

A new species of *Stygonitocrella* (Crustacea: Copepoda: Ameiridae), the first report of the genus in North America

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Abstract.—A new species of ameirid harpacticoid copepod, *Stygonitocrella sequoyahi*, was collected in streambeds in Arkansas and Oklahoma, U.S.A., and is described herein. The new taxon shares with its congeners the 1-segmented endopodite of leg 4, but differs in having much longer caudal rami, as well as in the major armament of the swimming legs. Other species of *Stygonitocrella* are known from freshwater hypogean habitats in Europe, Central Asia, Argentina, and Cuba. This is the first record of a member of the genus from North America. No type species has ever been designated for the genus *Stygonitocrella*. In order to make the genus name available, we designate *Stygonitocrella montana* (Noodt) as the type species, and provide a diagnosis for the genus.

Collections from the hyporheic zones of streams in the Ozark region of Arkansas and Oklahoma, south-central U.S.A., resulted in the discovery of a previously undescribed species assignable to *Stygonitocrella*, a genus proposed by Petkovski (1976). The ameirid harpacticoid copepods which have been assigned to this genus have been reported from freshwater hypogean habitats in Europe, Central Asia, the Ryukyus, Argentina, and Cuba. The species described herein constitutes the first record of the genus from North America. We describe the species and provide information on its habitat.

Eleven freshwater subterranean species of the family Ameiridae are presently included in *Stygonitocrella*. Petkovski (1976) revised the genus *Nitocrella* Chappuis, 1924, and proposed the erection of a new genus *Stygonitocrella* for species with much-reduced segmentation of the endopodites of swimming legs 2–4, i.e., with

combinations of 2,2,1; 2,1,1; or 1,1,1 segments in the endopodites of legs 2–4 respectively. As Petkovski (1976) noted, all the species then known have short conical caudal rami, about 1–2 times longer than wide. The few species described since also share this feature. The species are, as originally assigned by their authors: *Nitocrella dubia* Chappuis, 1937, from Spain; *Nitocrella karamani* Petkovski, 1959, from Yugoslavia (now Macedonia, near Skopje); *Nitocrella montana* Noodt, 1965, from Argentina; *Nitocrella ljevuschkini* Borutsky, 1967, from Transcaucasia; *Nitocrella colchica* Borutsky & Mikhailova-Neikova, 1970, from West Georgia; *Nitocrella tianschanica* Borutsky, 1972, from Kirghizstan; *Nitocrella orghidani* Petkovski, 1973, from Cuba; *Nitocrella pseudotianschanica* Štěrba, 1973, from Afghanistan; *Nitocrella djirgalanica* Borutsky, 1978, from Kirghizstan; *Stygonitocrella guadalfensis* Rouch, 1985, from Spain; and *Stygonitocrella petkovskii*

Pesce, 1985, from Lesbos, Greece. Another species, *Nitocrella insularis* Miura, 1962, from the Ryukyu Islands was included in *Stygonitocrella* by Petkovski (1976), but was transferred from *Stygonitocrella* to a new genus *Neonitocrella* by Lee & Huys (2002).

Petkovski (1976) did not designate a type species for the genus *Stygonitocrella*, nor has any subsequent investigator done so. Since definite type fixation by original designation or indication is a mandatory requirement for the availability of generic names published after 1930 (ICZN 1999 Art. 13.3), it follows that the name *Stygonitocrella* is unavailable. In order to maintain nomenclatural stability, we propose to re-establish *Stygonitocrella* as a new name, taking the date and authorship of the present paper. A similar action was taken by Galassi et al. (1999) in the case of *Nitocrellopsis*, another genus defined by Petkovski (1976), which now takes the authorship Galassi, De Laurentiis & Dole-Olivier, 1999.

Unfortunately, of the species originally included by Petkovski in the genus, the type material of several (*S. dubia*, *S. karamani*, *S. orghidani*) no longer exists. To satisfy the criteria both of available and accessible material and an accurate published description, we propose *S. montana* as the type species, and provide a diagnosis for the genus. Since species-group names must be published in combination with a generic name, but the latter need not be valid or even available (ICZN 1999 Art. 11.9.3.1), the unavailability of Petkovski's (1976) generic name has no implications for the species of *Stygonitocrella* described since 1976, other than that they will be treated as new combinations.

