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New Records and New Species of the Genus *Diacyclops* (Crustacea; Copepoda) from Subterranean Habitats in Southern Indiana, USA

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ABSTRACT

Ten species of the cyclopoid copepod crustacean genus *Diacyclops* were collected by Julian J. Lewis and his associates from caves, wells, and the hyporheic zone of streambeds in karst and non-karst terrain in southern Indiana, USA. These collections included six previously known species: *D. crassicaudis brachycercus*, *D. jeanneli*, *D. navus*, *D. nearcticus*, *D. sororum*, and *D. yeatmani*. *Diacyclops jeanneli*, which was originally described from Marengo Cave in Crawford County, is redescribed herein. A population of *D. jeanneli* still exists in Marengo Cave, and other populations were discovered in caves in Floyd, Harrison, and Orange counties. All the sites where *D. jeanneli* was collected are located in the Blue River faunal basin, which was never covered by the Illinoian or Wisconsonian glaciers. A new species, *D. conversus*, is described from a gravel bar in the Blue River, also in the Blue River faunal basin. Three new species, *D. salisae*, *D. lewisi*, and *D. indianensis*, are described from wells and a cave in Big Oaks National Wildlife Refuge. The refuge lies within the

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Muscatatuck faunal basin, which was covered by the Illinoian glacier. These three species show few or none of the morphological reductions that are normally associated with the subterranean habitat. They may have invaded subterranean habitats comparatively recently, i.e., after the Illinoian glacier began to retreat about 140,000 years ago. Female cyclopoids that are morphologically identical to *D. indianensis* were recently discovered in two caves in east-central Tennessee; therefore the primary habitat of *D. indianensis* may be groundwater rather than caves. Both *Diacyclops jeanneli* and *D. conversus* show several reductions that are typical of subterranean cyclopoids, and may be more ancient subterranean inhabitants than *D. salisae*, *D. lewisi*, and *D. indianensis*.

INTRODUCTION

For several years, Julian J. Lewis and his associates have collected invertebrates from subterranean habitats in southern Indiana. In this area lie two main karst regions (Fig. 1). The south-central karst region was formed in rocks of Mississippian age. The southern part of this region, including Orange, Washington, Crawford, and Harrison counties where samples were taken for the present report, was not affected by the Illinoian or Wisconsonian glaciers. The southeastern karst region, including much of Jennings and Jefferson counties, was formed in rocks of Ordovician to Devonian age, and was covered by the Illinoian but not the later Wisconsonian glacier. Most of the collections were made in caves, wells, and

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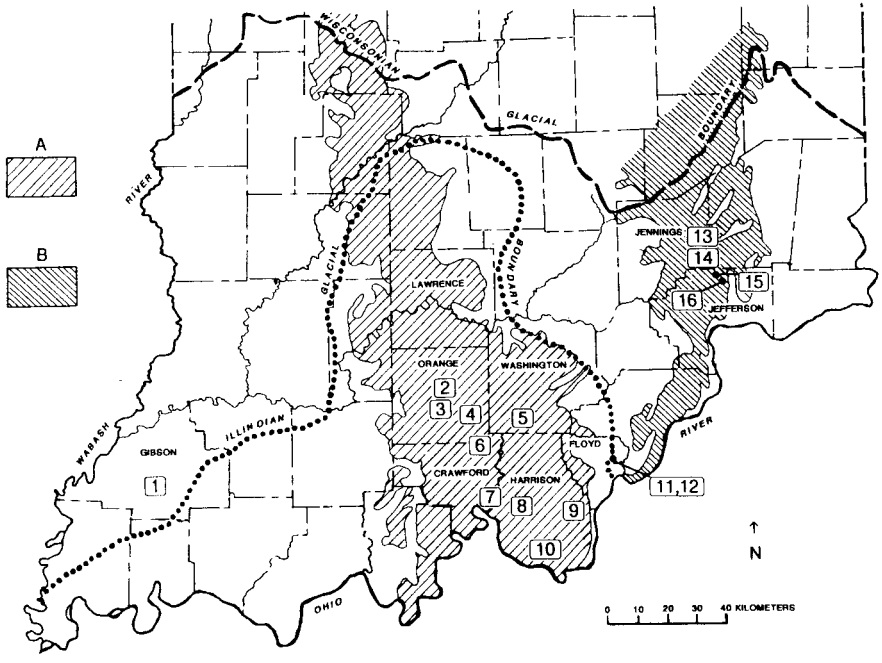
Fig. 1. Map of the southern part of the state of Indiana, USA, showing the collection localities in relation to the karst areas and the southernmost boundaries of the Illinoian and Wisconsonian glaciers (base map redrawn from Powell, 1961). Legend: A, The south-central karst region; B, The southeastern karst region. Localities: 1, Sollman's Well, Gibson County; 2, Murray Spring Cave, Paoli, Orange County; 3, Apple Cave, Orange County; 4, Bond Cave, Orange



County; 5, Fredericksburg Cave, Washington County; 6, Marengo Cave, Crawford County; 7, Old Rothrock Mill site, Blue River, Wyandotte, Crawford County; 8, Devils Graveyard Cave, Harrison County; 9, Hiser Spring Cave, Harrison County; 10, Squire Boone Caverns, Harrison County; 11, old well across Grant Line Road from Indiana University Southeast, New Albany, Floyd County; 12, cistern near intersection of I-265 and Grant Line Road, New Albany, Floyd County (Localities 11 and 12 are across Grant Line Road from each other and about 1 km apart); 13, well in Otter Creek drainage, section 31 SW 1/4, Big Oaks National Wildlife Refuge, Jennings County; 14, well in Graham Creek drainage, section 18, NW 1/4, Big Oaks National Wildlife Refuge, Jennings County; 15, well in Big Creek drainage, section 7 NE 1/4, Big Oaks National Wildlife Refuge, Jefferson County; 16, Henry Dilk Falls cave, Big Creek no. 08, Big Oaks National Wildlife Refuge, Jefferson County.

streambeds within the south-central and southeastern karst regions, and a few were made outside these regions.

Although the south-central karst fauna has been the focus of numerous studies, the only previous reports of copepod crustaceans from there are by Chappuis (1929, 1931). In both these articles, which repeated essentially the same information, Chappuis described a new species of cyclopoid, *Diacyclops jeanneli*, from Marengo Cave in Crawford County. He also described four new species, the cyclopoid *Megacyclops donnaldsoni* and the harpacticoids *Attheyella pilosa*, *Echinocamptus* (now *Bryocamptus*) *morrisoni*, and *Moraria cristata* from Donaldson Cave in Lawrence County. (Chappuis gave the name of this cave as "Donnaldson" in the 1929 article and as "Donnelson's" in the 1931 article.) There are no published reports of copepods from the southeastern karst region [see Lewis (1983) for a review of records of obligate subterranean invertebrates from this region].

The recent collections have yielded, among other copepod taxa, ten species of the cyclopoid genus *Diacyclops*. *Diacyclops* is a large genus whose members inhabit a wide range of surface and subterranean aquatic habitats, from the plankton of large lakes to the interstitial spaces in sandy streambeds or cave pools. Most of the species are known from temperate Eurasia or North America, with a few tropical and austral representatives living in South America, Africa, and Australia. A total of 24 species and subspecies have been reported in North America, mostly from surface-water habitats. The North American species north of Mexico were listed by Williamson & Reid (2001).

Five of the ten species were recorded from Indiana for the first time: *Diacyclops crassicaudis brachycercus* (Kiefer, 1929), *D. navus* (Herrick, 1882), *D. nearcticus* Kiefer, 1931, *D. sororum* Reid, 1992, and *D. yeatmani* Reid, 1988. A population of *D. jeanneli* is still living in Marengo Cave, and this species has also been found in caves in Washington, Harrison, and Orange counties and in a well in Floyd County. *Diacyclops jeanneli* is redescribed, and four new species are described herein. For each species,

detailed locality data for Indiana, and general information on the known habitats and geographical distribution are provided. The relative degrees of morphological adaptation to the subterranean habitat, and the geographical distributions of *D. jeanneli* and the four new species are discussed.

Recently, Julian Lewis sent to me for identification, copepods collected from caves in east-central Tennessee. Two of the samples contained a species of *Diacyclops*, of which the female is morphologically identical to the female of one of the new species from Indiana. These new records are listed herein as well.

MATERIAL AND METHODS

Copepods were collected with plankton nets or baited jars, and were fixed and preserved in 70% ethanol. For taxonomic examination, individual specimens were mounted temporarily in glycerin or lactic acid, or permanently in commercial CMC-10® (Masters Chemical Co., Wood Dale, Illinois) with a little chlorazol black E added to stain the integument. Measurements were made from specimens in glycerin. Total length was measured from the tip of the rostrum to the end of the caudal ramus, excluding the caudal setae. Drawings were made at magnifications of 400x, 600x, or 800x by the use of a Leica DMLB® microscope fitted with a drawing tube. Most of the specimens have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C., or in the Virginia Museum of Natural History (VMNH Accession No. and Crustacea Catalog Database – CrustCatDB No.), Martinsville, Virginia. Specimens which were collected from federally managed lands and are therefore held as loans by the VMNH were not accessioned and received only CrustCatDB numbers. A few specimens are in the collection of Julian Lewis.

Detailed information on the cave localities in Tennessee may be obtained from The Nature Conservancy of Tennessee, 2021 21st Avenue South, Suite C-400, Nashville, Tennessee 37212 (contact Heather Garland, Cave and

Karst Program Manager: hgarland@tnc.org), or from the Tennessee Cave Survey, Inc. (contact Gerald Moni: moni7597@aol.com).

RESULTS: LIST OF SPECIES AND TAXONOMIC DESCRIPTIONS

Diacyclops crassicaudis brachycercus (Kiefer, 1929)

Material examined

One adult female, from Indiana, Harrison County, Hiser Spring Cave, ca. 2 miles (3.6 km) north of Elizabeth, 10 May 1997, collectors J. J. Lewis and A. Pursell. Specimen in collection of J. J. Lewis.

Remarks

Diacyclops crassicaudis brachycercus is most often found in small ephemeral ponds and puddles, but occasionally occurs in groundwater-related habitats, especially in streambed sediments (the hyporheos). Most of the members of the circumboreal *Diacyclops crassicaudis*-complex have been recorded from Europe, but the ranges of two of its members, *D. c. brachycercus* and *D. crassicaudis* (G. O. Sars, 1863) s. str. extend to North America. Although several of the European subspecies are known only from caves, and *D. crassicaudis* s. str. is stygoxenic, *D. c. brachycercus* is seldom found in caves and is considered stygophilic (Pesce & Galassi, 1987). The North American range of *D. c. brachycercus*, as reviewed by Reid (1992), extends from Alaska as far south as Texas. Later records from southern Louisiana (Reid & Marten, 1995); southern Florida (Bruno et al., 2003), and Nova Scotia (Moseley, 1998) have somewhat amplified this distribution. The present record is the first from Indiana. As far as I am aware, this is only the third report of *D. c. brachycercus* from a cave in North America; the subspecies has also been found in caves in Texas (Reddell, 1965) and Nova Scotia (Moseley, 1998).

Diacyclops jeanneli Chappuis, 1929
Figs. 2-6

Synonymy

Cyclops (Diacyclops) Jeanneli Chappuis, 1929: 51-53, Figs. 1, 2.– Kiefer, 1929: 89, 95.– Chappuis, 1931: 348, Figs. 1, 2.– Chappuis, 1933: 11.
Cyclops (Diacyclops) Jeannelli.– Kiefer, 1931: 612.
Cyclops (Diacyclops) jeanneli.– Yeatman, 1944: 1, 5, 8, 58-60, Figs. 112, 113.– Wilson & Yeatman, 1959: 806, Fig. 29.124.
Cyclops jeanneli.– Yeatman, 1943: 29, 30, 32-33.– Pennak, 1953: 398.– Pennak, 1963: 359.– Yeatman, 1964: 98.– Bunting, 1973: 140.– Franke, 1989: 107.– Pennak, 1989: 427.
Acanthocyclops jeanelli.– Damian-Georgescu, 1963: 41.
Diacyclops jeanneli.– Monchenko, 1974: 273, 275.– Reid, 1988: 36.– Williamson, 1991: 810.– Reid & Strayer, 1994: 256, Table 2.– Lewis, 1995: 230, 231, 235.– Monchenko & Vaupel Klein, 1999: 256, Appendix.– Williamson & Reid, 2001: 953, Table III.
Diacyclops jeannelli.– Pesce, 1994: 14.
Non *Diacyclops* nr. *jeanneli*.– Strayer & Reid, 1999: 82, 84, 86, Tables 1, 3.

Material examined

Four adult females (1 dissected on slide), 1 adult male, and 2 copepodid juveniles, from Indiana, Crawford County, Marengo Cave, rimstone pool and mud-bottomed drip pool next to trail in upper level passage, 15 November 1997, collector J. J. Lewis (USNM 243525). Ten adult females, 5 adult males, and 19 copepodid juveniles, from Indiana, Floyd County, New Albany, across Grant Line Road from Indiana University Southeast, old well (21 feet or 6.4 m deep), shrimp-baited jar on bottom of well, 26 April 1995, collector J. J. Lewis (USNM 264239). One adult male, from Indiana, Washington County, Fredericksburg Cave, 1.7 miles (3.06 km) north-

northeast of Fredericksburg, plankton tow of upper-level drip pool, 26 May 1997, collectors J. J. Lewis and T. Sollman (USNM 243548). Forty-one adult females, 9 adult males, and 4 copepodid juveniles, from Indiana, Harrison County, Devils Graveyard Cave, repeated dippings from isolated rimstone pools, 29 March 1998, collectors J. J. Lewis, V. Lewis, and R. Burns (USNM 243663). One adult female, from Indiana, Orange County, Paoli, Paoli Country Club, Murray Spring Cave, upper-level drip pool, 30 April 1998, collectors J. J. Lewis and S. T. Rafail (USNM 243677). Three adult females, 3 adult males, and 7 copepodid juveniles, from Indiana, Orange County, Apple Cave, ca. 2 miles (3.6 km) southwest of Paoli, rimstone pools, upper level, 20 July 2002, collectors J. J. Lewis, S. T. Rafail, and D. Rosenthal (VMNH Accession No. 2002-114, CrustCatDB No. 437).

The following redescription is based on the specimens from the type locality, Marengo Cave (USNM 243525), with a few references to the original description of Chappuis (1929).

Description of Adult Female

Lengths of 4 specimens ranging from 782 to 968 μm (length given by Chappuis, 1929 as 0.9 mm); additional measurements given in Table 1. Body (Fig. 2A) in dorsal view slender, pediger (pedigerous somite) 2 slightly expanded laterally, pedigers 3-5 little expanded and lateral margins rounded, without surface spines. Genital double-somite (Fig. 2A, B) slightly wider than long, tapering posteriorly. Seminal receptacle with wide anterior and posterior expansions and with short wide lateral arms; genital pore large and sclerotized; pore-canal short and sclerotized. Hyaline frills on posterior borders of prosomites and pediger 5 smooth, frills of abdominal somites crenate. Anal somite (Fig. 2C, D) with small spines along most of posterior margin, these spines increasing in size ventrally; anal operculum not sclerotized, only slightly crescentic, its free margin slightly irregular.

