

RHEOCYCLOPS, A NEW GENUS OF COPEPODS FROM THE SOUTHEASTERN AND CENTRAL U.S.A. (COPEPODA: CYCLOPOIDA: CYCLOPIDAE)

*Janet W. Reid, David L. Strayer, J. Vaun McArthur,
Suzanne E. Stibbe, and Julian J. Lewis*

A B S T R A C T

The new genus *Rheocyclops* is proposed to accommodate the cyclopoid copepods *Diacyclops virginianus* Reid, from Virginia, and the new species *R. carolinianus* from South Carolina, *R. talladega* and *R. hatchiensis* from Alabama, and *R. indiana* from Indiana, U.S.A. Most species were collected from the hyporheic zones of stream beds, except *R. indiana* which was found in a drip pool in a cave. The new genus is distinguished by a combination of characters: anal operculum produced; antennule 11-segmented; antenna lacking exopodite seta; rami of legs 1-4 all 3-segmented, or some rami 2-segmented; leg 5 with proximal segment fused to somite and reduced to small protrusion bearing seta inserted near distal (free) segment, and free segment cylindrical with 2 terminal setae.

Diacyclops virginianus Reid, 1993, from Goose Creek, Virginia, was tentatively placed in the genus *Diacyclops* by its author. The fifth leg of *D. virginianus*, with the proximal segment reduced to a small knob fused to the somite, and two setiform terminal appendages on the distal segment, does not conform to the usual condition in *Diacyclops*. Pesce (1994) observed correctly that assignment of *D. virginianus* to the genus *Diacyclops* confused the status and definition of the genus, although he then designated this species as the type of his "*Diacyclops virginianus*-group." Following the discovery and analysis of four additional species similar to *D. virginianus*, from hyporheic zones of streams and a drip pool in a cave in the southeastern and central U.S.A., we propose to separate these in a new genus.

MATERIALS AND METHODS

For taxonomic examination, the Formalin- or ethanol-fixed specimens were transferred gradually to glycerine, then to lactic acid. Dissected specimens were permanently mounted in polyvinyl lactophenol, with a little chlorazol black E added in some cases. Drawings were made at 600x or 1,000x (the latter using an oil immersion lens), with the aid of a drawing tube mounted on a Wild M30 microscope. The specimens were deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution.

Order Cyclopoida G. O. Sars, 1886
Family Cyclopidae Burmeister, 1834

Subfamily Cyclopinae Dana, 1853, char.
emend. Kiefer, 1927

Rheocyclops Reid and Strayer,
new genus

Diagnosis.—Cyclopidae, Cyclopinae. Small species with stout, compact habitus. Body with or without pseudosomite between pedi-

ger 5 and genital double-somite. Genital double-somite broader than long; seminal receptacle with large anterior and (when visible) posterior expansions, copulatory duct recurved and heavily sclerotized. Anal operculum produced, crescentic or triangular. Caudal ramus short (less than 3 times longer than wide). Medialmost terminal caudal seta equal in length or shorter than outermost terminal caudal seta. Antennule of 11 segments. Antenna lacking exopodite seta; and endopodite segment 2 with 6 or 7 setae. Rami of swimming legs broad and paddlelike, basically 3-segmented but showing oligomerization in some species, and sexually dimorphic. Leg 5 composed of 2 segments, proximal segment fused to somite, visible as tiny expansion lateral to free segment, and bearing lateral seta set close to distal segment; distal segment distinct, cylindrical, with 2 thin terminal setae, medial seta shorter than lateral seta.

Type Species.—*Diacyclops virginianus* Reid, 1993, by designation.

Additional Species.—*Rheocyclops carolinianus* Reid, new species; *R. hatchiensis* Reid and Strayer, new species; *R. talladega* Reid and Strayer, new species; and *R. indiana* Reid, new species.

Gender.—Masculine.

Etymology.—From the Greek *rheos*, stream, prefixed to the genus name *Cyclops*.

***Rheocyclops carolinianus* Reid,**
new species
Figs. 1, 2

Material Examined.—Holotype: 1 ♀, dissected on slide (USNM 284146). From hyporheic sediments of Meyers

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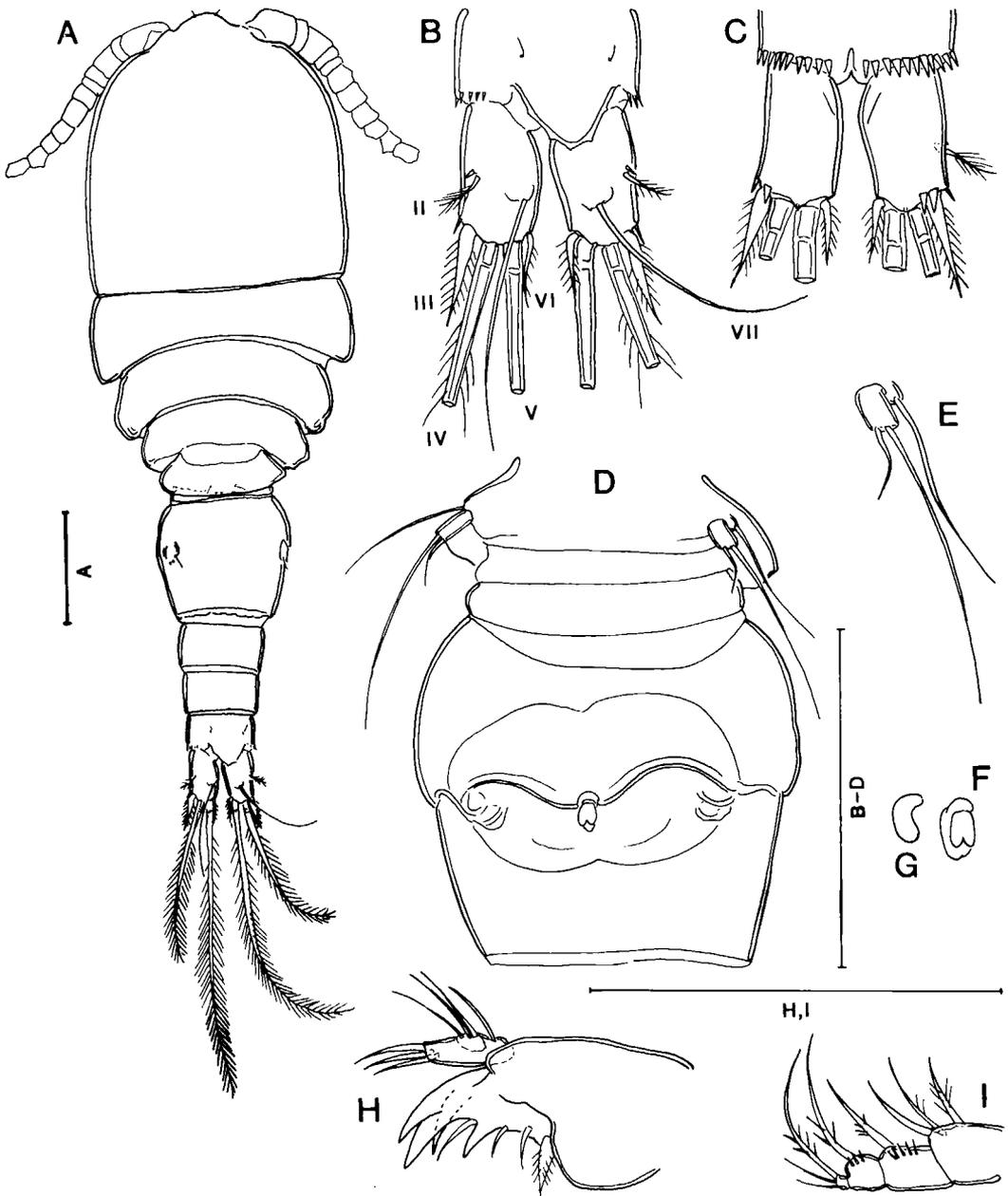


