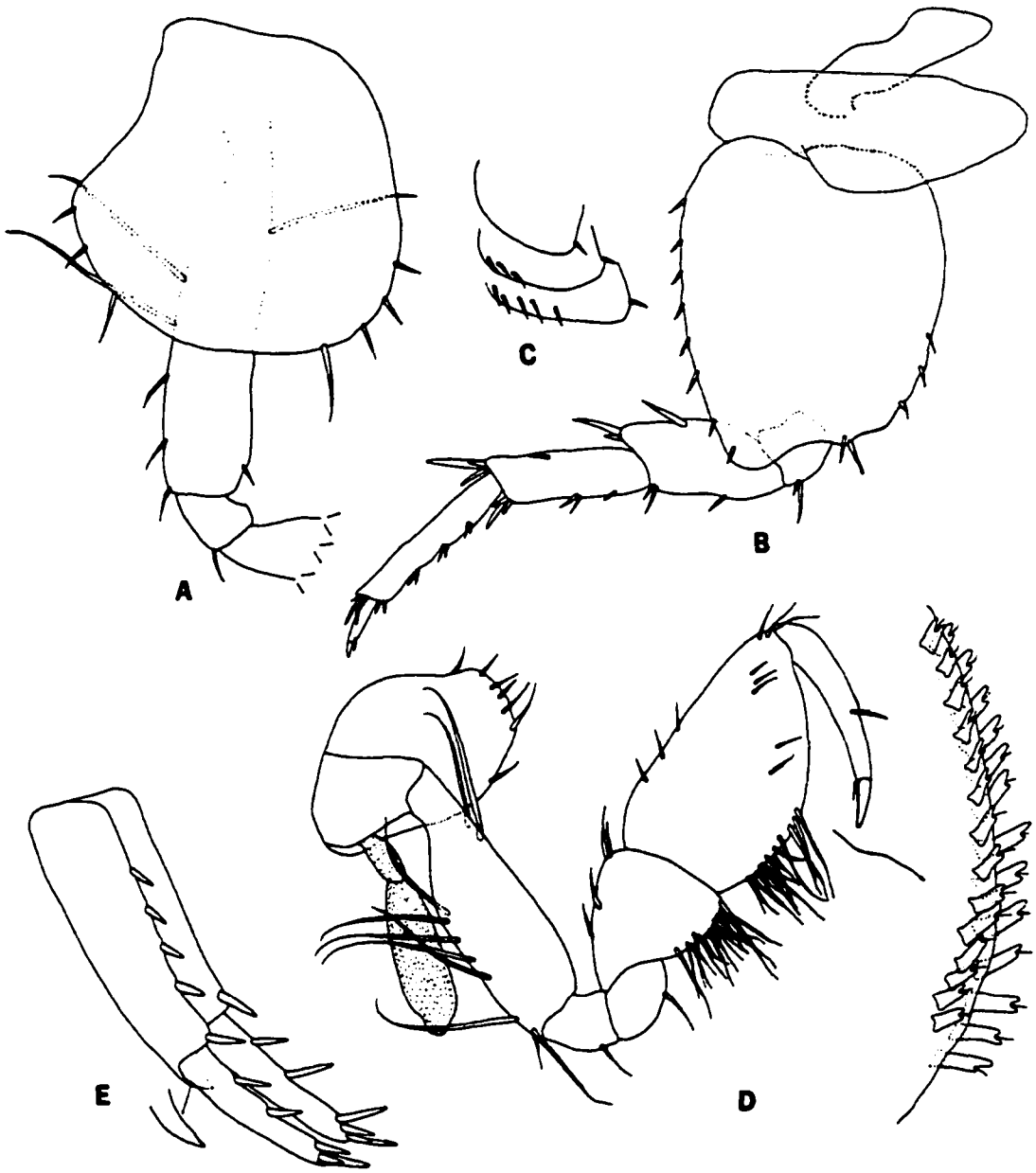

Fig. 48. ***Stygobromus latus*****, new species, female paratype (5.6 mm), Millers Spring No. 1, Spokane County, Washington: A, pereopod 4 (in part); B, pereopod 6; C, pleonal plates; Male paratype (6.0 mm), D, gnathopod 2; E, uropod 1.**

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates narrow but apparently submature on material examined.

Pleonal plates: posterior margin of plate 1 nearly straight, with 1 seta near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 3 spines, that of plate 3 with 5 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 66 percent length of peduncle, with 6 spines; outer ramus with 6 spines; peduncle with 7 spines.

Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 11 spines; outer ramus with 3 spines; peduncle with 2 spines.

Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 45-50 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with tiny median notch between spine clusters, bearing 12-13 relatively long spines.

Male. Differing from female as follows: Gnathopod propods slightly shorter, palm of propod 2 shorter in relation to posterior margin and with more teeth on palmar margin. Peduncular process of uropod 1 about 25 percent length of outer ramus, pointed distally, upper margin minutely serrate; inner ramus with 6 spines; peduncle with 5 spines. Uropod 2: inner ramus with 9 spines, peduncle with 3 spines. Telson with 8 apical spines.

Type locality. Millers Spring no. 1, approximately 26 km S. of Cheney, Spokane Co., Washington (see Mohammad, 1995, for detailed description).

Distribution and ecology. This species is recorded from six springs located to the south and southwest of Cheney, WA (Mohammad, 1995). They include Giffords, TNWR, Millers 1 and 2 springs, Spokane Co.; Rock Lake Spring, Whitman Co.; and Dragon Spring, Adams Co (Figs. 93, 96). This species co-occurs with *Stygobromus rallus*, n. sp. (described below) in Millers Spring No. 1 and Rock Lake Spring.

Etymology. The epithet *latus* is from the Latin, meaning "broad," in reference to the broad bases of the pereopods, which easily distinguishes this species from most others in the genus *Stygobromus*.

Remarks. This species was not described but mentioned by Ibrahim Mahammad in his 1995 unpublished Master's thesis in the Department of Biology at Eastern Washington University, Cheney. He refered to it as "*Stygobromus* species (stocky body)."

Stygobromus limbus, new species

(Figs. 49-50)

Material examined. TEXAS. Culberson Co.: Border Cave, HOLOTYPE ♀ (slides in part) (USNM), W. C. Welbourn, 1 Nov. 1976; 12 ♀, paratypes, 16 juvs., S. J. Harden and C. T. Lindblom, 4 July 1985; 8 ♀, 1 ♂, S. J. Harden and C. T. Lindblom, 15 Aug. 1986.

Diagnosis. A relatively large cavernicolous species possibly related to *S. azisonensis* in structure of the gnathopods but distinguished from that species as follows: maxillae 1 and 2 with more setae on inner plate; maxilliped with more long setae on inner plate; distoposterior lobe of pereopod 6 better developed; coxal plates 3-4 with more setae on margin; pleonal plates 2-3 with more spines on ventral margin; uropods 1-2 with more spines on rami and peduncle; telson with shorter apical spines and slight notch. Largest ♀, 12.5 mm; ♂ unknown.

Female. Antenna 1: 50 percent length of body, 45 percent longer than antenna 2; primary flagellum with 19-20 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with row of 8 long setae on inner margin; palp segment 3 bearing 1 B seta, 11 D setae, and 5 setae E, lacking both A and C setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 11 apical, plumose setae; palp with 8 stiff setae subapically. Maxilla 2: inner plate with oblique row of 13 plumose setae on inner margin.

Maxilliped: inner plate with 3-4 bladelike spines, 5 plumose spines, 1 naked seta apically, and 5 plumose setae on inner margin; outer plate with setae on inner margin and apex, and single small spine near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and approximately 2 times longer than length of posterior margin, armed with 20 spine teeth in double row; defining angle with 2 spine teeth on outside, 4 shorter ones on inside; posterior margin lacking setae; 2-3 superior medial setae; 2-3 inferior medial setae; dactyl nail rather long; coxa broader than deep, margin with 3 setae.

Gnathopod 2: propod subrectangular, deeper than broad; palm straight or slightly concave and armed with 20 spine teeth in double row; defining angle with 1 spine tooth on outside, 1 shorter spine tooth on inside; posterior margin 50 percent as long as palm, with 2 sets of doubly inserted setae; 10 superior medial setae, triple inserted; 5 inferior medial setae; coxa deeper than broad, margin with 3 setae.

Pereopod 3: coxal plate deeper than broad, margin with 6 setae.

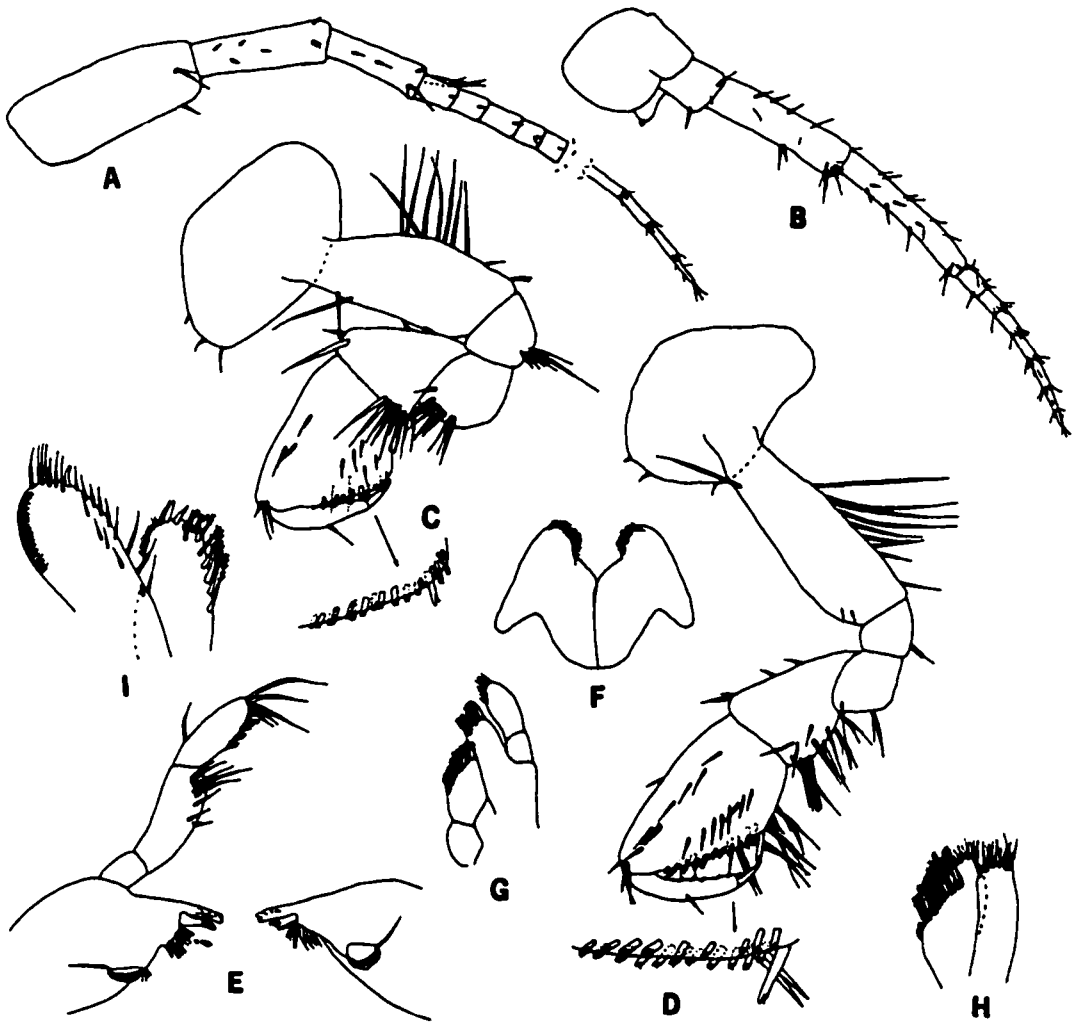

Fig. 49. *Stygobromus limbus*, new species, female paratype (10.0mm), Border Cave, Culberson County, Texas: A, B, antennae 1,2; C, D, gnathopods 1, 2 (palms enlarged); E, left mandible and dentate part of right mandible; F, lower lip; G, H, maxilla 1, 2; I, inner and outer plates of maxilliped (enlarged).

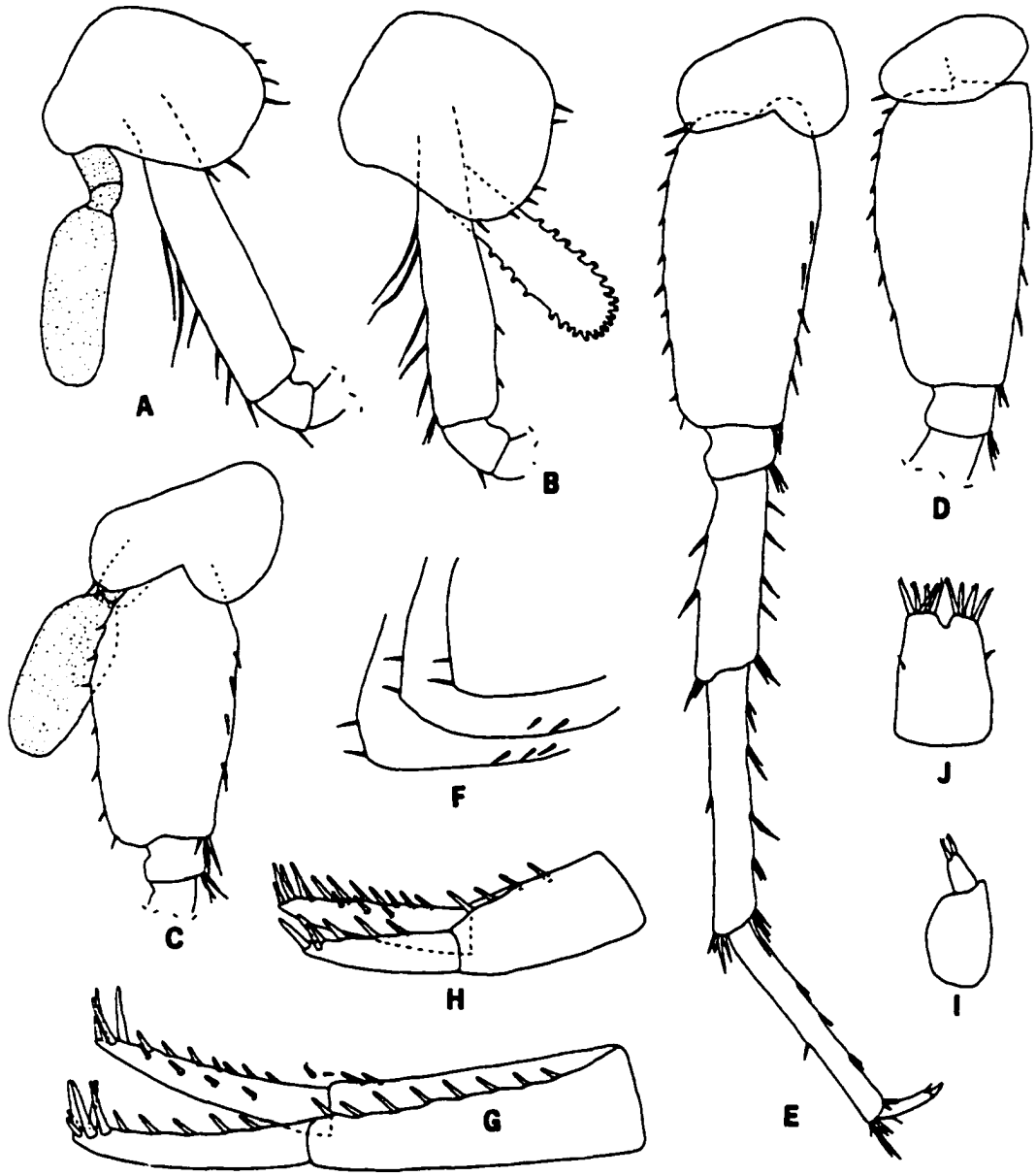

Fig. 50. ***Stygobromus limbus*****, new species, female paratype (10.0mm), Border Cave, Culberson County, Texas: A, B, C, pereopods 3, 4, 5; D, E, pereopods 7, 6; F, pleonal plates; G, H, I, uropods 1, 2, 3; J, telson.**

Pereopod 4: coxal plate relatively broad, reaching about 35 percent length of basis, margin with 6 setae.

Pereopod 6 little longer than pereopod 7, about 55 percent length of body, 30 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than the distally; posterior margins weakly convex; distoposterior lobes poorly developed; anterior margin with 3-5 spines, posterior margins with numerous spines; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 20 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 3 convex, with 2 setules near distoposterior corner, that of 1 and 2 less convex, each also with 2 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral superior margin of plate 2 with 2 spines, that of plate 3 with 3 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 15 spines; outer ramus with 11 spines; peduncle with 10 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 16 spines; outer ramus with 6 spines; peduncle with 5 spines.

Uropod 3: peduncle usually without small setae; ramus approximately 50 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, taped distally; apical margin with small notch between spine clusters, bearing 8-9 relatively long spines.

Type locality. Border Cave, Culberson County, Texas (Figs. 93, 97), is developed in gypsum bedrock and accesses phreatic water on its lower level.

Distribution and ecology. This species is known only from its type-locality, where it has been collected on several occasions from phreatic lakes on the cave's lower level. Samples were collected from rocks in deep lakes with the stygobiont isopod *Lircealus modulus* Lewis (see Lewis 2001). All of the females collected by Harden and Lindblom in the summer of 1985/86 were ovigerous.

Etymology. This species is named for the type-locality, Border Cave. The epithet *limbus* is from the Latin, meaning "border".

Stygobromus mackenziei Holsinger, 1974

Stygobromus mackenziei Holsinger, 1974: 32-35, figs. 18-19 [type-locality: Empire Cave, Santa Cruz Co., California].

Material examined. CALIFORNIA. Santa Cruz Co.: Empire Cave, 5 ♀, D. C. Rudolph, D. Cowan and B. van Ingen, 22 Apr. 1979; 2 ♀, T. S. Briggs, 4 Dec. 1983.

Diagnosis. A small cavernicolous species, distantly related to species of the Mother Lode region of California and distinguished by having 4 apical spines on inner plate of Maxilliped: lightly spined palms of gnathopodal propods, relatively large, deep coxal plates of gnathopods and pereopods 3 and 4; proportionately broad bases of pereopods 5-7, lightly spined peduncles of uropods 1 and 2, and 8 apical spines on telson. Largest ♀ 6.0 mm; largest ♂ 4.0 mm.

Distribution and ecology. This species is known only from its type-locality, Empire Cave, Santa Cruz Co., California (Figs. 93, 95). Several of the females in the April 1979 sample measured 6.0 mm and had setose brood plates. One specimen was ovigerous with 7 embryos in the brood pouch. This collection also contained 1 specimen of *S. imperialis* n. sp. (described above). The December 1983 collection was taken from a flooded room in the company of 2 stygobiont isopods of the genus *Caecidotea*.

Stygobromus myersae, new species

(Figs. 51-53)

Material examined. CALIFORNIA. Inyo Co.: Black Canyon Spring, ca. 11 km E of Bishop, HOLOTYPE ♀ (USNM), 10 ♂ and 11 ♀ paratypes, 1 juv., M. Myers, 17 July 1997; 2 ♂, 6 ♀, 3 juvs., M. Myers, 4 Aug. 1996; unnamed hillside spring, ca. 7 km S of Black Canyon Spring, 5 juvs., M. Myers, 29 July 1998; 7 juvs., unnamed hillside spring in Marble Canyon, ca. 7 km S of Blank Canyon Spring, 3 Nov. 1998; NEVADA. Esmeralda Co.: Log Spring, ca. 64 km E of Black Canyon Spring, 40 ♂, 19 ♀, M. Myers, 30 Oct 1997.

Diagnosis. A medium-sized groundwater species distinguished as follows: propod of gnathopod 1 relatively with long posterior margin; propod of gnathopod 2 proportionately smaller; posterior margin of pleonal plates with few spines and telson lacking apical notch. Largest ♀, 6.0 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 46 percent length of body, 45 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with row of 4

rather long setae on inner margin; palp segment 3 with 8 D setae, 4 E setae, lacking A, B and C setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 7 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 3-4 naked setae apically, and 2 plumose spines on inner margin; outer plate with setae on inner margin and setae and 1 or 2 small spines on apex.

Gnathopod 1: propod little smaller than propod of gnathopod 2; palm straight or slightly convex, and subequal in length to posterior margin, armed with 16 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae, 4 singly inserted inferior medial setae; dactyl nail rather short; coxa broader than deep, margin with 3 setae.

Gnathopod 2: propod relatively small, longer than broad; palm straight and armed with 16 spine teeth in double row; defining angle with 1 very long spine tooth of unequal length on outside, 1 shorter spine tooth on inside; posterior margin 50 percent length of palm, with 1 set of mostly doubly inserted (occasionally triply) setae; 6 doubly inserted inserted supperior medial setae, 4 singly inserted inferior medial setae; coxa about as broad as deep, margin with 3 setae.

Pereopod 3: coxal plate little deeper than broad, margin with 4 setae.

Pereopod 4: coxal plate about as deep as broad, reaching about 40 percent length of basis, margin with 6 setae.

Pereopod 6 little longer than pereopod 7, about 62 percent length of body, 33 percent longer than pereopod 5.

Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 30 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, those of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 without spines, that of plate 3 with 1 spine.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 90 percent length

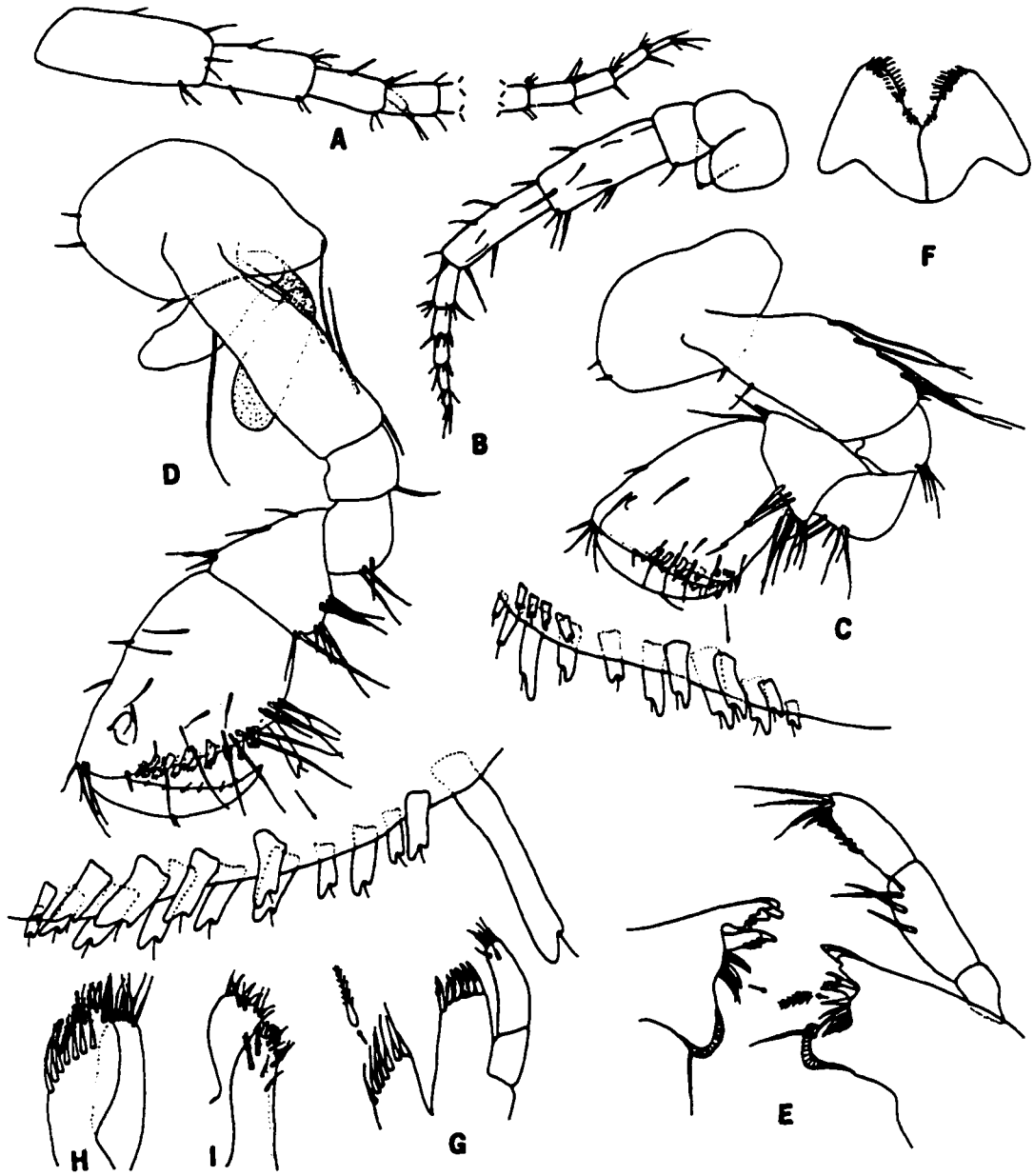

Fig. 51. ***Stygobromus myersae*****, new species, female paratype (5.0 mm), Black Canyon Spring, Inyo County, California: A, B, antennae 1, 2; C, D, gnathopods 1, 2 (palms enlarged); E, right mandible and dentate part of left mandible; F, lower lip; G, H, maxilla 1, 2 (apical setae enlarged); I, inner and outer plates of maxilliped (enlarged).**

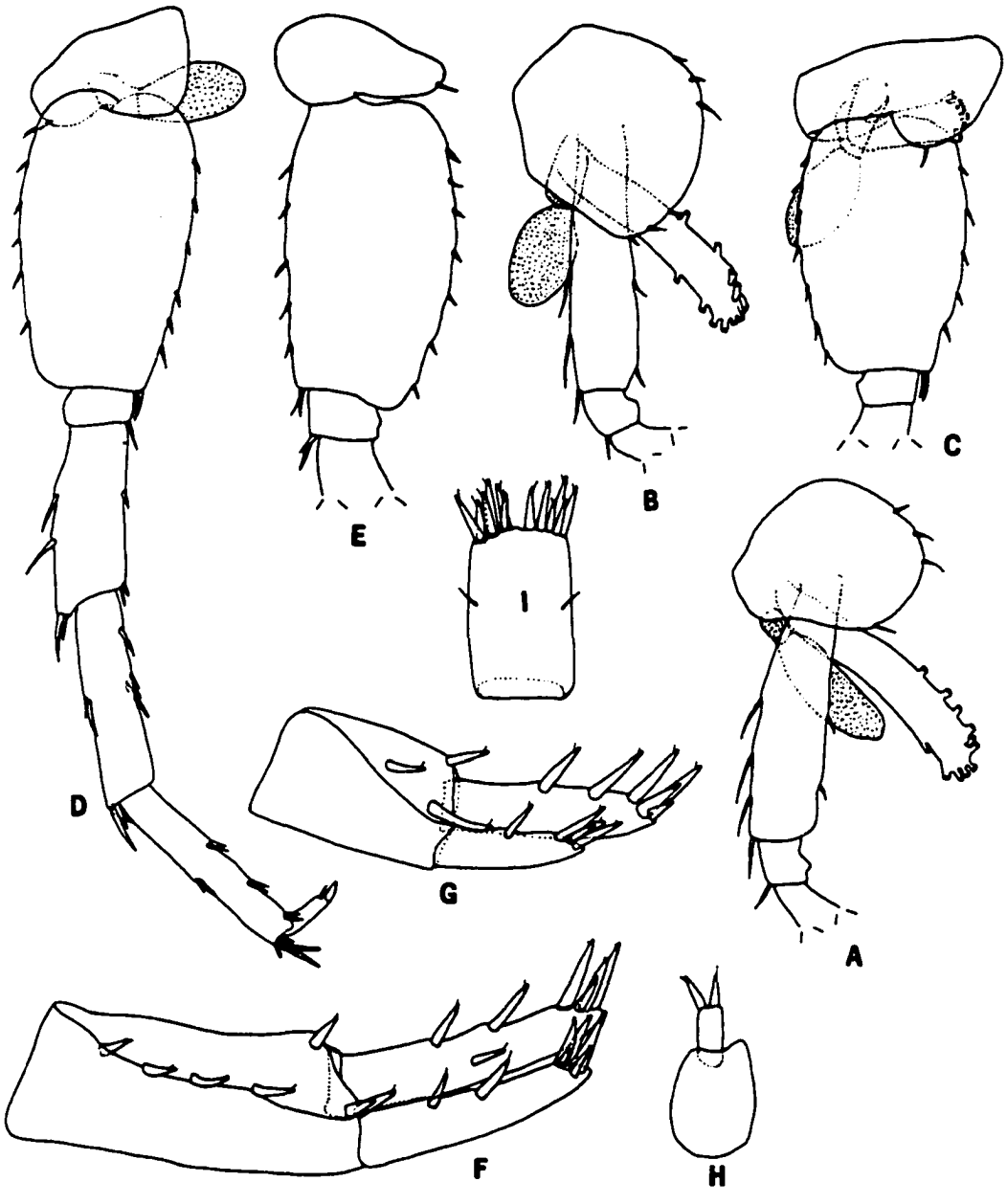

Fig. 52. ***Stygobromus myersae*****, new species, female paratype (5.0 mm), Black Canyon Spring, Inyo County, California: A, B, C, pereopods 3, 4, 5; D, E, pereopods 6, 7; F, G, H, uropods 1, 2, 3; I, telson; J, pleonal plates.**

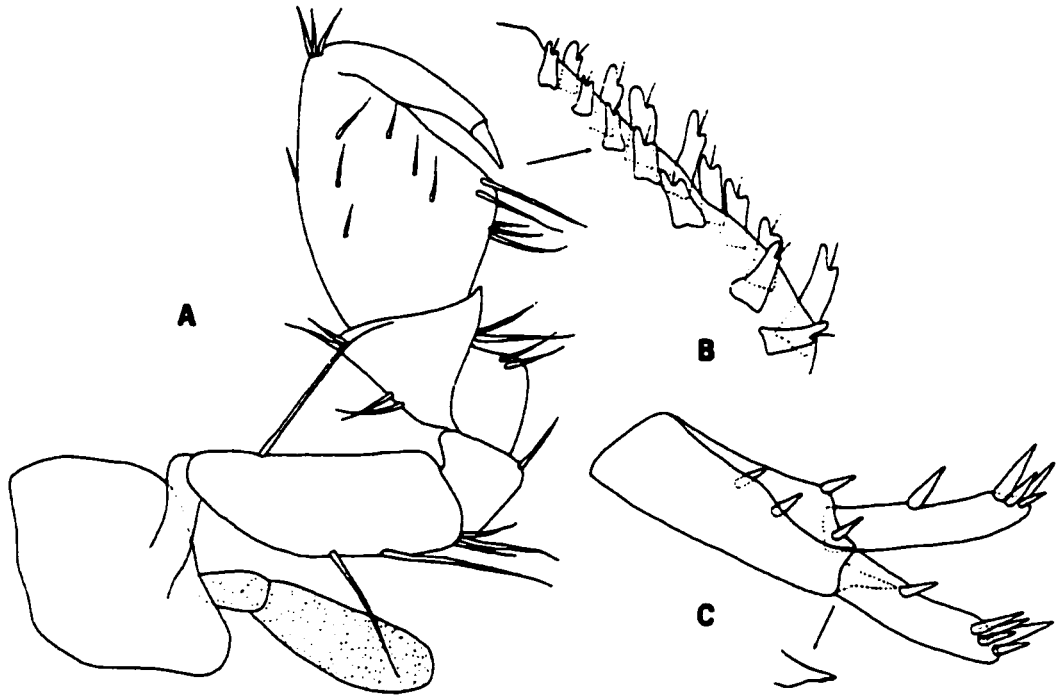

Fig. 53. ***Stygobromus myersae*****, new species, Male paratype (3.8 mm), Black Canyon Spring, Inyo County, California: A, B, gnathopod 2, enlarged palm; C, uropod 1.**

of peduncle, with 7 spines; outer ramus with 7 spines; peduncle with 7 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 6 spines; outer ramus with 5 spines; peduncle with 3 spines.

Uropod 3: peduncle usually without small setae; ramus approximately 55 percent length of peduncle, with 2 apical spines.

Telson subrectangular, longer than broad; apical margin typically entire, occasionally with tiny median notch or "break" between spine clusters, bearing 12 relatively long spines.

Male. Differing from female as follows: Gnathopod propods proportionately shorter, palm of propod 2 slightly longer in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process 33 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 4 spines. Uropod 2: inner ramus with 7 spines, peduncle with 4 spines. Telson with 12-14 apical spines.

Type locality. Black Canyon Spring, about 11 km east of Bishop, Inyo County, California.

Distribution and ecology. This species is recorded from two springs, approximately 7 km apart, in Inyo Co., California, and one spring in Esmeralda Co., Nevada, about 64 km to the east (Figs. 93, 95). Samples from the Black Canyon Spring were abtained through a PVC pipe pushed into the substrate and with an aquarium net (M. Myers pers. comm.). The water temperature in the spring was about 10°C. Elsewhere, in the unnamed spring in Marble Canyon, the water temperature was about 12.8°C. Females ranging in size from 5.0 - 6.0 mm have setose brood plates and are sexually mature.

Etymology. This species is named in honor of its collector, Marilyn Myers, who collected several good samples of this species and furnished useful data on its ecology.

Stygobromus mysticus Holsinger, 1974

Stygobromus mysticus Holsinger, 1974: 49-52, figs. 30-31 [type-locality: subterranean habitat, Greenview, Siskiyou Co., California].

Diagnosis. A medium-sized subterranean species, distinguished by possession of relatively small gnathopod propods; deep coxal plates; broadly expanded bases of pereopods 5-7; narrow outer rami of uropod 1 and 2; telson long and distally tapering. Largest ♀, 8.0 mm; male unknown.

Distribution and ecology. This species is known only from subterranean habitat, possibly from a well, in the Klamath Mountains, Siskiyou Co., California (Figs. 93, 95) (Holsinger, 1974).

Stygobromus oregonensis Holsinger, 1974

Stygobromus oregonensis Holsinger, 1974: 13-16, figs. 6-7 [type-locality: small unnamed cave near Roseburg, Douglas Co., Oregon].

Material examined. OREGON. Douglas Co.: a small cave near Roseburg (type-locality), 2 topotypes ♀, Jim Riggs, 1 Jan. 1983.

Diagnosis. A moderately cavernicolous species easily distinguished from other species of the *hubbsi* group by numerous long, stiff setae and slender spines on peduncular segments 4 and 5 of antenna 2; proportionately large propod gnathopod 1 with very long, heavily spined palm; convex palm of gnathopodal propod 2 with double row of 16 spine teeth; convex posterior margins of bases of pereopods 5-7; midlateral position of posterior subacute distoposterior corners of pleonal plates 2 and 3; larger ramus of uropod 3. Largest ♀ 13.0 mm; male unknown.

Distribution and ecology. This species is known only from type-locality, an unnamed cave in Douglas Co., Oregon (Figs. 93, 96). Two samples, containing only females to date, have been collected from a pool in the bottom of the cave. According to Jim Riggs (pers. comm.), the cave is a single passage developed in the Eocene-aged Umpqua formation, which was formed by faulting and/or fissuring in sandstone or siltstone conglomerate. It is not developed in basalt as stated earlier by Holsinger (1974).

Stygobromus pennaki Ward, 1977

Stygobromus pennaki Ward, 1977: 458-461, figs. 3-5 [type-locality: hyporheic in North Fork of the South Platte River, Jefferson Co., Colorado].

Material examined. COLORADO. Arapahoe Co.: interstitial waters of "shore zone" with Bou-Rouch pump South Platte River, Littleton (ca. 2.5 km below Chatfield reservoir), 1♀, 1 ♂, S. P. Canton, 9 Feb. 1988; Jefferson Co.: hyporheic habitats in North Fork of South Platte River by S. P. Canton as follows: 0.48 km W of S. Platte, 2 ♀, 26 Mar. 1985; 2 ♀, 5 Apr. 1985 and 5 ♀, 9 Apr. 1985; 0.8 km W. S. Platte, 3 ♀, 1 ♂, 5 Apr. 1985; behind S. Platte Hotel, 5 ♀, 5 Apr. 1985, 7 ♀, 9 Apr. 1985, and 14 ♀, 5 Nov. 1985; 100 m downstream from jct. with N. Fork, 3 ♀, 5 Apr. 1985; near gaging station in S. Platte, 2 ♀, 9 Apr. 1985.

Diagnosis. A small hyporheic species, apparently related to *S. puteanus* but distinguished by longer gnathopodal propod 1 with more oblique palm; more teeth on palmar margin; fewer marginal setae on coxal plates 3 and 4; more spines on posterior margin of pleonal plates, fewer

spines on ventral margins; uropod 3 similar with proportionately larger ramus. Largest♀, 4.3 mm; largest ♂, 4.1 mm.

Distribution and ecology. This species is known from hyporheic habitats in the North Fork of South Platte River, Jefferson County, and interstitial waters of the shore zone, Arapahoe County, Colorado (see also Pennak and Ward, 1986) (Figs. 93, 97). As noted above, this species was often collected with *S. coloradensis* in hyporheic habitats in the South Platte River.

Stygobromus putealis Holmes, 1909

Stygobromus putealis (Holmes), 1909: 77-78, figs. 6 [type-locality: well at Waupun, Dodge Co., Wisconsin]. -- Schellenberg, 1936:37. -- Shoemaker, 1942a:5. -- Hubricht, 1943:71. -- Barnard, 1958:74. -- Hubricht, 1959:878. -- Nicholas, 1960:129. -- Holsinger, 1972:70-71. -- Barnard, 1983:441, map16. -- Fitzpatrick, 1983:146.-- Holsinger, 1986:547. -- Holsinger and Shaw, 1986:99. -- Peck and Christiansen, 1990:75.

Diagnosis. A medium-sized groundwater species, morphologically closely similar to many members of the *hubbsi* group much farther west. This species lacks sternal processes and setae on the posterior margin of the propod of gnathopod 1. Largest ♀, 6.0 mm; largest ♂, 4.0 mm.

Distribution and ecology. To date all collection of this species have been from wells in southeastern Wisconsin, approximately 56 km east of the "Driftless Area" (Fig. 93). It is the only species of the *hubbsi* group found in central North America east of the western Cordillera.

Remarks: A detailed redescription of this species is being prepared by Holsinger (in ms.).

Stygobromus puteanus Holsinger, 1974

Stygobromus puteanus Holsinger, 1974: 11-13, figs. 4-5 [type-locality: an unnamed well near an unnamed well near Three Forks, Gallatin Co., Montana].

Diagnosis. A medium-sized subterranean species apparently related to *S. tritus* but distinguished from that species by the straight to slightly convex palms of gnathopodal propods, broader bases of pereopods 5-7; more apical spines on uropod 3 and telson. Largest ♀, 6.5 mm; male unknown (see Holsinger, 1974).

Distribution and ecology. This species is known only from its type locality, an unnamed well near Three Forks, Gallatin Co., Montana (Figs. 93, 96).

Stygobromus quatsinensis Holsinger and Shaw, 1987

Stygobromus n. sp. Holsinger and Shaw, 1986: 79.

Stygobromus quatsinensis Holsinger and Shaw, 1987: 222-229, figs. 1-3 [type-locality: Thanksgiving Cave, Vancouver Island, British Columbia, Canada]. -- Holsinger *et al.*, 1997: 347-348.

Diagnosis. A medium-sized groundwater species, distinguished from most other members of the *hubbsi* group by presence of 2 or 3 submarginal setae on distal part of posterior margin of propod of gnathopod 1, inserted below defining angle; and absence of distal peduncular process on uropod 1 of male. Largest ♀ 9.0 mm; largest ♂ 7.0 mm.

Distribution and ecology. This species was originally described from two cave populations on Vancouver Island, British Columbia, Canada (Holsinger and Shaw, 1986, 1987). Subsequently, the species has been found in caves elsewhere on Vancouver Island and in karst groundwater habitats (caves and resurgences) on several islands in the Alexander Archipelago of southeastern Alaska (figs. 93, 96) (Holsinger et al., 1997). Ovigerous females (6.0-7.0 mm) occurred in two July samples from Alaska.

Stygobromus rallus, new species

(Figs. 54-56)

Material examined. WASHINGTON. Whitman Co.: Rock Lake Spring, HOLOTYPE ♀ (USNM), 3 ♂ and 3 ♀ paratypes, 2 juvs., I. Mohammad, 2 July 1992; Spokane Co.: Millers Spring No. 2, 2 ♂, 2 ♀, I. Mahammad, 5 Dec. 1992.

Diagnosis. A relatively large groundwater species, closely related to *S. duplus* in gnathopods and uropods 1-2, but distinguished from that species as follows: propod of gnathopod 1 with short posterior margin and more teeth on palmar margin; gnathopod 2 with more teeth on palmar margin; bases of pereopods 4-7 more narrow; uropod 3 with more spines on rami; telson lacking notch on apical margin and with longer and stouter spines. Largest ♀, 11.0 mm; largest ♂, 10.0 mm.