Caudal ramus about 3.9 times longer than wide, its surface smooth, lacking spines at bases of lateral and lateralmost terminal setae. Lateral seta inserted at

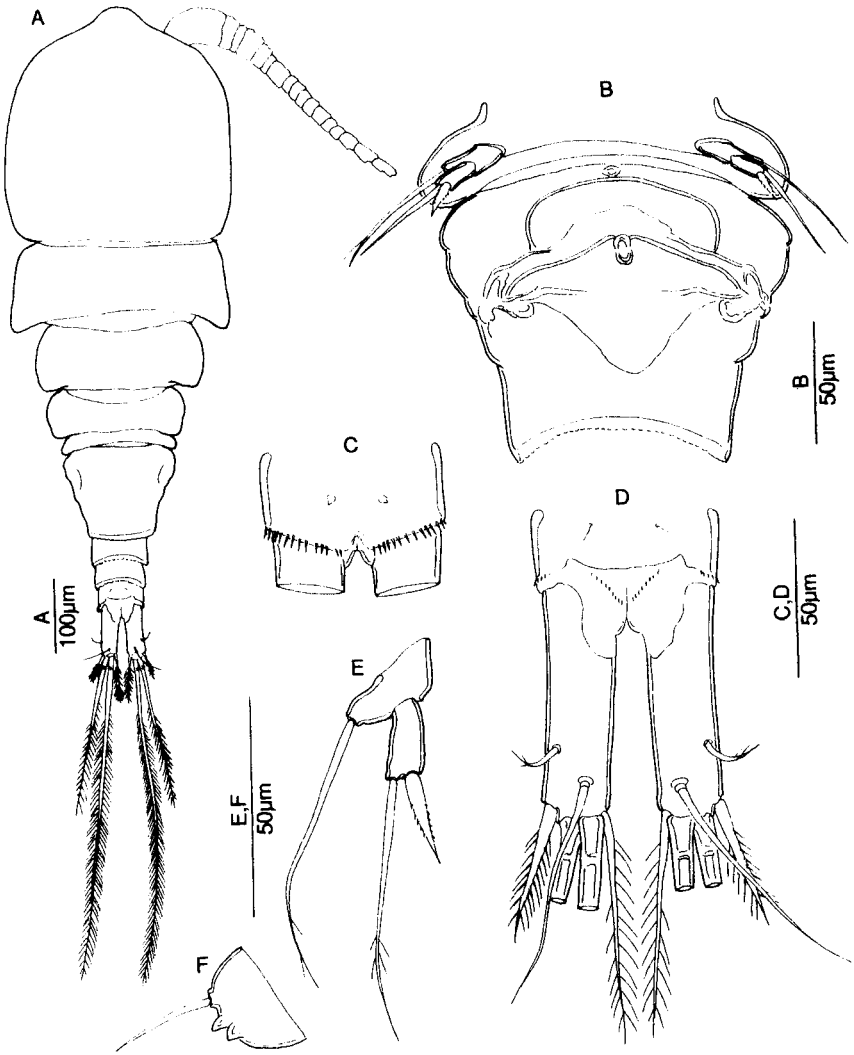


Fig. 2. *Diacyclops jeanneli* Chappuis, female: A, Habitus, dorsal; B, Pediger 5 and genital double-somite, ventral; C, Anal somite and part of caudal rami, ventral; D, Anal somite and caudal rami, dorsal; E, Leg 5; F, Leg 6.

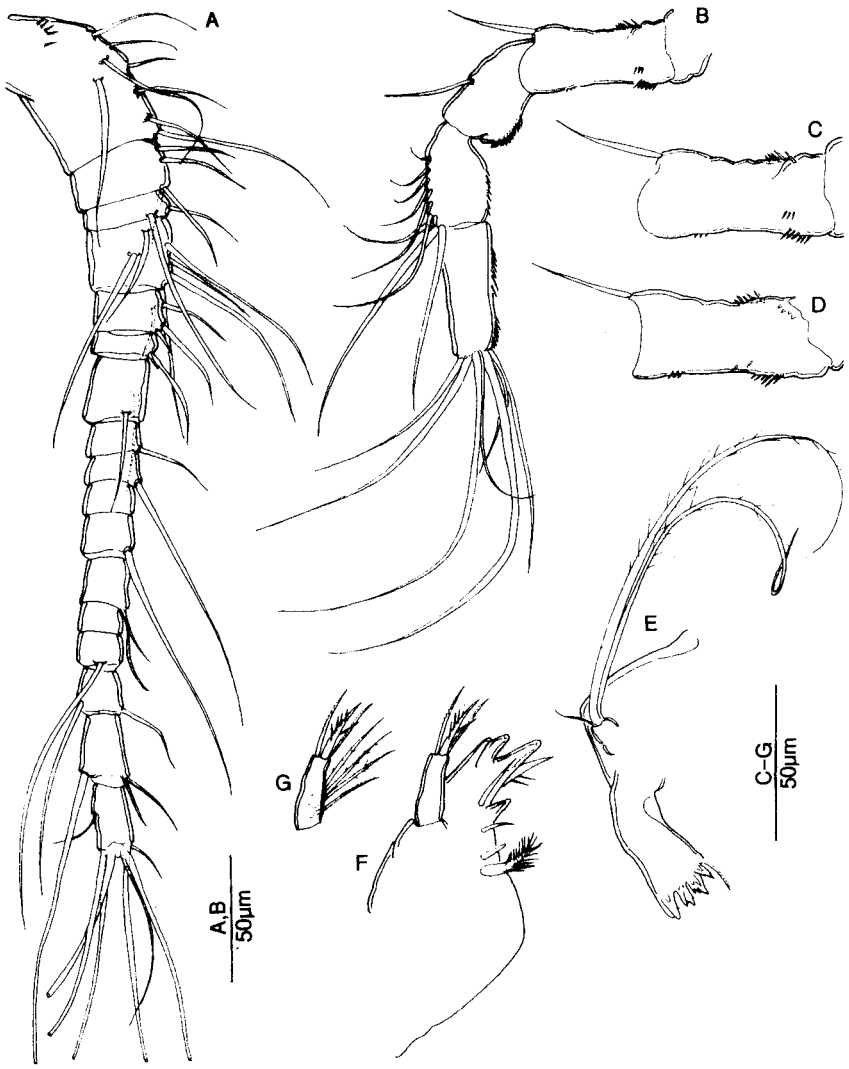


Fig. 3. *Diacyclops jeanneli* Chappuis, female: A, Antennule; B, Antenna, caudal; C, Antennal basipodite, caudal; D, Antennal basipodite, frontal; E, Mandible; F, Maxillule; G, Maxillular palp.

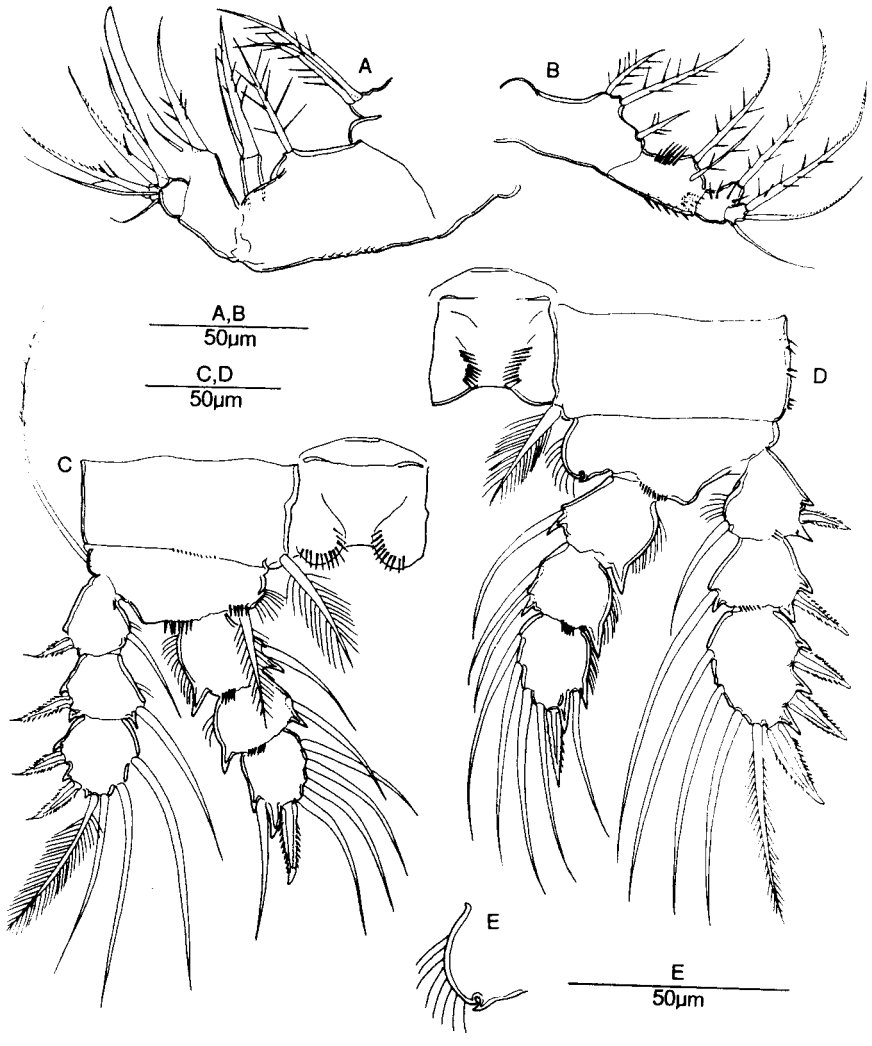


Fig. 4. *Diacyclops jeanneli* Chappuis, female: A, Maxilla; B, Maxilliped; C, Leg 1 and coupler (intercoxal sclerite), frontal; D, Leg 2 and coupler, frontal; E, Leg 2, medial expansion of basipodite (enlarged).

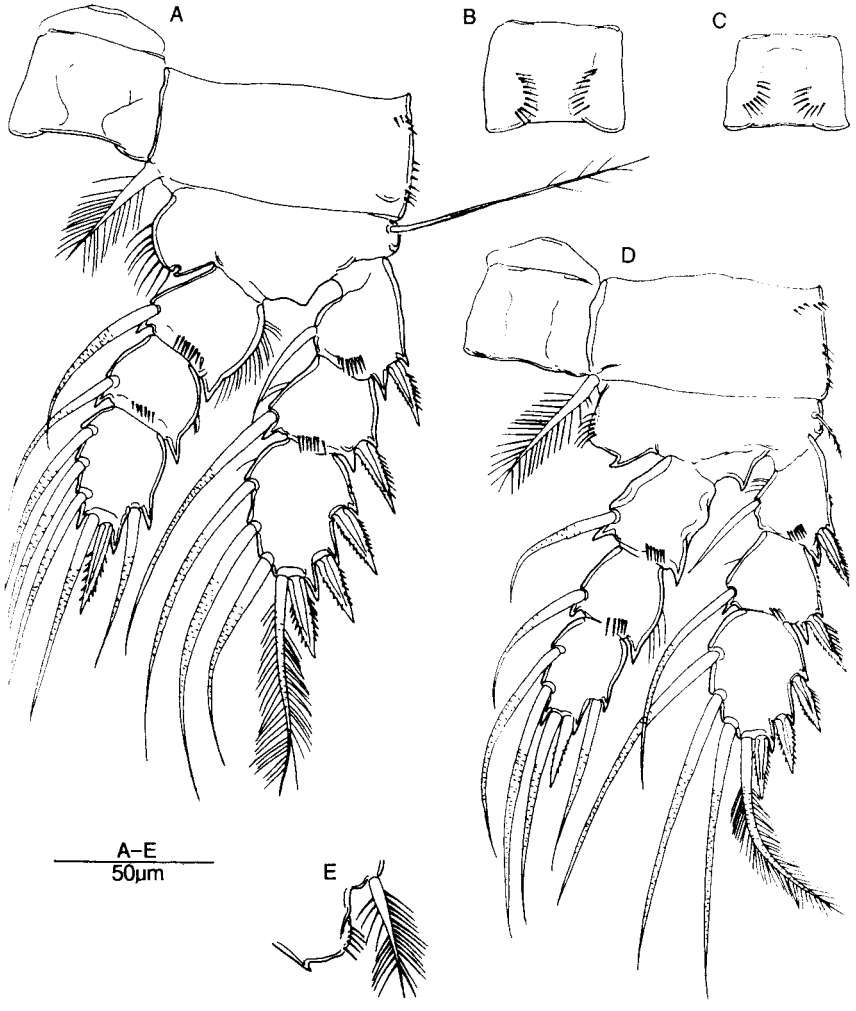


Fig. 5. *Diacyclops jeanneli* Chappuis, female: A, Lĕg 3 and coupler, caudal; B, Leg 3 coupler, frontal; C, Leg 4 coupler, frontal; D, Leg 4 and coupler, caudal; E, Leg 4, medial expansion of basipodite, frontal (enlarged).

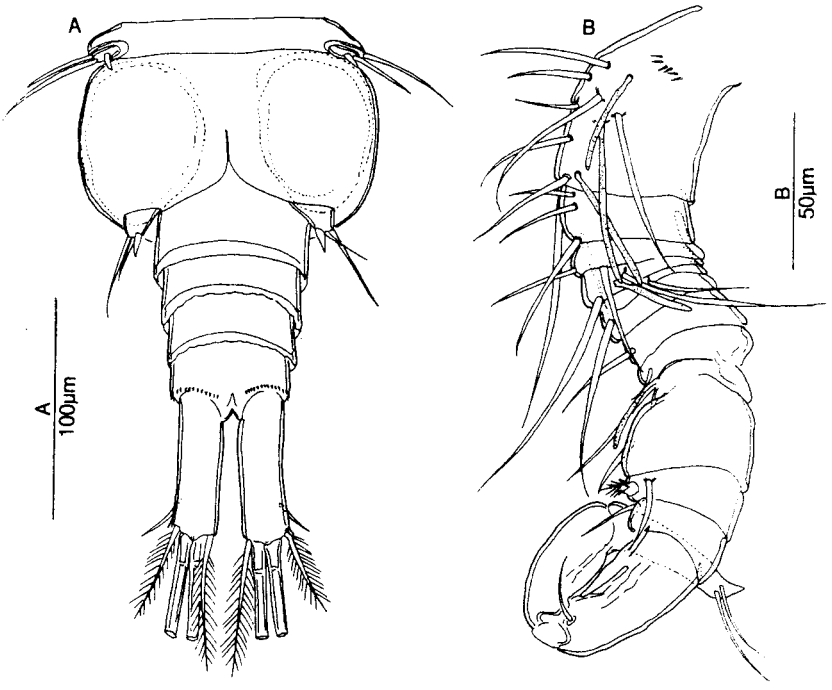


Fig. 6. *Diacyclops jeanneli* Chappuis, male: A, Urosome, ventral; B, Antennule.

Caudal ramus about 3.9 times longer than wide, its surface smooth, lacking spines at bases of lateral and lateralmost terminal setae. Lateral seta inserted at about posterior 3/4 of ramus. Dorsal seta smooth, lateral and terminal setae finely and homogeneously plumed. Lengths of caudal setae given in Table 1.

Antennule (Figs. 2A and 3A) when bent back reaching about middle of pediger 2; composed of 17 segments, bearing elements as follows (Roman numeral = segment, Arabic numeral = number of setae, sp = spine, ae = aesthetasc): I-8 + row of spines, II-4, III-2, IV-6, V-4, VI-1 + sp, VII-2, VIII-1, IX -1, X-0, XI-1, XII-1+ae, XIII-0, XIV-1, XV-2, XVI-2 +ae, XVII-7 + ae. Aesthetasc on segment XII reaching about midlength of segment XV. Segments XVI and XVII without visible hyaline membrane.

Antenna (Fig. 3B-D), basipodite with 1 seta on anterior distal corner and no exopodite-seta on posterior distal corner; endopodite segments 1-3 with 1, 9, and 7 setae respectively. Ornamentation of basis consisting of 2 rows of spines along posterior margin, 1 short row of spines on caudal surface, few spines on frontal surface, 1 row along anterior margin, and 1 transverse row of tiny spines proximally on frontal surface.

Mandible (Fig. 3E) with no surface ornamentation, palp with 1 short and 2 long setae.

Maxillule (Fig. 3F, G) as in figure; palp with no spines on surface.

Maxilla (Fig. 4A), claw with no teeth along inner margin.

Maxilliped (Fig. 4B), segments 1-4 with 3, 2, 1, and 3 setae respectively; segments 2 and 3 also ornamented with surface spines.

Swimming legs 1-4 (Figs. 4C-E and 5) all with 3-segmented rami. Exopodite segments 1 and 2 and endopodite segment 1 each with 1 medial seta. Endopodite segment 2 of legs 1-4 with 1,2,1,1 setae respectively. Exopodite terminal segments with 2,3,3,3 spines and 4,4,4,4 setae respectively. Couplers (intercoxal sclerites) of all legs with paired rounded protrusions on free margins, protrusions of legs 3 and 4 shallow. Each coupler ornamented with 2 rows of spines on frontal surface, its caudal surface bare. Seta present on distomedial corner of each coxopodite, plumage of seta of leg 4 slightly stouter than plumage of remaining setae. Leg 1 basipodite distomedial corner bearing long spiniform seta that reaches nearly to end of endopodite segment 2. Medial expansions of all basipodites with slender hairlike setules ("hairs"), hairs on basipodites of legs 3 and 4 thicker and stiffer than hairs of legs 1 and 2; medial expansions of legs 1 and 4 with shallow groove, medial expansions of legs 2 and 3 with small but deep round notch. Coxa of leg 4 ornamented with only few rows or groups of spines on caudal and lateral surfaces. Spines on exopodite of leg 1 with slender hairlike tips. Leg 4 endopodite segment 1 with medial and lateral margins sculptured. Leg 4 endopodite segment 3 about 1.4 times longer than wide, and bearing 2 medial, 1 terminal, and 1 lateral setae and 1 terminal spine; all setae extending far past end of terminal spine. Terminal spine short, about 0.7 times length of segment.

