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The Subterranean Amphipod Crustacean Fauna of An Artesian Well in Texas

John R. Holsinger
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Introduction

Subterranean amphipod crustaceans were first reported from Texas by Benedict (1896), who described *Crangonyx flagellatus* (now *Stygobromus flagellatus*) from specimens obtained from an artesian well (Figure 1) drilled by the United States Fish Commission in San Marcos, Hays County, Texas, in late 1895 or early 1896. Water issuing from the newly opened well also brought forth troglobitic isopods, *Lirceolus smithii* (Ulrich) and *Cirolanides textensis* Benedict; shrimps, *Palaemonetes antrorum* Benedict; and salamanders, *Typhlomolge* (or *Eurycea*?) *rathbuni* Stejneger (Mitchell and Redell, 1971:35). In the years following these spectacular new discoveries and until recently, few new taxa of subterranean organisms were obtained from the well. The troglobitic helecinid snail *Horatia micra* (Pilsbry and Ferris) was reported from the well in 1906, and in 1940 Leslie Hubricht collected four amphipods that were later described as *Mexiweckelia* (= *Texiweckelia*, new genus, in part) *texensis* by Holsinger (1973).

The artesian well and old Federal Fish Hatchery were deeded to Southwest Texas State University as an Aquatic Station in 1964. In December 1973 Longley initiated an intensive, ongoing sampling program designed to survey the subterranean fauna of the underlying Edward Aquifer. As a result of this program the list of troglobitic and/or phreatobitic species from the well has increased considerably with the addition of the planarian *Sphalloplana mohri* Hyman, a second species (undescribed) of the snail *Horatia*, two undescribed species of cyclopoid copepods, one undescribed species of ostracod, the thermosbaenacean *Monodella texana* Maguire, the dytiscid beetle *Haideoporus texanus* Young and Longley, and eight amphipods, seven of which are new species.

Amphipod crustaceans of the suborder Gammaridea represent by far the most taxonomically diverse group of subterranean organisms recorded from the artesian well. The troglobitic amphipod fauna is composed of five families, six genera, and 10 species, of which one family, four genera, and six species are newly described herein. In overall taxonomic diversity the amphipod fauna of this well is probably the richest in the world, and in number of species it is rivaled only by those of certain groundwater biotopes in France and Yugoslavia.

Amphipods were collected by placing a 500μm mesh nylon net over the discharge from the flowing artesian well at the Aquatic Station. The majority of specimens utilized in this study were obtained by continuous sampling from 14 May 1974 to 16 December 1975. The inside diameter of the well-discharge pipe is 30.4 cm. The well was originally drilled to a depth of 426 m, but it was later plugged back, and at present the main source of water is a 1.5-m-high cave passage at the depth of 59.5 m. The water in this cave passage is part of the San Marcos pool of the extensive Edwards Aquifer, which parallels the Balcones Escarpment and Fault Zone of

John R. Holsinger, Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23508. Glenn Longley, Aquatic Station, Southwest Texas State University, San Marcos, Texas 78666.

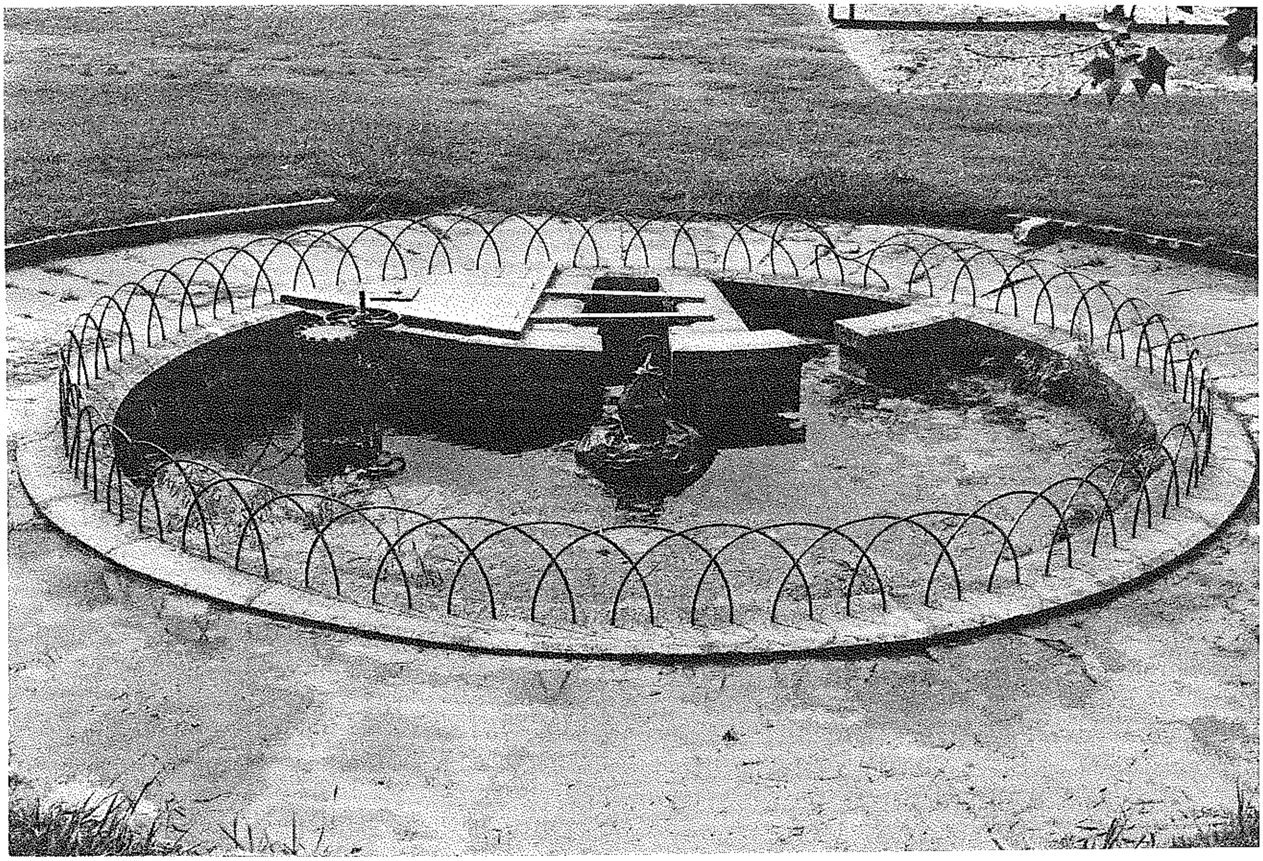

FIGURE 1.—The artesian well on the grounds of the Aquatic Station (former Federal Fish Hatchery) of Southwest Texas State University, San Marcos, Texas. (Photograph by Longley.)

south-central Texas (Figure 2). The escarpment was formed by extensive faulting of Cretaceous age limestone. The largest concentration of caves in Texas occurs along and adjacent to this escarpment and many are partially or completely filled with water from the Edwards Aquifer. This acquifer is also the source of water for nearby San Marcos Springs, a first magnitude spring located approximately 0.8 km northeast of the Artesian Well.

In addition to their occurrence in the artesian well, several species of amphipods have also been taken from San Marcos Springs and deep artesian wells located near Von Ormy, approximately 93 km southwest of San Marcos and approximately 20 km from the center of San Antonio (see Figure 2). The water in the Von Ormy wells is also from the Edwards Aquifer. The artesian well shares four species (in two genera) with San Marcos Springs and four species (in three genera) with the wells near Von Ormy. At least one species from the artesian well has also been found in the phreatic water of two caves in San Marcos. *Hyalella azteca* (Saussure), a common, widespread, epigean amphipod of the family Hyalellidae, has also been taken occasionally in samples from both the artesian well and San Marcos Springs, but in each case it apparently entered the sampling net from surrounding surface water.

The taxonomic work in this paper is that of Holsinger as indicated; the remainder of the paper is the work of both of us. A second paper treating additional ecological aspects of the artesian well amphipod fauna will be published separately (Longley and Holsinger, in prep).

ACKNOWLEDGMENTS.—A number of persons were of assistance to us during this study and to all of them we are grateful. Henry Karnei, Jr., and Joe Kolb assisted with the sampling program and sorting material. Gary W. Dickson, James A. Estes, and Julian J. Lewis helped with the sorting of speci-

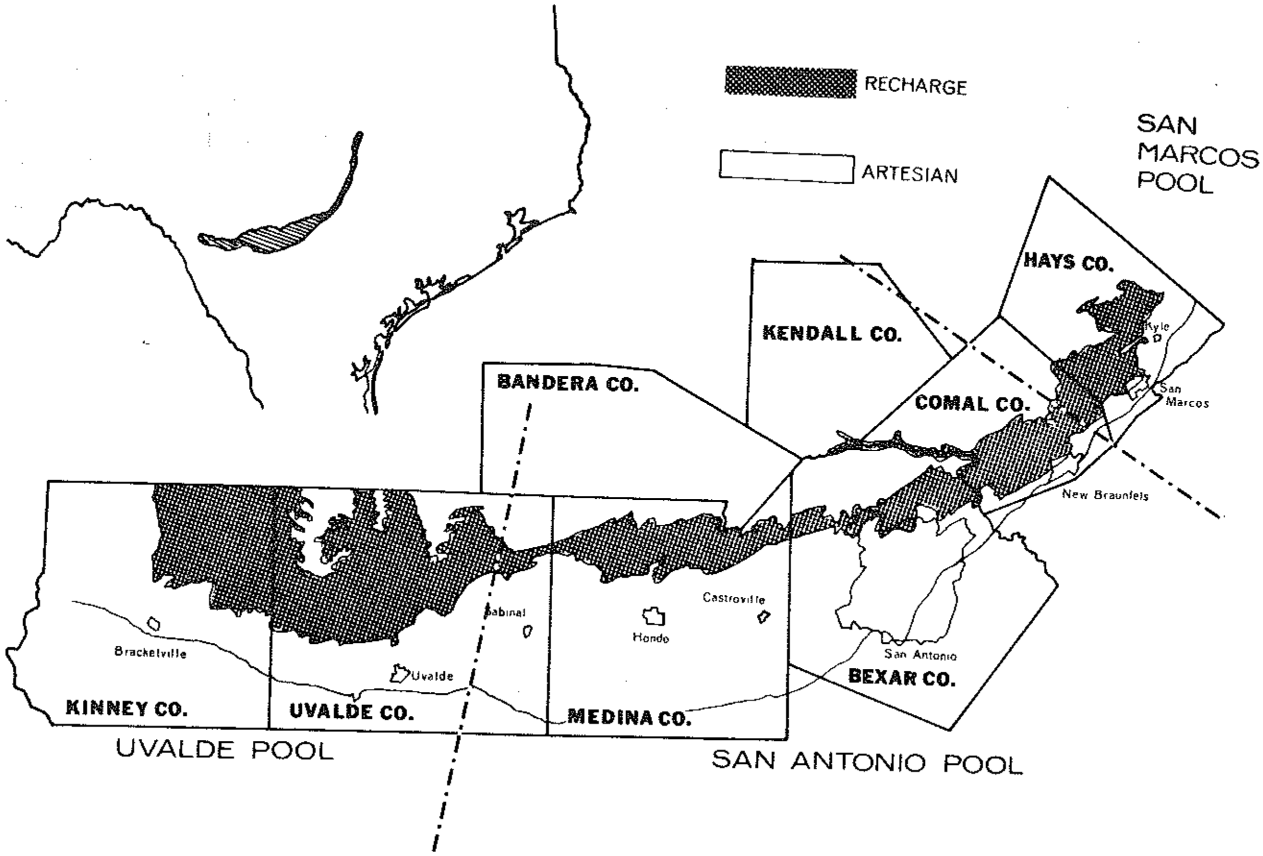

FIGURE 2.—Balcones Fault Zone and Edwards Aquifer of south-central Texas. Small map in upper left shows extent of the Balcones Fault Zone (shaded) in Texas. Large map shows extent and details of the Edwards Aquifer. Balcones Escarpment and Fault Zone lies parallel to, and generally overlaps, the southern and eastern boundary of the recharge area.

mens, inking of plates, and compilation of collection data. William C. Rhodes also helped with the compilation of data. Andy G. Grubbs and James R. Reddell donated additional specimens from localities in Hays County, Texas, other than the artesian well.

Conversations and exchange of information with Drs. J. Laurens Barnard, E. L. Bousfield, David C. Culver, Gordan S. Karaman, Randall S. Spencer, and Jan H. Stock were especially helpful in giving us a better insight into some of the taxonomic, geologic, and ecological problems encountered in the study. Drs. Barnard, Bousfield, Culver, Thomas E. Bowman, and John E. Cooper reviewed all or parts of the manuscript and made many useful suggestions. Drs. Janine Gibert, René Ginet, and Boris Sket supplied useful comparative data from their studies on groundwater amphipods in Europe.

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Taxonomic Procedure

DEPOSITION OF TYPE MATERIAL.—Holotypes are deposited in the National Museum of Natural History (Smithsonian Institution) under the catalog numbers of the former United States National Museum (USNM). Paratypes are deposited in the collections of the authors and in the following museums: National Museum of Natural History (Washington), National Museum of Natural Sciences (Ottawa), Zoölogisch Museum (Amsterdam), Museo Civico Di Storia Naturale (Verona), and The Museum of Texas Tech University (Lubbock).

TERMINOLOGY.—"Gammaridan" (sensu Barnard, 1976:421) is used in lieu of "gammaroidean" (sensu Bousfield, 1977:282) in reference to amphipods of the old family Gammaridae (sensu lato). The use of "gammaridan" seems to us to be more appropriate since, taken out of context, "gammaroidean" could easily be misconstrued as meaning amphipods of the superfamily Gammaroidea.

We have adopted and utilized the following terms suggested by Barnard (1976:421) and Zimmerman and Barnard (1977:566) to describe the third uropod of gammaridan amphipods: *Dispariramus,* inner and outer rami dissimilar; *Aequiramus,* inner and outer rami similar in length, shape and patterns of armament; *Magniramus,* inner ramus extending as far as outer ramus.

"Ventrolateral spine(s)" is employed to designate the row of one to four (frequently strong) spines that occur on the ventral (lower), lateral (outer) margin or face of the peduncle of uropod 1. These spines have also been called "anterior proximal," "ventroproximal," "basofacial," or "basoventral" by amphipod workers, but they are not always proximal or basal in position because in some taxa one or more of these spines may be inserted distal to the midpoint of the peduncle. Moreover, ventral is preferable to anterior, since in amphipods, uropods 1 and 2 are normally directed backward instead of downward.

The terms "plesiomorphic" and "apomorphic" are used in the sense of Hennig (1966) and other practitioners of cladistics to describe, respectively, ancestral and derived character states.

CLASSIFICATION.—Recent suggestions by various workers (e.g., Bousfield, 1973; Barnard, 1976; Holsinger, 1974b, 1977a) to divide the large, heterogeneous amphipod family Gammaridae into smaller taxonomic units that better reflect phylogenetic relationships and identify morphologically homogeneous (natural) groups have resulted in an attempt by Bousfield (1977) to reclassify the family. Six superfamilies encompassing 25 family groups were proposed, and a few taxa were transferred to nongammaridan families and superfamilies. The superfamilies (with number of family groups in parentheses) are: Gammaroidea (10), Melitoidea (3), Crangonyctoidea (4), Niphargoidea (3), Bogidielloidea (2), and Melphidippoidea (3). The superfamily name Melitoidea should be changed to Hadzioidea, however, since according to the *International Code of Zoological Nomenclature* (Stoll et al., 1964:23), "A family-group taxon formed by the union of two or more taxa of that group takes the oldest valid family-group name among its components . . . ." Bousfield (1977) assigned three families to his newly proposed superfamily: Hadziidae (Karaman, 1943), Melitidae (Bousfield, 1973) and Carangoliopsidae (Bousfield, 1977). Therefore, Hadziidae should be the nominate family of the new group.

In classifying the taxa treated in this paper, we have followed Bousfield's new system by recognizing the families Crangonyctidae Bousfield (see also Holsinger, 1977a), Hadziidae Karaman, and Bogidiellidae Hertzog and assigning them to their respective superfamilies. Artesiidae, a new family proposed herein, is placed within the Bogidielloidea. The family Sebidae, a previously described marine family new to the freshwater subterranean environment, is left unassigned to a superfamily, pending further study of the relationships among higher taxa in the suborder Gammaridea. Bousfield (1977:308) suggested placing the families Sebidae, Synopiidae, Argissidae, Liljeborgiidae, and Salentinellidae in a single superfamily group, but we question the close relationship of Sebidae to the other taxa of this group and are therefore reluctant to accept this new arrangement (see additional remarks under "Family Sebidae," elsewhere this paper).

Key to the Genera and Species of Amphipods

1. Uropod 3 with single, short ramus 2
   Uropod 3 biramous, rami well developed 4
2. Length of adult 2.0 mm or less; palms of gnathopod propods transverse; coxal plates of pereopods 3 and 4 greatly enlarged; telson without apical spines .... ***Seborgia relicta,*** new species
   Length of adult 5.0 mm or more; palms of gnathopod propods oblique; coxal plates of pereopods 3 and 4 not enlarged; telson with apical spines *(Stygobromus)* 3

3. Bases of pereopods 5–7 narrowing distally, distoposterior lobes narrow and poorly defined; telson up to 50 percent longer than broad .... ***Stygobromus flagellatus*** (Benedict)
   Bases of pereopods 5–7 about as broad distally as proximally, distoposterior lobes broad and well defined; telson up to 20 percent longer than broad... ***Stygobromus russelli*** (Holsinger)
4. Palp absent from mandible; antenna 1 longer than body (*Texiweckelia*, new genus) 5
   Palp present on mandible; antenna 1 shorter than body 8
5. Gnathopods sexually dimorphic; propod of female gnathopod 1 weak, palm short, transverse, armed with weak spine teeth; segment 6 of pereopods 5 and 6 without long setae on posterior margin 6
   Gnathopods not sexually dimorphic; propod of female gnathopod 1 strong, palm rather long, armed with strong spine teeth; segment 6 of pereopods 5 and 6 with long setae on posterior margin .... ***Allotexiweckelia hirsuta***, new genus, new species
6. Bases of pereopods 5–7 broadly expanded; coxal gills ellipsoidal in shape; inner plate of maxilla 2 with oblique row of approximately 100 setae .... ***Texiweckelia samacos***, new species
   Bases of pereopods 5–7 not broadly expanded; coxal gills ovate or subovate in shape; inner plate of maxilla 2 with oblique row of 50 or fewer setae 7
7. Pereopods 6 and 7 subequal to body in length; antenna 1 up to 40 percent longer than body; coxal gills moderately large and subovate; apical margin of telson incised approximately 45 percent of distance to base .... ***Texiweckelia texensis*** (Holsinger)
   Pereopods 6 and 7 only about 55 percent length of body; antenna 1 up to 20 percent longer than body; coxal gills small and ovate; apical margin of telson incised approximately 60–70 percent of distance to base .... ***Texiweckelia insolita***, new species
8. Bases of pereopods 5 and 6 greatly expanded; peduncle of uropod 1 with large, ventrolateral spines; uronites 1 and 2 with dorsolateral spines .... ***Artesia subterranea***, new genus, new species
   Bases of pereopods 5 and 6 very small; peduncle of uropod 1 without ventrolateral spines; (*Parabogidiella*, new genus) 9
9. Telson not much longer than broad, apical margin with shallow excavation .... ***Parabogidiella americana***, new genus, new species
   Telson distinctly longer than broad, apical margin not excavate .... ***Parabogidiella***(?), new species (undescribed)

Family CRANGONYCTIDAE

Genus *Stygobromus* Cope

Stygobromus Cope.—Holsinger, 1978:3 [with references].

REMARKS.—This genus is currently being revised by Holsinger (1974a, 1978, in prep.). Two other North American, subterranean amphipod genera, *Apocrangonyx* and *Stygonectes*, are now considered synonymous with *Stygobromus* (Karaman, 1974; Holsinger, 1977a, 1978). *Stygobromus*, as presently understood, is composed of 93 described species and approximately 50 undescribed but provisionally recognized species, all of which, with the exception of one poorly known species from Siberia, occur in subterranean groundwaters of North America north of Mexico. The genus is well represented in the groundwaters of the Edwards Plateau of Texas, where 10 species (in three species groups) have been described principally from caves. Several species from Texas are still undescribed.

Stygobromus flagellatus (Benedict)

Stygonectes flagellatus (Benedict).—Holsinger, 1967:115–116 [with references].—Mitchell and Reddell, 1971:59–60.
Stygobromus flagellatus (Benedict).—Karaman, 1974:111.—Holsinger, 1977a:261.

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, 3 ♀, 5 ♂, 31 Mar 1973 to 1 Nov 1973; 424 ♀, 592 ♂, 306 juvs, and 3 fragments from continuous sampling between 14 May 1974 and 16 Dec 1975; Ezells Cave in San Marcos, 4 ♀, 3 ♂, J. R. Reddell and R. W. Mitchell, 28 Oct 1967; Rattlesnake Cave in San Marcos, 2 ♀, A. G. Grubbs, 9 Mar 1975 and 1 ♀, 1 ♂, 2 May 1975; San Marcos Springs, 10 ♀, 2 ♂, and 15 juvs (from large spring opening), 25 Nov 1975; 9 ♀, 2 ♂ (from large pipe spring), 5 Dec 1975; 12 ♂, 2 ♂, and 7 juvs (from large pipe spring), 7 Dec 1975; 7 ♀, (from large pipe spring), 19 Jan 1977.

REMARKS.—*Stygobromus flagellatus* was the first species of amphipod crustacean discovered and described from the artesian well in San Marcos, Texas (see Holsinger, 1966, for details). It was originally assigned to *Crangonyx* by Benedict (1896) but subsequently designated the type-species of *Stygonectes* by Hay (1903). Since *Stygonectes* was recently lumped with *Stygobromus*, we now consider *S. flagellatus* to be a member of the latter genus.

Stygobromus flagellatus is at present authentically recorded from the artesian well (type-locality), San Marcos Springs, and Ezells and Rattlesnake caves, all located within 6.5 km of each other in the environs of San Marcos. All four localities are situated along the San Marcos Springs Fault (Russell, 1976) at the edge of the Balcones Escarpment and are presumably connected by an extensive subterranean network of phreatic water. Two specimens from Carson Cave near Mondell in Uvalde County, located approximately 210 km west of San Marcos, appear to be nearly identical with specimens of *S. flagellatus* from Hays County, but a definitive determination awaits further study.

Stygobromus flagellatus is the nominate species of the *flagellatus* group, which is composed of four described species from caves, springs, and deep phreatic water in the Edwards Plateau of south-central Texas (Holsinger, 1967). The *flagellatus* group is distinguished from the *tenuis* group, with which it overlaps in central Texas, by the gnathopods, which are subequal in size, relatively narrow bases of pereopods 5–7, and elongate telson, which is tapered distally. The *flagellatus* group is further divided into two subgroups composed of two species each and distinguished from each other primarily by differences in the lengths of the antennae and pereopods (Holsinger 1967). The *flagellatus* subgroup includes *S. flagellatus* and *S. longipes* (Holsinger), the latter being recorded from two caves situated approximately 55 km west of San Marcos in Kendall County. The *pecki* subgroup, on the other hand, is based on two species from single localities (a cave and spring) in Comal and Kendall counties.

The *flagellatus* group is probably far more complex than it appeared when first designated by Holsinger in 1967 and is in need of further, detailed study. Recent collections from a pit in Comal County, boxed springs in Kerr County, and a cave in Uvalde County contain specimens referrable to the *flagellatus* group, but none of these populations can yet be assigned to previously described species with certainty. *Stygobromus flagellatus* is itself somewhat variable within its tightly circumscribed range, and some of its characters appear to intergrade with those of other species in the group.

Stygobromus flagellatus is the second most frequently collected amphipod from the artesian well, where, during the continuous sampling period of 14 May 1974 to 16 December 1975, 1325 specimens (representing 26.37 percent of the total amphipod fauna collected) were obtained (Table 2). The sex ratio for this period was 1.4:1.0 in favor of males. Juveniles were numerous in most samples and were collected during all four seasons of the year. Females (6.5 to 15.5 mm) with setose brood plates were also collected during all seasons of the year but only one specimen (7.2 mm) from a sample on 27 August 1975 was ovigerous. The largest males were 12.5 mm but most did not exceed 10.0 mm in length; the largest female was 15.5 mm but most did not exceed 13.0 mm.

The specimens of *S. flagellatus* from San Marcos Springs were taken in association with other subterranean amphipods, viz., *Stygobromus bifurcatus* (Holsinger), *S. russelli* (Holsinger), and *Texiweckelia* (new genus) *texensis* (Holsinger), and the epigean amphipod *Hyallella azteca* (Saussure). In the samples from Ezells and Rattlesnake caves, *S. flagellatus* was unaccompanied by other amphipods. In the former cave the species was taken from a shallow pool, where it was attracted by liver bait (J. R. Reddell, Texas Tech University, in litt.); in the latter cave it was collected from two very deep pools of phreatic water with the troglobitic shrimp *Palaemonetes antrorum* Benedict (A. G. Grubbs, Texas Speleological Survey, in litt.).

Stygobromus russelli (Holsinger)

Stygonectes russelli Holsinger, 1967:95–101, figs. 23, 24 [with references].—Mitchell and Reddell, 1971:59–60, fig. 38.
Stygobromus russelli (Holsinger).—Karaman, 1974:118.—Holsinger, 1977a:262.

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, 7 ♀, 7 ♂, and 39 juvs from continuous sampling between 14 May 1974 and 16 Dec 1975; San Marcos Springs, 1 ♀, 1 ♂, and 1 juv (from large spring opening), 25 Nov 1975; 1 ♀, 1 ♂ (from large pipe spring), 5 Dec 1975; 2 ♀, 1 ♂, and 1 juv (from large pipe spring), 7 Dec 1975; 75 adults (♀ and ♂) and 14 juvs (from deep spring outlet), 15 Nov 1976; 2 ♂ (from large pipe spring), 19 Jan 1977.

REMARKS.—*Stygobromus russelli* is a member of the *tenuis* group, which is composed of 14 described species from subterranean waters of the eastern and southern United States (Holsinger, 1967, 1978). Five of these species are found in central Texas, and four of them are endemic to this region. *Stygobromus russelli* is the most widely distributed and morphologically variable troglobitic amphipod in Texas. Its range covers most of the eastern half of the cavernous limestone area of central Texas, but more than one-third of its populations are recorded from caves just west and northwest of Austin in Travis County (Holsinger, 1967; Mitchell and Reddell, 1971). The samples from the artesian well and San Marcos Springs mark the first Hays County records for this species, but they do not materially extend its range. The species is currently recorded from 10 counties in the state.

As indicated by the data obtained during the continuous sampling period of May 1974–December 1975, *S. russelli* is apparently uncommon in the artesian well. Only 53 specimens, representing 1.05 percent of the total amphipod fauna, were collected during this period (Table 2). These samples contained numerous juveniles (39) but only 14 subadults. None of the females (size range, 4.0–7.0 mm) had setose brood plates. The size range of males was approximately that of the females; juveniles ranged in size from 2.0 to 5.0 mm and were found during all seasons of the year.

Out of the five samples from San Marcos Springs, *S. russelli* was collected together with *S. flagellatus* (four samples), *S. bifurcatus* (one sample), *Texiweckelia* (new genus) *texensis* (Holsinger) (two samples), and *Hyalella azteca* (three samples). Two ovigerous females (8.0 and 8.5 mm) were found in the 15 November 1976 collection.

Family HADZIIDAE

Texiweckelia Holsinger, new genus

Mexiweckelia Holsinger and Minckley, 1971:426 [in part].

DIAGNOSIS.—Without eyes and pigment, of subterranean facies. Head sometimes produced into tiny triangular-shaped rostrum between 1st antennae; interantennal (lateral) lobe distinct, rounded anteriorly; inferior antennal sinus indistinct. Antenna 1: elongate, longer than body, longer than antenna 2; esthetascs present or absent on flagellar segments; accessory flagellum reduced to tiny vestigial stub or absent. Peduncular segment 4 (and sometimes 5) of antenna 2 with few dorsal spines. Buccal mass prognathous. Upper lip symmetrical, rounded or subtruncate apically, with or without apical incision. Mandible: molar rather prominent, triturative; lacinia mobilis absent from right; molar seta absent from left; palp lacking. Maxilla 1: inner plate with numerous naked, apical setae; outer plate with 7–15 apical, serrate and/or pectinate spines; palp 2-segmented, with spines apically and setae subapically. Maxilla 2: inner plate broader than outer, bearing oblique row of numerous, naked setae; both plates with numerous coarse setae apically. Maxilliped: variable; inner plate with bladelike spines and short setae apically and row of naked setae on inner margin; outer plate bearing bladelike spines apically and/or subapically; palp 4-segmented. Lower lip: outer lobes high, well developed; inner lobes vestigial or absent; lateral (mandibular) processes relatively long and slender.

Gnathopods sexually dimorphic. Gnathopod propod 1 of female elongate, weak; palm short, transverse, with 1 or 2 bent setae and small spine teeth; male propod 1 less elongate, proportionately broader, palm longer, oblique, with or without bent setae, with more spine teeth. Posterior margin of segment 5 of gnathopod 1 in both sexes broadly lobiform and pubescent. Gnathopod propod 2 of female longer than propod 1; palm short but slightly oblique, with small spine teeth, with or without bent setae; propod 2 of male proportionately broader, palm longer and more oblique, with more spine teeth. Posterior margin of segment 5 of gnathopod 2 in both sexes lobiform and pubescent toward distal end. Dactyl of gnathopod 2 of male with inner marginal spines. Coxal plates of gnathopods enlarged, deeper than corresponding body segments. Pereopods 3 and 4 subequal; coaxal plates generally similar, comparatively much smaller than those of gnathopods, shallower than corresponding body segments. Pereopods 6 and 7 subequal in length, more than 50 percent length of body; dactyls of pereopods 5–7 with several setules on distal part of anterior margin. Coxal gills pedunculate, variable in shape and size, on pereopods 2–6. Sternal gills absent. Brood plates sublinear but fully developed (i.e., setose) in only one species in the material studied.