Fig. 1. *Rheocyclops carolinianus* Reid, new species, holotype female (USNM 284146): A, habitus, dorsal; B, anal somite and caudal ramus, dorsal; C, caudal ramus, ventral; D, pediger 5 and genital double-somite, ventral; E, leg 5 (enlarged); F, area of copulatory pore and copulatory duct (enlarged); G, copulatory duct (enlarged); H, maxillule; I, maxilliped. Scales = 50 μ m.

Branch, Savannah River Site, U.S. Department of Energy, South Carolina, about 33°10'N, 81°34'W, June 1994, collected by S. E. Stibbe. Average water temperature in June was 20°C, electrical conductivity 120 μ S/cm, and pH 7.4.

Female.—Length, exclusive of caudal setae, 355 μ m. Body (Fig. 1A) compact, postero-

lateral corners of pedigers 2–4 slightly lobate, without ornamentation. Sclerotized pseudo-somite (Fig. 1A, D) present between pediger 5 and genital double-somite. Genital double-somite (Fig. 1A, D) ovate, slightly broader than long; seminal receptacle with broad an-

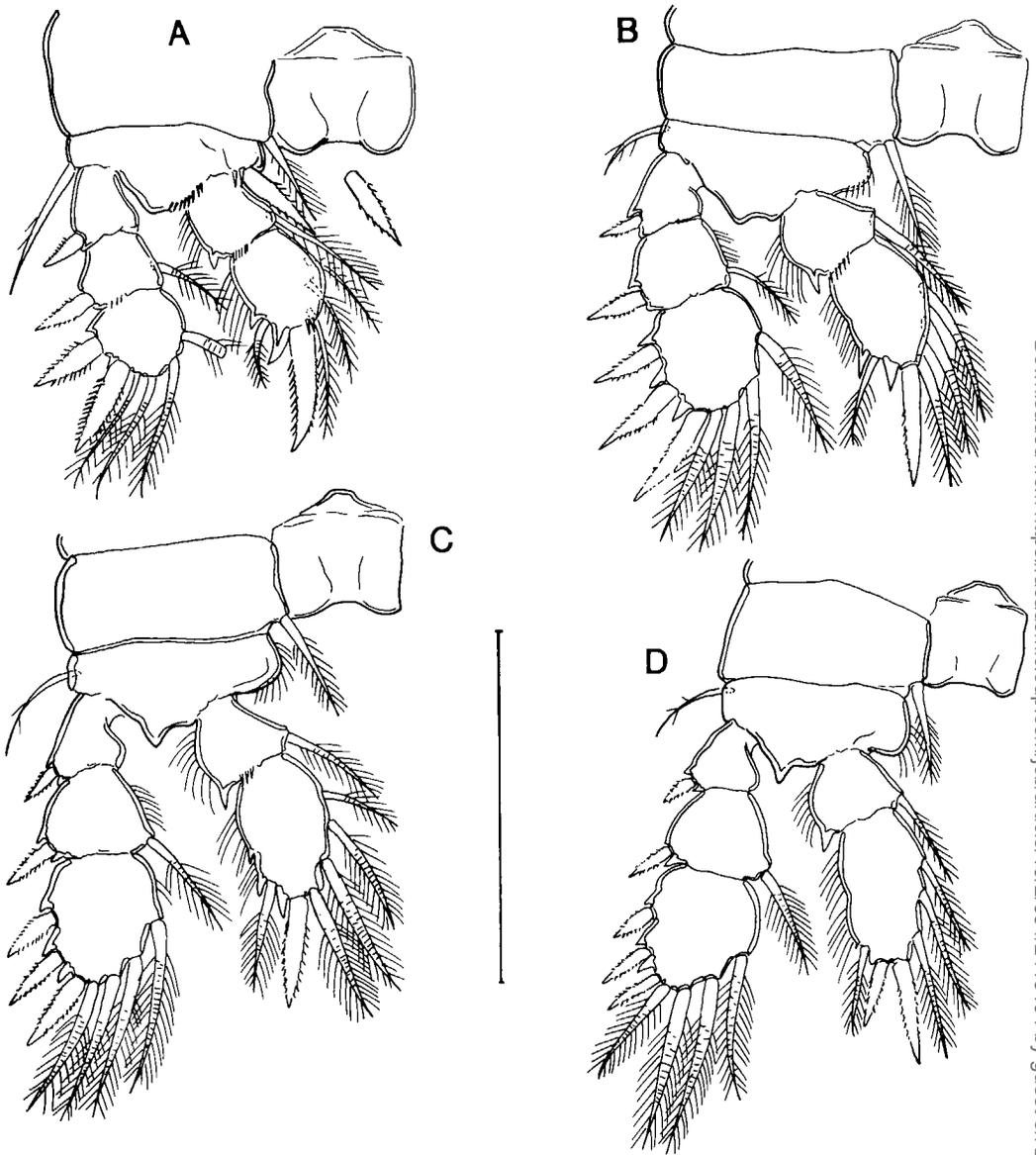


Fig. 2. *Rheocyclops carolinianus* Reid, new species, holotype female (USNM 284146): A, leg 1 and coupler, frontal, with detail of basipodite spine; B, leg 2 and coupler, frontal; C, leg 3 and coupler, frontal; D, leg 4 and coupler, frontal. Scale = 50 μ m.

terior and posterior expansions, transverse ducts narrow and curved, copulatory pore and copulatory duct (Fig. 1D, F, G) heavily sclerotized. Anal somite (Fig. 1A–C) with row of spinules along posterior margin; anal operculum produced posteriorly, its sclerotized margin with several tiny knoblike projections. Caudal ramus (Fig. 1A–C) about 2.8 times longer than broad, without ornamentation except unsocketed spinules at bases of lateral and lateralmost terminal setae. Lengths of

caudal setae in μ m: lateral (II) 7, dorsal (VII) 35, outermost to innermost terminal (III–VI) 16, 78, 137, 9 (setae numbered according to system of Huys and Boxshall, 1991).