Female. Antenna 1: 70 percent length of body, 62 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 13 rather long setae on inner margin; palp segment 3 bearing 3 B setae, 16 D setae, and 4 E setae, lacking both A and C setae.

Inner lobes of lower lip vestigial.

Maxilla 1: inner plate with 8 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 11 plumose setae, 5 naked setae apically, and 4 coarse setae on inner margin; outer plate with setae on inner margin and apex, some slightly plumose, and 1 small spine.

Gnathopod 1: propod subequal in size to that of gnathopod 2; palm slightly convex and about five times longer than posterior margin in length, armed with 27 spine teeth in double row; defining angle with 4 spine teeth on outside, 4 shorter ones on inside; posterior margin with row of 4 setae; approximately 8 superior medial setae, mostly triply inserted; 5-6 singly inserted inferior medial setae; dactyl nail rather short; coxa rather narrow and broader than deep, margin with 2 setae.

Gnathopod 2: propod palm weakly convex and armed with 29-30 spine teeth in double row; defining angle with 4 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 3 sets of mostly triply inserted setae; 10 superior medial setae, mostly triply inserted; 5 singly inserted inferior medial setae; coxa little broader than deep, margin with 3 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae.

Pereopod 4: coxal plate broader than deep, reaching about 30 percent length of basis, margin with 4 setae.

Pereopod 6 little longer than pereopod 7, about 78 percent length of body, 43 percent longer than pereopod 5.

Pereopods 5-7: bases narrowing in larger specimens, broader proximally than distally; posterior margins convex; distoposterior lobes distinct (but less so on pereopod 7); anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from segment 7.

Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners teny but distinct; ventral margin of plate 2 without spines, that of plates 3 with 3 to 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 70 percent length of peduncle, with 9 spines; outer ramus with 9 spines; peduncle with 14 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 8

spines; outer ramus with 8 spines; peduncle with 6 spines.

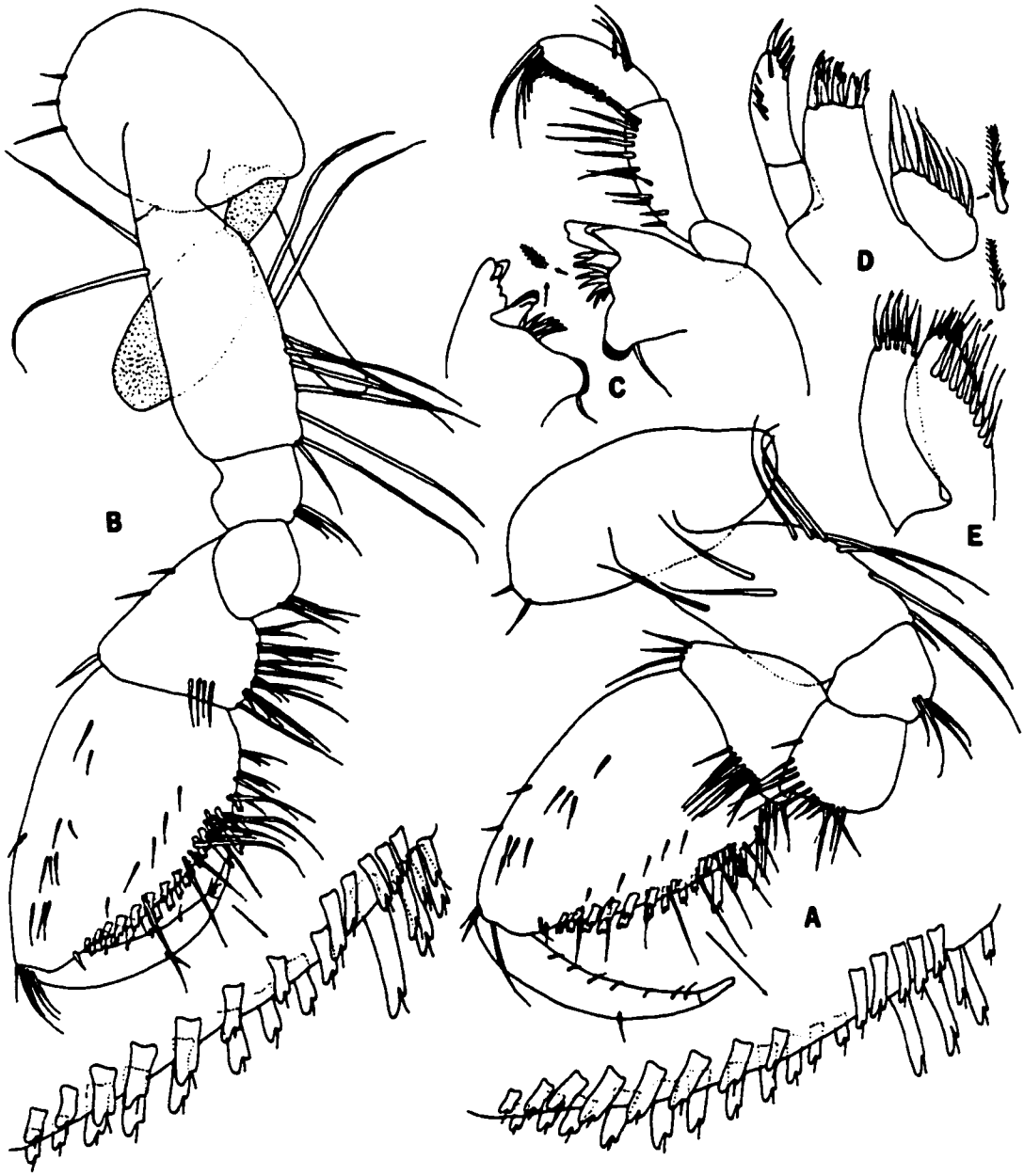

Fig. 54. ***Stygobromus rallus*****, new species, female paratype (7.6 mm), Rock Lake Spring, Whitman County, Washington: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, E, maxilla 1, 2 (apical setae enlarged).**

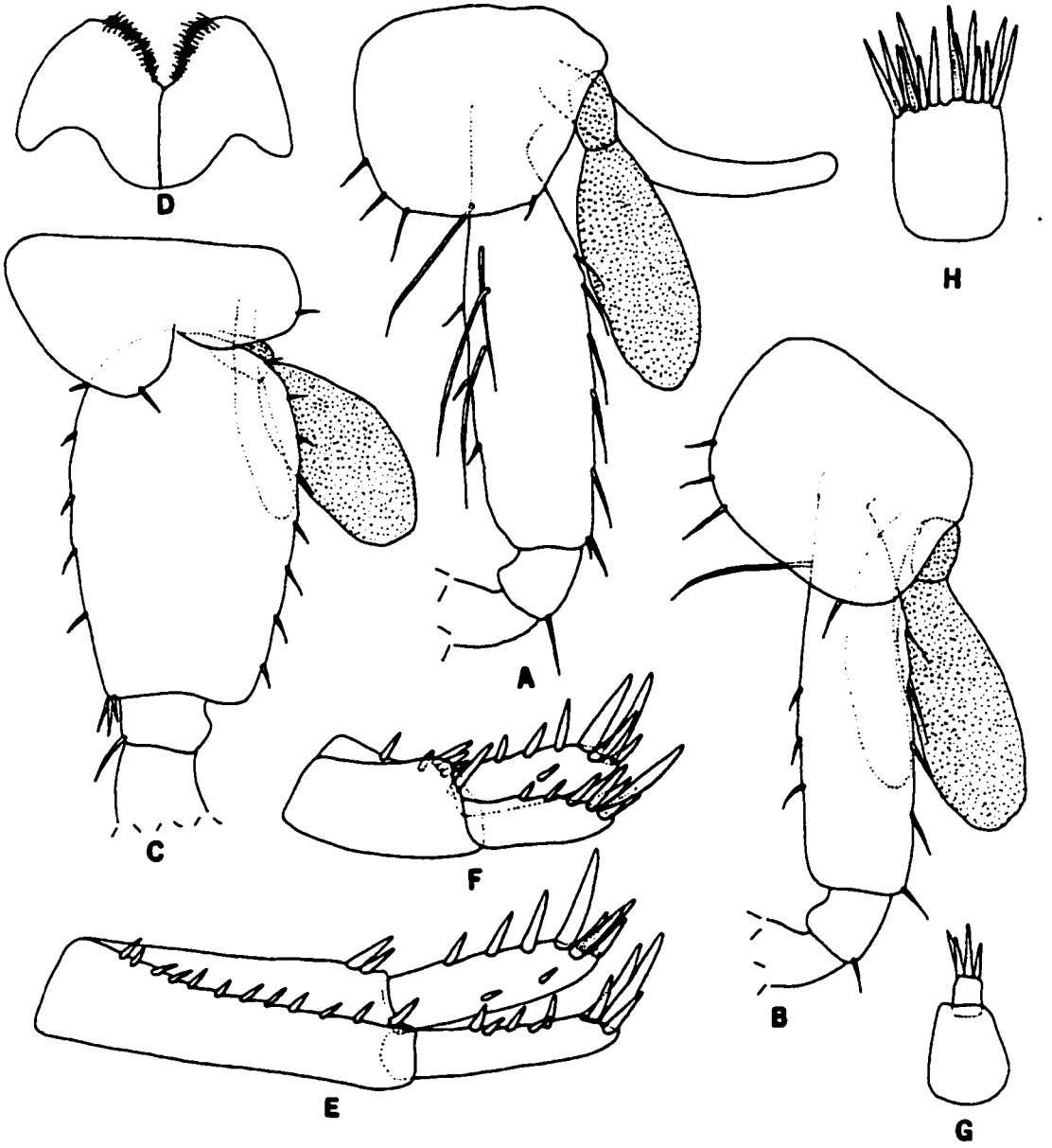

Fig. 55. ***Stygobromus rallus*****, new species, female paratype (7.6 mm), Rock Lake Spring, Whitman County, Washington: A, B, C, pereopods 3, 4, 5; D, lower lip; E, F, G, uropods 1, 2, 3; H, telson; I, pleonal plates.**

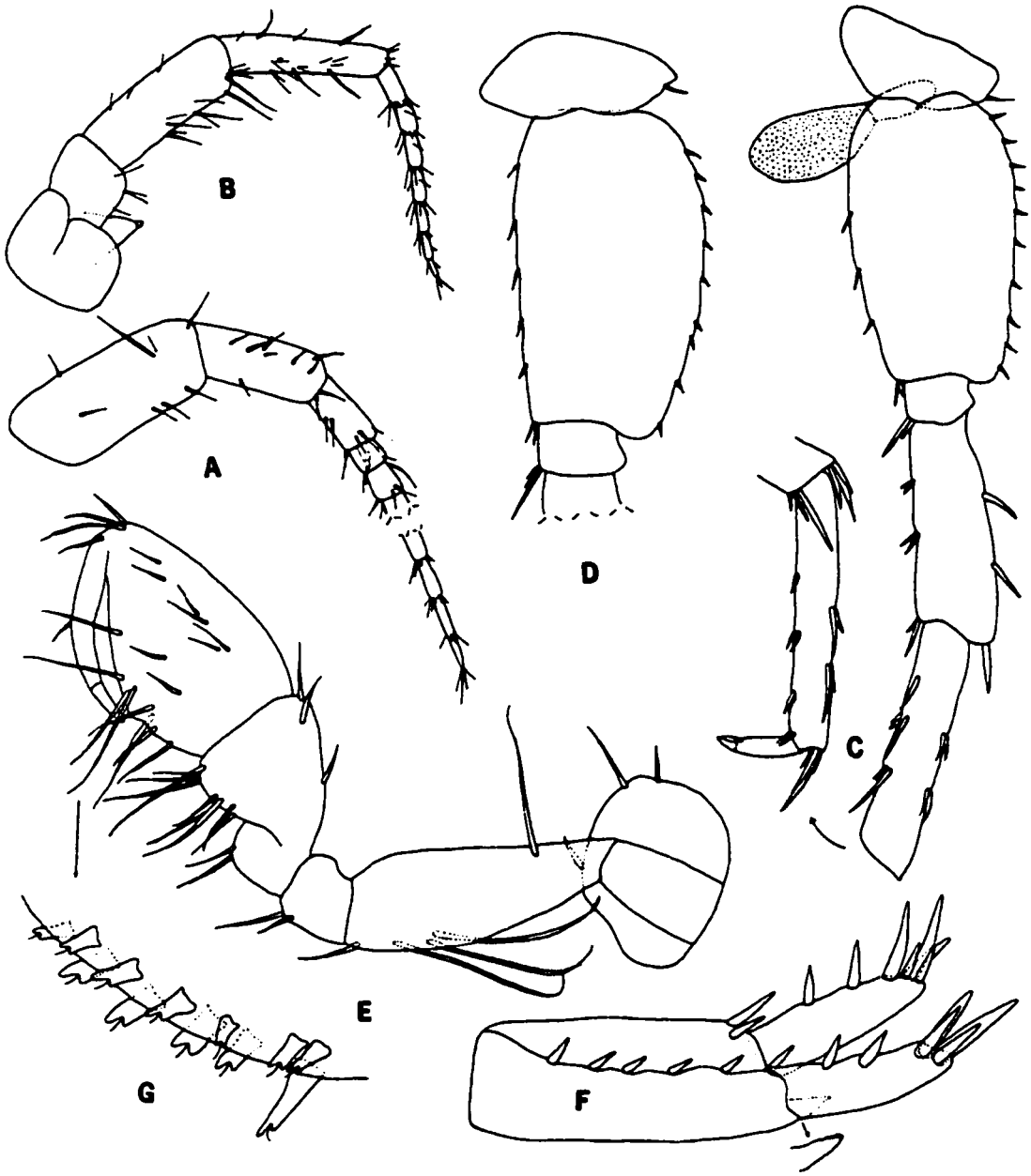

Fig. 56. ***Stygobromus rallus*****, new species, Female paratype (7.6 mm), Rock Lake Spring, Whitman County, Washington: A, B, antennae 1, 2; C, D, pereopods 6, 7; Male paratype (4.5 mm), E, G, gnathopod 2, enlarged palm; F, uropod 1.**

Uropod 3: ramus approximately 45 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, apical margin typically with tiny median notch between spine clusters, bearing 14 - 18 relatively long spines.

Male. Differing from female as follows: Gnathopod propods shorter and narrower, palm of propod 2 longer in relation to posterior margin and with fewer teeth on palmer margin. Uropod 1: peduncular process approximately 25 percent length of outer ramus, narrowing distally, upper margin minutely serrate distally; inner ramus with 7 spines; peduncle with 8 spines. Uropod 2: inner ramus with 9 spines, peduncle with 6 spines. Telson with 14 long apical spines.

Type locality. Rock Lake Spring, approximately 28 km S of Cheney, Whitman County, Washington.

Distribution and ecology. In addition to Millers Spring no. 2 and Rock Lake Spring (the type-locality), Mohammad (1995) reported this species from Millers Springs no. 3 and 4, Spokane Co., WA and Dragon Spring, Adams Co., Washington (Figs. 93, 96). This species co-occurs with *S. latus* in Rock Lake Spring and Millers Spring No. 2.

Etymology. The epithet *rallus* means "thin" or "narrow," in reference to the bases of pereopods 5 - 7, which are relatively narrow in comparison to those of the sympatric *S. latus*.

Remarks: This is the same species that Ibrahim Mohammad named *Stygobromus chrissi* in his unpublished 1995 master's degree thesis at Eastern Washington University.

Stygobromus rudolphi, new species

(Figs. 57-59)

Material examined. CALIFORNIA. Santa Barbara Co.: Montgomery Spring in Los Padres National Forest, HOLOTYPE ♀ (USNM), 6 ♀, 1 ♂ paratypes, D. C. Rudolph, 10 May 1974.

Diagnosis. A medium-sized species closely similar to *S. grahami* and *S. gradyi* but distinguished from these 2 species as follows: palm of gnathopod 1 straight; coxal plates 1-2 with fewer setae; coxal plates 3 and 4 broader than deep and with fewer setae; pleonal plate 2 with fewer ventral spines; peduncle of uropod 3 with a long spine; telson with more spines on apical margin. Largest ♀, 6.0 mm, largest ♂, 3.0 mm (probably immature).

Female. Antenna 1: 52 percent length of body, 57 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 with 3-4 C setae, 9 or more D setae, 4 E setae, lacking A and B setae.

Inner lobes of lower lip small to vestigial.

Maxilla 1: inner plate with 12 apical, plumose setae; palp with 6 stiff setae or slender spines on apical margin. Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 4 plumose spines, 3 naked setae apically, plumose spines and/or coarse setae absent from inner margin; outer plate with numerous naked setae on inner margin and lightly plumose setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2, palm straight, 67 percent longer than posterior margin, armed with 21 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin not bearing setae; 3-4 superior medial setae, singly inserted; 6-7 inferior medial setae; dactyl nail small; coxa broader than deep, margin with 4 setae.

Gnathopod 2: propod deeper than broad; palm concave medially and armed with 20 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin less half length of palm, with 2 sets of doubly inserted setae; 5 medial setae; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 6 setae.

Pereopod 4: coxal plate broader and deeper than that of pereopod 3, reaching about 40 percent length of basis, margin with 6 setae.

Pereopod 6 little longer than pereopod 7, about 60 percent length of body, about 50 percent longer than pereopod 5.

Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 33 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates slightly expanded distally.

Pleonal plates: posterior margins of plate 1 and 3 convex, each with 1 setule near distoposterior corner, that of 2 less convex, with 1 setule near distoposterior corner; distoposterior corners rounded and distinct; ventral margin of plate 2 with 1 spine, that of plate 3 with 4 spines.

Uronites free. Uropod 1: inner ramus subequal to outer ramus, about 80 percent length of peduncle, with 10 spines; outer ramus with 9 spines; peduncle with 8 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle and with 8 spines;

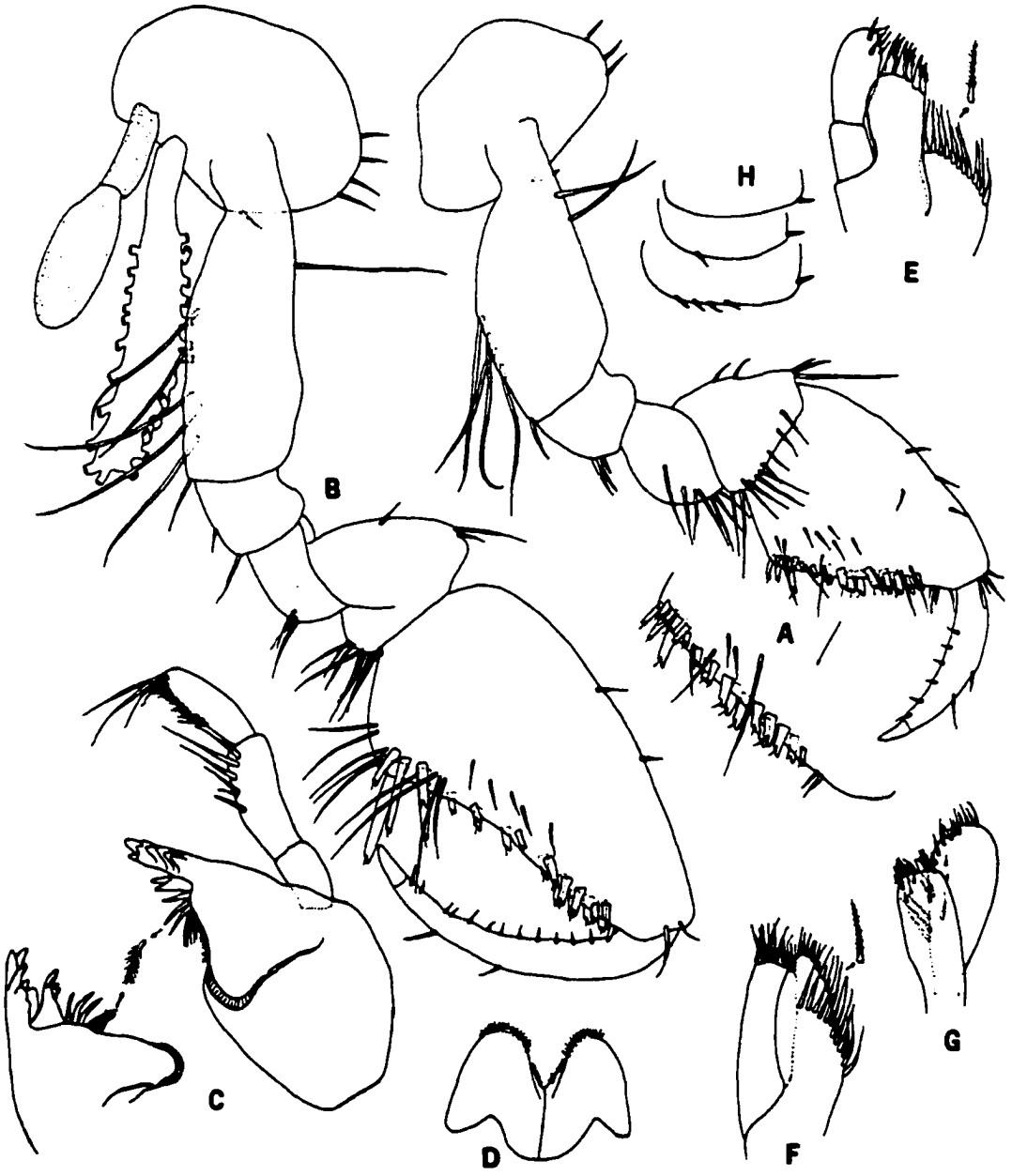

Fig. 57. ***Stygobromus rudolphi*****, new species, female paratype (7.0 mm), Montgomery Spring, Santa Barbara County, California: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged); H, pleonal plates.**

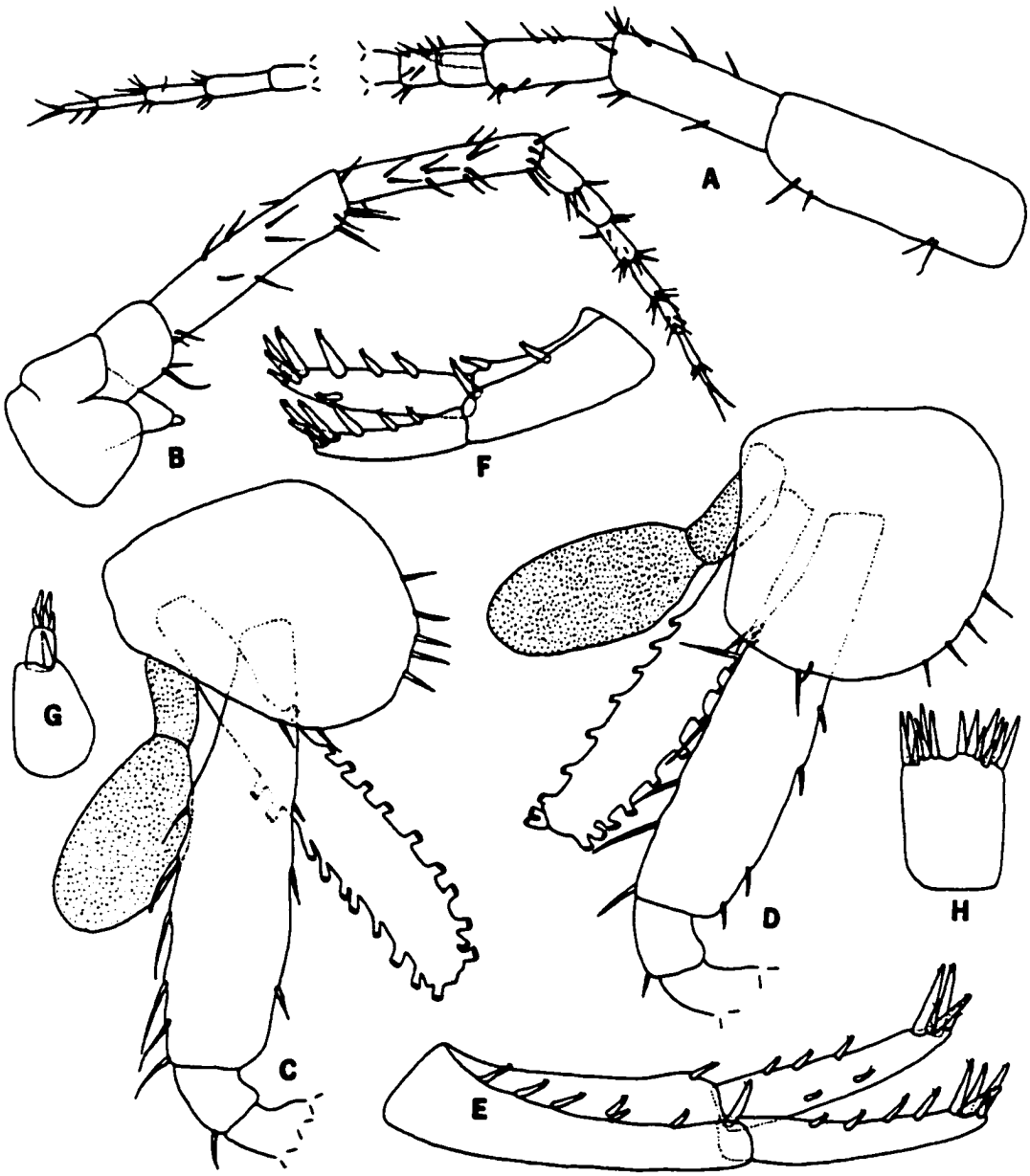

Fig. 58. ***Stygobromus rudolphi*****, new species, female paratype (7.0 mm), Montgomery Spring, Santa Barbara County, California: A, B, antennae 1, 2; C, D, pereopods 3, 4; E, F, G, uropods 1, 2, 3; H, telson.**

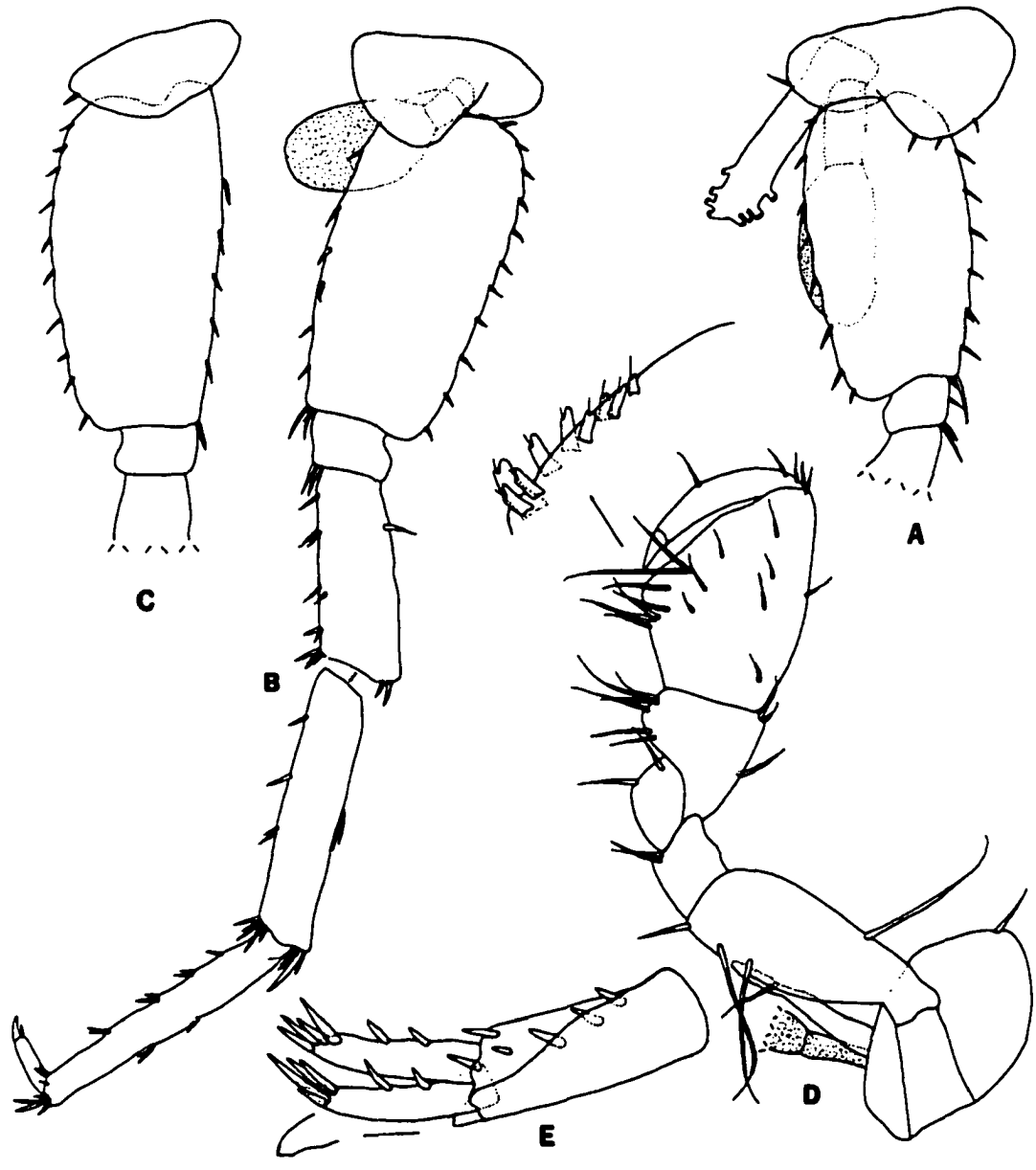

Fig. 59. ***Stygobromus rudolphi*****, new species, female paratype (7.0 mm), Montgomery Spring, Santa Barbara County, California: A, B, pereopods 5, 6; C, pereopod 7; Male paratype (3.0 mm), D, gnathopod 2; E, uropod 1.**

outer ramus with 7 spines; peduncle with 3 spines.

Uropod 3: peduncle bearing one spine apically; ramus approximately 33 percent length of peduncle, bearing 5 apical spines.

Telson longer than broad, apex with tiny median notch between spine clusters, bearing 14 relatively long spines.

Male. Differing from female as follows: Palm of gnathopod 2 shorter in relation to posterior margin; palmar margin convex and with fewer teeth; Uropod 1: peduncular process 25 percent length of outer ramus, inner ramus with 6 spines; peduncle with 6 spines. Uropod 2: inner ramus with 7-8 spines, peduncle with 3-4 spines. Telson with 14-17 long apical spines.

Type locality. Montgomery Spring in Los Padres National Forest, Santa Barbara County, California. The spring is apparently developed in sandstone. The specimens were collected from a water tank fed from a small seep-like spring (D. C. Rudolph, pers. comm.).

Distribution and ecology. The range of the species is known only from its type-locality in Montgomery Spring, Los Padres National Forest, Santa Barbara County, California (Figs. 93, 95). This species was collected from a water tank fed by a small seep-like spring in the San Rafael Mountains.

Etymology. This species is named in honor of its collector, D. Craig Rudolph, who discovered it during a survey of the subterranean invertebrates of California.

Stygobromus saltuaris, new species

(Figs. 60-61)

Material examined. OREGON. Lane Co.: hyporheic/seep area, Trail Creek, Willamette National Forest, HOLOTYPE ♀ (slides in part) (CMN), 1 ♀ paratype (CMN), G. W. Courtney, 25 June 1987;

Diagnosis. A medium-sized hyporheic species, related to *S. oregonensis* in structure of pleonal plates but distinguished by the following: gnathopods 1 and 2 with proportionately longer posterior margin; palm of gnathopod 2 concave; uropod 1 and 2 with fewer long and stout spines on rami and peduncle; uropod 3 peduncle broad; telson lacking notch and with fewerspines. Largest ♀, 5.0 mm; ♂ unknown.

Female. Antenna 1: 66 percent length of body, 80 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 4 plumose spines; palp segment 2 with row of 2 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 4-5 C setae, few D setae, and 3 E setae,

lacking A setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 4 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 8 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, and 3 naked setae apically, and 1 stiff setae on inner margin; outer plate with short setae on inner margin and 1 small bladelike spine on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm straight or slightly concave about 2 times longer than posterior margin, armed with 13-14 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; 4 superior medial setae; 2 or 3 inferior medial setae; dactyl nail rather long; coxa about as broad as deep, margin with 2 setae.

Gnathopod 2: propod subrectangular, 2 times longer than broad; palm slightly concave medially and armed with 13 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin approximately 70 percent length of palm, with 3-4 sets of doubly inserted setae; 6 superior medial setae, singly inserted; 3 singly inserted inferior medial setae; coxa little broader than deep, margin with 4 setae.

Pereopods 3-4: coxal plates about as deep as broad, margins with 3 setae.

Pereopod 6 little longer than pereopod 7, about 55 percent length of body, and 22 percent longer than pereopod 5.

Pereopods 5-7: bases of about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively elongate, that of pereopod 6 about 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates slightly expanded distally.

Pleonal plates: posterior margin of plates 1 and 2 slightly concave or nearly straight, with 1 setule near distoposterior corner, that of 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 6 spines.

Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7

spines; outer ramus with 4 spines; peduncle with 4 spines.

Uropod 3: peduncle usually not bearing small setae; ramus approximately 50 percent length of peduncle, with 3 apical spines.

Telson approximately 30 percent longer than broad, narrowing distally; apical margin with

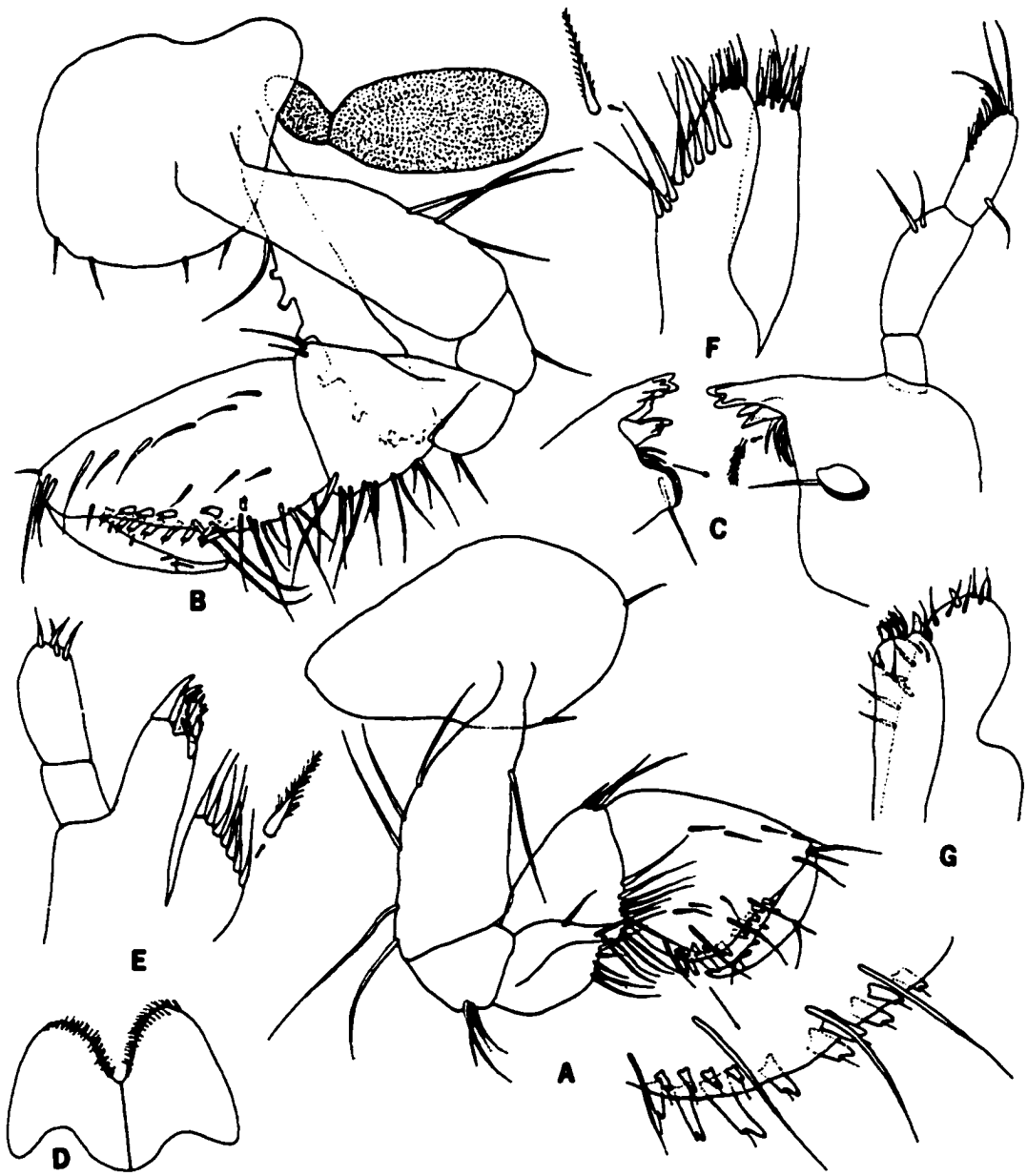

Fig. 60. *Stygobromus saltuaris*, new species, female paratype (4.7 mm), hyporheic area, Trail Creek, Lane County, Oregon: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).

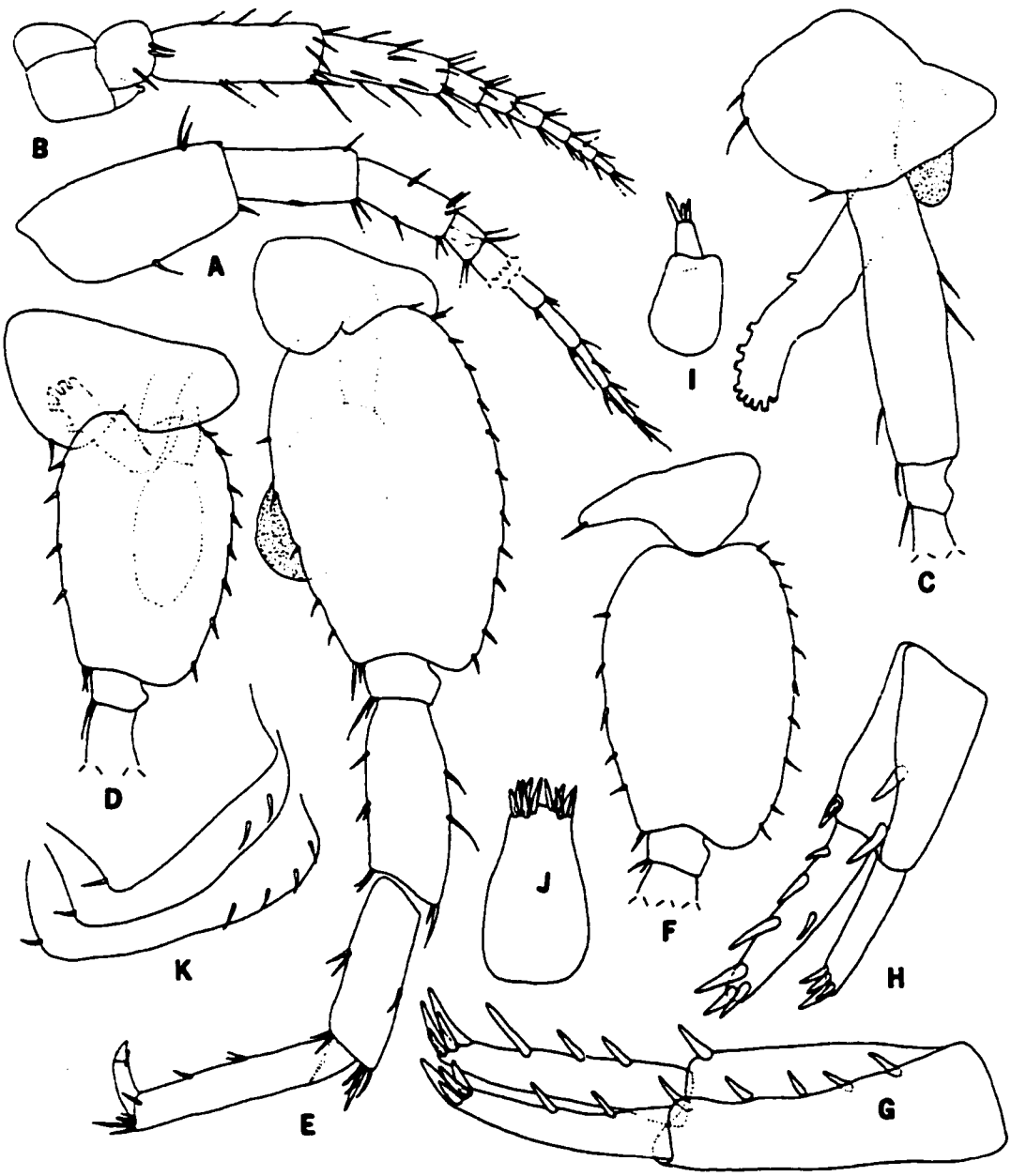

Fig. 61. ***Stygobromus saltuaris*****, new species, female paratype (4.7 mm), hyporheic area, Trail Creek, Lane County, Oregon: A, B, antennae 1, 2; C, pereopod 4 (in part); D, pereopod 5 (in part); E, pereopod 6; F, pereopod 7 (in part); G, H, I, uropods 1, 2, 3; J, telson.**

tiny median notch between spine clusters, bearing 10 relatively long spines.