Posterior corners of pleonal plates typically rounded, bearing 1 setule each, produced in plates

2 and 3; ventral margins without spines. Pleopods biramous, 1 and 2 typically subequal in length, 3 a little shorter; peduncles with 3–8 coupling spines on inner margin distally. Uronites free (not fused) with few dorsolateral spines. Uropods 1 and 2 not sexually dimorphic; rami and peduncles bearing normal spines; peduncle of uropod 1 also armed with ventrolateral spines. Uropod 3 comparatively long, biramous; rami 1-segmented, generally of equal length (magniramus) but different slightly in width and setal pattern (dispariramus). Telson relatively small but variable in length and width; apical margin incised from 45 to 75 percent the distance to base; apical lobes with few spines and often threadlike setae; lateral margins with or without spines.

TYPE-SPECIES.—*Mexiweckelia texensis* Holsinger. Gender feminine.

ETYMOLOGY.—The generic name is derived by a combination of *Texi,* which alludes to geographic placement in Texas, and *Weckelia,* the name of a related, Greater Antillean genus.

FAMILY RELATIONSHIP.—The classification of hadzioid amphipods is currently in a state of flux and confusion, owing chiefly to the numerous parallelisms and mosaic patterns of evolution among many genera and species in the group. Karaman (1943) was the first worker to recognize the "hadziid Gestalt" as distinct from other Gammaridae, and he proposed the family Hadziidae to include the subterranean genus *Hadzia,* then known only from two troglobitic species in Yugoslavia. Although most workers subsequently failed to accept the family concept suggested by Karaman, they did, however, recognize a *Hadzia* group within the family Gammaridae, which eventually was expanded to include about eight genera of typically brackish and/or freshwater, subterranean amphipods with a circumtropical distribution (Ruffo, 1953; Holsinger and Minckley, 1971; Stock, 1977a; and others). Bousfield (1973:61) assigned the marine genus *Melita* and some of its closest allies, including the weckeliid genera of the greater Caribbean region described to that time, to a new family Melitidae. Bousfield did not, however, include *Hadzia* and several other *Hadzia*-like genera, although by implication they probably should have been included since his concept of the new family did not differ significantly from that of Hadziidae (see Holsinger, 1974b:317). Usage of the term "weckeliid genera" in this paper is not necessarily meant to imply group (taxonomic) status. It is, rather, used as a convenience for designating subterranean genera of the greater Caribbean region, whose names are formed from the surname "Weckel."

In 1975 at the Third International Colloquium on *Gammarus* and *Niphargus* in Schlitz, West Germany, Bousfield proposed the superfamily Melitoidea (=Hadzioidea; see "Taxonomic Procedure" elsewhere in this paper) to include three families: Hadziidae, Melitidae, and Carangoliopsidae (Bousfield, 1977:296–299). In Bousfield's 1975 scheme, the weckeliid genera are unequally distributed in two unnamed subfamily groups of Hadziidae. Following Bousfield's work, Barnard (1976) proposed a Hadzioid supergroup of gammaridans that he divided into groups encompassing, among others, melitids, hadziids, weckeliids, ceradocids, and eriopisellids. Shortly thereafter, Zimmerman and Barnard (1977) revived the family Hadziidae but, largely on the basis of the special form of female gnathopod 2, they restricted its composition to three genera: *Hadzia, Protohadzia,* and *Dulzura*. Barnard's 1976 scheme, while not establishing formal names, would nevertheless by implication elevate the weckeliid genera (excluding *Paraweckelia,* which he placed with the ceradocids) to a family group, fully equivalent in rank with the hadziids, melitids, ceradocids, etc.

Finally, Stock (1977a:3–4) in another recent paper adopted the basic concept of Bousfield's 1975–1977 classification of Hadziidae and, with the exclusion of *Metacrangonyx,* he assigned 11 genera to this family group. Whereas Bousfield (1977) and Stock (1977a) appear to be in rather close agreement, Barnard (1976) and Zimmerman and Barnard (1977) strongly differ by their fine splitting of the hadzioids into many small, narrowly defined family groups and by restricting Hadziidae to only three genera. Considering the large amount of variation in the structure of the second gnathopod of the hadzioids, the separation of the hadziids from the weckeliid genera at the family level principally on the basis of small differences in female gnathopod 2 is questionable. In our opinion neither of the classification schemes proposed to date offer a completely satisfactory solution, although at the moment we generaly favor the scheme of Bousfield and Stock over that of Barnard and Zimmerman. However, considerably more study is clearly called for and, pending that, we have elected to assign the weckeliid genera of mainland North America to the family Hadziidae and the superfamily Hadzioidea.

GENERIC RELATIONSHIP.—The weckeliid genera include: *Texiweckelia*, new genus (three species), and *Allotexiweckelia* (monotypic new genus described below) from phreatic water in Texas; *Mexiweckelia* Holsinger and Minckley (two species) from a cave and shallow phreatic water in northern Mexico; *Mexiweckelia particeps* Holsinger (transfered to a monotypic new genus by Holsinger, in press) from shallow phreatic water in northern Mexico; *Mayaweckelia* Holsinger (two species) from caves on the Yucatan Peninsula in southern Mexico; *Weckelia* Shoemaker (one species) from caves in western Cuba; *Paraweckelia* Shoemaker (one species) from a cave in central Cuba; *Alloweckelia* Holsinger and Peck (one species) from a cave in Puerto Rico; and *Saliweckelia* Stock (two species) from mostly interstitial, hyperhaline habitats in the Netherlands Antilles (islands of Curaçao and Bonaire). Dancău (1973a) divided *Weckelia* into subgenera and described a second species in the genus, but because his distinguishing criteria are questionable (Holsinger, 1977b; Stock, 1977a:69), we consider *Weckelia* (*Neoweckelia*) *cubanica* Dancau a synonym of *Weckelia caeca* (Weckel).

In all of the weckeliid genera the third uropod is either magniramus or approaches that condition, but in *Saliweckelia* the outer ramus has a short second segment that is absent in the other weckeliid genera but present in *Hadzia, Metaniphargus,* and other nonweckeliid genera recently assigned to Hadziidae by Stock (1977a). The structure of the third uropod may therefore indicate a closer relationship of *Saliweckelia* with *Hadzia, Metaniphargus,* etc., than with the other weckeliid genera. *Paraweckelia* may also differ rather sharply from the other weckeliid genera and is clearly not as closely allied with *Alloweckelia* as one of us (Holsinger, 1977b:268) mistakenly indicated (see also Stock, 1977a:69). Primarily because gnathopod 2 differs rather significantly from that of the other weckeliid genera, Barnard (1976:425) and Zimmerman and Barnard (1977:569) excluded *Paraweckelia* from their "weckeliid group concept," pointing out that this genus was probably more closely aligned with the marine ceradocids and that it might reflect a transitional stage in a hypothesized derivation of "weckeliids" from "ceradocids."

Since the five weckeliid genera of the North American mainland are geographically restricted to a continental landmass, are exclusively subterranean freshwater inhabitants with the exception of *Mayaweckelia*, which was recorded once from slightly brackish water (Holsinger, 1977c:25), and share a number of important diagnostic characters, they would appear at first glance to form a rather homogeneous group. Closer examination, however, reveals some fundamental intergeneric differences with respect to the structure of the accessory flagellum of the first antenna, mouthparts, gnathopods, uropods, and telson. With the exception of the gnathopods that are characterized and discussed below, the other major differences are summarized in Table 1.

Basically four types of female gnathopods are seen in the mainland weckeliid genera and are exemplified as follows. (1) *Mexiweckelia* and *Texiweckelia:* gnathopod 1 propod weak, palm transverse and weakly armed, segment 5 posteriorly lobate and pubescent, segment 4 not as large as segment 5 and with small pubescent posterior lobe; gnathopod 2 stronger, palm oblique, segment 5 posteriorly lobate or tumid and pubescent. (2) *Mexiweckelia particeps:* gnathopod propod 1 about like type 1, segment 5 not posteriorly lobate or pubescent, segment 4 about like type 1; gnathopod 2 propod a little broader distally than type 1, segment 5 lacking posterior lobe and pubescence. (3) *Mayaweckelia:* gnathopod 1 propod generally weak, palm transverse and weakly armed, segment 5 with weak posterior lobe but not pubescent, segment 4 as large and as long as segment 5 with large, pubescent posterior lobe; gnathopod propod 2 about like type 2 except more slender, segment 5 about like type 2. (4) *Allotexiweckelia:* gnathopods convergent; gnathopod 1 propod relatively strong, palm oblique and strongly armed, segment 5 with large, pubescent posterior lobe, segment 4 not enlarged or lobate; gnathopod 2 propod slender but palm more heavily armed than type 3, segment 5 with small pubescent posterior lobe.

The shape and size of the gnathopod coxal plates also differ to some extent among the genera, but these differences are highly variable and do not

TABLE 1.—Comparison of the weckeliid amphipod genera of mainland North America

Genus	Accessory flagellum of ant.1	Man-dibular palp	Outer plate of maxilla 1	Inner lobes of lower lip	Gnatho-pods 1 sexually dimorphic	Ventro-lateral spine(s) on uropod 1	Uropod 3	Telson cleft % distance to base
Mayaweckelia	3 segs.	absent	9 spines	small to vestigial	yes	absent	magniramus & dispariramus, spines/setae	100
Mexiweckelia	vestigial or absent	absent	7 spines	vestigial or absent	yes	present	magniramus & dispariramus, spines/setae	50–65
M. particeps [2]	1 seg.	absent	9 spines	absent	no	present	magniramus & dispariramus, spines/setae	90
Texiweckelia	vestigial or absent	absent	7-15 spines	absent	yes	present	magniramus & dispariramus, spines/setae	45–75
Allotexiweckelia	vestigial or absent	absent	7 spines	small to vestigial	no	present	magniramus & dispariramus, spines/setae	65

[1] Other differences in gnathopods discussed in text.

[2] Monotypic new genus in press by Holsinger.

appear to fall into definable types. Despite the differences noted in the gnathopods, all four types agree in having segment 5 elongate, although it is more elongate in some than in others. With the exception of the presence or absence of a pubescent lobe on segment 5, types 1 and 2 are generally similar. Type 3, however, diverges rather radically from the basic plan seen in types 1 and 2 in having segment 4 of gnathopod 1 enlarged and prominently lobate. Type 4, on the other hand, corresponds to types 1 and 2 in the structure of segments 4 and 5 but differs significantly in having a much stronger and more heavily armed propod on gnathopod 1.

In those weckeliid genera having sexually dimorphic gnathopods, the first gnathopod propod of the male has an oblique palm and is a little broader than that of the female, and the second gnathopod propod of the male is typically broader and more strongly armed in the palmar region.

Texiweckelia is more closely allied morphologically and geographically with *Mexiweckelia* than any other weckeliid genus, and because these two genera share so many apomorphic characters they should be considered sister groups. Nevertheless, *Texiweckelia* is distinguished from *Mexiweckelia* by the following characters: (a) antenna 1 is longer than the body, whereas it is only about 50 percent as long in *Mexiweckelia;* (b) the lacinia mobilis is absent from the right mandible but present on both mandibles in *Mexiweckelia;* (c) the coxal plate of gnathopod 1 is proportionately much larger, reaching ⅔ to ¾ of the length of segment 2, as opposed to only ¼ to ⅓ the length in *Mexiweckelia;* (d) the dactyls of pereopods 5–7 have two or more setules on the anterior margins in contrast to only 1 setule per margin in *Mexiweckelia;* (e) the posterior corners of the pleonal plates are produced, whereas they are not produced in *Mexiweckelia.*

INTERSPECIFIC VARIATION.—As can be seen from the following descriptions there is considerable variation among the three species presently assigned to *Texiweckelia.* The most prominent variation is associated with the mouthparts, structures generally found to be "conservative" in the majority of gammaridan amphipod genera. Strictly on the basis of differences in mouthpart morphology, one might be persuaded to assign these species to three separate genera. But, considering that some of the interspecific variation is discordant, that several characters considered important on the generic level are generally similar in all three species, and that mouthpart morphology might have been strongly influenced by ad hoc adaptations to narrow resource partitioning in a rigorous and restricted subterranean environment, we have elected to include these species in a single genus for the time being. The discovery of additional *Texiweckelia*-like forms in the groundwaters of Texas and Mexico may necessitate change in our present classification, however.

Texiweckelia texensis (Holsinger)

FIGURES 3–5

Mexiweckelia texensis Holsinger, 1973:6–10, figs. 4–6 [in part; type-locality: Artesian well, San Marcos, Hays County, Texas].

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, 2 syntypes (partly on slide mounts) (USNM 142357) collected by Leslie Hubricht, 14 May 1940. Topotypes collected from same locality include 1 juv on 25 Apr 1973, and 79 ♀, 82 ♂, 250 juvs, and 1 fragment from continuous sampling between 14 May 1974 and 16 Dec 1975. Additional material collected from San Marcos Springs, Hays County includes: 1 ♀, 2 ♂, and 1 juv from large spring opening, 25 Nov 1975; 1 ♀ and 1 fragment from large pipe spring, 7 Dec 1975; 1 ♂ from deep spring outlet, 15 Nov 1976.

DIAGNOSIS.—A medium-sized, fragile-bodied subterranean species distinguished by slender body; long, attenuated appendages, with 1st antenna up to 40 percent longer than body and 7th pereopod typically as long as body; large coxal plates of gnathopods; relatively large, subovate coxal gills; proportionately short telson, incised approximately 45 percent the distance to base. Largest males, 6.5 mm; largest females, 7.8 mm.

FEMALE.—Antenna 1: 35–40 percent longer than body, approximately 70 percent longer than antenna 2; primary flagellum with 40–45 segments, esthetascs absent or at least not discernible; accessory flagellum reduced to tiny, vestigial stub or absent; peduncular segment 1 subequal in length to combined lengths of segments 2 and 3. Antenna 2: flagellum with 10–12 segments; peduncular segment 5 longer than 4. Head produced into small triangle between 1st antennae; interantennal lobe small, sharply rounded. Upper lip pyriform, apex with slight incision. Mandible large, molar large and prominent, palp lacking; right mandible with 2 spines in spine row and 1 molar seta, lacinia mobilis lacking; left mandible with small lacinia mobilis, 3 spines in spine row, molar seta lacking. Maxilla 1: inner plate with about 22 naked, apical setae; outer plate with 7 apical, serrate spines; palp with 6 apical, bladelike spines and several subapical setae. Maxilla 2: inner plate with oblique row of about 27 naked setae on inner margin. Maxilliped: inner plate with 3 small, bladelike spines and several short setae apically and row of longer setae (mostly naked) on inner margin; outer plate with 2 stiff setae apically and row of small, bladelike spines on distal half of inner margin. Lower lip with long, lateral (mandibular) processes; inner lobes vestigial or absent.

Propod of gnathopod 1 weak, narrow, about twice as long as broad; palm short, transverse, with small spine teeth (some weakly bifid) and 1 long, bent seta; posterior margin elongate, pubescent, without long setae; anterior margin with row of long setae. Dactyl of gnathopod 1 short and thick at base, lacking inner marginal spines; nail short. Segment 5 of gnathopod 1 longer and broader than propod; posterior margin broadly lobiform and pubescent. Coxal plate of gnathopod 1 broad and deep, deeper than corresponding body segment; ventral margin broadly rounded, with 7 to 8 short setae. Propod of gnathopod 2 elongate, subrectangular, about twice length of propod 1; palm short, slightly oblique, armed with double row of 6–7 weak, mostly bifid spine teeth; posterior angle with 2 long, thick setae; posterior margin elongate, with 3–4 sets of long, mostly doubly inserted setae; anterior margin with row of long, singly inserted setae. Dactyl of gnathopod similar to that of gnathopod 1. Segment 5 of gnathopod 2 elongate, subequal in length to propod; posterior margin lobiform and pubescent toward distal end. Coxal plate of gnathopod enlarged but proportionately a little smaller than coxal plate of gnathopod 1, deeper than corresponding body segment, margin with 4 short seta (setules). Coxal plates of pereopods 3 and 4 comparatively small, shallower than corresponding body segments, about as broad as long, margins with 2 setules each. Pereopod 7 long and slender, typically equal in length to body but sometimes only 90–95 percent as long, subequal to pereopod 6 in

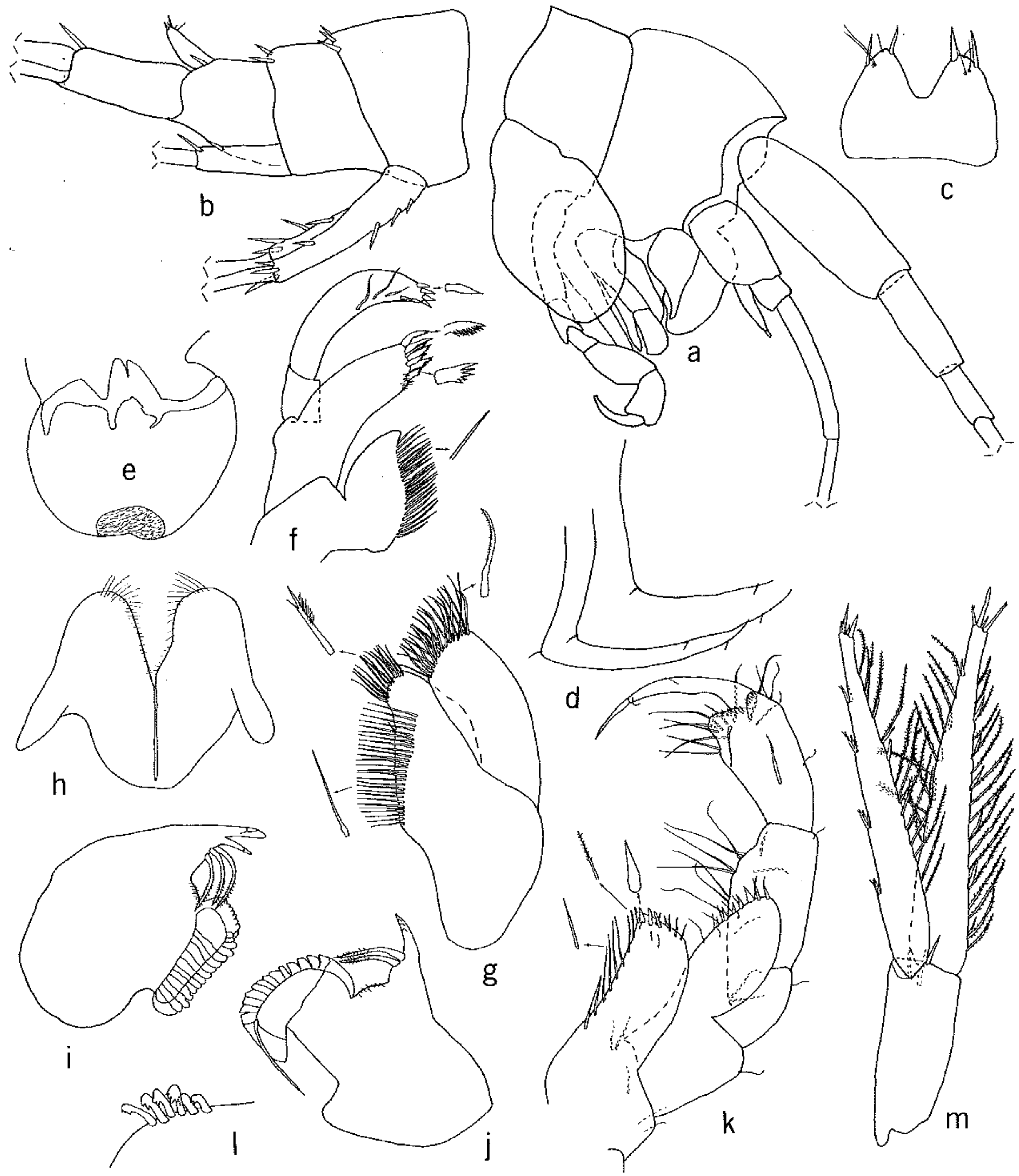

FIGURE 3.—*Texiweckelia texensis* (Holsinger), topotypes, artesian well, Hays County, Texas, male (6.0 mm): *a*, head region (setae and spines omitted); *b*, uronites with telson and uropods (in part). Female (6.0 mm): *c*, telson; *d*, pleonal plates; *e*, upper lip; *f*, *g*, maxillae 1, 2 (apical setae and spines enlarged); *h*, lower lip; *i*, left mandible; *j*, right mandible; *k*, maxilliped (setae and spines enlarged); *l*, coupling spines from peduncle of pleopod 2. Female (7.0 mm): *m*, uropod 3. (All mouthparts to same scale; head and uronites to same scale.)

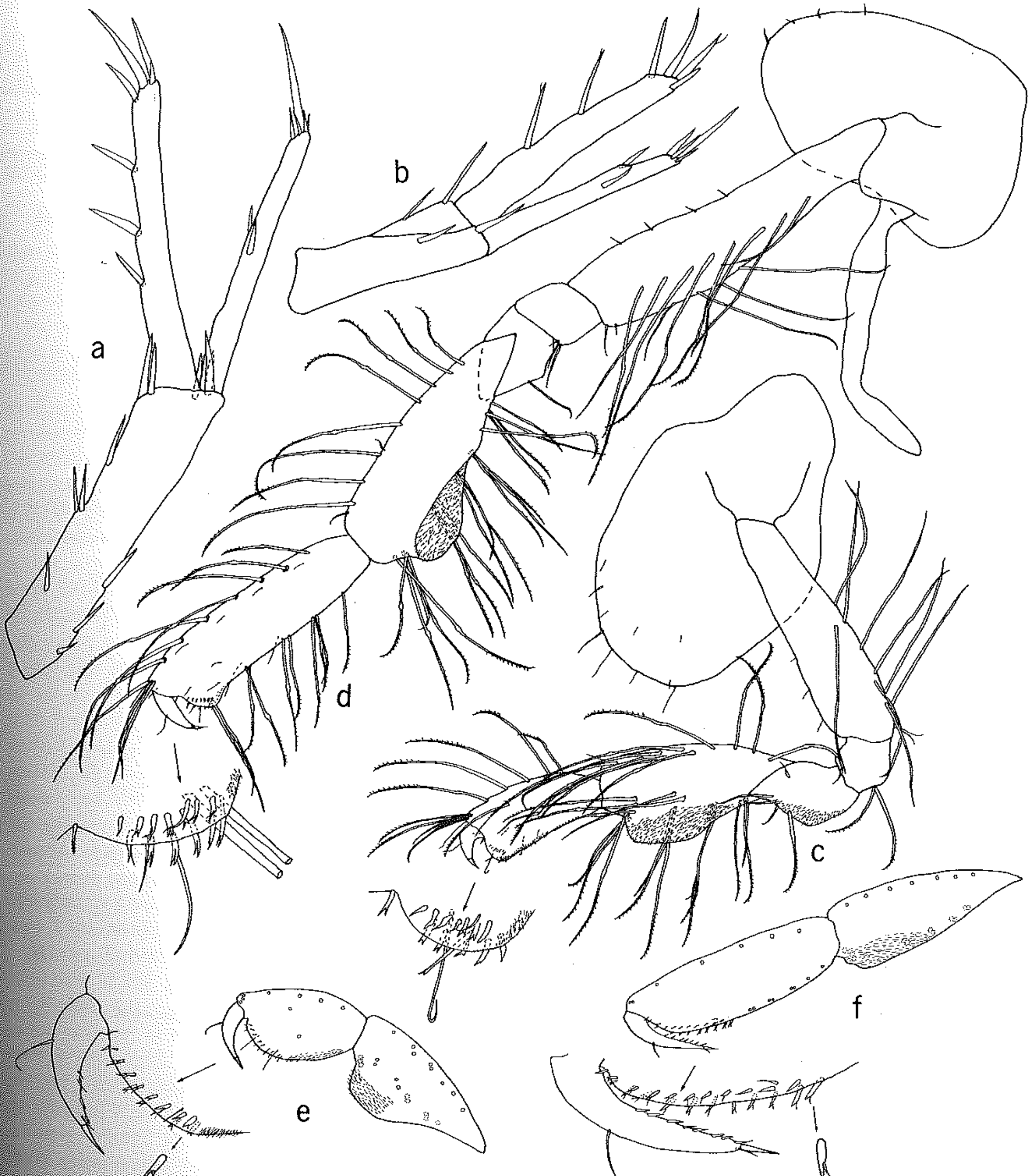

FIGURE 4.—*Texiweckelia texensis* (Holsinger), topotypes, artesian well, Hays County, Texas, female (6.0 mm): *a*, *b*, uropods 1, 2. Female (7.0 mm): *c*, *d*, gnathopods 1, 2 (palms enlarged). Male (6.0 mm): *e*, *f*, segments 5, 6, and 7 of gnathopods 1, 2, respectively (setal insertations indicated by small circles; spines enlarged). (Male gnathopods to same scale as those of female.)

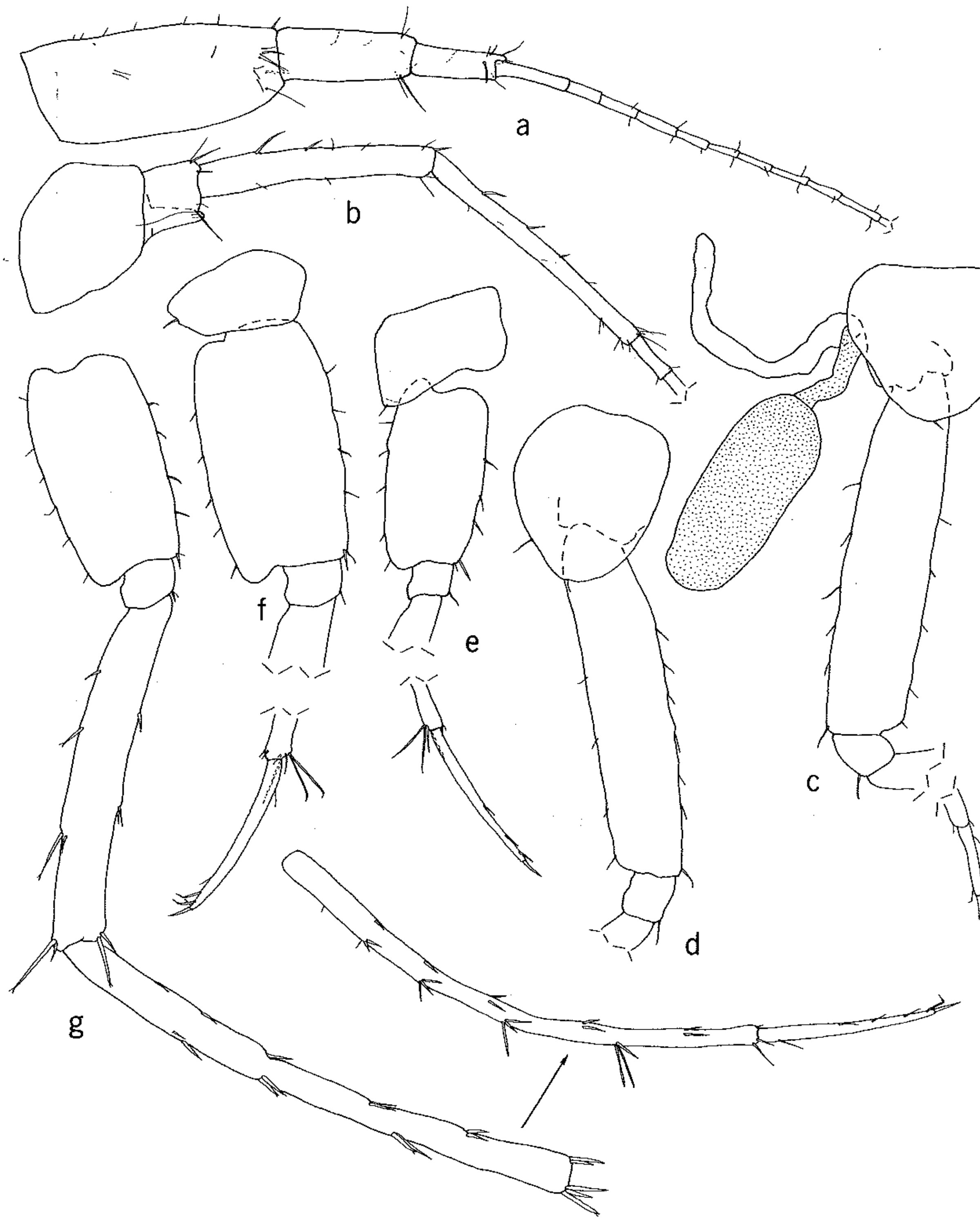

FIGURE 5.—*Texiweckelia texensis* (Holsinger), topotype, artesian well, Hays County, Texas, female (6.0 mm): *a*, *b*, antennae 1, 2; *c*, *d*, pereopods 3, 4 (in part); *e*, *f*, pereopods 5, 7 (in part); *g*, pereopod 6 (continuation of appendage indicated by arrow).

length, 15–20 percent longer than pereopod 5. Bases of pereopods 5–7 comparatively short; posterior margins nearly straight; distoposterior lobes small, bluntly rounded. Dactyls of pereopods 5–7 attenuate, with several setules on distal part of anterior margin; dactyl of pereopod 5 about 40–45 percent length of corresponding propod, that of pereopod 6 about 38–40 percent of corresponding propod, that of pereopod 7 about 30 percent. Coxal gills large, subovate, with long peduncles. Brood plates linguiform, nonsetose in material examined.

Pleonite 3 with 4 small dorsal spines. Pleonal plates: posterior margin of plate 1 generally straight, corner obsolescent, with 1 setule, posterior margins of 2 and 3 slightly concave, corners weakly produced and rounded, with 1 setule each; ventral margins with 1–2 setules each. Pleopods 1 and 2 subequal in length, 3 a little shorter; inner rami slightly shorter than outer; peduncles with 5–8 coupling spines each. Uronite 1 with 6 dorsodistal spines, 2 with 4 spines, 3 with 2 spines. Uropod 1: inner ramus a little longer than outer ramus, 90–95 percent length of peduncle, armed with 7 spines; outer ramus with 7 spines; peduncle with 12 spines, 3 of which are ventrolateral. Uropod 2: inner ramus longer than outer ramus and peduncle, armed with 6 spines; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3 relatively long, approximately 25 percent length of body; rami of equal length but outer ramus slightly narrower and lacking plumose setae on outer margin. Telson short, broader than long, broadest at base; apical margin with large incision extending about 45 percent the distance to base; apical lobes armed with 2 spines and 3 threadlike setae each.