Antennule (Fig. 1A) shorter than cephalosome, of 11 segments, segment I with row of spinules, remaining segments lacking surface ornamentation; no hyaline membrane visible on terminal segments. Proportions of segments as in *R. virginianus* and *R. hatchiensis*, new species (cf. Fig. 3E). Numbers of

setae (Arabic numerals), spines (sp), and aesthetascs (ae) on segments (Roman numerals) as follows: I(7), II(4), III(5), IV(2), V(2 + sp), VI(1), VII(3), VIII(2 + ae), IX(2), X(2 + ae), XI(7 + ae).

Antenna exactly as in *R. virginianus*, i.e., with only 1 seta on anterior corner of basis, exopodite seta absent, and endopodite segments I–III with 1, 6, and 7 setae, respectively; no ornamentation visible on surface of basipodite. Labrum not observed. Mandible as in *R. virginianus*. Maxillule as in Fig. 1H. Maxilla as in *R. hatchiensis* (cf. Fig. 3F). Maxilliped (Fig. 11) similar to that of *R. virginianus*, i.e., composed of 4 short segments, proximal to distal segments bearing 3, 1, 1, and 3 setae, respectively; middle segments with surface spinules.

Legs 1–4 (Fig. 2) with 3-segmented exopodites and 2-segmented endopodites. Couplers (intercoxal sclerites) without surface ornamentation, free margins each with shallow double curvature. Distomedial corner of leg 1 basis with short, stout, finely serrate spine. Exopodite segment 1 of all legs lacking seta; exopodite segment 2 and endopodite segment 1 with 1 medial seta. Spine formula 2,3,3,3; seta formula 4,4,4,4. All setae short, barely longer than segment bearing them; more distal setae of legs 2–4 rather stout. Leg 3 endopodite segment 2 with spiniform process on lateral margin indicating site of former division of segment; endopodites of legs 2 and 4 with shallow notches at corresponding sites. Leg 4 endopodite segment 2 about 1.7 times longer than broad, ending in 2 terminal spines, medioterminal spine 1.4 times longer than lateroterminal spine.

Leg 5 (Fig. 1D, E) remnant of proximal segment visible as small knob bearing long

slender seta; distal segment about twice longer than broad, with 2 slender terminal setae, lateral seta about 3.7 times longer than medial seta. Leg 6 (Fig. 1A) consisting of small plate bearing 1 short dorsal seta and 2 tiny ventral spines.

Male.—Unknown.

Remarks.—*Rheocyclops carolinianus* is one of three species in this genus with 2-segmented endopodites of legs 1–4. It differs from *R. virginianus* (Reid, 1993a) mainly in having the exopodites completely divided into 3 segments, while the distalmost 2 segments of exopodites of legs 3 and 4 are only partly divided laterally in *R. virginianus*. The distal setae of legs 2–4 are shorter and stouter, and the leg 5 setae are much longer in *R. carolinianus* than in *R. virginianus*. Except for these aspects, the basic structure of the swimming legs is identical in both species. *Rheocyclops hatchiensis*, new species, has all swimming legs with 2-segmented exopodites as well as endopodites (see description following). *Rheocyclops carolinianus* also differs from all known congeners in having the anal operculum subtriangular.

***Rheocyclops hatchiensis* Reid and Strayer,
new species
Figs. 3, 4**

Material Examined.—Holotype ♀, dissected on slide (USNM 243665), well 2, 70 cm. Allotype ♂, dissected on slide, well 2, 70 cm (USNM 243666). Paratypes: 8 ♀♀, 4 ♂♂, and 3 copepodids (USNM 243671), well 2, 70 cm; 1 ♂, ethanol-preserved (USNM 243672), well 1, 40 cm; 1 ♂, slide, and 2 ♂♂, ethanol (USNM 243667), well 1, 70 cm; 1 ♀, slide (USNM 243668), well 6, 10 cm; 1 ♀, ethanol (USNM 266464), well 3, 70 cm, Sample 75; 1 ♂, ethanol (USNM 266462) and 2 ♀♀, 1 ♂, and 2 copepodids, semidissected on slide (USNM 266463), well 4, 40 cm, Sample 187. All from Hendrick Mill Branch, 4

Table 1. Physical and chemical features of the collection sites of *Rheocyclops hatchiensis* and *R. talladega*. Numbers are means from several samples per site. HM, Hendrick Mill Branch, Alabama; CC, Choccolocco Creek, Alabama.

A. Sediment granulometry and organic matter content.		Particle size distribution (%)					
Site	Loss on ignition (%)	>16 mm	4–16 mm	1–4 mm	0.25–1 mm	62–250 μm	<62 μm
HM	1.1	13	57	20	8	2	0.4
CC	0.7	12	25	20	40	3	1

B. Water chemistry (ppm).								
Site	Ca	Mg	K	Na	NO ₃ -N	SO ₄	Cl	DOC
HM	22.2	11.6	0.5	0.7	0.9	1.8	1.2	0.5
CC	10.5	3.1	1.0	3.0	0	4.2	1.5	1.6

Table 2. Measurements (μm) of *Rheocyclus hatchiensis* Reid and Strayer, new species, from Hendrick Mill Branch, Alabama. Ten individuals of each sex were measured. Abbreviations: L = length; W = width; CR = caudal ramus; CR II–VII = caudal setae II–VII (Fig. 1B); P4enp2 = leg 4 endopodite segment 2; P4 m sp = length of P4enp2 medioterminal spine; P4 l sp = length of P4enp2 lateroterminal spine.

Structure	Median	Range	Median	Range
Body L	272	260–304	252	236–284
CR L	23	21–25	21	20–22
CR W	13	12–13	12	12
CR II	7	6–8	5	4–7
CR III	13	13–14	12	11–14
CR IV	73	68–80	74	70–78
CR V	128	112–135	130	120–133
CR VI	10	8–12	8	7–12
CR VII	35	29–55	28	23–35
P4enp2 L	18	17–22	17	16–20
P4enp2 W	14	13–14	12	11–13
P4 m sp	8	1–11	7	6–8
P4 l sp	14	13–17	13	12–15

October 1990, collected by D. L. Strayer. Additional specimens in collection of D. L. Strayer.

Hendrick Mill Branch is a third-order stream running on the limestone terrain of the Valley and Ridge. The sampling site is near Alabama Route 75 about 20 km northeast of Pinson, Blount County, Alabama (33°52'12"N, 86°33'57"W). This is a crystal-clear, unpolluted spring-fed stream 3–6 m wide, running through mixed hardwood forest. The bottom varies from sand to exposed bedrock, with a predominance of coarse sand, angular gravel, and small (10–15 cm) stones. Generally, the alluvium is thin, but a large deposit of sand and gravel is held in place by a low (approximately 3 m high) dam (Table 1). The emergent part of this deposit is 3–4 m wide, about 30 m long, and reaches about 0.5 m above the stream water level. The dam leaks from its base, with water flowing down and through the bar. The alluvium is deep (almost 2 m) and extremely permeable, especially below a depth of 15–20 cm, and dissolved oxygen concentrations were 0–8.0 ppm, with most readings 2–6 ppm. The fauna was very rich in terms of numbers of individuals and species, including bathynellaceans, stygobiont isopods, amphipods, and oligochaetes.