Type locality. Hyporheic habitat in seep area near Trail Creek in the Williamette National Forest, Lane County, Oregon (Figs. 93, 96).

Distribution and ecology. This species is only known from its type-locality, the elevation of which is about 640 m (G. W. Courtney, pers. comm.). The larger female (5.0 mm) in the series of two has setose brood plates.

Etymology. The epithet *saltuaris* is from the Latin, meaning "forest," in reference to the location of the type-locality in the Williamette National Forest.

Stygobromus sheldoni Holsinger, 1974

Stygobromus sheldoni Holsinger, 1974: 37-40, figs. 22-23 [type-locality: bog spring (elevation 1,920 m) tributary to Sagehen Creek, Nevada Co., California].

Material examined. CALIFORNIA. Nevada Co.: outflow pipe from boxed spring, Sagehen Field Research Station, north of Truckee, 1 ♂, 1 ♀, C. B. Barr and W. D. Shepard, 24-26 Sept. 1999.

Diagnosis. A small to medium-sized groundwater species probably closely related to both *S. mackensiei* and *S. sierrensis*. It differs from the latter by smaller size at sexual maturity, fewer spine teeth on palms of propod of gnathopod 1 of both sexes, proportionately smaller gnathopodal propod 2 of male, proximally broader bases of pereopods 5-7; 2 apical spines on ramus of uropod 3. Largest ♀, 5.5 mm; largest ♂, 4.8 mm.

Distribution and ecology. This species is recorded from a series of springs situated at elevations between 1915 and 2340 m (above sea level) that feed Segehen Creek in Nevada Co., California (Figs. 93, 95 and also see Holsinger, 1974).

Remarks. In the recent (1999) sample by Barr and Shepard, both the male and female are at least 1.5 mm longer than any of the type specimens described by Holsinger (1974) and differ slightly from the previously reported material as follows. The larger female has 3, instead of 2, apical spines on the ramus of uropod 3; and 12, instead of 10, apical spines on the telson. The larger male has a few more spine teeth on the gnathopod propods and 2-4 more apical spines on the telson.

Stygobromus sierrensis Holsinger, 1974

Stygobromus sierrensis Holsinger, 1974: 35-37, figs. 20-21 [type-locality: an unnamed spring in Trosi Canyon, Sierra Co., California].

Diagnosis. A medium-sized groundwater species and distinguished by shallow coxal plates of gnathopod 2 and pereopods 3 and 4; 2 ventral spines each on pleonal plates; proportionately short ramus of uropods 3; and near absence of notch on telson. Largest ♀, 7.0 mm; largest ♂, 5.2 mm.

Distribution and ecology. This species is known only from its type-locality, an unnamed spring in Trosi Canyon, Sierra Co., California (Figs. 93, 95).

Stygobromus tahoensis Holsinger, 1974

Stygobromus tahoensis Holsinger, 1974: 40-44, figs. 24-25 [type-locality: Lake Tahoe, at about 61 m depth, between Skunk Harbor and Tahoe City, Placer Co., California].

Material examined. CALIFORNIA.: Lake Tahoe in Chara bed at 200 feet depth, 15 ♀, 3 ♀ paratypes, E. R. Byron, fall 1979.

Diagnosis. A medium-sized, deep-lake dwelling, stygomorphic species, apparently related to *S. sierrensis* and *S. sheldoni*, but distinguished from these 2 species by the diagnosis and description of Holsinger (1974). Largest ♀ 6.5 mm; largest ♂ 5.0 mm.

Distribution and ecology. This species is known only from Lake Tahoe (Figs. 93, 95), where a majority of specimens were collected at depths of 60-495 m (see Holsinger, 1974).

Stygobromus trinus, new species

(Figs. 62-64)

Material examined. CALIFORNIA. Trinity Co.: Hall City Cave, HOLOTYPE ♀ (USNM), 3 ♀ paratypes, D. C. Rudolph, B Martin and S. Winterath, 11 Apr. 1979.

Diagnosis. A medium-sized cavernicolous species, closely similar to *S. grahami* but distinguished as follows: maxilla 2 with fewer setae on inner plate; palms of gnathopods 1 and 2 straight; coxal plate of pereopod 3 broader than deep; pleonal plates 1 and 2 with more ventral spines; uropod 3 with tiny ramus; and telson apical margin almostwithout notch. Size of largest ♀ 7.0 mm, ♂ unknown.

Female. Antenna 1: 60 percent length of body, 80 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles: spine row with 6 plumose spines; palp segment 2 with 8 long setae on the inner side; palp segment 3 with 10-11 C setae, few D setae, 3 E setae, lacking A and B setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 9 apical, plumose setae; palp with 6 stiff setaeor slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spine, 2 naked setae apically, and 3 plumose setae on inner margin and apex; outer plate with 1 bladelike spine and 5 or 6 small serrate pines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and about 50 percent longer than posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 4 superior medial setae; 4-5 inferior medial setae, all singly inserted; dactyl nail short; coxa approximately 2 times deeper than broad, margin with 4 setae.

Gnathopod 2: propod subrectangular, longer than broad; palm concave medially and armed with 23 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2-3 shorter spine teeth on inside; posterior margin about 33 percent length of palm, with 2 sets of triply inserted setae; 8 doubly inserted superior medial setae; 4 inferior medial setae, singly inserted; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate about as broad as deep, margin with 5-6 setae.

Pereopod 4: coxal plate broader than deep, reaching about 40 percent length of basis, margin with 5 setae.

Pereopod 6, slightly longer than pereopod 7, about 60 percent length of body, 33 percent longer than pereopod 5.

Pereopods 5-7: bases as broad or slightly broader proximally; posterior margins nearly straight; distoposterior lobes distinct but not well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with variable spines; dactyls of pereopods 5-7 not elongate, that of pereopod 6 about 30 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates narrowing distally.

Pleonal plates: posterior margin of plates 2 and 3 slightly convex, with 1 seta each near distoposterior corner, that of 1 less convex, with 1 setule near distoposterior corners; distoposterior corner rounded and indistinct, ventral margin of plate 1 with 4 spines; ventral margin of plate 2 with 3 spines, that of plate 3 also with 4 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length

of peduncle, with 9 spines; outer ramus with 8 spines; peduncle with 8 spines.

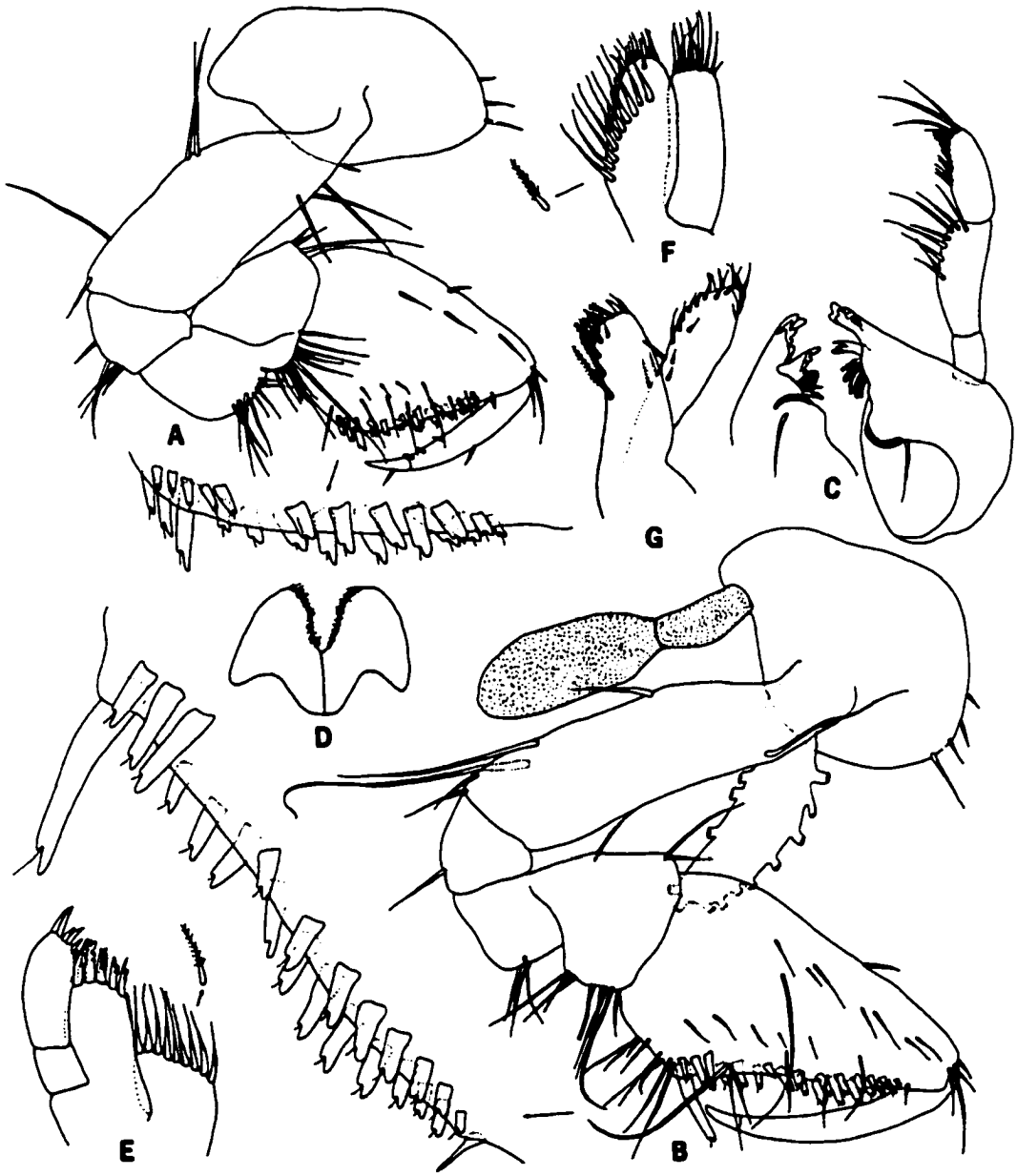

Fig. 62. ***Stygobromus trinus*****, new species, female paratype (7.0 mm), Hall City Cave, Trinity County, California: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

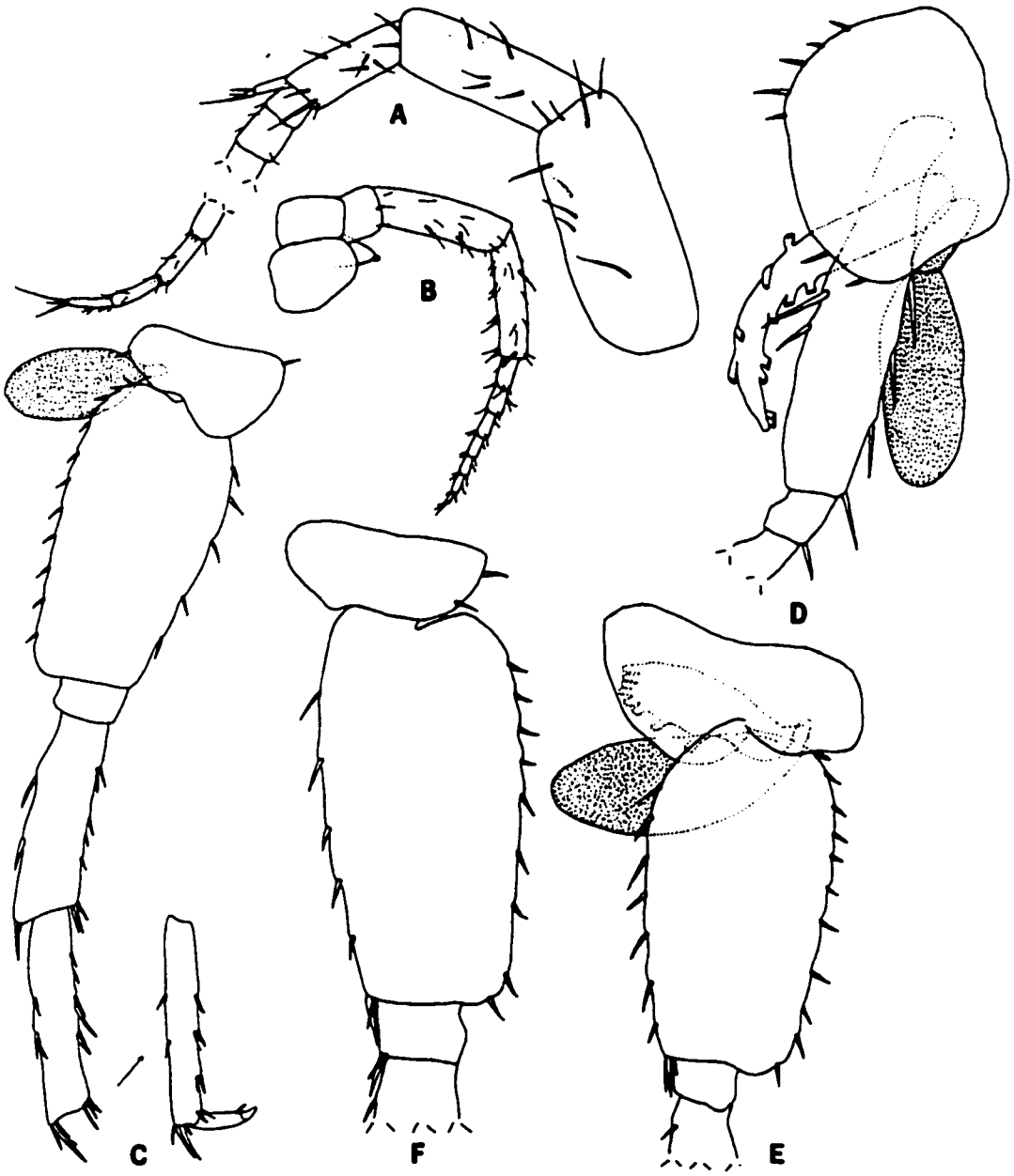

Fig. 63. ***Stygobromus trinus*****, new species, female paratype (7.0 mm), Hall City Cave, Trinity County, California: A, B, antennae 1, 2; C, pereopod 6; D, E, F, pereopods 4, 5, 6.**

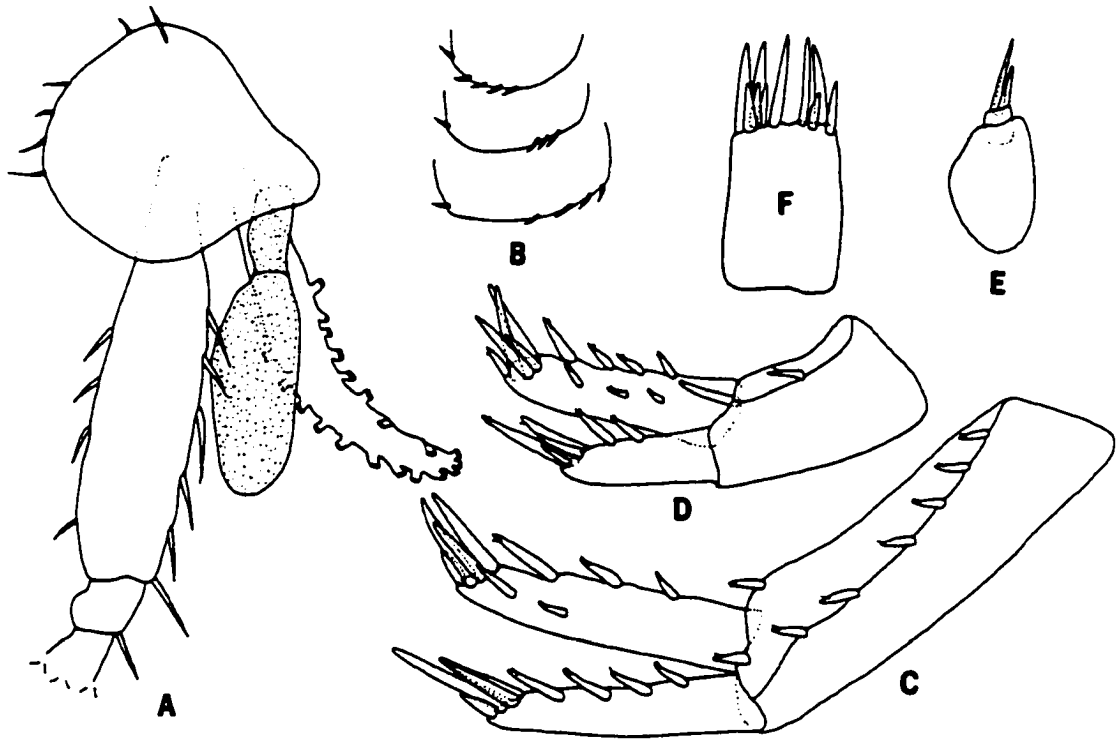

Fig. 64. ***Stygobromus trinus*****, new species, female paratype (7.0 mm), Hall City Cave, Trinity County, California: A, pereopod 3; B, pleonal plates; C, D, E, uropods 1, 2, 3; F, telson.**

Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 12 spines; outer ramus with 6 spines; peduncle with 2 spines.

Uropod 3: peduncle without setae; ramus approximately 30 percent length of peduncle, with 3-4 apical spines.

Telson longer than broad, subrectangular; apical margin typically entire but occasionally with tiny median notch between spine clusters, bearing 10-12 relatively long spines.

Type locality. Hall City Cave, approximately 54.4 km west of Redding, Trinity County, California.

Distribution and ecology. This species is known only from its type-locality, Hall City Cave, Trinity Co., California (Figs. 93, 95). It was collected from wood debris near the edge of a deep pool (D. C. Rudolph, pers. comm.).

Etymology. The epithet *trinus* is from the Latin, which is based on the geographic place name, Trinity County.

Stygobromus tritus Holsinger, 1974

Stygobromus tritus Holsinger, 1974: 8-11, figs. 2-3 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Material examined. MONTANA. Missoula Co.: shallow water wells (2.6-6.6 m depth) in Missoula, 14 ♀, 4 ♂, 1 juv., M. E. Ver Hey, May 1986.

Diagnosis. A rather small subterranean species distinguished by the diagnosis and description of Holsinger (1974). Largest ♀, 5.0 mm; largest ♂, 4.5 mm.

Distribution and ecology. This species is recorded from a well at Victor Crossing, Ravalli Co. Montana (see Holsinger, 1974) and wells in Missoula County (see above) (Figs. 93, 96). Females ranging in length from 4.5 to 5.0 mm have setose brood plates and are sexually mature.

Taxonomic remarks: Re-examination of male specimens revealed an apically serrate peduncular process on uropod 1, which was not described in the original description by Holsinger (1974).

Stygobromus urospinatus, new species

(Figs. 65-68)

Styogobromus sp. A.-- Ward and Holsinger, 1981: 64-67.

Material examined. COLORADO. Larimer Co.: Belluve Spring, HOLOTYPE ♀ (USNM), 13 ♀ paratypes, J. V. Ward, 15 Sept. 1977; 1 ♂, 16 ♀, J. V. Ward, 2 Apr. 1978; 3 ♂, 3 ♀, J. V. Ward, 29 Jan. 1978; Redstone spring no. 1, west of Horsetooth Reservoir, 1 ♂, J. V. Ward, 30 Oct 1976; spring at base of Spring Canyon Dam of Horsetooth Reservoir, 9 ♀, J. V. Ward, 28 Apr. 1975.

Diagnosis. A medium-sized groundwater species apprarentely related to *S. holsingeri* but differing as follows: palms of gnathopods 1 and 2 straight; coxal plates of pereopods 3 and 4 deeper than broad; pleonal plates 1-3 with fewer ventral spines but more setules on posterior margin; uropods 1-3 more heavily spinose; telson with numerous and longer spineson apical margin. Largest ♀, 7.0 mm; largest ♂, 6.0 mm.

Female. Antenna 1: 46 percent length of body, 8 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 8 segments.

Mandibles subequal: spine row with 8 plumose spines; palp segment 2 with about 12 long setae on inner margin, segment 3 bearing 1 long B seta, 2 C setae, approximately 14 D setae, and 5 E setae, lacking A setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 10 apical, plumose setae; palp with 13 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 11 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 1 naked seta apically and 2 plumose setae on inner margin; outer plate with setae on inner margin and 5 setae on or near apex.

Gnathopod 1: propod subequal in size to gnathopod 2; palm straight and nearly 2 times longer than posterior margin, armed with 26 spine teeth in double row; defining angle with 3 spine teeth on outside, 4 shorter ones on inside; posterior margin without setae; bearing single superior medial seta and lacking inferior medial setae; dactyl nail short; coax approximately 2 times broader than deep, margin with 3 setae.

Gnathopod 2: propod longer than broad; palm long and straight, armed with 29 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin relatively short, only approximately 33 percent length of palm, with 3 sets of setae, 2 mostly triply inserted; bearing 4 doubly inserted superior setae and 4 singly inserted inferior medial setae; coxa little broader than deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae.

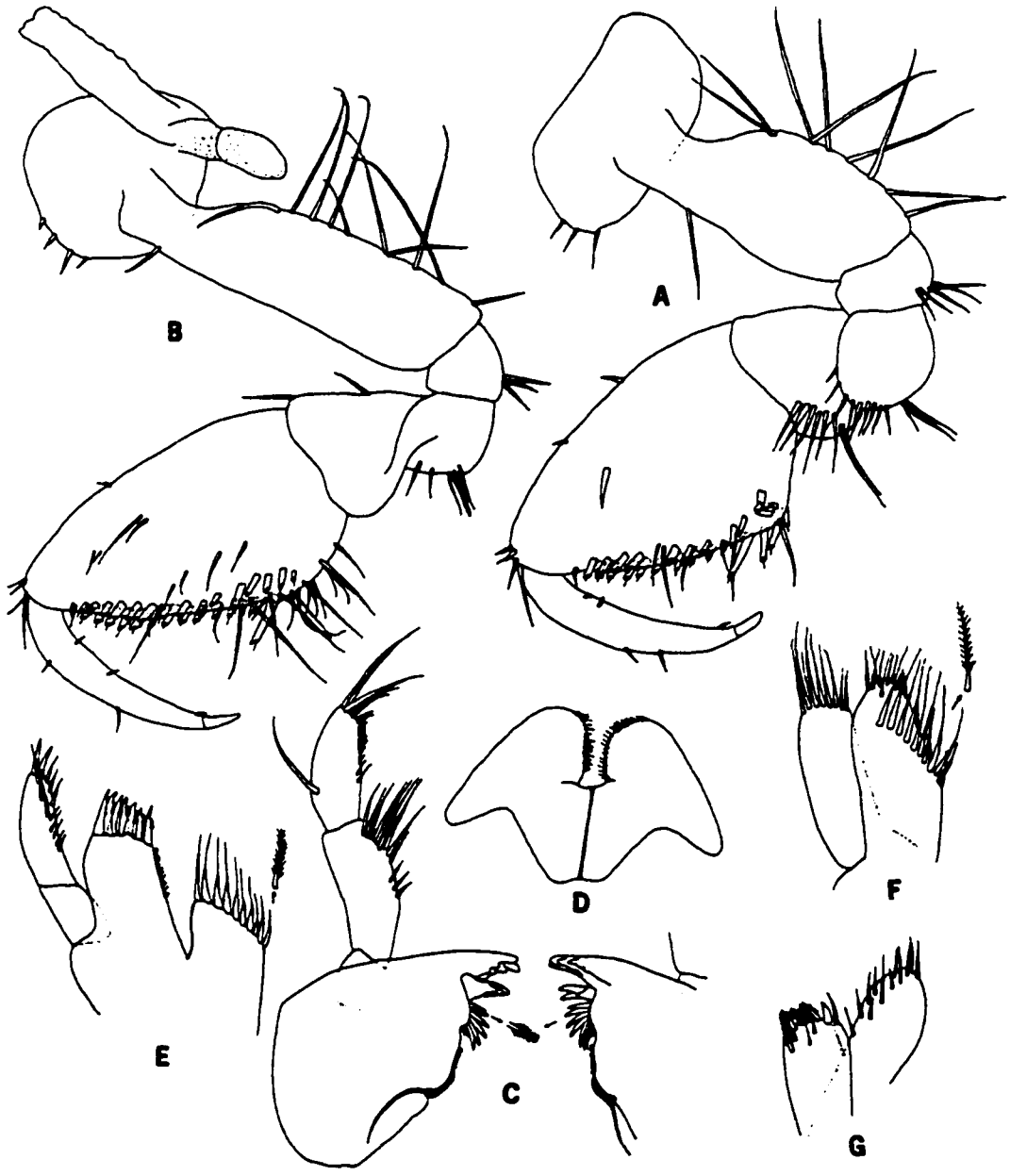

Fig. 65. ***Stygobromus urospinatus*****, new species, female paratype (7.0 mm), Belluve Spring, Larimer County, Colorado: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

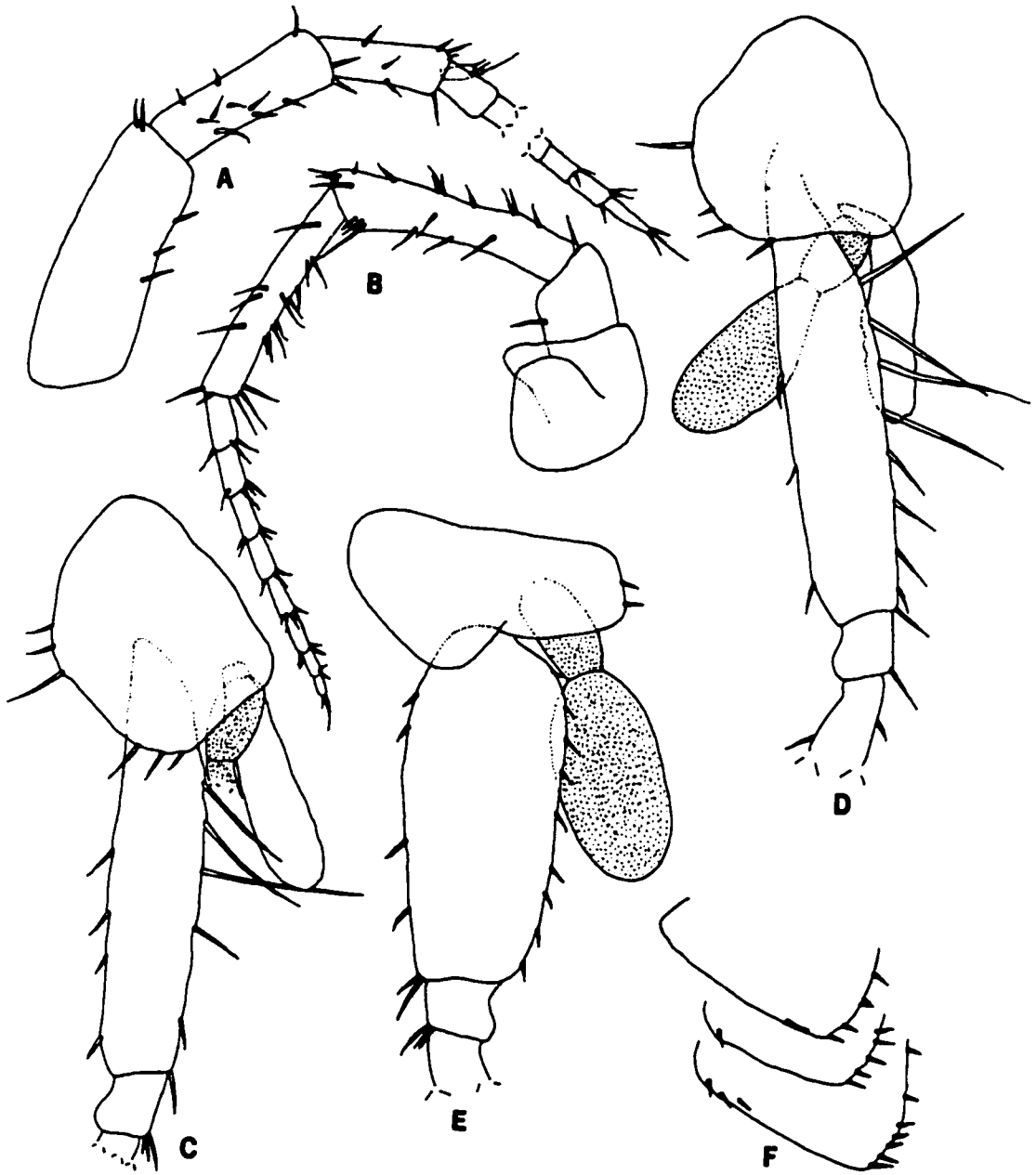

Fig. 66. ***Stygobromus urospinatus*** **, new species, female paratype (7.0 mm), Belluve Spring, Larimer County, Colorado: A, B, antennae 1, 2; C, D, E, pereopod 3, 4, 5; F, pleonal plates.**

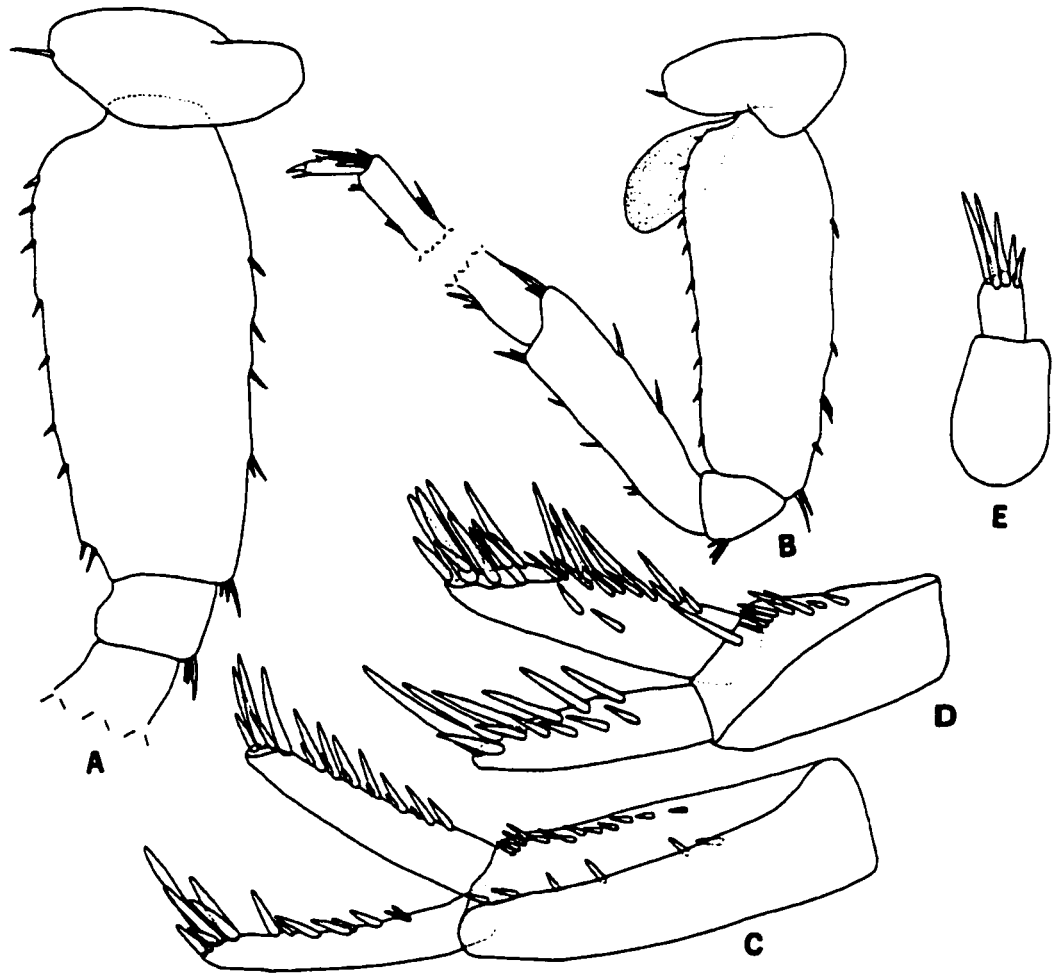

Fig. 67. ***Stygobromus urospinatus*****, new species, Female paratype (7.0 mm), Belluve Spring, Larimer County, Colorado: A, pereopod 7; B, pereopod 6; C, D, E, uropod 1, 2, 3.**

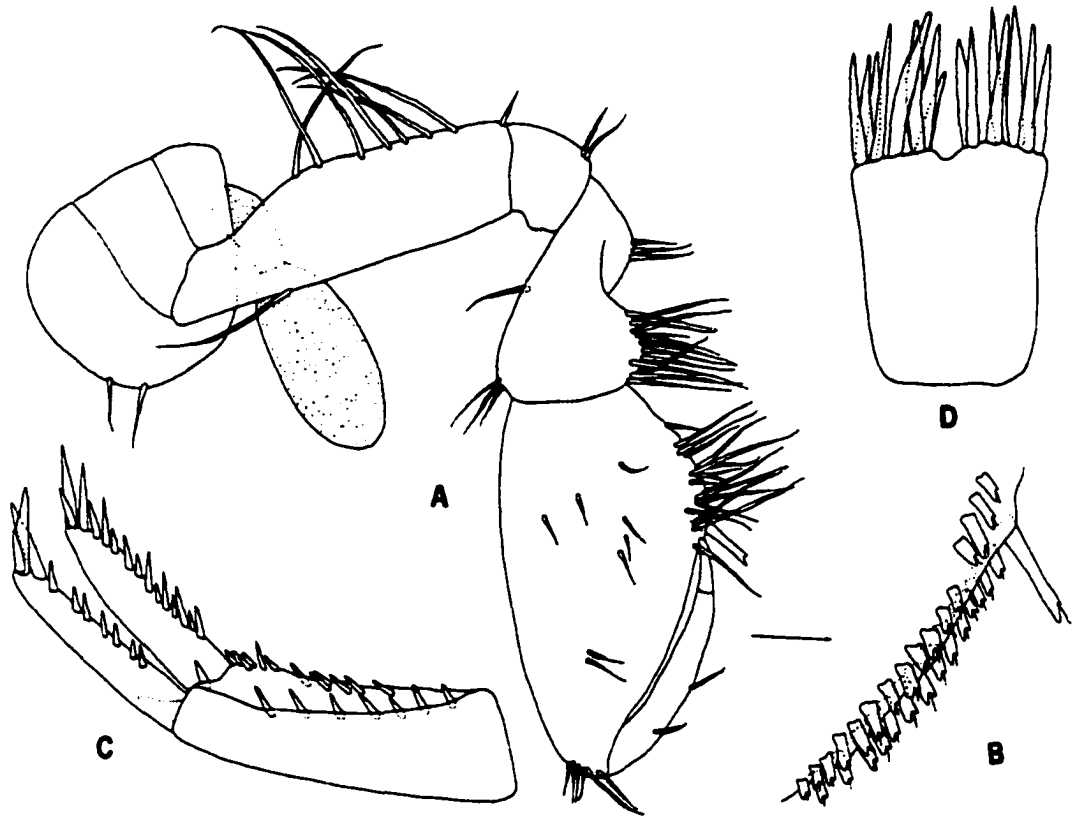

Fig. 68. ***Stygobromus urospinatus*****, new species, Male paratype (6.0 mm), Belluve Spring, Larimer County, Colorado: A, B, gnathopod 2, enlarged palm; C, uropod 1. Female paratype (7.0 mm), D, telson.**

Pereopod 4: coxal plate broader than deep, reaching approximately 25 percent length of basis, margin with 6 setae.

Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 33 percent longer than pereopod 5.

Pereopods 5-7: bases narrow, about as broad proximally as distally; posterior margins nearly straight; distoposterior lobes almost indistinct, not broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically about 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Pleonal plates: posterior margins weakly convex, with 7 setules on posterior margin of plate 3 and 5 setules on margins of plates 1 and 2; distoposterior corner indistinct; ventral margin of plates 1 and 2 bearing 1 spine, that of plate 3 bearing 3 spines.

Uronites free. Uropod 1: heavily spinose, especially inner ramus; inner ramus subequal in length to outer ramus, about 70 percent length of peduncle, with 18 long spines; outer ramus with 15 spines; peduncle with 19 long, strout spines.

Uropod 2: heavily spinose overall, inner ramus longer than outer ramus and peduncle, with 30 long, strout spines; outer ramus with 14 mostly long spines; peduncle with 10 spines.

Uropod 3: peduncle without setae; ramus approximately 50 percent length of peduncle, with 5 apical spines (3 relatively long).

Telson longer than broad, little broader distally, apical margin with tiny median notch between spine clusters, bearing 16 relatively long, strout spines.

Male. Differing from female as follows: Gnathopod propods slightly broader; palm of propod 2 slightly longer in comparison with posterior margin and bearing more sets of setae. Uropod 1: peduncular process 25 percent length of outer ramus, tapered to a point distally, inner ramus with 15-17 long spines; peduncle with 20 spines. Uropod 2: inner ramus with 28-35 long spines, peduncle with 10-12 spines. Telson with 16-19 apical spines.

Type locality. Bellvue Spring, approximately 1.6 km southeast of Bellvue, Larimer County, Colorado.

Distribution and ecology. This species is recorded from Bellvue Spring, the type-locality, and two other springs near Horsetooth Reservoir, west of Ft. Collins (Figs. 93, 97). It was collected together with 1 specimen of *S. holsingeri* on 30 Oct. 1976 from Redstone Spring no. 1. All sites are in Larimer County.

Etymology. The epithet *urospinatus* is from the Latin, meaning "spines on uropods," in reference to the presence of many long, stout spines on the uropods of this species.

Stygobromus utahensis, new species

(Figs. 69-70)

Material examined. UTAH. Duchesne Co.: Pole Creek Cave, HOLOTYPE ♀ (USNM), 70 ♀, 13 ♂, paratypes, 1 juv., S. J. Peck, 5 Aug. 1979.

Diagnosis. A medium-sized cavernicolous species apparently closely related to *S. azisonensis* in gnathopods and uropod 1-2, but distinguished from those species as follows: coxal plates 3-4 broader than deep; bases of pereopods 6-7 with fewer spines on distoposterior margin; pleonal plates 1-3 lacking spines on ventral margin and fewer setules near distoposterior corner; peduncular process of uropod 1 of male sharply pointed apically; telson with only slight notch. Largest ♀, 5.5 mm, largest ♂, 4.0 mm.

Female. Antenna 1: 55 percent length of body, 50 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 8-9 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 bearing 1 B seta, 9 D setae, and 3 setae E, lacking both A and C setae.

Inner lobes of lower lip vestigial.

Maxilla 1: inner plate with 8 apical, plumose setae; palp with 4 stiff setae subapically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine, 1 naked seta apically, and 3 setae on inner margin; outer plate with setae on inner margin and 4-5 on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly concave, 2 times longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 4 doubly inserted superior medial setae; 3 singly inserted inferior medial setae; dactyl nail rather long and sharply pointed; coxa about 2 times broader than deep, margin with 2 setae.

Gnathopod 2: propod longer than broad; palm straight or slightly convex, strongly oblique, armed with 13 spine teeth in double row; defining angle with 1 spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 30 percent length of palm, with 2 sets of doubly inserted setae; 7 superior medial setae, most doubly inserted; 5 inferior medial setae, most singly inserted; coxa about as broad as deep, margin with 3 setae.