MALE.—Differing principally from female in the structure of the gnathopods as follows: Propod of gnathopod 1 proportionately shorter and broader; palm oblique, convex, armed with double row of 8 weak, bifid spine teeth. Dactyl of gnathopod 1 with several small spines on inner margin. Propod of gnathopod 2 proportionately a little broader; palm oblique, armed with double row of 10–11 weak, bifid spine teeth; defining angle obsolescent, without long setae. Dactyl of gnathopod 2 longer, inner margin lined with row of small spines. Segment 5 of gnathopod elongate but a little shorter than propod. Gnathopods with fewer setae overall.

DISTRIBUTION AND ECOLOGY.—This species is recorded from the artesian well and from San Marcos Springs. Based on the samples obtained from the artesian well between 14 May 1974 and 16 December 1975, *T. texensis* represented 8.38 percent of the total amphipod fauna collected (Table 2). The sex ratio appears to be about 1.1 but with a preponderance of juveniles. Although many of the females examined to date appeared sexually mature, none had setose brood plates. The presence of juveniles from nearly every month of the sampling period would tend to indicate, however, that breeding takes place the year round.

TABLE 2.—Frequency distribution of amphipod species from the artesian well in San Marcos, Texas, based on continuous sampling between 15 May 1974 and 16 December 1975

Species	Number of specimens	Percent of total fauna
Texiweckelia insolita	3065	61.01
Stygobromus flagellatus	1325	26.37
Texiweckelia texensis	421	8.38
Seborgia relicta	56	1.11
Artesia subterranea	54	1.07
Stygobromus russelli	53	1.05
Allotexiweckelia hirsuta	33	0.66
Texiweckelia samacos	13	0.26
Parabogidiella americana	2	0.04
Parabogidiella (?) n. sp.	2	0.04

In the San Marcos Springs collections, *T. texensis* has been found in association with three other subterranean amphipods: *Stygobromus flagellatus*, *S. russelli*, and *Texiweckelia insolita*, new species. In all three samples the species of *Stygobromus* occurred in far greater numbers.

REMARKS.—The above description of *T. texensis* supercedes the previous one by Holsinger (1973:6–9). The original description was based on four fragments collected from the artesian well in 1940. After study of additional material from the well, it became obvious that the 1973 description of *T. texensis* was a composite of three different species, including *T. texensis*, *T. insolita*, new species, and *Allotexiweckelia hirsuta*, new genus, new species. Only two of the four fragments designated as syntypes are actually *T. texensis;* the remaining two have been redesignated paratypes of *T. insolita* and *A. hursita* as indicated elsewhere in this paper.

Texiweckelia insolita Holsinger, new species

FIGURES 6–8

Mexiweckelia texensis Holsinger, 1973:6–10, figs. 4–6 [in part].

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♀ (USNM 171149), 6–9 Sept 1974. Paratypes from same locality as follows: 1 fragment collected by L. Hubricht, 14 May 1940; 1 ♀, 1 ♂, 21 Apr 1973; 1 ♀, 2 ♂, 25 Apr 1973; 1696 ♀, 1025 ♂, 322 juvs, and 21 fragments from continuous sampling between 14 May 1974 and 16 Dec 1975. Additional material from Texas as follows. HAYS COUNTY: San Marcos Springs (large spring opening), 1 ♀, 25 Nov 1975. BEXAR COUNTY: Verstraeten well no. 1 near Von Ormy, 16 fragments (♀, ♂), 6 Apr 1977.

DIAGNOSIS.—A relatively small, fragile-bodied, subterranean species with rather slender body, easily distinguished from *T. texensis* by structure of mouthparts (i.e., upper lip without apical incision, outer plate of maxilla 1 with 14–15 apical spines, inner plate of maxilla 2 with 38–40 inner marginal setae, inner plate of maxilliped broad and setose); proportionately shorter 1st antenna and 6th and 7th pereopods; small, ovate coxal gills with short peduncles; convex posterior margins of gnathopod propods; and more deeply incised telson. Largest male, 4.5 mm (rarely execeeding 4.0 mm); largest female, 4.9 mm (rarely execeeding 4.5 mm).

FEMALE.—Antenna 1: 20 percent longer than body, 30 percent longer than antenna 2; primary flagellum with 45–55 segments; esthetascs absent or at least not discernible; accessory flagellum reduced to tiny vestigial stub or absent; peduncular segment 1 longer than combined lengths of segments 2 and 3. Antenna 2: flagellum with 12–15 segments; peduncular segment 4 longer than 5. Head produced into small triangle between 1st antennae; interantennal lobe small, bluntly rounded. Upper lip subquadrate, apical margin entire. Mandible small in comparison with other mouthparts, palp lacking; incisor reduced; right mandible with 3 spines in spine row and 1 molar seta, lacinia mobilis lacking; left mandible with lacinia mobilis (larger than incisor), 3 spines in spine row, molar seta lacking. Maxilla 1: inner plate with 20–24 naked, apical setae; outer plate with 14–15 apical, serrate spines; palp with 2 slender spines apically and single row of small setae medially. Maxilla 2: inner plate with oblique row of 38–47 naked setae on inner margin. Maxilliped: inner plate broadly expanded apically, about 25 percent broader than outer plate, apex with 3–4 bladelike spines and row of setae, inner margin with row of naked setae, inner face with numerous short setae on distal half; outer plate with 3 bladelike spines apically and several setae on inner margin. Lower lip with long, lateral processes; outer lobes large and prominent; inner lobes absent.

Propod of gnathopod 1 weak, narrow, more than twice as long as broad; palm short, transverse, with several small spine teeth and 2 long, bent setae; posterior margin elongate, convex, pubescent, with 3 long, bent setae; anterior margin with several long setae. Dactyl of gnathopod 1 rather short, nail also short. Segment 5 of gnathopod 1 subequal in length to propod; posterior margin broadly lobiform and pubescent. Coxal plate of gnathopod 1 broad and deep, deeper than corresponding body segment; ventral margin convex, with about 5 setules. Propod of gnathopod 2 elongate, subrectangular, a little longer than propod 1; palm short, slightly oblique, armed with few weak spines and 2 long setae; posterior angle without spines or setae; posterior margin elongate, slightly convex, pubescent, with 3 long setae; anterior margin with row of several long setae. Dactyl of gnathopod 2 longer and more slender than that of 1st gnathopod. Segment 5 of gnathopod 2 elongate, a little longer than propod; posterior margin lobiform and pubescent near distal end. Coxal plate of gnathopod 2 deeper than corresponding body segment but only about ½ as broad as 1st coxal plate; margin narrowly rounded, with 1 stiff seta. Coxal plates pereopods 3 and 4 comparatively small, shallower than corresponding body segments, about as broad as long, margins with 3 setae each. Pereopods 6 and 7 subequal in length, about 55 percent length of body, 5–10 percent longer than pereopod 5. Bases of pereopods 5–7 comparatively short; posterior margins nearly straight to slightly convex; distoposterior lobes rather prominent. Dactyls of pereopods 5–7 comparatively long, with several setules on distal part of anterior margin; dactyls of pereopods 6 and 7 about 45 percent length of corresponding propods, that of pereopod 5 about 55 percent. Coxal gills rather small, oval, with short peduncles. Brood plates elongate and narrow, margins with long setae.

Pleonite 3 with up to 4 small, dorsal spines. Pleonal plates: posterior margins somewhat variable,

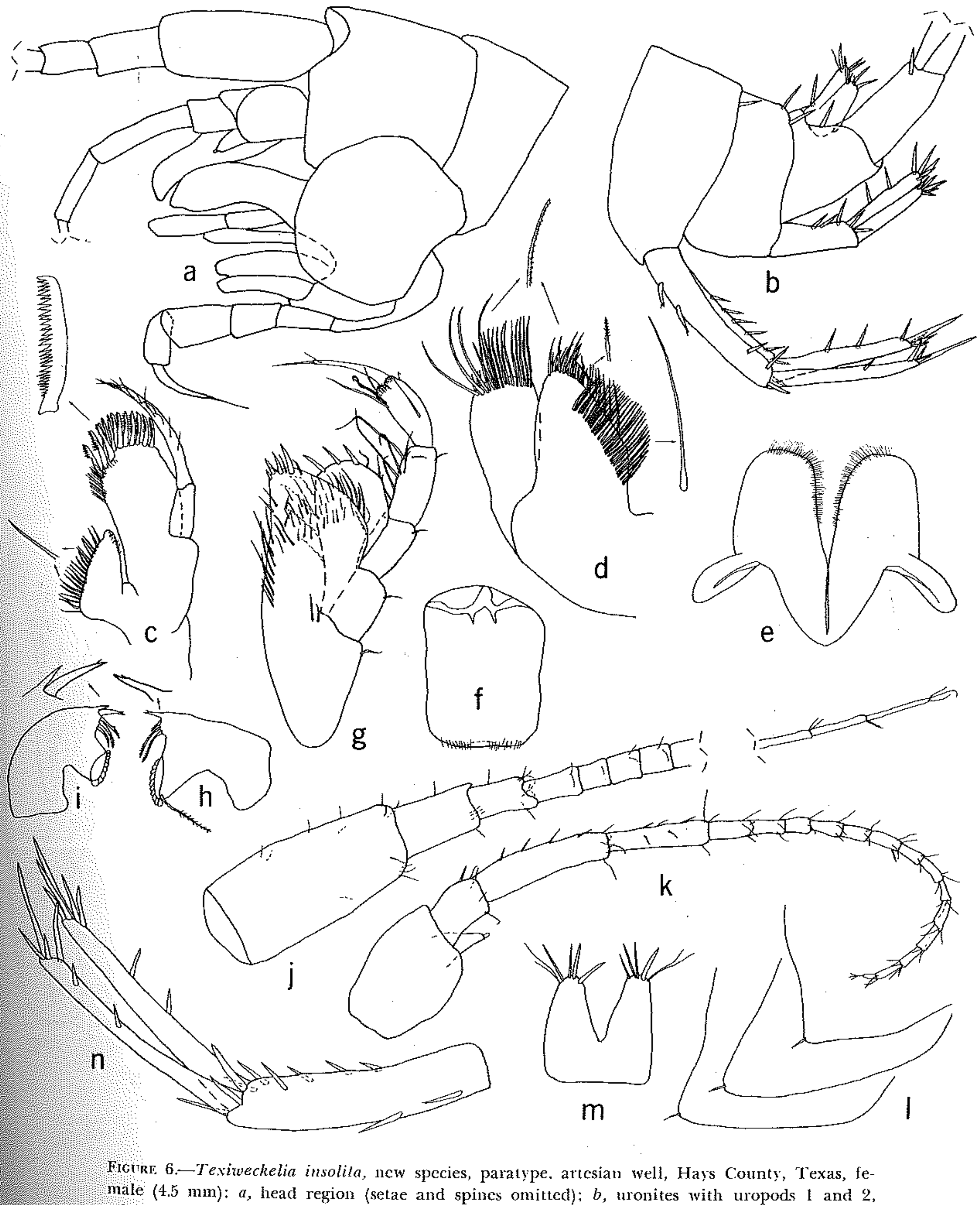

FIGURE 6.—*Texiweckelia insolita*, new species, paratype, artesian well, Hays County, Texas, female (4.5 mm): *a*, head region (setae and spines omitted); *b*, uronites with uropods 1 and 2, telson and uropod 3 in part; *c*, *d*, maxillae 1, 2 (setae and spines enlarged); *e*, lower lip; *f*, upper lip; *g*, maxilliped; *h*, right mandible (incisor enlarged); *i*, left mandible (incisor and lacinia mobilis enlarged); *j*, *k*, antennae 1, 2; *l*, pleonal plates; *m*, telson; *n*, uropod 1. (All mouthparts to same scale; head and uronites to same scale.)

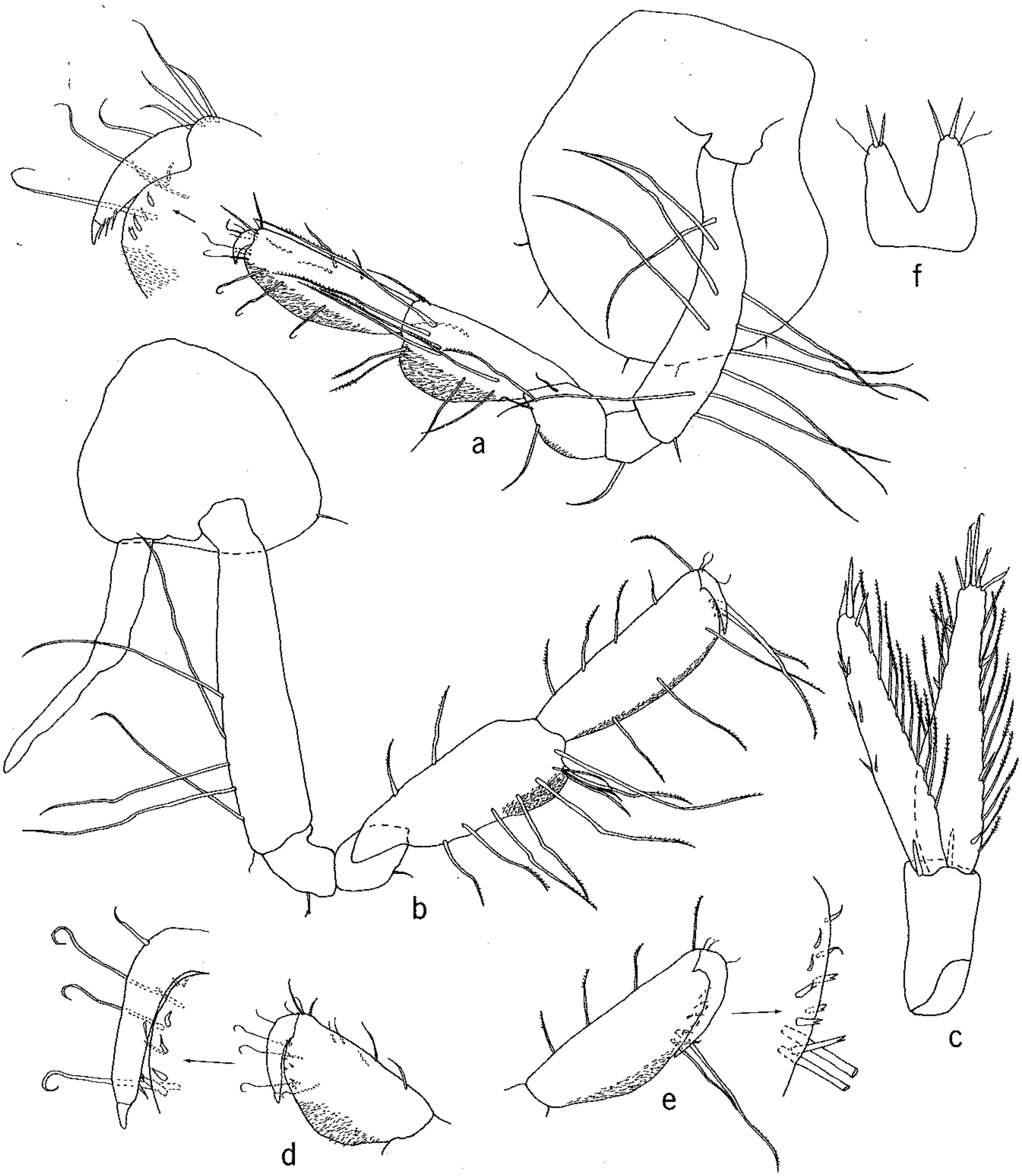

FIGURE 7.—*Texiweckelia insolita*, new species, paratypes, artesian well, Hays County, Texas, female (4.7 mm): *a*, *b*, gnathopods 1, 2 (palm enlarged). Female (4.5 mm): *c*, uropod 3. Male (4.0 mm): *d*, *e*, gnathopod propods 1, 2 (palms enlarged; same scale as those of female); *f*, telson.

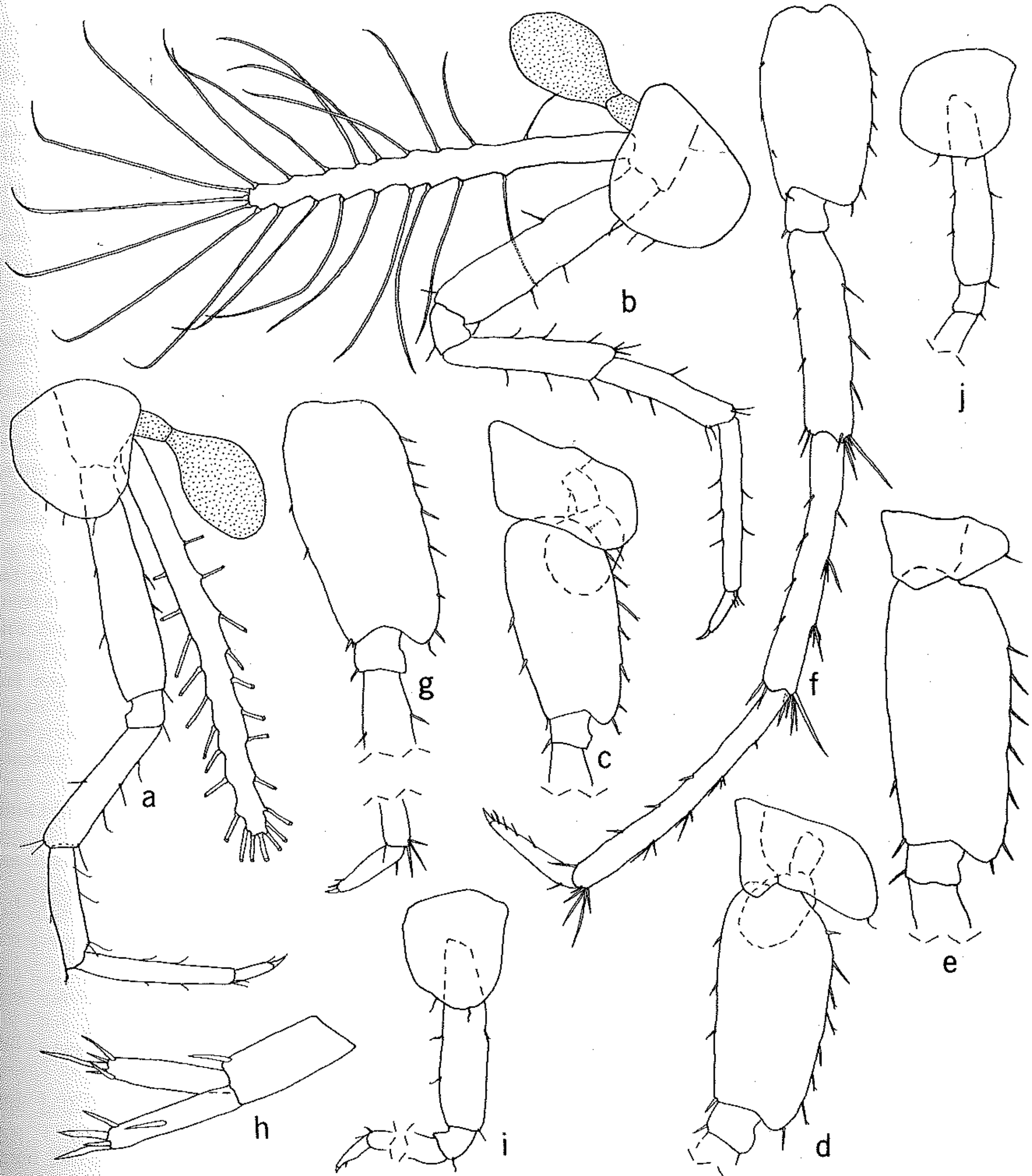

FIGURE 8.—*Texiweckelia insolita*, new species, paratypes, artesian well, Hays County, Texas, female (4.5 mm): *a*, *b*, pereopods 3, 4; *c*, *d*, *e*, pereopods 5, 6, 7 (in part). Another female (4.5 mm) (pereopods drawn to smaller scale than for preceding female): *f*, pereopod 6; *g*, pereopod 7 (in part). Male (4.0 mm): *h*, uropod 2; *i*, *j*, pereopods 3, 4 (in part).

those of plates 1 and 3 slightly concave, that of 2 generally straight; posterior corner of plate 1 weakly produced, bluntly rounded, bearing 1 setule; posterior corners of plates 2 and 3 rather strongly produced, otherwise like that of 1st plate; ventral margins without spines or setae. Pleopods decreasing slightly in overall length posteriorly; inner rami slightly shorter than outer; peduncles with 3–4 coupling spines each. Uronites 1 and 2 each with 2 (rarely 4) slender spines dorsodistally; 3 with 2–4 such spines. Uropod 1: inner ramus subequal in length to outer ramus and peduncle, armed with 6–7 spines; outer ramus with 5–6 spines; peduncle with 11–12 spines, 2 of which are ventrolateral. Uropod 2: inner ramus subequal in length to outer ramus and peduncle, armed with 5–7 spines; outer ramus with 5 spines; peduncle with 5 spines. Uropod 3 proportionately elongate, 35–40 percent length of body; rami about equal in length but outer ramus slightly narrower proximally and lacking plumose setae on outer margin. Telson relatively short, about as broad as long; apical margin with large V-shaped incision extending about 60–70 percent the distance to base; apical lobes armed with 4 slender spines and 2 threadlike setae each.

MALE.—Differing principally from female as follows: Propod of gnathopod 1 proportionately shorter and broader; palm longer, oblique, bearing few more spine teeth and 3 long, bent setae; posterior margin broadly expanded, nearly lobiform, without setae. Dactyl of gnathopod 1 a little longer. Segment 5 of gnathopod 1 with few less setae. Propod of gnathopod 2 proportionately a little broader; palm longer, more oblique, bearing few more weak spine teeth and 2 long setae near defining angle; posterior margin more convex, without setae. Dactyl proportionately longer, bearing 2 tiny spines on inner margin. Segment 5 subequal in length to propod, with few less setae. Peduncle of uropod 1 with about 9 spines; that of uropod 2 with 2 spines (only 1 shown in Figure 8h). Apical lobes of telson with 2 slender spines each.

TYPE-LOCALITY.—The artesian well in San Marcos, Hays County, Texas.

DISTRIBUTION AND ECOLOGY.—This species is recorded from the type-locality and nearby San Marcos Springs in Hays County, but also apparently occurs in deep subterranean aquifers near Von Ormy in Bexar County. Outside of San Marcos, however, the species is known only from the fragments of 16 specimens collected from the Verstraeten well, and the poor condition of this material has made positive determination difficult.

On the basis of 2722 sexable specimens obtained from the artesian well between 14 May 1974 and 16 December 1975, a sex ratio of approximately 1.6: 1:00 in favor of females was calculated. Although adults outnumbered juveniles 8.45 to 1 in these samples, the latter were collected during nearly every month of the sampling period but occurred in greater numbers during late summer and fall than during other seasons of the year. Many of the females examined to date appeared sexually mature, but only five specimens had setose brood plates. Four of these females, ranging in size from 4.1 to 4.5 mm, were collected from the artesian well in June, July, and August 1975, and the other was collected from the Verstraeten well in April 1977.

Of the 10 subterranean amphipod species recorded from the artesian well, *S. insolita* is by far the most common and represented 61.01 percent of the total amphipod fauna collected from this locality during the May 1974–December 1975 sampling period (Table 2). This species is much less common in San Marcos Springs, however, where a single specimen was taken in association with four *Texiweckelia texensis*, 27 *Stygobromus flagellatus*, and three *S. russelli* on 25 November 1975.

ETYMOLOGY.—The epithet *insolita* is from Latin, meaning "unusual" or "strange."

Texiweckelia samacos Holsinger, new species

FIGURES 9–12

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♀ (USNM 171148), 1–4 Feb 1975. Paratypes from same locality as follows: 3 ♀, 8 ♂, and 1 juv from continuous sampling between 14 May 1974 and 16 Dec 1975.

DIAGNOSIS.—A medium-sized, fragile-bodied subterranean species, easily distinguished from *T. texensis* and *T. insolita* by more heavily setose inner plates of maxillae and maxilliped (i.e., inner plate of maxilla 1 with 40 setae, inner plate of maxilla 2 with oblique row of 100 setae, maxilliped with row of numerous setae on inner margin), larger coxal gills, broader bases of pereopods 3–7 (esp.

5–7), and proportionately longer and more deeply incised telson. Largest male, 7.1 mm; largest female, 7.3 mm.

FEMALE.—Antenna 1: 25–30 percent longer than body, 70–75 percent longer than antenna 2; primary flagellum with 65–69 segments, esthetascs on some flagellar segments; accessory flagellum reduced to tiny, vestigial stub or absent; peduncular segment 1 longer than combined lengths of segments 2 and 3. Antenna 2: flagellum with about 15 segments; peduncular segment 4 longer than 5. Head without triangular-shaped rostrum between 1st antennae; interantennal lobe small, bluntly rounded. Upper lip tapering slightly distally, apex entire. Mandible comparatively large and slender (not compact), palp lacking; right mandible with 3 spines in spine row and 1 molar seta, lacinia mobilis lacking; left mandible with small lacinia mobilis, 3 spines in spine row, molar seta lacking. Maxilla 1: inner plate expanded distally, with 40 naked, apical setae; outer plate with 7 apical, serrate spines; palp with 4 bladelike spines apically and 5–6 slender setae subapically. Maxilla 2: enlarged; inner plate elongate, with oblique row of 100 naked setae on inner margin. Maxilliped: inner plate elongate, subrectangular, with 4 bladelike spines, 4 plumose setae and row of naked setae apically, inner margin with long row of numerous naked setae; outer plate expanded distally, with 3 small, bladelike spines and several short setae apically and subapically and row of few slender setae on inner margin. Lower lip with long, lateral processes; outer lobes large and prominent; inner lobes absent.

Propod of gnathopod 1 weak, narrow, more than twice as long as broad; palm short, transverse, with irregular double row of small spine teeth (some weakly bifid) and 1 long, bent seta; posterior margin elongate, pubescent, with 1 or 2 slender setae; anterior margin with row of long setae. Dactyl of gnathopod 1 short; nail short. Segment 5 of gnathopod 1 longer and much broader than propod; posterior margin broadly lobiform and pubescent. Coxal plate of gnathopod 1 broad and deep, deeper than corresponding body segment; ventral margin broadly rounded, with 2 slender setae. Propod of gnathopod 2 elongate, subrectangular, about 35 percent longer than propod 1; palm short, slightly oblique, armed with irregular double row of weak, mostly bifid spine teeth and 2 or 3 long setae; posterior angle without spines or setae; posterior margin elongate, with 5 sets of long, mostly triply inserted, setae; anterior margin with row of long, singly inserted setae. Dactyl of gnathopod 2 generally similar to that of gnathopod 1. Segment 5 of gnathopod 2 elongate, a little shorter than propod; posterior margin lobiform and pubescent toward distal end. Coxal plate of gnathopod 2 nearly as deep but less broad than 1st coxal plate; margin with 2 slender setae. Coxal plates of pereopods 3 and 4 comparatively small, shallower than corresponding body segments, that of 3 longer than broad, that of 4 about as long as broad; margins with 2 setules each. Bases of pereopods 3 and 4 somewhat expanded, more than twice as broad as segments 4, 5, or 6. Pereopods 6 and 7 subequal in length and structure, 65 percent length of body, 20 percent longer than pereopod 5. Bases of pereopods 5–7 broadly expanded, anterior and posterior margins convex; anterior margins armed with rather heavy spines; distoposterior lobes large, broadly rounded. Dactyls of pereopods 5–7 rather long, with 4–6 setules on distal half of anterior margin; dactyls of pereopods 6 and 7, 30–35 percent length of corresponding propods, that of pereopod 5 about 50 percent length of corresponding propod. Coxal gills large, prominent, ellipsoidal, with peduncles. Brood plates small, sublinear, and nonsetose in material examined.