Female.—Length 260–304 μm (Table 2). Body (Fig. 3A) compact, similar to congeners. No pseudosomite present between pediger 5 and genital double-somite. Genital double-somite (Fig. 3A, D) ovate, slightly broader than long; seminal receptacle with broad anterior and posterior expansions, copulatory pore and recurved copulatory duct (Fig. 3D) heavily sclerotized. Anal somite (Fig. 3A–C) with row of spinules along lateral and ventral posterior margin; anal operculum broad, crescentic, produced posteriorly just past margin of anal somite, sclerotized margin smooth. Caudal ramus (Fig. 3A–C) about 2.0 times longer than broad, without ornamentation except unsocketed spinules at

bases of lateral and lateralmost terminal setae. Lengths of caudal setae as in Table 2.

Antennule (Fig. 3E) shorter than cephalosome, of 11 segments, segment I with row of spinules, other segments lacking surface ornamentation; no hyaline membrane visible on terminal segments. Proportions of segments as in *R. virginianus* and *R. carolinianus*. Numbers of setae (Arabic numerals), spines (sp), and aesthetascs (ae) on segments (Roman numerals) as follows: I(7), II(4), III(5), IV(2), V(1 + sp), VI(2), VII(3), VIII(2 + ae), IX(2), X(2 + ae), XI(7 + ae).

Antenna, labrum, and mandible as in *R. virginianus*; maxillule as in *R. carolinianus*. Maxilla (Fig. 3F) with slender claw bearing few tiny teeth. Maxilliped similar to that of *R. virginianus*, i.e., composed of 4 short segments, proximal to distal segments with 3, 1, 1, and 3 setae, respectively.

Legs 1–4 (Figs. 3F, G, 4A, B) with 2-segmented exopodites and endopodites. Couplers (intercoxal sclerites) without surface ornamentation, free margins with shallow double curvature. Distomedial corner of leg 1 basis with short, stout, finely serrate spine. Exopodite and endopodite, proximal segment of all legs with 1 medial seta. Spine formula 3,4,4,4; seta formula 5,4,5,5. All setae slender, more distal setae of legs 3 and 4 exopodites particularly long. Leg 4 endopodite segment 2 about 1.6 times longer than broad, with 2 terminal spines, lateroterminal spine 1.6 times longer than medioterminal spine.

Leg 5 (Fig. 3D) much as in *R. carolinianus*. Leg 6 (Fig. 3A, D) ventrolateral, consisting

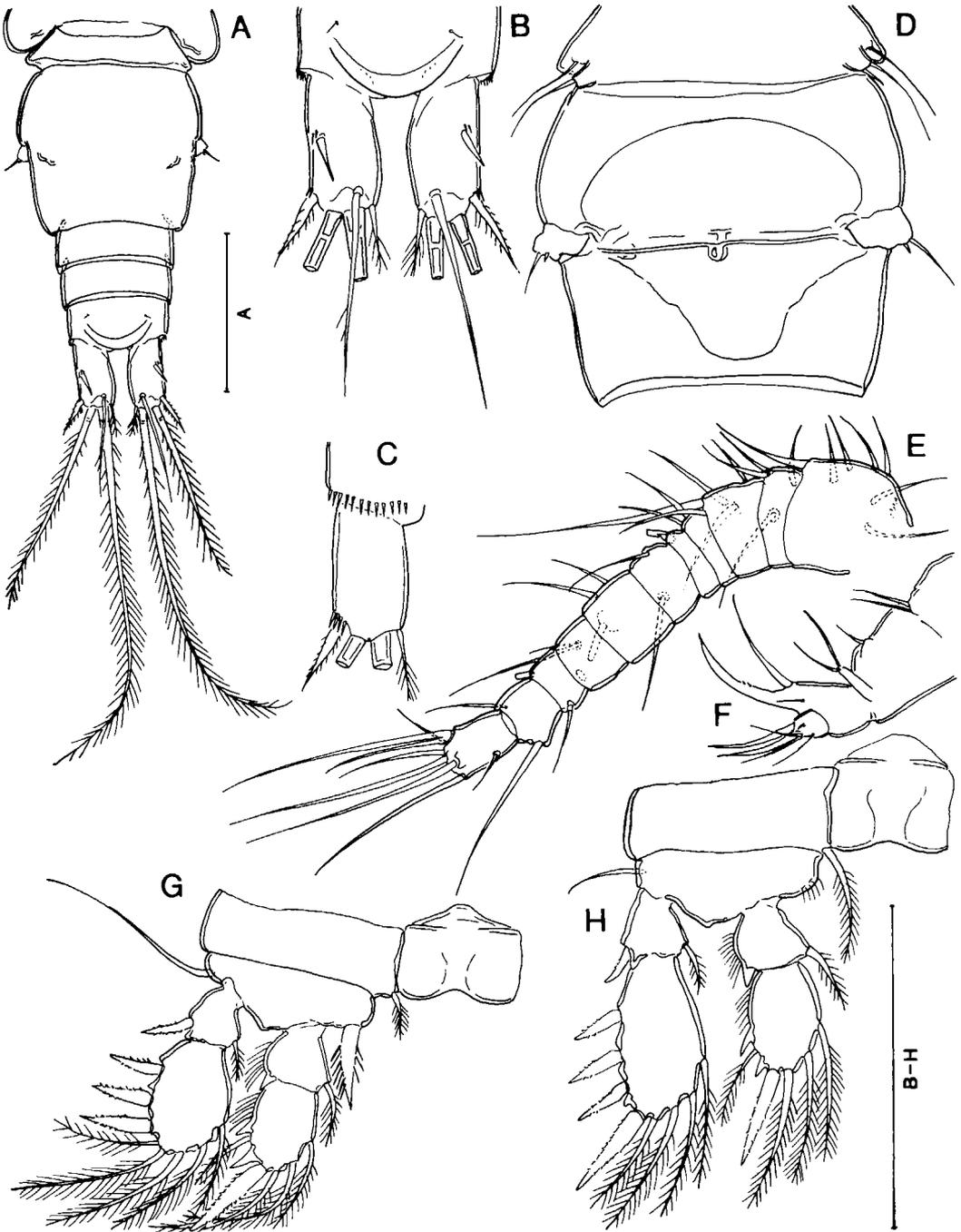


Fig. 3. *Rheocyclops hatchiensis* Reid and Strayer, new species, holotype female (USNM 243665): A, pediger 5 and urosome, dorsal; B, anal somite and caudal rami, dorsal; C, right caudal ramus, ventral; D, pediger 5 and genital double-somite, ventral; E, antennule; F, maxilla; G, leg 1 and coupler, frontal; H, leg 2 and coupler, frontal. Scales = 50 μ m.