Methods

Samples were collected from wells driven into the stream substrates. Hyporheic samples, pumped from the wells with a hand pump, were concentrated with a 63

μm mesh net and preserved in 5% formalin. Detailed information on the sampling method and habitat parameters in Sager Creek and Baron Fork was provided by Hunt & Stanley (2000). Station data and information on the hydrology and water chemistry of all the streams were presented by Hunt (1999). Sorting, facilitated by the addition of rose bengal stain, was done using an Olympus dissecting microscope. For morphological examination, specimens were transferred to glycerin and then to lactic acid. All the specimens were extremely fragile, and the appendages broke easily during dissection. To compensate for this fragility, the habitus and larger appendages were drawn from whole specimens in lactic acid under supported cover glasses. Mouthparts were drawn and details of all appendages were verified and in some cases re-drawn after the specimens were dissected and permanently mounted in CMC-10[®] (Masters Chemical Co., Wood Dale, Illinois, U.S.A.) with a little chlorazol black E stain added. Drawings were made using a Wild M30[®] compound microscope fitted with a drawing tube, at magnifications of 600 \times or 1000 \times . Details were verified using a Leica DMLB[®] microscope equipped with phase-contrast and differential interference contrast illumination. The specimens were deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Order Harpacticoida

Family Ameiridae Monard, 1927

Genus *Stygonitocrella*, new genus

Diagnosis.—Ameiridae. Antennule of female 8-segmented, segment 1 not elongated. Antennule of male geniculate. Antenna with basis and 1-segmented exopodite bearing 2 or 3 setae. Medial spine on leg 1 basipodite modified in male. Basipodites of legs 1–4 all with lateral (outer) spine or seta. Exopodites of legs 1–4 and endopodite of leg 1 3-segmented. Endopodites of legs 2–4 with 2,2,1; 2,1,1; or 1,1,1 seg-

ments respectively, or leg 4 endopodite reduced to tiny nub without seta. Baseopodite and exopodite of leg 5, if present, either distinct or fused. Caudal ramus short, about 1–1.5 times longer than wide, or long and cylindrical. Lacking eye and pigment.

Type species.—*Stygonitocrella montana* (Noodt, 1965), new combination.

Additional species.—*Stygonitocrella colchica* (Borutsky & Mikhailova-Neikova, 1970), new combination; *S. dubia* (Chapuis, 1937), new combination; *S. djirgalanica* (Borutsky, 1978), new combination; *S. guadalupensis* (Rouch, 1985), new combination; *S. karamani* (Petkovski, 1959), new combination; *S. ljovuschkini* (Borutsky, 1967), new combination; *S. petkovskii* (Pesce, 1985), new combination; *S. pseudotianshanica* (Štěrba, 1973), new combination; *S. tianshanica* (Borutsky, 1972), new combination; and *S. sequoyahi*, new species.

Species incertae sedis.—*Stygonitocrella orchidani* (Petkovski, 1973), new combination.

Stygonitocrella sequoyahi, new species

Figs. 1–4

Material examined.—Holotype ♀, dissected on slide (USNM 288040); allotype ♂, dissected on slide (USNM 288041); paratypes: 1 ♀, dissected on slide, and 1 ♀ and 4 copepodids (USNM 288042), preserved in 70% ethanol, all from depths of 5–20 and 60–75 cm at 2 stations in streambed of Sager Creek, Benton Co., Arkansas, about 36°12'N, 94°35'W, 29 Jul 1997, collector G. W. Hunt. Additional paratypes, all ethanol-preserved: 1 ♀, 2 ♂♂, and 4 copepodids (USNM 288043), from 30–45 cm depth in streambed of Snake Creek, Cherokee Co., Oklahoma, about 36°09'N, 95°08'W, 27 Jun 1996, collectors G. W. Hunt and E. H. Stanley; 8 ♀♀, 5 ♂♂, and 5 copepodids (USNM 288044), from several depths combined in streambed of Baron Fork, Cherokee Co., Oklahoma, about 35°55'N, 95°51'W, 2 Jan 1997, collector G. W. Hunt.

Female.—Length of holotype (measured

from anterior margin of cephalosome to apex of caudal ramus and excluding caudal setae) 0.56 mm; range of lengths of paratypes from 0.444–0.548 mm, median length 0.470 mm ($n = 11$). Habitus (Fig. 1A, B, drawn extended in lactic acid) slender, prosome dorsoventrally compressed. Intercalary membranes broad, i.e., body quite flexible. Prosome ornamented only with scattered hairs (setules). Cephalic shield (Fig. 1A, C) with irregularly round dorsal integumental window. Pedigers 2–4 each with 1 round integumental window on each side. Genital double-somite (Fig. 1A, D), both original somites completely fused, with no trace of previous separation. Genital field (Fig. 1D) short, copulatory pore located at anterior 1/4 of genital double-somite. Leg 6 (Fig. 1D) consisting of tiny plate bearing 1 hairlike seta. Genital double-somite and next urosomite each with lateroventral row of tiny spinules near posterior border; following urosomite with lateral row of similar spinules near posterior border. Anal somite (Fig. 1A, D, E) with few rows of tiny spinules near anteroventral border, and larger spinules along posterior border. Anal operculum (Fig. 1E) crescentic, reaching approximately to posterior end of anal somite, bordered with tiny teeth. Caudal ramus (Fig. 1A, D, E) about 5 times longer than wide, with 6 main setae, tiny accessory seta next to anterior lateral (outer) seta, and few small spines at bases of posterior lateral, dorsal, and medialmost (innermost) terminal setae. Dorsal seta longer than ramus, doubly articulated at base. Medialmost terminal seta shorter than lateralmost terminal seta, and with slightly enlarged base. Medialmost terminal seta about as long as urosome, without breaking plane.