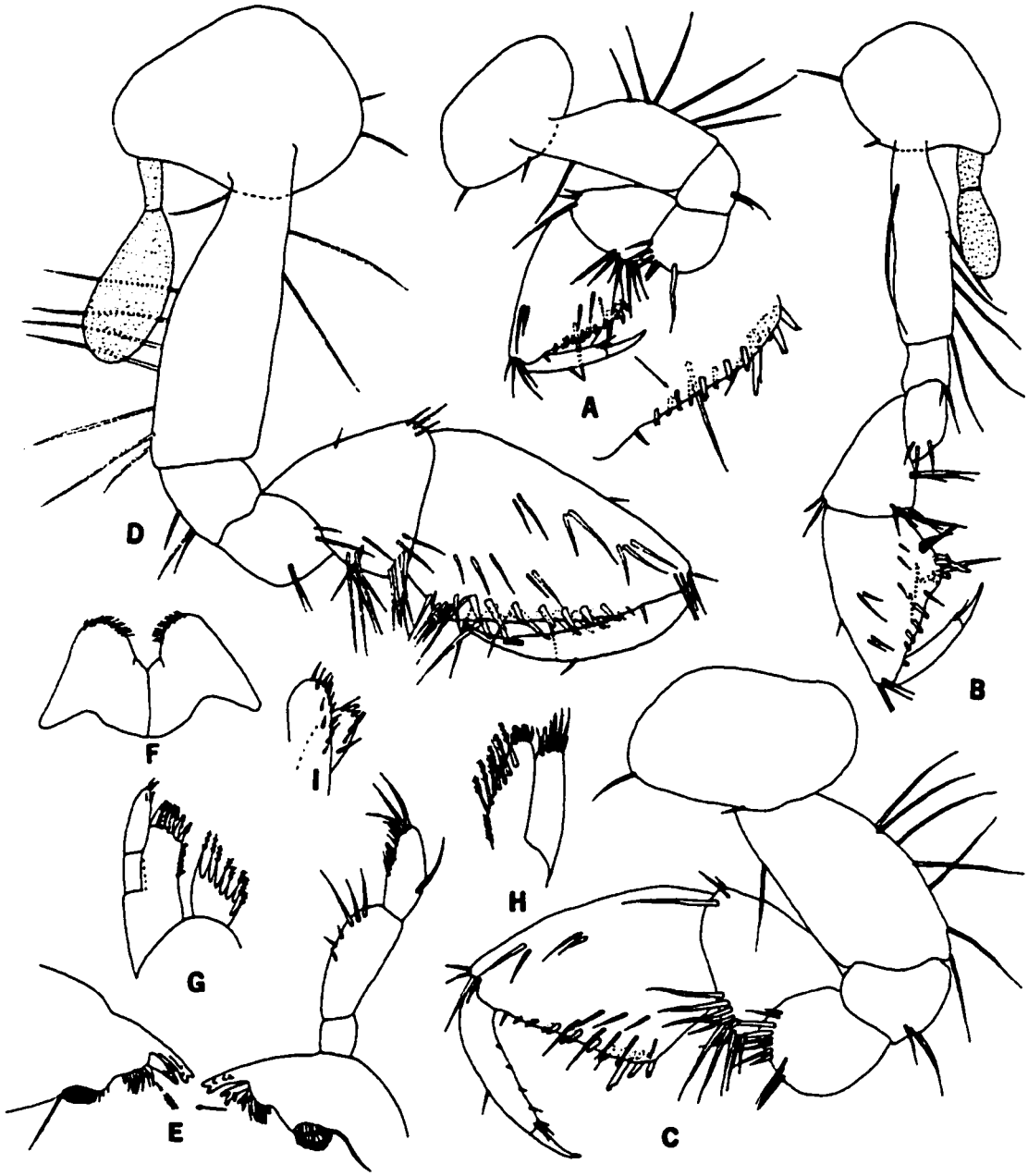

Fig. 69. ***Stygobromus utahensis*****, new species, Male paratype (4.0 mm), Pole Creek Cave, Duchesne County, Utah: A, B, gnathopods 1, 2 (palm enlarged); Female paratype (5.5 mm), C, D, gnathopods 1, 2; E, right mandible and dentate part of left mandible; F, lower lip; G, H, maxilla 1, 2 (apical setae enlarged); I, inner and outer plates of maxilliped (enlarged).**

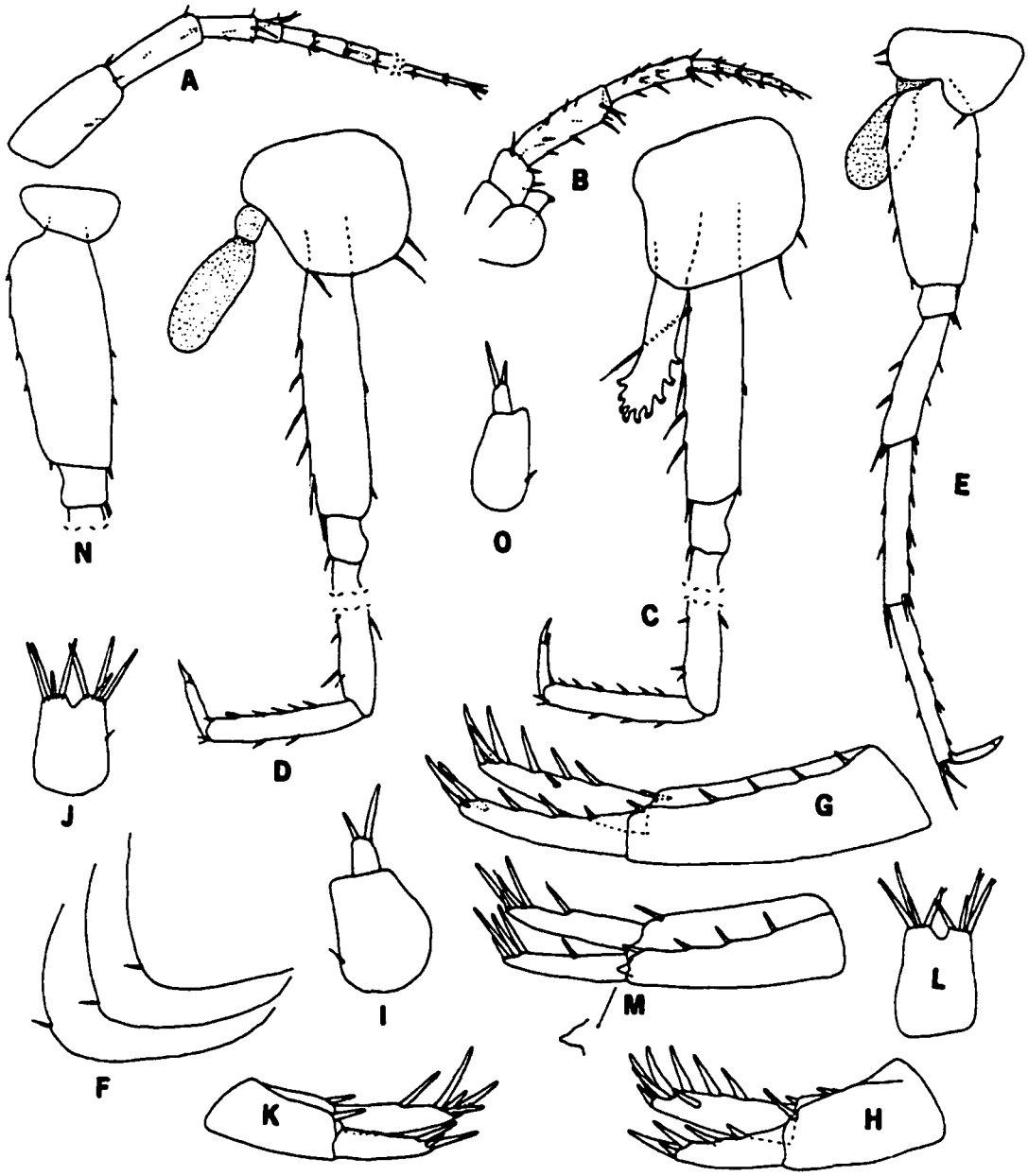

Fig. 70. ***Stygobromus utahensis*****, new species, female paratype (5.5 mm), Pole Creek Cave, Duchesne County, Utah: A, B, antennae 1, 2; C, D, pereopods 4, 3; E, pereopod 6; F, pleonal plates; G, H, I, uropods 1, 2, 3; J, telson; Male paratype (4.0 mm), K, uropod 2; L, telson; M, uropod 1; N, pereopod 7 (in part); O, uropod 3.**

Pereopod 3: coxal plate slightly broader than deep, margin with 3 setae.

Pereopod 4: coxal plate broader than deep, reaching about 30 percent length of basis, margin with 2 setae.

Pereopod 6 little longer than pereopod 7, about 58 percent length of body, 20 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than the distally; posterior margins convex; distoposterior lobes poorly developed and almost indistinct; anterior and posterior margins with 24 spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 about 35 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates little expanded distally.

Pleonal plates: posterior margins of plate 1 - 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plates 1, 2 and 3 lacking spines.

Uronites free. Uropod 1: inner ramus subequal to outer ramus, about 60 percent length of peduncle, with 8 spines; outer ramus with 8 spines; peduncle with 6 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 8 spines; outer ramus with 5 spines; peduncle with 3 spines.

Uropod 3: peduncle not bearing small setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with small median notch between spine clusters, bearing 8 relatively long spines.

Male. Differing from female as follows: Gnathopod propods smaller and shorter, palm of propod 2 longer in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process 10 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 6 spines. Uropod 2: inner ramus with 5 spines, peduncle with 2 spines. Telson with 8 apical spines.

Type locality. Pole Creek Cave, approximately 37 km NNW of Roosevelt, Duchesne County, Utah. The elevation of the cave is approximately 2128 m.

Distribution and ecology. This species is only known from its type-locality (Figs. 93, 95).

Etymology. The species is named for the state of Utah.

Stygobromus wahkeenensis, new species

(Figs. 71-73)

Stygobromus sp.-- Bousfield and Holsinger, 1989: 968.

Material examined. OREGON. Multnomah Co.: railroad bank spring, Wakkeena Creek in Columbia River gorge, HOLOTYPE ♀ (on slides) (USNM), R. W. Wisseman, 17 Mar. 1989; seep or hyporheic habitat associated with Wahkeena Creek, ca. 3.1 km SSW of Bonneville, 3 ♀ paratypes, 2 juvs. (CMN), G. W. Courtney, 19 Apr. 1985, 1 ♂, 1 ♀ (CMN), 6 Mar. 1986.

Diagnosis. A small groundwater species distinguished as follows: palm of gnathopod 2 straight or slightly concave medially and with few teeth on palmar margin; maxilliped with bladelike spine on outer plate; bases of pereopods 5-7 rather narrow; pleonal plates 2-3 with 3 ventral spines each; uropod 1-2 moderately spinose; telson longer than broad. Largest ♀, 4.0 mm, largest ♂, 3.0 mm.

Female. Antenna 1: 50 percent length of body, 46 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4 plumose spines; palp segment 2 with row of 4 long setae on inner margin; palp segment 3 with 6 D setae and 4 E setae, lacking both A, B and C setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 4 plumose spines, and 3 naked setae apically, and 1 plumose spine on inner margin; outer plate with setae on inner margin and apex, and small bladelike spine on or near apex.

Gnathopod 1: propod 1 subequal in size to that of gnathopod 2 but of different shape; palm straight or slightly concave and approximately 65 percent longer than posterior margin, armed with 16 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4 superior medial setae; 4-5 inferior medial setae; dactyl nail short; coxa about 2 times broader than deep, margin with 1 seta.

Gnathopod 2: propod longer than broad; palm straight or slightly concave medially and armed with 14 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin 30 percent length of palm, with 2 sets of doubly inserted setae; 6-7 doubly inserted superior medial setae; 2 inferior medial setae; coxa broader than deep, margin

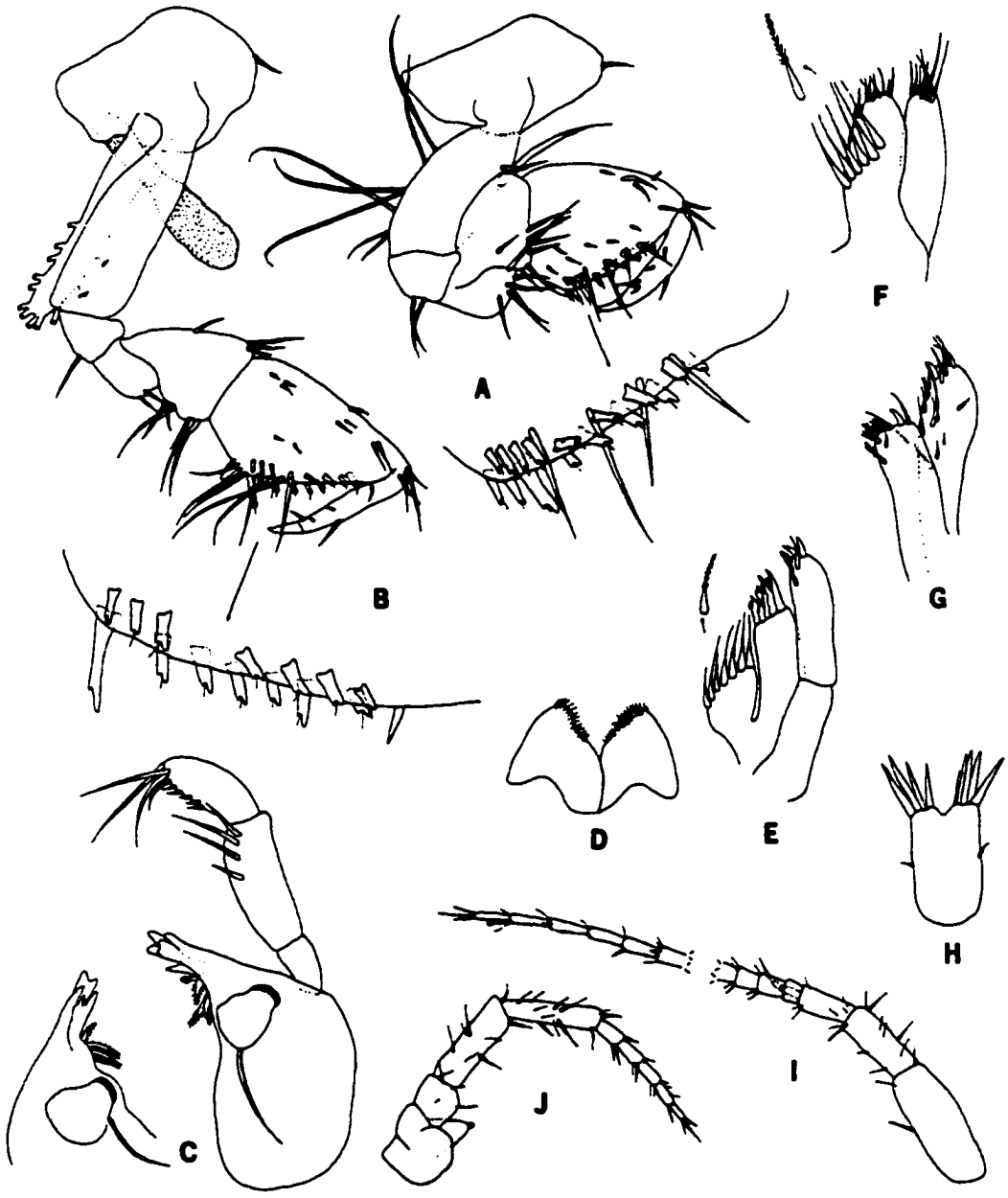

Fig. 71. ***Stygobromus wahkeenensis*****, new species, female holotype (3.8 mm), railroad back spring, Multnomah County, Oregon: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged); H, telson; I, J, antennae 1, 2.**

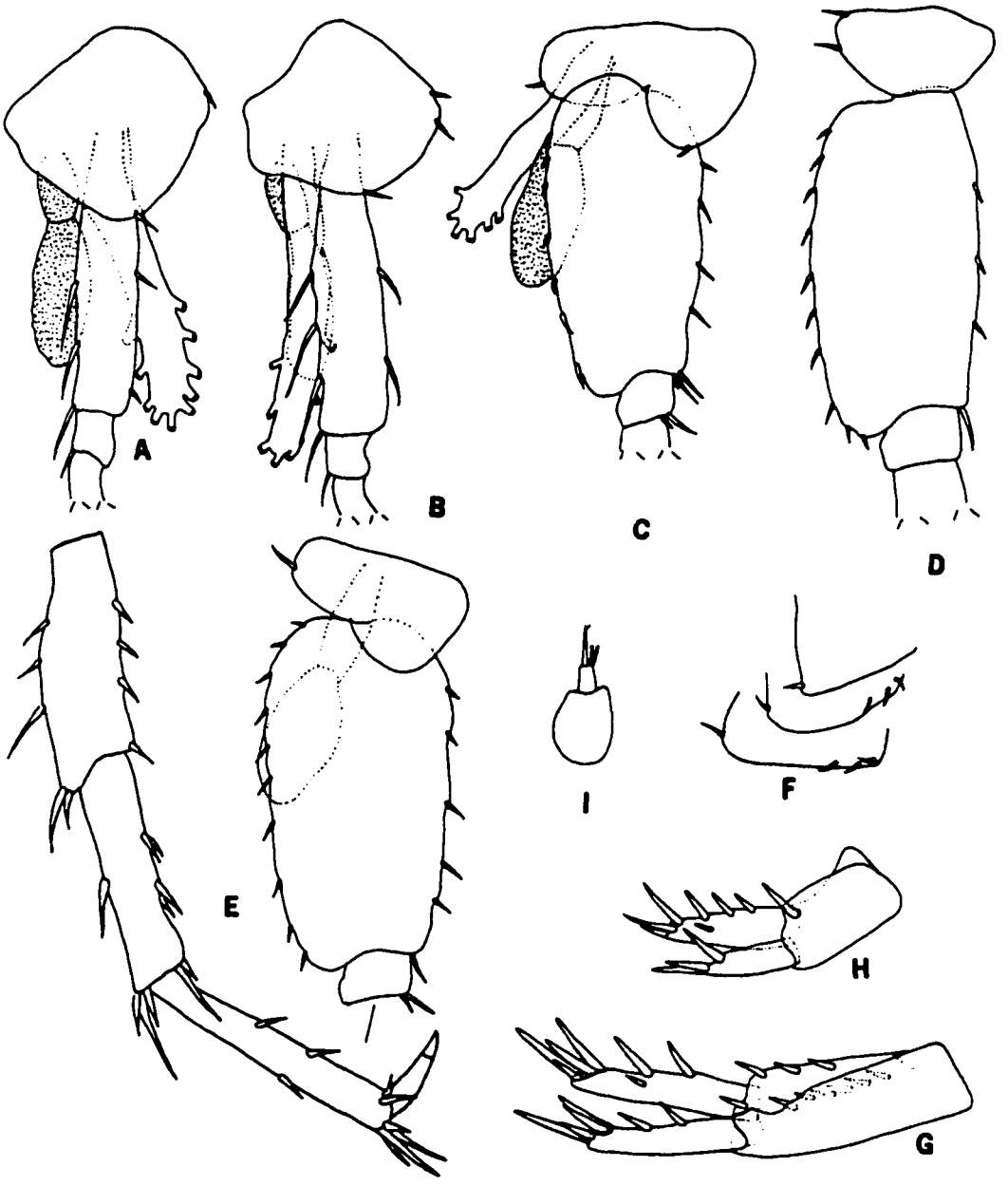

Fig. 72. ***Stygobromus wahkeenensis*****, new species, female holotype (3.8 mm), railroad back spring, Multnomah County, Oregon: A, B, C, pereopods 3, 4, 5 (in part); D, E, pereopods 6, 7 (in part); F, pleonal plates; G, H, I, uropods 1, 2, 3.**

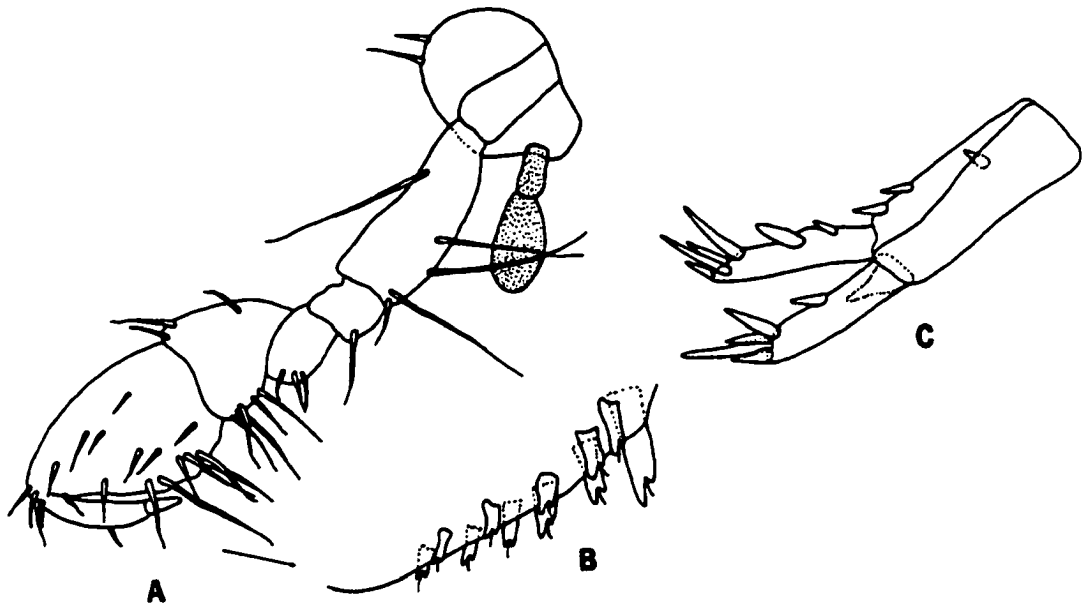

Fig. 73. ***Stygobromus wahkeenensis*****, new species, Male paratype (3.0 mm), railroad back spring, Multnomah County, Oregon: A, B, gnathopod 2, enlarged palm; C, uropod 1.**

with 1 seta.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae.

Pereopod 4: coxal plate little broader than deep, reaching about 30 percent length of basis, margin with 2 setae.

Pereopod 6 little longer than pereopod 7, about 60 percent length of body, 40 percent longer than pereopod 5.

Pereopods 5-7: bases about as broad proximally as distally; posterior margins weakly convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 35 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

Brood plates sublinear or slightly narrowing distally.

Pleonal plates: posterior margins of plate 1 - 3 straight or slightly convex, with 1 setule each near distoposterior corner; distoposterior corners rounded and that of plate 3 indistinct; ventral margin of plates 2 and 3 each with 3 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 45 percent length of peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 11 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 7 spines; outer ramus with 3 spines; peduncle with 1 spine.

Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 45 percent length of peduncle, with 3 apical spines.

Telson subractangular, longer than broad, apex with tiny median notch between spine clusters, bearing 9-10 relatively long spines.

Male. Differing from female as follows: Gnathopod propods broader, palm of propod 2 shorter in relation to posterior margin, with fewer teeth on palmar margin. Uropod 1: peduncular process 30 percent length of outer ramus, narrowing distally, upper margin minutely serrate; inner ramus with 6 spines; peduncle with 3 spines. Uropod 2: inner ramus with 6 spines, peduncle with 2 spines. Telson with 10-12 apical spines.

Type locality. Railroad bank springs, Wahkeena Creek, in Columbia River gorge, (elevation 183 m above sea level), Multnomah County, Oregon.

Distribution and ecology. This species is recorded from the type-locality spring and a nearby seep and/or hyporheic zone associated with Wahkeena Creek in Multnomah Co., Oregon

(Figs. 93, 96). The collection of March 1986 and 1989 also contained 18 and 9 specimens of *Stygonyx courtneyi* Bousfield and Holisnger (see Bousfield and Holsinger, 1989).

Etymology. The epithet *wahkeenensis* is in reference to the association of this species with Wahkeena Creek.

Stygobromus wengerorum Holsinger, 1974

Stygobromus wengerorum Holsinger, 1974: 29-32, figs. 16-17 [type-locality: Bower Cave, Mariposa Co., California].

Material examined. CALIFORNIA. Mariposa Co.: Centipede Cave, 1 ♂, 6 ♀, S. J. Shimek, 30 July 1975.

Diagnosis. A relatively large cavernicolous species, closely similar to but differing from other cavernicolous species of the Mother Lode region by proportionately larger gnathopodal propods with more spine teeth on palms and more spines on ventral margins of pleonal plates. Largest ♀, 10.0 mm; largest (and only known) ♂ 5.5 mm.

Distribution and ecology. This species is only known from two caves in Mariposa Co., California (Figs. 93, 95).

Taxonomic Remarks: The peduncular process present of the male is small and triangular in shape. Male otherwise like female.

Other Species

The following nine species from western North America have not been assigned to the *hubbsi* group and are treated separately in this section. They are distinguished from the *hubbsi* group species by possessing sternal gills (or processes).

Stygobromus canadensis Holsinger, 1980

Stygobromus canadensis Holsinger, 1980: 290-297, figs. 1 [type-locality: Castleguard Cave, Alberta, Canada]. -- Holsinger, 1981: 93 - 95. -- Holsinger et al., 1983: 546 - 547.

Diagnosis. A small to medium-sized subterranean species, distinguished from all other species of *Stygobromus* by presence of paired sternal gills on pereonites 2-5, also distinguished by having few segments of pleopod rami. Largest ♀, 5.0 mm; largest ♂, 5.5 mm.

Distribution and ecology. To date this species is known only from a stream in its type-locality, Castleguard Cave (Figs. 93, 96). This is a large alpine-type cave situated partly beneath a glacier and located about 90 km south of Cadomin in the Banff National Park, Alberta, Canada (see Holsinger, 1980; Holsinger et al., 1983).

Stygobromus curroae, new species

(Figs. 74-76)

Material examined. NEW MEXICO. Taos Co.: groundwater discharge into Gallina Creek, HOLOTYPE ♀ (USNM), 2 ♀ paratypes, J. Curro, 23 Nov. 1994 and 1 ♂, 5 July 1994.

Diagnosis. A relatively small goundwater species, with some resemblance to *S. holsingeri* and *S. arizonensis* but easily distinguished as follows: maxillae 1 and 2 with fewer setae on inner plates; palm of propod of gnathopod 1 with more spine teeth; coxal plates 3 and 4 with more setae; relative long distally expanded telson, with 18- 20 apical spines and rather deep notch; uropods 1-2 with more long and thick spines on rami; and tiny, simple, paried lateral sternal gills on pereonites 6 and 7. Largest ♀, 4.8 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 55 percent length of body, 40 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 6 plumose spines; palpsegment 2 with row of 6 setae on inner margin; palp segment 2 with 6 long setae in inner margin; palp segment 3 bearing 1 B seta, 5 C setae, 9 D setae, and 3 E setae, lacking A setae.

Inner lobes of lower lip absent.

Maxilla 1: inner plate with 6 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 3 bladelike spines, 2 plumose spines, 1 naked seta apically, and 1 plumose spine on inner margin; outer plate with setae on inner margin, and 1 lightly plumose seta and 1 bladelike spine on or near apex.

Gnathopod 1: propod little smaller than that of gnathopod 2; palm straight or slightly convex, approximately 2 times longer than posterior margin, armed with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; posterior margin without setae; 1 superior medial setae; 2-3 inferior medial setae; dactyl nail relatively short; coxa little broader than deep, margin with 5 setae.

Gnathopod 2: propod deeper than broad; palm slightly convex and armed with 15-16 spine

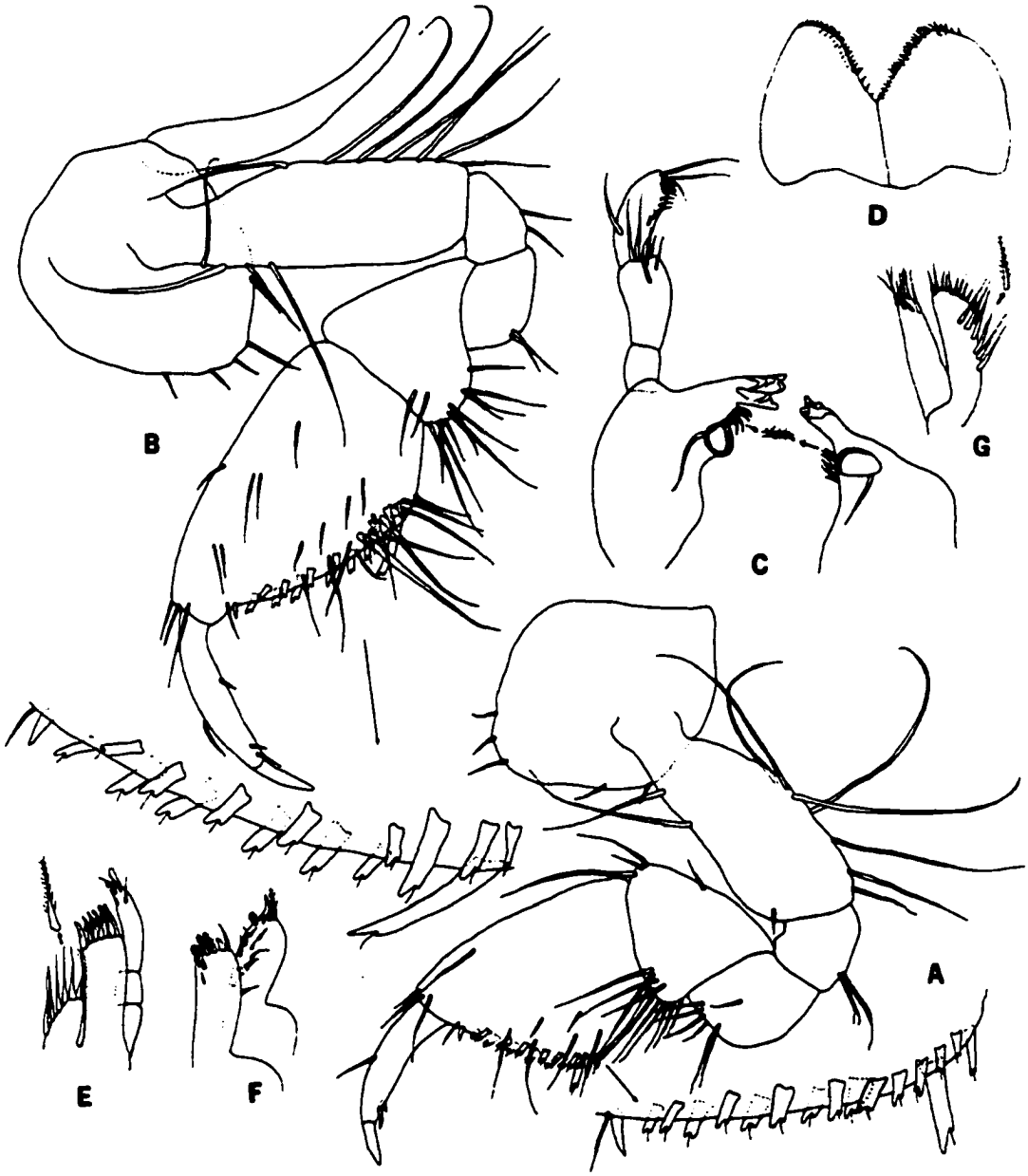

Fig. 74. ***Stygobromus curroae*****, new species, female paratype (4.4 mm), Gallina Creek, Taos County, New Mexico: A, B, gnathopods 1, 2 (palms enlarged); C, left mandible and dentate part of right mandible; D, lower lip; E, F maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

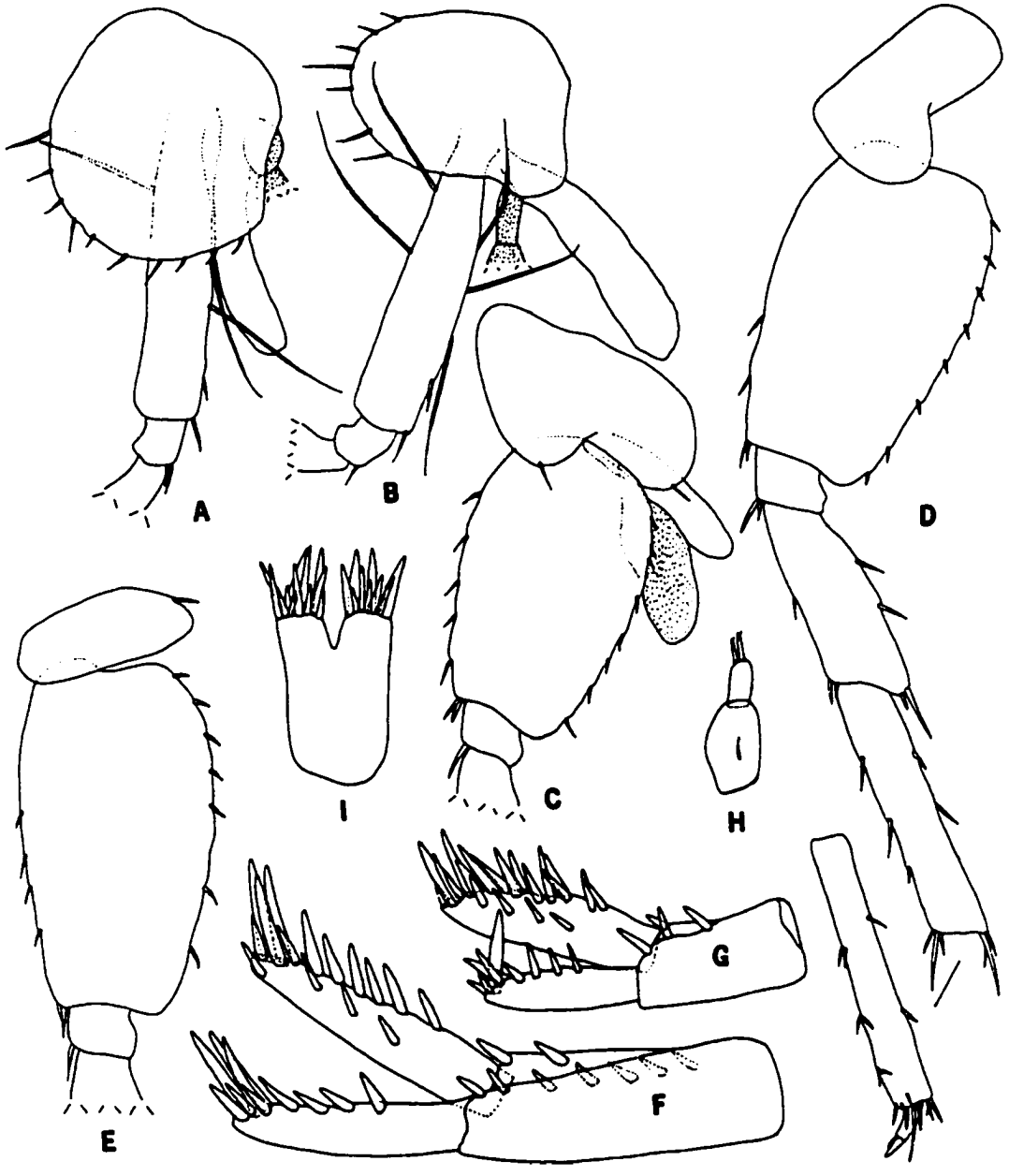

Fig. 75. ***Stygobromus curroae*****, new species, female paratype (4.4 mm), Gallina Creek, Taos County, New Mexico: A, B, pereopods 4, 3; C, D, E, pereopods 5, 6, 7; F, G, H, uropods 1, 2, 3; I, telson.**

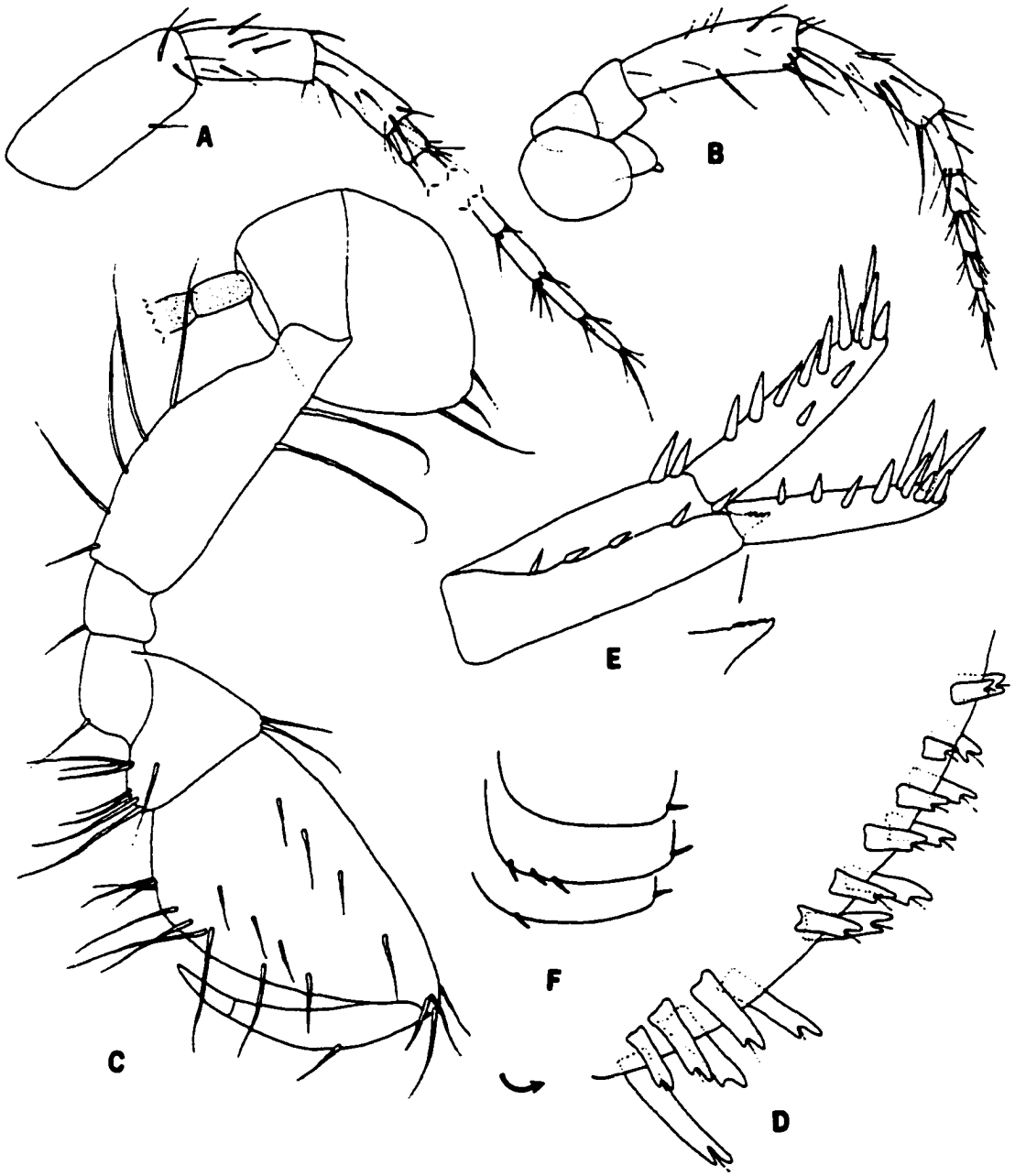

Fig. 76. ***Stygobromus curroae***, **new species, female paratype (4.4 mm), Gallina Creek, Taos County, New Mexico: A, B, antennae 1, 2; F, pleonal plates. Male paratype (4.5 mm), C, D, gnathopod 2, enlarged palm; E, uropod 1.**

teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 or 2 setae; 4 - 5 doubly inserted superior medial setae; 4 inferior medial setae; coxa little broader than deep, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 7 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 50 percent length of basis, broadly convex margin with 10 setae.

Pereopod 6 little longer than pereopod 7, about 77 percent length of body, 42 percent longer than pereopod 5.

Pereopods 5-7: bases broader proximally than distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and short, that of pereopod 6 approximately 25 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from pereopod 7.

Brood plates little expanded distally, but not setose in material examined.

Pleonal plates: posterior margin of plates, 1 - 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded, indistinct; ventral margin of plate 2 with 3 spines, that of plate 3 with 1 spines.

Uronites free. Uropod 1: inner ramus spinose, little longer than outer ramus, about 95 percent length of peduncle, with 15 mostly robust spines; outer ramus with 10 spines; peduncle with 9 spines.

Uropod 2: inner ramus longer than outer ramus, heavily spinose, longer than peduncle, with approximately 20 spines; outer ramus with 9 spines, 1 very large; peduncle with 4 spines.

Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 55 percent length of peduncle, with 2 apical spines.

Telson 25 - 30 percent longer than broad, gently expanded distally; apical margin typically with relatively deep "V" shaped median notch between spine clusters, bearing 19-20 relatively long spines.

Male. Differing from female as follows: Gnathopod propods slightly broader, palm of propod 2 shorter in comparison with posterior margin, with more teeth on palmar margin. Uropod 1: peduncular process sharply pointed distally, with lightly serrate upper margin, approximately 20 percent length of outer ramus; inner ramus with 14-15 spines; peduncle with 7 spines. Uropod 2: inner ramus with approximately 22-25 spines, peduncle with 4-5 spines. Telson with 18-21 apical

spines.

Type locality. Hyporheic groundwater, approximately 30 cm beneath Gallina Creek in the Sangre de Cristo Mountains near Taos, Taos Co., New Mexico (Figs. 94, 97).

Distribution and ecology. This species is only known from its type locality, where it was sampled from the hyporheic zone with a PVC pipe and pump from a depth of 30 cm (J. Curro, pers. comm.).

Etymology. This species is named in honor of its collector, Julia Curro.