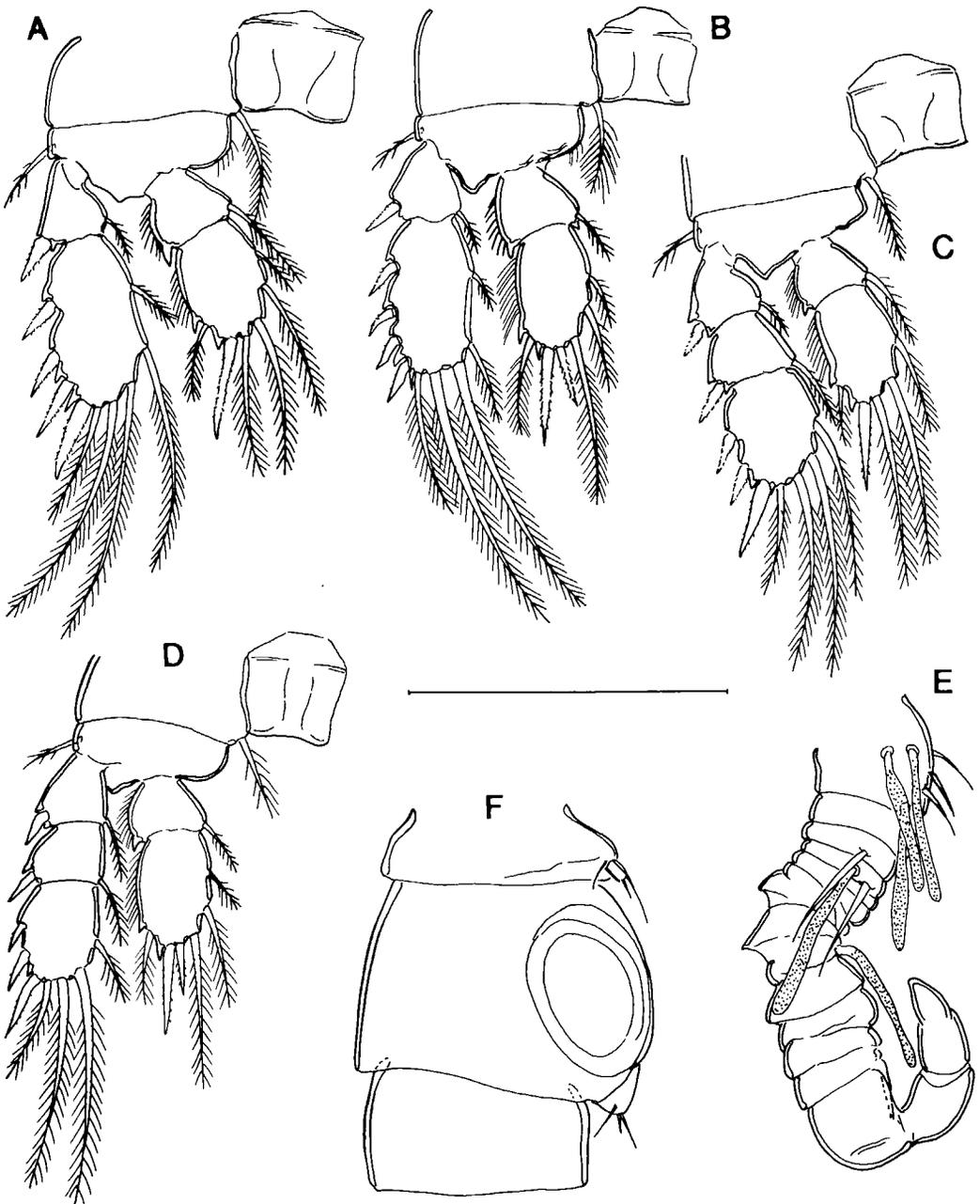


Fig. 4. *Rheocylops hatchiensis* Reid and Strayer, new species: A, B, holotype female (USNM 243665); C–F, allotype male (USNM 243666): A, leg 3 and coupler, frontal; B, leg 4 and coupler, frontal; C, leg 3 and coupler, frontal; D, leg 4 and coupler, frontal; E, antennule (some setae omitted); F, anterior urosomites. Scale = 50 μ m.

of small irregularly shaped plate bearing 1 short dorsal seta and 1 tiny ventral spine.

Male.—Lengths 236–284 μ m (Table 2). Habitus, caudal ramus, and anal operculum as in female except for normal sexual di-

morphism. Antennule (Fig. 4E) with long broad aesthetascs. Antenna, mouthparts, and legs 1 and 2 as in female. Legs 3 and 4 (Fig. 4C, D) with 3-segmented exopodites. Leg 6 (Fig. 4F) consisting of small triangular plate bearing 3 setae, middle seta shortest.

Type Locality.—Hendrick Mill Branch, Blount County, Alabama.

Etymology.—Species appellation from the Creek Indian word “hatchi” or “hatchee,” meaning creek or stream (Gatschet, 1884).

Remarks.—*Rheocyclops hatchiensis* differs from its congeners in having all swimming legs with 2-segmented rami in the female, and in both sexes, exopodite 1 of each swimming leg with a medial seta.

***Rheocyclops talladega* Reid and Strayer,
new species
Fig. 5**

Material Examined.—Holotype ♀, partly dissected on slide under left cover slip (USNM 243669), well 4, 10 cm, Choccolocco Creek, 25 October 1991, collected by D. L. Strayer. Allotype ♂, dissected on slide (USNM 243670), well 6, 10 cm, Hendrick Mill Branch, 4 October 1991, collected by D. L. Strayer.

Choccolocco Creek is a small, unpolluted third-order stream northeast of Anniston, Calhoun County, Alabama (33°49'43"N, 85°34'49"W). The collection site lies 1–2 km south of Rabbittown Road, about 1.5 km east of the Cleburne County line. The site is on sandstone terrain in the piedmont province. Much or all of the watershed is in the Talladega National Forest, which is hilly and covered by second growth (less than 50 year-old) pines and mixed hardwoods. At baseflow Choccolocco Creek is 4–8 m wide, less than 0.5 m deep, perfectly clear, and has moderately soft water (Table 1). The creek is well shaded by deciduous trees. Bedrock outcrops along the stream, and the alluvium of coarse sand, gravel, and angular stones is thin, less than 1 m. The floodplain is broad, but the channel appears stable and riffles and pools are only moderately well marked. The samples came from a small (3 × 14 m), low (<25 cm above low water level) bar immediately adjacent to the stream. The bar, 25–60 cm deep, was composed of blocky cobbles up to 30 cm in diameter, embedded in compact coarse sand, and bounded on the landward side by a low (0.5 m high) bank. Since the sediments were too compact to allow for the free flow of water, levels of dissolved oxygen within the bar were low (0.4–3.3 ppm) and H₂S was distinctly present in two samples. The fauna was numerically sparse, but included typical groundwater animals (bathynellaceans, stygobiont isopods).

For description of Hendrick Mill Branch see comments for *R. hatchiensis*.