Rostrum (Fig. 1C) short, broad, and continuous with cephalic shield.

Antennule (Figs. 1A, 2A) longer than cephalosome, 8-segmented. Segments (indicated by Roman numerals) with numbers of setae (indicated by Arabic numerals) and aesthetascs (ae) as follows: I (1), II (6), III (6), IV (3 + ae), V (1), VI (2), VII (3), VIII

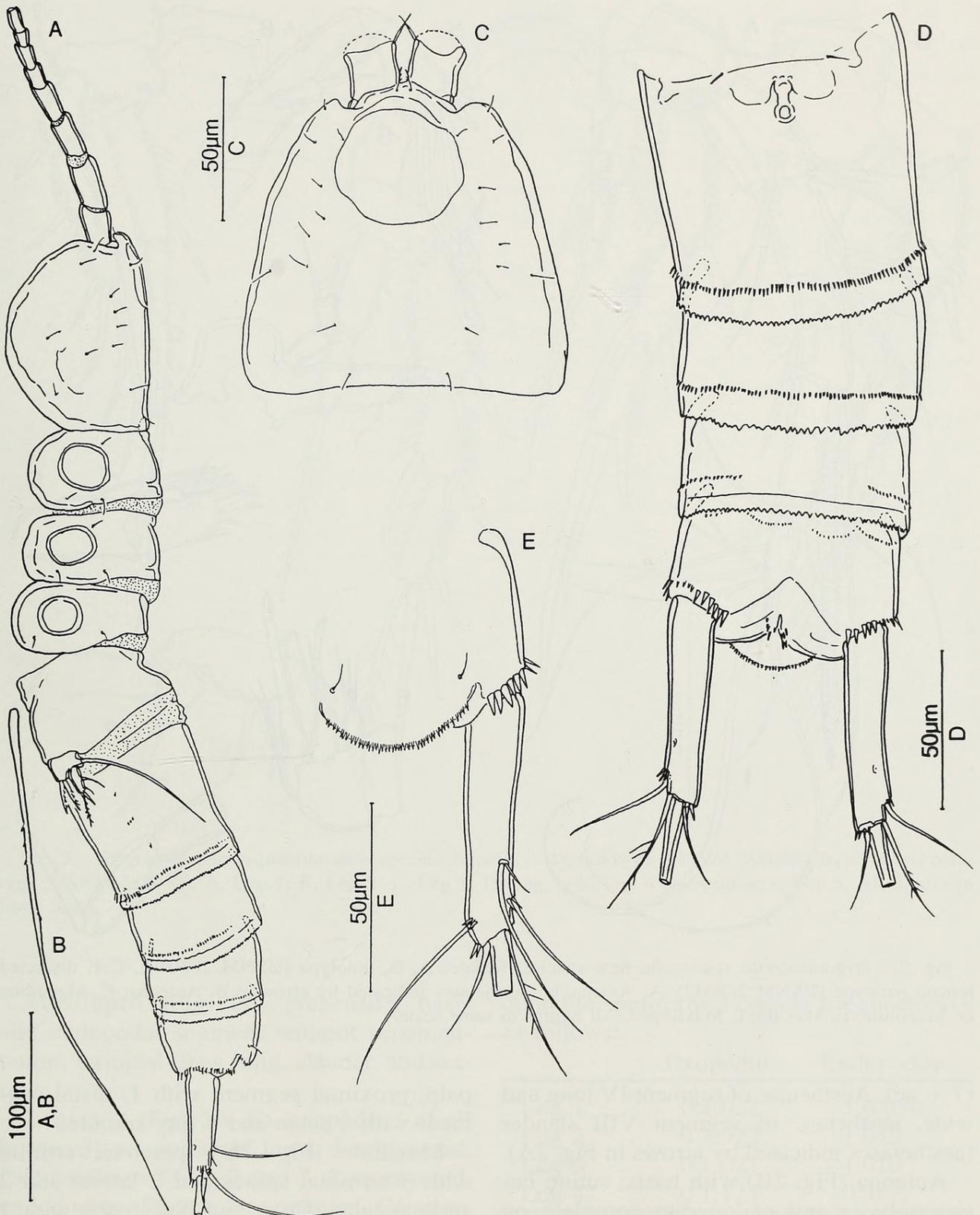


Fig. 1. *Stygonitocrella sequoyahi*, new species, female, holotype (USNM 288040). A, Habitus, left lateral; B, Middle terminal caudal seta; C, Cephalosome, dorsal; D, Urosome (somite bearing leg 5 omitted), ventral; E, Anal somite and right caudal ramus, dorsal.