Stygobromus glacialis, new species

(Figs. 77-78)

Material examined. MONTANA. Flathead Co.: Algal Cave, 2 ♀, J. Chester, 25 Aug. 1977; 4 ♀, P. Hendricks, 27 Sept. 1999; Logan Creek springhead, Logan Poss, 100(+) speciemens, (female, male, juv.), (MTEC), J. Giersch, 20 Aug. 2000; stream in an unnamed cave on Trail Creek in Flathead National Forest, ca. 12.8 km S of Canadian border, 1 ♀, J. A. Stanford, 25 Nov. 1980; Glacier Co.: Zoo Cave, HOLOTYPE ♀ (USNM), 1 ♀ paratype, J. Chester, 27 Aug. 1977;.

Diagnosis. A relatively small to medium-sized cavernicolous species, distinguished from all other species of *Stygobromus* by the possession of 3 pairs of lateral sternal on pereonites 5, 6 and 7; and further differing as follows: posterior margin of gnathopod 1 longer proportionally; coxae 1and 2 with fewer setae on margin; bases of pereopods 5-7 slender; lacking distinct distoposterior lobe on pereopod 6 or poorly developed; coxal plates 3-4 with fewer setae on margins; pleonal plates 1-3 with more spines on posterior margin; uropods 1and 2 with fewer spines on rami and peduncle; uropod 3 with proportionately longer peduncle; telson longer, with shorter apical spines and with notch on apical margin. Largest ♀, 7.0 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 40 percent length of body, 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 9 long setae on inner margin; palp segment 3 bearing 2 B setae, 9 D setae, and 4 setae E, lacking both A and C setae.

Inner lobes of lower lip vestigial or absent.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 8 stiff setae apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 5 plumose spines, 2 nakedsetae apically, and 3 plumose spines on inner margin; outer plate with setae on inner margin and 3 lightly plumose setae

on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm slightly convex medially and almost 2 times longer than posterior margin, armed with 18 spine teeth in double row; defining angle with 2 spine teeth on outside, 1 shorter one on inside; posterior margin lacking setae; 4 doubly inserted superior medial setae; 5 inferior medial setae; dactyl nail long and slender; coxa approximately 2 times broader than deep, margin with 2 setae.

Gnathopod 2: propod longer and broader than first peropod, longer than broad; palm straight or little convex medially, armed with 20 spine teeth in double row; defining angle with 1 spinetooth on outside, 3 shorter spine teeth on inside; posterior margin 33 percent length of palm, with 2 sets of doubly inserted setae; 7 - 8 superior medial setae doubly and triply inserted, about 5 singly inserted inferior medial setae; coxa broader than deep, margin with 3 setae.

Pereopod 3: coxal plate deeper than broad, margin with 1 setae.

Pereopod 4: coxal plate relatively broad and about as broad as deep, reaching about 45 percent length of basis, margin with 7 setae.

Pereopod 6 little longer than pereopod 7, about 50 percent length of body, 25 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than distally; posterior margins slightly convex; distoposterior lobes poorly developed and indistinct; anterior and posterior margins with 2-4 spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 30 percent length of corresponding propod.

Coxal gills on pereopods 2 - 6, absent from 7.

Three pairs of long, slender and simple lateral sternal gills present on pereonites 5 - 7, longest gills present on 6 and 7, all other sternal gills absent.

Brood plates rather narrow, not setose on specimen illustrated.

Pleonal plates: posterior margins of plates 1 - 3 convex, each with 2 or 3 setules; distoposterior corners rounded and indistinct; ventral margins of plates 1-3 lacking spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 7 spines; outer ramus with 7 spines; peduncle with 6 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 5 spines; outer ramus with 7 spines; peduncle with 3 spines.

Uropod 3: peduncle usually bearing 1-2 small setae; ramus approximately 20 percent length of peduncle, with 3 apical spines.

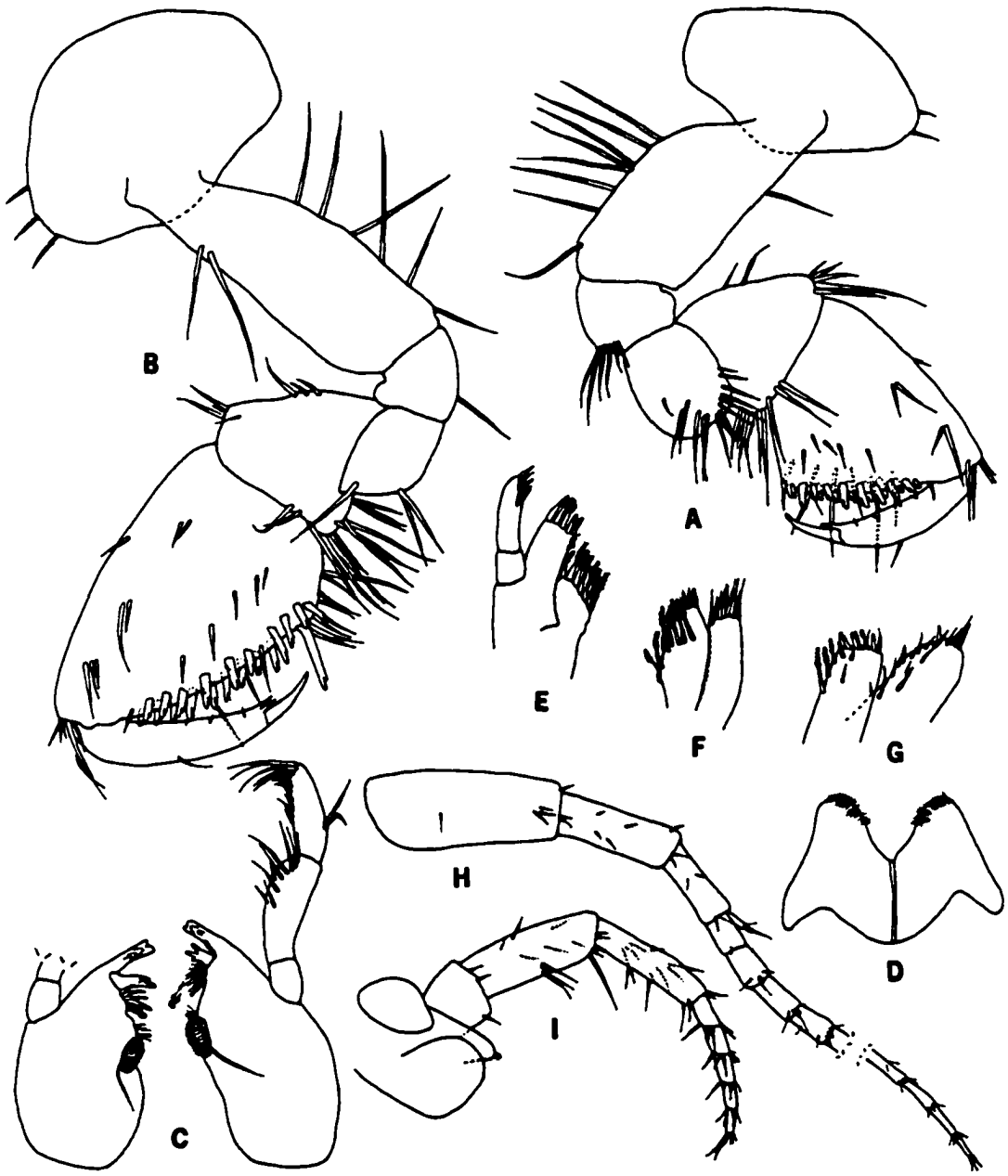

Fig. 77. ***Stygobromus glacialis*****, new species, female paratype (6.5 mm), Zoo Cave, Glacier County, Montana: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2; G, inner and outer plates of maxilliped (enlarged); H, I, antennae 1, 2.**

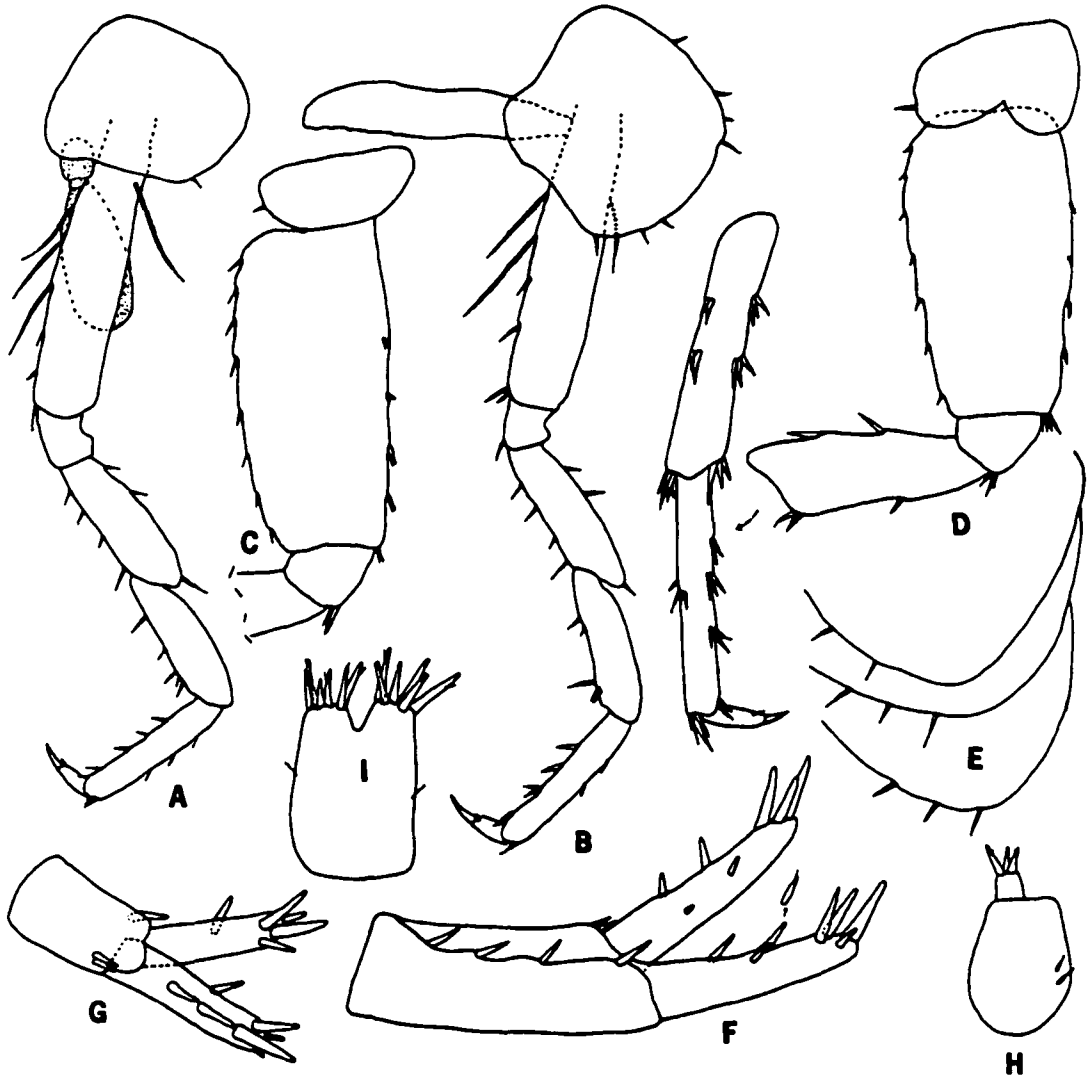

Fig. 78. ***Stygobromus glacialis*****, new species, female paratype (6.5 mm), Zoo Cave, Glacier County, Montana: A, B, pereopods 3, 4; C, pereopod 7; D, pereopod 6; E, pleonal plates; F, G, H, uropods 1, 2, 3; I, telson.**

Telson longer than deep, apical margin with small median notch, bearing 12 relatively long spines.

Type locality. Zoo Cave, located approximately 16 km west of Babb in Glacial National Park, Glacier County, Montana.

Distribution and ecology. The species is recorded from Zoo Cave in Glacier County and Algal Cave (= West Tunnel Cave), an unnamed cave on Trail Creek and Logan Creek springhead in adjoinning Flathead County (Figs. 93, 96). Algal and Zoocaves and the spring are in Glacier National Park, whereas the unnamed cave is just outside the park's western boundary. According to Paul Hendricks (pers. comm.), who made the most recent collection of this species from Algal Cave in 1999, the specimens were taken from a series of three silt-bottom pools with a slight flow between them. He also reported seeing 30-40 amphipods that were not collected. Stygobiont isopods, *Salmasellus stegonathrix* Bowman., also inhabit the pools (Lewis 2001). The 2 ovigerous females measured 5.8 mm long and each had 2 embryos in the brood pouch, although four embryos were loss in the vial. The other females were 5.0 mm long and had setose brood plates but were not ovigerous. The temperature of the Algal Cave stream pools was 6.5 °C.

A very recent (August 2000) collection of this species was made by Joe Giersch, who obtained a large sample of more than 100 individuals form the Springhead of Logan Creek in Logan Poss at elevation of 2159 m. According to J. Giersch (pers. comm.), the species is abundant in gravels on the substrate of the spring flow.

Etymology. The epithet *glacialis* is from the Latin, meaning "ice" or "frozen," in reference to the occurrence of this species in Glacier National Park.

Stygobromus idahoensis, new species

(Figs. 79-81)

Material examined. IDAHO. Lemhi Co.: Wilson Creek, HOLOTYPE ♀, 1 ♂ and 3 ♀ paratypes, P. Koetsier, probably late 1986 (no exact date on the collection label).

Diagnosis: A small groundwater species, distinguished by small size, rather broad bases of pereopods 5 - 7, especially 7, and 2 long spine teeth at defining angle of pereopod of gnathopod 2. Largest ♀, 3.5 mm, largest ♂, 3.0 mm.

Female. Antenna 1: 47 percent length of body, 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 5-7 plumose spines; palp segment 2 with row of 3 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 6 D setae, and 4 E setae, lacking both A

and C setae.

Inner lobes of lower lip small to vestigial.

Maxilla 1: inner plate with 6 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 5 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 4 plumose spines, and 2-3 naked setae apically, and 2 plumose setae on inner margin; outer plate with setae on inner margin and 6-7 lightly plumose setae on or near apex.

Gnathopod 1: propod little smaller than propod of gnathopod 2; palm straight, little longer than posterior margin, armed with 11 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae; 2-3 inferior medial setae; dactyl nail moderately short; coxa approximately about as broad as deep; margin with 4 setae.

Gnathopod 2: propod longer than broad; palm weakly convex and armed with 11 spine teeth in double row; defining angle with 2 long spine teeth on outside, 2 shorter spine teeth on inside; posterior margin shorter than palm, with 1 or 2 setae; few superior medial setae doubly and singly inserted; 2 singly inserted inferior medial setae; dactyl nail moderately long; coxa deeper than broad; margin with 3 setae.

Pereopod 3: coxal plate deeper than broad, margin with 4 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 55 percent length of basis, margin with 9 setae.

Pereopod 6 little longer than pereopod 7, about 54 percent length of body, 20 percent longer than pereopod 5.

Pereopods 5-7: bases of about broadest proximally; posterior margins of 5 and 7 strongly convex and expanded, that of 6 less so; distoposterior lobes distinct and broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 35 - 40 percent length of corresponding propod.

Coxal gills present on pereopods 2 - 6, absent from 7.

Simple, lateral sternal gills present on pereonites 6 and 7.

Brood plates slightly narrowing distally.

Pleonal plates: posterior margins of plates 1 - 3 weakly convex, with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 1 with 1

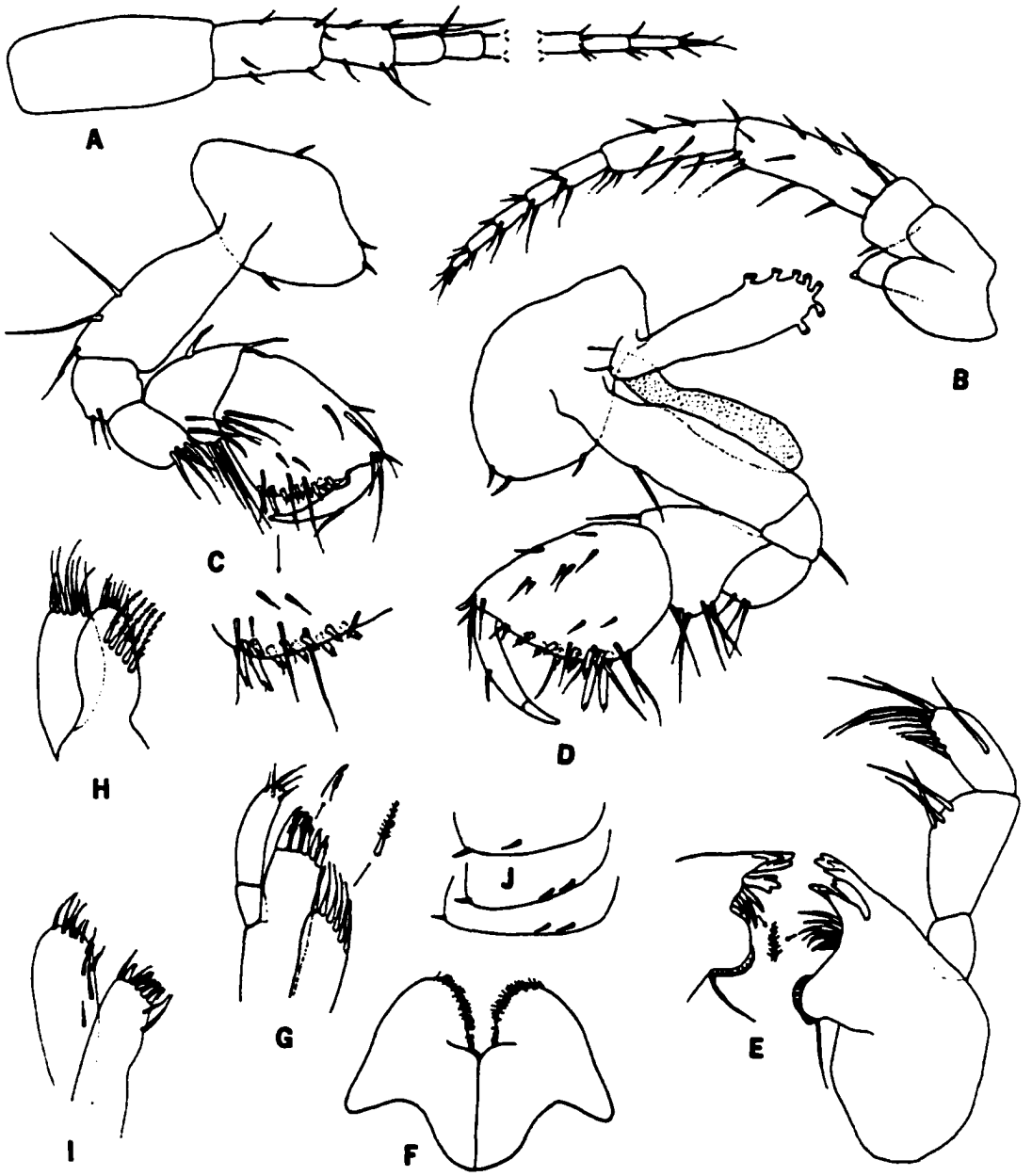

Fig. 79. ***Stygobromus idahoensis*****, new species, female paratype (3.5 mm), Wilson Creek, Lemhi County, Idaho: A, B, antennae 1, 2; C, D, gnathopods 1, 2 (palms enlarged); E, left mandible and dentate part of right mandible; F, lower lip; G, H, maxilla 1, 2 (apical setae enlarged); I, inner and outer plates of maxilliped (enlarged).**

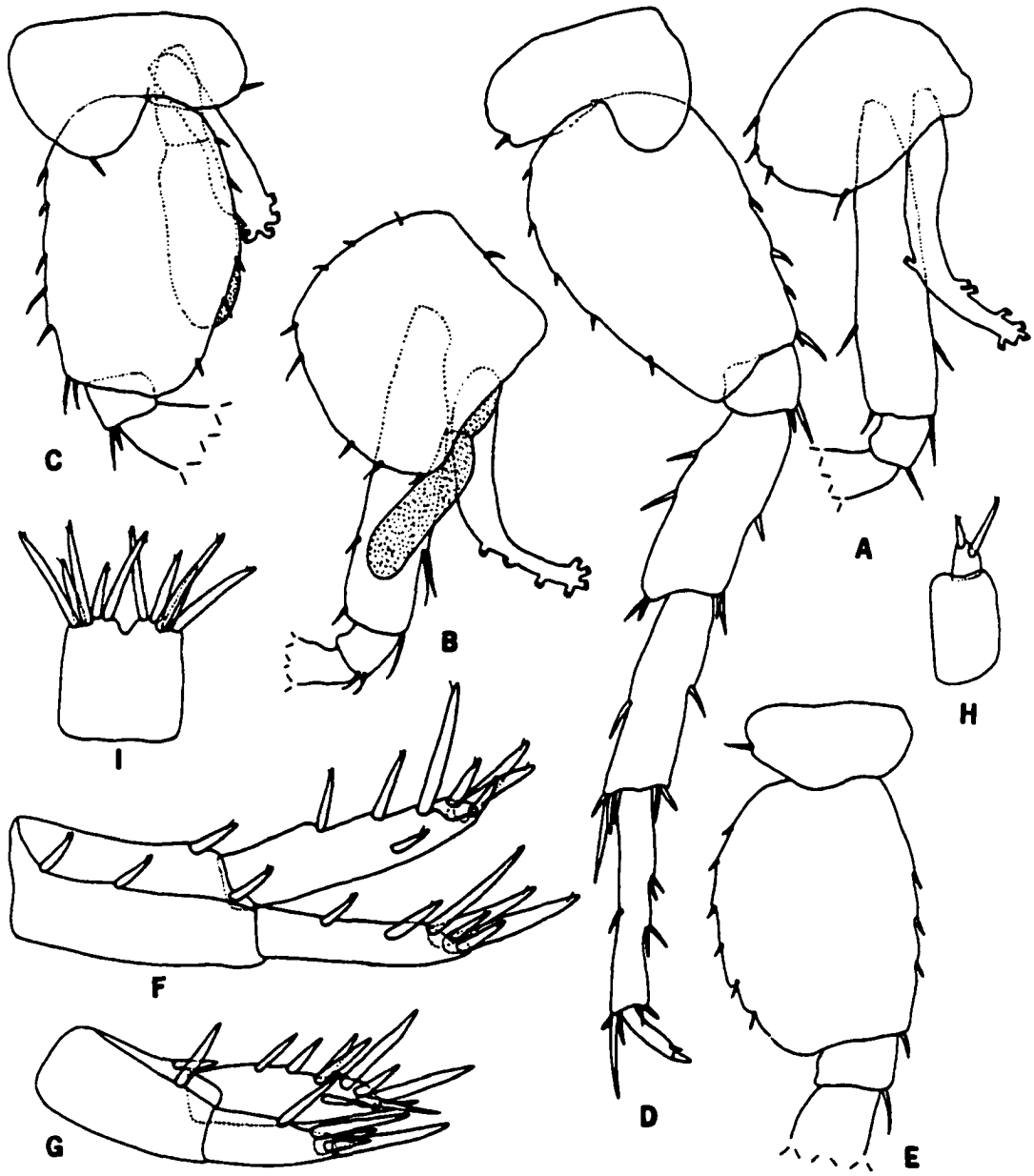

Fig. 80. ***Stygobromus idahoensis*****, new species, female paratype (3.5 mm), Wilson Creek, Lemhi County, Idaho: A, B, C, pereopods 3, 4, 5 (in part); D, pereopod 6; E, 7 (in part); F, G, H, uropods 1, 2, 3; I, telson.**

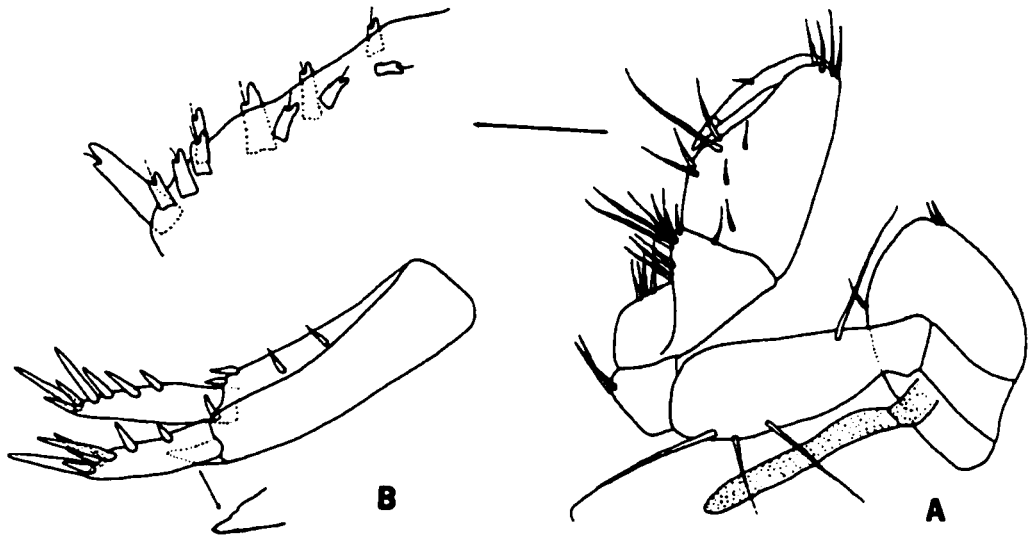

Fig. 81. ***Stygobromus idahoensis*****, new species, Male paratype (3.0 mm), Wilson Creek, Lemhi County, Idaho: A, gnathopod 2, B, uropod 1.**

spine, that of plates 2 and 3 with 2 spines each.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, 10 percent longer than length of peduncle, with 8 spines, 1 elongate; outer ramus with 7 spines, 3 elongate; peduncle with 4 spines.

Uropod 2: rami heavily spinose; inner ramus longer than outer ramus, subequal in length to peduncle, with 11 spines; outer ramus with 5-6 robust spines; peduncle with 2 spines.

Uropod 3: peduncle without setae, ramus only 30 percent length of peduncle, with 2 apical spines.

Telson subquadrate, about as long as broad, apical margin with tiny median notch between spine clusters, bearing 10 relatively long spines, some as long as telson.

Male. Differing from female as follows: Gnathopod propods narrower, palm of propod 2 shorter in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process about 50 percent length of outer ramus, tapering to blunt point distally, upper margin minutely serrate toward apex; inner ramus with 7-8 spines; peduncle with 5 spines. Uropod 2: inner ramus with 9-12 spines, peduncle with 3 spines. Telson, with 13-14 long apical spines.

Type locality. Shallow hyporheic habitat at mouth of Wilson Creek, a tributary to the middle fork of Salmon River, Lemhi County, Idaho. This site is located at 45° 02'57" N, 114°43'31" W (Figs. 93, 96).

Distribution and ecology. This species is only known form its type-locality, where according to its collector Peter Koetsier (pers. comm.), the material was collected with a Surber bottom sampler.

Etymology. This species is named for the state of Idaho.

Stygobromus montanensis Holsinger, 1974

Stygobromus montanensis Holsinger, 1974: 52-55, figs. 32-33 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Diagnosis. A small to medium-sized subterranean species, distinguished by possession of few setae on posterior margin of gnathopodal propod 1 and presence of 2 pairs of tiny simple lateral sternal gills on pereonites 6 and 7 (Holsinger, 1974). Largest ♀, 5.5 mm; male unknown.

Distribution and ecology. This species is known only from its type-locality (Figs. 93, 96), where it has been collected with two other species of *Stygobromus* (see Holsinger, 1974).

Stygobromus obscurus Holsinger, 1974

Stygobromus obscurus Holsinger, 1974: 55-58, figs. 34-35 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Diagnosis. A small to medium-sized subterranean species, apparently unrelated to other known species of *Stygobromus* in western North America and distinguished by: relatively slender propods of gnathopods; shallow coxal plates of gnathopod 2 and pereopods 3 and 4; narrow bases of pereopods 5-7 which lack distoposterior lobes; 2 pairs of simple, lateral sternal gills; absence of ventral spines on pleonal plates; heavily spinose uropods and telson; and relatively long spines on uropods 3 and telson. Largest ♀, 7.0 mm; male unknown.

Distribution and ecology. This species is known only from its type-locality (Figs. 94, 96), where it has been collected with two other species of *Stygobromus* (see Holsinger, 1974).

Stygobromus secundus Bousfield and Holsinger, 1981

Stygobromus secundus Bousfield and Holsinger, 1981: 1827-1830, figs. 1 [type-locality: a spring 24 km southwest of Rocky Mountain House, Alberta, Canada].

Diagnosis. A small to medium-sized groundwater species, distinguished from all other species of *Stygobromus* by presence of simple, paired, lateral sternal gills on pereonites 4 and 5; and in general by comparatively large ramus of uropod 3, less than half length of peduncle; and absence of a peduncular process on uropod 1 of the male. Largest ♀, 5.2 mm; largest ♂, 4.0 mm.

Distribution and ecology. This species is known only from its type-locality, a spring, 24 km SW of Rocky Mountain House, Alberta, Canada (Figs. 94, 96) (see Bousfield and Holsinger, 1981).

Stygobromus simplex, new species

(Figs. 82-83)

Material examined. COLORADO. Rio Blanco Co.: Spring Cave, southeast of Meeker, HOLOTYPE ♀ on slides in part (USNM), M. Tate and K. Tate, 4 Oct 1995.

Diagnosis. A medium-sized cavernicolous species that resembles *S. holsingeri* in structure of gnathopods and uropods 2-3, but is distinguished from that species as follows: maxilla 1-2 with fewer setae on inner plate; maxilliped with bladelike spines on inner plate; gnathopods 1-2 with more teeth on palmar margin; bases of pereopods 3-7 with fewer spines on posterior margins; pleonal plates 2-

3 with more ventral margin spines and presence of relatively long, lateral sternal gills. Largest ♀, 5.0 mm, male unknown.

Female. Antenna 1: 44 percent length of body, 34 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4-6 plumose spines; palp segment2 with row of 6 rather long setae on inner margin; palp segment 3 with 8 D setae, 4 E setae, without A, B and C setae.

Inner lobes of lower lip restigial or absent.

Maxilla 1: inner plate with 6 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 2 naked setae apically, and 2 plumose setae on inner margin; outer plate with setae on inner margin and apex.

Gnathopod 1: propod little shorter than that of gnathopod 2; palm weakly convex, about 2 times longer than posterior margin, armed with 21-22 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 1 or 2 superior medial setae; 8 - 10 singly inserted inferior medial setae; dactyl nail rather long and sharply pointed; coxa deeper than broad, margin with 1 seta.

Gnathopod 2: propod about 2 times longer than broad; palm convex and armed with 19-20 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of triply inserted setae; 3 or 4 superior medial setae; 3 singly inserted inferior medial setae; coxa about as broad as deep, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 2 setae.

Pereopod 4: coxal plate relatively broad and deep, reaching about 40 percent length of basis, margin with 4 setae.

Pereopod 6 little longer than pereopod 7, about 76 percent length of body, 20 percent longer than pereopod 5.

Pereopods 5-7: bases relatively narrow, but little broader proximally than distally; posterior margins weakly convex, not expanded; distoposterior lobes poorly developed, almost indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 35 - 40 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7.

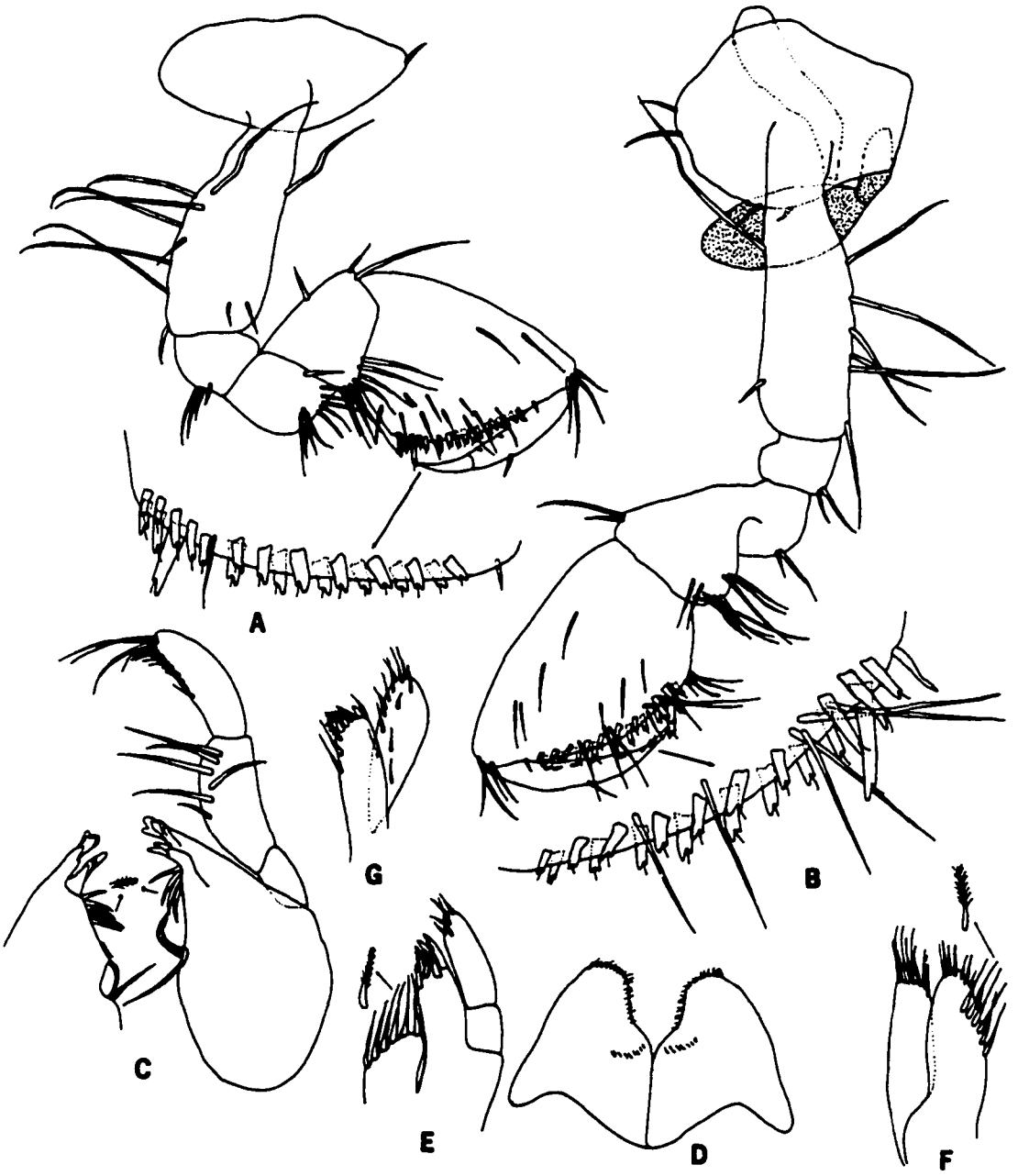

Fig. 82. ***Stygobromus simplex*****, new species, female paratype (5.0 mm), Spring Cave, Rio Blanco County, Colorado: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

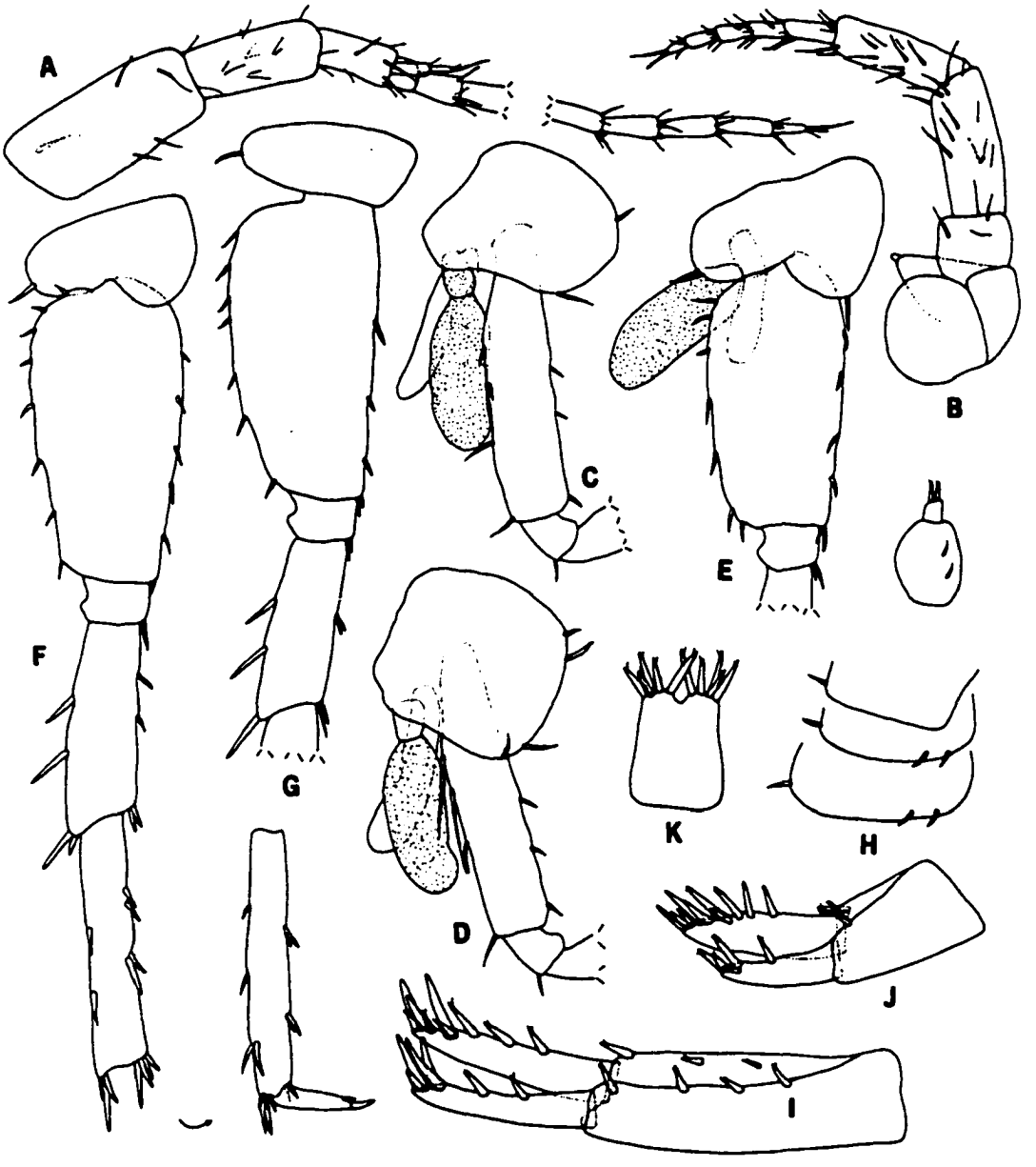

Fig. 83. ***Stygobromus simplex*****, new species, female paratype (5.0 mm), Spring Cave, Rio Blanco County, Colorado: A, B, antennae 1, 2; C, D, E, pereopods 3, 4, 5; F, G, pereopods 6, 7; H, pleonal plates; I, J, K, uropods 1, 2, 3; L, telson.**

Relatively long, simple, lateral sternal gills present on pereonites 6 and 7.

Brood plates little expanded distally.

Pleonal plates: posterior margins of plate 1 - 3 weakly convex, with 1 setule near distoposterior corner, distoposterior corners rounded and indistinct; ventral margins of plates 2 and 3 with 2 spines each.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 60 percent length of peduncle, with 9 spines; outer ramus with 6 spines; peduncle with 7 spines.

Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 9-10 spines; outer ramus with 5-6 spines; peduncle with 3 spines.

Uropod 3: peduncle usually bearing 2 small setae; ramus approximately 35 percent length of peduncle, with 2-3 apical spines.

Telson little longer than broad, gently tapered distally; apical marginwith tiny median notch between spine clusters, bearing 10-12 spines.

Type locality. Spring Cave, located southeast of Meeker in Rio Blanco County, is one of the longest caves in Colorado (Parris, 1973). It contains a stream and lake.

Distribution and ecology. This species is known only from its type-locality (Figs. 93, 97), and to date it is based on a single female specimen.

Etymology. The epithet *simplex* is from the Latin, meaning "simple" or "uncomplicated," in reference to the simplicity of a species based on a single specimen.

Stygobromus wardi, new species

(Figs. 84-86)

Material examined. COLORADO. Eagle Co.: Fulford Cave, HOLOTYPE ♀ (USNM), 3 ♂ and 4 ♀ paratypes, 1 juv., J. V. Ward and J. R. Holsinger, 6 July 1980; Blue Butt Cave, 6 ♀, J. V. Ward and J. R. Holsinger, 6-7 July 1980.

Diagnosis. A small cavernicolous species, possibly related to *S. holsingeri* and *S. coloradensis* in structure of gnathopods and uropod 1-2 but distinguished from these speceis as follows: antenna 1 about 2 times as long as antenna 2; maxilla 1-2 with more setae on inner plate; coxal plates 3-4 broader than deep; bases of pereopods 6-7 with fewer spines on posterior margin; pleonal plates 2-3 with fewer spines on ventral margin; presence of lateral sternal processes; telson broader than deep and with longer apical spines. Largest ♀, 5.0 mm; largest ♂, 3.5 mm.