Leg 5 (Fig. 2E), segment 1 with long lateral expansion bearing seta; segment 2 about 2.2 times longer than wide, bearing long terminal seta and slender serrate subterminal spine, this spine slightly longer than segment.

Leg 6 (Fig. 2F) consisting of small plate located slightly dorsally on genital double-somite, without surface ornamentation and with 1 tiny seta and 2 short stout spines on its free margin.

Description of Adult Male

Body length of single specimen from Marengo Cave, 600 μm. Habitus similar to that of adult female except for usual sexual dimorphisms including the unfused genital somite and the geniculate antennules.

Genital somite (Fig. 6A) markedly swollen, as wide as pediger 5.

Caudal ramus (Fig. 6A) as in female except about 3.6 times longer than wide, and with tiny spines at base of lateralmost terminal seta. Lengths of caudal setae given in Table 1.

Antennule (Fig. 6B) geniculate, composed of 16 segments. Segment 1 with 3, and segments 4 and 9 each with 1 aesthetasc. Aesthetascs slender.

Leg 6 (Fig. 5A) consisting of small smooth plate bearing 1 medial spine and 2 setae on its margin, of which the spine is the shortest element.

Ethanol-preserved specimens colorless, transparent.

Remarks

Chappuis (1929) described *Diacyclops jeanneli* from specimens collected in Marengo Cave by R. Jeannel. As was customary at that time, Chappuis provided a partial written description of the new species, and illustrated only the fifth leg and the terminal segment of the leg 4 endopodite of the female. In a later article, Chappuis (1931) repeated his earlier description and figures without changes. In the collections of the Emil Racovitza Speleological Institute in Cluj, Romania, where Chappuis was a member of the staff at the time of writing those articles, there are two slide preparations labelled "*Diacyclops jeanneli*, female, Marengo." Each contains an undissected specimen, which may have been mounted in glycerol; both are in very poor condition, dry and full of dust (S. Iepure, pers. comm., 2003). Two prepared slides of "*Cyclops jeanneli*" are listed in the catalog of the Kiefer Collection held at the Staatliches Museum für Naturkunde in

Karlsruhe, Germany (Franke, 1989); the locality is given as "Marengo-Höhle, USA", but the date and collector are not listed, and the slides are not labeled as types. Although it is possible that some or all of the older specimens were used by Chappuis to prepare his description, the poor condition of the specimens in Cluj and the incomplete label information makes it difficult to be certain. Therefore, the redescription presented here was done entirely from the recently collected material. No type material is designated at this time.

The rimstone pool and mud-bottomed drip pool where Julian Lewis made the recent collections are located in the upper-level passage, the same passage as the "Crystal Palace" where the original collection of *D. jeanneli* was made. In this section of the cave there is no stream, and water enters only through seepage and drip input (J. J. Lewis, pers. comm., 2002).

These specimens coincide closely with most of Chappuis' (1929) description. There are slight differences in the proportions of the caudal ramus, which Chappuis gave as 3.5 times longer than wide, and the leg 4 endopodite segment 3, which Chappuis gave as 1.5 times longer than wide.

Diacyclops jeanneli is easily distinguished from most of its North American congeners by having a terminal spine and seta rather than 2 terminal spines on leg 4 endopodite segment 3. *Diacyclops jeanneli putei* (Yeatman, 1943), known from a well in North Carolina, shares this character of terminal spine and seta on leg 4, but has the antennule composed of only 11 segments in the female. A morph from Alabama reported as "*Diacyclops* nr. *jeanneli*" by Strayer & Reid (1999) from Alabama also shares this character, but has the female antennule composed of 16 segments. All the Indiana populations of *D. jeanneli* have the female antennule of 17 segments, and therefore the Alabama population cannot be ascribed to this taxon.

Diacyclops jeanneli shows several of the most typical features of cyclopoids that live in subterranean habitats (see Reid & Strayer, 1994; Monchenko & Vaupel Klein, 1999). These features include the lack of the large antennal exopodite-seta, as well as the lack of one of the two setae that

are usually present on the anterodistal corner of the antennal basipodite. The genital double-somite of the female and the genital somite of the male are relatively large. Other unusual morphological features of this species, which may or may not be related to its subterranean existence, include the lack of teeth on the maxillar claw, the presence of ornamentation on the frontal rather than the caudal surfaces of all of the couplers of the swimming legs, the small but deep notches in the medial expansions of the basipodites of legs 2 and 3, and the modified stiff hairs on the basipodites of legs 3 and 4.

Following its description, *D. jeanneli* was included in various checklists and keys, but was not actually found again until these recent collections. A population is still present in the type locality, Marengo Cave in Crawford County. Other populations were discovered in several caves in Harrison, Orange, and Washington counties, and in an old well in Floyd County. The populations in all of the caves were found in rimstone pools and drip pools, isolated from streams. According to Chappuis (1929), Jeannel collected by sampling the "rassemblements" of water with a fine net; the term "rassemblements" may refer to these pools. As suggested by J. J. Lewis (pers. comm., 2003), its distribution within the caves suggests that its true habitat is within the epikarst, from which it enters caves through drip water. *Diacyclops jeanneli* has never been found in a cave stream.

Diacyclops navus (Herrick, 1882)

Material examined

One adult female and 1 copepodid juvenile, from Indiana, Floyd County, New Albany, cistern near intersection of highway I-265 and Grant Line Road, jar placed on bottom of cistern for 24 hours baited with fresh uncooked shrimp, 27 April 1996, collector J. J. Lewis (USNM 278140). One adult female and 1 copepodid juvenile, from Indiana, Gibson County, Sollman residence located 5.6 km east of Fort Branch, hand-dug brick-lined

well dug in 1929 into glacier lake bed sediment, with grayish sand at bottom, depth 6 m (no date), shrimp-baited jar, collector T. Sollman. Specimen in collection of J. J. Lewis.

Remarks

Diacyclops navus occurs from southern Alaska to Louisiana (Reid, Hare, & Nasci, 1989). It is primarily an epigean species, usually found in temporary ponds or pools which hold water for brief to extended periods, and in shallow wells; it may also occur in water-filled artificial containers, such as discarded tires (Reid, Hare, & Nasci, 1989; Reid & Marten, 1995). These are the first records from Indiana.

Diacyclops nearcticus Kiefer, 1931

Material examined

Two adult females, 5 adult males, and 2 copepodid juveniles, from Indiana, Orange County, Bond Cave, 0.5 mile (0.9 km) south of Chambersburg, 30 March 2002, collectors J. J. Lewis and R. Burns (VMNH Accession No. 202-114, CrustCatDB No. 438). One adult female and 2 copepodid juveniles, from Indiana, Crawford County, Wyandotte, Blue River, gravel bar at old Rothrock Mill site, Bou-Rouch pump inserted into bar to a depth of about 1 m, 9 July 2000, collector J. J. Lewis (USNM 252724).

Remarks

Diacyclops nearcticus was described by Kiefer (1931) from a pond in Massachusetts, and later redescribed by Reid (1992) from the single type specimen. Bruno, Reid, & Perry (2000) described the male, and reviewed confirmed records of *D. nearcticus* that were made after Reid's (1992) revision of the *nearcticus*-group. The known range of *D. nearcticus* includes

the eastern and central USA, from Massachusetts and the Laurentian Great Lakes to Florida and Alabama. The present records are the first from Indiana.

Members of the *nearcticus*-group appear to be common and widespread in the hyporheos of streams (Strayer & Reid, 1999). In the Everglades, *D. nearcticus* was found in driven wells in seasonally dry karstic terrain (Bruno, Reid, & Perry, 2000). The Blue River gravel bar is typical of the usual habitat of *D. nearcticus*. The record from Orange County is the first from a cave.

Diacyclops sororum Reid, 1992

Material examined

One adult female, 1 adult male, and 1 copepodid juvenile, from Indiana, Crawford County, Wyandotte, Blue River, gravel bar at old Rothrock Mill site, from shallow "well" consisting of a piece of perforated PVC pipe buried to a depth of about 35 cm in the bar, 24 August 1997, collectors J. J. Lewis and A. Pursell (USNM 260740). Three adult females and 2 adult males, from Indiana, Harrison County, Squire Boone Caverns, ca. 12 miles (21.5 km) south of Corydon, from shallow pools in upper level of cave, water dipped and strained through plankton net, 26 June 1999, collectors J. J. Lewis and S. T. Rafail (USNM 252813).

Remarks

Diacyclops sororum is a member of the *nearcticus*-group, which is distinguished by the possession of a stout spiniform seta, rather than the long slender setiform seta that is usual in cyclopoids, on the lateral margin of leg 4 endopodite segment 3. This species was described from the sandy sediments of the hyporheic zone of Goose Creek, in the Piedmont of northeastern Virginia (Reid, 1992). Strayer & Reid (1999) reported it from

streams in south-central Kentucky, western Virginia, and northern Florida. The present records are the first in Indiana and the first from a cave, and extend its distribution somewhat westward. Strayer & Reid (1999) included this among the so-called "southern" species, i.e., those which in their study had not been found north of the glacial border.

Diacyclops yeatmani Reid, 1988

Synonymy

Cyclops (*Diacyclops*) *clandestinus* Yeatman, 1964: 95-98, Figs. 1-23.
Diacyclops clandestinus Yeatman.– Dussart & Defaye, 1985: 95.
Cyclops clandestinus Yeatman.– Pennak, 1989: 427.
Diacyclops yeatmani, nomen novum, Reid, 1988: 31, 36.– Reid & Strayer, 1994: 256, Table 2.– Monchenko & Vaupel Klein, 1999: 259, appendix table (I).– Williamson & Reid, 2001: 953, Table III.
Diacyclops yetmani Reid.– Pesce, 1994: 14 (lapsus).
Non *Cyclops* (now *Diacyclops*) *languidoides clandestinus* Kiefer, 1926: 276, Figs. 5-7.
Non *Diacyclops* nr. *yeatmani* Reid.– Strayer & Reid, 1999: 82, 84, 86, Tables 1, 3.

Material examined

One adult female and 1 adult male, from Indiana, Crawford County, Wyandotte, Blue River, gravel bar at old Rothrock Mill site, Bou-Rouch pump at about 1 m depth in bar, 27 August 1998, collector J. J. Lewis (USNM 288049).

Remarks

The name *Diacyclops yeatmani* was proposed by Reid (1988) as a nomen novum for *Diacyclops clandestinus* Yeatman, 1964, because Yeatman's name was preoccupied by *D. languidoides clandestinus* (Kiefer,

1926). Because of this change in name, the complete synonymy of *D. yeatmani* is provided.

The original description of Yeatman (1964) was based on several specimens from Bigmouth Cave in Grundy County, Tennessee, and other specimens collected from a drainage tile emptying into a creek near Fairmont, Vermillion County, Illinois. These two populations were so similar morphologically that Yeatman (1964) included them in the same taxon, although he considered the Illinois copepods as a "variant." The Indiana female specimen closely resembles Yeatman's description of the specimens from Illinois, in particular the proportions of the caudal ramus and leg 4.

Strayer & Reid (1999) reported "*Diacyclops* nr. *yeatmani*" from northern Alabama, but the material which they examined differed in several minor respects from both of the populations described by Yeatman. It is likely that there exists a complex of cryptic species with only minor morphological differences.

Diacyclops salisae, new species

Figs. 7-10

Material examined

Holotype, adult female; allotype, adult male; paratypes, 1 adult male and 1 copepodid juvenile, all from Indiana, Jennings County, Big Oaks National Wildlife Refuge, well in Otter Creek drainage, section 31, southwest 1/4, shrimp-baited jars, 2-3 February 2001, collectors J. J. Lewis and S. T. Rafail (VMNH CrustCatDB No. 346).

Description of Adult Female

Body length of holotype 1410 µm. Body (Fig. 7A) slender; in dorsal view pedigers 2 and 3 laterally expanded, pediger 4 rounded, pediger 5 laterally produced and ending in small papilla. Genital double-somite (Fig. 7A, B) slightly longer than wide, tapering posteriorly. Seminal receptacle indistinct, rounded

anteriorly and appearing little expanded posteriorly, with short wide lateral arms; genital pore small, sclerotized, pore-canal not visible in this specimen. Hyaline frills of all somites smooth. Anal somite (Fig. 7C, D) with small spines along most of posterior margin; anal operculum not sclerotized, little produced, with irregular free margin.

Caudal ramus 133 μm long and 28 μm wide, thus 4.75 times longer than wide; lateral surface without ornamentation except for several tiny spines at insertion of outermost terminal seta; medial surface with 3 small transverse rows or groups of tiny spines. Lateral seta inserted at about posterior 3/4 of ramus. Dorsal seta smooth, lateral and terminal setae finely and homogeneously plumed. Lengths of dorsal, lateral, and medialmost to lateralmost terminal setae 110, 47, 122, 610, 420, and 75 μm respectively.

Antennule (Figs. 7A and 8A) when bent back reaching approximately to middle of pediger 2; composed of 17 segments, with following armature: I-8 + row of spines, II-4, III-2, IV-6, V-4, VI-1 + sp, VII-2, VIII-1, IX -1, X-0, XI-1, XII - 1+ae, XIII-0, XIV-1, XV-2, XVI-2 +ae, XVII-7 + ae. Aesthetasc on segment XII reaching about midlength of segment XV. Segments XVI and XVII without visible hyaline membrane.

Antenna (Fig. 8B, C), basipodite with 2 setae on anterior distal corner and exopodite-seta on posterior distal corner; endopodite segments 1-3 with 1, 9, and 7 setae respectively. Ornamentation of basis consisting of 2 rows of spines along posterior margin, 2 short rows of 4 spines on caudal surface, and 1 row of 5 spines on frontal surface, in addition to 2 transverse rows of tiny spines proximally on frontal surface.

Mandible (Fig. 8D), without surface ornamentation, palp with 1 short and 2 long setae.

Maxillule (Fig. 8E) as in figure; palp with no spines on surface.

Maxilla (Fig. 8F), claw with numerous large teeth along its midlength.

Maxilliped (Fig. 8G), segments 1-4 with 3, 2, 1, and 3 setae respectively; segments 2 and 3 ornamented with surface spines.