Female.—Length of dissected holotype undetermined. Habitus apparently similar to congeners. No pseudosomite present between pediger 5 and genital double-somite. Genital double-somite and seminal receptacle (Fig. 5A, B) similar to congeners. Anal somite (Fig. 5A), posterior margin with lateroventral spines; anal operculum broad crescentic, reaching just past posterior margin of anal somite, free margin smooth, sclerotized. Caudal ramus (Fig. 5A) 2.0 times longer than

broad, without ornamentation except small spines at bases of lateral and lateralmost terminal setae. Dorsal seta rather stout, nearly as long as ramus. Lengths of caudal setae in μm: dorsal 20, lateral 6, medialmost to lateralmost terminal 7, 133, 85, 14.

Antennule, antenna, and mouthparts as in *R. hatchiensis*.

Legs 1–4 (Fig. 5D–G) with all rami 3-segmented. Couplers without surface ornamentation, free margins with shallow double curvature. Distomedial corner of leg 1 basipodite with short, stout, finely serrate spine. Exopodite of leg 2 as corresponding structure of leg 3. Proximal segments of exopodites of all legs lacking medial seta. Spine formula 2,3,3,2; seta formula 4,4,4,4. Setae rather short and stout. Leg 4 endopodite segment 2 about 1.3 times longer than broad, with 2 terminal spines, medioterminal spine about 1.5 times length of lateroterminal spine.

Leg 5 (Fig. 5B, C) with lateroterminal seta only slightly longer than medioterminal seta. Leg 6 (Fig. 5A) small, placed slightly dorso-laterally.

Male.—Length 340 μm. Habitus, including anal somite and caudal rami similar to female except for normal sexual dimorphism. Lengths of caudal setae in μm: dorsal 35, lateral 8, medialmost terminal 10, next medialmost broken, next lateralmost 82, lateralmost 14.

Antennule as in *R. hatchiensis*. Antenna, mouthparts, and leg 5 as in female. Legs 1–4 as in female, except left leg 4 exopodite 1 with medial seta. Leg 6 (Fig. 5H) much like that of *R. hatchiensis*.

Type Locality.—Choccolocco Creek, Talladega National Forest, Cleburne County, Alabama.

Etymology.—Named for the Talladega National Forest; proposed as a noun in apposition.

Comparisons.—*Rheocyclops talladega* differs from *R. virginianus*, *R. carolinianus*, and *R. hatchiensis* primarily in having all rami of the swimming legs completely 3-segmented. Its differences from *R. indiana*, new species, are described in the following section.

***Rheocyclops indiana* Reid, new species
Fig. 6**

Material Examined.—Holotype ♀ preserved whole in ethanol (USNM 243664), Ladder Cave, Indiana, 8 March 1998, collected by J. J. Lewis and R. Burns.

Ladder Cave is located approximately 18 km SSW of Salem, Washington County, Indiana. The pit entrance of the cave breaches the sandstone that caps the ridge and

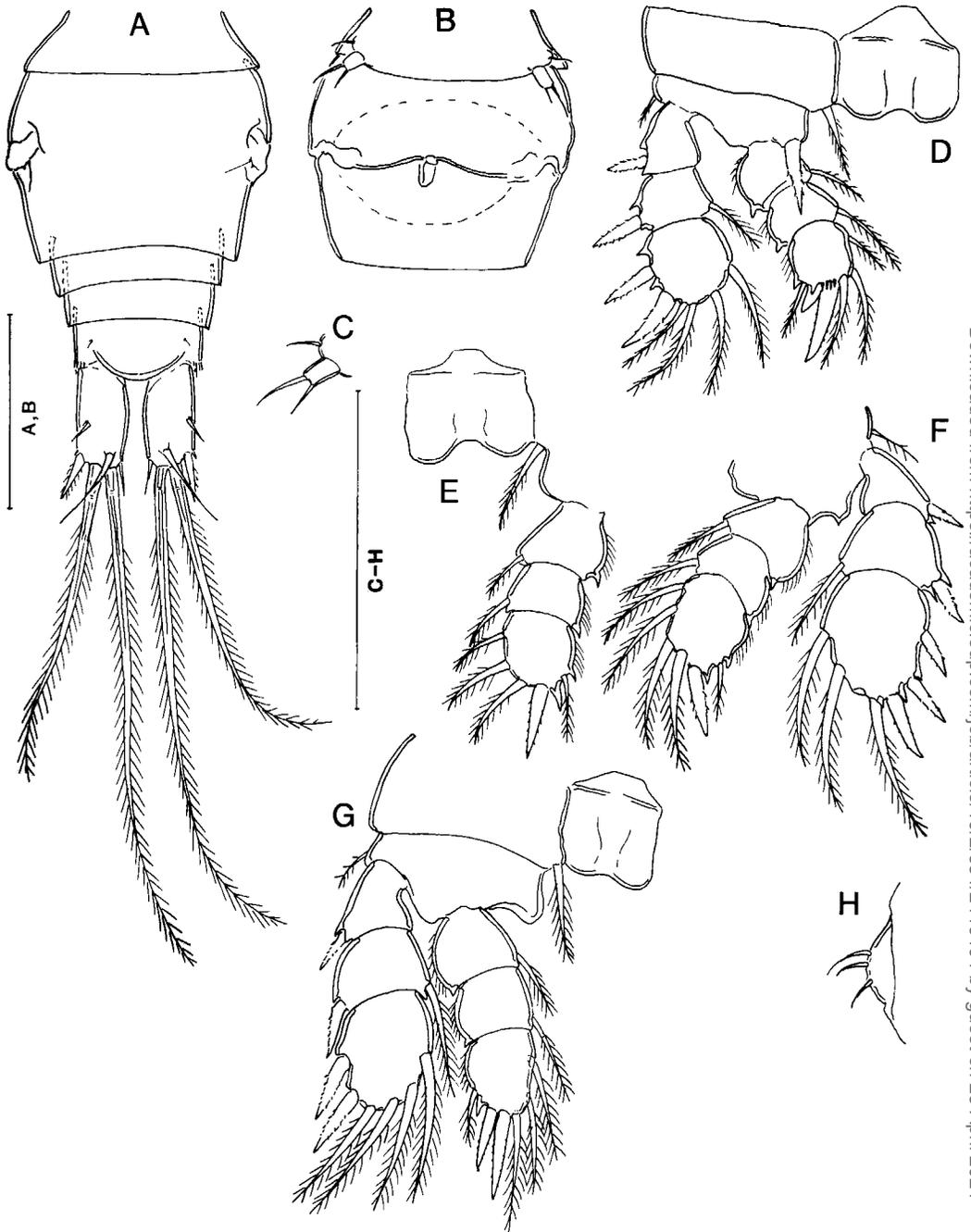


Fig. 5. *Rheocyclops talladega* Reid and Strayer, new species: A–G, holotype female (USNM 243669); H, allotype male (USNM 243670): A, urosome, dorsal; B, pediger 5 and genital double-somite, ventral; C, leg 5 (enlarged); D, leg 1 and coupler, frontal; E, leg 2 endopodite and coupler, frontal; F, leg 3; G, leg 4 and coupler, frontal; H, leg 6. Scales = 50 μ m.

penetrates the limestone in which the cave was formed. The cave itself consists of a short (100+ m), streamless passage (Powell, 1961). On the date of collection, the only aquatic habitat was shallow (approximately 1 cm in depth, 30 cm in diameter) pools on the floor of the passage, fed

by water slowly dripping from the cave ceiling. The bottom of the pools consisted of sand and pebbles. Fauna taken from the pool consisted of the single copepod and one specimen of a previously unknown species of the crangonyctid amphipod genus *Stygobromus*.