Female. Antenna 1: 46 percent length of body, approximately 2 times longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 5-6 plumose spines; palp segment 2 with 3 long setae on inner margin; palp segment 3 bearing 1 B seta, 6 D setae, 3 E setae, lacking A and C setae

Inner lobes of lower lip small to vestigial.

Maxilla 1: inner plate with 7 apical, plumose setae; palp with 4 stiff setae subapically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin.

Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 3-4 naked setae apically, and 1 plumose spine on inner margin; outer plate with 7 or 8 setae on inner margin, 4 setae on or near apex.

Gnathopod 1: propod subequal in size to gnathopod 2; palm straight, approximately same length as posterior margin, armed with 7 spine teeth in double row; defining anglewith 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; without superior medial setae; 1-3 inferior medial setae; dactyl nail rather long; coxa broader than deep, margin with 1 seta.

Gnathopod 2: propod longer than broad; palm straight or slightly concave and armed with 8 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin little shorter than palm, with 1 set of doubly or triply inserted setae; 3 superior medial setae, one rather long; 2 inferior medial setae; coxa deeper than broad, margin with 1 seta.

Pereopod 3: coxal plate deeper than broad, margin with 2-3 setae.

Pereopod 4: coxal plate subquadrate, about as broad as deep, reaching about 30 percent length of basis, margin with 3 setae.

Pereopod 6 little longer than pereopod 7, about 65 percent length of body, 33 percent longer than pereopod 5.

Pereopods 5-7: bases little broader proximally than the distally; posterior margins nearly straight or slightly convex; distoposterior lobes indistinct; anterior and posterior margins with fewer (2-4) spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically up to 40-45 percent length of corresponding propod.

Coxal gills present on pereopods 2-6, absent from 7;

Two pairs of simple lateral sternal processes on pereonites 6 and 7.

Brood plates slightly expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner,

Fig. 84. ***Stygobromus wardi*****, new species, female paratype (3.7 mm), Fulford Cave, Eagle County, Colorado: A, B, gnathopods 1, 2 (palms enlarged); C, right mandible and dentate part of left mandible; D, lower lip; E, F, maxilla 1, 2 (apical setae enlarged); G, inner and outer plates of maxilliped (enlarged).**

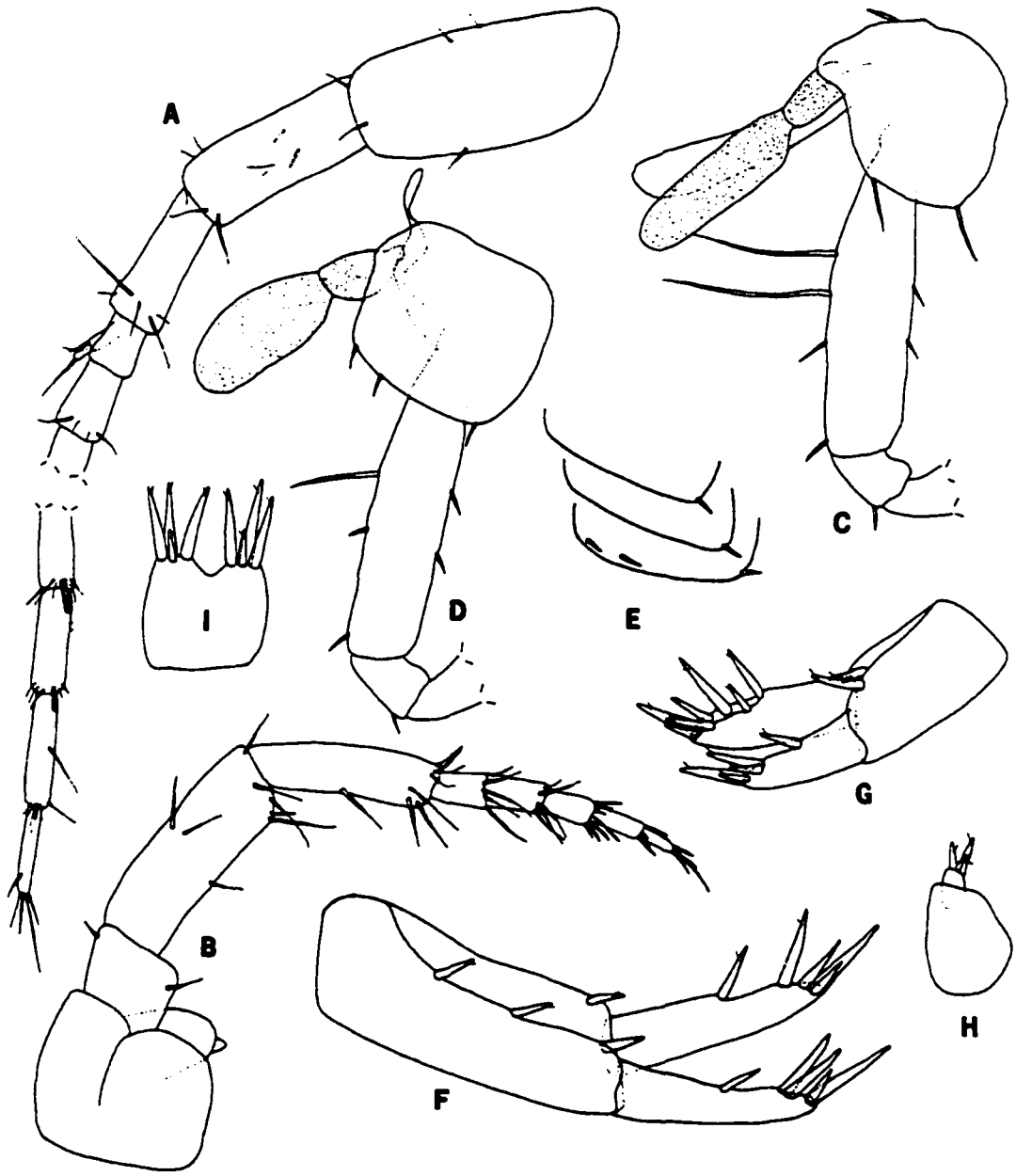

Fig. 85. ***Stygobromus wardi*****, new species, female paratype (3.7 mm), Fulford Cave, Eagle County, Colorado: A, B, antennae 1, 2; C, D, pereopod 3, 4; E, pleonal plates; F, G, H, uropods 1, 2, 3; I, telson.**

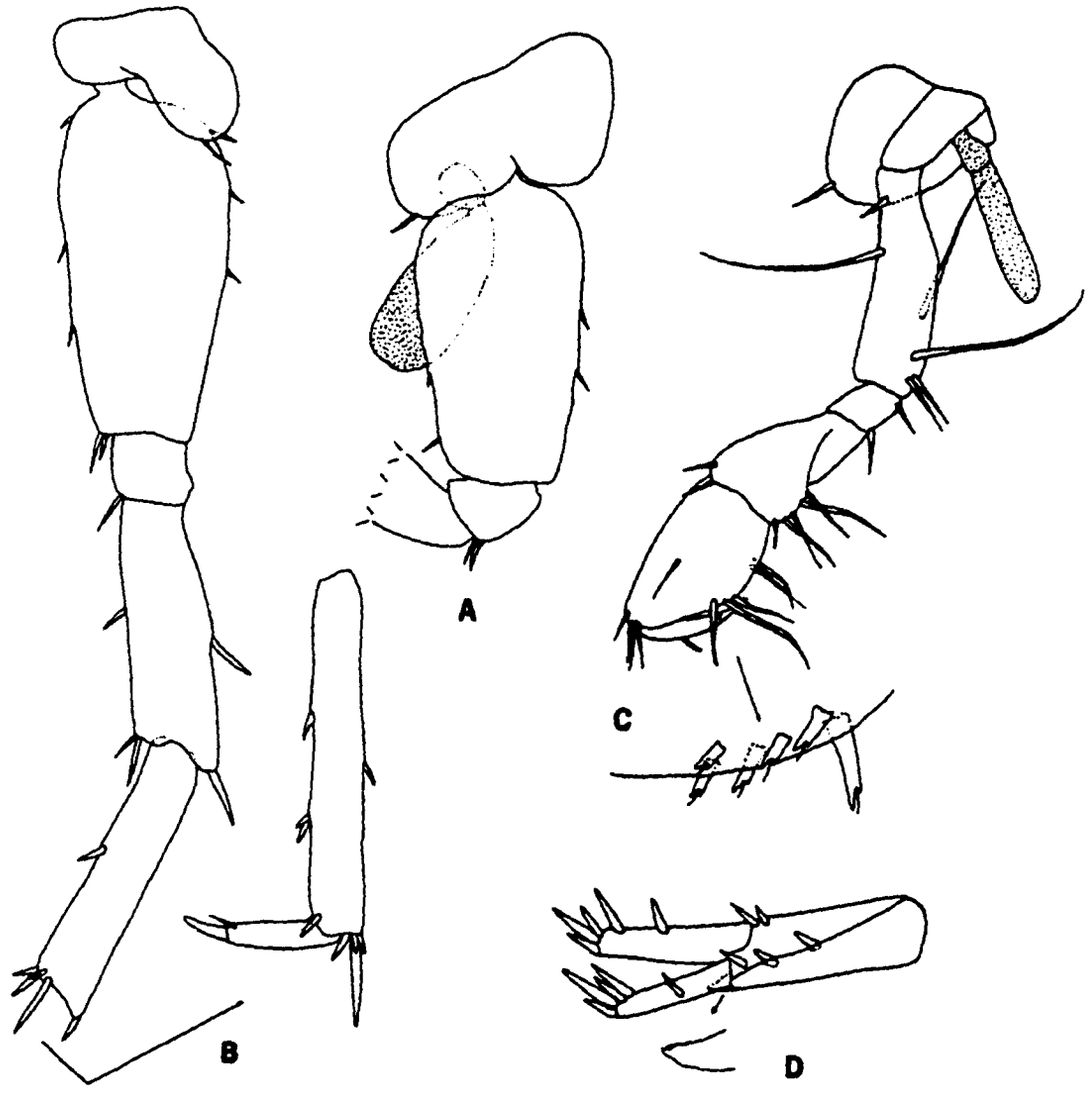

Fig. 86. ***Stygobromus wardi,*** **new species, female paratype (3.7 mm), Fulford Cave, Eagle County, Colorado: A, B, pereopods 5, 6; Male paratype (3.5 mm), C, gnathopod 2; D, uropod 1.**

that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margins of plates 1 and 2 without spines, that of plate 3 with 2 spines.

Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 5 spines; outer ramus with 5 spines; peduncle with 4 spines.

Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 2 spines.

Uropod 3: peduncle without setae; ramus approximately 30 percent length of peduncle, with 3 apical spines.

Telson little broader than long, lateral margins slightly convex; apical margin with shallow median notch between spine clusters, bearing 8 mostly long spines.

Male. Differing from female as follows: Gnathopod propods proportiona tely shorter, palm of propod 2 longer in relation to posterior margin and with fewer teeth. Uropod 1: peduncular process present, reaching about 25 percent length of outer ramus, pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 5 spines. Uropod 2: inner ramus with 8 spines, peduncle with 3-4 spines. Telson with 6-9 apical spines.

Type locality. Fulford Cave, located south of Eagle in Eagle County, Colorado, is one of the larger and better known cave in the state (Parris, 1973).

Distribution and ecology. This species is known only from small streams in two caves in Eagle Co., Colorado, at elevations of approximately 2902 and 3,048 m (above sea level) (Figs. 94, 97). It was collected from gravels and assorted rubble in a rapid, high gradient stream in Fulford Cave, where the water temperature was 4.5 °C. In Blue Butt Cave, 6 specimens were collected from the silty substrate of the cave stream by a conbination of Surber bottom sampler and overnight drift net. A single female (4.0 mm) in the July sample from Blue Butt Cave had 2 large embryos in the brood pouch. The water temperature near the entrance to this cave was 8°C.

Etymology. This species is named in honor of Prof. Dr. James V. Ward, who helped with the discovery and collection of this species and has made many other significant contributions to the study of subterranean amphipods in Colorado.

Stygobromus species

The following populations were recognized as two distinct species in this study but are not described because of the lack of mature specimens or enough material. These specimens and detailed habitat data were donated by Richard Casey and Gary Byrtus from the Alberta Environmental Center in Vegreville, AB, Canada.

Species No. 1. A single immature male (ca. 4.0 mm), collected by G. Byrtus from a groundwater well on the grounds of the Glencoe Golf and Country Club, just west of Calgary, Alberta, Canada (Figs. 94, 96). This species has small, simple lateral sternal gills; telson with small apical notch; uropod 3 with 2 apical spines; and gnathopod 2 larger than gnathopod 1. Its overall morphology is rather typical for species of the *hubbsi* group with exception of the sternal gills. This specimen was collected with speciemens of a second undescribed species, which is listed immediately below (see species no. 2).

Species No. 2. Eleven tiny specimens from: a) groundwater well on grounds of Glencoe Golf and Country Club, just west of Calgary (3 specimens collected by G. Byrtus, 19 Oct. 1993); b) groundwater wells on grounds of Kananaskis Country Golf Course, 60 km west of Calgary (7 apparently immature specimens in 5 samples collected by G. Byrtus from 3 June 1992 to 1 June 1993); c) groundwater well on grounds of Canmore Golf and Curling Club, about 70 km west of Calgary (1 tiny specimen collected by G. Byrtus, 4 May 1993) (Figs. 94, 96).

CHAPTER IV

PHYLOGENETIC ANALYSIS

CHARACTERS AND CHOICE OF OUTGROUP

Characters

The choice of characters used in the analysis is based on descriptions from the literature and illustrations. The matrix emphasizes morphological characters. A total of thirty-two morphological characters were coded. Most characters are binary, but three are multistate. The characters were treated in two ways during the cladistic analysis: unordered and ordered. Ordering was sequential as follows: 0↔1↔2↔3. Treatment of multistate characters as ordered or unordered constitutes an assumption about evolutionary process (Hauser and Presch 1991; Wilkinson 1992; Barriel and Tassy 1993; Slowinski 1993) that must be faced *a priori* in cladistic analysis.

Unordered multistate characters assume that one character state can transform directly into any other character state without passing through an intermediate character state. Ordered multistate characters, however, assume that transformations pass through such an intermediate stage. Wilkinson (1992) argued that ordering certain characters is a logical extension of Hennig's auxiliary principle and "explains the similarity between a subset of the character states in terms of synapomorphy" (Wilkinson 1992). Slowinski (1993) demonstrated that neither ordering nor unordering characters necessarily increases taxonomic congruence, which is one measure of phylogenetic accuracy. He concluded that either way of treating multistate characters is valid (Slowinski 1993) and proposed ordering as favorable if a transformation series describes morphoclinal variation. The characters treated as ordered here mean hierarchical morphological change, and treating these characters as unordered would not result in a loss of informational importance of phylogenetic reconstruction.

Polymorphic characters, for example, varying numbers of long setae on the inner plate of maxilla 1, were coded according to the scaled method, but not strictly (Wiens 1995) because the presence of four or five long setae on the inner plate of maxilla 1, for example, could not be treated as two states. In most cases, it would have been more satisfactory to code polymorphic characters in relation to their frequencies. If the majority of the specimens with four long setae, for example, four setae will be treated as coded state. However, such information is not always

available since some species descriptions are merely based on an inadequate number of specimens. In this case relevant information of related species is used as reference.

Adaptation to groundwater/interstitial habitats is typically corelated to reduction or loss of some morphological structures that would reduce functionality of mobility or sense organs in interstitial environments. These morphological modifications might involve eyes, pleopodal and uropodal appendages, gills, and coxal plates. Morphological structures can either display different stages of reduction or evolve into organs or instruments with new, specialized pleopodal and uropodal rami (Notenboom 1991). For the coding of those characters, the basic functional model of an epigean amphipod was considered as the common ancestor of the *Stygobromus*. Character states nearest to this morphological prototype were coded as plesiomorphic (i.e., state 0). The loss or acquisition of small structures, however, is very likely to occur as homoplasies within a lineage, not only as apomorphies. For this reason, the reduction of spines and setae was not strictly considered as apomorphic and their coding remains hypothetical at this phase of cladistic analysis (see also, Stock 1981; Lindeman 1991; Notenboom 1991; Koenemann and Holsinger 1999). If not explicitly stated, a character is by default unordered and/or unweighted. The former is called first run in the following context. The second run means ordered and partially weighted run.

In some of the species, the occurrence of a character showed a variable or transitional state, for example, the number of apical and subapical spines on the inner ramus of uropod 1 and uropod 2 (character 19 and 21). These variations were treated as separate morphological conditions. Another problem encountered during the analysis was the pronounced degree of interspecific variation. For example, the shape of propodal palm of gnathopods 1 and 2 is straight in species A, concave in species B and convex in species C. Two different approaches were used to deal with it. For the first, variable characters were coded as question marks if their morphological/evolutionary significance is not sure. Alternatively, it was coded according to the majority of their occurrence frequency in all species (Wiens 1995). Because the basic difference of the resulting trees was the degree of polytomy, better-resolved trees of the Majority Rule method were chosen as representatives. A third solution to this problem may be obtained by an inferred ground-plan character state (Exemplary Method). In this approach, the ancestral state of a polytomic OTU (Operational Taxonomic Unit) is determined by a partial cladistic analysis of some exemplary species (or higher taxa), investigating the variable character only (Yeates 1995; Koenemann and Holsinger 1999). This method was not employed because of limitation of materials and time.

Character Independence

An assumption of parsimony analysis is that the characters used in a phylogenetic analysis are independent. As discussed by Kluge and Wolf (1993), independence in phylogenetic analysis should be addressed in two forms: (1) logical independence of characters, and (2) concurrent origin of the characters. The most egregious violation of the assumption of independence is to score redundant characters, i.e., those that fail the test of logical independence. Farris (1983) described an example of two characters that are not logically independent as scoring "tarsal segments and twice that number" separately.

The second criterion for independence, concurrent origin, is much more difficult to verify (Kluge and Wolf 1993). Rejection of the hypothesis that two synapomorphies evolved independently requires knowledge of ontogenetic relationships that "even our best-supported phylogenetic propositions do not provide" (Kluge and Wolf 1993). Numerous biological processes (e.g., genetic, selective, developmental) may contribute to the non-independence of different characters. However, as Kluge and Wolf (1993) pointed out, "the actual processes responsible for non-independent evolution cannot be read from even the most detailed patterns of organism relationship." It can be interpreted that similar distribution of character states in two or more characters is not necessarily indicative of the non-independence of those characters. Hence, to dismiss covarying character without exquisite knowledge of ontogenetic relationships risks a priori dismissal of phylogenetic signal (character congruence). I therefore included all logically independent characters in the analysis.

Choice of Outgroup

Assumptions about morphological adaptations of amphipods to subterranean or interstitial environments seem to have achieved a broad consensus in the literature (Stock 1981; Notenboom 1991; Holsinger 1993, 1994; Koenemann *et al.* 1998). Therefore, morphological reductions/loss of structure are treated as apomorphies attributed to hypogean adaptation. Accordingly, each corresponding plesiomorphic condition was coded as state 0. The relatively frequent occurrences of homoplasies in stygobiont amphipods tend to impede the choice of effective outgroups and will most likely fail to produce a probable phylogenetic reconstruction of the *Stygobromus* (see Holsinger 1994; Koenemann *et al.* 1998; Koenemann and Holsinger 1999; Wang 1996; Wang and Mauries 1996; Wang and Zhang 1996a, 1996b). For this reason, I also considered a hypothetical, "all-zero" ancestor as an outgroup. For another choice of outgroup, three

"representative" species were chosen from three genera of the family Crangonyctidae, which are thought to be closely related to the genus *Stygobromus*.

CLADISTIC ANALYSES

A Macintosh (OS-7) was used to run the phylogenetic software programs PAUP 3.1 (Swofford 1993) and MacClade 3.01 (Maddison and Maddison 1993). Each series of runs was started with the Heuristic Search option, considering that the data matrix contained a relatively high number of terminal taxa or OTUs.

For the first run, only minimum trees were kept by Random Stepwise Addition, TBR Branch Swapping, and MULPARS options activated. For subsequent runs, all trees in memory from the preceding runs were used, activating MULPARS option and keeping all trees that were as short as or one step shorter than those loaded into memory. These steps were repeated until no shorter trees can be found. From the resulting trees, two different types of consensus trees were calculated (i.e., Strict and Majority Rule). The Majority Consensus tree was transferred to MacClade for a detailed investigation. This search procedure was conducted for numerous runs with modified character sets, i.e., 'unordered' and 'unweighted' versus 'ordered' and 'partially weighted' character sets. From the resulting parsimonious trees, consensus trees were calculated according to strict and majority rule. All consensus trees were finally evaluated and edited in MacClade 3.01. Each analysis was based on an identical data matrix (Table 1 and 2). In the first-run case, characters were treated as unordered and unweighted (randomly reversible states and equally weighted as 1), assuming that, for example, in character 12, any observed number of spines on the ventral margin of pleonal plate 3 could evolve directly.

The second run analysis was conducted with ordered and partly weighted characters using the same data matrix. In this case, multistate characters were ordered, under the assumption that they have evolved in linear transformation series, moving progressively from one character state to the next. Some characters were weighted according to their possibly evolutionary significance and/or their complex evolution. In the following discussion, these two alternative analyses will be referred to as "first-run" and "second-run", respectively.

This analysis includes two categories: the first one chose a hyporthetical ancestor (character states coded all zero) as an outgroup; the second chose *Bactrurus brachycaudus*, *Crangonyx forbesi* and *Synurella ambulans* as outgroups. Although the resulting trees are not identical and have different lengths, there are many topologic similarities in the trees. Accordingly, congruent topologic patterns can be recognized in trees resulting from the first-runs, as well as the second-

runs. To a great extent, difference in tree length could result from different weighting of characters in the second-run, where this option was available.

RESULTS OF PHYLOGENETIC ANALYSES AND DISCUSSIONS

The analysis resulted in a relatively large number of cladograms. In order to facilitate the discussion of these phylogenetic results, a representative choice of 50% Majority-Rule consensus trees as depicted in Figs. 87-90.

I. Hypothetical Ancestor as Outgroup

The first-run (all characters unordered and unweighted) resulted in 99 trees of 212 steps each. The 50% Majority-Rule consensus trees supports the monophlyly of California-Oregon-Washington clade. This clade includes *S. imperialis*, *S. rudolphi*, *S. gallawayae*, *S. latus*, *S. grahami*, *S. wengerorum*, *S. harai*, *S. gradyi*, *S. elliotti*, *S. mysticus*, and *S. hubbsi* (Fig. 87).

The robustness of this cluster clade in each category (program or methed) is remarkable. It indicates that these species are closely related.

In each run, there is at least one consensus tree that presents the species of *S. grahami-gradyi* complex (*S. grahami*, *S. gradyi*, *S. harai*, *S. wengerorum*, *S. imperialis* and *S. rudolphi*,) as a monophyletic group (Figs. 87-88).

Another loosely stable congruent pattern of clades is represented by taxa that form following geographic species clusters:

(1) California-Oregon-Nevada species form a monophyletic clade (*S. imperialis*, *S. rudolphi*, *S. grahami*, *S. wengerorum*, *S. harai*, *S. gallawayae*, *S. gradyi*, *S. mysticus*, *S. hubbsi*, *S. cherylae*, *S. wahkeenensis*, *S. lacicolus* and *sierrensis*).

(2) Colorado-Arizona species form a cluster with *S. wardi*, *S. arizonensis*, *S. holsingeri*, *S. pennaki*, *S. coloradensis*, *S. uropsinatus*, *S. quatsinensis*, and *S. fontanalis* as a stable core (Fig. 87-88). In second-runs, *S. limbus* from Texas appears integrated into the cluster, which possibly implies that there is close relationship between Colorado-Arizona species and Texas species.

(3) Washington-Montana-Oregon species cluster composes of *S. canadensis*, *S. glacialis*, *S. secundus*, *S. obscurus*, *S. utahensis*, *S. tritus*, *S. duplus*, *S. rallus*, *S. puteanus* and *S. curroae*. An interesting thing is *S. idahoensis*. This species is paraphyletic with *S. canadensis* but a sister

Table 1: Character analysis of species of *Stygobromus* in western North America. Unless specifically indicated, characters were ordered and weighted by 1 in the second run.

Antenna

1. Ratio of length of antenna 1 to that of body.

   state 0: 50% or less

   state 1: more than 50%

   For delimiting plesiomorphic state and apomorphic state, a survey on ratio of antenna 1 length to the length of the body of *hubbsi*-group species of *Stygobromus* was conducted. Based on the result of the survey, the boundary between plesiomorphic and apomorphic states was delimited according to the evolutionary assumption, i.e., given a character, a popularly appearing character state possibly stands for the plesiomorphic. This assumption was also applied to the following character analysis. In second-run: ordered.

Maxillae

2. Plumose setae on inner plate of maxilla 1.

   state 0: more than 10

   state 1: equal or less than 10

   In second-run: ordered

3. Plumose setae in oblique row on inner plate of maxilla 2.

   state 0: more than 11

   state 1: equal or less than 11

   In second-run: ordered

Mandibles

4. B setae on segment 3 of mandibular palp:

   state 0: present

   state 1: absent

   In second-run: ordered

5. Spines in spine row of mandibles:

   state 0: more than 8

   state 1: equal or less than 8

   In second-run: ordered

Gnathopods 1 and 2

6. Shape of propodal palm of gnathopod 1.

   state 0: convex

   state 1: straight

Table 1, continued

state 2: concave

In second-run: ordered.

The palm shape of gnathopods 1 and 2 varies in the *Stygobromus* species. The terms "straight," "concave" and "convex" refer to the general shape of the propodal plam, e.g., concave palms of gnathopod 1 of *S. saltuaris* new species and *S. grahami* (see Holsinger, 1974), convex palms of gnathpod 1 of *S. hyporheicus* new species and *S. wengerorum* (see Holsinger, 1974), straight palms of gnathopod 1 of *S. boultoni* new species and *S. tahoensis* (see Holsinger, 1974).

7. Spine teeth on propodal palm of gnathopod 1:

state 0: more than 28

state 1: equal or less than 28

In second-run: ordered and weighted 2.

8. Shape of propodal plam of gnathopod 2.

state 0: convex

state 1: straight

state 2: concave

In second-run: ordered and weighted 2.

9. Ratio of length of posterior margin of propod of gnathopod 2 to that of propodal palm:

state 0: more than 30%

state 1: 30% or less

In second-run: ordered.

10. Sets of setae on posterior margin of propod of gnathopod 2:

state 0: present

state 1: absent

In second-run: ordered

11. Coxa of gnathopod 2 breadth and depth?

state 0: broader or equal

state 1: deeper

In second-run: ordered

12. Superior medial setae on propod of gnathopod 2:

state 0: present

state 1: absent

In second-run: ordered

Table 1, continued

Pereopods

13. Coxal depth compared to breadth of pereopod 3:

state 0: equal or deeper than broad

state 1: broader than deep In second-run: ordered.

14. Setae on coxal margin of pereopods 3-4:

state 0: more than 6

state 1: equal or less than 6

In second-run: ordered.

15. Coxal breadth of pereopods 5-7 compared to depth:

state 0: equal or longer

state 1: shorter

In second-run: ordered.

16. Pereopod 6 longer than 7:

state 0: yes

state 1: no

In second-run: ordered.

17. Shape of bases of pereopods 6 and 7:

state0: normal

state 1: broader

state 2: norrow

The term "normal" means that the ratio of breadth to depth of bases of pereopods 6 and 7 in length is similar to that of most of *Stygobromus* species. Species *S. duplus*, *S. rallus* and *S. latus* have the base shape to which the term "broader" refers in comparison with the normal shape (see figures of these species for detail). In second-run: ordered and weighted 2.

Sternal Gills/Processes

18. Sternal gill/process:

state 0: present

state 1: absent

This character plays an important role in separating the species of *Stygobromus* into *hubbsi* group (without sternal gills on pereonites) and non-*hubbsi* species group (with sternal gills on pereonites, typically 6 and 7). In second-runs ordered and weighted 8.

Table 1, continued

Pleonal plates

19. Setules on posterior margins of pleonal plates 2 and 3:

    state 0: 2 or more

    state 1: 1 In second-run: ordered.

20. Spines on ventral margin of pleonal plate 3:

    state 0: more than 3

    state 1: 1-3

    state 2: absent

    In second-run: ordered and weighted 4.

Uropods

21. Apical spines of inner ramus of uropod 1 about 50 percent as long as that of peduncle:

    state 0: no

    state 1: yes

    In second-run: ordered.

22. Spines on peduncle of uropod 1:

    state 0: more than 12

    state 1: equal or less than 12

    In second-run: ordered.

23. Length of inner ramus of uropod 1 compared to that of peduncle:

    state 0: equal or shorter

    state 1: longer

    In second-run: ordered.

24. Spines on inner ramus of uropod 2:

    state 0: equal or less than 12

    state 1: more than 12

    In second-run: ordered.

25. Length of inner ramus of uropod 2 compared with that of peduncle:

    state 0: equal or shorter

    state 1: longer

    In second-run: ordered.

26. Ratio of length of uropod 3 to that of peduncle:

    state 0: 25% or less

    state 1: more than 25% In second-run: ordered and weighted 3.

Table 1, continued

27. Spines on apical margin of uropod 3:

state 0: 1-2

state 1: 3 or more In second-run: ordered.

Telson

28. Telson notch:

state 0: present

state 1: absent

In second-run: ordered and weighted 2.

29. Telson notch depth compared to length of telson:

state 0: 25% or less

state 1: more than 25%

In second-run: ordered.

30. Spines on apical margin of telson:

state 0: 8 or less

state 1: more than 8

In second-run: ordered.

31. Length of apical spines of telson as long as that of telson:

state 0: no

state 1: yes

In second-run: ordered.

32. Ratio of telson length to width:

state 0: 1.5 times or less

state 1: more than 1.5 times

In second-run: ordered.

Table 2. Character data matrix. Question marks in the matrix refer to unknown character state.

Taxon\Character																															
1	*B. brachycaudus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2	*C. forbesi*	0	1	0	0	1	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
3	*S. ambulans*	1	0	0	0	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
4	*imperialis*	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
5	*cowani*	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0
6	*trinus*	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1
7	*hyporheicus*	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0
8	*rudolphi*	1	1	1	0	0	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
9	*gallawayae*	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0
10	*cherylae*	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	1	1	0
11	*myersae*	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	1	0	0
12	*herbsti*	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1
13	*urospinatus*	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0
14	*fontinalis*	1	0	1	1	1	0	0	0	0	0	?	0	0	0	0	1	0	0	1	?	1	0	1	0	0	1	0	0	0	1	0	0
15	*interstitialis*	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	2	0	0	1	1	0	0	0	0	0	1	1	1
16	*wardi*	0	0	0	1	0	0	0	0	0	1	?	0	1	0	0	1	0	0	0	?	1	0	1	1	0	1	0	0	0	1	1	0
17	*blinni*	1	0	0	1	0	0	1	0	0	0	?	0	0	1	0	1	0	0	0	?	0	0	1	0	0	0	0	0	0	1	1	0
18	*jemezensis*	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1
19	*lanensis*	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	1	0	0	1	1	0	0
20	*wahkeenensis*	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0
21	*rallus*	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0
22	*latus*	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0
23	*utahensis*	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0
24	*limbus*	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0
25	*boultoni*	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1
26	*hubbsi*	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0
27	*tritus*	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1
28	*puteanus*	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	1	0	1
29	*oregonensis*	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0
30	*elliotti*	1	1	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0
31	*grahami*	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0
32	*gradyi*	1	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0
33	*harai*	0	1	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0
34	*wengerorum*	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0
35	*mackenziei*	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
36	*sierrensis*	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1
37	*sheldoni*	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0
38	*tahoensis*	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0
39	*lacicolus*	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0
40	*arizonensis*	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0
41	*pennaki*	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0
42	*coloradensis*	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0
43	*holsingeri*	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0
44	*putealis*	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	1	1	0	1	1	1	0
45	*duplus*	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1
46	*saltuaris*	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0
47	*quatsinensis*	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	0
48	*mysticus*	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0
49	*canadensis*	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0
50	*currorae*	1	0	0	1	0	0	0	0	1	0	?	0	0	1	1	0	0	0	1	?	0	0	1	0	0	1	1	0	1	1	1	0
51	*glacialis*	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1
52	*idahoensis*	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	0	0	0	1	1	0
53	*montanensis*	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0
54	*obscurus*	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	1	0	2	1	0	1	1	0	1	0	0	0	1	0	0
55	*secundus*	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0
56	*simplex*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0

Note: *Bactrurus brachycaudus*, *Crangonyx forbesi* and *Synurella ambulans* are outgroup species.

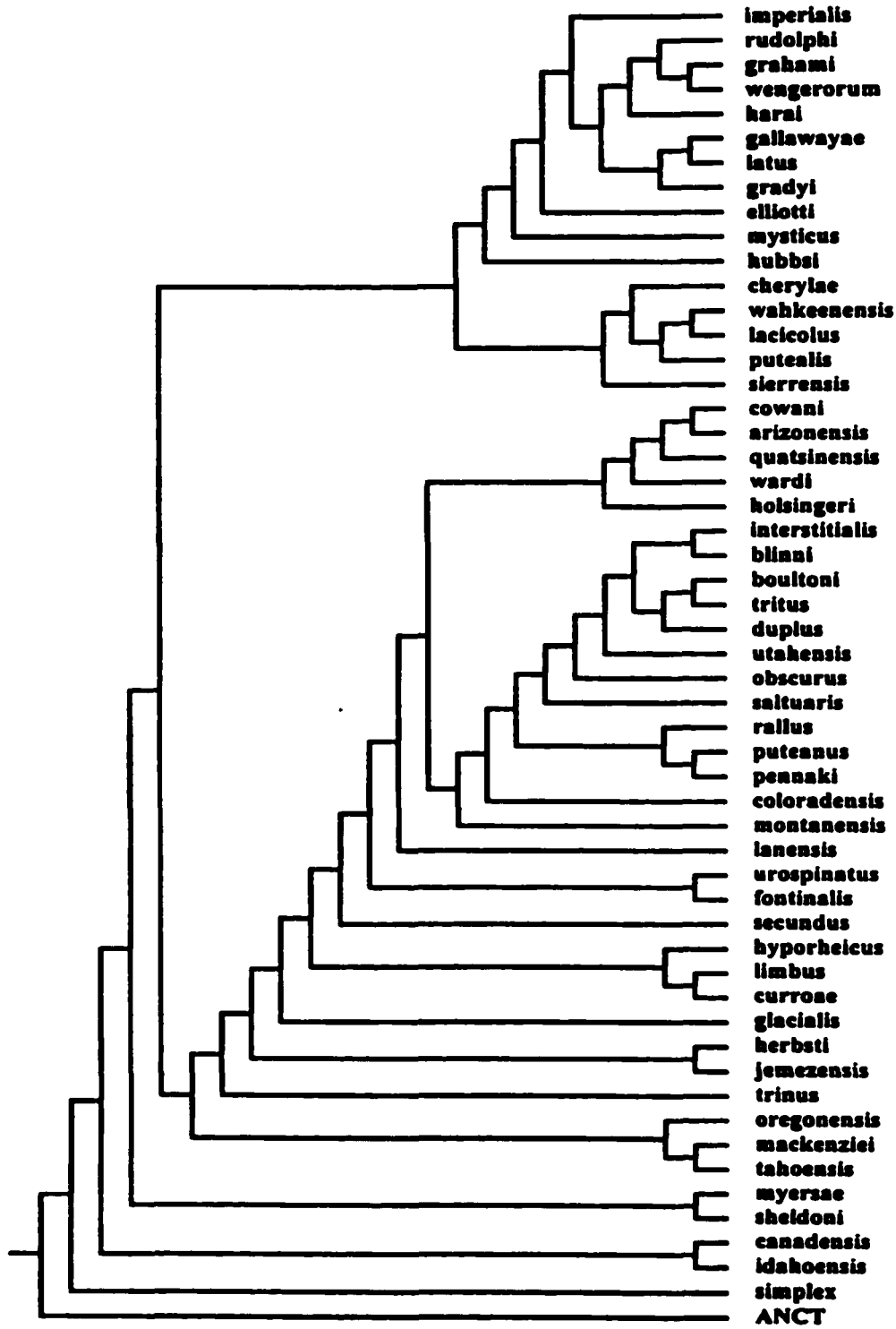

Fig. 87. Majority-Rule Consensus tree of the first-run using "all-zero" theoretical ancestor as an outgroup (see Cladistic Analysis for details); Characters not weighted and not ordered (CI: 0.16, RI: 0.52, tree length: 212).

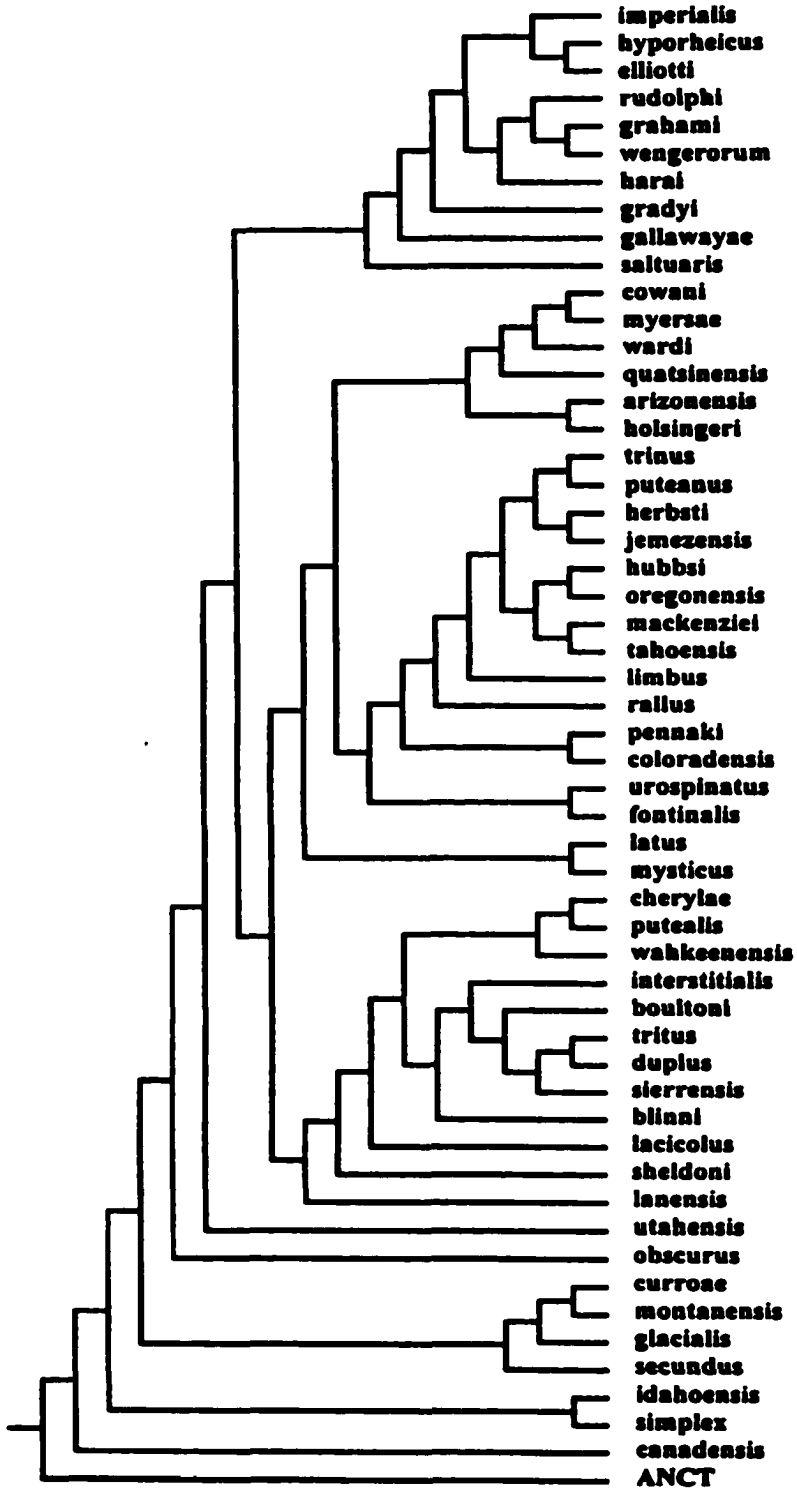

Fig. 88. Majority-Rule Consensus tree of the second-run using "all-zero" theoretical ancestor as an outgroup (see Cladistic Analysis for details); Characters partially weighted and ordered (CI: 0.15, RI: 0.47, tree length: 232).