Swimming legs 1-4 (Fig. 9) all with 3-segmented rami. (Leg 3 not illustrated; exactly like leg 2 except slightly larger.) Exopodite segments 1 and 2 and endopodite segment 1 each with 1 medial seta, endopodite segments 2 with 2 medial setae; exopodite terminal segments with 3,4,4,4 spines and 4,4,4,4 setae

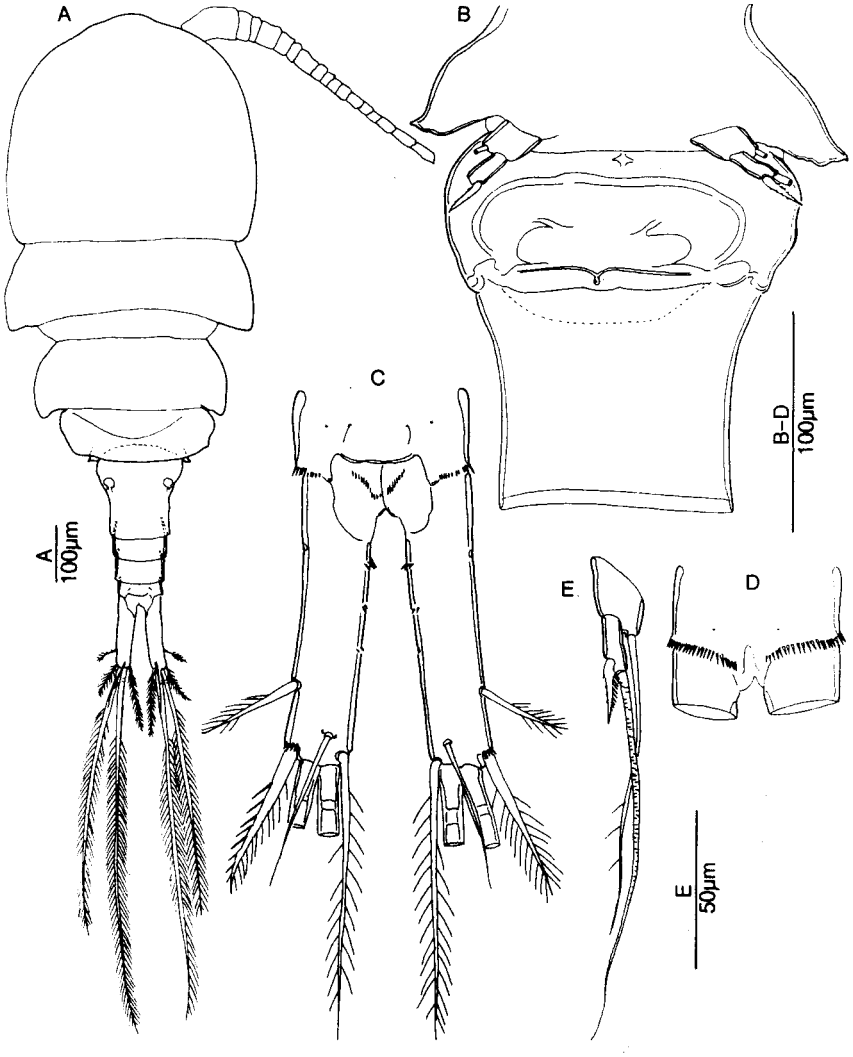


Fig. 7. *Diacyclops salisae*, new species, female: A, Habitus, dorsal; B, Pediger 5 and genital double-somite, ventral; C, Anal somite and caudal rami, dorsal; D, Anal somite and part of caudal rami, ventral; E, Leg 5.

respectively. Couplers of all legs with paired rounded protrusions on free margins, protrusions of leg 4 coupler shallower. Coupler of leg 1 bare, couplers of legs 2 and 3 each ornamented with 2 vertical rows of long spines on its frontal surface, and coupler of leg 4 with transverse row of tiny spines on its caudal surface. Leg 1 basipodite, distomedial corner with long spiniform seta that reaches past end of endopodite segment 2. Expanded medial margins of all basipodites ornamented with fine hairs, and margin of leg 4 basipodite with double spiniform tip. Coxa of leg 4 ornamented with several rows of spines on caudal and lateral surfaces. Spines on exopodite of leg 1 with slender hairlike tips. Leg 4 endopodite segment 1 with grooved lateral margin. Leg 4 endopodite segment 3, 85 μm long and 30 μm wide, thus about 2.8 times longer than wide, and bearing 2 medial setae, 2 terminal spines, and 1 lateral seta; setae extending slightly past ends of terminal spines. Medial terminal spine 55 μm long, thus only about 1.1 times longer than lateral terminal spine (50 μm long). Medial terminal spine directed medially at an angle from lateral terminal spine.

Leg 5 (Fig. 7B, E), segment 1 with short lateral expansion bearing relatively long seta; segment 2 about 2.6 times longer than wide, bearing long terminal seta and slender serrate subterminal spine, this spine slightly longer than segment.

Plate of leg 6 (not illustrated) located slightly dorsally on genital double-somite. Plate without surface ornament, and with 1 tiny seta and 2 short spines on its margin.

Description of Adult Male

Body length of allotype specimen 1300 μm, length of paratype specimen 1000 μm. Habitus similar to that of female except for usual sexual dimorphisms. Both allotype and single male paratype overgrown with bacteria; as far as can be seen, general structure and fine details of appendages as in female, except in the following respects.

Genital somite (Fig. 10A) not markedly swollen, slightly narrower than pediger 5.

Caudal ramus (not illustrated) as in female except with tiny spine at base of lateral seta; medial surface overgrown, ornamentation, if present, not visible. Caudal ramus of allotype 103 μm long and 21 μm wide, thus 4.9 times longer than wide; ramus of paratype 90 μm long and 22 μm wide, thus 4.1 times longer

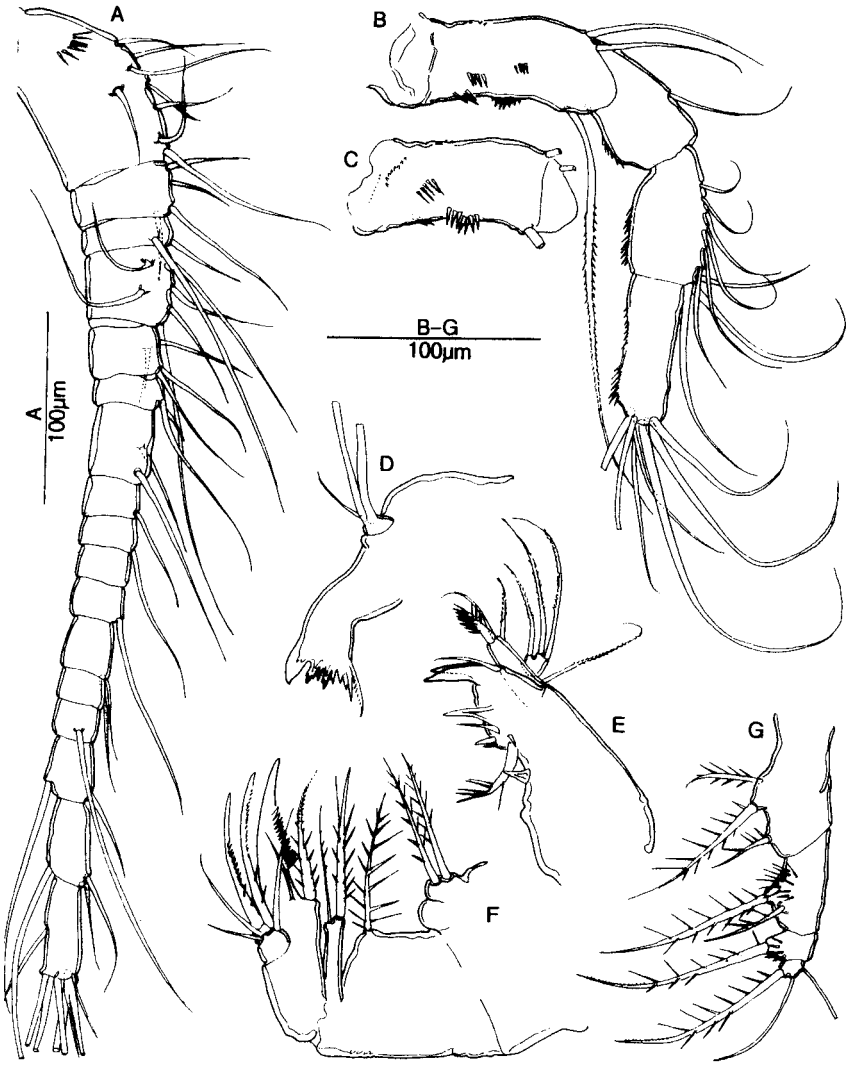


Fig. 8. *Diacyclops salisae*, new species, female: A, Antennule; B, Antenna, caudal; C, Antennal basipodite, frontal; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped.

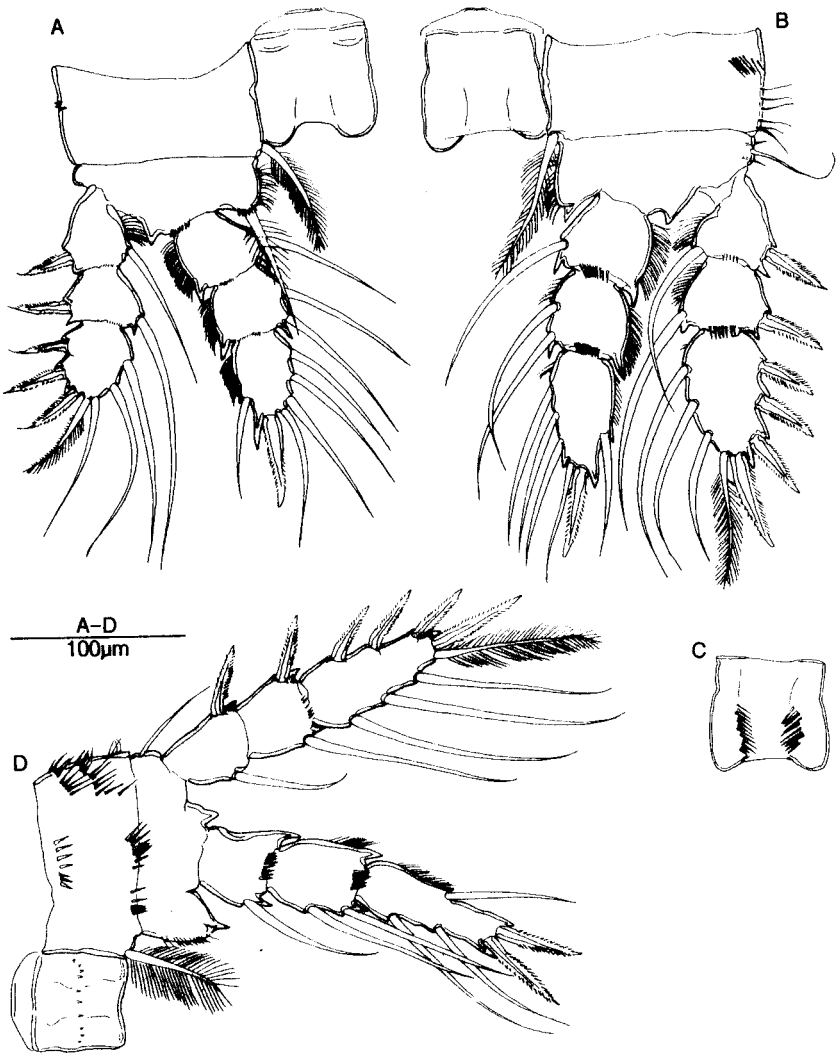


Fig. 9. *Diacyclops salisae*, new species, female: A, Leg 1 and coupler, frontal; B, Leg 2 and coupler, caudal; C, Leg 2 coupler, frontal; D, Leg 4 and coupler, caudal.

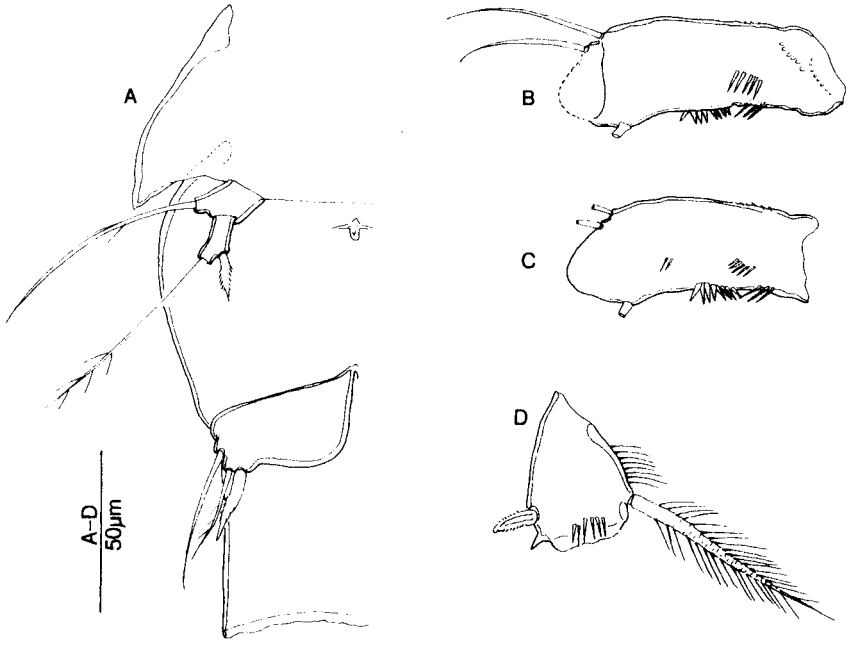


Fig. 10. *Diacyclops salisae*, new species, male: A, Pediger 5 and genital and succeeding somites, ventral; B, Antennal basipodite, frontal; C, Antennal basipodite, caudal; D, Leg 2 exopodite segment 1.

than wide. Lengths of dorsal, lateral, and medialmost to lateralmost terminal setae, respectively, of allotype 80, 33, 117, 520, 330, and 62 µm; of paratype 90, 38, 113, 662, 315, and 61 µm.

Antennule (not illustrated) geniculate, composed of 16 segments. Segment 1 with 3 aesthetascs and segments 4, 9, and 12 each with 1 aesthetasc. All aesthetascs short and slender.

Antennal basipodite (Fig. 10B, C), general pattern of spine rows similar to that of female.

Couplers of legs 1-4 ornamented as in female, except leg 4 coupler with 2 vertical rows of long spines. Leg 2 exopodite segment 1 (Fig. 10D), lateral spine stout and with blunt tip as in female, but differs in curving slightly caudad. Leg 4 endopodite segment 3 slightly stouter than in female, about 2.4 times longer than wide; medial terminal spine relatively longer (1.2 times) in proportion to lateral terminal spine.

Leg 6 (Fig. 10A) consisting of smooth subrectangular plate bearing 1 serrated spine and 2 setae on its margin, of which spine is shortest element.

Ethanol-preserved specimens colorless, transparent.

Type Locality

Well in Otter Creek drainage, section 31, Big Oaks National Wildlife Refuge, Jennings County, Indiana.

Name

The species name honors Ms. Salisa Taylor Rafail, for her indefatigable efforts and invaluable help to Julian Lewis in collecting subterranean invertebrates.

Remarks

The major morphological features of *Diacyclops salisae* include the 17-segmented antennule; the uniformly 3-segmented rami of the swimming legs; the spine formula 3,4,4,4; and on the leg 4 endopodite, the 2 terminal spines and lack of modifications of the setae. Minor features which are also customarily used to distinguish species of cyclopids include the distinctive ornamentation pattern of the couplers of legs 2-4 and the caudal rami.

No other member of the genus combines all these attributes. The relatively few *Diacyclops* species in North America which have spines or hairs on the caudal ramus are the four members of the *uruguayensis*-group, all of which have legs 1-4 with spine formula 2,3,3,3 (Fiers, Ghenne, &

Suárez-Morales, 2000); and some members of the *nearcticus*-group, all of which have a spine rather than a seta on the lateral margin of leg 4 endopodite segment 3 (Reid, 1992). Some populations of *D. thomasi* (S. A. Forbes, 1882) may also have stiff hairs on the caudal ramus, but these are long and fine, not short, and *D. thomasi* has legs 1-4 with spine formula 2,3,3,3, among other differences from *D. salisae*.

On the other hand, the combination of characters present in *D. salisae* raises once again the old question of the distinction of the genus *Diacyclops* Kiefer, 1927 from the genus *Acanthocyclops* Kiefer, 1927. Both genera are widely distributed and include many species that show a wide range of morphological features. Because of this wide range of variation, the only character which effectively separates the genera is the relative length of the subterminal spine of leg 5: in *Diacyclops*, this spine is "long", which in practice is usually taken to be as long as, or longer than the terminal segment, and relatively wide; while in *Acanthocyclops* it is "short", i.e., usually half or less the length of the terminal segment, and much narrower than the width of the segment (compare illustrations of members of *Acanthocyclops* given by Einsle, 1996). S. Dodson (pers. comm., 2003) has found one individual belonging to the *Acanthocyclops vernalis-robustus* group with one leg 5 typical of *Acanthocyclops* and the other typical of *Diacyclops*. However, usually the structure of leg 5 is conservative, and because of this conservatism it has been traditionally used as the fundamental character distinguishing cyclopid genera. The long subterminal spine of *D. salisae* is clearly typical of members of *Diacyclops*.

Certain other characters of *D. salisae* resemble those of the *Acanthocyclops vernalis-robustus* group, which in North and Central America and the Antilles includes several named and unnamed morphs, in a largely still-unresolved species-complex (Dodson, 1994; Reid & Suárez-Morales, 1999; Fiers, Ghenne, & Suárez-Morales, 2000; Dodson et al., 2003). This group is characterized by a 17-segmented antennule which lacks a hyaline membrane on its terminal segments, swimming legs 1-4 with 3-

segmented rami and base spine formula 3,4,4,4 (except for variations in some taxa), the leg 4 endopodite segment 1 with a distinct notch on the lateral margin (in most taxa), and the seminal receptacle little expanded posteriorly. *Diacyclops salisae* shares all these characters. Nevertheless it differs from all the members of the *vernalis-robustus* group in the combination of minor features, in particular the lack of modified setae on legs 1-4, and the pattern of spine ornamentation on the couplers of legs 1-4 and the caudal ramus. Even though the genus attribution of these specimens may be arguable, they clearly represent a previously undescribed taxon.