Pleonite 3 without spines. Pleonal plates: posterior margin of plate 1 nearly straight, corner quadrate, with 1 setule; posterior margin of plate 2 generally straight, corner weakly produced, with setule; posterior margin of plate 3 concave, corner rather strongly produced, sharply rounded, with 1 setule; ventral margins without spines or setae. Pleopods 1 and 2 subequal in length, 3 slightly shorter; inner rami slightly longer than outer; peduncles with 6–7 coupling spines each. Uronites 1 and 2 each with 2 dorsodistal spines, 3 with 4 spines. Uropod 1: inner ramus a little shorter than outer ramus, about 75 percent length of peduncle, armed with 6 spines; outer ramus with 7 spines; peduncle with 11 spines, 3 of which are ventrolateral. Uropod 2: inner ramus subequal in length to peduncle, a little shorter than peduncle, armed with 6 spines; peduncle with 5 spines. Uropod 3 relatively long, approximately 20 percent length of body; rami of equal length but outer

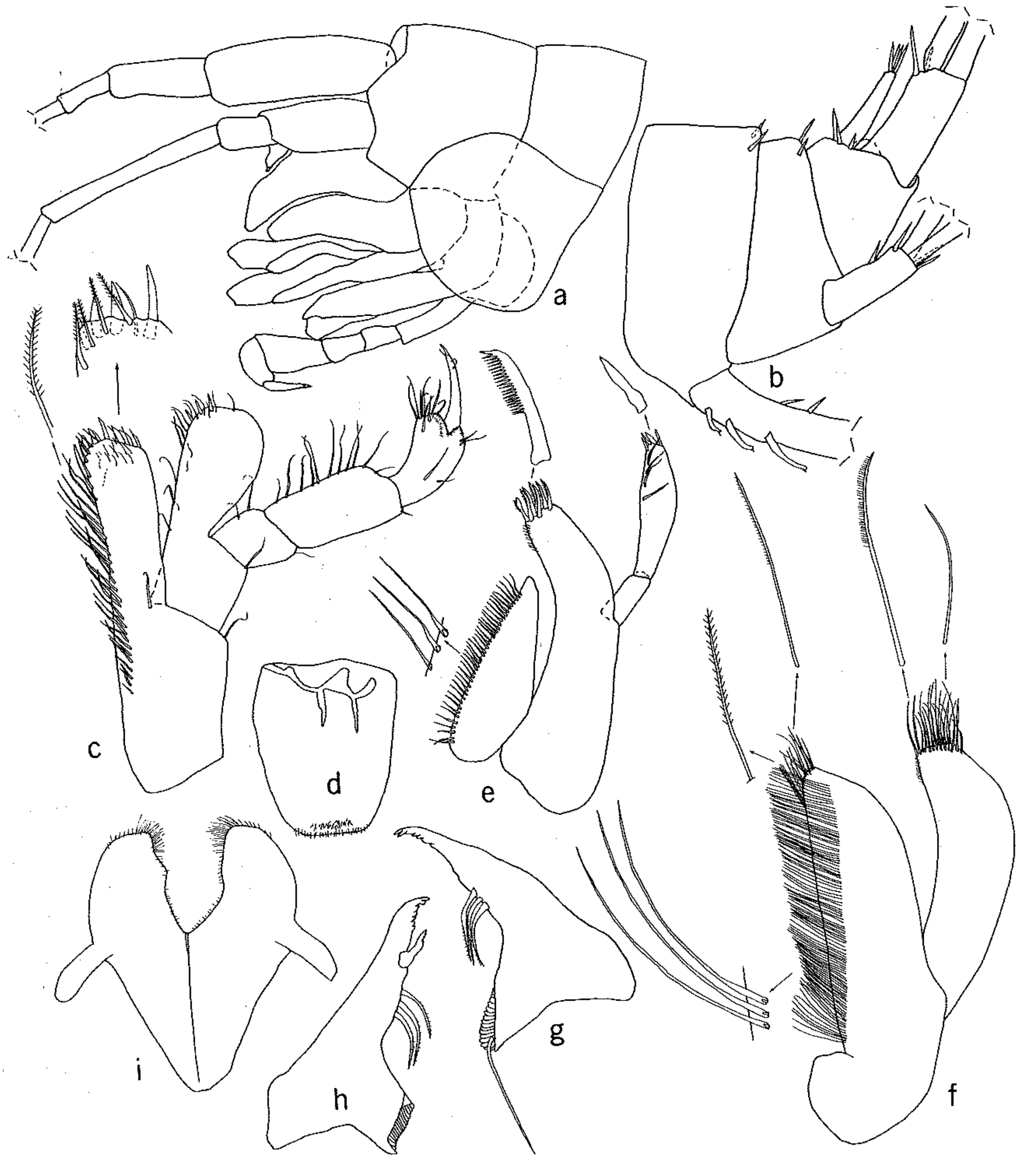

FIGURE 9.—*Texiweckelia samacos*, new species, paratypes, artesian well, Hays County, Texas, male (7.0 mm): *a*, head region (setae and spines omitted); *b*, uronites with telson and uropods (in part). Female (7.3 mm): *c*, maxilliped (setae and spines enlarged); *d*, upper lip; *e*, *f*, maxillae 1, 2 (setae and spines enlarged). Male 6.3 mm: *g*, *h*, right and left mandibles. Male (7.0 mm): *i*, lower lip. (Mouthparts to same scale except mandibles, which are at larger scale; head and uronites to same scale.)

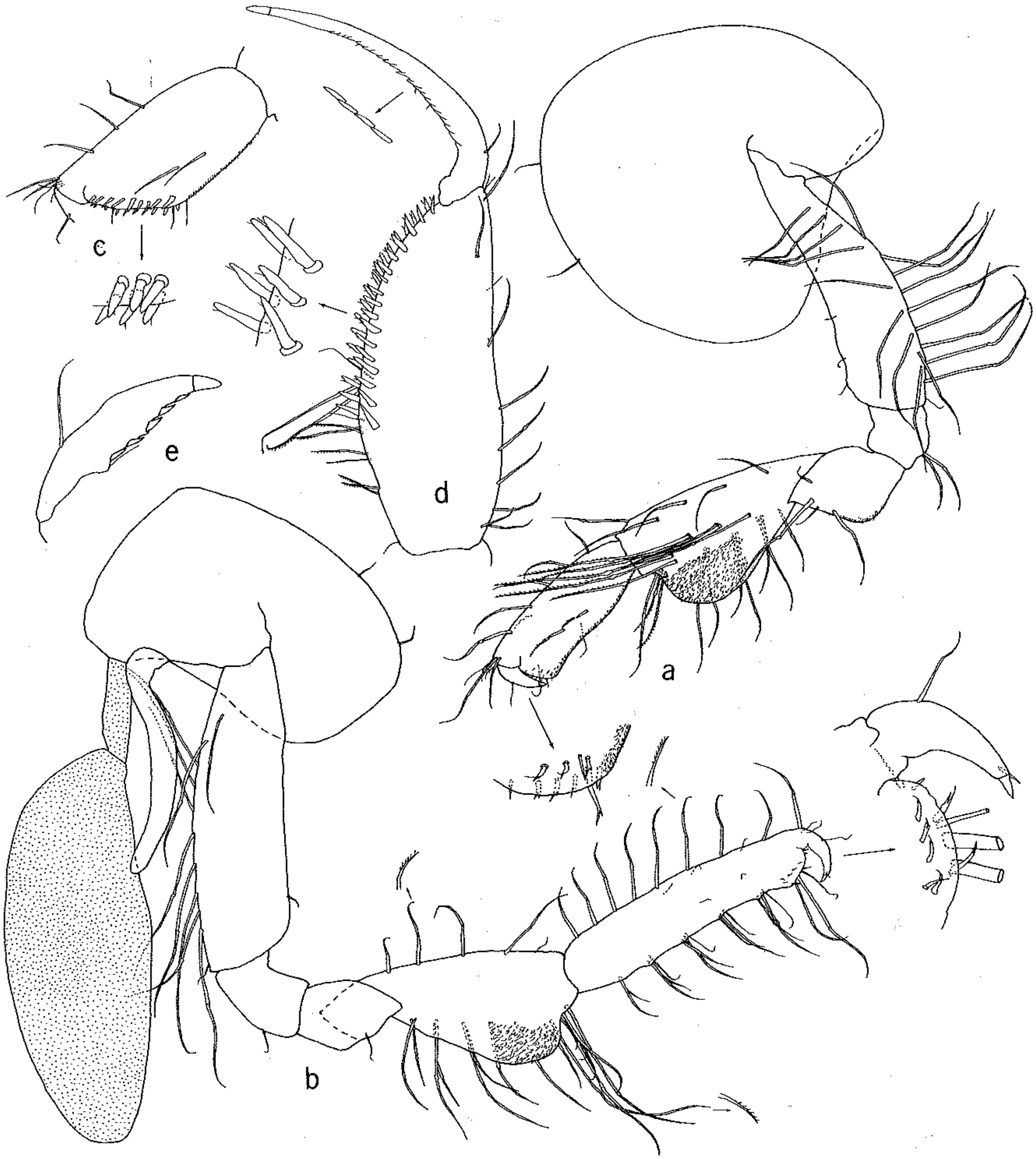

FIGURE 10.—*Texiweckelia samacos*, new species, paratypes, artesian well, Hays County, Texas, female (7.3 mm): *a*, *b*, gnathopods 1, 2 (palms enlarged). Male (7.0 mm): *c*, *d*, gnathopod propods 1, 2 (spines enlarged); *e*, dactyl of gnathopod 1 (enlarged). (Gnathopods of both sexes to same scale.)

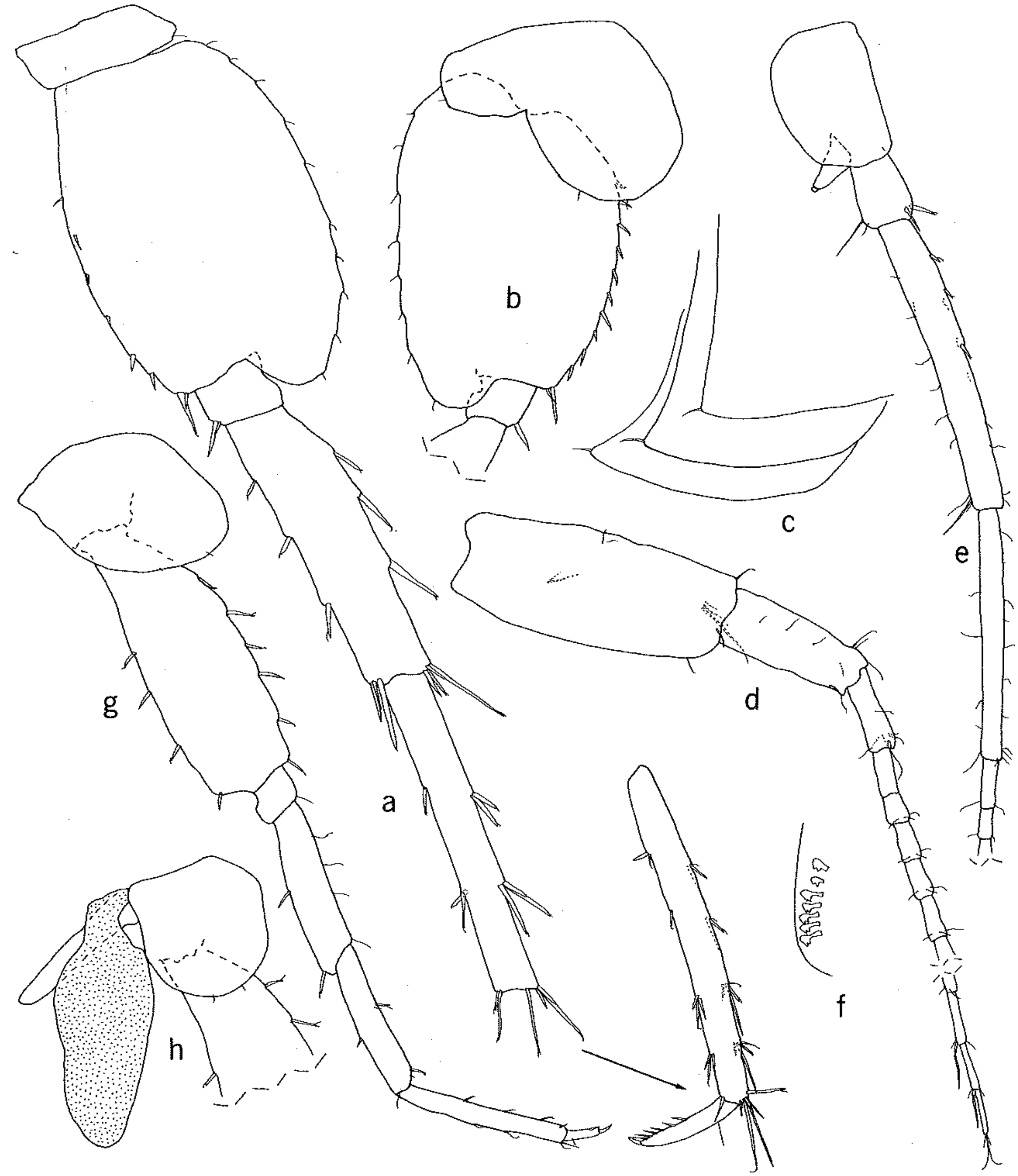

FIGURE 11.—*Texiweckelia samacos*, new species, paratype, artesian well, Hays County, Texas, female (7.3 mm): *a*, pereopod 7 (continuation of appendage indicated by arrow); *b*, pereopod 5 (in part); *c*, pleonal plates; *d*, *e*, antennae 1, 2; *f*, coupling spines of peduncle of pleopod 2; *g*, pereopod 3; *h*, pereopod 4 (in part) with coxal gill and brood plate.

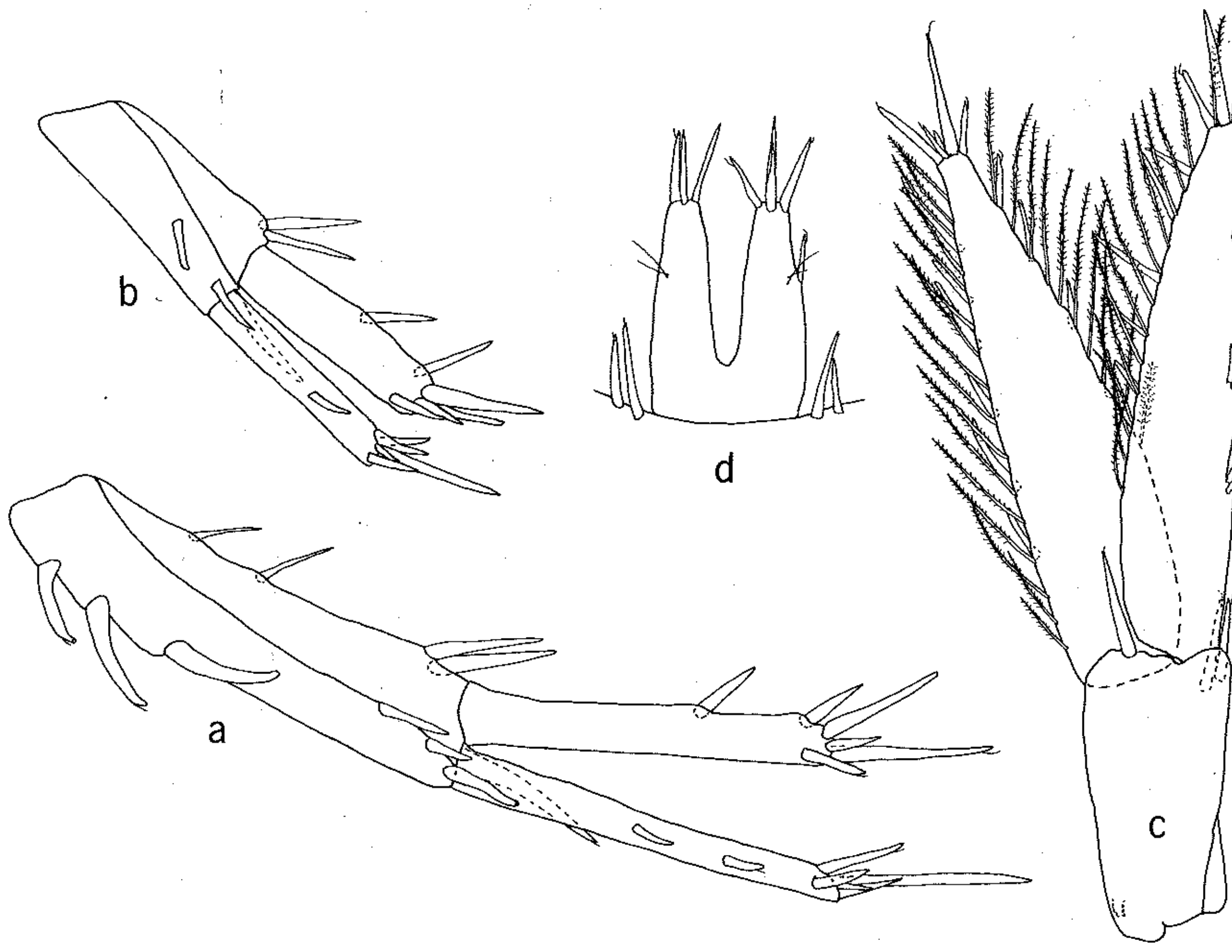

FIGURE 12.—*Texiweckelia samacos*, new species, paratype, artesian well, Hays County, Texas, female (7.3 mm): *a, b, c,* uropods 1, 2, 3; *d,* telson (with spines of uronite 3). (Uropods and telson to same scale.)

ramus slightly narrower and lacking plumose setae on outer margin. Telson rather long and narrow, about 35 percent longer than broad; apical margin incised about 75 percent the distance to base; apical lobes armed with 3–4 heavy spines; lateral margins sometimes with single spines.

MALE.—Differing principally from female in structure of gnathopods as follows: Propod of gnathopod 1 proportionately shorter and broader; palm oblique, armed with double row of 8–9 nonbifid spine teeth. Dactyl of gnathopod 1 with row of bladelike spines on inner margin. Segment 5 of gnathopod 1 subequal in length to propod but otherwise like female. Propod of gnathopod 2 proportionately broader; palm oblique, convex, armed with double row of 17 rather large, nonbifid spine teeth and 2 long, bent setae near posterior angle; posterior margin shorter than palm, with 3 sets of doubly inserted setae. Dactyl long and slightly curved, closing beyond palm spines; inner margin with row of small, bladelike spines; nail short and blunt. Segment 5 of gnathopod about 60 percent length of propod but otherwise about like that of female.

TYPE-LOCALITY.—The artesian well in San Marcos, Hays County, Texas.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality, where, in comparison with other species in the genus *Texiweckelia,* it is quite rare. During the 19-month sampling period (May 1974–December 1975), only 13 specimens (0.26 percent of the total amphipod fauna) were collected (Table 2). Of the four females obtained to date, three measured 6.9–7.3 mm in length and appeared sexually mature but lacked setae on the brood plates. A single juvenile (3.1 mm) was collected in January 1975. The remaining specimens examined were males, ranging in size from 5.0 to 7.1 mm.

ETYMOLOGY.—The epithet *samacos* is a contraction of the place name "San Marcos."

Allotexiweckelia Holsinger, new genus

DIAGNOSIS.—Without eyes and pigment, of subterranean facies. Head produced into tiny triangular-shaped rostrum between 1st antennae; interantennal lobe distinct, rounded anteriorly; inferior antennal sinus indistinct. Antenna 1: elongate, longer than body, longer than antenna 2; esthetascs on most flagellar segments; accessory flagellum reduced to tiny, vestigial stub or absent. Antenna 2: segments 3–5 of peduncle armed with conspicuous lateral spines. Upper lip symmetrical, rounded apically, without apical incision. Mandible: molar rather prominent, triturative; lacina mobilis absent from right; molar seta absent from left; palp lacking. Maxilla 1: inner plate with naked, apical setae; outer plate with 7 apical, serrate and/or pectinate spines; palp 2-segmented, with spines apically and subapically. Maxilla 2: inner plate broader than outer, bearing oblique row of naked setae; both plates with numerous coarse setae. Maxilliped: inner plate with bladelike spines and naked setae apically and row of naked setae on inner margin; outer plate with row of bladelike spines extending from apex onto inner margin; palp 4-segmented, segment 2 the longest. Lower lip: outer lobes rather low; inner lobes small to vestigial; lateral processes slender.

Gnathopods not sexually dimorphic, heavily setose; propods comparatively large but 2nd longer and more slender than 1st, palms oblique, armed with double row of large nonbifid spine teeth; segment 5 shorter than propod, posterior margin lobiform and pubescent distally; dactyls with row of spines on inner margin. Coxal plate of gnathopod 1 enlarged, deeper than corresponding body segment. Pereopods 3 and 4 subequal; coxal plates shallower than corresponding body segments; bases broadly expanded; dactyls with row of setules on anterior margin. Pereopods 6 and 7 subequal in length, approximately 50 percent of body, longer than pereopod 5; segment 6 of pereopods 5–7 with numerous spines on anterior margin; dactyls with row of setules on anterior margins. Segment 6 of pereopods 5 and 6 with row of numerous long setae on posterior margin. Rather large, pedunculate coxal gills on pereopods 2–6. Sternal gills absent. Brood plates small and narrow.

Posterior corners of pleonal plates rounded, produced in plates 2 and 3. Pleopods biramous, 1 and 2 subequal in length, 3 a little shorter; peduncles with 7–10 coupling spines on inner margin distally. Uronites free (not fused), with few dorsolateral spines. Uropods 1 and 2 not sexually dimorphic; rami and peduncles bearing normal spines; peduncle of uropod 1 also armed with ventrolateral spines. Uropod 3 comparatively long, biramous; rami 1-segmented, subequal in length and differing slightly in width and setal pattern. Telson longer than broad; apical margin with large incision; apical lobes and lateral and medial margins bearing spines.

TYPE-SPECIES.—*Allotexiweckelia hirsuta*, new species. Gender is feminine.

ETYMOLOGY.—The generic name is derived from a combination of *Allo*, which is from Greek, meaning "another kind," and *Texiweckelia*.

RELATIONSHIP.—Although *Allotexiweckelia* and *Texiweckelia* share several important morphological characters, the former differs from the latter in a number of important ways: (a) peduncular segments 3–5 of antenna 2 are heavily spinose in contrast to the comparatively weakly spined condition in *Texiweckelia;* (b) the outer lobes of the lower lip are rather low, whereas in *Texiweckelia* they are rather high; (c) the gnathopods are not sexually dimorphic as in *Texiweckelia;* (d) the propod of the 1st gnathopod of the female is rather powerful and has an oblique palm armed with strong spine teeth and lacking long, bent setae, all of which are in contrast to the female propod of gnathopod 1 in *Texiweckelia*, which is weak and has a short, transverse palm armed with weak spine teeth and 1 or 2 long, bent setae; (e) the bases of pereopod 3 and 4 are broadly expanded anteriorly with heavily spinose margins unlike *Texiweckelia*, which has "normal" pereopod bases; (f) segment 6 of pereopods 5 and 6 has long setae on the posterior margin, and segment 6 of pereopods 5–7 has a heavily spinose anterior margin, whereas in *Texiweckelia,* pereopods 5 and 6 lack long setae and the 6th segment of pereopods 5–7 has a weakly spined anterior margin; (g) the telson is armed with prominent lateral and medial spines, as opposed to this structure in *Texiweckelia,* which lacks medial and usually lateral spines; (h) the inner ramus of uropod 3 is a little longer than the outer ramus, whereas in *Texiweckelia* the rami are generally equal in length.

Except for the gnathopod propods and the 6th segment of pereopods 5 and 6, which differ markedly between the two genera, the other differences appear to be of less importance at the generic level. The structure of the 1st gnathopod propod of the female, however, signals a significant departure from the *Mexiweckelia-Texiweckelia* line, as well as from other weckeliid genera, and the presence of long setae on pereopods 5 and 6 is unique among all known genera of the weckeliid complex.

Allotexiweckelia hirsuta Holsinger, new species

FIGURES 13–15

Mexiweckelia texensis Holsinger, 1973:6–10, figs, 4–6 [in part].

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♂ (USNM 171144), 18–20 May 1974. Paratypes from same locality as follows: 1 fragment collected by L. Hubricht, 14 May 1940; 10 ♀, 5 ♂, and 17 juvs from continuous sampling between 14 May 1974 and 16 Dec 1975. Additional material from Bexar County, Texas, as follows: O. R. Mitchell well no. 2 near Von Ormy, ♂ (?), 25 Mar 1977; Verstraeten well no. 1 near Von Ormy, 1 ♀, 6 Apr 1977.

DIAGNOSIS.—A medium-sized, fragile-bodied subterranean species clearly distinguished by elongate 1st antenna; spinose peduncular segments 3–5 of antenna 2; large, setose gnathopods with double row of prominent spine teeth on palms; broadly expanded bases and setose dactyls of pereopods 3–7; long setae on segment 6 of pereopods 5 and 6; heavy anterolateral spines of uropod 1; and telson that is spinose on distal half and broadly incised. Largest male, 7.9 mm; largest female, 10.1 mm.

DESCRIPTION.—Sexes generally similar except mature female apparently larger than mature male. Antenna 1: 10–15 percent longer than body in female, about 28 percent longer in male, 45–50 percent longer than antenna 2; peduncular segment 1 longer than combined lengths of segments 2 and 3; primary flagellum with 77–79 segments, esthetascs on most flagellar segments; accessory flagellum reduced to tiny, vestigial stub or absent. Antenna 2: flagellum with 28–31 segments; peduncular segment 4 a little longer than 5; peduncular segments 3–5 armed with lateral and medial spines. Head produced into small triangle between 1st antennae; interantennal lobe rather well developed, rounded anteriorly. Upper lip small, narrowing and rounded apically. Mandible: molar large, palp lacking; right mandible with 3 spines in spine row and 1 molar seta, lacinia mobilis lacking; left mandible with well-developed lacinia mobilis, 3 spines in spine row, molar seta lacking. Maxilla 1: inner plate with 12–13 naked, apical setae; outer plate with 7 serrate spines; palp of left maxilla with 7 bladelike spines apically, 4 stiff setae (spinules ?) subapically and 4 slender spines on inner margin distally; palp of right maxilla with 13 bladelike spines apically and on inner margin distally. Maxilla 2: inner plate with oblique row of 14 naked setae on inner margin. Maxilliped: inner plate broadly rounded apically, with 4 bladelike spines and several naked setae apically, row of naked setae on inner margin; outer plate broadly rounded apically, with row of bladelike spines on apex extending onto distal half of inner margin. Lower lip: outer lobes rather low and broadly rounded; inner lobes small to vestigial.

Propod of gnathopod 1 rather powerful, longer than broad, heavily setose; palm oblique, slightly convex, armed with double row of 10–12 prominent, nonbifid spine teeth; posterior margin a little longer than palm, with 4 sets of setae; anterior margin with row of mostly doubly inserted setae; medial setae singly inserted. Dactyl of gnathopod 1 rather long, inner margin lined with bladelike spines; nail short. Segment 5 of gnathopod 1 a little shorter than propod, heavily setose; posterior margin produced into broad, pubescent lobe bearing numerous long, naked setae. Segments 2 and 3 of gnathopod 1 bearing numerous long setae, some of which are weakly plumose. Coxal plate of gnathopod 1 deeper than corresponding body segment, broadly expanded distally, margin with 2 setules. Propod of gnathopod 2 proportionately elongate, longer than 1st propod; palm oblique, slightly convex, bearing double row of 10–15 prominent, nonbifid spine teeth and 3 long, jointed setae; posterior angle obsolescent; anterior margin with row of singly inserted setae; posterior margin with 7 sets of mostly

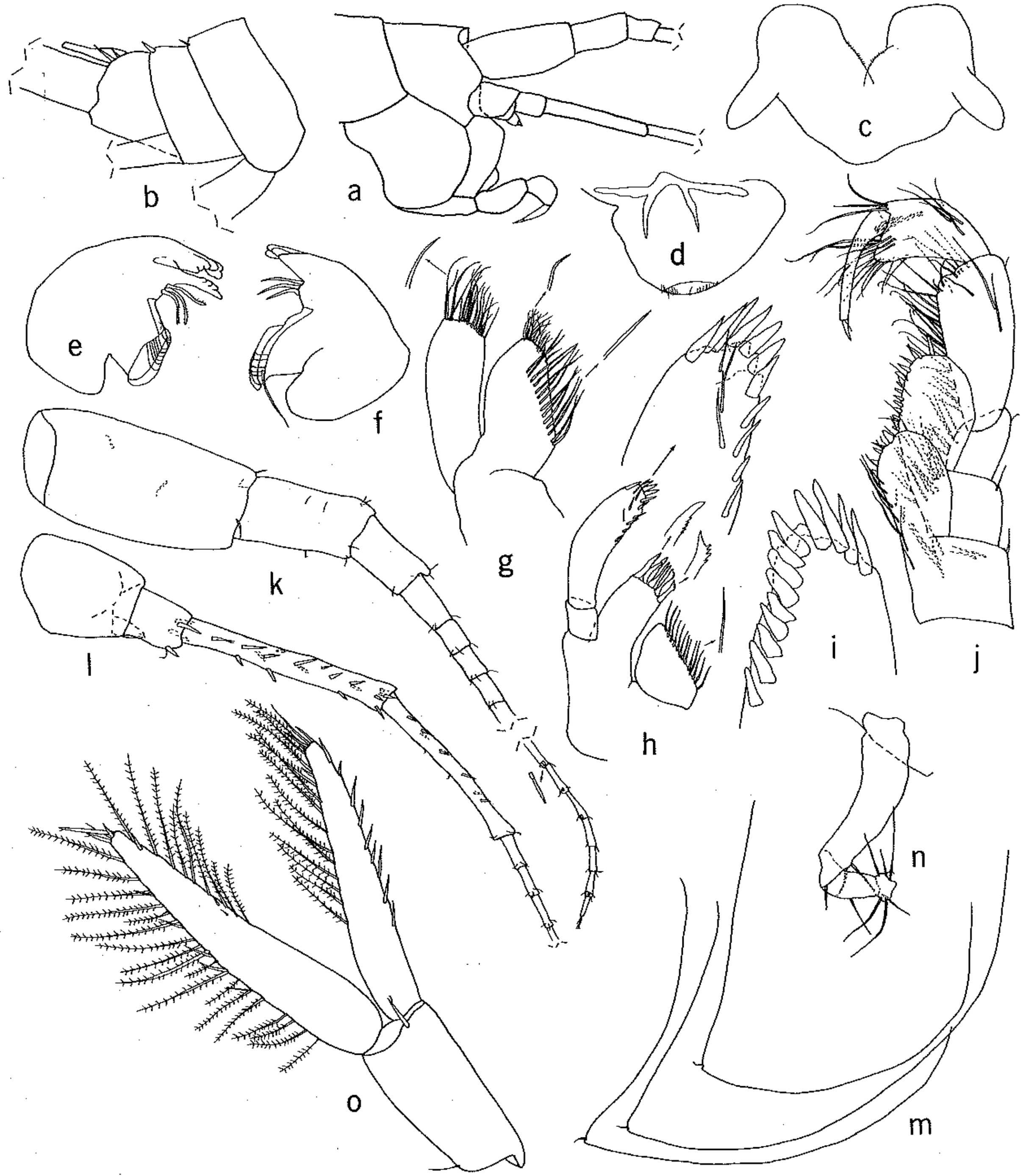

FIGURE 13.—*Allotexiweckelia hirsuta*, new species, artesian well, Hays County, Texas, male paratype (7.0 mm): *a*, head region (setae and spines omitted); *b*, uronites (to same scale as head region). Female paratype (9.0 mm): *c*, lower lip; *d*, upper lip; *e, f*, left and right mandibles; *g*, maxilla 2 (setae enlarged); *h*, left maxilla 1 (apex of palp, spines, and setae enlarged); *i*, apex of palp of right maxilla enlarged to same scale as left; *j*, maxilliped; *k, l*, antennae 1, 2; *m*, pleonal plates. Female paratype (10.1 mm): *n*, setose brood plate from gnathopod 2. Male holotype (7.5 mm): *o*, uropod 3.