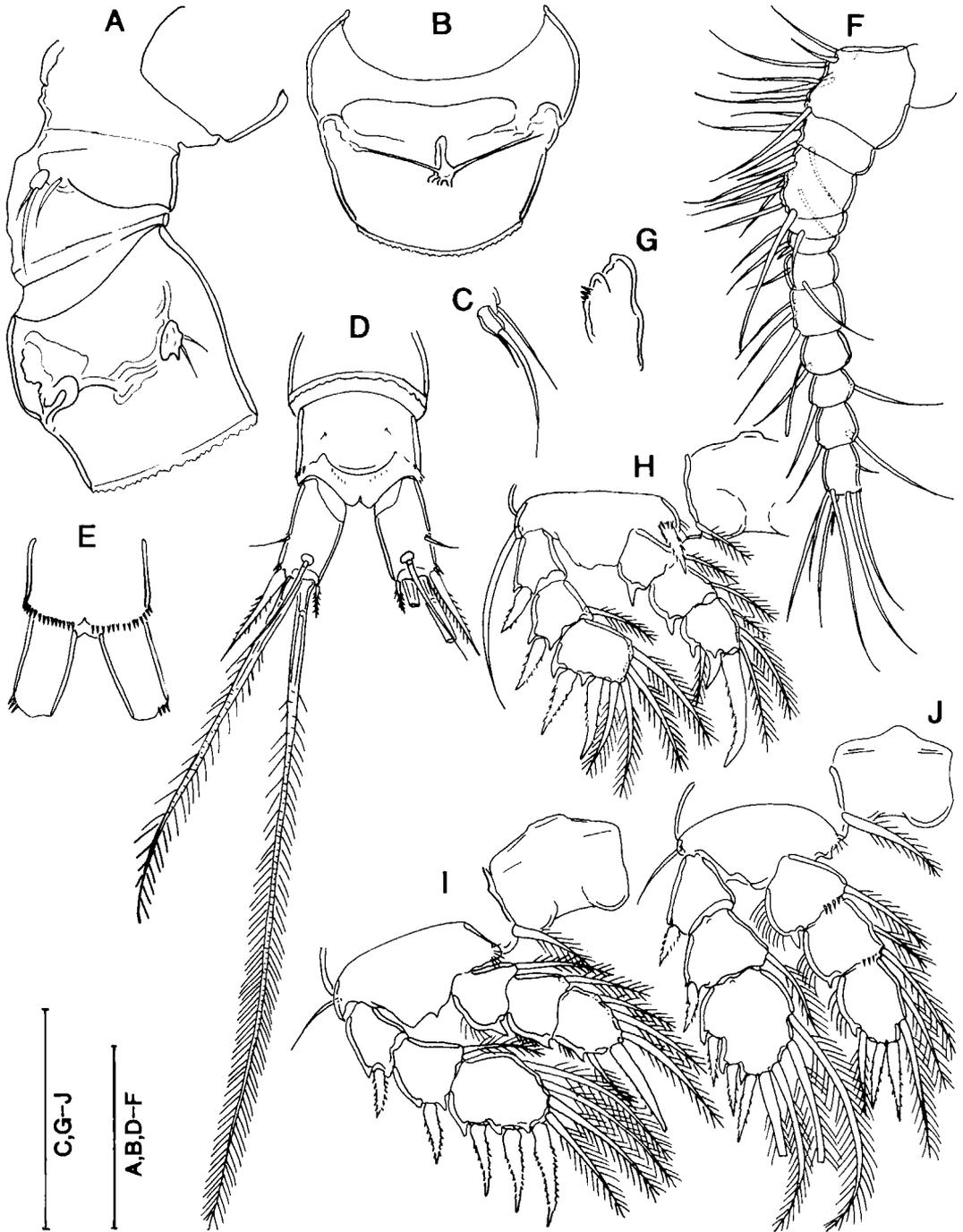


Fig. 6. *Rheocyclops indiana* Reid, new species, holotype female (USNM 243664): A, pediger 5 and genital double-somite, left lateral; B, genital double-somite, ventral; C, left leg 5, ventral; D, last two urosomites and caudal rami, dorsal; E, anal somite and caudal rami, ventral; F, antennule; G, left paragnath, ventral; H, right leg 1 and part of coupler, frontal; I, right leg 2 and coupler, frontal; J, right leg 4 and coupler, frontal. Scales = 50 μ m.

Female.—Length 520 μm . Habitus similar to congeners. Pseudosomite (Fig. 6A) present between pediger 5 and genital double-somite. Genital double-somite (Fig. 6A, B) similar in shape to congeners; seminal receptacle with broad anterior expansion, posterior expansion not visible, copulatory pore and recurved copulatory duct strongly sclerotized. Anal somite (Fig. 6D, E) with spinulate posterior margin; anal operculum broad, crescentic, reaching posterior end of anal somite, margin smooth, sclerotized. Caudal ramus (Fig. 6D, E) about 2.1 times longer than broad, its only ornamentation consisting of tiny unsocketed spinules at bases of lateral and lateralmost terminal setae. Dorsal seta longer than ramus. Lengths of caudal setae in μm : dorsal 27, lateral 10, medialmost to lateralmost terminal 9, 196, 112, 27.

Antennule (Fig. 6F) of 11 segments, setation as in *R. hatchiensis* except segment III with 8 setae, VIII with 1 seta + aesthetasc, and X with no aesthetasc visible. No hyaline membrane visible on segments X and XI. Antenna (not illustrated) with 7 setae on margin of endopodite segment 1; i.e., with 1, 1, 7, and 7 setae on proximal to distalmost segments, respectively. Labrum, mandible, maxillule, and maxilla as in *R. virginianus*. Paragnath (Fig. 6G) with 4 tiny spines on medial surface. Maxilliped with 3, 2, 1, and 3 setae on proximal to distalmost segments.

Legs 1–4 (Fig. 6H–J) all with 3-segmented exopodites and endopodites. Leg 3 (not illustrated) slightly larger than leg 2, otherwise identical. Couplers without surface ornamentation. Distomedial corner of leg 1 basis with short, stout, finely serrate spine. Proximal segments of all legs, exopodite with no medial seta, endopodite with 1 medial seta. Spine formula 2,3,3,3; seta formula 4,4,4,4. All setae rather slender. Leg 4 endopodite segment 3 about 1.2 times longer than broad, with 2 terminal spines, lateroterminal spine about 0.6 length of medioterminal spine.