Most of the morphological features of *D. salisae* are typical of benthic epigean cyclopids: the relatively large body size and slender body shape, the long caudal rami and caudal setae, and the lack of any oligomerization or loss of the normal complement of setae and spines on the appendages. In particular, the large antennal exopodite-seta is present. These animals likely live primarily in the more open groundwater subhabitats, such as the well where they were found.

Diacyclops lewisi, new species
Figs. 11-15

Material examined

Holotype, adult female; allotype, adult male; each dissected on 1 slide; paratypes: 18 adult females, 3 adult males, and 27 copepodid juveniles, all from Indiana, Jennings County, Big Oaks National Wildlife Refuge, well in Graham Creek drainage section 18, northwest 1/4, shrimp-baited jars, 2-3 February 2001, collectors J. J. Lewis and S. T. Rafail (VMNH CrustCatDB No. 348). Additional paratypes: 1 adult male and 3 copepodid juveniles, all from Indiana, Jefferson County, Big Oaks National Wildlife Refuge, Big Creek drainage section 7, northeast 1/4, well, shrimp-baited jars, 2-3 February 2001, collectors J. J. Lewis and S. T. Rafail (VMNH CrustCatDB No. 347).

Description of Adult Female

Body length of holotype 1320 μm; certain other measurements given in Table 2. Body (Fig. 11A) slender, in dorsal view pedigers 2 and 3 laterally expanded, pediger 4 rounded, pediger 5 slightly produced laterally. Genital double-somite (Fig. 11A, B) about as long as wide, tapering posteriorly. Seminal receptacle little expanded anteriorly and much expanded posteriorly, with wide lateral arms; pore-canal short and prominently sclerotized. Hyaline frills of prosomites smooth, frills of urosomites crenulate. Anal somite (Fig. 11C, D) with small spines along ventral part of posterior margin only; anal operculum not sclerotized, little produced, its free margin irregular.

Caudal ramus 4.8 times longer than wide, medial and lateral surfaces without ornamentation. Lateral seta inserted at approximately posterior 2/3 of ramus. Dorsal seta smooth, lateral and terminal setae finely and homogeneously plumed. Lengths of caudal setae given in Table 2.

Antennule (Figs. 11A and 12A) when bent back reaching middle of pediger 2; composed of 17 segments, with the following elements: I-8 + row of spines, II-4, III-2, IV-6, V-3, VI-1 + sp, VII-2, VIII-1, IX -1, X-0, XI-1, XII -1+ae, XIII-0, XIV-1, XV-2, XVI-3, XVII-7 + ae. Aesthetasc on segment XIII reaching about end of segment XIV. Narrow, finely serrated hyaline membrane present on segments XVI and XVII.

Antenna (Fig. 12B-D), basipodite with 2 setae on anterior distal corner and exopodite-seta present on posterior distal corner; endopodite segments 1-3 with 1, 9, and 7 setae respectively. Basis with several spines along posterior margin, 3 short rows of 4 or 6 spines on caudal surface, and row of 7 spines on frontal surface.

Mandible (Fig. 12E), surface without ornamentation, palp with 1 short and 2 long setae.

Maxillule (Fig. 13A) as in figure, palp without spines on surface.

Maxilla (Fig. 13B), claw with numerous fine teeth along its middle third.

Maxilliped (Fig. 13C), segments 1-4 with 3, 2, 1, and 3 setae respectively, segment 2 also with several groups of spines.

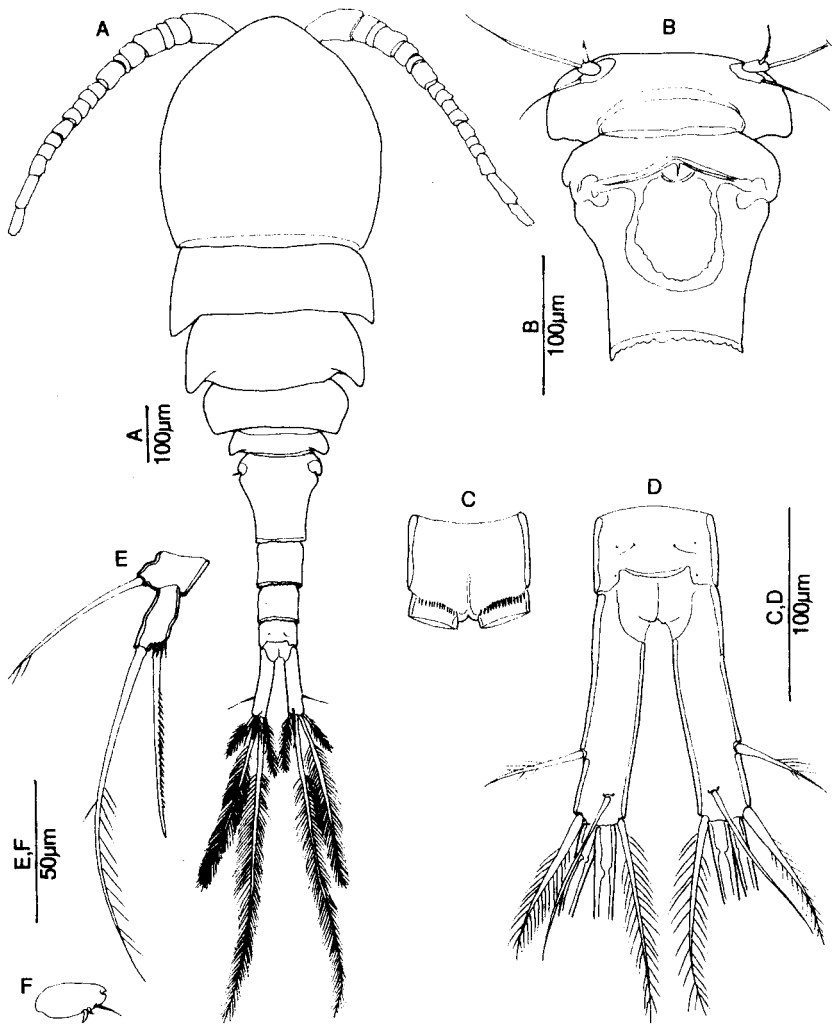


Fig. 11. *Diacyclops lewisi*, new species, female: A, Habitus; B, Pediger 5 and genital double-somite, ventral; C, Anal somite and part of caudal rami, ventral; D, Anal somite and caudal rami, dorsal; E, leg 5; F, Leg 6.

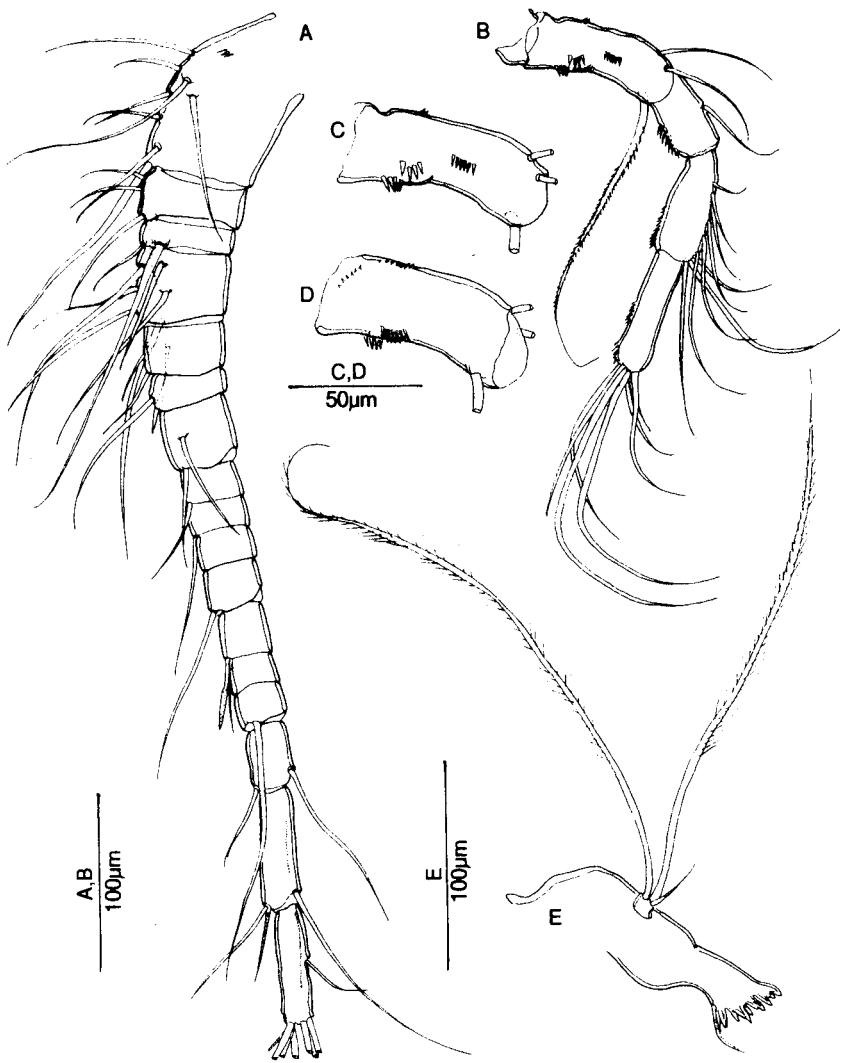


Fig. 12. *Diacyclops lewisi*, new species, female: A, Antennule; B, Antenna, caudal; C, Antennal basipodite, caudal; D, Antennal basipodite, frontal; E, Mandible.

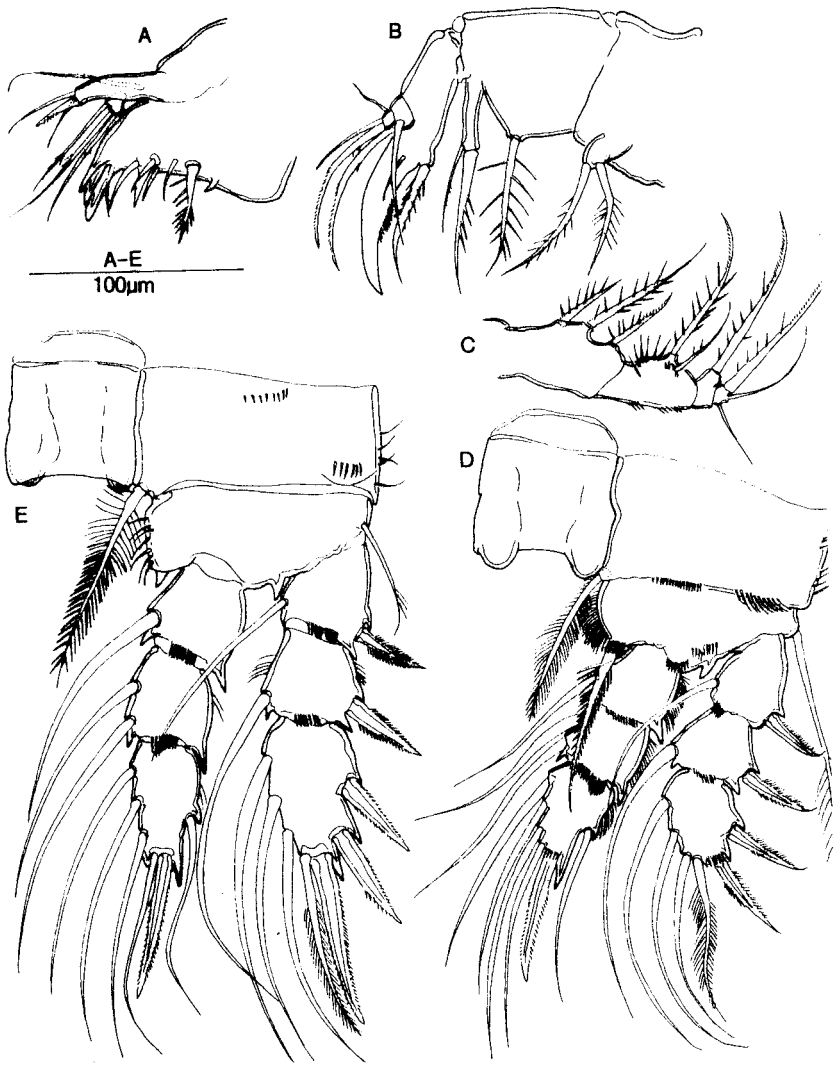


Fig. 13. *Diacyclops lewisi*, new species, female: A, Maxillule; B, Maxilla; C, Maxilliped; D, Leg 1 and coupler, caudal; E, Leg 2 and coupler, frontal.

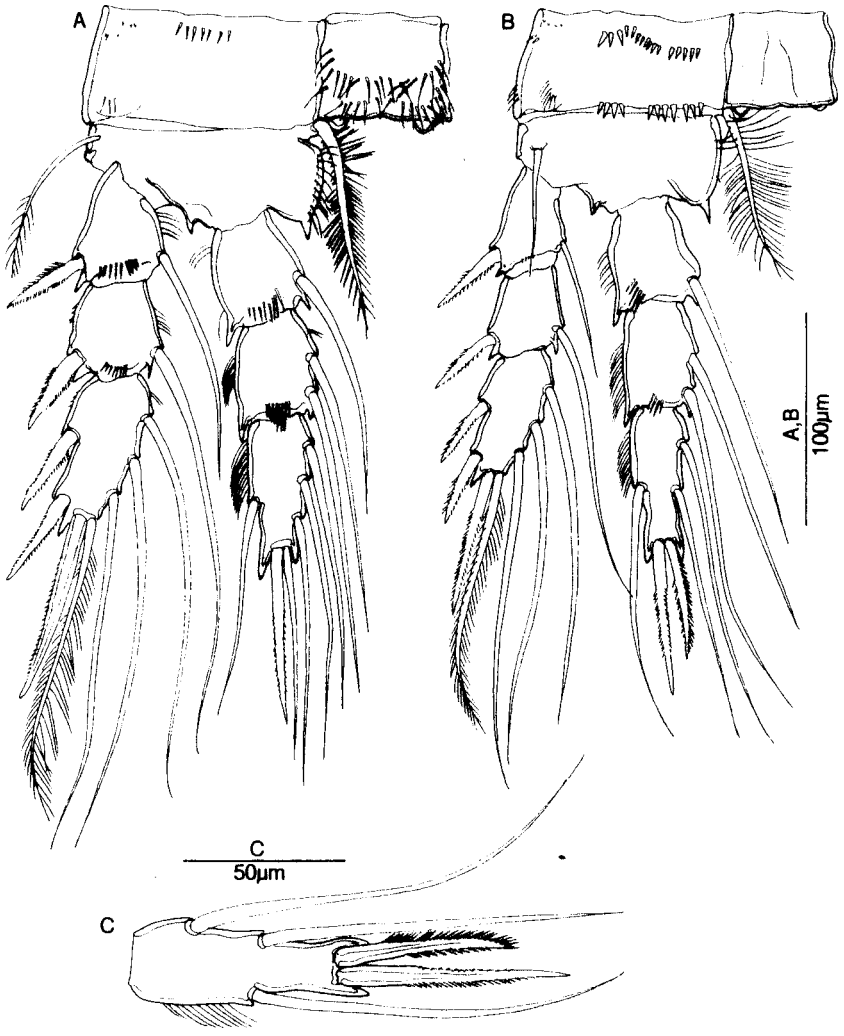


Fig. 14. *Diacyclops lewisi*, new species, female: A, Leg 3 and coupler, caudal; B, Leg 4 and coupler, caudal; C, Leg 4 endopodite segment 3.