FIGURE 14.—*Allotexiweckelia hirsuta,* new species, female paratype, artesian well, Hayes County, Texas, female (9.0 mm): *a, b,* gnathopods 1, 2 (spines and setae enlarged); *c,* coupling spines from peduncle of pleopod 1; *d,* telson (with spines of uronite 3).

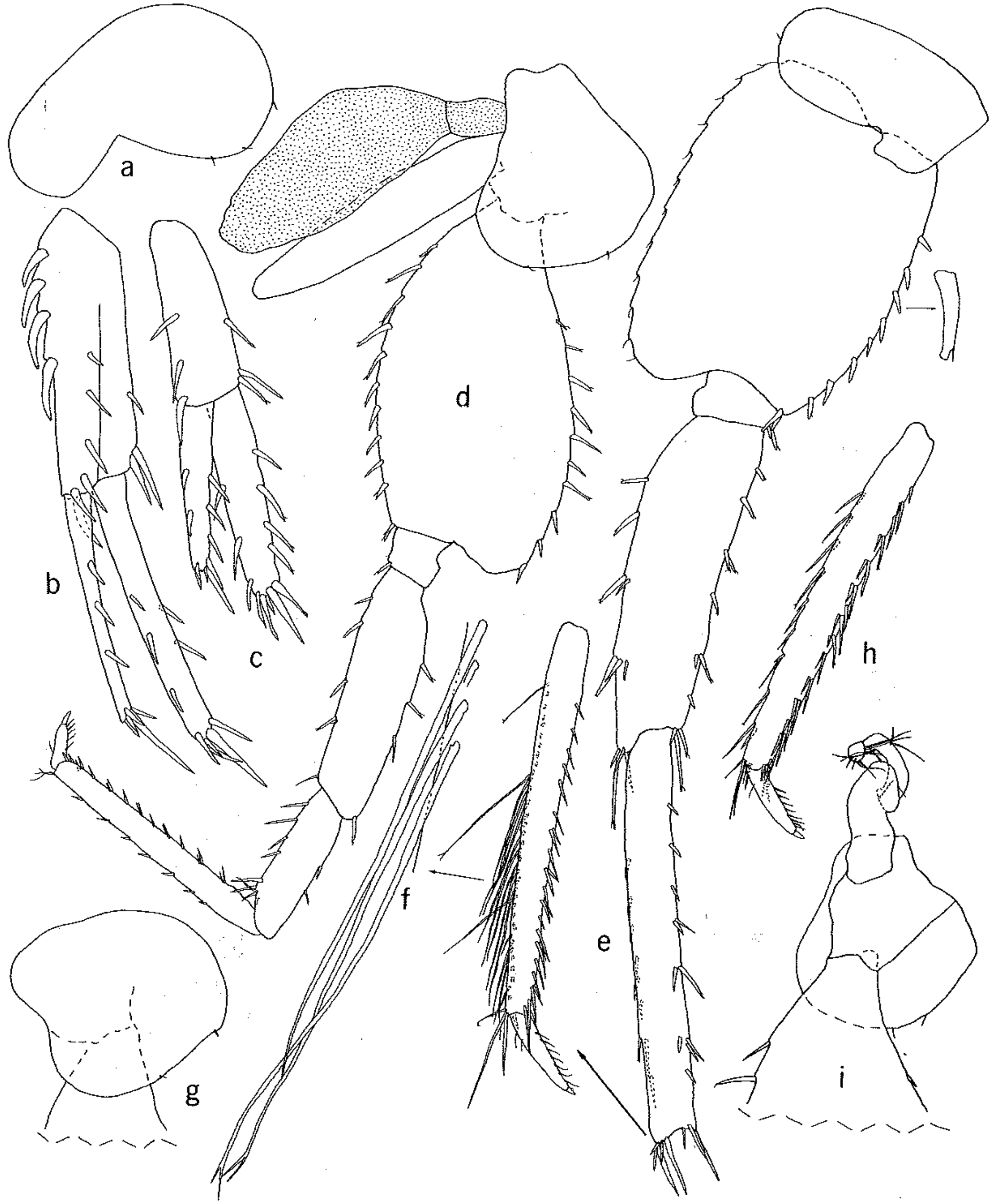

FIGURE 15.—*Allotexiweckelia hirsuta*, new species, paratypes, artesian well, Hays County, Texas, female (9.0 mm): *a*, coxal plate of pereopod 5; *b*, *c*, uropods 1, 2; *d*, pereopod 3; *e*, pereopod 6 (continuation of appendage indicated by arrow; spine of basis enlarged): *f*, several setae on segment 6 of pereopod 6 greatly enlarged; *g*, coxal plate of pereopod 4; *h*, segments 6 and 7 of pereopod 7. Female (10.1 mm): *i*, pereopod 3 (upper part) with setose brood plate.

doubly and triply inserted setae; medial setae reduced to few setules. Dactyl of gnathopod 2 long, inner margin with row of bladelike spines; nail short. Segment 5 of gnathopod 2 shorter than propod; posterior margin produced into small, pubescent lobe distally, bearing about 7 sets of long setae. Coxal plate of gnathopod 2 significantly smaller than that of 1st gnathopod, longer than broad, shallower than corresponding body segment; margin with 2 setules. Pereopods 3 and 4: coxal plates comparatively small and shallow, a little broader than long, margins with 2 setules each; bases broadly expanded, especially anteriorly; margins convex and armed with row of spines; dactyls with 5 setules each on anterior margins. Pereopods 6 and 7 subequal in length, 50–60 percent length of body, 20–25 percent longer than pereopod 5. Bases of pereopods 5–7 broad; distoposterior lobes prominent, broadly rounded; anterior margins with row of rather strong spines. Dactyls of pereopods 5–7 about 25 percent length of corresponding propods, with 7–8 setules on anterior margins. Segment 6 of pereopods 5 and 6 bearing row of numerous long setae and several long, slender spines on posterior margins and numerous slender spines on anterior margins. Segment 6 of pereopod 7 without long setae on posterior margin but with numerous slender spines on posterior and anterior margins. Coxal gills rather large and ellipsoidal, peduncles short and rather stout. Brood plates short, narrow, convoluted, and bearing few short setae near distal end when fully developed.

Pleonal plates: posterior margin generally straight, corner rounded, not produced, bearing 1 setule in tiny indentation; posterior margins of plates 2 and 3 concave (but more so in plate 3), corners rounded and produced, each bearing 1 setule in tiny indentation; ventral margins without setae or spines. Rami of pleopods subequal in length; pleopods 1 and 2 with 10 coupling spines each on peduncles; pleopod 3 with 7 coupling spines. Uronites 1 and 2 with 2 dorsodistal spines each; 3 with 4 such spines. Uropod 1: inner ramus longer than outer ramus, subequal in length to peduncle, bearing 10 spines; outer ramus with 8 spines; peduncle with 13 spines, 4 of which are ventrolateral. Uropod 2: inner ramus longer than outer ramus and peduncle, bearing 12 spines; outer ramus with 10 spines; peduncle with 6 spines. Uropod 3 relatively long, approximately 23 percent length of body; outer ramus slightly shorter (?) and narrower than inner ramus; inner ramus with long, plumose setae laterally and medially, outer ramus with plumose setae medially and slender spines only laterally. Telson rather long, longer than broad; apical margin with broad incision extending about 65 percent the distance to base; apical margins with 2–3 spines each; lateral and medial margins with spines toward distal end.

Type-Locality.—The artesian well in San Marcos, Hays County, Texas.

Distribution and Ecology.—This species is recorded from the type-locality and two deep artesian wells near Von Ormy. The wells near Von Ormy have each yielded only one specimen of the species to date. Thirty-two specimens of *A. hirsuta,* representing 0.66 percent of the total amphipod fauna collected, were obtained from the artesian well in San Marcos during the continuous sampling period of 14 May 1974 to 16 December 1975 (Table 2). Although a number of females (7.5–9.5 mm) appeared to be nearly sexually mature, only one specimen (10.1 mm in length) collected on 7 October 1975 from the artesian well had setose brood plates. Juveniles (size range=2.1–3.5 mm), however, occurred in samples during all seasons of the year.

Etymology.—The epithet *hirsuta* is from Latin, meaning "hairy" (i.e., setose).

Family BOGIDIELLIDAE

Parabogidiella Holsinger, new genus

Diagnosis.—Closely allied morphologically with *Bogidiella* but differing from that genus by the absence of setae on inner plate of maxilla 1, 1-segmented palp of maxilla 1, reduction and fusion of inner and outer plates of maxilla 2, presence of 5 pairs of coxal gills (on pereopods 2–6), and multisegmented inner rami of the pleopods, which are a little longer than the outer rami.

Without eyes and pigment, of subeterranean facies. Body slender; coxal plates very shallow, not contiguous. Head lacking rostrum; interantennal (lateral) lobe distinct, sharply rounded anteriorly; inferior antennal sinus indistinct. Antenna 1 longer than antenna 2; esthetascs present on most flagellar segments; accessory flagellum 1-segmented. Upper lip symmetrical, broadly rounded, without apical incision. Mandible: molar reduced to small cone; incisor and lacinia mobilis well developed; palp 3-segmented, setae reduced in number. Maxilla 1: inner plate without setae; outer plate with 7 apical spines; palp reduced to 1 segment bearing few apical setae. Maxilla 2: inner plate reduced and fused to outer plate except near apex; both plates bearing few apical setae. Maxilliped: inner and outer plates short, with few apical setae; palp strong, 4-segmented, with few setae. Lower lip: inner and outer lobes well developed; lateral processes short.

Gnathopods relatively large, powerfully subchelate; propod 1 larger than 2, palms of propods elongate, oblique, armed with double row of spines; segment 5 short, posteriorly lobate and pubescent. Pereopods 3 and 4 subequal. Pereopod 7 proportionately elongate, more than 50 percent length of body, approximately 50 percent longer than pereopods 5 and 6. Bases of pereopods 5–7 very narrow. Coxal gills pedunculate, rather small, suboval, attached to pereopods 2–6. Sternal gills lacking. Brood plates unknown.

Posterior corners of pleonal plates distinct but not produced, bluntly rounded. Pleopods reduced but biramous, decreasing slightly in overall length posteriorly; inner and outer rami multisegmented and subequal in length; peduncles with 2 coupling spines each on inner margins distally. Uronites free, without dorsal spines. Uropods 1 and 2 apparently not sexually dimorphic; rami and peduncles bearing spines. Uropod 3 relatively long, biramous; rami 1-segmented, of equal length and armament (aequiramus). Apical margin of telson with shallow excavation; lobes armed with several spines and plumose setae.

TYPE-SPECIES.—*Parabogidiella americana* by monotypy. Gender is feminine.

ETYMOLOGY.—The generic name is derived from a combination of *Para,* which is from Greek, meaning "near" or "beside," and *Bogidiella,* the name of a closely related genus.

RELATIONSHIP.—*Parabogidiella* is clearly a member of the family Bogidiellidae, which was recently resurrected from synonymy with Gammaridae and redefined by Bousfield (1977:305–306). In order to assign the genus to this family, however, a part of Bousfield's diagnosis (1977:306) should be amended to read: "... pleopods reduced, inner ramus with 1 to several segments or lacking." Bousfield (1977:305) suggested assigning five genera to the family: *Bogidiella, Bollegidia, Pseudingolfiella, Kergueleniola,* and *Spelaeogammarus.* Similarly, Ruffo and Vigna Taglianti (1977:169) sugested that these genera belong together in a single group (the *Bogidiella* group), but they did not recognize this group on the family level in preference to retaining it in Gammaridae. However, the uropods of *Pseudingolfiella* are greatly reduced, especially the third, which is reduced to a single ramus with two short segments (see Coineau, 1977:292), and, primarily for this reason, the assignment of this genus to Bogidiellidae or the *Bogidiella* group is questionable. *Spelaeogammarus* is also aberrant vis-à-vis the other genera, and its systematic position in the family (or group) is likewise questionable (see also comments by Bousfield, 1977:306). This genus is discussed in greater detail below.

In general body shape and in the structure of the lower lip, gnathopods, coxal plates, pereopods, uropods, and telson, *Parabogidiella* is closely allied morphologically with *Bogidiella.* It differs from *Bogidiella,* however, by having reduced mouthparts (especially the maxillae), five pairs of coxal gills, and multisegmented inner rami of the pleopods. Unlike many of the species of *Bogidiella* described from southern Mexico and Guatemala by Ruffo and Vigna Taglianti (1973, 1977) and some species of this genus from Europe and Asia, *Parabogidiella* lacks lenticular organs (=Hertzog's organs of some authors) on the pereopod bases. Finally, in most species of *Bogidiella* the accessory flagellum of the first antenna has two or three segments, the mandibular molar is typically a little stronger, the inner and outer plates of the maxilliped bear a few spines, and the peduncle of uropod 1 bears a ventrolateral spine, in contrast to *Parabogidiella,* which possesses a 1-segmented accessory flagellum, a weak, cone-shaped molar, bears setae only on the plates of the maxilliped, and lacks a ventrolateral spine on the peduncle of uropod 1.

In comparison with *Bogidiella, Parabogidiella* possesses both plesiomorphic and apomorphic characters. Like most other gammaridan amphipods, *Parabogidiella* has at least five pairs of coxal gills and multisegmented inner rami of the pleopods, whereas in contrast, *Bogidiella* is apomorphic for these characters and has only three pairs of coxal gills (with one exception, see below), and the inner rami of the pleopods are reduced to a single small segment or are completely absent. The mouthparts of *Parabogidiella* are in general more apomorphic than in *Bogidiella,* however, as evidenced by the reduction in the number of setae on the maxillae, loss of one segment from the palp of maxilla 1, reduction in size of the mandibular molar, and loss of spines from the plates of the maxilliped.

To some extent, *Parabogidiella* is also allied morphologically with *Bollegidia,* a genus that is in turn closely related to, but more apomorphic than, *Bogidiella.* Although probably convergent, the mouthparts of *Bollegidia* are remarkably similar to those of *Parabogidiella,* especially the mandible and maxilla 1. In *Bollegidia,* however, the pleopods are greatly reduced, the outer ramus of uropod 1 is absent, and in at least one species (*B. capensis*) there are four pairs of coxal gills.

At present the genus *Bogidiella* is composed of 28 described species and several provisionally recognized species (Ruffo, 1973; Dancău, 1973b; Ruffo and Vigna Taglianti, 1973, 1975, 1977; Ruffo and Schiecke, 1976; Matsumoto, 1976; Stock, 1978; Boris Sket, Ljubljana University, pers. comm., 1978), principally from the European-Mediterranean and Central America-Caribbean regions but with satellite species from South America (Brazil), east-central Africa (Somalia), Asia (Turkmen S.S.R., Afghanistan, China, and Japan), and the Indian Ocean (Réunion Island). Species of the genus inhabit a rather broad spectrum of subterranean biotopes, including mesopsammic marine, littoral interstitial, freshwater hyporheic, and freshwater caves. Ruffo (1973:75) has shown an interesting qualitative correlation of morphology with habitat, whereby the cavernicolous species fall into one group and the mesopsammic interstitial species fall into another. Considering its broad, disjunct distribution and occurrence in a wide latitude of habitats, the genus is relatively homogeneous morphologically, with the exception of *B. somala* (see Ruffo, 1970) from east-central Africa. This form departs rather significantly from other species in the genus in the peculiar development of the mandible, the large coxal plates, and the broadened bases of pereopods 5–7, and further study may indicate that it warrants separate generic or subgeneric status.

Bollegidia is at present composed of two tiny, littoral interstitial species, one from Andaman and Nicobar Islands in the Bay of Bengal (Coineau and Chandrasekhara Rao, 1972) and the other from Table Bay at Cape Town, South Africa (Ruffo, 1974). Coineau and Chandrasekhara Rao (1972 originally assigned the species from Bengal Bay to *Bogidiella,* but its morphological affinities are clearly with *Bollegidia* as indicated by Ruffo (1974: 411–412).

REMARKS.—*Parabogidiella americana* is the first bogidiellid-like amphipod to be described from North America north of southern Mexico and the Lesser Antilles, and its presence in Texas extends the range of the family Bogidiellidae in the western hemisphere to the north approximately 1200 km.

In his description of *Bogidiella bredini* from the island of Barbuda in the Caribbean Sea, Shoemaker (1959:275, fig. 1) indicated that this species had five pairs of coxal gills on pereopods 2–6. Ruffo's (1973: 55) examination of topotypic material revealed only three pairs of coxal gills on pereopods 4–6, however, and a recent examination of the female holotype, male allotype, and a topotype female in the Smithsonian Institution by one of us (J.R.H.) similarly revealed only three pairs of gills. It would appear then that Shoemaker's description was in error on this point, and that all previously described species of *Bogidiella* have three pairs of coxal gills. However, according to G. S. Karaman of Titograd, Yugoslavia (pers. comm., 1978), Ulrich Schiecke of West Germany has in press the description of a species of *Bogidiella* from an interstitial brackish water habitat in the Bay of Naples with four pairs of coxal gills. Stock (1978:110, 113) has also alluded to this species (viz., *B. tyrrhenica*), which was apparently first recognized by Schiecke in a dissertation in 1973.

Parabogidiella americana Holsinger, new species

FIGURES 16–18

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♂ (?) (USNM 171145), 7–9 Dec 1974, and paratype ♂ (?), 4–7 Dec 1974. Additional material from Bexar County, Texas, as follows: O. R. Mitchell well no. 2 near Von Ormy, 1 ♂ (?), 6 Apr 1977; Verstraeten well no. 1 near Von Ormy, 4 specimens, 6 Apr 1977.

Diagnosis.—A small, slender-bodied subterranean species distinguished by the characters of the genus. Largest specimens (males ?), 3.5 mm; female unknown (?).

Description.—Antenna 1: 40–45 percent length of body, 20 percent longer than antenna 2; peduncular segment 1 subequal in length to combined lengths of peduncular segments 2 and 3; primary flagellum with 12 segments; accessory flagellum short, 1-segmented, about 50 percent length of 1st segment of primary flagellum. Antenna 2: peduncular segments 4 and 5 subequal in length, bearing few setae or spinules; flagellum with 5 segments. Mandible: molar reduced, not triturative, bearing subapical setule; incisor and lacinia mobilis broad; spine row with 3–4 nonplumose spines; palp segment 2 with 1 inner marginal seta, segment 3 with 2 long, apical setae. Maxilla 1: inner plate tapering distally, without setae; outer plate with 7 simple apical spines; palp 1-segmented, bearing 2 apical setae or spines. Maxilla 2: inner plate smaller than outer plate, fused to latter except near apex, bearing 2 apical setae; outer plate with 3 apical setae. Maxilliped: inner plate subrectangular, with 3 apical setae; outer plate about 50 percent length of inner plate, with 3 apical setae and several inner marginal setae; palp proportionately long, segments 2 and 3 subequal in length. Lower lip: inner lobe as broad as, but more shallow than, other lobes; lateral processes short, bluntly rounded.

Propod of gnathopod 1 proportionately large, longer than broad, larger than 2nd propod; palm elongate, oblique, armed with double row of 5 peg-like spine teeth and 2 large spine teeth on outside near defining angle; posterior margin very short, without setae; medial setae few in number, singl

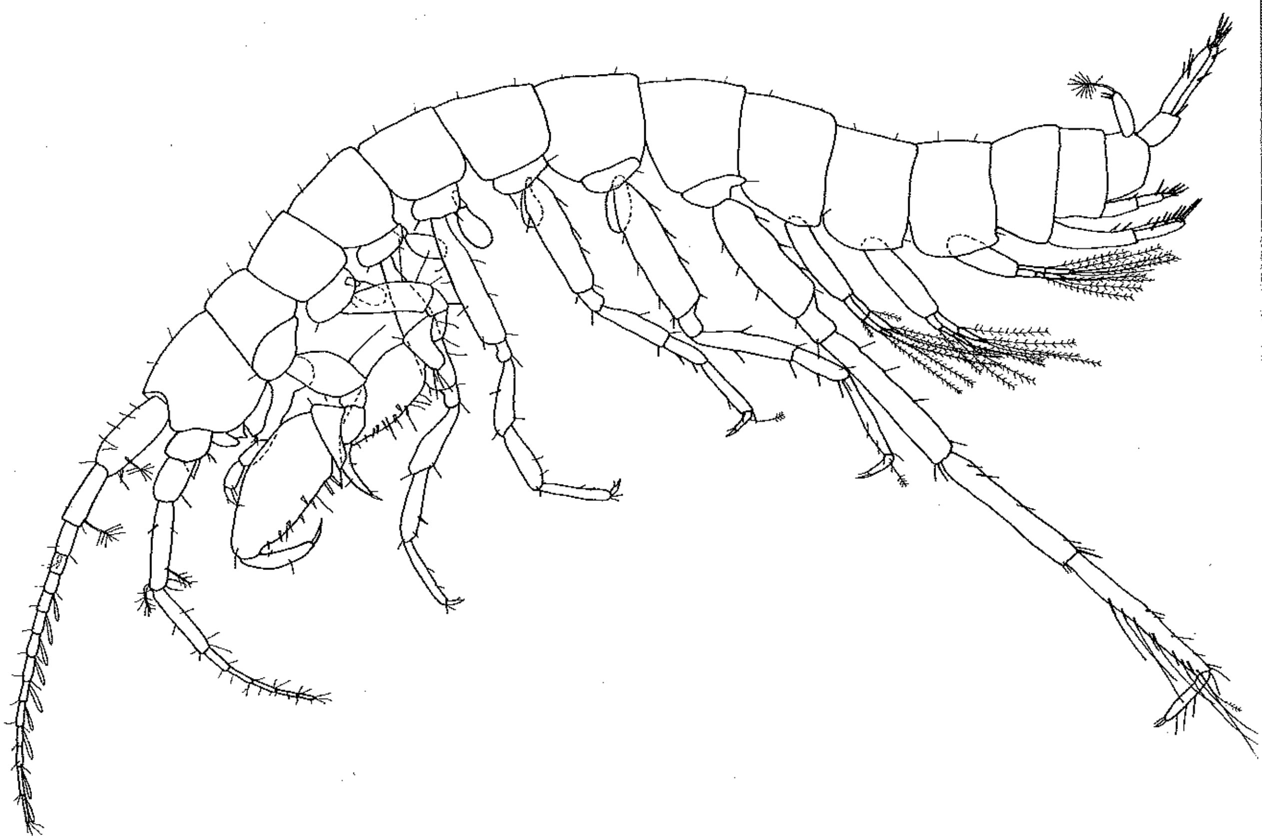

Figure 16.—*Parabogidiella americana*, new species, artesian well, Hays County, Texas, male (?) paratype (3.5 mm).

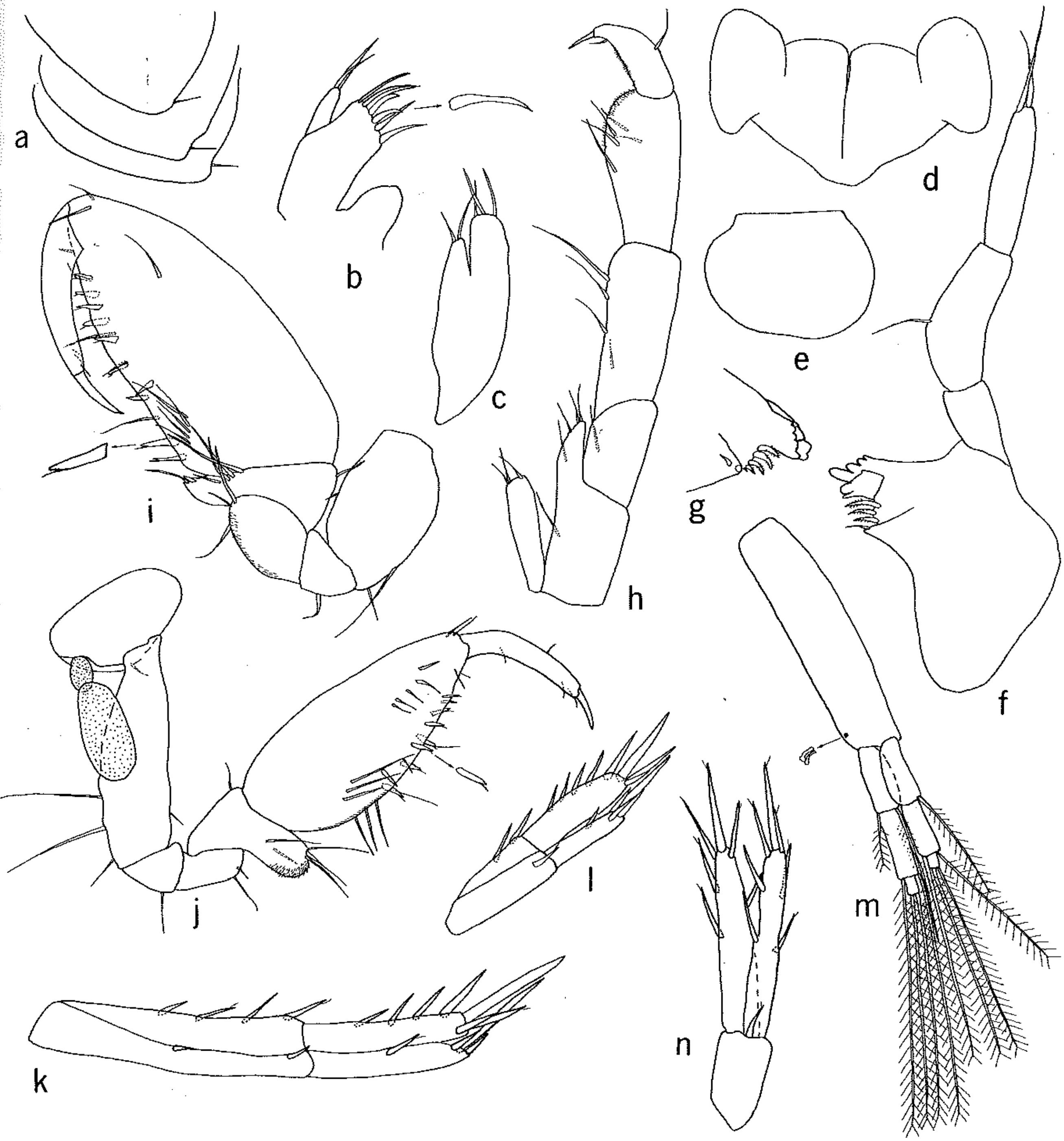

FIGURE 17.—*Parabogidiella americana*, new species, artesian well, Hays County, Texas, male (?) paratype (3.5 mm): *a*, pleonal plates; *b*, *c*, maxiliae 1, 2 (apical spine enlarged); *d*, lower lip; *e*, upper lip; *f*, right mandible; *g*, dentate part of left mandible; *h*, maxilliped; *i*, *j*, gnathopods 1, 2 (palmar spines enlarged); *k*, *l*, uropods 1, 2; *m*, pleopod 1 (coupling spines enlarged). Male (?) holotype (3.5 mm): *n*, uropod 3. (All mouthparts to same scale, gnathopods to same scale.)

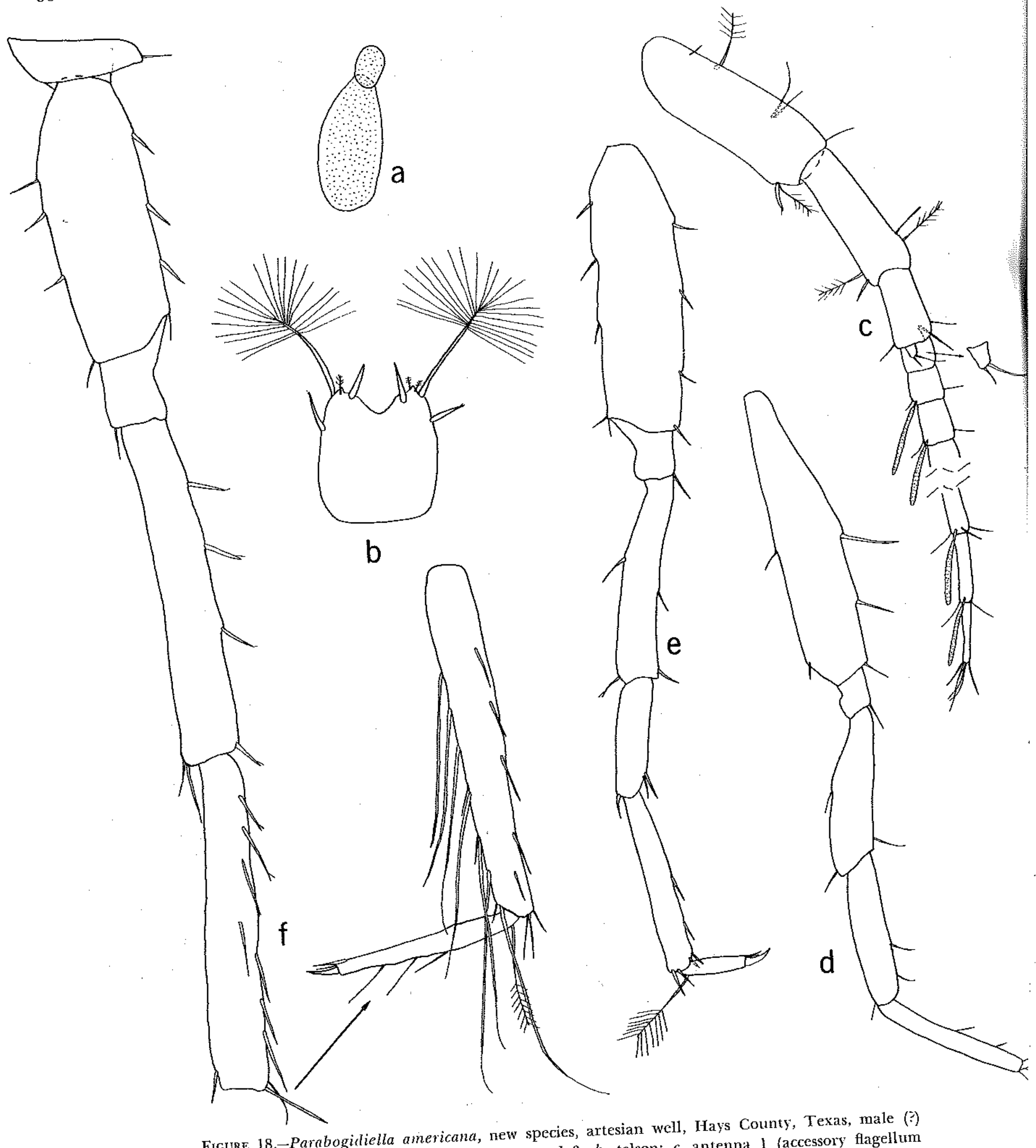

FIGURE 18.—*Parabogidiella americana*, new species, artesian well, Hays County, Texas, male (?) paratype (3.5 mm): *a*, coxal gill from pereopod 3; *b*, telson; *c*, antenna 1 (accessory flagellum enlarged); *d*, pereopod 3; *e*, *f*, pereopods 6, 7 (continuation of appendage indicated by arrow). (All pereopods to same scale.)

inserted. Dactyl of gnathopod 1 closing distal to defining angle; nail rather long and curved. Segment 5 of gnathopod 1 short; posterior margin lobiform and pubescent. Propod of gnathopod 2 subpyriform; palm rather long, oblique, armed with double row of 5 peglike spine teeth; defining angle indistinct; posterior margin shorter than palm, convex, weakly pubescent, bearing row of 3 setae; medial setae in two rows, singly inserted. Segment 5 of gnathopod 2 short; posterior margin lobiform and pubescent. Coxal plates of gnathopods small and shallow, margins with 1 or 2 setules each. Pereopods 3 and 4 subequal; coxal plates small and very shallow, margins with 2 setules each. Pereopod 7 proportionately elongate, 65 percent length of body, approximately 45 percent longer than pereopod 6, 55–60 percent longer than pereopod 5; segment 6 with row of long, threadlike setae on anterior margin; dactyl with 1 long, plumose seta and 3 naked setae on posterior margin. Segment 6 of pereopods 5 and 6 without long setae; dactyls with 1 plumose seta each but lacking other setae on posterior margin. Bases of pereopods 5–7 narrow, margins subparallel; dactyls elongate, 60–65 percent length of corresponding propods.

