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APALACHOCYCLOPS GEN. NOV. (COPEPODA, CYCLOPOIDA,
CYCLOPIDAE): A NEARCTIC “DOPPELGÄNGER” OF
THE EUROPEAN SPEOCYCLOPINES

BY

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ABSTRACT

A new genus and species of Cyclopinae, collected in one of the most extended cave systems, Endless Caverns, in the state of Virginia (U.S.A.) is described. *Apalachocyclops minotaurus* gen. n., sp. n. combines a curious mixture of highly advanced characteristics and features referable to the ground pattern of the Cyclopinae. The new genus is largely characterized by its curious flattened body, the striking differences between the segmentation of male and female legs 3 and 4, and the particular modifications of the terminal elements of the leg 3 endopodite in the male. *Rheocyclops*, *Itocyclops*, the *jeanneli* species-group of *Diacyclops*, and *Apalachocyclops* gen. n. are assumed to constitute the North American counterpart of the European subterranean cyclopid fauna, here referred to as “speocyclopines”.

RÉSUMÉ

Une nouvelle espèce d'un nouveau genre de Cyclopinae, collecté dans l'un des systèmes cavernicoles les plus étendus, Endless Caverns, dans l'état de Virginie (U.S.A.) est décrite. *Apalachocyclops minotaurus* gen. n., sp. n. combine un étonnant mélange de caractéristiques hautement avancées et de traits renvoyant au patron de base des Cyclopinae. Le nouveau genre est caractérisé par son corps de forme curieuse, aplati, par les différences frappantes de segmentation des pattes natatoires 3 et 4 entre le mâle et la femelle, et par les modifications particulières des éléments terminaux de l'endopodite de la patte 3 chez le mâle. *Rheocyclops*, *Itocyclops*, le groupe d'espèces *jeanneli* du genre *Diacyclops*, et *Apalachocyclops* gen. n. sont supposés constituer l'équivalent nord-américain de la faune des cyclopidés souterrains d'Europe, ici dénommés “speocyclopinés”.

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INTRODUCTION

Our current perception of the diversity and distribution of subterranean copepods on the North American continent is rather scanty. Compared to the steep number of cyclopines known to occur in European groundwaters (Lescher-Moutoué, 1986; Deharveng et al., 2009) the number of obligate subterranean representatives reported from the Nearctic is surprisingly low (Culver & Sket, 2000; Culver et al., 2003). Hence, the vastness of suitable habitats (see for example the distribution of evaporites and karst massifs in Veni, 2002 and Vesper, 2008) is undeniable promising and has been inspiring from the early days of biospeleology on, when C. Bolivar and R. Jeannel made extensive collections in 1928 (Bolivar & Jeannel, 1931).

The current picture of subterranean aquatic diversity in the Nearctic is mainly formed by the larger, more visible, representatives, i.e., amphipods, isopods, and decapods (Taylor, 2004). Their presence and diversity is unmistakably demonstrative for our limited insights into the richness of the “smaller” crustacean fauna thriving in this environment. Fortunately, the situation for the North American continent seems to come to a turn. When, at the dawn of the present decade, only 4 cyclopines figured between a 900-items long list of (obligate) names of cave animals (Culver et al., 2003), a recent listing of cyclopine cave inhabitants, either obligate subterraneans or not, from the Interior Low Plateaus raised the number promptly to 40, some waiting formal description (Lewis & Reid, 2007). Clearly, an undisclosed treasure box awaits to be explored.

A small set of vials containing unidentified copepods collected in the early seventies in springs and caves located in the states of Virginia, Kentucky, and Texas (U.S.A.) held a remarkable diversity of cyclopines. The species spectrum encountered corresponds largely to those described in Strayer & Reid (1999) and Lewis & Reid (2007) and comprises a mixture of epigean and typical subterranean representatives. Particularities of the species observed will form a separate contribution. In the present one, an apparently well adapted stygobiont cyclopine is described from a sample originating from the Endless Caverns in the state of Virginia. The particular combination of characters displayed by this small cyclopine, viz., body shape, leg segmentation, and dimorphism, provide sufficient grounds to propose a new genus to accommodate it. The general appearance of the here described *Apalachocyclops minotaurus* gen. n., sp. n., is in many ways reminiscent of that of the European obligate subterranean cyclopines, referred to as “speocyclopines”. Hence, the allusion to the “Doppelgänger” [= double] in the present title.