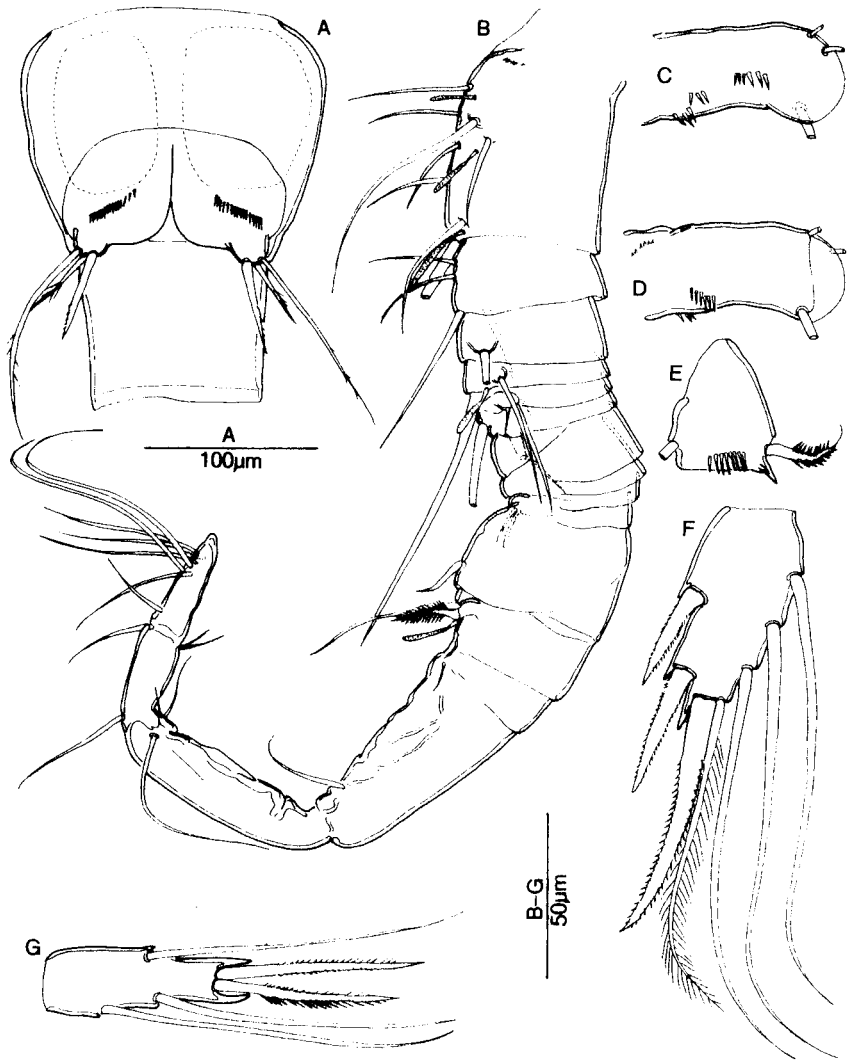


Fig. 15. *Diacyclops lewisi*, new species, male: A, Genital and succeeding somites, ventral; B, Antennule (some setae omitted); C, Antennal basipodite, caudal; D, Antennal basipodite, frontal; E, Leg 2 exopodite segment 1; F, Leg 4 exopodite segment 3; G, Leg 4 endopodite segment 3.

Swimming legs 1-4 (Figs. 13D and E, 14) all with 3-segmented rami. Exopodite segments 1 and 2 and endopodite segment 1 each with 1 medial seta, endopodite segment 2 each with 2 medial setae; exopodite terminal segments with 2,3,3,3 spines and 4,4,4,4 setae respectively. Couplers of all legs with prominent paired rounded protrusions on free margins. Couplers of legs 1, 2, and 4 bare; coupler of leg 3 ornamented with 2 rows of long spines on its caudal surface, its frontal surface bare. Leg 1 with long, coarsely serrate spiniform seta present on distomedial corner. Medial expansions of basipodites of legs 1-3 ornamented with hairs, these hairs on legs 2 and 3 fewer and markedly stouter than corresponding hairs on leg 1. Medial expansions of leg 4 basipodite with only 1 or 2 tiny hairs. Coxopodite of leg 4 ornamented with several rows of spines on caudal surface plus few hairlike spines on lateral surface. Spines on exopodite of leg 1 with slender hairlike tips. Leg 4 endopodite segment 3 about 2.4 times longer than wide, and bearing 2 medial setae, 2 terminal spines, and 1 lateral seta; all setae extending well past ends of terminal spines; lateral terminal spine about 1.2 times length of medial terminal spine. Medial terminal spine directed slightly medially, with a pronounced inward curve.

Leg 5 (Fig. 11E), segment 1 with short lateral expansion bearing relatively short seta; segment 2 with plumose terminal seta and long slender serrate subterminal spine, this spine about 4 times longer than segment and with several tiny spines at its base.

Plate of leg 6 (Fig. 11A and F) located slightly dorsally on genital double-somite, with 1 tiny seta and 2 short spines on its free margin.

Description of Adult Male

Body length of allotype specimen 940 μm; additional measurements given in Table 2. Habitus similar to that of female except for usual sexual dimorphisms. Genital somite (Fig. 15A) swollen, wider than pediger 5.

Antennule (Fig. 15B) geniculate, composed of 16 segments. Segment 1 with 3 aesthetascs and segments 4, 9, and 12 each with 1 aesthetasc, all aesthetascs short and slender.

Antennal basipodite (Fig. 15C and D), general pattern of spine rows similar to that of female, except with fewer spines in some of the rows.

Leg 2 exopodite segment 1 (Fig. 15E), lateral spine slender, curved proximally, serrate with long hairlike tip.

Leg 3 exopodite segment 3 (Fig. 15F), apical spine distinctly curved outwards.

Leg 4 endopodite 3 (Fig. 15G) slightly more slender than in female (2.6 times longer than wide), and medial and lateral spines slightly closer in length (lateral terminal spine about 1.15 times length of medial terminal spine).

Leg 6 (Fig. 15A) consisting of wide plate ornamented with 1 diagonal row of small spines, and bearing 1 spine and 2 setae on its margin, middle seta the shortest element.

Ethanol-preserved specimens colorless, transparent.

Type Locality

Well in Graham Creek drainage section, Big Oaks National Wildlife Refuge, Jennings County, Indiana.

Name

The species name honors Dr. Julian J. Lewis, in appreciation of his dedication to the discovery and better understanding of the subterranean fauna of Indiana.

Remarks

The most similar species to *D. lewisi* is the normally epigean *D. navus*. Both are relatively large-bodied, with none of the usual modifications found in hypogean species. They are similar in major morphological aspects, such as the large rounded seminal receptacle with prominent copulatory pore, the 17-segmented antennule in the female, the antenna with the exopodite-seta present, the legs 1-4 with all rami 3-segmented, and the number and arrangement of spines and setae on the swimming legs (compare the redescription of *D. navus* by Reid, Hare, & Nasci, 1989). *Diacyclops lewisi* differs from *D. navus* mainly in having a longer caudal ramus, relatively longer setae and spines on several appendages (especially the antennule, antenna, maxilliped, and legs 1-5), the modified, stout plumage on the medial

setae of the coxopodites and the medial margins of the basipodites of legs 2 and 3, and most noticeably in the presence of the two rows of large spines on the leg 3 coupler (which are lacking in *D. navus*). The male of *D. navus* has two rows of small spines on the leg 6 plate, as opposed to the single row present in the male of *D. lewisi*.

The modified plumage of the coxopodite-setae and basipodites of legs 2 and 3, and the ornamentation on the leg 3 coupler, which are present in both sexes of *D. lewisi*, are unusual features. In other species, coupler ornamentation, if present, may occur on the couplers of all the swimming legs, or only on the coupler of leg 4, the posteriormost swimming leg pair. To my knowledge this is the only member of the genus with coupler ornamentation present only on leg 3.

This species shows few sexual dimorphisms (other than the usual modifications of the genital segment, antennule, and leg 6) except for the slightly reduced spine ornamentation of the antennal basipodite and the modified spine on leg 2 exopodite segment 1 in the male. Similar dimorphisms are known to occur in other members of the family. For instance, males of some species of *Mesocyclops* have reduced antennal basipodite ornamentation (Hołyńska, 2000). Modified leg 2 spines are known to be present in males of some species of *Acanthocyclops* and *Diacyclops* (e.g., Fiers, Ghenne, & Suárez-Morales, 2000). The slightly modified, outwardly curved terminal spine of the leg 3 exopodite of the male of *D. lewisi* is an unusual feature.

Fiers et al. (1996) speculated that the progressively more elongated appendages, spines, and setae of *Mesocyclops chaci* and *M. yutsil*, which live in crevicular spaces and the open waters of cenotes (sinkholes) in the karstic Yucatan Peninsula, evolved as modifications of their putative ancestor, the primarily epigean *M. reidae*, as adaptations for a planktonic existence in these more open-water environments. It is possible that *D. lewisi* has evolved from *D. navus*, undergoing an analogous elongation of the appendages.

***Diacyclops indianensis*, new species**
Figs. 16-18

Material Examined

Holotype, adult female, dissected on 1 slide; paratypes, 3 copepodid juveniles, all from Indiana, Jefferson County, Big Oaks National Wildlife Refuge, Big Creek No. 08, Henry Dilk Falls Cave, from gravel interstices, Karaman-Chappuis method, 8 May 2001, collectors J. J. Lewis, S. Miller, and E. Laudermilk (VMNH CrustCatDB No. 349).

Non-paratypes: 1 adult female and 1 copepodid juvenile, from Tennessee, Pickett County, Cordell Hull Birthplace State Park, Bunkum Cave, ca. 1 km east of Bloomington, stream, gravel washings by Karaman-Chappuis technique, 12 September 2003, collectors J. J. Lewis, S. Rafail, and H. Garland (VMNH CrustCatDB No. 520). 1 adult female, 2 adult males, and 1 copepodid juvenile, all from Tennessee, Fentress County, Jim Creek Nature Preserve, Redbud Cave, ca. 4.8 km east of Pall Mall, residual pool, gravel washings by Karaman-Chappuis technique, 14 September 2003, collectors J. J. Lewis, S. Rafail, and H. Garland (VMNH CrustCatDB No. 521).

Description of Adult Female

Body length of holotype 1052 µm. Body (Fig. 16A) slender, prosomites with rounded margins in dorsal view. Genital double-somite (Fig. 16A, B) slightly wider than long, tapering rather abruptly in posterior third. Seminal receptacle unusually narrow, little expanded anteriorly and posteriorly, with wide lateral arms; pore-canal long, sclerotized. Hyaline frills of prosomites smooth, frills of urosomites slightly crenulate. Anal somite (Fig. 15C, D) with small spines along nearly all of posterior margin; anal operculum not sclerotized, wide and slightly crescentic, its free margin smooth.

Caudal ramus 85 µm long and 23 µm wide at widest point, thus 3.7 times longer than wide. Medial and lateral surfaces of ramus without ornamentation except for few spines at insertion of outermost terminal seta. Lateral seta inserted

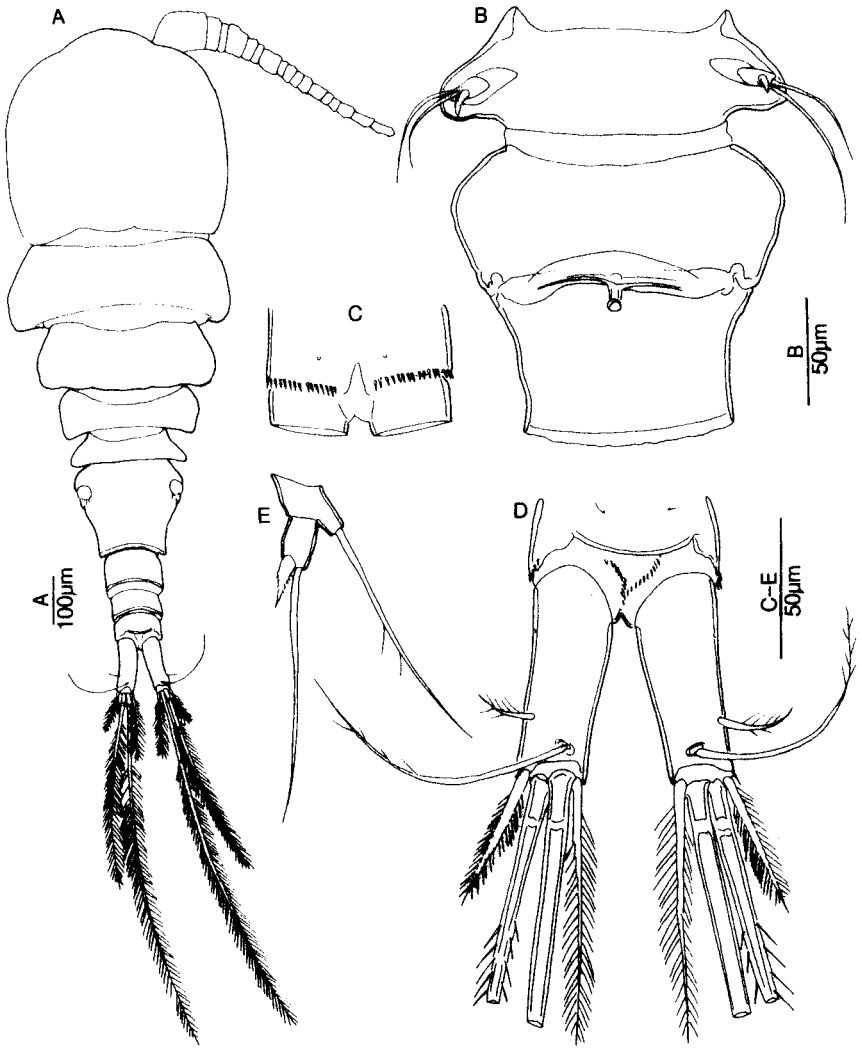


Fig. 16. *Diacyclops indianensis*, new species, female: A, Habitus, dorsal; B, Pediger 5 and genital double-somite, ventral; C, Anal somite and part of caudal rami, ventral; D, Anal somite and caudal rami, dorsal; E, leg 5.

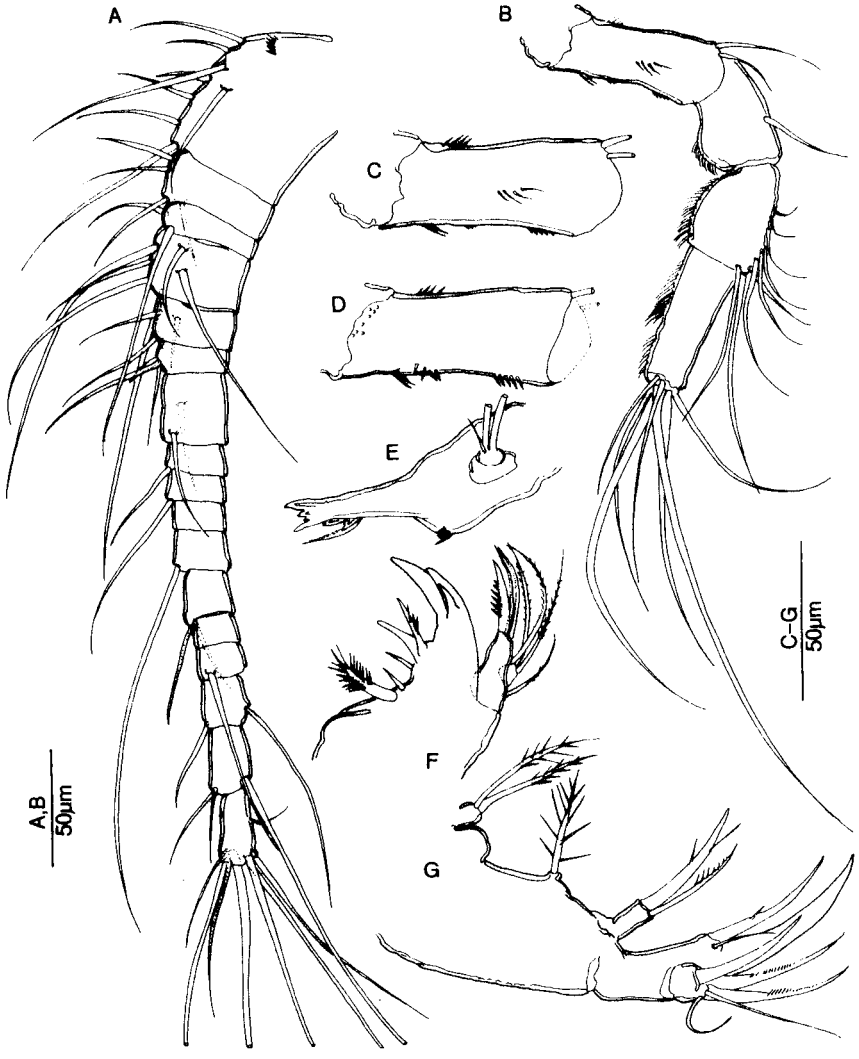


Fig. 17. *Diacyclops indianensis*, new species, female: A, Antennule; B, Antenna, caudal; C, Antennal basipodite, caudal; D, Antennal basipodite, frontal; E, Mandible; F, Maxillule; G, Maxilla.