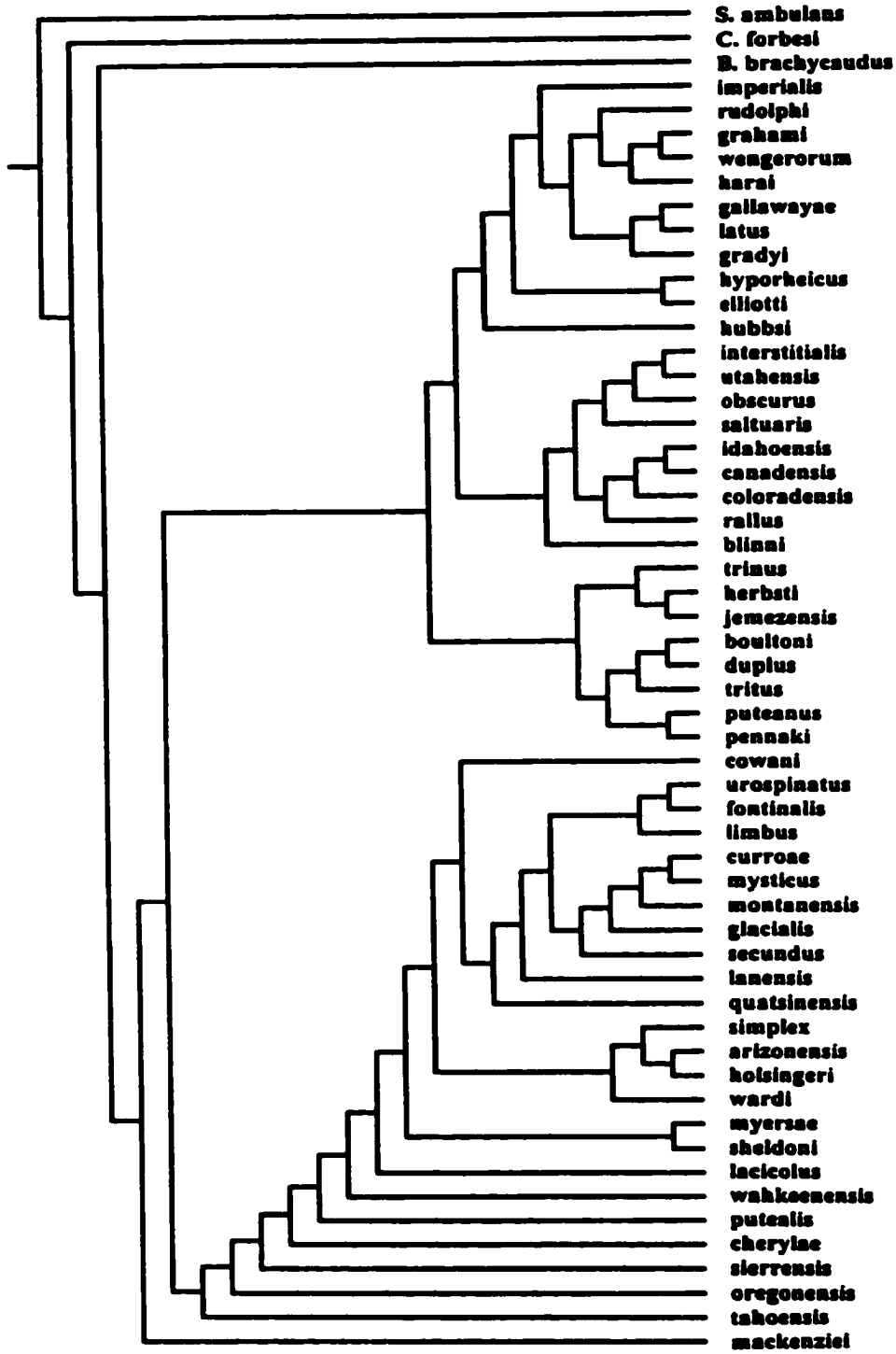

Fig. 89. Majority-Rule Consensus tree of the first-run using three non-*Stygobromus* species as outgroups (see Cladistic Analysis for details); Characters not weighted and not ordered (CI: 0.16, RI: 0.50, tree length: 232).

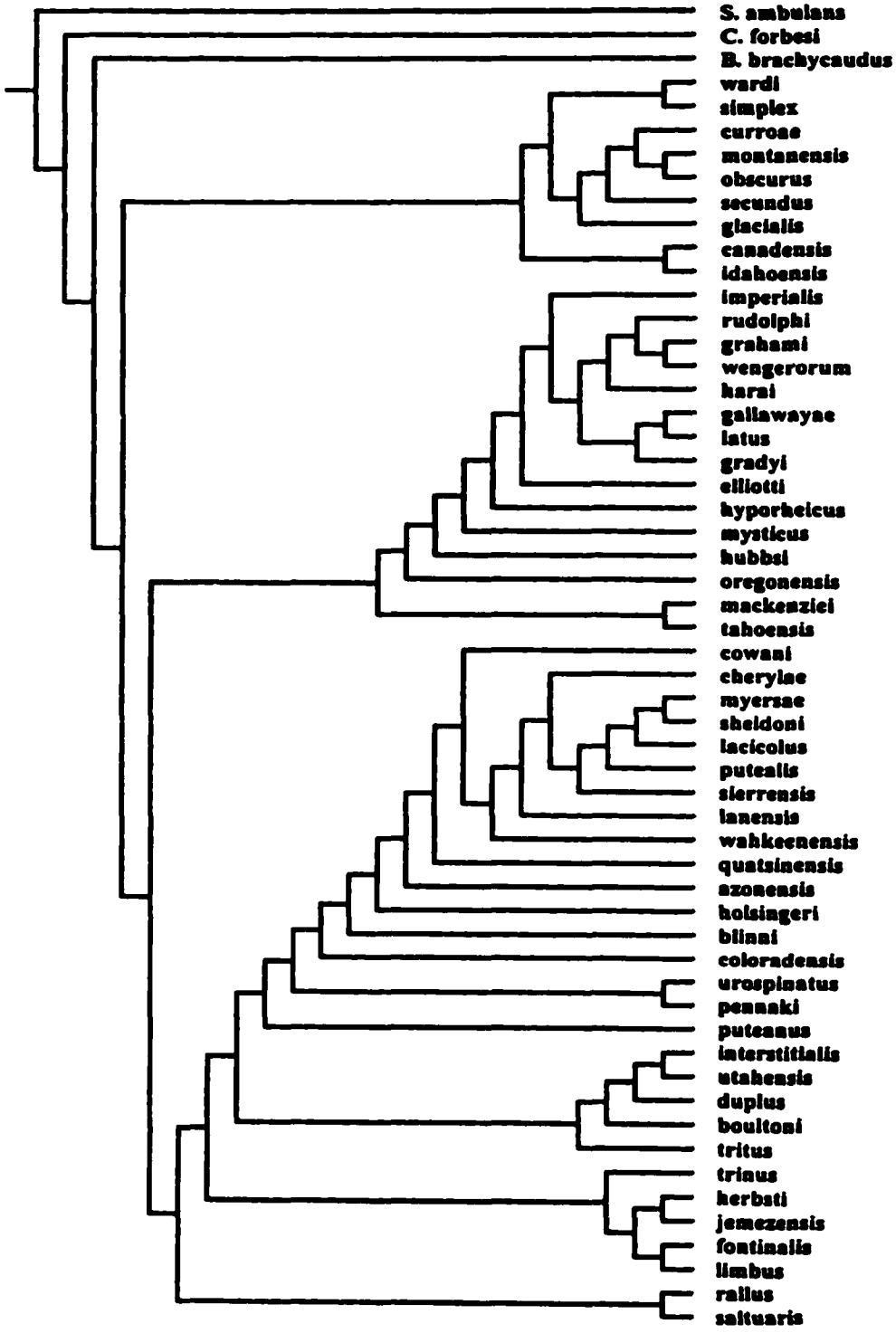

Fig. 90. Majority-Rule Consensus tree of the second-run using three non-*Stygobromus* species as outgroups (see Cladistic Analysis for details); Characters partially weighted and ordered (CI: 0.16, RI: 0.51, tree length: 229).

group species with Colorado species *S. simplex*. Such relationship implies that *S. idahoensis* close related with Washington-Montana-Oregon species cluster.

Except for these three more or less constant clusters, some pattern of related taxa can be traced in each category, either arranged as doublets or triplets within alternating larger clades with incongruous geographic distribution ranges. *S. wahkeenensis* and *S. lacicolus*, *S. puteanus* and *S. pennaki*, *S. herbsti* and *S. jemezensis* form a robust doublets, respectively (Fig.88). Moreover, *S. hyporheicus*, *S. limbus* and *curroae* (Figs. 87), *S. tritus*, *S. duplus*, *and S. sierrensis* form a stable triplets, respectively (Figs. 88).

II. Three non-*Stygobromus* Species as Outgroups

In comparison with the analysis using "all-zero" theoretical ancestor as an outgroup, an analysis was also conducted using three non-*Stygobromus* species from three genera which are thought to be closely related to *Stygobromus*. The four genera all belong to the family Crangonyctidae.

The first-run most consensus tree and second-run most consensus tree are very similar in composition of some clades. The most consensus tree also supports the monophlyly of California-Oregon-Washington clade, including *S. imperialis*, *S. rudolphi*, *S. grahami*, *S. gallawayae*, *S. latus*, S. *wengerorum*, *S. harai*, *S. gradyi*, *S. elliotti*, and *S. hubbsi* except *S. mysticus* (Figs. 89-90). The consensus trees also support two loosely stable pattern of geographic clusters which are similar to that of alternative analysis above:

1) California-Oregon-Washington species cluster, including *S. imperialis*, *S. rudolphi*, *S. grahami*, *S. wengerorum*, *S. harai*, *S. gallawayae*, *S. latus*, *S. gradyi*, *S. elliotti*, *S. hyporheicus*, and *S. hubbsi*.

2) Colorado-Arizona species cluster, including *S. urospinatus*, *S. fontanalis*, *S. holsingeri* and *S. arizonensis*.

For the second-run, *hubbsi* group and non-*hubbsi* group species (Fig. 90) can be also recognized. This possibly resulted from partially weighted data set during the analysis. The robustness of the two cluster clades in each category is remarkable. It indicates that these species are closely related.

Besides these two major constant clusters, some pattern of related taxa can be also traced in both runs, either arranged as doublets or triplets within alternating larger clades with incongruous geographic distribution ranges. The species *S. puteanus* and *S. pennaki*, *S. tritus* and *S. duplus*

form a robust doublets, respectively. Furthermore, *S. tritus, S. duplus, and S. boultoni, S. urospinatus, S. fontinalis* and *S. limbus* (Fig. 90) form a stable triplets.

Discussion and Conclusions

The resulting trees of the analyses indicate an impressively congruent topology. These congruencies are characterized by (1) a stable monophyletic clade of geographically related taxa, most belonging to California-Oregon species group; (2) the constant appearance of the same. "foreign" taxa (i.e., species which are not in the same physical area) in constant double/triplet configurations in some geographic clusters; and (3) several loose constant congruent clusters of taxa with geographic relation.

The existence of a relatively robust clade in each category of consensus trees implies phylogenetic relationships that are associated with certain large geographic regions. These regions comprise large parts of western North America rather than "smaller region" such as a state of the United States. If speciation events did occur at high rates in *Stygobromus,* distinct phylogenetic patterns of species from small areas with a remarkable diversity could be expected. The California-Oregon species, as well as Colorado-Montana species seem to indicate such peripatric or sympatric speciation events, typically resulting from interstitial dispersal of mature individuals or populations (see Notenboom, 1991; Holsinger, 1987b, 1993, 1994). The fact that *S. lanensis* and *S. saltuaris* in Oregon, *S. holsingeri* and *S. urospinatus* in Colorado co-exist in the same habitat seems to support such prediction and rationale.

A pattern of descent that encircles large regions is more obvious and conspicuous than speciation on a small scale, for example, the California-Oregon-Washington, as well as Colorado-Arizona-New Mexico species. The two major geographic clusters mentioned before have two features in common: first, they do not include all species found in that specific area; second, they are accompanied by "foreign" species. For example, Washington species *S. latus* and New Mexico species *S. curroae* appeares in the California-Oregon clade (Fig. 87, Figs. 89-90). Such phylogenetic pattern resembles a mosaic with complete parts and missing pieces. Moreover, it also implies that the species of these three geographic areas are closely related.

Stygobromus putealis found in Wisconsin particularly illustrates such rationale and vicariant biogeography of *Stygobromus*. It is discussed in the following Biogeogrphy section. To date, *S. putealis* is known only from a few wells in Wisconsin just east of the Driftless Area. It consistently appears in the California-Oregon clade in both runs and could be considered as a "foreign" taxon in the California-Oregon cluster since it has not been found in western North

America. Accordingly, however, other constant taxa in some geographic clusters (e.g., *S. puteanus*, *S. arizonensis*, *S. duplus*, *S. jemezensis*, see Figs. 87, Figs. 89-90) could either be misinterpreted as "foreign" species because of missing distribution data or be explained as evidence that the "foreigner" and its accompanied cluster are closely related. However, I tend to accept the latter scenario since it is more evolutionary significant and makes sense in terms of biogeography (also see Holsinger, 1986a, 1987b and 1994).

The appearance of "foreign" species seems to support the concept of mosaic evolution and vicariant biogeography in amphipods, with an assumed ancient, Mesozoic origin (Stock, 1981; Barnard and Barnard, 1983; Holsinger, 1978; Notenboom, 1991). However, the assumption of an ancient origin, whose present phylogentic pattern is still clouded by missing information or data, should not be ruled out. Various conceivable scenarios may have resulted in the present distribution of stygobiont amphipods, including major and minor ancient vicariant events, dispersal by rivers/currents and others.

This cladistic analysis in this study draw an outline picture of the phylogeny of the western North America species of *Stygobromus*. However, subsequent study could provide further insight by using molecular systematic techniques. In addition, a more robust view of the evolution of *Stygobromus* may be realized by an extended outgroup comparison using species of *Bactrurus*, *Stygonectes*, *Synurella*, and *Crangonyx*.

CHAPTER V

BIOGEOGRAPHY AND HABITATS

BIOGEOGRAPHY

The family Crangonyctidae is assumed to be derived from ancient freshwater ancestry, probably dating back at least to the Mesozoic (Holsinger 1978, 1986). Two lines of evidence support this theory: the first is that crangonyctids are exclusively freshwater and showing no apparent relationship with any marine species; second, the three largest genera (*Crangonyx*, *Stygobromus* and *Synurella*) of the family have a Holarctic distribution (Holsinger 1994, 1995), which suggests that they were well established on the Laurasian landmass prior to continental breakup in the late Mesozoic. Putative ancestors of the genus *Stygobromus* probably originated as an ancient freshwater lineage dating to the Mesozoic or earlier. Three lines of evidence support this hypothesis.

The first one is that *Stygobromus* is apparently represented in Eurasia by three species (*S. apscheronia*, *S. kazkhstanica* and *S. pusillus*) (Martynov 1930; Derzhavin 1945; Holsinger 1974, 1977, 1987). Furthermore, in view of the fact that large areas of Siberia have not been explored for aquatic crustaceans (Bowman and Holmquist 1975), the chances of finding additional species of *Stygobromus* in remote subterranean habitats there cannot be ruled out.

The second is that *S. quatsinensis*, a member of *hubbsi* group, is found in Vancouver Island, Canada and Alaska. Vancouver Island is presently isolated from the mainland on the east and south by marine waters of the Georgia and Juan de Fuca straights, respectively. Georgia Strait is a major feature of the general physiographic region known as the "Georgia Depression," a downward trending trough thought to have originated during a period of tectonic activity in the Late Cretaceaous (Jeletzky 1965; Sutherland Brown 1966). Two alternative hypotheses are proposed by Holsinger *et al.* (1987) to explain *S. quatsinensis* on a glaciated island separated from the mainland by marine straits. One theory suggests that it evolved from putative ancestors that were present on the island before development of the Juan de Fuca Strait in the Eocene. The other suggests that it gained access to the island from the mainland through interstitial dispersal in coarse sediments of the Quadra Sand which infilled parts of the Georgia Strait in the late Pleistocene. Both theories assume that this species has survived glaciation in subglacial groundwater refugia and does not conflict with the hypothesis of origin of *Stygobromus* above.

The third is that *S. putealis*, a member of the *hubbsi* group found in eastern Wisconsin, occurs approximately 1760 km east of the range of the western species of *Stygobromus*. If we assume

that species of the *hubbsi* group were derived from a common ancestral species or a cluster of closely related species and that the similarity of *S. putealis* to western species is more than coincidental, then the presence in Wisconsin of a species belonging to a group otherwise known only from the far western United States must clearly be regarded a relict distribution. Since the middle of the Cenozoic, climates have become increasingly drier, and in the west-central United States (i.e., across the Great Plains), north of central Texas, is nearly devoid of freshwater amphipods, either epigean or hypogean. If there was a continuous distribution of the *hubbsi* group progenitors across the west-central United States then it must have occurred prior to the Miocene while the climate in this region was still humid and provided support of aquatic habitats.

To explain these relict distributions, it was hypothesized that under certain conditions some aquatic subterranean species might have survived extended periods of glaciations in deep groundwater refugia beneath the ice and that their present ranges have not resulted from northward migration since Wisconsin time but instead probably reflect very old, preglacial distributions (Holsinger 1978, 1980, 1981; Lipps *et al.* 1979; Bruchhausen *et al.* 1979). The fact that most of species of the *hubbsi* group are found south of the southern extent of Pleistocene glaciation in North America strengthens this hypothesis.

As shown in Figures 91-93, the geographic distribution of species of *Stygobromus* in the western United States is widespread and scattered. Many of these species display highly insular ranges and all but nine are known only from a single locality. With one exception, even those species represented in two or more localities are restricted to small ranges.

An interesting question arises that is why species diversity of *Stygobromus* decreases from east to west in North America (see Holsinger 1986a)? From the discussion of phylogeny section in this paper, the *hubbsi* group appears to be a distinct evolutionary group within the genus (Fig. 94). With the exception of *S. putealis* from Wisconsin, the *hubbsi* group (and the other three species described above) is geographically disjunct from all other species of *Stygobromus* and occupies a position well isolated from all other subterranean amphipod genera of North America. The present distributional patterns of the western species have probably resulted from fragmentation of previously more widespread populations. The western United States has been marked by a series of major geological changes and climatic shifts since the Laramide Revolution, and modern landforms and climates are the result of events in the middle to late Tertiary such as the Cascadian Revolution and extensive regional volcanism. Numerous, isolated belts of cavernous limestone that characterized much of the karst terrane of this region played a

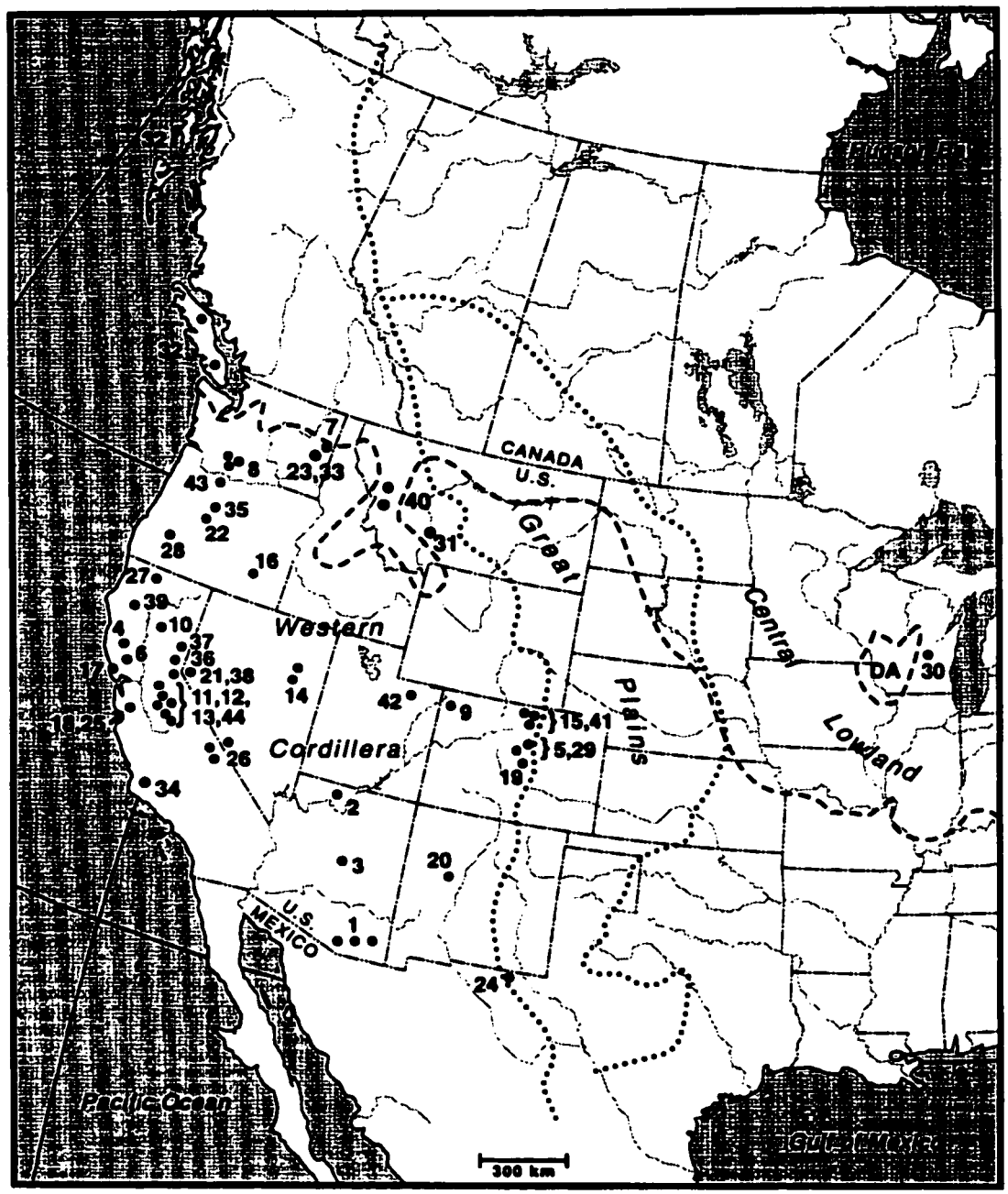

Fig. 91. Geographic distribution of 44 species of *Stygobromus* in the *hubbsi* group in North America. A closed circle indicates one to many closely proximate locality records for a species. 1, *S. arizonensis*; 2, *S. blinni*; 3, *S. boultoni*; 4, *S. cherylae*; 5, *S. coloradensis*; 6, *S. cowani*; 7, *S. duplus*; 8, *S. elliotti*; 9, *S. fontinalis*; 10, *S. gallawayae*; 11, *S. gradyi*; 12, *S. grahami*; 13, *S. harai*; 14, *S. herbsti*; 15, *S. holsingeri*; 16, *S. hubbsi*; 17, *S. hyporheicus*; 18, S. *imperialis*; 19, *S. interstitialis*; 20, *S. jemezensis*; 21, *S. lacicolous*; 22, *S. lanensis*; 23, *S. latus*; 24, *S. limbus*; 25, *S. mackenziei*; 26, *S. myersae*; 27, *S. mysticus*; 28, *S. oregonensis*; 29, *S. pennaki*; 30, *S. putealis*; 31, *S. puteanus*; 32, *S. quatsinensis*; 33, *S. rallus*; 34, *S. rudolphi*; 35, *S. saltuaris*; 36, *S. sheldoni*; 37, *S. sierrensis*; 38, *S. tahoensis*; 39, *S. trinus*; 40, *S. tritus*; 41, *S. urospinatus*; 42. *S. utahensis*; 43, *S. wahkeensis*; 44, *S. wengerorum.* The heavy dashed line represents the approximate southern extent of Pleistocene glaciation. DA = the Wisconsin Driftless Area.

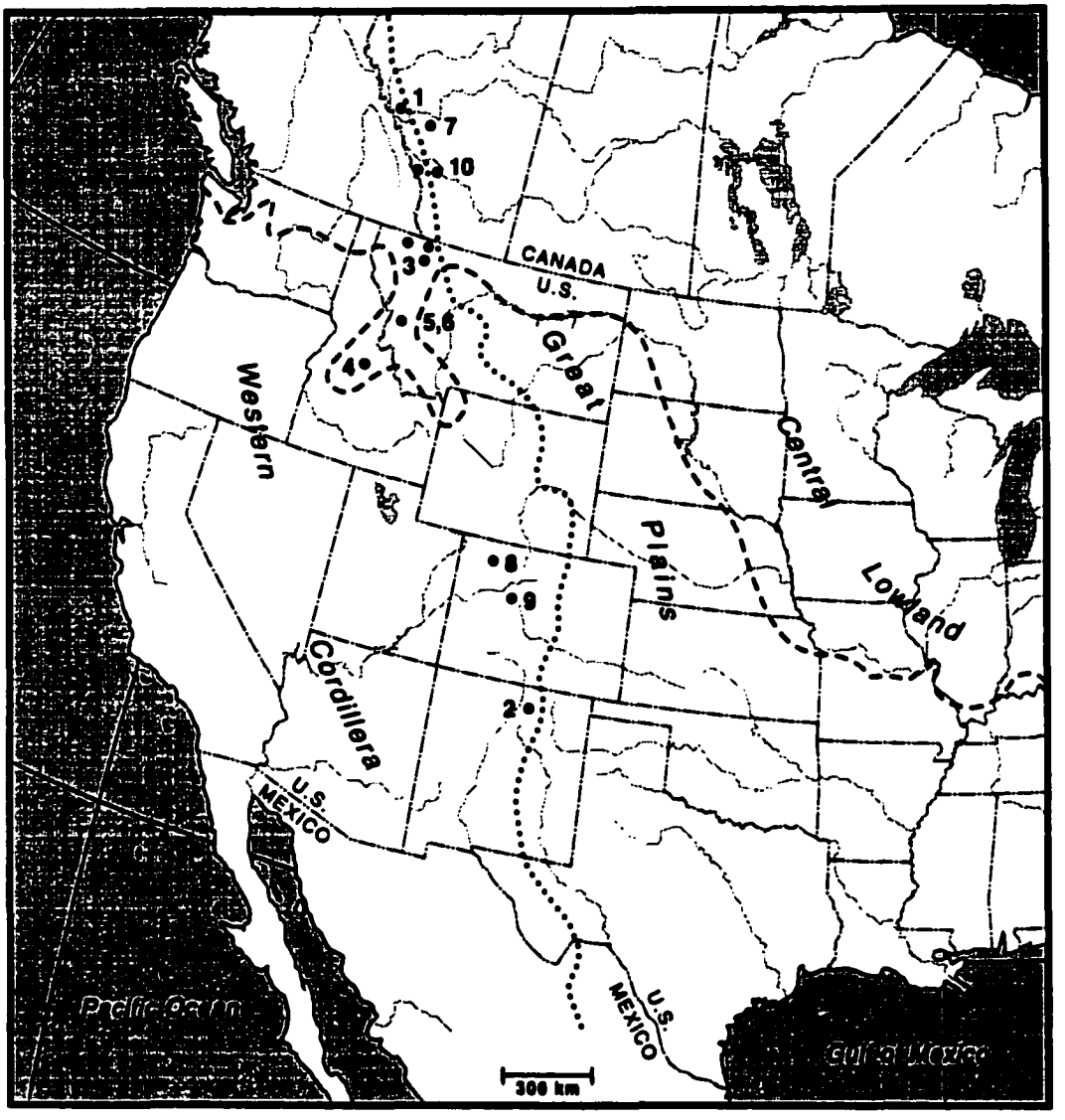

Fig. 92. Geographic distribution of non-*hubbsi* group species of *Stygobromus* in the western Cordillera of North America: 1, *S. canadensis*; 2, *S. curroae*; 3, *S. glacialis*; 4, *S. idahoensis;* 5, *S. montanensis*; 6, *S. obscurus*; 7, *S. secundus*; 8, *S. simplex*; 9, *S. wardi*; 10, specimens of 2 new species of *Stygobromus* from 3 localities west of Calgary that cannot be described without additional material. The heavy dashed line represents the approximate southern extent of Pleistocene glaciation.

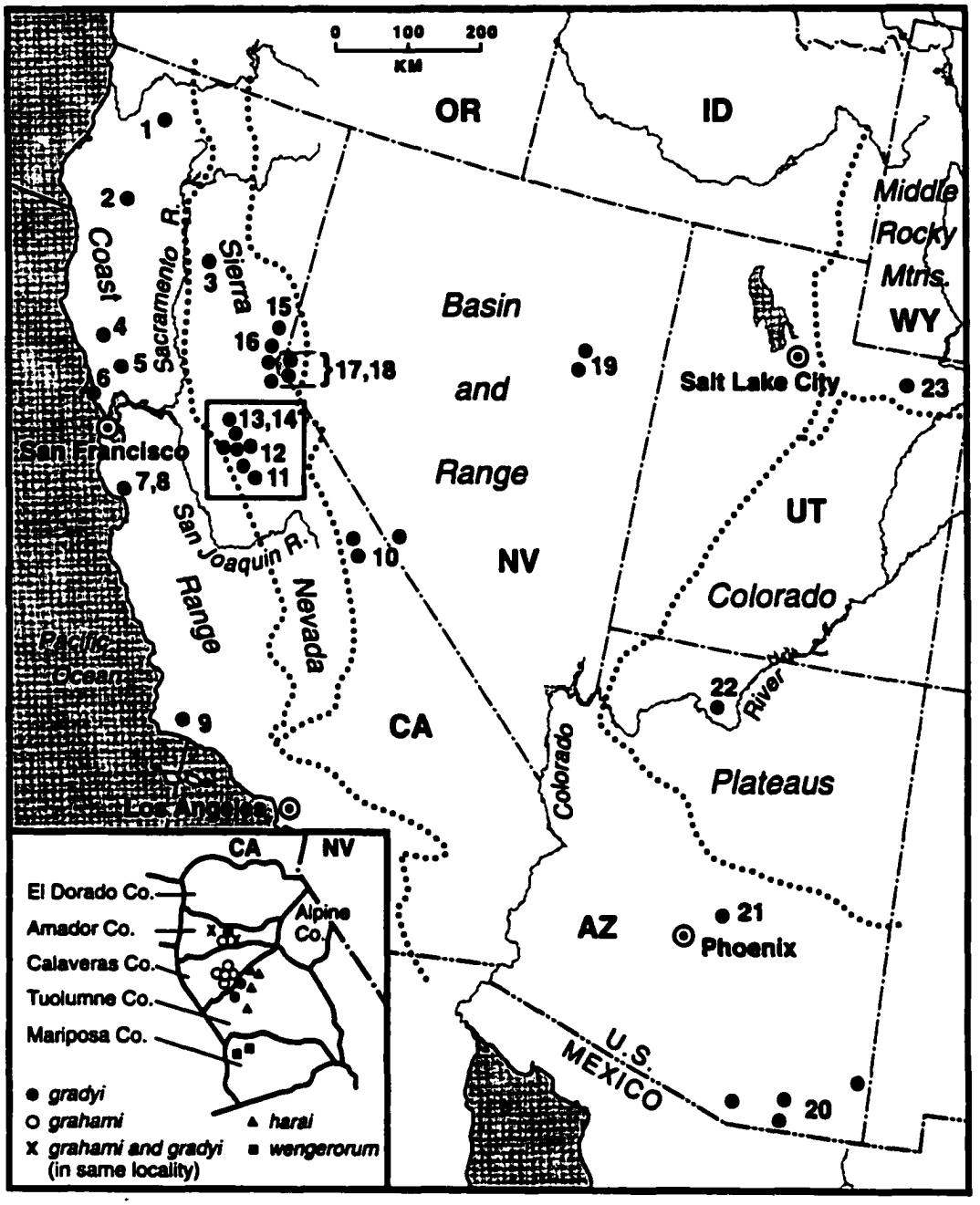

Fig. 93. Geographic distribution of *Stygobromus* in Arizona, California, Nevada and Utah, USA. A closed circle indicates one to several closely proximate localities for a species (number of recorded localities in parentheses). *hubbsi group*: 1, *S. mysticus* (1 loc.); 2, *S. trinus* (1 loc.); 3, *S. gallawayae* (1 loc); 4, *S. cherylae* (1 loc.); 5, *S. cowani* (1 loc.); 6, *S. hyporheicus* (1 loc.); 7, *S. imperialis* (1 loc.); 8, *S. mackenziei* (1 loc.); 9, *S. rudolphi* (1 loc.); 10, *S. myersae* (3 locs.); 11, *S. wengerorum* (2 locs.); 12, *S. harai* (4 locs.); 13, *S. grahami* (8 locs.); 14, *S. gradyi* (5 locs.); 15, *S. sierrensis* (1 loc.); 16, *S. sheldoni* (4 or 5 locs.); 17, *S. tahoensis* (9 or 10 sites in Lake Tahoe); 18, *S. lacicolous* (5 sites in Lake Tahoe); 19, *S. herbsti* (10 locs.); 20, *S. arizonensis* (4 locs.), 21, *S. boultoni* (2 locs.); 22, *S. blinni* (1 loc.); 23, *S. utahensis* (1 loc.). Insert: open circles, *S. grahami*; closed circles, *S. gradyi*; x, localities with both *S. grahami* and *S. gradyi*; closed triangles, *S. harai*; closed boxes, *S. wengerorum*.

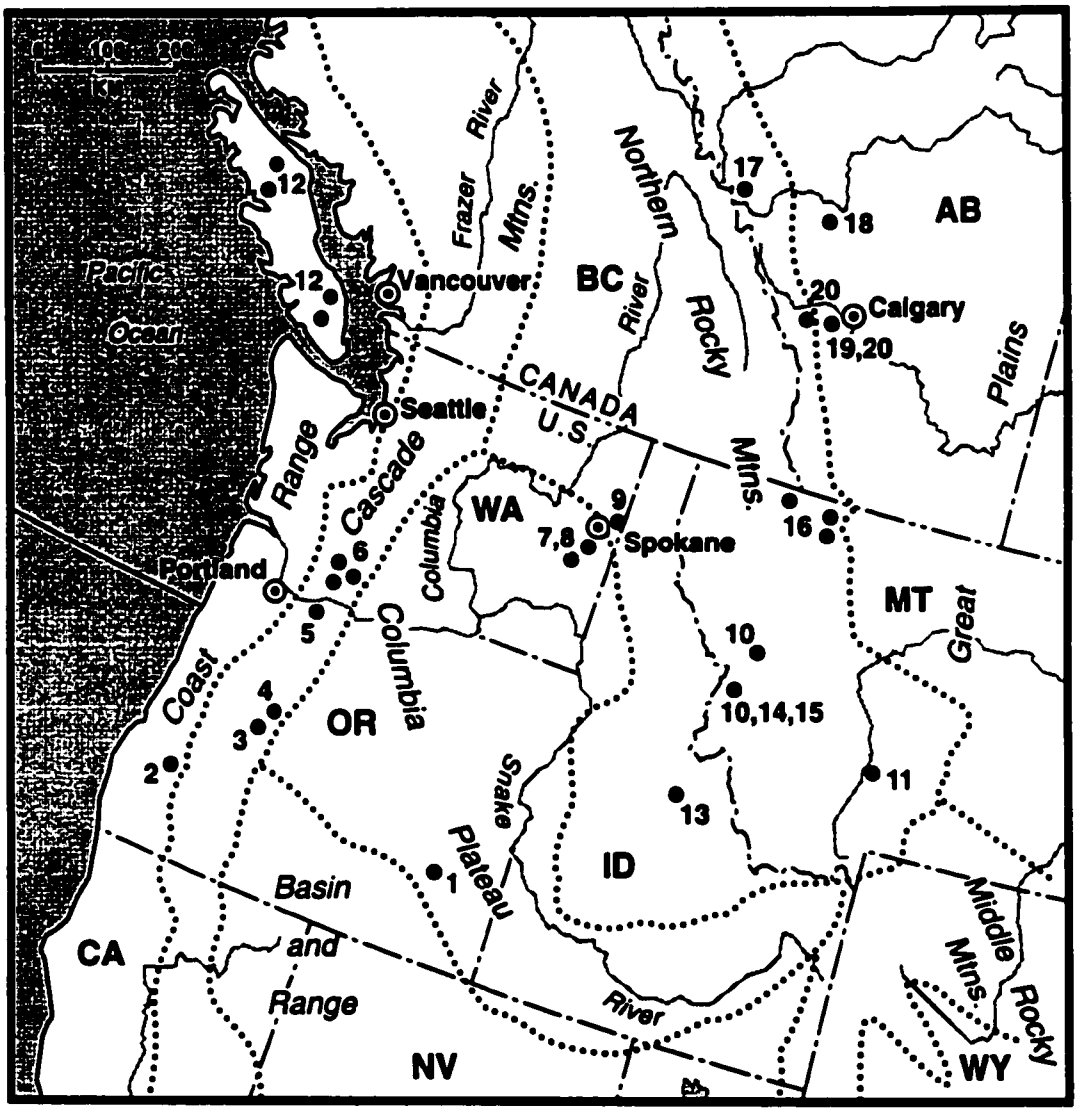

Fig. 94. Geographic distribution of *Stygobromus* in Idaho, Montana, Oregon, and Washington, USA; and Alberta and British Columbia, Canada. A closed circle indicates one to several closely proximate localities for a species (number of recorded localities in parentheses). *hubbsi* group: 1, *S. hubbsi* (1 loc.); 2, *S. oregonensis* (1 loc.); 3, *S. lanensis* (1 loc.); 4, *S. saltuaris* (1 loc.); 5, *S. wahkeenensis* (2 locs.); 6, *S. elliotti* (3 locs.); 7, *S. latus* (3 locs.); 8, *S. rallus* (2 locs.); 9, *S. duplus* (2 locs.); 10 *S. tritus* (2 locs.); 11, *S.,puteanus* (1 loc.); 12, *S. quatsinensis* (4 localities on Vancouver Island; 26 in southeastern Alaska not shown). Other species: 13, *S. idahoensis* (1 loc.); 14, *S. montanensis* (1 loc.); 15, *S. obscurus* (1 loc.); 16, *S. glacialis* (3 locs.); 17, *S. canadensis* (1 loc.); 18, *S. secundus* (1 loc.); 19 & 20, S. spp.(2).

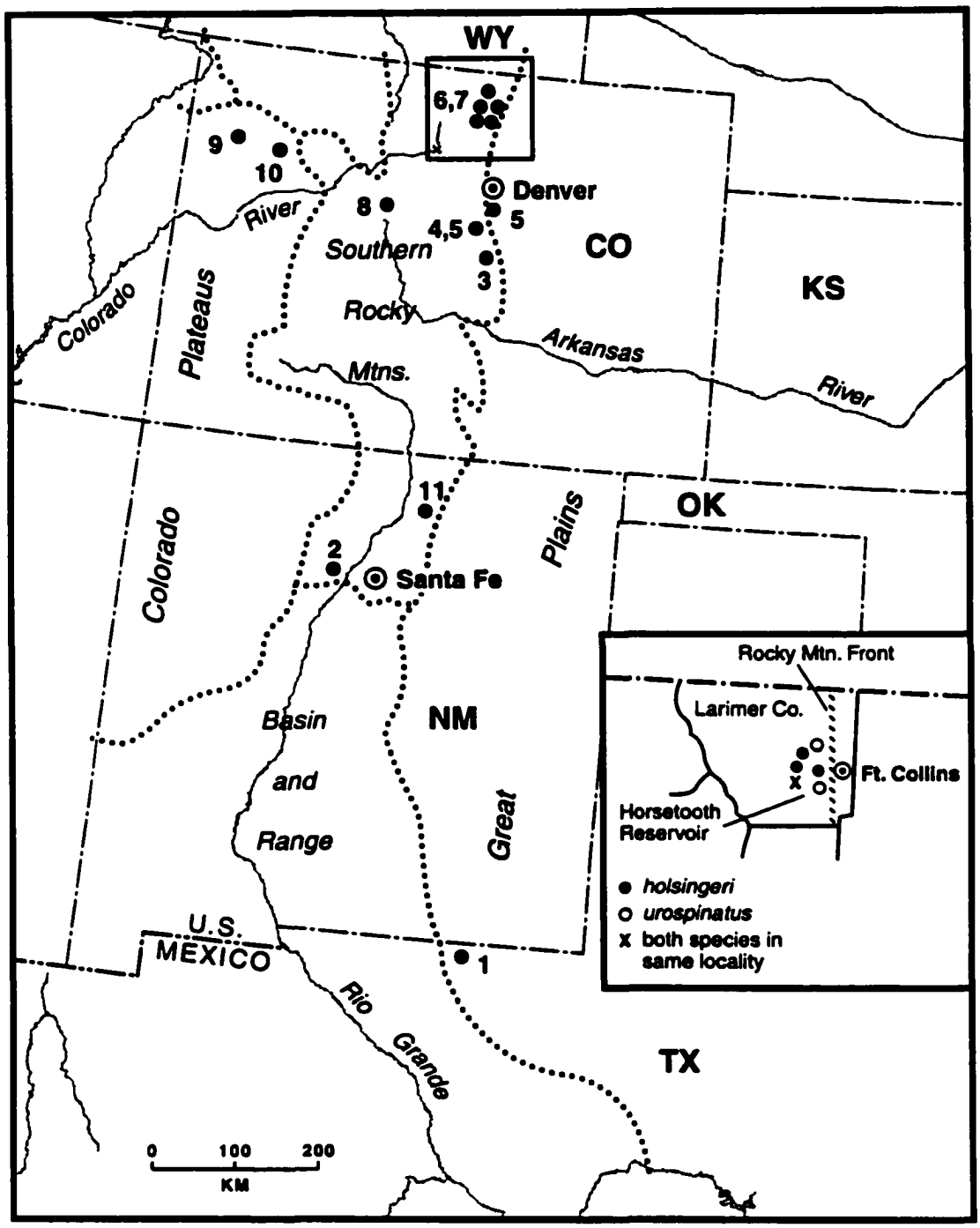

Fig. 95. Geographic distribution of *Stygobromus* in Colorado, New Mexico and far western Texas, USA. A closed circle indicates one to many closely proximate localities for a species (number of recorded localities in parentheses). *hubbsi* group: *S. limbus* (1 loc.); 2, *S. jemezensis* (1 loc.); 3, *S. interstitialis* (3 locs.); 4, *S. coloradensis* (8 or 9 locs.); 5, *S. pennaki* (7 or 8 locs.); 6, *S. holsingeri* (approx. 25 locs.); 7, *S. urospinatus* (3 locs.); 8, 9, *S. fontinalis* (2 locs.). Other species: 9, *S. wardi* (2 locs.); 10, *S. simplex* (1 loc.); 11, *S. curroae* (1 loc.). Insert: closed circles, *S. holsingeri;* open circles, *S. urospinatus;* x, both species from same locality.