Coxal gills, pleopods, and uronites as described for the genus. Pleonal plates: posterior margins weakly convex, each bearing 1 setule near corner; ventral margins without setae or spines. Uropod 1: inner ramus subequal in length to outer ramus, about 60 percent length of peduncle, armed with 7 spines; outer ramus with 4 spines; peduncle with 6 spines, none of which are ventrolateral. Uropod 2: inner ramus longer and broader than outer ramus, subequal in length to peduncle, armed with 8 spines; outer ramus with 5 spines; peduncle with 3 spines. Uropod 3 about 12 percent length of body; rami of equal length and armament. Telson a little longer than broad; apical margin with shallow excavation, apical lobes each bearing 2 spines, 1 long plumose seta and 2 or 3 very short plumose setae.

TYPE-LOCALITY.—The artesian well in San Marcos, Hays County, Texas.

DISTRIBUTION AND ECOLOGY.—This species is recorded from its type-locality and two deep artesian wells near Von Ormy. Only two specimens of this species, representing 0.04 percent of the total amphipod fauna collected from the artesian well in San Marcos during the continuous sampling period of 14 May 1974 to 16 December 1975, have been recorded from the type-locality (Table 2). Four specimens (sex undetermined) from the Verstraeten well were collected in association with one *Allotexiweckelia hirsuta*, 16 *Texiweckelia insolita*(?) and six specimens representing two bogidiellid-like species that are still undescribed.

REMARKS.—The type-specimens (3.5 mm in length) from San Marcos are probably males, but the genital papillae are not clearly discernible. The specimens from the wells near Von Ormy, which measure approximately 3.0 mm in length, lack secondary sex characters and are apparently immature. Although the Von Ormy specimens are apparently conspecific with those from San Marcos, we have not designated them paratypes.

ETYMOLOGY.—The epithet *americana* is based on the fact that this is the first species of bogidiellid amphipod discovered in North America north of Mexico.

Parabogidiella? species

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, 1 specimen, 7 Jul 1975; 1 specimen, 5 Aug 1975. BEXAR COUNTY: Verstraeten well no. 1 near Von Ormy, 4 specimens, 6 Apr 1977.

REMARKS.—The material from the artesian well in San Marcos consists of two fragments, each about 3.7 in length and one possibly a female. The material from the well near Von Ormy is in better shape, but all specimens are missing the 7th pereopods and most are missing other critical appendages. These specimens measure about 3.0 mm in length and one appears to have tiny (rudimentary ?) brood plates.

The combination of attenuated body, small, noncontiguous coxal plates, reduced mouthparts, powerful gnathopods, 5 pairs of coxal gills, slender bases, reduced pleopods (both rami multisegmented however), aequiramus 3rd uropods, and uncleft telson strongly indicates the placement of this undescribed form in the genus *Parabogidiella*. Without a fully intact specimen, however, it can neither be adequately described nor positively assigned to any given genus.

Only two specimens of this rare, new form were obtained from the artesian well in San Marcos during the continuous sampling period of 14 May 1974 to 16 December 1975 and represent 0.04 percent of the total amphipod collected (Table 2). The specimens from the Verstraeten well were collected in association with one *Allotexiweckelia hirsuta,* 16 *Texiweckelia insolita* (?), four *Parabogidiella americana,* and two specimens of another bogidiellid-like amphipod which is still undescribed.

ARTESIIDAE Holsinger, new family

DIAGNOSIS.—Head small, narrowing anteriorly; eye and rostrum lacking. Body relatively slender; uronites free (not coalesced), with few spines. Antennae, telson, and sometimes pereopod dactyls with few conspicuous, threadlike, plumose setae. Antennae strong, 1st slightly longer than 2nd; accessory flagellum 1-segmented. Mouthparts weak, somewhat reduced in size and armament. Mandibular molar obsolescent. Inner plate of maxilla 1 without apical setae; outer plate with 7 apical spines; palp 1-segmented. Inner and outer plates of maxilla 2 weak, partly coalesced, inner plate lacking inner marginal setae. Inner and outer plates of maxilliped reduced in size, palp stronger, 4-segmented. Inner and outer lobes of lower lip distinct.

Gnathopods proportionately large, powerfully subchelate, not sexually dimorphic; propod 1 larger than 2, palm of propods elongate, with row of peglike spine teeth on outside; segment 5 short, lobate; coxal plates shallow. Coxal plates of pereopods 3 and 4 shallow. Coxal plates of pereopods 5 and 6 enlarged, broadly expanded distally, that of pereopod 7 normal. Pedunculate coxal gills on pereopods 2–6; sternal gills lacking. Brood plates small and narrow.

Pleopods biramous, uropods 1 and 2 not sexually dimorphic, 1st with large ventrolateral spines on peduncle. Uropod 3 biramous, rami equal or subequal in length. Telson cleft, apical lobes with spines.

TYPE-GENUS.—*Artesia* Holsinger, new genus. At present this family is known only from the type-genus.

RELATIONSHIP.—Although the unique character combination of the new family Artesiidae serves to differentiate it from other families of gammaridans, several morphological attributes tend to indicate an affinity with the bogidielloids and it is to this superfamily group that we are assigning it. Artesiidae has a rather strong morphological affinity with Bogidiellidae as seen in the overall similarities of the head, mouthparts, gnathopods, uropods, and setation of segment 6 of pereopod 7. But, it differs from most other bogidiellids in having broader coxal plates (especially those of pereopods 5 and 6), broadened basis of pereopod 7, unreduced pleopods (although the number of segments in the rami is low when compared with many other gammaridan genera), uronites with dorsal spines, setae on the margins of the rami of uropod 3, and deeply cleft telson.

Artesia Holsinger, new genus

DIAGNOSIS.—With the characters of the family. Without eyes and pigment, of subterranean facies. Interantennal (lateral) lobe of head rather prominent, sharply rounded anteriorly; inferior antennal sinus lacking. Antenna 1 at least 50 percent length of body; esthetascs present on flagellar segments. Peduncular segment 4 of antenna 2 longer than peduncular segment 5, with few slender spines; gland cone long and narrow. Upper lip symmetrical, apical margin rounded and entire. Mandible: incisor and lacinia mobilis broad; spine row with several nonplumose spines; palp 3-segmented, bearing few setae. Maxilliped: inner and outer plates with few slender spines and/or stiff setae. Lower lip with well-developed inner and outer lobes, lateral (mandibular) processes short.

Gnathopod propods armed with row of peglike (unnotched) spine teeth on outer margin of palm; segment 5 short, with posterior lobe. Pereopods 3 and 4 subequal. Pereopods 6 and 7 subequal in length, more than 50 percent length of body, longer than pereopod 5. Coxal plates of pereopods 5 and 6 large and prominent, bases narrow. Coxal plate and basis of pereopod 7 unmodified but segments 5 and 6 with row of long setae on anterior margins. Coxal gills oblong.

Pleonal plates: posterior corners slightly produced, bluntly rounded, with 1 setule each; ventral margins without spines or setae. Pleopods decreasing slightly in overall length posteriorly; peduncles with 2 coupling spines each on inner margins distally. Uronites 1 and 2 with few dorsal spines. Uropod 3 comparatively long; rami 1-segmented, of equal or subequal length (magniramus) but differing slightly in width and setal pattern (dispararamus). Telson a little longer than broad, apical margin deeply cleft.

TYPE-SPECIES (by monotypy).—*Artesia subterranea* Holsinger, new species. Gender is feminine.

ETYMOLOGY.—The generic name *Artesia* is a shortened form of the word "artesian."

RELATIONSHIP.—The unusual combination of characters displayed by this new genus clearly distinguishes it from all other bogidielloids and, furthermore, in our judgment, warrants its placement in a family separate from Bogidiellidae. Although *Bogidiella somala* Ruffo (1970) from wells in Somalia has broadened coxal plates somewhat reminiscent of *Artesia*, it is otherwise, with the exception of the peculiar structure of the mandible, a member of the genus *Bogidiella*. The similarity of its coxal plates to *Artesia* is probably due to convergence.

The monotypic *Spelaeogammarus behiensis* da Silva Brum (1975) from a cave in Bahia, Brazil, is not as easily distinguished from *Artesia*, however, and the similarities between these two genera may be more than convergent or superficial. This genus is undoubtedly a bogidielloid as indicated by a number of its major characters, but owing in part to a less than adequate description, a complete diagnostic comparison with *Artesia* is impossible, and its systematic position among the bogidielloids is presently unclear. *Spelaeogammarus* resembles *Artesia* by the structure of gnathopod 1, large coxal plates of pereopods 5 and 6, row of strong ventrolateral spines on the peduncle of uropod 1, and subequal (length) rami of uropod 3 with spines and setae. It differs, however, in having a 3-segmented accessory flagellum; better developed mouthparts, especially the mandible (?) and maxillae; broad bases of pereopods 5 and 6; unsegmented inner rami of the pleopods; uronites without spines (?); and a "typical" bogidiellid telson that is only slightly incised and possesses heavy lateral spines.

As far as a comparison can be made under the present circumstances (i.e., without seeing material or better illustrations), the differences between *Spelaeogammarus* and *Artesia* appear to be as significant as the similarities, and the assignment of this genus to Artesiidae does not appear to be feasible at the present time. Further study of *Spelaeogammarus* is obviously needed and should shed more light on the taxonomic and phylogenetic relationship of this genus to *Artesia*, and to other bogidielloid genera as well.

Artesia subterranea Holsinger, new species

FIGURES 19–22

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♂ (USNM 171147), 16–18 May 1974. Paratypes from the same locality as follows: 17 ♀, 21 ♂, and 15 juvs from continuous sampling between 14 May 1974 and 16 Dec 1975.

DIAGNOSIS.—A medium-sized, relatively slender-bodied, subterranean species, distinguished by the characters of the family and the genus. Largest male, 6.6 mm; largest female, 7.4 mm.

DESCRIPTION.—Sexes generally similar. Antenna 1: 50 percent longer than body, only slightly longer than antenna 2; peduncular segment 1 as long as combined lengths of segments 2 and 3; primary flagellum with 11 segments; esthetascs on most flagellar segments; accessory flagellum 1-segmented. Antenna 2: flagellum with 5 segments. Mouthparts not protruding, relatively weak and reduced. Mandible: molar feeble, obsolescent, with seta; spine row with 5 or 6 nonplumose spines; incisor and lacinia mobilis broad; segment 2 of palp with 1 inner marginal seta, segment 3 with 4 apical setae. Maxilla 1: inner plate subconical, lacking apical seta(e); outer plate with 7 apical, nonserrate spines; palp reduced to 1 small segment with 2 apical setae. Maxilla 2: plates small and weak, with few slender, apical setae; outer plate a little larger than inner. Maxilliped: inner plate with 3 slender spines or stiff setae apically; outer plate with several slender spines or stiff setae apically and subapically; palp comparatively robust, segment 2 the largest. Lower lip: inner lobes lower but about as broad as outer lobes; lateral processes short, bluntly rounded apically.

Propod of gnathopod 1 large and prominent, about 18 percent length of body; palm elongate, slightly convex distally, with row of about 8 peg-like spine teeth and few setae on outside margin, row of short setae on inside margin; defining angle slightly humped, with 2 large spine teeth on outside; posterior margin very short, without setae; medial setae restricted in number. Dactyl of gnathopod 1 long and curved, nail relatively long with blunt tip. Segment 5 of gnathopod 1 short and

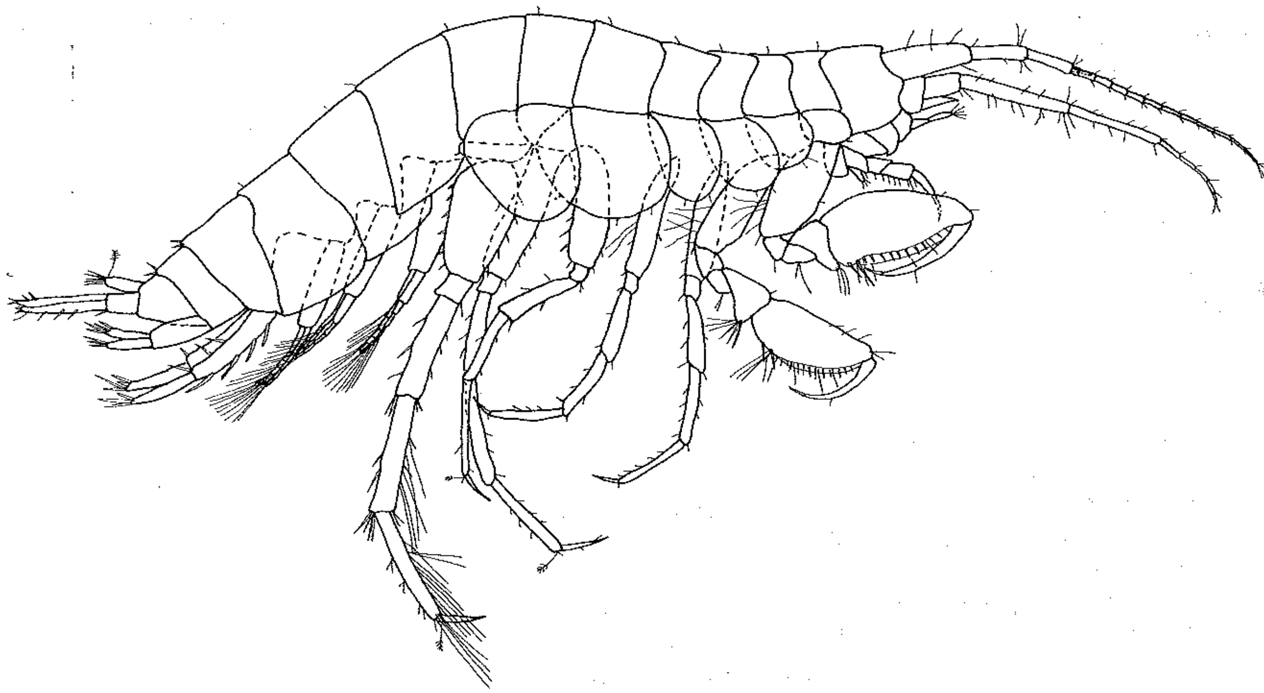

FIGURE 19.—*Artesia subterranea,* new species, artesian well, Hays County, Texas, female paratype (6.1 mm).

lobate posteriorly. Coxal plate of gnathopod 1 very small, shallower than corresponding body segment, broader than long, margin with 2 setae. Propod of gnathopod 2 large and prominent, about 15 percent length of body, proportionately rather narrow, longer than broad; palm elongate, convex distally, with 10 or 11 peglike spine teeth and several long setae on outside margin, row of short setae on inside margin; defining angle broadly rounded, with 1 long spine and 2 sets long setae; posterior margin about ⅓ length of palm, without setae; superior medial setae singly inserted, inferior medial setae in one small cluster near defining angle. Dactyl of gnathopod 2 long and curved, nail rather short with blunt tip. Segment 5 of gnathopod 2 longer than that of gnathopod 1 but not elongate, posterior margin lobate, with cluster of long setae. Coxal plate of gnathopod 2 small, shallower than corresponding body segment, about as broad as long, margin with 2 setae.

Pereopods 3 and 4 generally similar, coxal plates about as deep as corresponding body segments, longer than broad, margins with 2 setae each. Pereopods 6 and 7 about equal in length, 60–70 percent length of body, 20–25 percent longer than pereopod 5. Coxal plates of pereopods 5 and 6 greatly enlarged, broader and deeper than corresponding body segments; ventral margins broadly rounded, with 1–3 short setae. Bases of pereopods 5 and 6 comparatively slender, narrowing proximally. Pereopod 7: coxal plate very shallow; basis "normal," broadest proximally, distoposterior lobe indistinct; segments 5 and 6 with row of long, slender setae on anterior margins. Dactyls of pereopods 5–7 rather long; that of 7, 40–50 percent length of corresponding propod, those of 5 and 6, 50–60 percent length of corresponding propods. Coxal gills oblong, peduncles short. Brood plates of females small and narrow, lacking setae in specimens examined.

Pleonal plates as described for the genus. Inner rami of pleopods slightly longer than outer. Uronites 1 and 2 with 2 dorsolateral spines each. Uropod 1: inner ramus subequal in length to outer ramus, 60–65 percent length of peduncle, armed with 5 apical spines; outer ramus with 4 apical spines; peduncle with 4 posterior spines and 4 long, curved ventrolateral spines with blunt tips. Uropod 2: inner ramus subequal in length to, but broader than, outer ramus, about 75 percent length

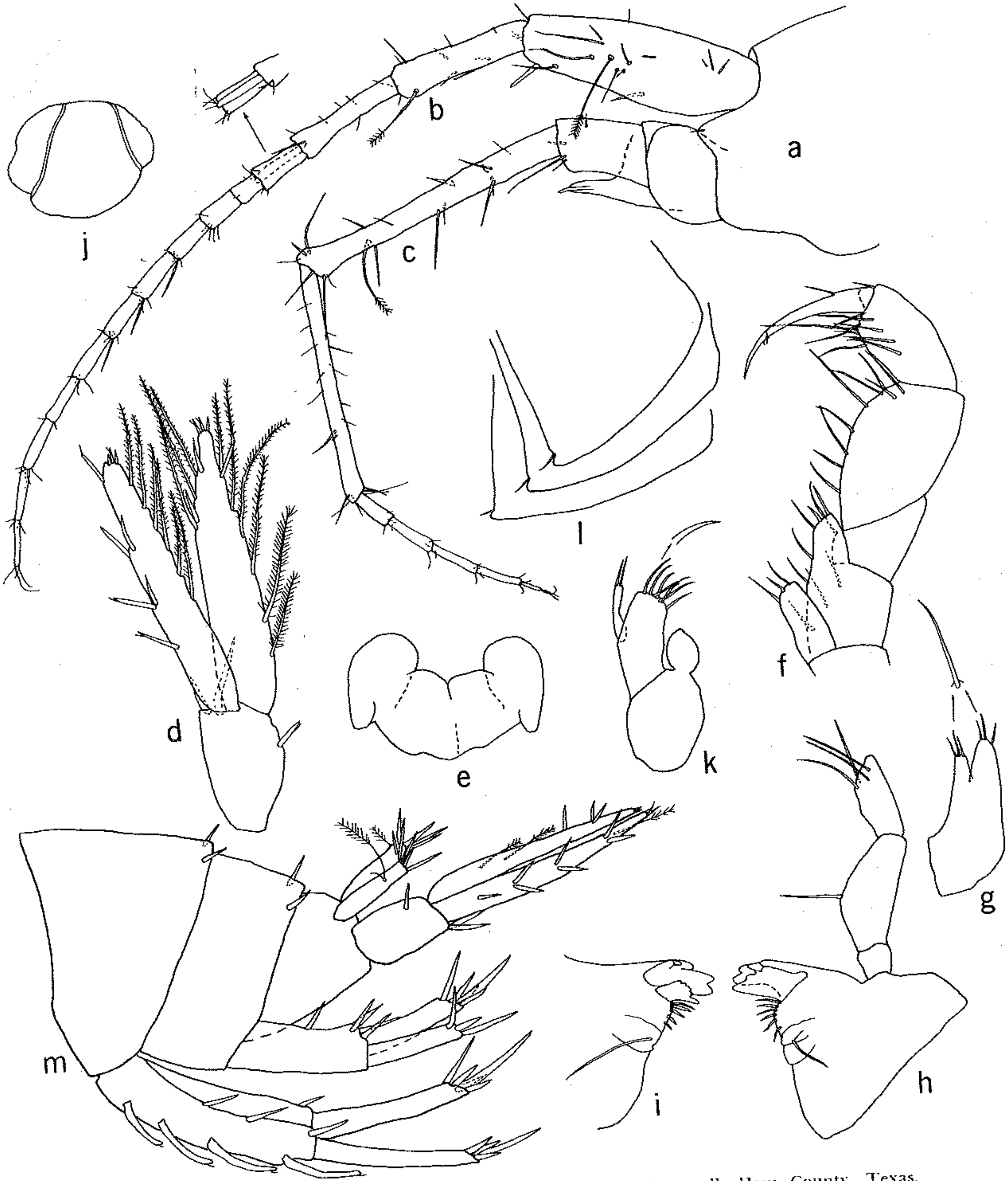

FIGURE 20.—*Artesia subterranea*, new species, paratypes, artesian well, Hays County, Texas, female (5.5 mm): *a*, head; *b*, *c*, antennae 1, 2 (head and antennae shown intact, medial view of accessory flagellum also shown); *d*, uropod 3; *e*, lower lip; *f*, maxilliped; *g*, maxilla 2 (setae enlarged); *h*, right mandible; *i*, dentate part of left mandible. Male (5.0 mm): *j*, upper lip; *k*, maxilla 1 (spine enlarged); *l*, pleonal plates. Male (6.6 mm): *m*, uronites with uropods and telson (some setae omitted from uropod 3). (All mouthparts of both sexes to same scale.)

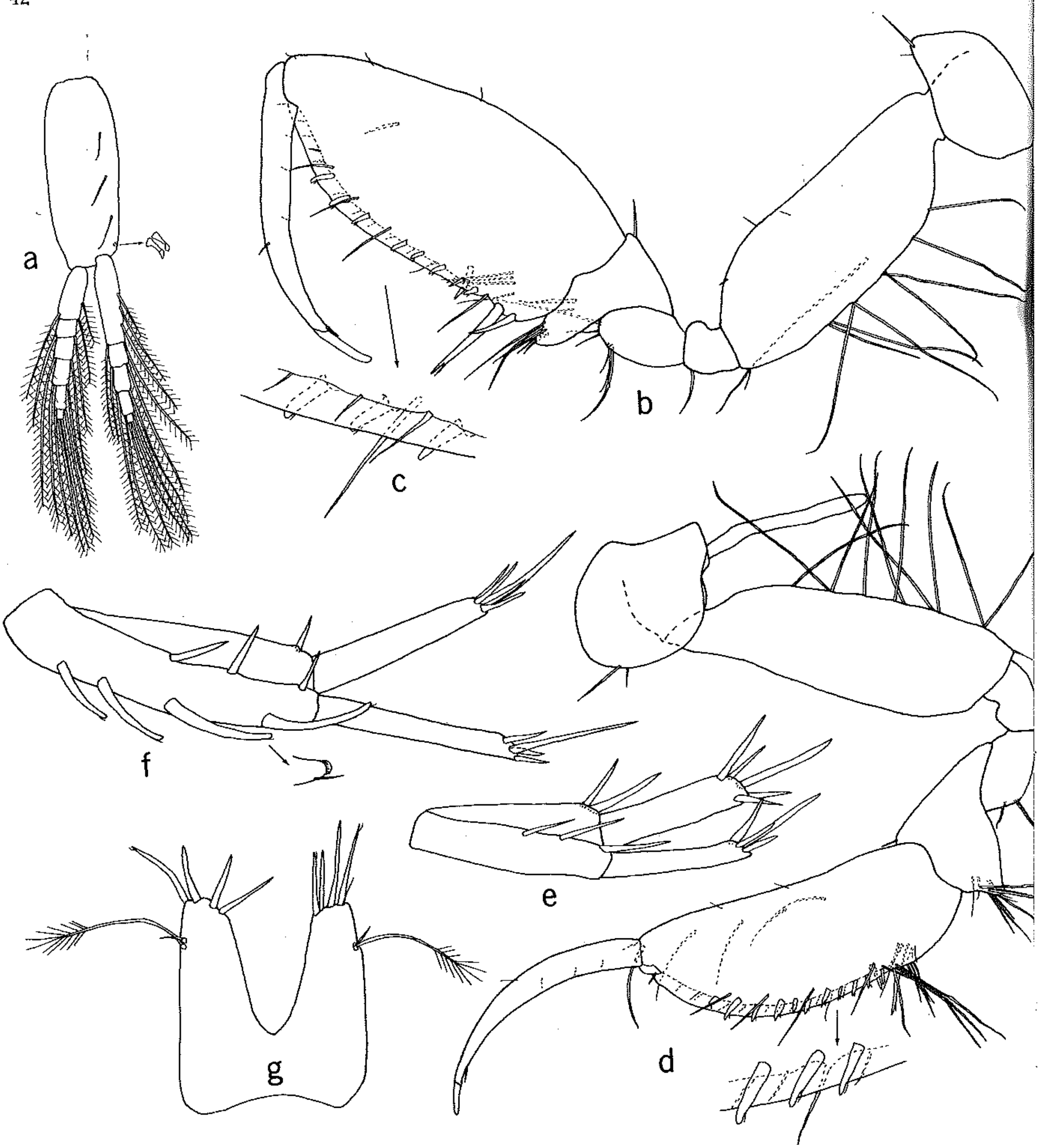

FIGURE 21.—*Artesia subterranea*, new species, paratype, artesian well, Hays County, Texas, female (5.5 mm): *a*, pleopod 3 (coupling spines enlarged); *b*, gnathopod 1 (lateral view); *c*, medial view of part of palm (enlarged); *d*, gnathopod 2 (lateral view; spines enlarged); *e*, uropod 2. Male (5.0 mm); *f*, uropod 1 (apex of spine enlarged); *g*, telson.

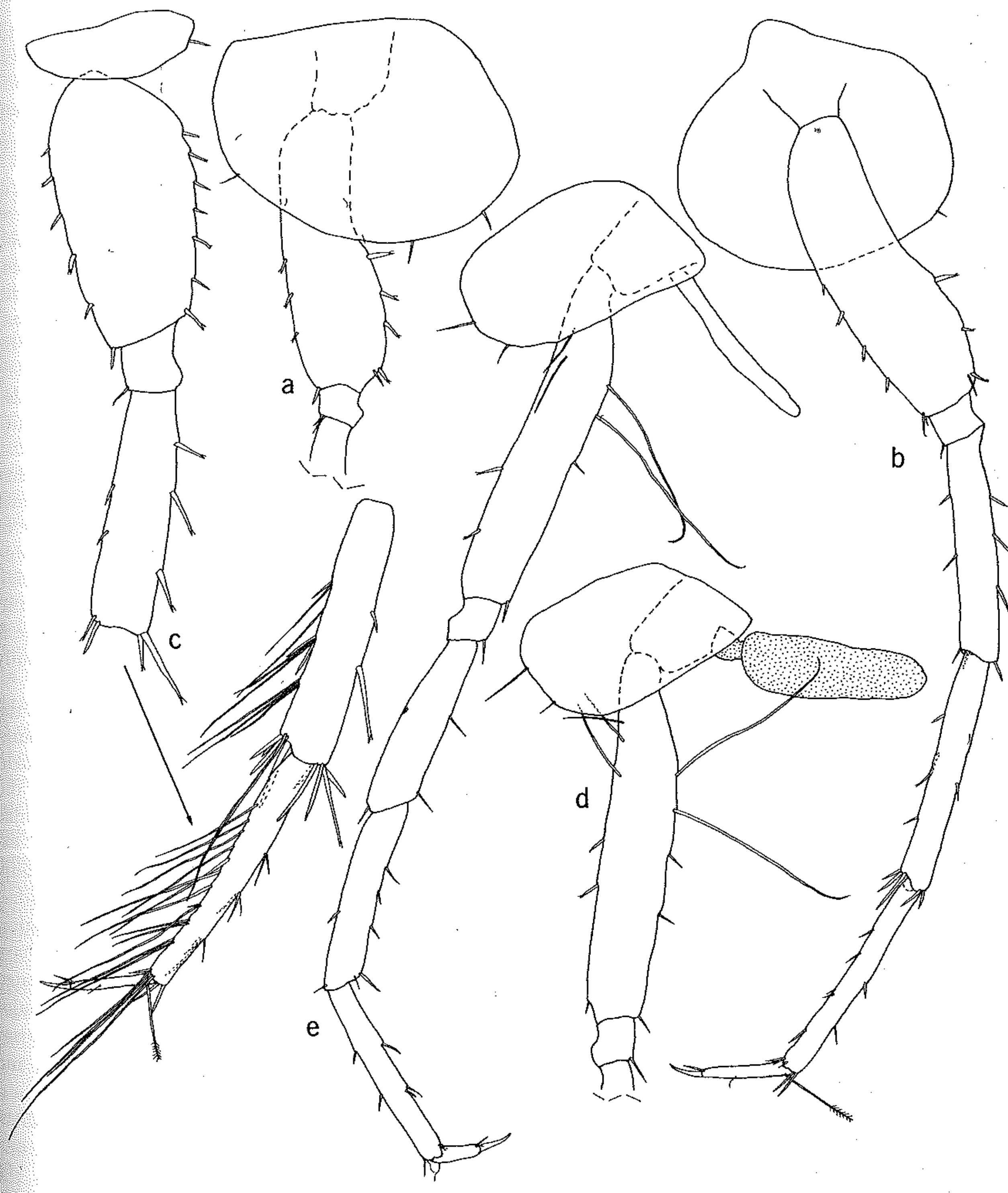

FIGURE 22.—*Artesia subterranea*, new species, artesian well, Hays County, Texas, female (5.5 mm): *a*, pereopod 5 (in part); *b, c*, pereopods 6, 7 (continuation of appendage indicated by arrow); *d*, pereopod 3 (in part); *e*, pereopod 4. (Pereopods 3 and 4 to slightly smaller scale than other pereopods.)

of peduncle, armed with 5 apical spines; outer ramus with 4 apical spines; peduncle with 5 spines. Uropod 3 comparatively long, 18–20 percent length of body; rami equal or subequal in length but outer ramus narrower and lacking plumose setae on outer margin. Telson a little longer than broad; apical margin incised 65 to 70 percent the distance to base; apical lobes armed with 4–6 spines each; lateral margins with 1 long, threadlike, partially plumose seta each near distal end.