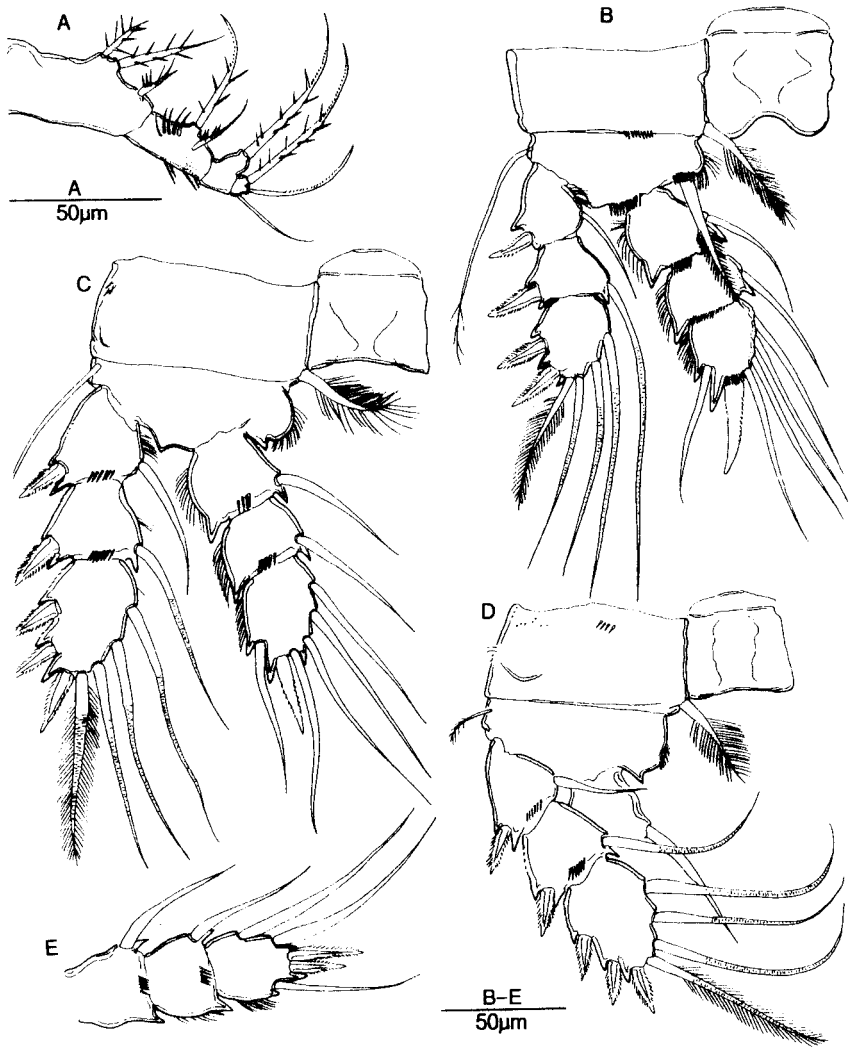


Fig. 18. *Diacyclops indianensis*, new species, female: A, Maxilliped; B, Leg 1 and coupler, frontal; C, Leg 3 and coupler, caudal; D, Leg 4 and coupler (endopodite only partly illustrated), caudal; E, Leg 4 endopodite, caudal.

at posterior 3/4 of ramus. Caudal setae finely plumed, plumage of dorsal seta sparse. Lengths of dorsal, lateral, and medialmost to lateralmost terminal setae 110, 20, 105, 532, 293, and 51 μm respectively.

Antennule (Figs. 16A and 17A) when bent back reaching middle of pediger 2; composed of 17 segments, with following armature: I-8 + row of spines, II-4, III-2, IV-6, V-4, VI-1 + sp, VII-2, VIII-1, IX -1, X-0, XI-1, XII -1+ae, XIII-0, XIV-1, XV-2, XVI-2 +ae, XVII-7 + ae. Aesthetasc on segment XIII reaching nearly to end of segment XV. No hyaline membrane visible on distalmost segments.

Antenna (Fig. 17B-D), basipodite with 2 setae on anterior distal corner but lacking exopodite-seta. Endopodite segments 1-3 with 1, 9, and 7 setae respectively. Basipodite with 3 groups of spines along posterior margin, 1 group of 4 spines on caudal surface, and 1 group of 4 spines on proximal part of anterior margin.

Mandible (Fig. 17E), transverse row of spines present distal to palp; palp with 1 short and 2 long setae.

Maxillule (Fig. 17F), as in figure; palp without surface ornamentation.

Maxilla (Fig. 17G), claw with no teeth along its margin.

Maxilliped (Fig. 18A), segments 1-4 with 3, 2, 1, and 3 setae respectively; 3 groups of spines present on surface of segment 2.

Swimming legs 1-4 (Fig. 18B-E) all with 3-segmented rami. Structure of leg 2 like that of leg 3 (illustrated) except leg 2 is slightly smaller. Exopodite and endopodite segments 1 and 2 of each leg with 1 medial seta; exopodite terminal segments with 2,3,3,3 spines and 4,4,4,4 setae respectively. Couplers with no surface ornamentation. Basipodite of leg 1, margin of medial expansion smoothly convex, with fine hairs and long spiniform seta. Basipodites of legs 2 and 3 identical, ornamented with fine hairs, medial expansions with shallow but distinct distal notch next to spiniform process. Basipodite of leg 4, medial margin convex but with haired groove along its middle part. Coxopodite of leg 4 ornamented with few rows or groups of spines on caudal and lateral surfaces. Leg 4 endopodite, segment 1 with medial margin thickened and grooved; segment 3, 38 μm long and 34 μm wide, thus about 1.1 times longer than wide, and bearing 2 medial setae, 2 terminal spines, and 1 lateral spine; lateral terminal spine 24 μm long, medial terminal spine 32 μm long, thus about 1.3 times longer than lateral terminal

spine.

Leg 5 (Fig. 16B and E), segment 1 with short lateral expansion bearing long seta; segment 2 with terminal seta and subterminal spine, this spine more than 3 times wider at its base than base of terminal seta, and about as long as segment. Plate of leg 6 (Fig. 16A) located slightly dorsally on genital double-somite, without surface ornament and with 1 tiny seta and 2 short spines on its margin.

Ethanol-preserved specimens colorless, transparent.

Adult Male

Not described.

Type Locality

Henry Dilk Falls Cave, Big Oaks National Wildlife Refuge, Jefferson County, Indiana.

Additional Localities

Redbud Cave, Jim Creek Nature Preserve, Fentress County, Tennessee; and Bunkum Cave, Cordell Hull Birthplace State Park, Pickett County, Tennessee.

Name

The species name is given for the state in which the type specimens were collected.

Remarks

The combination of the 3-segmented rami and the lack of acute protrusions on the couplers of the swimming legs, the leg 4 endopodite 3 with 2 terminal spines of which the lateral terminal spine is shorter, the antennule composed of 17 segments, the caudal ramus about 3.7 times longer than wide and lacking surface ornamentation, and the lack of an antennal exopodite-seta distinguish the adult female of *D. indianensis* from its congeners.

Additional distinguishing microcharacters are the lack of a hyaline membrane on the distal segments of the antennule, the row of spines on the surface of the mandible, the notched medial margins of the basipodites of legs 2 and 3, the haired groove of the basipodite of leg 4, and the short wide subterminal spine of leg 5. The seminal receptacle is unusually narrow, but may simply be undeveloped in the single specimen collected from the type locality; however, both the female specimens from Tennessee also have narrow receptacles.

Like *D. lewisi* and *D. salisae*, *D. indianensis* shows few of the typical features of hypogean species. It does show two reductions: the lack of the antennal exopodite-seta and the teeth on the claw of the maxilla, which are present in nearly all congeneric species.

The two female specimens collected from Tennessee are morphologically indistinguishable from the holotype. Nevertheless, because of the great distance between the type locality and these recently discovered populations in Tennessee, it seems the more conservative course to delay describing the male until specimens from the type locality become available.

Henry Dilk Falls Cave consists of 617 feet (188 m) of mapped stream passage. The substrate is scalloped limestone with occasional gravel bars, from which the copepods were withdrawn. The specimens from Tennessee were also collected from gravel washings (J. J. Lewis, pers. comm., 2003).

Diacyclops conversus, new species

Figs. 19-22

Material Examined

Holotype, adult female, dissected and mounted on slide (USNM 1014258); allotype, adult male (USNM 1014259); paratype, 1 adult male (USNM 288051), all from Indiana, Crawford County, Wyandotte, Blue River, gravel bar at old Rothrock Mill site, Bou-Rouch pump at depth of 1 m, 27 August 1998, collector J. J. Lewis.

Description of Adult Female

Length of holotype 775 μm. Body (Fig. 19A) slender, most prosomites with rounded margins in dorsal view, pediger 5 slightly produced laterally. Genital double-somite (Fig. 19A-C) about as long as wide, tapering in posterior third. Seminal receptacle indistinct, appearing little expanded anteriorly and posteriorly, with wide lateral arms; pore-canal short, sclerotized. Hyaline frills of prosomites slightly crenulate, those of urosomites more deeply crenulate. Anal somite (Fig. 18D and E) with small spines along nearly all of posterior margin; anal operculum not sclerotized, little produced and slightly crescentic, its free margin irregular.

Caudal ramus 3.6 times longer than wide, without surface ornamentation. Lateral seta inserted at posterior 2/3 of ramus. Dorsal and lateral setae smooth, terminal setae finely plumed. Lengths of dorsal, lateral, and medialmost to lateralmost terminal setae 43, 12, 38, (broken), 175, and 34 μm.

Antennule (Figs. 19A and 20A) when bent back reaching middle of pediger 2; composed of 12 segments, bearing elements as follows: I-8 + row of spines, II-4, III-2, IV-6, V-4, VI-1 + sp, VII-2, VIII-3, IX-2+ae, X-2, XI-2 +ae, XII-7 + ae. Aesthetasc on segment IX reaching about end of segment X. No hyaline membrane visible on distalmost segments.

Antenna (Fig. 20B and C), basipodite with 2 setae on anterior distal corner but lacking exopodite-seta. Endopodite segments 1-3 with 1, 9, and 7 setae respectively. Basipodite with several spines along posterior margin, and 2 groups of few spines on caudal surface.

Mandible (Fig. 20D), palp with 2 long and 1 short setae.

Maxillule (Fig. 20E and F), as in figure; palp without surface ornamentation.

Maxilla (Fig. 20G), claw with few teeth along middle third.

Maxilliped (Fig. 20H), segments 1-4 with 2, 2, 1, and 3 setae respectively; 1 group of spines present on each of segments 2 and 3.

Swimming legs 1-4 (Fig. 21) all with 3-segmented rami; leg 3 like leg 2 (illustrated) except slightly larger. Exopodite and endopodite segments 1 and 2 of each leg with 1 medial seta; exopodite terminal segments with 2,3,3,3 spines and 4,4,4,4 setae respectively. Couplers of all legs ornamented with 2 short rows of long spines on their frontal surfaces. Medial margins of basipodites of legs 1-3 ornamented with few hairs, basipodite of leg 4 with 1 tiny stiff hair. Coxopodite

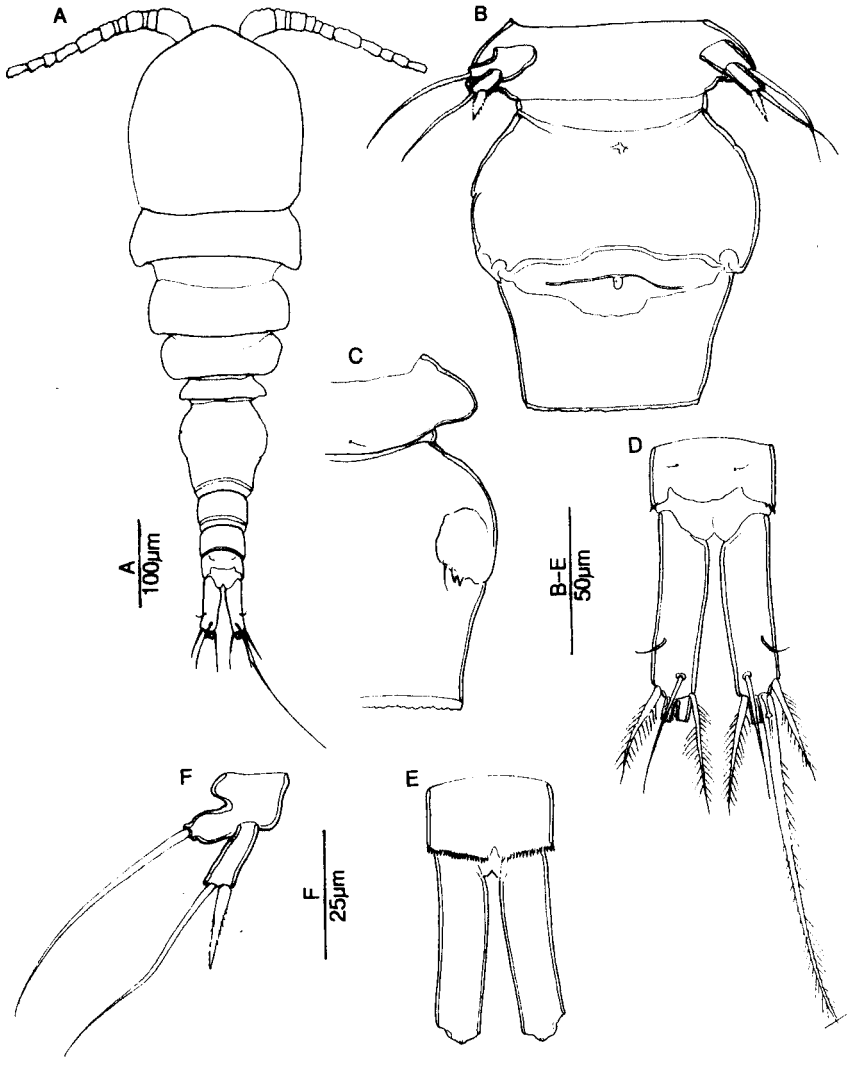


Fig. 19. *Diacyclops conversus*, new species, female: A, Habitus, dorsal (three of four middle terminal setae broken); B, Pediger 5 and genital double-somite, ventral; C, Pediger 5 and genital double-somite, dorsal; D, Anal somite and caudal rami, dorsal; E, Anal somite and caudal rami, ventral (setae omitted); F, Leg 5.

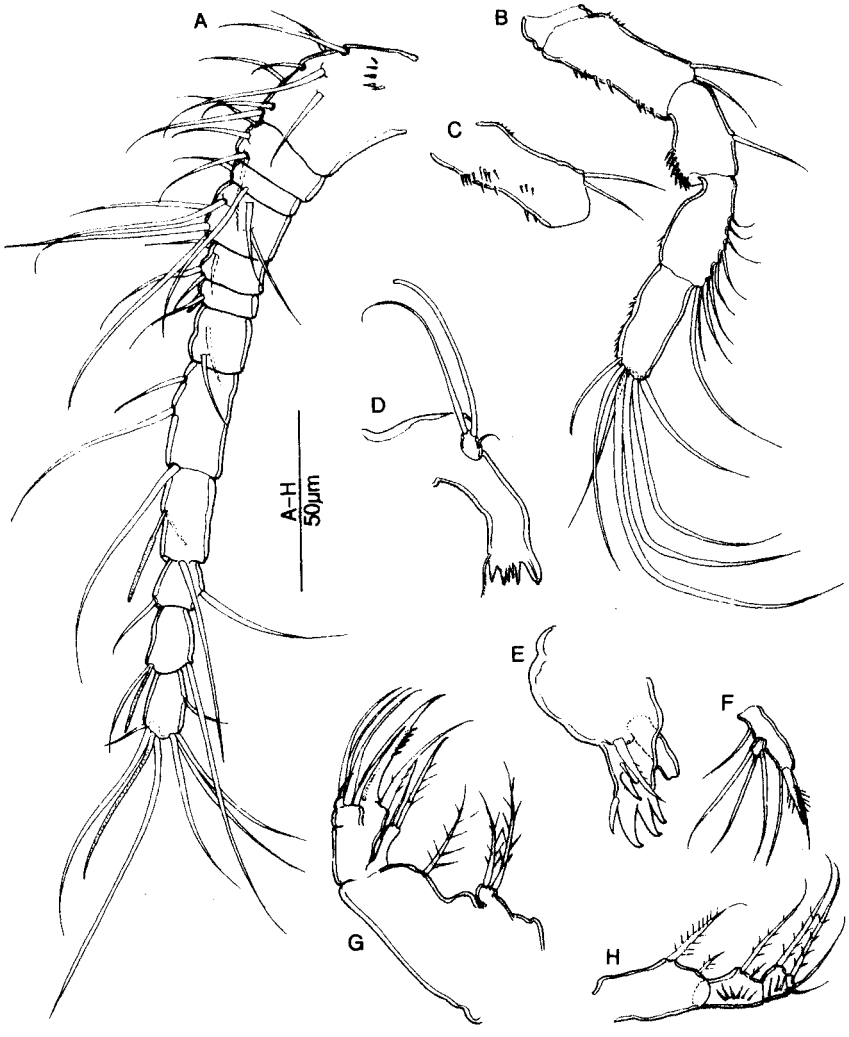


Fig. 20. *Diacyclops conversus*, new species, female: A, Antennule; B, Antenna, frontal; C, Antennal basipodite, caudal; D, Mandible; E, Maxillule (palp only partly illustrated); F, Maxillular palp; G, Maxilla; H, Maxilliped.