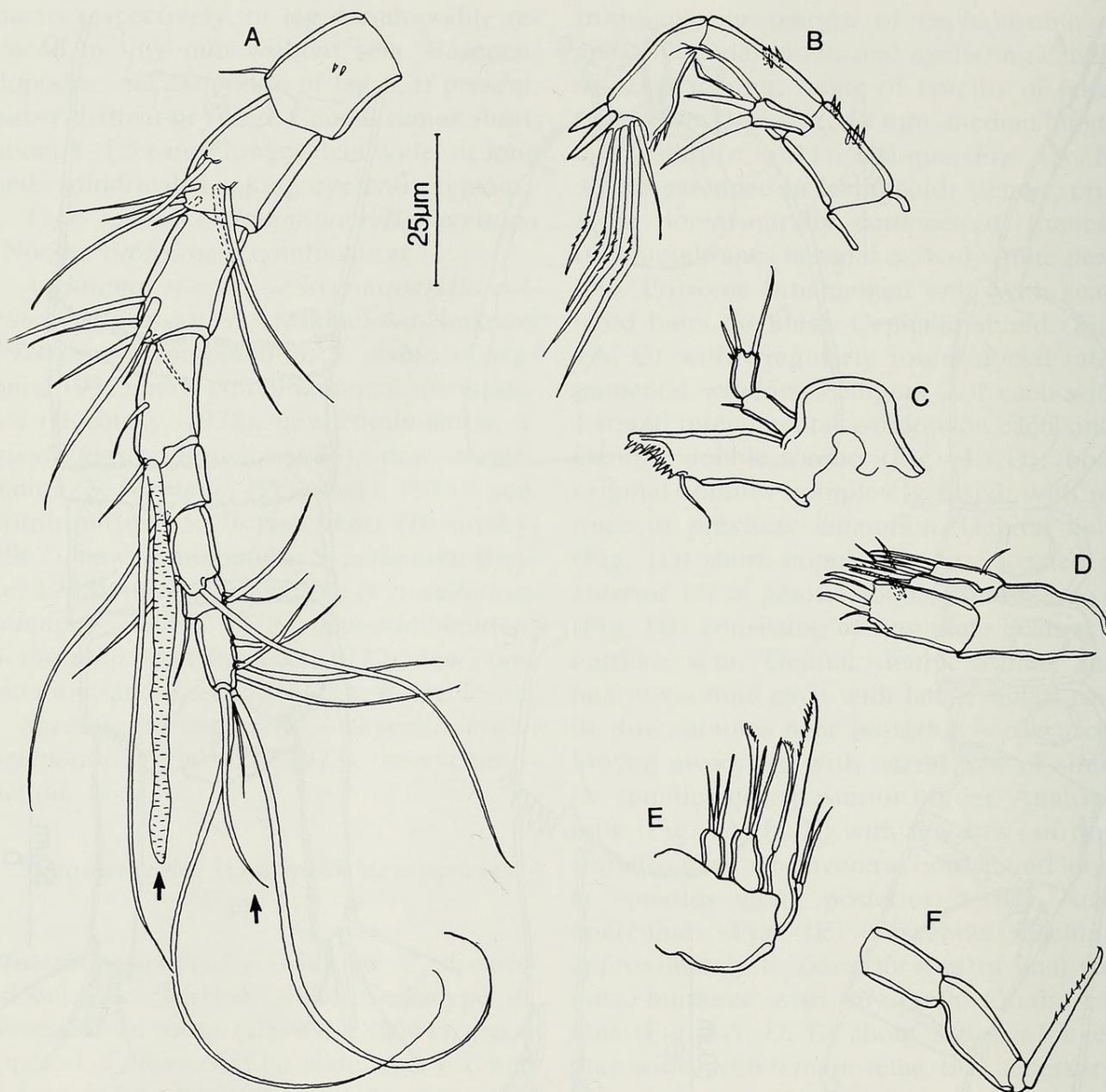


Fig. 2. *Stygonitocrella sequoyahi*, new species, female; A, B, holotype (USNM 288040), C–F, dissected female paratype (USNM 288042). A, Antennule (aesthetascs indicated by arrows); B, Antenna; C, Mandible; D, Maxillule; E, Maxilla; F, Maxilliped. All figures to same scale.

(7 + ae). Aesthetasc of segment IV long and wide, aesthetasc of segment VIII slender (aesthetascs indicated by arrows in Fig. 2A).

Antenna (Fig. 2B) with basis; suture between basis and endopodite complete on both sides. Antennal exopodite 1-segmented, bearing 1 setiform and 2 spiniform elements. Segment 1 of endopodite with few spinules along inner margin; segment 2 with few spinules, 2 socketed spines, and 5 terminal setae, 4 of these setae geniculate.

Mandible (Fig. 2C) with 2-segmented

palp, proximal segment with 1, distal segment with 3 setae and 1 tiny spinule.

Maxillule (Fig. 2D), precoxal arthrite with 3 terminal spines and 2 lateral and 2 surface setae. Coxa and basis each with 3 terminal setae. Exopodite represented by tiny nodule bearing 1 seta.