TYPE-LOCALITY.—The artesian well in San Marcos, Hays County, Texas.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality where, based on continuous sampling between 14 May 1974 and 16 Dec 1975, it represented 1.07 percent of the total amphipod fauna collected (Table 2). Based on this material, the sex ratio was 1.3:1.0 in favor of males. Males ranged in size 3.2 to 6.6 mm but most were between 4.5 and 6.1 mm. Females ranged in size from 3.5 to 7.4 mm but most were between 5.0 and 6.5 mm. The juvenile size range was 2.7 to 3.7 mm with most around 3.0 mm. Some of the larger females appeared to be sexually mature but lacked setose brood plates. Juveniles occurred in samples from fall, winter, spring, and early summer.

ETYMOLOGY.—The epithet *subterranea* is from Latin, meaning "underground."

REMARKS.—During the preparation of this paper a second species of *Artesia* was discovered in a cave in Culberson County, Texas (ca. 650 km WNW of San Marcos), by W. C. Welbourn of Ohio State University, and is being described by Holsinger.

Family SEBIDAE

Subfamily SEBINAE, new status

DIAGNOSIS.—Inner plate of maxilla 1 with apical seta(e), palp 1-segmented. Maxilla 2 with 2 plates. Inner lobes of lower lip partly fused or lacking. Gnathopod 2 chelate, segment 3 relatively elongate. Uronites 2 and 3 fused. Apical margin of telson tapering to point.

TYPE-GENUS.—*Seba* Stebbing, 1875 (see Karaman, 1971:84–86).

SEBORGIINAE Holsinger, new subfamily

DIAGNOSIS.—Inner plate of maxilla 1 lacking apical seta(e), palp 2-segmented. Maxilla 2 reduced to single plate. Inner lobes of lower lip well developed. Gnathopods subchelate; segment 3 of gnathopod 2 not elongate. Uronites 2 and 3 free (not fused). Apical margin of telson subtruncate.

TYPE-GENUS.—*Seborgia* Bousfield, 1970.

REMARKS.—Prior to the description of the new species below, the family Sebidae was composed of 10 or 11 strictly marine species of the genus *Seba* (see Karaman, 1971, and Thurston, 1974, for summaries), and a single brackish water species of the genus *Seborgia* (see Bousfield, 1970). The original definition of the family was somewhat modified by Bousfield (1970:163–164) in order to accommodate his new and rather unusual genus. Bousfield also pointed out that *Seborgia* differed rather significantly from *Seba*, but he did not divide Sebidae into subfamilies. He did, however, indicate that such a division might be warranted after additional material became available. With the discovery of another species of *Seborgia*, it now appears feasible to divide this heterogeneous family into subfamilies, which reflect obvious patterns of morphological and ecological divergence. The subfamily Seborgiinae is easily distinguished from the nominate subfamily Sebinae by the diagnosis given above.

Based on what he viewed as similarities in the general form of the head and antennae, mouthparts, urosome, uropods, and telson, Bousfield (1977:308) suggested aligning Sebidae with the European subterranean family Salentinellidae (*Salentinella* and *Parasalentinella*) and several exclusively marine families in a superfamily group. In our examination of Sebidae and Salentinellidae we found a number of fundamental morphological differences between these two families and hav concluded that they are not closely enough relate to be assigned to the same superfamily. Majo morphological differences were found in the struc ture of the mouthparts, gnathopods, uropods, an telson as follows.

The sebids have a weak, nontriturative mandibu lar molar as opposed to a generally strong, tritura tive one in the salentinellids. In the sebids th inner plate of maxilla 1 has no more than on short seta, the outer plate has seven apical spin and the palp narrows apically and bears a few seta only; whereas in the salentinellids the inner pla bears at least two long setae, the outer plate has nine apical spines, and the apex of the palp is broad and armed with several strong, bladelike spines. The inner and outer plates of maxilla 2 in the sebids are either partially or completely fused and the inner plate (when distinct) lacks facial setae; whereas in the salentinellids these plates are separate and the inner one sometimes bears one or two facial setae. The inner and outer plates of the maxilliped of the sebids are reduced in size and weakly armed with setae and sometimes a few weak spines; but in the salentinellids these plates are proportionately larger and strongly armed with bladelike spines. In the sebids the inner lobes of the lower lip are usually present and strongly developed in *Seborgia*, while in the salentinellids they are absent. Gnathopod 1 in the sebids is typically subchelate and strong with a transverse palm, gnathopod 2 is chelate or subchelate and if subchelate then the palm is transverse, and segment 5 is not especially elongate; however, in the salentinellids the gnathopods are subchelate and weak and the palms are oblique, and segment 5 is typically elongate (especially in gnathopod 2). Coxae 1–4 are proportionately large in the sebids, whereas in the salentinellids coxae 1–3 and sometimes 4 are proportionately small. The rami of uropods 1 and 2 of the sebids bear only a few weak spines, but in the salentinellids they always bear a number of strong spines. Uropod 3 of the sebids is proportionately short and uniramous in contrast to that of the salentinellids, which is proportionately long and unequally biramous (except in the aberrant, monotypic *Parasalentinella*, which has a reduced third uropod that is uniramous but not in the same manner as in the sebids). The telson of the sebids is never incised, whereas in the salentinellids it is incised except in *Parasalentinella*, in which this structure is reduced to a short, stout, rounded plate (see Bou, 1971:488).

In our opinion the resemblance between sebids and salentinellids is superficial and results almost entirely from the fact that in both groups the species are tiny, the antennae are of subequal length, the bases of pereopods 5–7 are broadened (especially posteriorly), and the pleopod rami have relatively few segments. Based on the form of the mouthparts, gnathopods, uropods, and telson, we have concluded that Salentinellidae is of gammaridan facies and is probably an apomorphic member of the superfamily Hadzioidea (see also Barnard, 1976:425).

Genus *Seborgia* Bousfield

Seborgia Bousfield, 1970:164.

Seborgia relicta Holsinger, new species

FIGURES 23–25

MATERIAL EXAMINED.—TEXAS. HAYS COUNTY: Artesian well in San Marcos, holotype ♀ (USNM 171146), 23 Sept 1975. Paratypes from the same locality as follows: 45 ♀ and 10 ♂ from continuous sampling between 14 May 1974 and 16 Dec 1975.

DIAGNOSIS.—A very small subterranean species distinguished from *Seborgia minima* Bousfield (the only other species in the genus) by a distinct rostrum, lacking inferior antennal sinus, gnathopods of unequal size (in both sexes), proportionately longer ramus of uropod 3, produced and acuminate posterior corners of pleonal plates, and lacking spines on the telson. Largest male, 1.5 mm; largest female, 1.9 mm.

DESCRIPTION.—Sexes generally similar. Without eyes and pigment, of subterranean facies. Head with distinct rostrum; interantennal (lateral) lobe not produced, broadly rounded; inferior antennal sinus lacking. Antenna 1: approximately 33 percent length of body, about 25 percent longer than antenna 2; peduncular segment 1 shorter than combined lengths of segments 2 and 3; primary flagellum with 4 segments, with few esthetascs; accessory flagellum 2-segmented, very short, only ¼ to ⅓ length of 1st flagellar segment, terminal segment rudimentary. Antenna 2: peduncular segments 4 and 5 subequal in length, both lacking spines; flagellum with 3 or 4 segments, most bearing tiny esthetascs. Upper lip broadly rounded, apical margin incised. Mandible: molar weak, conical, with apical setule; incisor and lacinia mobilis well developed; spine row with 3–4 spines; palp segment 2 with 2–4 setae on inner margin distally, segment 3 with 3 apical setae and pilose inner margin. Maxilla 1: inner plate small, tapering distally, lacking apical seta(e); outer plate with 7 very weakly serrate, apical spines; palp with 3 stiff setae on apex and row of very fine setae on outer margin. Maxilla 2 having single plate with broad base and 3 or 4 stiff

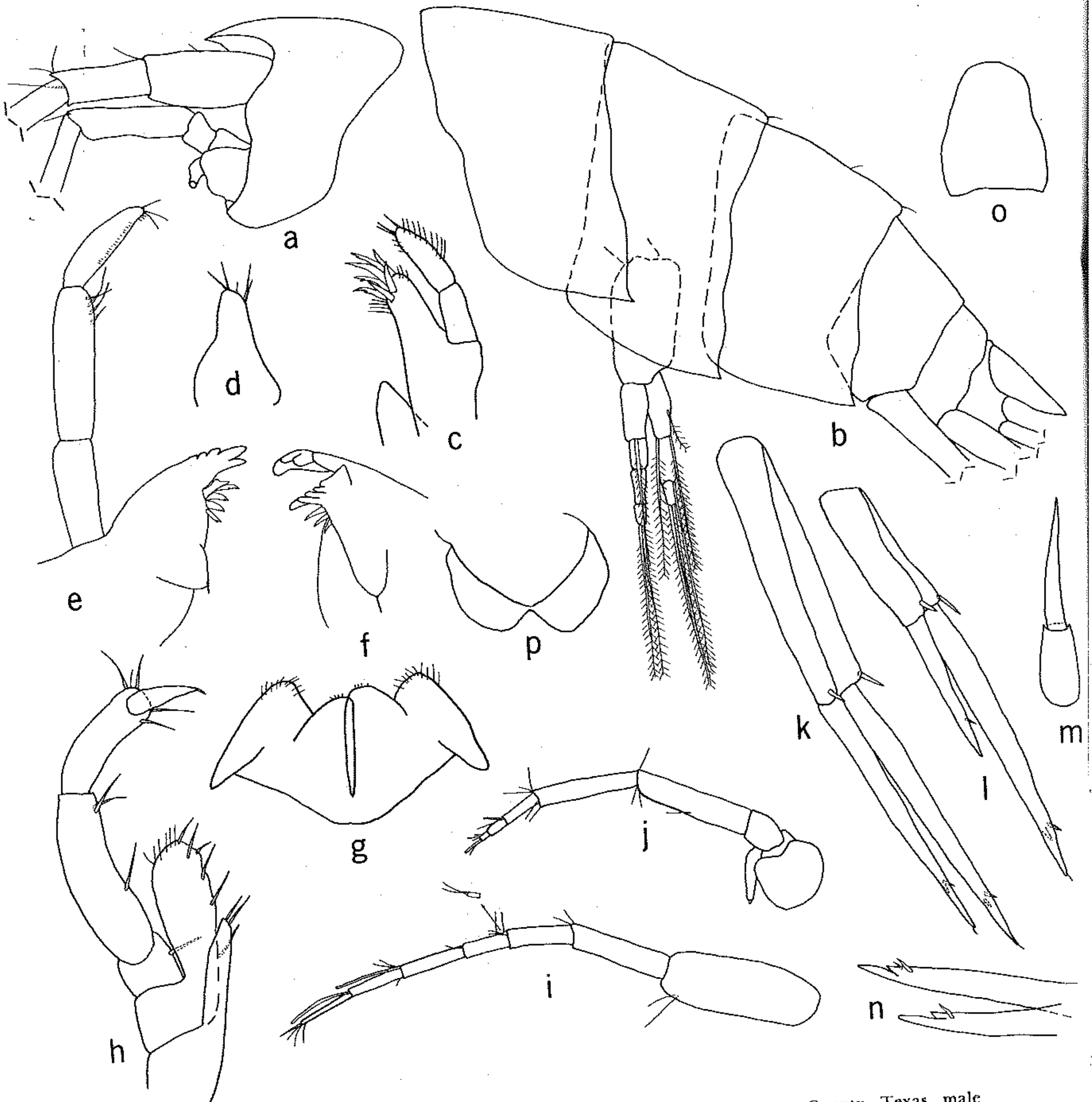

FIGURE 23.—*Seborgia relicta*, new species, paratypes, artesian well, Hays County, Texas, male (1.3 mm): *a*, head; *b*, pleonites and uronites with pleopod 2 and telson shown intact. Female (1.9 mm): *c*, *d*, maxillae 1, 2; *e*, left mandible; *f*, dentate part of right mandible; *g*, lower lip; *h*, maxilliped; *i*, *j*, antennae 1, 2; *k*, *l*, *m*, uropods 1, 2, 3. Male (1.3 mm): *n*, medial view of rami of uropod 1. Female (1.5 mm): *o*, telson; *p*, upper lip. (All mouthparts to same scale; head, pleonites, and uronites to same scale.)

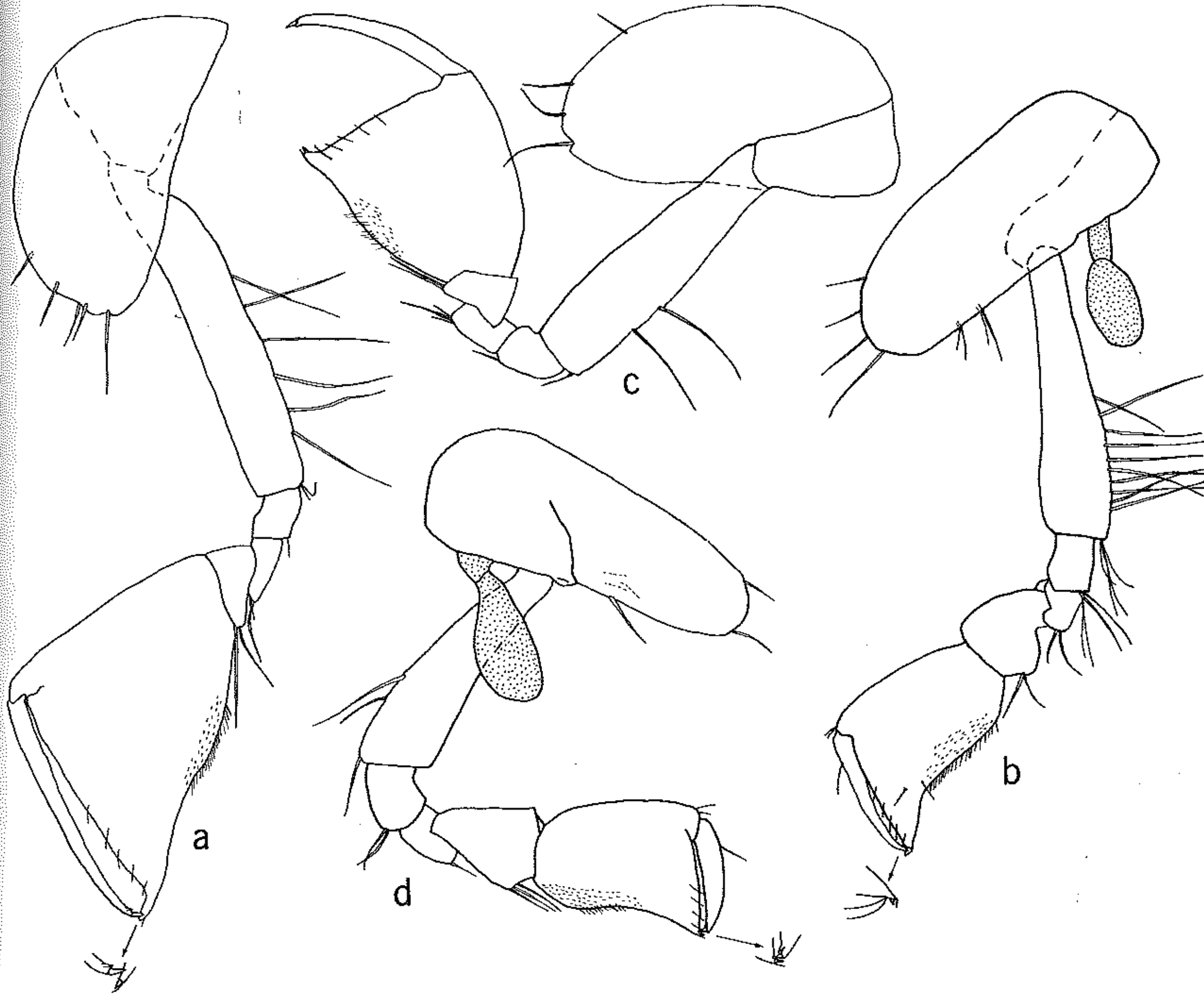

FIGURE 24.—*Seborgia relicta*, new species, paratypes, artesian well, Hays County, Texas, female (1.9 mm): *a*, *b*, gnathopods 1, 2 (lateral view). Male (1.5 mm): *c*, *d*, gnathopods 1, 2 (medial view). (Tip of dactyls and defining angles enlarged.)

setae apically. Maxilliped: inner plate weak, sublinear, armed with 2 stiff setae apically; outer plate much broader but not extending to base of palp segment 3, apex rounded with mostly fine setae, inner margin with few stiff setae (or slender spines ?); palp weakly armed with few setae, segment 2 the longest. Lower lip: inner lobes a little lower than, but as broad as, outer lobes; lateral (mandibular) processes tapering distally.

Gnathopods subchelate, not sexually dimorphic. Propod of gnathopod 1 large, strong, widest distally, nearly 2 times size of 2nd propod; palm transverse, a little shorter than posterior margin, bearing few setules; defining angle produced into narrow boss with short, stout terminal spine; posterior margin elongate, uneven, medially piliferous; media setae lacking. Dactyl of gnathopod 1 long and slender, nail short. Segment 5 of gnathopod 1 very short, segment 2 long and slender. Coxal plate of gnathopod 1 deeper than corresponding body segment, longer than broad, margin with 4–5 setae. Propod of gnathopod 2 widest distally, palm transverse, 60–75 percent length of posterior margin, bearing few setules; defining angle distinct but not produced into boss, bearing short, stout spine; posterior margin elongate, uneven, medially piliferous; inferior medial setae of about 2. Dactyl of gnathopod 2 similar to that of 1st gnathopod. Segment 5 of gnathopod 2 not elongate but about 50 percent length of propod, segment 2 long and slender. Coxal

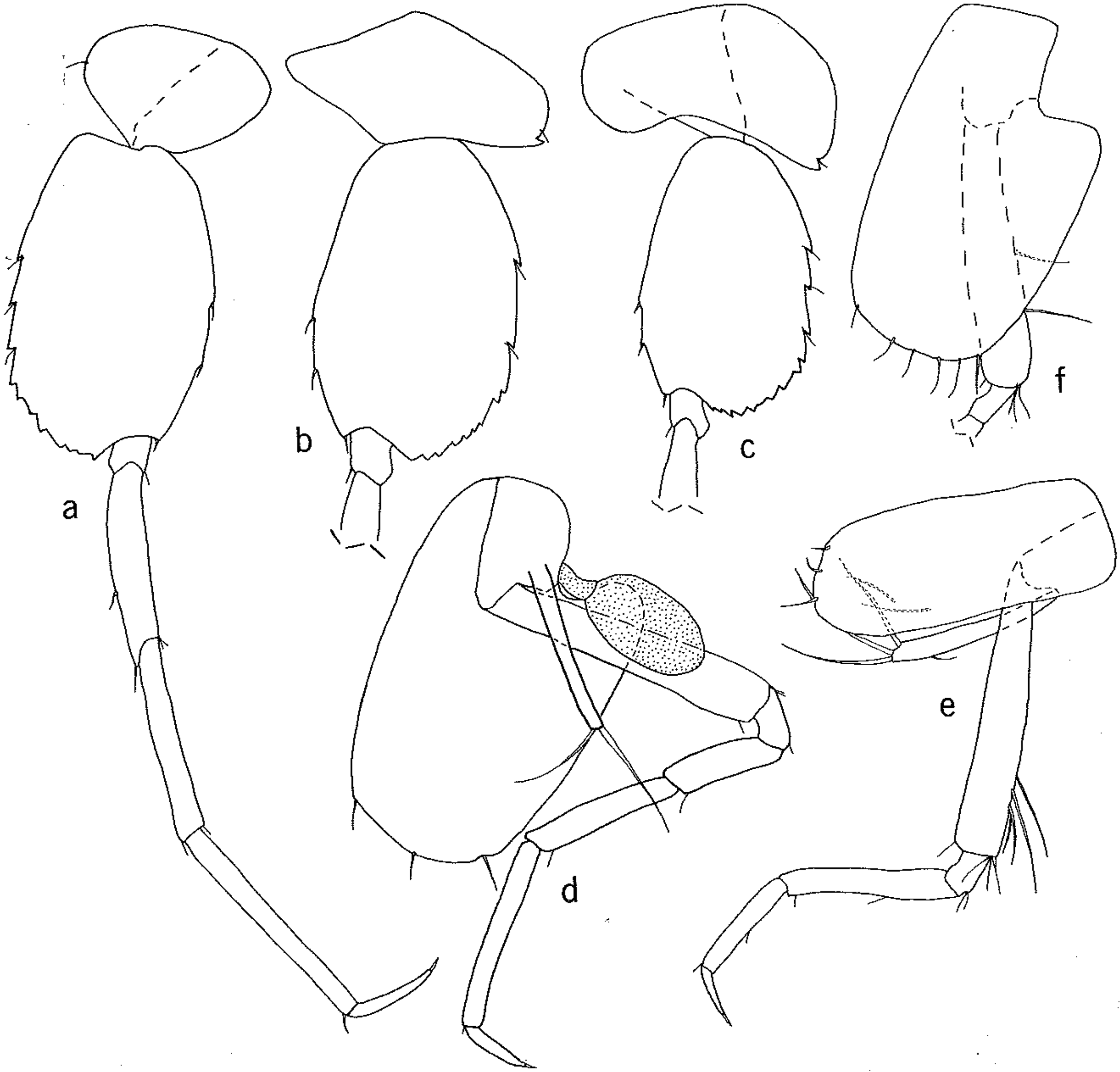

FIGURE 25.—*Seborgia relicta*, new species, paratypes, artesian well, Hays County, Texas, female (1.5 mm): *a*, pereopod 7; *b*, pereopod 6 (in part); *c*, pereopod 5 (in part); *d*, pereopod 4. Female (1.9 mm): *e*, pereopod 3; *f*, pereopod 4 (in part).

plate of gnathopod 2 deeper than corresponding body segment, subrectangular, margin with variable number of setae, apparently depending on age of specimen. Coxal plate of pereopod 3 very deep, subrectangular, extending approximately 70 percent length of basis (segment 2), margin with about 3 setae. Coxal plate of pereopod 4 deeper and proportionately broader than that of pereopod 3, extending about 90 percent length of basis, margin with 3–6 setae. Pereopod 7 subequal in length to, or slightly longer than, pereopod 6, 45–50 percent length of body, longer than pereopod 5. Pereopods 5–7 very weakly armed; posterior margins of bases unevenly serrate and broadly expanded distally; dactyls of 6 and 7 about 45 percent length of corresponding propods, that of 5 about 55–60 percent length of corresponding propod. Coxal gills pedunculate, suboval, on pereopods 2–6. Sternal gills lacking. Brood plates of sexually mature female short, sublinear, with 2 or 3 long, apical setae.

Pleonal plates: posterior corners weakly produced, acuminate; posterior and ventral margins without setae or spines. Pleopods short, decreasing slightly in overall length posteriorly; peduncles with 2 coupling spines each on inner margin distally; rami with few segments, outer slightly longer than inner. Uronites free (not coalesced), without spines. Uropod 1: inner ramus a little longer than outer ramus and peduncle, armed with 2 short spines near distal end; outer ramus with 1 or 2 short spines near distal end; rami lanceolate, usually with narrow marginal incisions near distal spines; peduncle with 2 spines posterodistally. Uropod 2: inner ramus about 50 percent longer than outer ramus and peduncle, armed with 2 short spines near distal end; outer ramus with 1 short spine near distal end; rami lanceolate, with or without marginal incisions; peduncle with 2 spines posterodistally. Uropod 3 uniramous; peduncle about ⅔ length of ramus; ramus lanceolate, without spines but sometimes with apical seta. Telson a little longer than broad, gently tapering distally, without setae or spines; apical margin entire, subrounded.

VARIATION.—Larger, and presumably older, specimens have a few more setae on the coxal plates and bases of the gnathopods and pereopods 3 and 4, and on the bases of pereopods 5–7. In larger specimens there is also a trend toward elongation of the gnathopod propods and narrowing of the gnathopod dactyls.

TYPE-LOCALITY.—The artesian well in San Marcos, Hays County, Texas.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type-locality where, based on continuous sampling between 14 May 1974 and 16 December 1975, it represented 1.11 percent of the total amphipod fauna collected (Table 2). Of the 56 specimens obtained, 46 were females and 10 were males, giving a sex ratio of 4.6 to 1 in favor of females. Out of the 46 females, 23 were ovigerous and 11 had setose brood plates but were not ovigerous. Ovigerous females were collected during all seasons of the year, and this fact, combined with the high percentage of sexually mature females, probably indicates continuous breeding throughout the year.

The clutch size of the 23 ovigerous females, ranging in size from 1.2 to 1.9 mm ($\bar{X}$=1.50, SD=0.20, C.V.=0.13) is summarized as follows: N=23, range=1–3 eggs or embryos, $\bar{X}$=1.43, SD=0.66, C.V.=0.46. Larger females (i.e., over 1.5 mm) were observed to generally brood more eggs than smaller females. The embryos measured approximately 0.35 mm in diameter. Males were also collected during all seasons of the year but were far less abundant and smaller than females. The size range for males was 1.0 to 1.5 mm. Juveniles, which by inference would be in the size range of 0.35 to 1.0 mm, were not found in the samples, but this might be explained by a loss through the sampling net of such tiny specimens or by a single molt upon emerging from the brood pouch that allows for a spurt of growth to 1.0 mm.

ETYMOLOGY.—The epithet *relicta* is from Latin, meaning "relict."

TAXONOMIC AFFINITIES.—The description of *S. relicta* brings the number of species in the genus *Seborgia* to two and extends the generic range from the Indo-West Pacific to the Nearctic. Considering the fact that the other species, *S. minima,* inhabits an oligohaline-brackish water lake on Rennell Island in the British Solomon Islands of the South Pacific and that *S. relicta* occurs some 7,400 km to the northeast in a freshwater, subterranean aquifer in central Texas, the morphological similarity of the two species is striking. This is especially obvious in the close correspondence of the mouthparts, gnathopods, pereopods, uropods, and overall size and shape of the body.

Seborgia relicta does, however, differ from *S. minima* in several important characters, but these differences do not appear at the moment to be significant enough to warrant separation of the two species at the generic level. *Seborgia relicta* is distinguished from *S. minima* by having a distinct rostrum of the head, antennae of unequal length, proportionately larger inner lobes and comparatively smaller lateral processes of the lower lip, gnathopods of unequal size, weakly produced and acuminate posterior corners of the pleonal plates, and proportionately longer ramus of uropod 3; and by lacking an inferior antennal sinus, spines on uropod 3 of the male, and spines on the telson.

The ramus of uropod 3 of the male of *S. minima* is also apparently 2-segmented but only indistinctly so (Bousfield, 1970:166).

The diagnosis of *Seborgia* by Bousfield (1970:164) was based on *S. minima*. In order to accommodate *S. relicta*, the diagnosis should be extended to include the following provisions: (a) head with or without distinct rostrum and inferior antennal sinus, (b) antennae subequal or 1st longer than 2nd, (c) gnathopods 1 and 2 subequal or 1st larger than 2nd, (d) pereopods 6 and 7 typically subequal in length, and (e) posterior corners of pleonal plates 2 and 3 subquadrate or weakly produced and acuminate.

REMARKS.—*Seborgia relicta* is the first species of the family Sebidae to be described from a freshwater habitat and is thus of great interest zoogeographically and ecologically.

Zoogeographic and Ecological Considerations

The rich gammarid amphipod fauna of the artesian well is a curious mixture of locally endemic species apparently derived from both marine and freshwater ancestors during and since the Cretaceous period. The taxonomic diversity of this fauna is unprecedented and its zoogeographic and ecological implications are profound.

The frequency distribution of the amphipod species obtained from the well during the continuous sampling period of May 1974 to December 1975 is given in Table 2. Both in numbers of genera and species the subterranean amphipod diversity of the artesian well far exceeds any other groundwater community studied in North America. Few caves, wells, or hyporheic habitats investigated on this continent to date have yielded more than two coexistent subterranean amphipod species, with three being the maximum (Culver, 1970, 1973; Holsinger, 1967, 1974a, 1978; Ruffo and Vigna Taglianti, 1977; Ward, 1977). In many cases at least two of the coexistent species were members of the same genus.