Leg 5 (Fig. 6A, C) much as in congeners, except lateroterminal seta of distal segment rather long. Leg 6 plate (Fig. 6A) set slightly dorsally.

Male.—Unknown.

Type Locality.—Ladder Cave, Washington County, Indiana.

Etymology.—The species bears the name of the state where it was collected, proposed as a noun in apposition.

Remarks.—The female of *R. indiana*, like *R. talladega*, has legs 1–4 with completely 3-segmented rami. The spine formula of the former species is 2,3,3,3, and of the latter, 2,3,3,2. In *R. indiana*, the outermost terminal caudal seta is more than three-fourths the length of the caudal ramus, while in *R. talladega* the outermost terminal caudal seta is about one-half the length of the caudal ramus. The eight setae of antennular segment III are also unusual in the genus.

KEYS TO THE SPECIES OF *RHEOCYCLOPS*

Females:

1. Legs 1–4, all rami 3-segmented
- Legs 1–4, endopodites all 2-segmented, exopodites variously 2- or 3-segmented
2. Legs 1–4, spine formula 2,3,3,2; outermost terminal caudal seta about one-half length of caudal ramus *R. talladega*
- Legs 1–4, spine formula 2,3,3,3; outermost terminal caudal seta more than three-fourths length of caudal ramus *R. indiana*
3. Legs 1 and 2, exopodites 3-segmented; legs 1–4, exopodite segment 1 with no medial seta
- Legs 1 and 2, exopodites 2-segmented; legs 1–4, exopodite segment 1 with medial seta *R. hatchiensis*
4. Anal operculum crescentic, little produced; legs 3 and 4, exopodites 2-segmented, with distal segments only partly divided *R. virginianus*
- Anal operculum nearly triangular, much produced; legs 3 and 4, exopodites 3-segmented, i.e., distal segments completely divided *R. carolinianus*

Known males:

1. Legs 1–4, exopodite segment 1 with medial seta *R. hatchiensis*
- Legs 1–4, exopodite segment 1 without medial seta *R. carolinianus*

DISCUSSION

In the absence of a modern systematic scheme of the family Cyclopidae, subfamily Cyclopiniae (cf. comments by Reid, 1993b) it is difficult to assess the phylogenetic relationships of *Rheocyclops*. Following the classical arrangement of Kiefer (1927, 1929) who placed most emphasis on the structure of leg 5, we compare known genera that are similar in having the proximal segment, usually indicated by a remnant seta, fused to the somite, and a distinct (free) distal segment bearing 2 socketed appendages. These genera are *Metacyclops* Kiefer, 1927, sensu Lindberg, 1961, *Muscocyclops* Kiefer, 1937, *Speocyclops* Kiefer, 1937, *Apocyclops* Lindberg, 1942, *Menzeliella* Lindberg, 1954, *Cochlacocyclops* Kiefer, 1955, *Goniocyclops* Kiefer, 1955, *Teratocyclops* Pleša, 1981, *Hesperocyclops* Herbst, 1984, and *Fimbricyclops*

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Reid, 1993b. The fifth legs in several genera (*Apocyclops*, *Fimbricyclops*, *Goniocyclops*, *Hesperocyclops*, *Menzeliella*, *Metacyclops*, and *Teratocyclops*) have the remnant seta inserted dorsally, rather far from the free segment (in most cases separated by at least twice the width of the free segment), and the medioterminal appendage of the free segment is spiniform. In most, the rami of the swimming legs are exclusively 2-segmented as well. In *Muscocyclops* the medioterminal appendage of the free segment is setiform, but the remnant seta is inserted far from the free segment. Species of *Muscocyclops* further differ from *Rheocyclops* in having a distinctive band-shaped seminal receptacle, no spine on the medial corner of the leg 1 basipodite, legs 1–4 always with 2-segmented rami, and much reduced spination and setation compared to *R. hatchiensis* (see Reid, 1987; Rocha and Bjornberg, 1987). *Cochlacocyclops* was described from a single female with incomplete fifth legs, and may well belong to *Metacyclops* (see Kiefer, 1955).

The European genus *Speocyclops* has leg 5 structured similarly to *Rheocyclops*, with the proximal segment reduced to a small protrusion bearing a seta, which is inserted near the distal segment. The distal segment in turn is fused to the somite in most species, but is distinct in a few. The medioterminal appendage of the free segment may be spiniform or setiform, but is usually as thin as the setiform mediolateral appendage. *Speocyclops* differs from *Rheocyclops* in having a transverse dorsal suture on the genital double-somite of the female, the rami of legs 1–4 always 2-segmented, and leg 4 endopodite segment 2 with an apical seta and spine.

In the European genus *Graeteriella*, the distal segment of leg 5 is distinct or fused to the somite, but no trace of the proximal segment remains, except the remnant seta in a few specimens of *G. rouchi* (Lescher-Moutoué, 1968). Leg 1 always has 2-segmented rami, legs 2–4 may have 2- or 3-segmented rami, and the setation of the endopodites is more reduced than in *Rheocyclops*.

The species of *Rheocyclops* form a distinct group, in which the fifth leg is more reduced than in *Diacyclops* but less so than in *Graeteriella* and *Speocyclops*. In *Diacyclops*, both segments of the fifth leg are usually present and distinct, although in a few species (reviewed by Reid, 1993a) the proximal segment

may be occasionally fused to the somite. In *Diacyclops*, the medioterminal appendage of leg 5 is spiniform. Two rare and incompletely described European species presently assigned to *Diacyclops*, *D. trajani* Reid and Strayer, 1994 (a nomen novum for *D. minutissimus* sensu Petkovski, 1954) and *D. stygius* sensu stricto (Chappuis, 1924) might upon re-examination bear additional resemblance to *Rheocyclops*.

The habitats of most species of *Rheocyclops* can best be characterized as highly permeable, coarse-grained stream sediments. We suspect that *Rheocyclops* eventually will be found to be rather widespread in karst and aquifers of coarse alluvium as well.

As Wägele *et al.* (1995), among others, have pointed out, the most probable explanation for the presence of closely related interstitial and subterranean faunal elements on both sides of the Atlantic ocean is vicariance via continental drift. *Rheocyclops* is conceivably a North American counterpart to *Graeteriella* and *Speocyclops*, and perhaps became differentiated from an ancestral common stock some time after the continents split. Additional examples of North American cyclopoids apparently related to Eurasian taxa include *Acanthocyclops parasensitivus* Reid, 1998, *Stolonicyclops heggiensis* Reid and Spooner, 1998, and other examples discussed by Reid (1998).

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Addresses: (JWR) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia 20560-0163, U.S.A. (e-mail: reid.janet@nmnh.si.edu); (DLS) Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545-0129, U.S.A.; (JVM) Savannah River Ecology Laboratory, Drawer E, University of Georgia, Aiken South Carolina 29802, U.S.A.; (SES) Box 4718, Mississippi State, Mississippi 39762, U.S.A.; (JLL) 217 W. Carter Avenue, Clarksville, Indiana 47129, U.S.A.

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