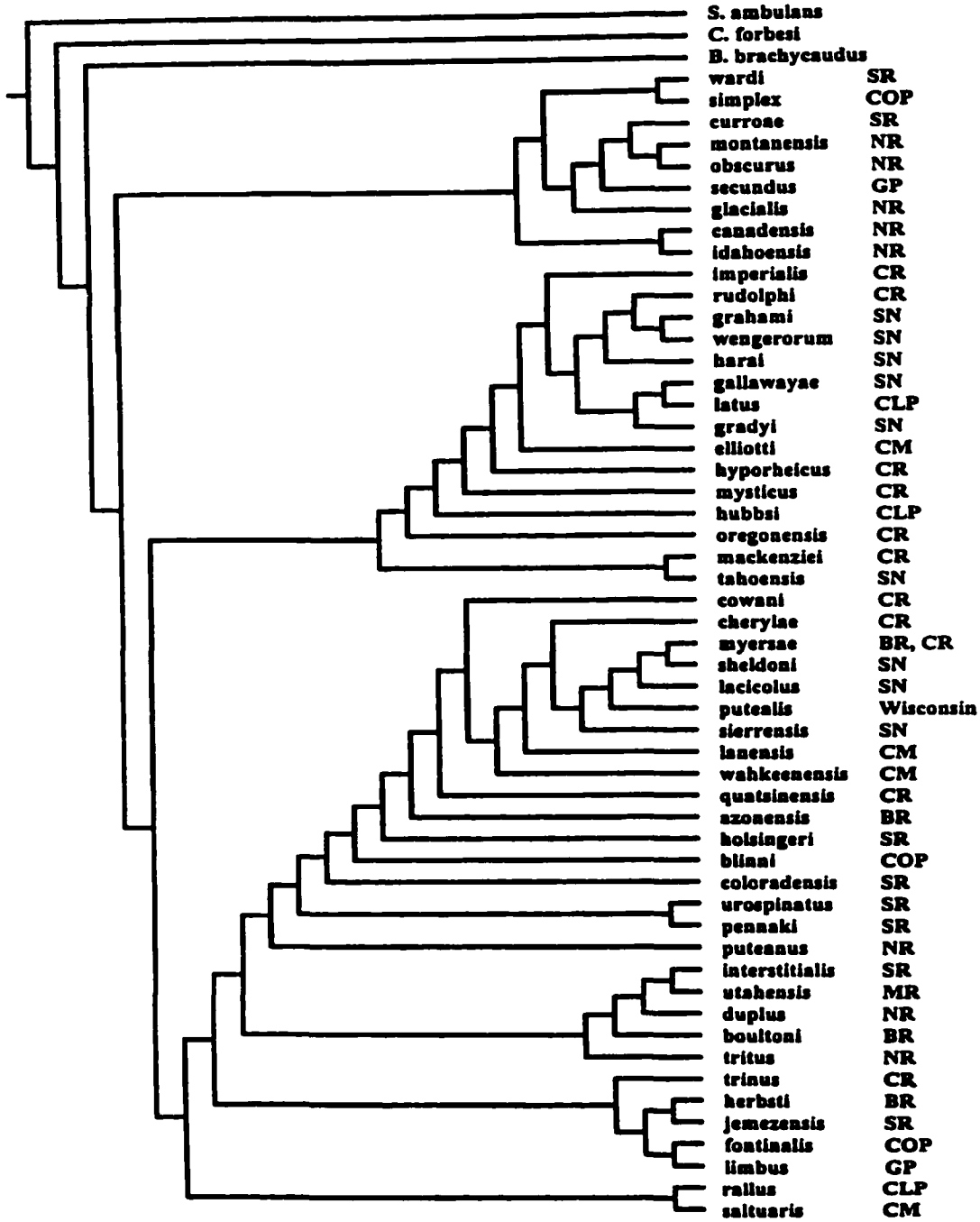

Fig. 96. Area cladogram of the second-run using three non-*Stygobromus* species (*Synurella ambulans*, *Bactrurus brachycaudus* and *Crangonyx forbesi*)as outgroups; Characters ordered and partially weighted. BR: Basin and Range (4 species), COP: Colorado Plateaus (3 species), NR: Northern Rocky Mountains (8 species), MR: Middle Rocky Mountains (1 species), SR: Southern Rocky Mountains (8 species), CLP: Columbia Plateau (3 species), CM: Cascade Mountains (4 species), SN: Sierra Nevada Mountains (9 species), CR: Coastal Range (10 species) and GP: Great Plains (2 species).

prominent role in promoting geographic speciation by physically isolating founder populations in discontinuous groundwater aquifers. According to King (1958), both regional and local relief and climatic contrasts have been greater in the Cordillera since the mid-Tertiary than at any other time and many habitats presently occupied by species of *Stygobromus* are not older than the Pleistocene. Moreover, as in the case of the Oregon and Washington lava tubes, they are even more recent. This fact may account for much of the overall decrease in numbers of species from eastern to western North America that has been documented for *Stygobromus*. As Pennak (1958) has pointed out for aquatic invertebrates in general: "the western states appear to present a set of conditions that should encourage isolation and speciation, especially in certain taxa containing macroscopic forms, and the West should theoretical have a unique population of freshwater of invertebrates."

Why are the *hubbsi* group species so morphologically similar? Although the 44 species of the *hubbsi* group comprise a relatively homogeneous assemblage, several patterns of speciation are discernible. The most obvious pattern is demonstrated by the four closely related cave species of the Sierra Nevada of California (Fig. 92: 3, 4, 5, 6), two species in Coast Range (Fig. 92: 2, 12) and nine species in Northern Rocky Mountains. The close morphological similarity of these species (especially in regard to their mouthparts and gnathopods), combined with their geographic proximity and similarity in habitats, is strongly indicative of their descent from a recent common ancestor (Fig. 91 and Fig. 92). The isolated nature of limestone caves in these regions could readiy provide dispersal barriers to troglobites (or phreatobites), thus effectively isolating populations to single caves or small clusters of caves.

Eleven other species appear to be closely related to the four species bound in the Sierra Nevada of California (see Figs. 91-92). While these species differ in the structure of their mouthparts (i.e., fewer plumose setae on the maxillae and fewer spines on the inner plate of the maxillipeds), their gnathopodal propods 1 and 2 are very similar to the Sierra Nevada species, and two of these species occupy habitats only 50 to 75 miles north of the California cave region. *Stygobromus hubbsi*, on the other hand, occurs in a lava cave approximately 560 km north of the Mother Lode region. Moreover, aside from their smaller size and other minor differences, four other species from California - S. *tahoensis*, *S. mackenziei*, *S. imperialis* and *S. sheldoni* also show affinity with the Sierra Nevada cave species.

In the remaining six species of the *hubbsi* group, three from Columbia Plateau and one in the Great Plains (Figs. 91-92), differ more significantly from the Sierra Nevada species. Most of them are far geographically separated, and occur on the periphery of the two mountain ranges. Thus, it would appear that at least two major centers of speciation within the *hubbsi* group have

taken place in the Cascade-Sierra Nevada range and Northern Rocky Mountains range, producing species which have successfully colonized a diversity of groundwater habitats, including caves, springs, and a deep lake Lake Tahoe.

The alternative hypothesis to explain the close morphological similarity is that it could result from habitat similarity. As indicated in Table 3, more than 50 percent of the cave species of *Stygobromus* in the western North America are known from cave pools and/or streams. Poulson and White (1969) suggested that the ability of troglobites to move between caves depends mainly on their size and suggested small species attained wide geographic distribution because they can move through stream gravels, soils, and various interstial media outside of caves. However, this generalization is too broad as pointed out by Holsinger (1978) since some larger species in a number of troglobitic and/or phreatobitic groups, such as beetles and amphipods, frequently have a wider range than the smaller species (Bar and Holsinger, 1971). But it is clear that dispersal among interstitiices or microspaces played an important role in distribution of *Stygobromus* if considering their small or tiny size and their swimming mobility. Therefore, geological more recent landform (e.g., Cascade Mountains and Rocky Mountains) and similar habitats may play a significant role in the morphological similarity of western species of *Stygobromus* in western North America.

Four instances of sympatric distribution among western species of *Stygobromus* strengthen the hypothesis above. The first sympatry is the curious association of three species in a well at Victor Crossing in Ravalli County, Montana (Fig. 94). Of the three species, however, only *S. tritus* is a member of the *hubbsi* group. A second member of the trio, *S. montanensis*, while showing a remote affinity with the *hubbsi* group, is at best only distantly related to any of the other western species of the genus. Unfortunately, very little is known about the well at Victor Crossing and it is not known whether these three species continuously share the same habitat or only occasionally come in contact. The second sympatric association occurs in Lake Tahoe, where both *S. tahoensis and S. lacicolus* (see Figs. 91-92) were obtained in periodic samples made in the early 1960s. Of the 16 samples studied, however, the two species were found together only twice, and *S. tahoensis* appeared to be much more abundant than *S. lacicolus*. The third sympatric occurrence is *S. holsingeri* and *S. urospinatus* in Larimer Co., Colorado (Fig. 95). The fourth sympatric association is *S. rallus* and *S. latus* in Spoken Co., Washington.

The hypothesis for the origin of *Stygobromus* in North America assumes that these genera or their ancestors were already established in continental freshwaters by the middle of Mesozoic (see Bousfield, 1958; Holsinger, 1974, 1978). From the discussions in the phylogenetic analysis section, *Stygobromus* and *Bactrurus* are established as sister groups. Although the hypothesized

cladistic relationship (Figs. 91-92) cannot give us a very clear picture of what the ancestor of *Stygobromus* looked like, they all clearly support a two lineage evolutionary scheme, one lineage being non-*hubbsi* group species (*glacialis*-like, see Figs. 92 and 96) and the other being *hubbsi* group species (*imperialis*- and *rallus*-like). Most of the species of *Bactrurus* have as many ancestral characters as the *glacialis* and *imperialis* species clusters. In addition, The California-Oregon-Washington (CA-OR-WA) species cluster is morphologically similar and forms a monophyletic cluster. Another cluster, CO-UT-AZ species, apparently closely related and adapted for life in microspaces or interstitials of the subterranean environment and has several autapomorphic characters.

The ancestor of *Stygobromus* is assumed to have resembled *Bactrurus* and separated from the common ancestor of *Synurella* and *Crangonyx* somewhere on Laurasia landmass. Extensive diversification occurred in North America as more and more species evolved after the break up of Laurasia. In Europe the surface species were probably driven out by *Synurella*, which is more common and widespread in Eurasia than North America, and other surface amphipods such as *Gammarus*. However, a few survived in the subterranean habitats, where they now probably represent relict species.

The present distribution patterns may not reflect the actual ranges of all species, nor can the number of species now recorded from the western United States be regarded as final. With the exception of many of the caves in the Mother Lode region of California, some of the lava tubes of Washington and other studied spots such as Lake Tahoe, numerous potential *Stygobromus* habitats remain to be investigated in the rugged mountainous country of the west. Many habitats such as wells, seeps, and remote caves and springs and their hyporheic zone of numerous streams and rivers in the more inaccessible regions of the Sierra Nevada, Utah, Wyoming and other mountain ranges may be expected to yield additional and/or new species when they are carefully sampled.

HABITATS

Species of *Stygobromus* have exploited a wide variety of groundwater habitats in North America. In an attempt to gain further insight into the relationships between biogeography and ecology among these species, general descriptive data on the different freshwater biotopes inhabited by the species of genus *Stygobromus* are summarized in Table 3. The data are from observations by the collectors, wherever that can be determined. The number of different habitats recorded for some species may not be complete, because in many cases only a few collections or specimens were available.

Species of *Stygobromus* have been collected from five different types of aquatic habitats: (1) 19 species were collected from caves, e.g., cave springs/pools, lakes or streams, based on 47 records; (2) 20 species from springs based on 54 records; (3) 9 species from wells based on 16 records; (4) 10 from hyporheic habitats based on more than 39 records, and (5) 2 species from surface deep lakes (e.g., Lake Tahoe) based on 15 records. The most common habitat types are subterranean waters and springs. Some species are found in one or both of these habitats. Only 2 species are found in deep lakes (*S. lacicolus* and *S. tahoensis*).

A total of 74 species are found in subterranean waters (primarily caves, including species in lava cave-- *S. elliotti*). An additional eight species are found in wells and 14 species in springs. The remaining species are found in hyporheic habitats collected by pumping-out from underground. Based on the absence of eyes, no pigmentation and a strong association with isolated spots in cold spring waters, many of the spring/seep dwellers are apparently preadapted to the life in subterranean waters (Holsinger 1994; Hubbard and Wang 1997).

Table 3. Records of species of *Stygobromus* from five kinds of generalized habitats in western North America

Species	caves[1]	springs[2]	wells[3]	hyporheic[4]	deep lake[5]
arizonensis	3	1	-	-	-
blinni	1	-	-	-	-
boultoni	-	-	2	-	-
canadensis	1	-	-	-	-
cherylae	-	1	-	-	-
coloradensis	-	-	-	-	10(+)
cowani	-	1	-	-	-
curroae	-	-	-	1	-
duplus	-	-	2	-	-
elliotti	3	-	-	-	-
fontinalis	-	2	-	-	-
gallawayae	-	1	-	-	-
glacialis	3	-	-	-	-
grahami	8	-	-	-	-
gradyi	4	-	-	-	-
harai	3	1	-	-	-
herbsti	-	10	-	-	-
holsingeri	-	1	-	10(+)	-
hubbsi	1	-	-	-	-
hyporheicus	-	-	-	1	-
idahoensis	-	-	-	1	-
imperialis	1	-	-	-	-
interstitialis	-	-	-	3	-
jemezensis	-	-	1	-	-
lacicolus	-	-	-	-	5
lanensis	-	1	-	1	-
latus	-	6	-	-	-
limbus	1	-	-	-	-

1- include 1 mine records each for *S. arizonensis* and *S.harai* and caves in limestone or basalt for all others.
2- include PVC wells driven into stream beds.
3- include interrupted streams for *S. holsingeri*.
4- include only 2 species from Lake Tahoe (precise habitat is unknown).

Table 3, continued

Species	caves	springs	wells	hyporheic	deep lake
mackenziei	1	-	-	-	-
montanensis	-	-	1	-	-
myersae	-	3	-	-	-
mysticus	-	-	1	-	-
obscurus	-	-	1	-	-
oregonensis	1	-	-	-	-
pennaki	-	-	-	10(+)	-
*putealis**	-	-	5	-	-
puteanus	-	-	1	-	-
quatsinensis	9	8	-	-	-
rudolphi	-	1	-	-	-
rallus	-	5	-	-	-
saltuaris	-	-	-	1	-
sierrensis	-	1	-	-	-
sheldoni	-	5	-	-	-
secundus	-	1	-	-	-
simplex	1	-	-	-	-
tahoensis	-	-	-	-	10
trinus	1	-	-	-	-
tritus	-	-	2	-	-
urospinatus	-	3	-	-	-
utahensis	1	-	-	-	-
wardi	2	-	-	-	-
wengerorum	2	-	-	-	-
wahkeenensis	-	1	-	-	-

* This species was recordred in Wisconsin.

CHAPTER VI

SUMMARY AND CONCLUSIOINS

This dissertation presents a study of the systematics of the subterranean amphipod genus *Stygobromus* of family Crangonyctidae in western North America. A total of 53 species of *Stygobromus* from western North America (including one species from Wisconsin) are recognized, 28 of which are new to science. All species are described and illustrated using external morphological features. A key to the western North America species of *Stygobromus* is given, as well as a summary of habitats of the species.

Cladistic analyses are conducted using 32 external morphological characters and two categories of outgroup choices: "all-zero" theoretical ancestor and three non-*Stygobromus* species. The consensus trees of unordered/unweighted and ordered/partially weighted are developed. The results of both categories support one monophyletic species cluster, which includes most species in California. Two loose constant congruent species clusters were also recognized in the two category runs: a California-Oregon-Washington species cluster includes *S. imperialis*, *S. rudolphi*, *S. gallawayae*, *S. latus*, *S. grahami*, *S. wengerorum*, *S. harai*, *S. gradyi*, *S. elliotti*, *S. mysticus*, and *S. hubbsi*; a Colorado-Idaho-Montana species cluster includes *S. urospinatus*, *S. fontanalis*, *S. pennaki*, *S. coloradensis*, *S. canadensis*, and *S. idahoensis*. The number of species in each of the two loose constant clusters of the two categories is variable.

The species diversity of *Stygobromus* decreases from east to west in North America, possibly resulting from geologically more recent landforms in western North America. In addition, many habitats presently occupied by western species of *Stygobromus* may not be older than the Pleistocene. Some lava tubes in Oregon and Washington are even more recent. This explanation and the similarity of habitats may also account for close morphological similarity of *hubbsi* group species in western North America.

REFERENCES

Bar, T. C. 1968. Cave ecology and the Evol., of troglobites. Evol. Biol., **2**: 35-102.

Barr, T.C. and J. R. Holsinger 1971. Biogeography of troglobites. Nat. Speleologica Soc. Bul., **33**: 115-118.

Barr, T.C. and J. R. Holsinger 1985. Speciation in cave faunas. Ann. rev. ecol. syst., **16**; 313-337.

Barnard, J. L. 1958. Index to the families, genera, and species of the Gammaridean Amphipoda (Grustacea). Occasional Papers of the Allan Hanncock Found., **19**: 1-145.

Barnard, J. L. 1976. Affinities of *Paraniphargus lelouparum* Monod, A Blind Anchialine Amphipod (Crustacea) from the Galapagos Islands. Proc. Biol. Soc. Washington, **89**: 421-432.

Barnard, J. L. and G. S. Karaman 1991. The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Part I. Records of the Australian Mus. Suppl., **13**: 1-417.

Barnard, J. L. and C. M. Barnard 1983. Freshwater Amphipoda of the world. I. Evol.,ary patterns, II. Handbook and bibliography. Hayfield Associates, Mt. Vernon, Virginia, pp I- viii, 1-830.

Barriel, V. and P. Tassy 1993. Characters, observations and steps: Comments on Lipscomb's "Parsimony, homology and the analysis of multistate characters." Clad. 9:223-232.

Birstein, J. A. 1940. Malacostraca. *In*: Life in the fresh water of the USSR. p405-430

Bousfield, E. L. and J. R. Holsinger 1989. A new crangonyctid amphipod crustacean from hypogean fresh waters of Oregon. Canadian J.of Zool., **67**: 963-968.

Bousfield, E. L. 1958. Fresh-water amphipod crustaceans of glaciated North America. Canadian Field Nat., **72**:55 113.

Bousfield, E. L. 1961. New records of fresh-water amphipod crustaceans from Oregon. Nat. Hist. Papers of Nat. Mus. of Canada, **12**:1-7.

Bousfield, E. L. 1973. Shallow-water gammaridean Amphipoda of New England. Xii+312 pages. Ithaca: Cornell University Press.

Bousfield, E. L. 1977. A new look at the systematics of gammaroidean amphipods of the World. Proc. of the 3rd InterNat. Colloquium on *Gammarus* and *Niphargus*, Schlitz, West Germany, 1975. Crust. (supplement), **4**: 282-316.

Bousfield, E. L. 1982. A second new subterranean amphipod crustacean of the genus*Stygobromus* (Crangonyctidae) from Alberta, Canadian J. of Zool., **59** (9): 1827-1830.

Bowman, T. E. and C. Holmquist, 1975. *Asellus* (*Asellus*) *alaskensis*, n. sp., the first Alskan Asellus, with remarks on its Asian affinities (Crustacea: Isopoda: Asellidae). Proc. of Biol. Soc. of Washington, **88** (7): 59-72.

Cope, E. D. 1872. On the Wyandotte Cave and its fauna. Amer. Nat.. **6**: 406-422.

Creaser, E. P. 1934. A new genus and species of blind amphipod with notes on parallel Evol., in Gertain amphipod genera. Occasional Papers of the Univ. of Michigan Mus. of Zool., **282**: 105, 1 plate.

Culver, D.C. T.C. Kane and D.W. Fong 1995. Adaptation and Evol., in caves. Harvard University Press. Cambridge. pp223.

Culver, D. C. 1970a. Analysis of simple cave communities: niche separation and species packing. Ecol., **51**: 949-958.

Culver, D. C. 1970b. Analysis of simple cave communities, I: caves as islands. Evol.,, **24**: 463-474.

Culver, D. C. 1971a. Analysis of simple cave communities, III: Control of abundance. Amer. Midland Nat., **85**: 173-187.

Culver, D. C. 1971b. Caves as archipelagoes. Nat. Speleological Soc. Bull., **33**: 97-100.

Culver, D. C. 1973. Competition in spatially heterogeneous systems: an analysis of simple cave communities. Ecol., **54**: 102-110.

Culver, D. C. and J. R. Holsinger 1969. Preliminary observations on sex ratios in the subterranean amphipod genus *Stygonectes* (Gammaridae). Amer. Midland Nat., **82**: 631-633.

Culver, D. C., J. R. Holsinger and R. A. Baroody 1973. Toward a predictive cave biogeography: the greenbarier valley as a case study. Evol., **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. Amer. Midland Nat., **85**: 74-84.

Davies, W. E. 1958. Caverns of West Virginia. West Virginia Geol.and Econ. Surv., **19** (A): 1-330.

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 MicroBiol.). *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.

Dunbar, C. O. 1960. Historical Geology. New York, John Wiley & Sons, Inc. IX+500 pages.

Derzhavin, A.N. 1945. The subterranean amphipoda of *Transcaucasus*. Bull. of. Acad. Soc. Azerbaidjan. **8**: 27-43.

Farris, J. S. 1983. The logic basis of phylogenetic analysis. p1-36 in Advances in Clad., Vol. 2 (N.I. Platnick and V.V. Funk, eds.). Columbia University Press.

Farris, J. S. 1988. HENNIG86, ver. 1.5. Microcomputer program available from author: 41 Admiral St. Port Jefferson Station, New York 11776, USA.

Frumhoff, P. C. and H. K. Reeve 1994. Using phylogenies to test hypotheses of adaptation: A critique of some current proposals. Evol., **48**:172-180.

Frantz, T. C. and A. J. Cordone 1966. A preliminary checklist of invertebrates collected from Lake Tahoe, 1961-1964. Occasional Papers of Biol. Soc. of Nevada, **8**: 1-12.

Greeley, R. 1971. Geology of selected lava tubes in the Bend area, Oregon. Oregon Dept. of Geol. and Mineral Industries, **71**: 1-47, plates 1-3.

Halliday, W. R. 1962. Caves of California. Species Report of the Western Speleological Survey, pp140.

Halliday, W. R. 1963. Caves of Washington. Information Circular No. 40 of the Washington Division of Mines and Geology, pp132, 9 plates.

Hauser, D. L. and W. Presch. 1991. The effect of ordered characters on phylogenetic reconstruction. Clad. **7**: 243-265.

Holmes, S. J. 1909. Descriptioin of a new subterranean amphipod from Wisconsin. Trans. of the Wisconsin Acad. of Sci., Arts and Letters, **16**: 77-80, plates 6-7.

Hay, W. P. 1903. Observations on the crustacean fauna of Nickajack Cave, Tennessee and vicinity. Proc. of the United States Nat. Mus., **25** (1292): 417-439.

Hill, L. M. 2000. The end of the line – Malheur Cave survey. NSS Newsl **58** (2): 38-41.

Holsinger, J.R. 1964. The Biol. of Virginia caves. Pages 57-74 in H. H. Douglas, Caves of Virginia. Falls Church, Virginia: Econ-Print.

Holsinger, J.R. 1966. Subterranean amphipods of the genus *Stygonectus* (Gammaridae from Texas. Amer. Midland Nat., **76**: 100-124.

Holsinger, J.R. 1967. Systematics, speciation and distribution of the subterranean amphipod genus *Stygonectus* (Gammaridae). Bull. of U.S. Nat. Mus., **259**: 1-176.

Holsinger, J.R. 1969a. Biography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians, p19-50 *In* P. C. Holt, editor, The Distributional History of the biota of the southern Appalachians, Part I: Invertebrates, Blacksburg, Virginia: Virginia Polytechnic Institute and State university Press.

Holsinger, J.R. 1969b. The systematics of the North Amer. subterranean amphipod genus *Apocrangonyx* (Gammaridae), with remarks on ecology and zoogeography. Amer. Midland Nat.., **81** (1): 1-28.

Holsinger, J.R. 1971. A new spcies of the subterranean amphipod genus *Allocrangonyx* (Gammaridae), with a redescription of the genus and remarks on its zoogeography, Internat. J.. of Speleology, **3**:317-331, 7 plates.

Holsinger, J.R. 1972. The freshwater amphipods of North America-biota of freshwater ecosystems. Ident. man. U. S. EPA, **4**: 244-281.

Holsinger, J.R. 1973. Two new species of the subterranean amphipod genus Mexiweckelia (Gammaridae) from Mexico and Texas, with notes on the origin and distribution of the genus. Bull. of the Assoc. for Mexican Cave Studies, **5**:1-12.

Holsinger, J.R. 1974a. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States. Smithsonian Contributions to Zoology, **166**: 1- 63.

Holsinger, J.R. 1974b. Systematics of subterranean amphipod genus *Stygobromus* from Alberta, Canada. Canadian J. of Zool., **59**: 1827-1830.

Holsinger, J.R. 1975a. Descriptions of Virginia caves. Bull. of the Virginia Division of Mineral Resources, **85**: 1-450, 7 plates.

Holsinger, J.R. 1975b. Observation on the dispersal of the cavernicolus amphipod crustacean *Crangonyx antennatus* (Gammaridae). Assoc. of Southeastern Biologists Bull., **22**: 58[abstract].

Holsinger, J.R. 1976. The cave fauna of Pennsylvania. Pages 72-87 in W. B. White, editor, Geology and Biol. and Pennsylvania Caves. Pennsylvania Geol. Surv. General Geol. Rep., 4th seres, **66**: 103 pages.

Holsinger, J.R. 1977. A review of the systematics of the Holarctic amphipod family Crangonyctidae. Crust. Supplementary. **4**: 244-281.

Holsinger, J.R. 1978. Systematics of the subterranean amphipod genus *Stygobromus*, Part II: Species of the eastern United States. Smithsonian Contributions to Zool., **266**: 1-144.

Holsinger, J.R. 1980. *Stygobromus canadensis*, a new subterranean amphipod crustacean (Crangonyctidae) from Canada, with remarks on Wisconsin refugia. Canadian J. of Zool., **58**:290-297.

Holsinger, J.R. 1981. *Stygobromus canadensis*, a troglobitic amphipod crustacean from astleguard Cave, with remarked on the concept of cave glacial refugia. Proc. of the 8th InterNat. Congr. of Speleology, **1**: 93-95.

Holsinger, J.R. 1983. The subterranean crustacean fauna of Castleguard Cave, Columbia icefields, Alberta, Canada and its zoogeographic significance. Arctic and Alpine Research, **15** (4): 543-549.

Holsinger, J.R. 1986a. Zoogeographic patterns of North Amer. subterranean amphipod crustaceans. In: Crustacean Biogeography-ed. by Robert H. Gore and Kenneth L. Heck. Boston. pp85-106.

Holsinger, J.R. 1986b. Holarctic crangonyctid amphipods. In: Stygofauna Mundi-ed. Lazare Botosaneanu. Leiden. E. J. Brill, Netherlands. pp 535-549.

Holsinger, J.R. 1987a. Redescription of the Stygobiont amphipod crustacean *Stygobromus pusillus* (Crangonyctidae) from the Soviet Union, with comments on taxonomic and zoogeographic relationships. J. of Crust. Biol., **7** (2): 249-257.

Holsinger, J.R. 1987b. *Stygobromus quatsinensis*, a new amphipod crustacean from caves on Vancouver Island, British Columbia, with remarks on zoogeographic relationships. Candaian J. of Zool., **65**: 2202-2209.

Holsinger, J.R. 1988. Troglobites: the Evol., of cave-dwelling organisms. Amer. Sci. **76**: 146-153.

Holsinger, J.R. 1991. What can vicariance biogeographic models tell us about the distribution history of subterranean amphipods? Hydobiologia, **223**: 43-45.

Holsinger, J.R. 1993. Biogeographic patterns of North Amer. subterranean amphipods in the genus *Stygobromus* (Crangonyctidae). Proc. of the 11th InterNat. Congr. of Speleology, pp118-120.

Holsinger, J.R. 1994. Pattern and process in the biogeography of subterranean amphipods. Hydrobilogia, **287** (1): 131-145.

Holsinger, J.R. 1997. Biogeographic significance of recently discovered amphipod crustaceans (*Stygobromus*) in caves of southeastern Alaska and Vancouver Island. Proc. of the 12th Internat. Congr. of Speleology, **3**: 347-349.

Holsinger, J. R. and R. A. Baroody and D. C. Culver 1976. The invertebrate cave fauna of West Virginia. Bull. of the West Virginia Speleological Surv., **7**: 1-82.

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 1968. A new genus and species of subterranean amphipod (Gammaridae) from Puerto Rico, with notes on its ecology, Evol., and relationship to other Caribbean amphipods. Crust., **15**:249-262.

Holsinger, J.R. and S. B. Peck 1971. The invertebrate cave fauna of Georgia. Nat. Speleological Soc. Bull., **33**: 23-44.

Holsinger, J.R. and W. L. Minckley 1971. A nw genus and two new species of subterranean amphipod crustaceans (Gammaridae) from Northern Mexico. Proc. of Biol.. Soc. of Washington, **83**: 425-444.

Holsinger, J.R., J. S. Mort and A. D. Recklies 1983. The subterranean crustacean fauna of Castleguard Cave, Columbia Icefields, Alberta, Canada, and its zoogeographic significance. Arctic and Alpine Research, **15** (4): 543-549.

Holsinger, J.R. and D. P. Shaw 1986. A new stygobiont amphipod crustacean (Crangonyctidae, *Stygobromus*) from glaciated karst on Vancouver Island, Canada. Proc. of the 9th Internat. Congr. of Speleology, 98-101.

Holsinger, J.R., K.R. Carlson and D. P. Shaw 1997. Biogeographic significance of recently discovered amphipod crustacean (*Stygobromu*) in caves of southeastern Alaska and Vancouver Island. Proc. of the 12th Internat. Congr. of Speleology, **3**: 347-349.

Hubbard, D.A. and D. Wang 1997. A preliminary report on some invertebrate cave fauna of China. Proc. of 12th Internat. Congr. of Speleology, Switzerland, **3**: 311-313.

Hubricht, L. and J.G. Mackin 1940. Descriptions of nine new species of freshwater amphipod crustaceans with notes and new localities for other species. Amer.. Midland Nat., **23**: 187-218.

Hubricht, L. 1943. Studies on the Nearctic freshwater Amphipoda, III: Notes on the freshwater amphipods of eastern United States, with descriptions of ten new species. Amer. Midland Nat., **29**: 683-712.

Hyman, L. H. 1937. Sutdies on the morphology, taxonomy, and distribution of North Amer. Triclad Turbellaria, VIII: some cave planarians of the United States. Trans. of the Amer. Microscopical Soc., **56**: 457-477.

Kane, T.C. and D.C. Culver 1991. The Evol., of troglobites: *Gammarus minus* (Amphipoda: Gammaridae) as a case study. Mem. de Biospeleologie, **18**: 3-14.

Karaman, G.S. 1974. Contribution to the knowledge of the Amphipoda revision of the genus *Stygobromus* Cope 1872 from North America. Glas. Republ. Zovada Zast. Prirode *I* Prirodnjackog Muzeja Titogradu, **7**: 97-125.

King, P. B. 1958. Evol., of modern surface features of western North America. *in* C. L. Hubbs, editor, Zoogeography, 51: 3-60. Washington, D. C.: Amer. Assoc. for the Advancement of Sci..

Kluge, A. D. and A. J. Wolf 1993. Clad.: what's in a word? Clad. **9**:183-199.

Koenemann, S., R. Vonk and f. R. Schram, 1998. Cladistic analysis of 37 Mediterranean Bogidiellidae (Amphipoda), including *Bogidiella arista*, new species, from Turkey. J. of Crust. Biol., **18** (2): 384-404.

Koenemann, S. and J. R. Holsinger 1999. Phylogenetic analysis of the amphipod family Bogidiellidae S. Lat., and revision of taxa above the species level. Crust. **72** (8): 781-816.

Kulkira, L. I. 1992. *Stygobromus kazakhstanica* sp.n. (Amphipoda, Crangonyctidae) from underground waters of the Tien Shan. Zoologichesku Zhurnal, **71** (1): 40-45.

Kummel, B. 1961. History of the Earth. Xii+610pages. San Francisco: W. H. Freeman and Company.

Lewis, J. J. 2001. Three new species of subterranean Asellids from western North America, with a synopsis of the species of the region (Crustacea: Isopoda). Texas Mem. Mus., Speleog. Mongr., **5**: 1-15

Lindeman, D. 1991. Phylogeny and zoogeography of the New World terrestrial amphipods (landhoppers)(Crustacea: Amphipoda: Talitridae). Canadian J. of Zool., **69**: 1104-1116.

Madison, W.P. and D.R. Madison 1993. MacClade: Analysis of phylogeny and character Evol.,. Version 3.03. Sinauer Associates, Inc., Sunderland, Massachusetts.

Notenboom, J. 1991. Marine regression and the Evol., of groundwater-dwelling amphipods (Crustacea). J. of Biogeog., **18**: 437-454.

Parris, L. E. 1973. Caves of Colorado. 1st edition, Pruett Press, Inc. pp247.

Pennak, R. W. 1953. Freshwater invertebrates of the United States. Ix+769 pages, 470 figures. New York: Ronald Press Company.

Pennak, R. W. 1958. Some problems of freshwater invertebrate distribution in the western states. p223-230 in C. L. Hubbs, editor, Zoogeography, No. 51. Washington, D. C.: Amer. Association for the Advancement of Sci..

Pennak, B. W. and J. V. Ward 1986. Interstitail faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. Arch. Hydrobiol./suppl. **74**: 357-396.

Poulson, T. L., and W. B. White 1969. The cave environment. Sci., 165(4897): 971-981.

Rutherford, J. M. and R. H. Handley, 1976. The Greenbrier caverns. Nat. Speleological Soc. Bull., **38**: 41-52.

Schellenberg, A. 1936. Die Amphipodengattungen um *Crangonyx*, ihre Verbreitung und ihre3 Arten. Mitteilungen aus dem Zoologischen Mus. in Berlin, **22**: 31-43.

Shoemaker, C. R. 1942a. Notes on some Amer. freshwater amphipod crustaceans descriptions of a new genus and two species. Smithsonian Misc. Coll., **101**: 1-31.

Shoemaker, C. R. 1942b. A new cavernicolous amphipod from Oregon. Occasional Papers of the Mus. of Zool. of University of Michigan. **466**: 1-6.

Skalski, A. W. 1970. Groundwater inhabitants in Poland. Internat. J. of Speleology, **8**: 217-228.

Slowinski, J. B. 1993. "unordered" versus "ordered" characters. Syst. Biol., **42**:155-165.

Stock, J. H., 1980. Regression model Evol., as exemplified by the genus *Pseudoniphargus* (Amphipoda). Bijdragen Dierkunde. pp 105-144.

Stock, J. H. 1981. The taxonomy and zoogeography of the family of Bogidiellidae (Crustacea, Amphipoda), with emphasis on the West Indian taxa. Bijdragen tot de Dierkunde **51**: 345-374.

Stone, R. W. 1953. Caves of Pennsylvania. Nat. Speleological Soc. Bull., **15**: 1-143.

Swofford, D. L. 1993. PAUP: phylogenetic analysis using parsimony, ver. 3.1. Computer program distributed by the Illinois State Natural History Survey, Champaign, Illinois.

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.

Wang, D. 1996. A preliminary study on phylogeny and biogeography of the family Paracortinidae (Myriapoda: Callipodida) a cladistic analysis. In: Acta Myriapodologica. Groffroy J.J., Mauries J.P. and Nguyen Duy-Jacquenin M. (edited). Mem. Mus. Natn. Hist. Nat., **169**: 307-311.

Wang, D. and J.P. Mauries 1996. Review and perspective of study on Myriapodology of China. In: Acta Myriapodologica. Groffroy J.J., Mauries J.P. and Nguyen Duy-Jacquenin M. (eds). Mem. Mus. Natn. Hist. Nat., **169**: 81-99.

Wang, D. and C. Zhang 1993a. Diplopoda and Chilopoda. In: Animals of Longqi Mountains. Huang Chunmai (ed.) Chinese forestry Publishing House. Beijing. p845-851.

Wang, D. and C. Zhang 1993b. A new family of millipedes (Diplopoda: Callipodida) from southwestern China. Peking Nat. Hist. Mus., **53**: 375-390.

Ward, J. V. 1977. First records of subterranean amphipods from Colorado with descriptions of three new species of *Stygobromus* (Crangonyctidae). Translation of Amer. Microscope Soc., **96** (4): 452-466.

Ward, J. V. And J. R. Holsinger 1981. Distribution and habitat diversity of subterranean amphipods in the Rocky Mountains of Colorado, U. S. A. Internat.. J. of Speleology, **11**: 63-70.

Ward, J. V. And M. A. Palmer 1994. Distribution patterns of interstitial freshwater meiofauna over a range of spatial scales, with emphasis on alluvial river-aquifer systems. Hydrobiologia, **287** (1) 147-156.

Wiens, J. J. 1995. Polymorphic characters in phylogenetic systematics. Syst. Biol.. **44**: 482-500.

Wilkinson, M. 1992. Ordered versus unordered characters. Clad. **8**: 375-385.

Yeates, D. K. 1995. Groundplans and exemplars: paths to the tree of life. Clad., **11**: 343-357.

Zhang, J. 1997. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America. Dissertation, Old Dominion University library, Norfolk, Virginia, USA.

Zhang, C. and D. Wang 1993. Diplopoda in caves of Yunnan - I. A study of new genera and species of the millipede family Doratodesmidae (Diplopoda: Callipodida) In: Karst Landscape and Cave Tourism. Song Li-Hua ed. China Environmental Sci. Press. p205-215.

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Wang, D. and J.P. Mauries, 1996. Review and perspective of study on Myriapodology of China. In: *Acta Myriapodologica*. Groffroy J.J., Mauries J.P. and Nguyen Duy-Jacquenin M. (eds). *Mem. Mus. Natn. Hist. Nat.*, 169: 81-99.

Wang, D. and C. Zhang, 1993. Diplopoda and Chilopoda. In: Animals of Longqi Mountains. Huang Chunmai (ed.) Chinese forestry Publishing House. Beijing. pp845-851.

Wang, D. and C. Zhang, 1993. A new family of millipedes (Diplopoda: Callipodida) from southwestern China. *Peking Nat. Hist. Mus.*, 53: 375-390.

Zhang, C. and D. Wang, 1993. Diplopoda in caves of Yunnan - I. A study of new genera and species of the millipede family Doratodesmidae (Diplopoda: Callipodida) *In*: Karst Landscape and Cave Tourism. Song Li-Hua ed. China Environmental Science Press. pp205-215.