Maxilla (Fig. 2E), syncoxa with 2 endites bearing 3 setae each, 1 seta on distal endite modified with brushlike tip. Allobasis extended into strong claw bearing 1 modified seta; endopod 1-segmented, bearing 2 setae.

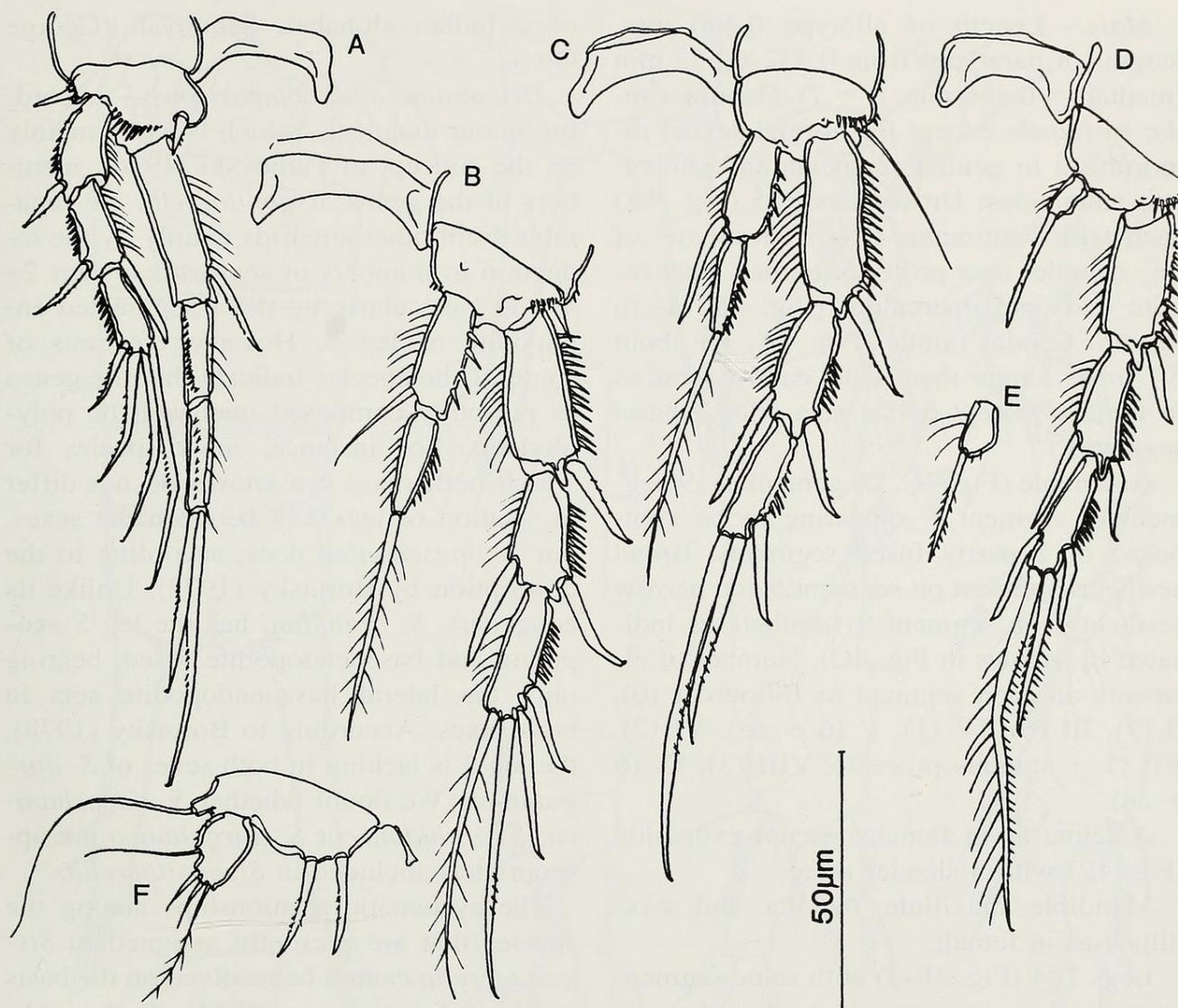


Fig. 3. *Stygonitocrella sequoyahi*, new species, female; A–D, holotype (USNM 288040), E, dissected paratype (USNM 288042). A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Leg 4 endopodite; F, Leg 5. All figures to same scale.

Maxilliped (Fig. 2F) prehensile, basis and endopodal segment without ornamentation, terminal claw long, slender, and serrate.