With the notable exception of the artesian well, several subterranean communities investigated in Europe appear to contain more amphipod species than those studied in North America. Using hierarchical diversity indices (see Pielou, 1975:17–18), the diversities of subterranean amphipods (i.e., troglobitic or phreatobitic) from different localities and groundwater habitats in Europe are compared with those of the artesian well in Table 3. While it might be argued that this comparison is misleading because of differences in the physical structure of the habitats (e.g., hyporheic vs. deep phreatic, etc.) and in the sampling techniques and periods utilized by difference workers, it nevertheless provides a useful way of quantifying amphipod diversity in groundwater communities in general. Based on the literature and correspondence with colleagues, the amphipod diversities given in Table 3 for European groundwater systems are believed to be among the highest recorded. In comparison with the artesian well system, however, only one of the European systems is equal in total species (whole community) diversity and none are equal in generic diversity. On the other hand, within genus diversity is higher in four of the five European systems than in the artesian well, but this can be credited largely to the presence of numerous species of the large, ubiquitous European subterranean amphipod genus *Niphargus*.

Representatives of at least four distinct phylogenetic lineages of gammarid amphipods are recognized from the artesian well:

1. The superfamily Crangonyctoidea, which is an old freshwater group of mostly groundwater-related species that are found in temperate regions of both the northern and southern hemispheres and are without contemporary marine relatives. The family Crangonyctidae, of which *Stygobromus flagellatus* and *russelli* are members, is restricted to the Holarctic region (Holsinger, 1977a) and is believed to have originated on the old Laurasian landmass prior to the separation of North America and Eurasia in the Jurassic (Holsinger, 1978:126). The crangonyctids are in turn allied morphologically at the superfamily level with several families living on landmass remnants of Gondwanaland in the Notogaean region (Holsinger, 1978:127). The crangonyctids are therefore believed to be an ancient group that was probably present in North American freshwaters prior to the Cretaceous. Since the Edwards Aquifier is developed in limestones of Cretaceous age, the presence of *Stygobromus* there would imply that members of this genus have invaded and colonized subterranean waters in this part of North America since the Cretaceous. Presumably these invasions were by ancestral immigrants from a part

TABLE 3.—Comparison of subterranean amphipod diversity from different localities and groundwater habitats using hierarchical diversity indices

Habitat and location	Families [1]	Number of genera	Species	Total (whole community) species diversity H′ (SG)	Generic diversity H′ (G)	Within genus diversity [2] H'_G (S)
Hyporheic (England) [3]	2	2	4	1.386	0.562	0.824
Hyporheic (Greece) [4]	5	5	6	1.792	1.560	0.231
Hyporheic (France) [5]	2	3	7	1.946	1.089	0.857
Hyporheic (Yugoslavia) [6]	2	2	10	2.303	0.500	1.803
Cave streams (Yugoslavia) [6,7]	3	3	9	2.197	0.687	1.513
Deep phreatic (Artesian Well, Texas)	5	6	10	2.303	1.695	0.606

[1] Number of families reflects recent subdivision of Gammaridae (see text).
[2] Within genus diversity averaged over all genera.
[3] From Gledhill (1977).
[4] From Bou (1975).
[5] From Gibert et al. (1977).
[6] From B. Sket (in litt. 1977).
[7] Represents several streams within the same cave system.

of the continent that remained uninnundated by marine waters during late Mesozoic times.

2. The superfamily Hadzioidea, which is composed of numerous epigean and hypogean genera and species living in marine, brackish, and freshwater habitats, largely in temperate and tropic regions throughout a greater part of the world. The majority of species inhabit brackish and marine habitats, however. Many of the hypogean hadzioids are of hadziid facies and are found in the old Tethys Sea region (i.e., the greater Caribbean and Mediterranean regions in particular) (see also, for example, Stock, 1977a, fig. 1). All bona fide freshwater species of the hadziid group (family Hadziidae) are troglobites or phreatobites. *Texiweckelia* and *Allotexiweckelia* are closely allied with subterranean freshwater genera living in Mexico (e.g., *Mexiweckelia* and *Mayaweckelia*) and on the Greater Antillean islands of Cuba and Puerto Rico (e.g., *Weckelia, Alloweckelia,* and possibly *Paraweckelia*). These genera are in turn more distantly related to the Caribbean genera *Metaniphargus* (formerly considered a synonym of *Hadzia* but see Stock, 1977a), *Saliweckelia,* and *Protohadzia,* all of which, except the fully marine, epigean *Protohadzia,* which has degenerate eyes, are primarily restricted to either brackish or marine waters of anchialine, interstitial, and cave habitats. Closely related hadziid genera of subterreanean facies also occur in brackish and freshwater habitats in the Mediterranean region (see Mateus, 1974; Stock, 1977a), in shallow marine and anchialine habitats at a few spots in the Pacific Ocean (Caroline and Hawaiian Islands and coast of southern California) (Zimmerman and Barnard, 1977; Barnard, 1977), and in interstitial habitats on Réunion Island in the Indian Ocean (Ruffo, 1956).

The distribution of hadziid amphipods is circumtropical and strongly Tethyan. The subterranean, freshwater weckeliid genera of North America and the Greater Antilles were probably derived from marine and/or brackish water ancestors at various times from the Late Cretaceous to the late Tertiary (Holsinger, 1974c, 1977c:25; Stock, 1977a: 11). The Texan and northern Mexican forms were probably relicted during the recession of marine waters in the Late Cretaceous, the Cuban and Puerto Rican forms during the early to middle Tertiary, and the Yucatan forms during the late Tertiary.

3. The superfamily Bogidielloidea, which is composed of subterranean species occupying a range of habitats that include mesopsammic marine, littoral interstitial, freshwater hyporheic, and freshwater caves. The majority of bogidielloids are presently assigned to the family Bogidiellidae. Whereas the distribution of this group is Tethyan to some extent and the majority of species are recorded from the greater Caribbean and Mediterranean regions, a significant number are also reported from outside

of the Tethyan realm, especially in the southern hemisphere. Bousfield (1977:306) placed the subterranean genera *Pseudocrangonyx* and *Procrangonyx* from east Asia, *Sternophysinx* from South Africa, and *Paracrangonyx* from New Zealand in this superfamily, but in our judgment, the morphological and zoogeographic affinities of these genera are unclear at present and their alliance with the Bogidielloids needs further study. Some of the characters of these genera, (e.g., the form of the gnathopods, pereopods, third uropod, and telson) tend to suggest a possible alliance with the crangonyctoids and require additional investigation.

Both Ruffo (1973:75) and Stock (1977b:136, 1978: 112–113) have made strong cases for the evolution of freshwater members of Bogidiellidae from marine ancestors, with freshwater invasion taking place at different places over a protracted period of time. Except that Artesiidae is so far unknown outside of Texas, its probable affinity with Bogidiellidae makes it likely that this family, too, had a marine origin. Assuming that both *Parabogidiella* (Bogidiellidae) and *Artesia* (Artesiidae) were derived from marine ancestors that were relicted in freshwater following the Cretaceous embayment of central Texas, the presence in southern North America of two of the most pleisomorphic members of the bogidielloid complex suggests that the most primitive members of this complex were present at the extreme western end of the old Tethys seaway in the late Mesozoic.

4. The family Sebidae, which is predominately marine and sparsely represented by 12 or 13 species in two genera. The members of this family are small, weakly pigmented, mostly eyeless species recorded from benthic habitats. *Seba* is exclusively marine (more than half of the described species occur in the southern hemisphere), whereas *Seborgia* now includes an eyeless, oligohaline-brackish water species from the Indo-West Pacific and a phreatobitic species from south-central Texas. Because of their small size, degenerate eyes, weak pigmentation, and predilection for bottom sediments, the sebids might be expected to have been good candidates for the colonization of interstitial freshwater habitats during marine transgressions. The presence of *Seborgia minima* in a land-locked, oligohaline-brackish water lake in the Rennell Islands of the South Pacific, presumably isolated there since the Late Pliocene (Bousfield, 1970:155), may indicate the manner in which the ancestral form of *Seborgia relicta* became isolated in, and adapted to, the transitional aquatic environment of south-central Texas during recession of sea water in the Late Cretaceous or early Tertiary.

Three broad explanations are suggested for the high taxonomic diversity of the amphipod fauna of the artesian well: (1) exposure of south-central Texas to an extensive marine embayment during the Cretaceous period; (2) complex geological structure of the Balcones Fault Zone and large size of the Edwards Aquifer; and (3) ecological complexity of aquatic communities in the Edwards Aquifer.

1. The strong possibility that many of the species recorded from the artesian well are derivatives of marine ancestors that invaded newly opened freshwater habitats during the Late Cretaceous has already been pointed out but needs further elaboration. Representatives of the hadzioids, bogidielloids and sebids all have unmistakable affinities with marine and brackish water relatives and, collectively, they comprise 80 percent of the amphipod fauna of the artesian well. Moreover, in certain parts of the world today, such as coastal regions of the Mediterranean and islands in the Indo-Pacific and Caribbean, where geological structure provides direct exposure of cave, anchialine, and interstitial habitats to warm marine waters, there is good evidence that species of these same taxonomic groups are still undergoing transition from shallow marine to subterranean freshwater environments (for examples see Ruffo, 1953, 1973; Bousfield, 1970; Holsinger, 1974d; Barnard, 1977; Zimmerman and Barnard, 1977; Stock, 1977a).

Conditions believed conducive to the invasion of subterranean freshwater habitats by marine and/or brackish water amphipods might have prevailed in central Texas during the Late Cretaceous, when an epeiric sea that had earlier extended from the Gulf of Mexico north to the Arctic Ocean receded from the continent (see Figures 26 and 27). Limestones of the Edwards Plateau and Balcones Fault Zone, which were deposited previously during the Early and Middle Cretaceous, were covered in part by warm marine water in the Late Cretaceous (Figure 27) (see also Dunbar, 1960:320; Dott and Batten, 1976:355–359; Schuchert and Dunbar, 1950:106). A part of Texas was again innundated by marine water during the early Tertiary (Dott

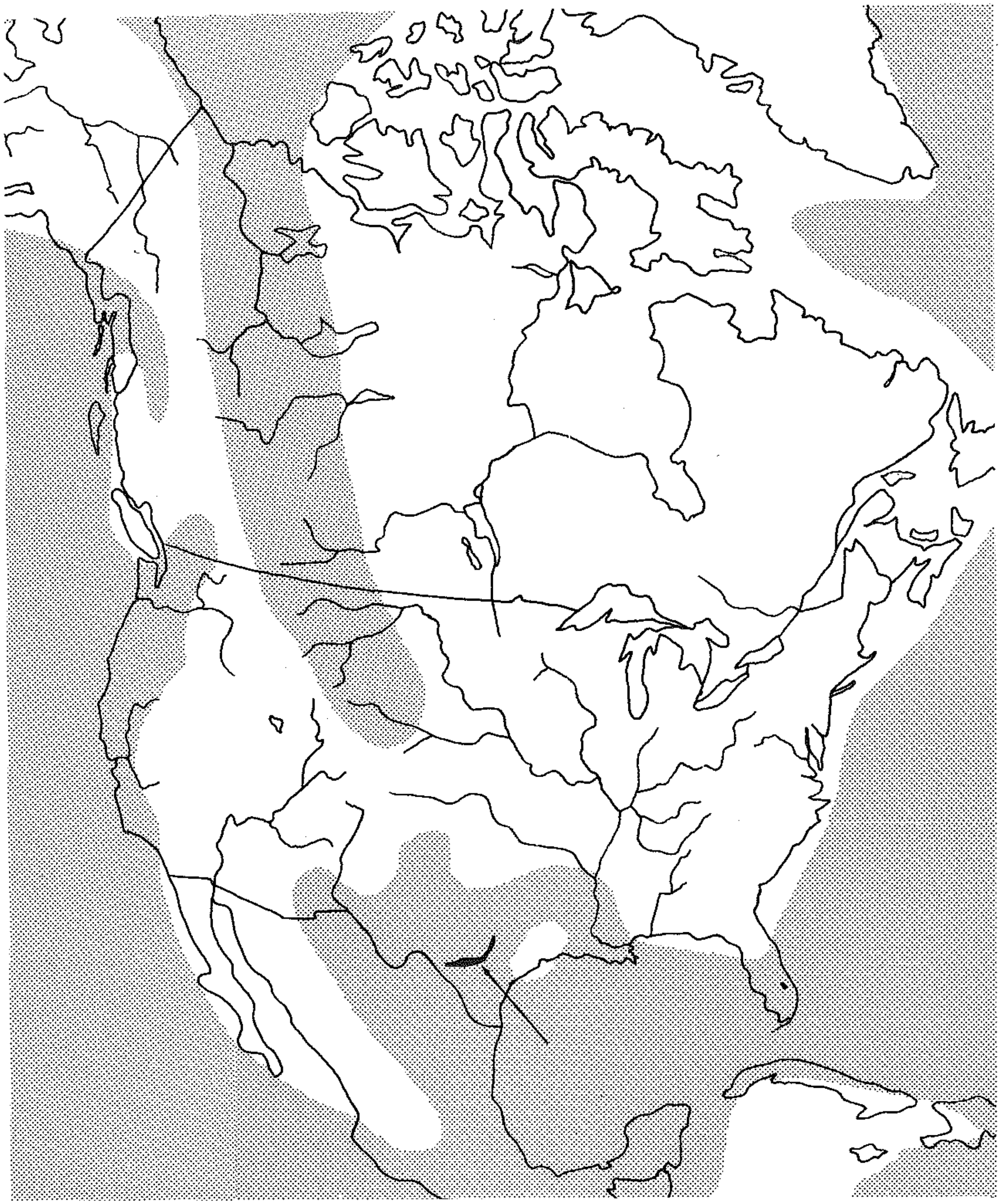

FIGURE 26.—Generalized paleogeographic map of North America showing marine transgression late in Early Cretaceous time (based on Dunbar, 1960:320). (Balcones Fault Zone superimposed and indicated by arrow; areas covered by marine water shaded.)

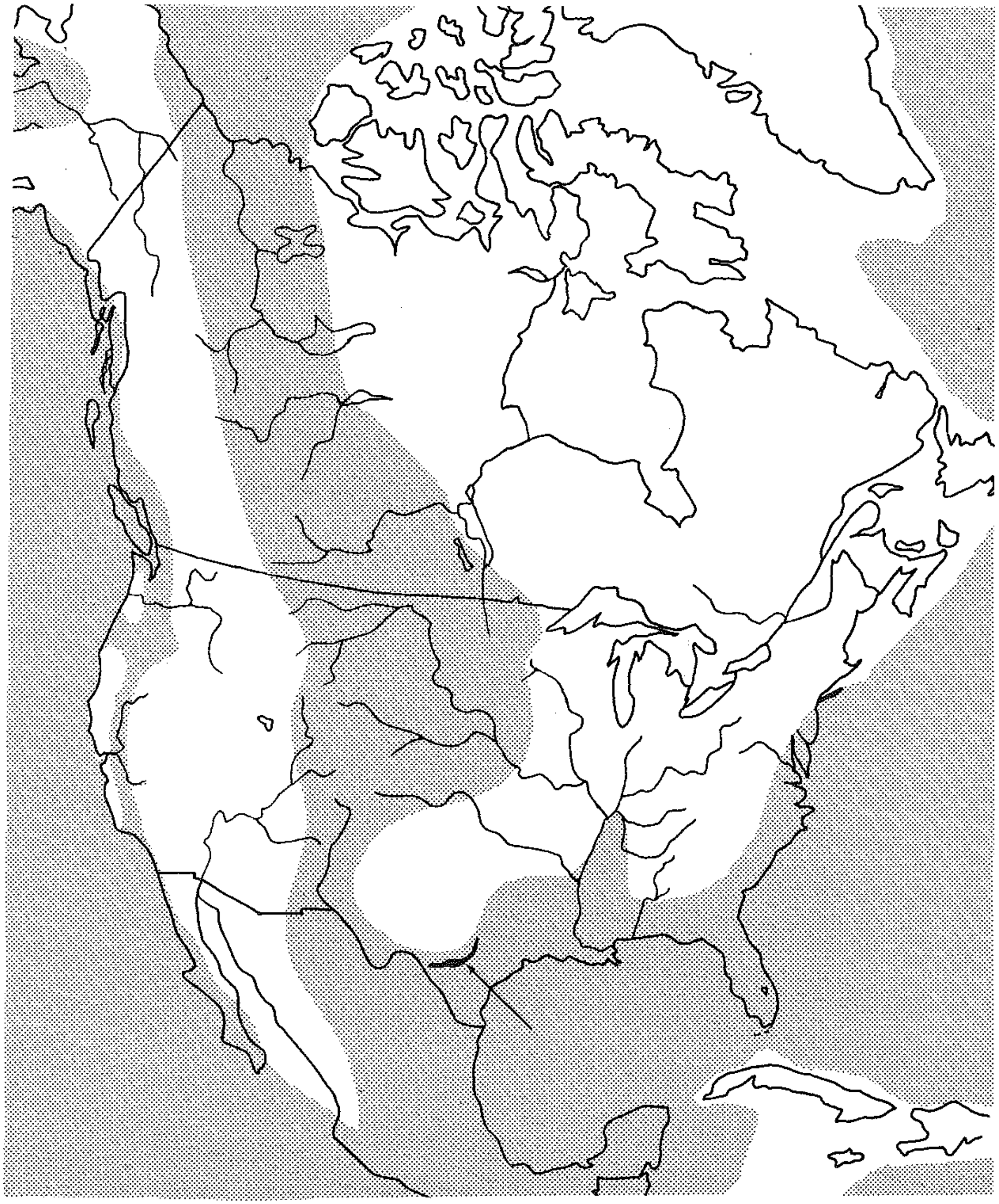

FIGURE 27.—Generalized paleogeographic map of North America showing maximum marine transgression in Middle to Late Cretaceous time (based on Dunbar, 1960:320 and Dott and Batten, 1976:357). (Balcones Fault Zones superimposed and indicated by arrow; areas covered by marine water shaded.)

and Batten, 1976:382; Schuchert and Dunbar, 1950:124), but at this time sea water apparently did not reach far enough inland to make contact with the limestone formations of central Texas.

The invasion and colonization of gradually freshened groundwater habitats by preadapted marine amphipods during the recession of sea water toward the end of the Cretaceous is therefore suggested as the most likely explanation for the presence of marine-related (relict) amphipods in the freshwater environment of south-central Texas. Moreover, the possibility that subsequent invasion of interstitial habitats in gravels and sands of the Coastal Plain took place to a limited extent during recession of shallow marine water in the Tertiary cannot be ruled out.

2. The Balcones Escarpment and Fault Zone, which separates the Edwards Plateau from the Gulf Coastal Plain, is traceable as a structural and topographic feature that extends from Del Rio east and north to Waco (see Figure 2). According to Russell (1976:8), "the fault zone is composed of numerous, individual, parallel and en echelon faults, generally downthrown to the south and southeast." This arcuate zone of faulting is believed to be of Miocene age (Kastning, 1978:2). According to Smith (1971:5), subterranean water of the Edwards Aquifer moves east from Kinney and Uvalde counties along faults in limetone members of the Edwards Group to join additional groundwater from the northern part of the region and emerges at large karst springs and through water wells at San Antonio, New Braunfels, and San Marcos. Further details of the complex geology of the fault zone and escarpment and its relationship to caves and karst groundwater are found in papers by Smith (1971), Longley (1975), Maclay and Small (1976), Russell (1976), and Kastning (1978).

In terms of size the Edwards Aquifer extends from Bracketville on the west approximately 283 km to Kyle in Hays County on the east, and is up to 48 km wide just west of San Antonio (Figure 2). Within the Balcones Fault Zone some parts of the aquifer are confined (artesian) and others are unconfined (water table) (Kastning, 1978:5). The combination of large size and partial confinement under artesian conditions makes this one of the worlds most unique karst aquifers. Despite changes in base level, erosional effects, and continued development and enlargement of solution channels and cave passages, the Edwards Aquifer has apparently remained relatively stable for a long period of time. Mitchell and Reddell (1971:87–88) have pointed out that the cavernous limestones of the Balcones Fault Zone were probably the first to be exposed in central Texas following uplift and extensive faulting of this region during the Miocene. Prior to that time, cavernous limestones presumably lay deeply buried under Late Cretaceous deposits. Although we postulate the existence of a groundwater amphipod fauna composed of marine relicts in central Texas in the early Cenozoic, the development of the Edwards Aquifer as presently understood could not have taken place until after geological events of the Miocene. Thus, whereas the Edwards Aquifer is probably no older than Miocene, it may well date from the late Miocene or early Pliocene.

The development of an extensive subterranean aquifer in a major fault zone that forms the boundary between two distinct physiographic regions of significantly different geological structure has undoubtedly influenced the diversity of its fauna. The Balcones Fault Zone not only provides a potential mixing zone for faunal immigrants from both the karst groundwater of the Edwards Plateau and the interstitial groundwater of the Coastal Plain, but, perhaps of equal importance, the intense faulting and fracturing of the bedrock of this region have probably resulted in the development of many smaller phreatic reservoirs that have periodically led to the physical isolation of populations of aquatic organisms. The latter effect, along with areal extent, could have easily facilitated speciation in different parts of the aquifer. Considering the long period of time during which faulting, erosion, and solution have effected changes in the subterranean networks of this limestone aquifer, there have probably been many opportunities for geographic speciation among the amphipods and other taxa as well. Although the within genus diversity of the artesian well amphipods appears to be comparatively low (Table 3), we predict that, given the immense part of the aquifer that is still unsampled and the species richness of the few wells that have been studied to date, a large number of amphipod taxa (especially sister species of those described in this paper) remain to be discovered in the Edwards Aquifer.

The periodic creation and elimination of dispersal barriers by long-term geological processes have probably influenced speciation as well as immigration, comingling and sympatry of many of the species of amphipods. And, in turn, these events have almost certainly contributed to the myriad of amphipod taxa recorded from the artesian well in San Marcos. The interconnectivity of numerous subterranean channels would provide pathways for immigration and result in the occasional mixing of faunal components that evolved in different parts of the aquifer. The prsesnce of some of the same amphipod species in artesian wells situated 93 km apart (viz., near Von Ormy and in San Marcos) is indicative of subterranean dispersal over comparatively great distances.

3. Cave communities are commonly regarded as relatively simple systems with few species and low productivity (Barr, 1968:38; Poulson and White, 1969:971–972; Culver, 1976:945). Apparently some of the cave communities of the Edwards Aquifer are exceptions to this rule. The aquatic fauna of the artesian well is possibly the richest of its kind in the world and includes 22 troglobitic species, nearly half of which are amphipod crustaceans (see also "Introduction"). Both the species richness and comparative abundance of many of the species of the artestian well are indicative of a complex, underlying cave ecosystem. In comparison, the aquatic community of Shelta Cave in Madison County, Alabama, considered to be one of the richest and most complex subterranean ecosystems in North America, has only 10 troglobitic species (e.g., 1 flatworm, 1 ostracod, 2 amphipods, 3 crayfishes, 1 shrimp, 1 salamander, and 1 fish) (Cooper, 1975).

In addition to the physical extent and heterogeneity, relative old age and comparative stability of the Edwards Aqifer, a high input of food, presence of several predators and large number of species, undoubtedly contribute significantly to the ecological complexity of the artesian well community. Furthermore, the high degree of morphological differentiation among the amphipods has equiped these organisms with the potential for fine resource partitioning and is probably responsible in part for the packing of so many species of a single taxon into a relatively limited area.

Because of the extensive recharge zone of the Edwards Aquifer (Figure 2), the probability is high that large amounts of organic material wash underground through sinkholes, fissures, and fault planes and gradually accumulate in a vast network of subterranean channels. Under these conditions, the buildup of decaying organic detritus would be considerable over a long period of time, and this material is believed to be the major source of energy input into the system. Washed-in organic debris not only provides food directly to detritus-feeding organisms, but perhaps, more importantly, it supports large populations of decomposer microorganisms (e.g., bacteria and fungi), which, in turn, provide food for many species of troglobites (see also Barr, 1968:51, 60; Dickson, 1975; Dickson and Kirk, 1976). Moreover, in the deeper, artesian parts of the aquifer, where subterranean passages are permanently filled with phreatic water, aquatic communities are probably "buffered" against the perturbations of periodic flooding initiated by heavy surface runoff and therefore remain "food rich" and relatively stable for long periods.

The influence of predation on species diversity has been discussed by Paine (1966), MacArthur (1972:191–194), Uetz (1974:120), and others. MacArthur has concluded that, depending on the structure of the environment, discriminate feeding by predators can lead to an increase in species diversity. Three predominately carnivorous groups—kenkiid planarians, dytiscid beetles, and plethodontid salamanders—are represented in the well fauna by potentially predatory species. Observations on the salamander *Typhlomolge rathbuni* in the laboratory by Longley (1978:24) and R. W. Mitchell (pers. comm.) of Texas Tech University have shown that this species feeds voraciously on amphipods; however, whether these salamanders discriminate among different species of amphipods in nautre is unknown. Laboratory observations are unavailable on the feeding habits of the dytiscid beetle *Haideoporus texanus*, but considering the fact that this species belongs to a group that is exclusively carnivorous and voracious (Pennak, 1953:596), one would expect it to be predaceous, at least in the larval stage. Since planarians are frequently carnivorous in nature, one would suspect that the large, polypharyngeal flatworm, *Sphalloplana morhi*, might also be predatory in the artesian well under certain conditions. In support of this possibility are the observations by Mitchell (1974:416–418), who found

Sphalloplana zeschi (a probable synonym of *S. mohri,* see Kenk, 1977:23) feeding on larger arthropods (including amphipods) in both the laboratory and in Zesch Ranch Cave (Mason County, Texas). Although the worms did not attack healthy, active individuals, they fed readily on injured or moribund animals. Based on thse observations, Mitchell speculated that the amphipod *Stygobromus russelli* (which is also present in the Artesian Well) probably constitutes one of the chief food sources of *S. zeschi* in Zesch Ranch Cave.

The artesian well amphipods are highly differentiated morphologically, and this fact may explain in part how so many species of a single taxon can coexist in a single cave community. Despite the unevenness or lack of equitability in the distribution of the amphipod species during the 19-month sampling period and the extreme rarity of the parabogidiellids and *T. samacos* (Table 2), we assume that all 10 species are in contact at least some of the time and that all share some part of the cave habitat underlying the artesian well. Major morphological differences among the amphipods species are noted especially in the size and shape of the body (e.g., tiny to relatively large; subvermiform, attenuated, or stocky); length of antenna 1, pereopods, and uropod 3; shape of the gnathopod propods and pereopod bases; and size, shape, and armament of the mouthparts. Undoubtedly, basic structural differences translate into differences in forging and feeding strategies, behavior, locomotion, and other aspects of the biology of these organisms. Precisely how, though, remains largely unknown, since few studies are available on correlations of structure and function in amphipods, especially in the subterranean forms.

Probably some of the best clues to niche utilization and resource partitioning can be gleaned from close examination of differences in mouthpart morphology. Many gammarid amphipods are assumed to be herbivorous or omnivorous (Marsall and Orr, 1960), but this is obviously a broad generalization inasmuch as very few observations have been made on specific feeding strategies in this group of crustaceans. Barnard (1969:28) has stated that gammaridean amphipods are regarded primarily as scavengers, which feed on debris and detritus, carrion, and dead plant fragments. He has also discussed in broad terms some of the more obvious structural-functional relationships in marine amphipod groups.

Basically four types of mouthparts are noted among the artesian well amphipods: (a) a generalized crangonyctid type (see Holsinger, 1977a) characterized by a triturative molar and moderately setose and spinose maxillary plates and palps, and exemplified by the two species of *Stygobromus;* (b) a modified hadziid type characterized by the mandible, which has a strong, triturative molar but lacks a palp and the right lacinia mobilis, relatively heavily setose and spinose maxillary plates and palps, and exemplified by *T. texensis* and *A. hirsuta;* (c) a highly specialized (apomorphic ?) hadziid type, similar to the above type in the structure of the mandible but differing in having expanded maxillary plates with supernumerary setae and spines, and exemplified by *T. insolita* and *T. samacos;* and (d) a reduced type, probably derived independently in several separate lineages, characterized by a small (nontriturative) obsolescent molar accompanied by a broad incisor and lacinia mobilis and reduced maxillary plates and palps with few setae, and exemplified by *Parabogidiella* spp., *A. subterranea,* and *S. relicta.*

Although further, detailed studies are obviously necessary, we have tentatively concluded that these mouthpart types represent a minimum of four distinctly different feeding patterns among the artesian well amphipods. Only on the crangonyctids, however, are there any observations available that will allow us to speculate with much probability of accuracy on the specific feeding habits of the artesian well amphipods. Dickson's studies (1978, 1979) on the troglobitic amphipod *Crangonyx antennatus,* which has mouthparts similar to those of *Stygobromus,* indicate that this species feeds on microorganisms living on decaying organic detritus (e.g., leaf litter and related material) in the mud-bottom pools and streams of caves. Presumably the crangonyctids in the artesian well community occupy a similar feeding niche. Beyond this, we might deduce from mouthpart morphology that the richly setose/spinose maxillary plates of *T. insolita* and *T. samacos* are somehow utilized in filter feeding and that the reduced mouthparts found in the parabogidiellids, *Artesia* and *Seborgia,* in which the grinding surface of the molar is missing and the maxillary plates and palps are reduced and sparsely armed, may be adapted for feeding on soft, pulpy substances.

Some rather striking differences in behavior have been observed between *S. flagellatus* and *T. insolita* in the laboratory, and these differences probably reflect to a large extent fundamental differences in the behavior of these species in nature. Both forms are slender bodied and have proportionately long appendages, but *T. insolita* is noticeably more fragile bodied and the appendages are more attenuated and some are longer. Moreover, there are major differences in the structure of the gnathopods, pereopods, uropods, and telson. In May 1977 a sample containing both species was taken from the artesian well and emptied into a large plastic pan in the laboratory. *Stygobromus flagellatus* was clearly a much better swimmer and was able to move quickly through the water by backward thrusts of the urosome. In addition, it was able to walk upright on the bottom of the pan in a manner similar to that observed in other crangonyctids, i.e., by extending the pereopods and flexing the urosome. In contrast, *T. insolita* was a very weak swimmer, often becoming suspended in the surface film, where it could not extricate itself without our assistance. Furthermore this species could not walk on the bottom of the pan but simply swam weakly around on its side, often in a slow, erratic manner. Although the plastic pan did not simulate the natural habitat of these species, it did provide us with the opportunity to observe what are obviously significant differences in the behavior of the two species.

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