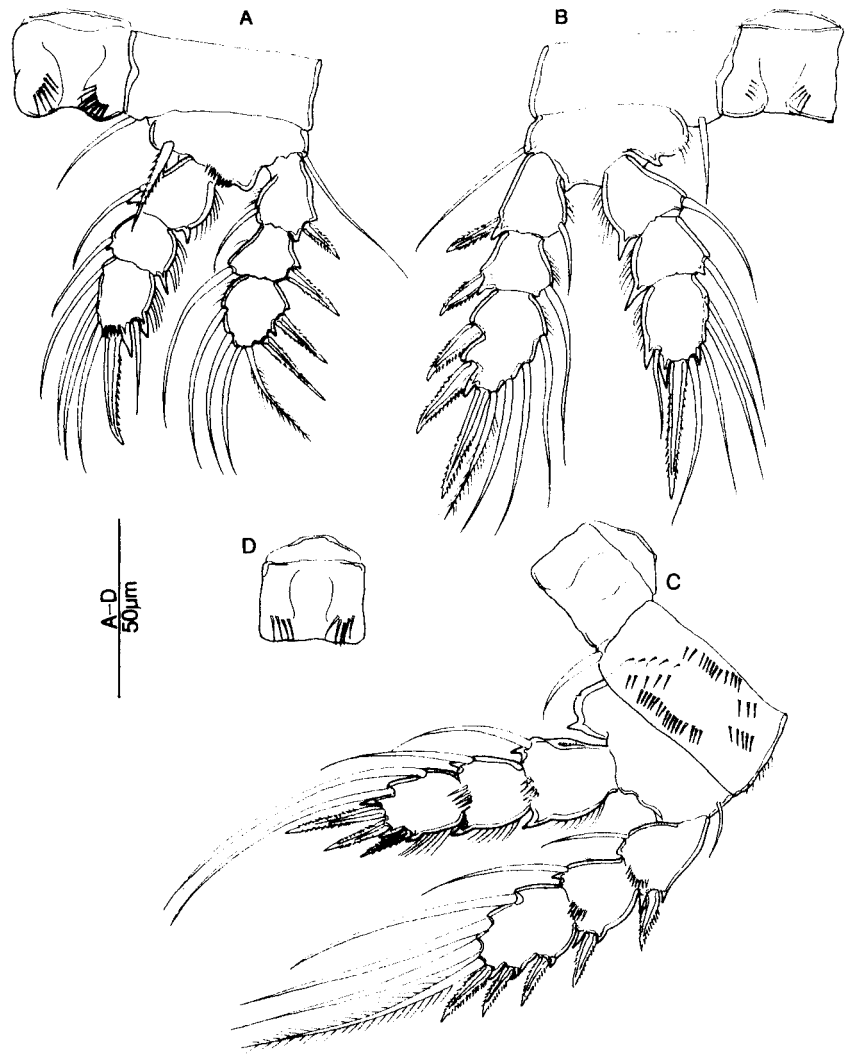


Fig. 21. *Diacyclops conversus*, new species, female: A, Leg 1 and coupler, frontal; B, Leg 2 and coupler, frontal; C, Leg 4 and coupler, caudal; D, Leg 4 coupler, frontal.

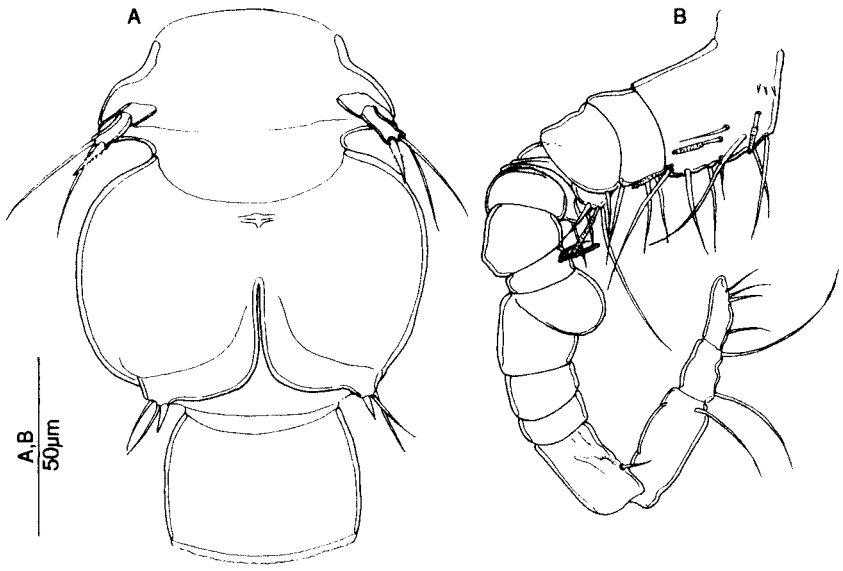


Fig. 22. *Diacyclops conversus*, new species, male: A, Pediger 5 and genital and succeeding somites, ventral; B, Antennule (several setae omitted).

of leg 4 ornamented with 6 rows of spines on caudal surface plus few thin spines on lateral surface. Leg 4 endopodite segment 3, length 25 µm and width 28 µm, thus about 1.1 times wider than long, and bearing 2 medial setae, 2 terminal spines, and 1 lateral spine; lateral terminal spine about 2/3 length of medial terminal spine.

Leg 5 (Fig. 19B, F), segment 1 with large lateral expansion bearing long seta; segment 2 with terminal seta and spine, spine about 1.2 times longer than segment.

Plate of leg 6 (Fig. 19C) located dorsolaterally on genital double-somite, without ornamentation and with 1 tiny seta and 2 short spines on its free margin.

Description of Adult Male

Lengths of allotype and paratype specimens 705 and 645 µm respectively. Habitus similar to that of female except for usual sexual dimorphisms. Genital

somite (Fig. 22A) swollen, wider than pediger 4, without surface ornamentation. Lengths of dorsal, lateral, and medialmost to lateralmost terminal caudal setae, respectively, of allotype 30, 12, 40, 315, 163, and 35 μm; of paratype 30, 14, 38, 295, 155, and 28 μm.

Antennule (Fig. 22B) geniculate, composed of 16 segments; segment 1 with 3, segments 4 and 9 each with 1 aesthetasc.

Mouthparts and most features of legs 1-5 as in female.

Leg 4 endopodite 3 slightly longer than wide, rather than wider than long as in female; its length and width in allotype, 21 and 17 μm; in paratype, 22 and 17 μm. Outer terminal spine closer in length (91 and 82%, in allotype and paratype respectively) to inner terminal spine.

Leg 6 (Fig. 22A) consisting of narrow curved unornamented plate bearing 1 short spine and 2 setae, longer than spine and of about equal lengths, on its free margin.

Ethanol-preserved specimens colorless, transparent.

Type Locality

Rothrock Mill site, Blue River at Wyandotte, Crawford County, Indiana.

Name

From the Latin "conversus" meaning turned around, to describe the unusual location of the spine ornamentation on the frontal sides of the couplers of the swimming legs.

Remarks

The *nearcticus*-group includes five species, all in North America. These have in common a relatively short leg 4 endopodite segment 3, which bears 1 lateral and 2 terminal spines in addition to 2 medial setae; spine formula 2,3,3,3; moderately long caudal rami; and the lack of the antennal exopodite-seta (Reid, 1992). *Diacyclops conversus* shares all these characters. The new taxon differs from its congeners primarily in having a 12-segmented

antennule in the female, versus 17 segments in *D. nearcticus* Kiefer, 1934, *D. chrisae* Reid, 1992, *D. harryi* Reid, 1992, and *D. sororum*, and 16 segments in *D. alabamensis* Reid, 1992.

Nearly all the records of members of the *nearcticus*-group are from hyporheic and other hypogean habitats. In addition to the lack of the antennal exopodite-seta, the short, 12-segmented antennule and the enlarged genital somites in both sexes of *D. conversus* are modifications for a hypogean mode of life.

In most members of the family Cyclopidae, ornamentation that may be present on the couplers of the swimming legs occurs either on the caudal, or on both the caudal and frontal surfaces. In the *nearcticus*-group, there is a tendency toward more ornamentation on the frontal surfaces. For example, in *D. alabamensis* only the caudal surface of the leg 4 coupler bears spines (Reid, 1992), which is the most usual case in the genus. In *D. nearcticus* all the couplers are bare (Reid, 1992; Bruno, Reid, & Perry, 2000). In *D. chrisae* and *D. harryi* the frontal surfaces of all couplers, but the caudal surfaces of only legs 1 and 4 couplers are ornamented; whereas in *D. sororum* the frontal surfaces of all the couplers, but the caudal surface of only leg 4 is ornamented (Reid, 1992). In *D. conversus*, with spine ornamentation only on the frontal surfaces of the couplers, this tendency is fully expressed.

DISCUSSION

In southern Indiana there are two main karst regions: the south-central karst belt, which developed in Mississippian strata (Fig. 1, area A); and the southeastern karst belt, which formed in strata of Ordovician to Devonian age (Fig. 1, area B). The most recent glaciation, the Wisconsonian, covered only the northern parts of these regions and began to retreat about 12,000 years ago. The earlier Illinoian glacier did not reach most of the south-central belt, but covered all of the southeastern belt until the glacier began to retreat

about 140,000 years ago. Thus, much of the southeastern karst region has been free of ice, and therefore available for colonization by subterranean fauna, for less than 100,000 years.

Ten members of the cyclopoid copepod genus *Diacyclops* have now been found in subterranean or groundwater-related habitats in southern Indiana. Four of these are primarily epigean species that are widespread in North America: *D. crassicaudis brachycercus* and *D. navus* mainly in ephemeral waters, and *D. nearcticus* and *D. sororum* mainly in streams. The remaining six species are exclusively hypogean. Two of these, *D. yeatmani* and *D. indianensis*, have been found outside Indiana; the remaining four, *D. jeanneli*, *D. salisae*, *D. lewisi*, and *D. conversus* are so far known only from southern Indiana.

The tendency of species of *Diacyclops* to succeed and diversify in hypogean, especially karstic habitats is well known. To take an example from the Americas, five of the six species of this genus which are known from the Yucatan Peninsula are hypogean (Fiers et al., 1996; Fiers, Ghenne, & Suárez-Morales, 2000). Therefore it is not surprising to find both a high number of species and a high proportion of hypogean species of *Diacyclops* in a particular karst region.

Three of the four new species, *D. indianensis*, *D. lewisi*, and *D. salisae*, occurred in Big Oaks National Wildlife Refuge. The refuge lies within the Muscatatuck Faunal Basin in parts of Jennings and Jefferson counties in the southeastern karst. The historical geology and aspects of the biogeography of several groups of invertebrates inhabiting the basin were discussed in detail by Lewis (1983, 1995). According to Lewis (1983), numerous obligatory hypogean species now occur in the caves and groundwaters of the southeastern karst, but these species are demonstrably less morphologically derived than are their relatives in the south-central karst. To explain this distribution pattern, Lewis (1983) suggested that certain species which were utilizing coldwater habitats entered caves and groundwaters only after the Illinoian glacier retreated, i.e., relatively recently in geological terms. With

the warming climate, these populations eventually became isolated in the subterranean waters. The three *Diacyclops* species from Big Oaks show few or none of the morphological modifications which are typically seen in hypogean cyclopoids. These modifications, which were reviewed in detail by Reid & Strayer (1994) and Monchenko & Vaupel Klein (1999), consist of shortening of the entire body and accompanying reductions of the appendages, which may include oligomerization or loss of some setae and spines. One of the most common changes is the loss of the antennal exopodite-seta. The slight degree of modification shown by the three hypogean species in the southeastern karst is consistent with Lewis' (1983) evolutionary scenario positing a relatively recent groundwater invasion by hypogean species into this region. *Diacyclops indianensis* now appears to be a widespread species, and its primary habitat is apparently groundwater-interstitial rather than caves per se. The distributions of both *D. lewisi* and *D. salisae*, which from their morphology also appear to be relatively generalist species, may similarly prove to extend outside the Muscatatuck Basin, although it is likely that both of them occur only in groundwater. Collections from surface waterbodies in Big Oaks National Wildlife Refuge and other localities in southern Indiana have yielded no species of *Diacyclops* (J. J. Lewis, pers. comm., 2003).

Both *D. jeanneli* and *D. conversus* are more strongly modified for hypogean existence, and both are apparently restricted to the unglaciated Blue River faunal basin in the south-central karst region. Strayer & Reid (1999), studying the distribution of hyporheic cyclopoids in glaciated and unglaciated sites in the eastern USA, suggested that there is a break in species composition near the Pleistocene glacial border, and that many of the more specialized interstitial species were unable to disperse into previously glaciated areas as the glaciers retreated. The presence of *D. jeanneli* and *D. conversus* in the Blue River basin, and their absence from the Muscatatuck basin, appears to be an example of this biogeographic faunal break.

The same gravel bar in the Blue River at the Rothrock Mill site yielded

four species of *Diacyclops* in different years: *D. sororum* in August 1997, *D. conversus* and *D. yeatmani* in August 1998, and *D. nearcticus* in July 2000. In some of the same Bou-Rouch pump samples were other typical but rarely collected groundwater animals such as an undescribed bathynellacean; the isopod *Caecidotea jordani* (Eberly, 1966); the amphipod *Crangonyx packardi* S. I. Smith, 1888; and the hydrobiid snail *Fontigens cryptica* Hubricht, 1973 (J. J. Lewis, pers. comm., 2003). This experience shows that, while occasional sampling in a particular hypogean habitat does yield valuable information, repeated sampling over the long term is necessary to gain a more complete picture of the fauna.

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Table 1. Measurements (in μm) of certain structures of 4 females and 1 male of *Diacyclops jeanneli* from the type locality, Marengo Cave. Abbreviations: Setae 1-4, medialmost terminal to lateralmost terminal caudal setae, respectively; P4enp3, leg 4 endopodite segment 3; TS, terminal spine.

Structure	Sex	Mean	Range
Total length	F	854	782 - 968
	M	600	
Caudal ramus			
Length	F	76.5	72 - 78
	M	68	
Width	F	19.7	19 - 20
	M	19	
Seta 1	F	71.7	62 - 80
	M	58	
Seta 2	F	433	422 - 453
	M	405	
Seta 3	F	230	215 - 240
	M	315	
Seta 4	F	42.7	41 - 45
	M	38	

Dorsal seta	F	67.5	55 - 80
	M	70	
Lateral seta	F	20.5	20 - 22
	M	20	
P4enp3			
Length	F	30.5	29 - 31
	M	28	
Width	F	22.0	21 - 23
	M	18	
P4enp3			
TS	F	21.7	21 - 23
	M	25	

Table 2. Measurements (in μm) of certain structures of 10 females and 4 males of *Diacyclops lewisi*, new species. Most abbreviations as in Table 1; MTS, medial terminal spine; LTS, lateral terminal spine.

Structure	Sex	Mean	Range
Total length	F	1271	1225-1331
	M	1076	940-1125
Caudal ramus			
Length	F	125	120-132
	M	96	82-105
Width	F	26	25-26
	M	21	20-22
Seta 1	F	114	107-122
	M	97	95-100
Seta 2	F	500	440-585
	M	506	495-520
Seta 3	F	328	312-340
	M	260	245-280
Seta 4	F	85	72-95
	M	73	65-83
Dorsal seta	F	96	57-120
	M	92	90-105

Lateral seta	F	40	38-43
	M	34	33-35
P4enp3			
Length	F	66	64-70
	M	56	53-58
Width	F	27	26-28
	M	21	20-22
P4enp3			
MTS	F	57	56-62
	M	55	52-58
LTS	F	69	65-74
	M	63	62-65