Legs 1–4 (Fig. 3A–E), exopodites of all legs and endopodite of leg 1 3-segmented. Endopodites of legs 2 and 3, 2-segmented, endopodite of leg 4, 1-segmented. Couplers (intercoxal sclerites) broad, without ornamentation. Leg 1 basipodite with small spine on anterior surface of distomedial (inner) corner. Leg 1 exopodite segment 2 with lateral (outer) spine. Medial setae of legs 1–4 exopodite 2, leg 3 endopodite 1, leg 4 exopodite 3, and terminal seta of leg 4 en-

dopodite spiniform. Formula for chaetotaxy as follows:

	Exopodite	Endopodite
Leg 1	0.1.022	1.0.030
Leg 2	0.1.022	1.010
Leg 3	0.1.021	1.010
Leg 4	0.1.121	010

Leg 5 (Fig. 3F) with 2 short spiniform setae on medial expansion of baseoendopodite; outer basal seta long and slender. Exopodite ovoid, with 2 terminal and 2 lateral setae, middle 2 setae shorter and slightly thicker than others. No ornamentation visible on surface of leg.

Male.—Length of allotype 0.460 mm, lengths of paratypes from 0.432–0.552 mm (median = 0.466 mm, $n = 7$). Habitus similar to female except for normal sexual dimorphism in genital segments and geniculate antennules. Urosomites 3–5 (Fig. 4A) each with continuous lateroventral row of tiny spinules near posterior border. Anal somite and anal operculum (Fig. 4B) as in female. Caudal ramus (Fig. 4A, B) about 5.7 times longer than wide; caudal setae as in female, except dorsal seta with 3 basal segments.

Antennule (Fig. 4C, D) geniculate, 9-segmented, segment 5 appearing to be composed of 2 partly fused segments. Broad aesthetasc present on segment 5 and narrow aesthetasc on segment 9 (aesthetascs indicated by arrows in Fig. 4C). Number of elements on each segment as follows: I (0), II (7), III (6), IV (1), V (6 + ae), VI (2), VII (1 + spinous process), VIII (3), IX (6 + ae).

Antenna as in female, except exopodite (Fig. 4E) with 3 slender setae.

Mandible, maxillule, maxilla, and maxilliped as in female.

Legs 1–4 (Fig. 4F–J) with same segmentation and major armament as in female. Leg 1 basipodite with modified spine on mediodistal corner (Fig. 4F, G). Some setae different from corresponding setae of female: particularly in legs 2 and 3, terminal setae of endopodites stouter and more spiniform, and medial setae of exopodite segment 2 and terminal setae of exopodite 3 thinner and more thickly plumed.

Leg 5 (Fig. 4A) with baseoendopodites partly fused at median line, each bearing 2 spiniform setae. Exopodite ovoid, with 2 medial, 1 terminal, and 1 lateral setae plus lateral hairlike setule.

Leg 6 (Fig. 4A) consisting of wide plate bearing 1 seta on free border.

Type locality.—Sager Creek, Benton County, Arkansas, U.S.A., about 36°12'N, 94°35'W.

Etymology.—The species name honors the great educator and inventor of the Cher-

okee Indian alphabet, Sequoyah (George Gist).

Discussion and comparisons.—According to our diagnosis, which is based mainly on the concept of Petkovski (1976), members of the genus *Stygonitocrella* are separable from other ameirids mainly by the reduction in numbers of segments of legs 2–4, and particularly by the 1-segmented endopodite of leg 4. However, features of some of the species indicate that the genus as presently composed may well be polyphyletic. For instance, most species for which both sexes are known do not differ in setation of legs 1–4 between the sexes, but *S. tianschanica* does, according to the description by Borutsky (1972). Unlike its congeners, *S. orghidani* has the leg 5 exopodite and baseoendopodite fused, bearing only the lateral baseoendopodite seta in both sexes. According to Borutsky (1978), the leg 5 is lacking in both sexes of *S. djirgalanica*. We doubt whether *S. tianschanica*, *S. orghidani*, or *S. djirgalanica* are appropriately included in *Stygonitocrella*.

The systematic relationships among the species that are presently assigned to *Stygonitocrella* cannot be resolved on the basis of the information available in the published descriptions. As Fiers & Iliffe (2000) noted, many of the present generic groupings in the family Ameiridae are merely a practical division of the diversity seen in this widely distributed and speciose family. Lee & Huys (2002) discussed the confused taxonomic subdivisions within the freshwater Ameiridae. They strongly criticized the practice of inferring relationships in derived lineages based on leg segmentation, which has led to the establishment of genera such as *Stygonitocrella*, which they characterized as “unnatural”. Lee & Huys (2002) also provided a table of known characters of appendages of members of the related genera *Stygonitocrella*, *Inermipes* Lee & Huys, 2002, *Neonitocrella*, and *Psammonitocrella* Rouch, 1992. Although they considered that the members of *Stygonitocrella* can be grouped into several discrete

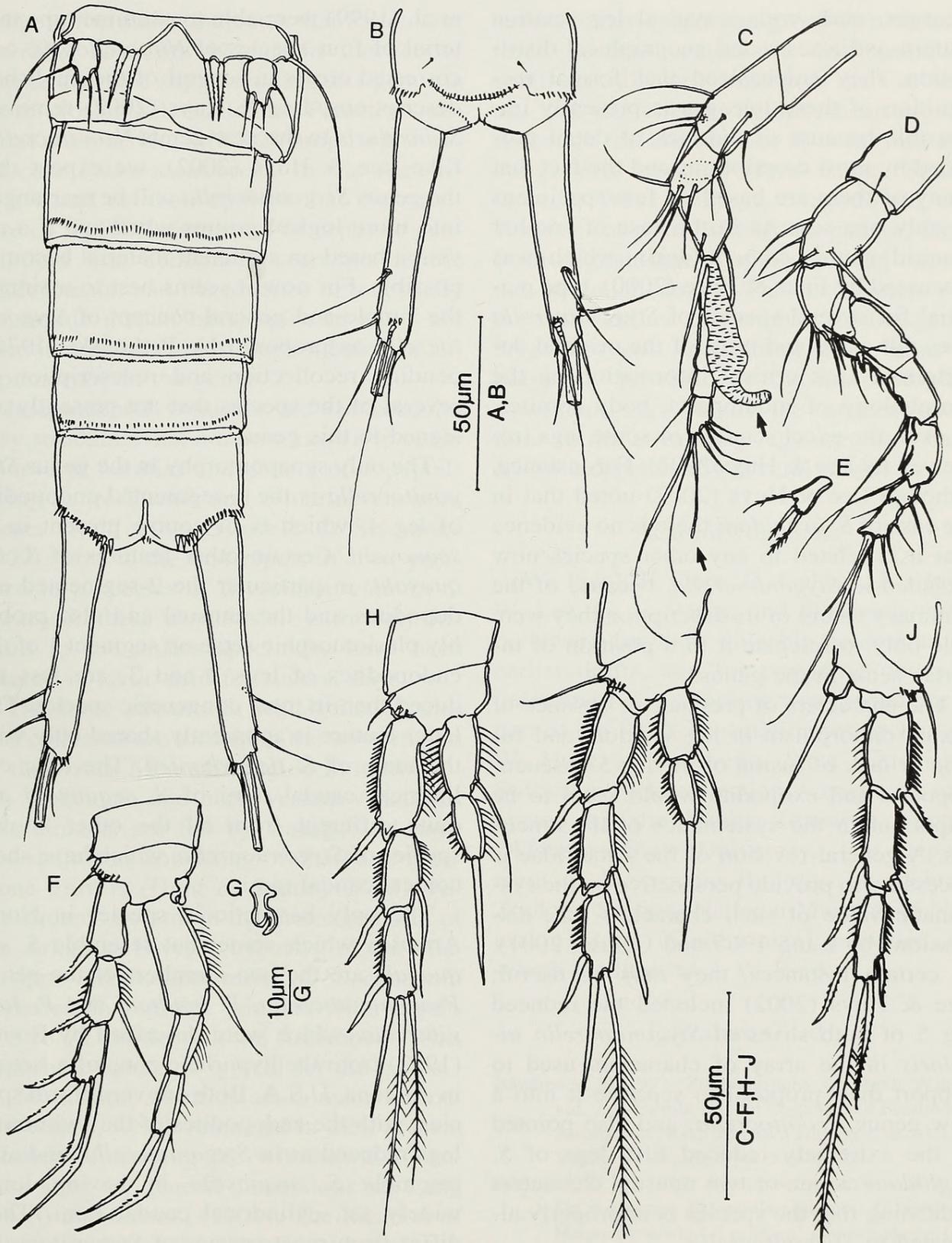


Fig. 4. *Stygonitocrella sequoyahi*, new species, male allotype (USNM 288041). A, Urosome, ventral; B, Anal somite and caudal rami, dorsal; C, Antennule, medial; D, Antennule, lateral; E, Antennal exopodite; F, Right leg 1; G, Spine on distomedial corner of left leg 1 basipodite (enlarged); H, Leg 2; I, Leg 3; J, Leg 4.

lineages, each with a typical leg setation pattern and a restricted geographical distribution, they emphasized that formal recognition of these lineages is presently impossible because of the lack of detail provided by most descriptions and the fact that many of them are based on few specimens or only one sex. As in the case of another ameirid genus, *Nitocrellopsis*, which was discussed by Fiers & Iliffe (2000), type material for several species of *Stygonitocrella* does not exist, and most of the original descriptions lack critical information on the morphology of mouthparts, body somites, or even the exact setation of some legs (reviewed by Lee & Huys 2002). For instance, although Lee & Huys (2002) noted that in the case of *S. orghidani* there is no evidence that it is related to any other species now included in *Stygonitocrella*, because of the summary nature of its description they were able only to relegate it to a position of incertae sedis in the genus.

The characters of presence or absence of sexual dimorphism in leg setation, and fusion or lack of fusion of the leg 5 baseopodite and exopodite would seem to be important in the systematics of the ameirids. A general revision of the Ameiridae is necessary to provide perspective on the systematic value of such characters (cf., discussions by Lang 1965 and Galassi 2001). In certain instances, they may be useful; Lee & Huys (2002) included the reduced leg 5 of both sexes of *Stygonitocrella insularis* in the array of characters used to support their proposal to separate it into a new genus *Neonitocrella*; and also pointed to the extremely reduced fifth legs of *S. orghidani* as one of two unusual characters indicating that the species is improperly allocated to *Stygonitocrella*.

Some of the problems in systematics of freshwater ameirids have been resolved on the basis of recently gathered information. Galassi et al. (1999) provided a diagnosis and designated a type species for *Nitocrellopsis*, another genus originally proposed by Petkovski (1976). In that case, Galassi

et al. (1999) were able to examine type material of four species of *Nitocrellopsis*, and corrected errors in several of the published descriptions. Lee & Huys (2002) removed *S. insularis* to the new genus *Neonitocrella*. Like Lee & Huys (2002), we expect that the genus *Stygonitocrella* will be rearranged into more logical groups when and if a revision based on sufficient material becomes possible. For now it seems best to maintain the simple and general concept of *Stygonitocrella* as proposed by Petkovski (1976), pending recollection and redescription of several of the species that are presently assigned to this genus.

The only synapomorphy in the genus *Stygonitocrella* is the 1-segmented endopodite of leg 4, which is of course present in *S. sequoyahi*. Certain other features of *S. sequoyahi*, in particular the 2-segmented endopodites and the unusual and also probably plesiomorphic setae on segment 1 of the endopodites of legs 2 and 3, are less reduced than in most congeneric species. The latter feature is apparently shared only with the male of *S. tianschanica*. The long cylindrical caudal rami of *S. sequoyahi* are quite different from all the other known species of *Stygonitocrella*, which have short conical caudal rami.

The only harpacticoid species in North America which somewhat resemble *S. sequoyahi* are the two members of the genus *Psammonitocrella*, *P. boultoni* and *P. longifurcata*, which were described by Rouch (1992) from the hyporheic zone of a stream in Arizona, U.S.A. Both are vermiform species, with the endopodites of the swimming legs reduced as in *Stygonitocrella*, and also resemble *S. sequoyahi* in having long, widely set, cylindrical caudal rami. They differ from most species of *Stygonitocrella* except *S. orghidani* in having the leg 5 exopodite fused to the baseopodite; and from all other known ameirid species in having the medial spine of the leg 1 basipodite not transformed in the male. Martinez Arbizu & Moura (1994) considered that the presence of an untransformed leg 1

spine in the males indicates that *Psammonitocrella* does not belong in the family Ameiridae, and suggested that this genus is more closely related to the Parastenocarididae. Lee & Huys (2002) proposed to re-allocate *Psammonitocrella* to the Ameiridae, based on their opinion that the structure of leg 5, the presence of separate genital and first abdominal segments in the adult female, and the absence of a sexually dimorphic medial basal spine in leg 1 are pedomorphic features, the last being an autapomorphy in the genus.

Integumental windows are osmoregulatory structures that are now known to occur in several families and genera of copepods living in freshwater and estuarine environments (Reid 1994, Hosfeld & Schminke 1997). This is the first report of their presence in a species of *Stygonitocrella*. In *S. sequoyahi* these windows are extremely difficult to see unless specimens have been cleared in lactic acid for several days.

The three streams in which this species was collected are located in the western part of the Ozark Mountain region in northeastern Oklahoma and northwestern Arkansas. The streams are fed by springs and have bed sediments consisting of chert and limestone gravels (Hunt & Stanley 2000). All the streams lie within the drainage basin of the Arkansas River, a tributary of the Mississippi. All the specimens of *S. sequoyahi* appeared in samples pumped from depths of 5 to 75 cm deep in the streambeds. This hyporheic habitat is typical for the genus.

Continental ameirids are considered marine relicts, which remained in their present locations following the withdrawal of ancient seas; for general discussions see Lang (1948) and Galassi (2001). The location of *S. sequoyahi* in the Ozarks, although not that of the two species of *Psammonitocrella* in Arizona, lies within the boundaries of the great North American inland sea, which receded in the early Paleocene (Bănărescu 1992). Fiers & Iliffe (2000) noted that the distribution of the genus *Nitocrellopsis* resembles the Tethyan distribution pattern of

several other crustacean groups which have three general centers of distribution in south-central North America, the Caribbean, and the circum-Mediterranean region. Although the locations of *S. sequoyahi* and congeneric species from Cuba, Spain, Greece, West Georgia, Macedonia, and Transcaucasia fall within this pattern, those from Afghanistan, Kirghizstan, and Argentina obviously do not. This incongruency of the distributions of members of the genus *Stygonitocrella*, in addition to the hints of polyphyly provided by the morphological characters, suggests that the extreme reductions in the swimming legs may well have arisen independently several times.

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