MATERIAL AND METHODS

The specimens, collected 8 June 1973 (collector anonymous), were fixed and stored in formalin; prior to examination, the specimens were transferred to 75% denaturated alcohol overnight and brought afterwards in glycerine for close observation; dissected animals are mounted in glycerine, preserved ones are stored now in 75% alcohol; the specimens are deposited in the copepod collection of the Royal Belgian Institute of Natural Sciences, Brussels (RBINSc COP). Observations were made with a Wild Dialux compound light microscope equipped with phase contrast, and illustrations with the aid of a drawing tube. Abbreviations in text and tables: aesth, aesthetasc; end/exo, endopodite/exopodite; sp, spine; T-plates, modified T-shaped structure on male antennule.

DESCRIPTION

Family CYCLOPIDAE Rafinesque, 1815

***Apalachocyclops* gen. nov.**

Diagnosis. — Cyclopidae, Cyclopinae, with a flattened and depressed body, devoid of particular integumental surface modifications; prosome–urosome transition not accentuated; anal operculum large, caudally produced; caudal rami cylindrical, with smooth surface and bearing 6 armature elements; genital double-somite inflated, without remnants of ancestral subdivision, widest in anterior half, and bearing leg 6 vestiges laterally; seminal receptacle located in middle of genital double-somite, narrow, and ribbon-shaped, with copulatory pore at caudal side and fitted in thick central cellular mass; prosomites without posterodorsal fringe, urosomites with wide fringe, irregularly serrated; female antennule 11-segmented, with basic set of setal armament; male antennule bi-geniculate, 16-segmented with 2 aesthetascs on segment I; antenna 4-segmented, lacking exopodite remnant seta; mandible with distinct palp bearing 3 setae; maxillary endopodite 2-segmented with 2 spines and 1 spine, 2 setae, on proximal and distal segment, respectively; maxilliped 4-segmented with (proximal to distal) 2.2.1.2 long and sparsely pinnate setae; leg 1-4 with medial coxal element and smooth intercoxal sclerite; leg 1 basis with medial spine; female legs with bimerous rami, male legs bimerous in legs 1 and 2, trimerous in legs 3 and 4; spine formula 3.4.4.4 in female, 3.4.3.3 in male; terminal endopodite segment of leg 4 in male and female without

outer subdistal element, and 2 apical spines; terminal endopodite segment of male leg 3 with: outer terminal element claw-shaped, inner terminal element minute, smooth, needle-shaped, and inner subdistal element short, sturdy and pinnate; leg 5 located at ventral side of pediger; (ancestral) basal segment obsolete, represented by a seta arising from minute socket adherent to (ancestral) terminal segment; the latter with 2 apical elements: outer one slender and setiform, inner one rigid, spiniform, distinctly longer than segment; female leg 6 represented by 1 short seta (outer element) and 2 long hyaline spiniform structures (median and inner one); male leg 6 vestiges represented by 3 prominent elements (2 setae, 1 spine) on large triangular valve.

Etymology. — *Apalacho-* after the Apalachee native tribe and the first cartographic reference to the Appalachian mountain chain (as “Apalachen”) appearing on the map of America drawn by the Spanish cartographer Diego Gutiérrez the Elder, and published in 1529 by his son Sancho; in conjunction with the generic name *Cyclops*. Gender masculine.

Type species. — *Apalachocyclops minotaurus* sp. n., designated by monotypy.

***Apalachocyclops minotaurus* sp. n.**

(figs. 1-5)

Type series. — Holotype: male specimen dissected and mounted on 4 slides, labelled RBINSc COP 9199 A-D; allotype: female dissected and mounted on 4 slides, labelled RBINSc COP 9200A-D; paratypes: 2 females (1 intact, 1 damaged) and 5 males, preserved in 75% denaturated ethylalcohol, and catalogued under number RBINSc COP 9201.

Description. — Female. Habitus (fig. 1C): body flattened and compact, semi-ovate in dorsal view; prosome widest at posterior margin of cephalothorax; metasome narrowing caudally, with posterior border as wide as anterior part of genital double-somite; prosome–urosome transition not remarkably accentuated; urosome less long than half body length; integument of each somite well sclerotized, lacking external depressions (pits) or retractile semi-perforations; posterior margins of prosomal tagma without hyaline frill; no eye pigment observed (animals fixed for over 30 years); body length 450-475 μm (2 females).

Pediger 5 rather wide with distinct, crescent pleural extension (fig. 2D); posterodorsal margin lacking fringe; genital double-somite conspicuously large and voluminous with, in dorsal view, wide anterior half, narrowing promptly and considerably in posterior half; longer than the 3 following somites combined; widest part slightly less wide than twice the width of

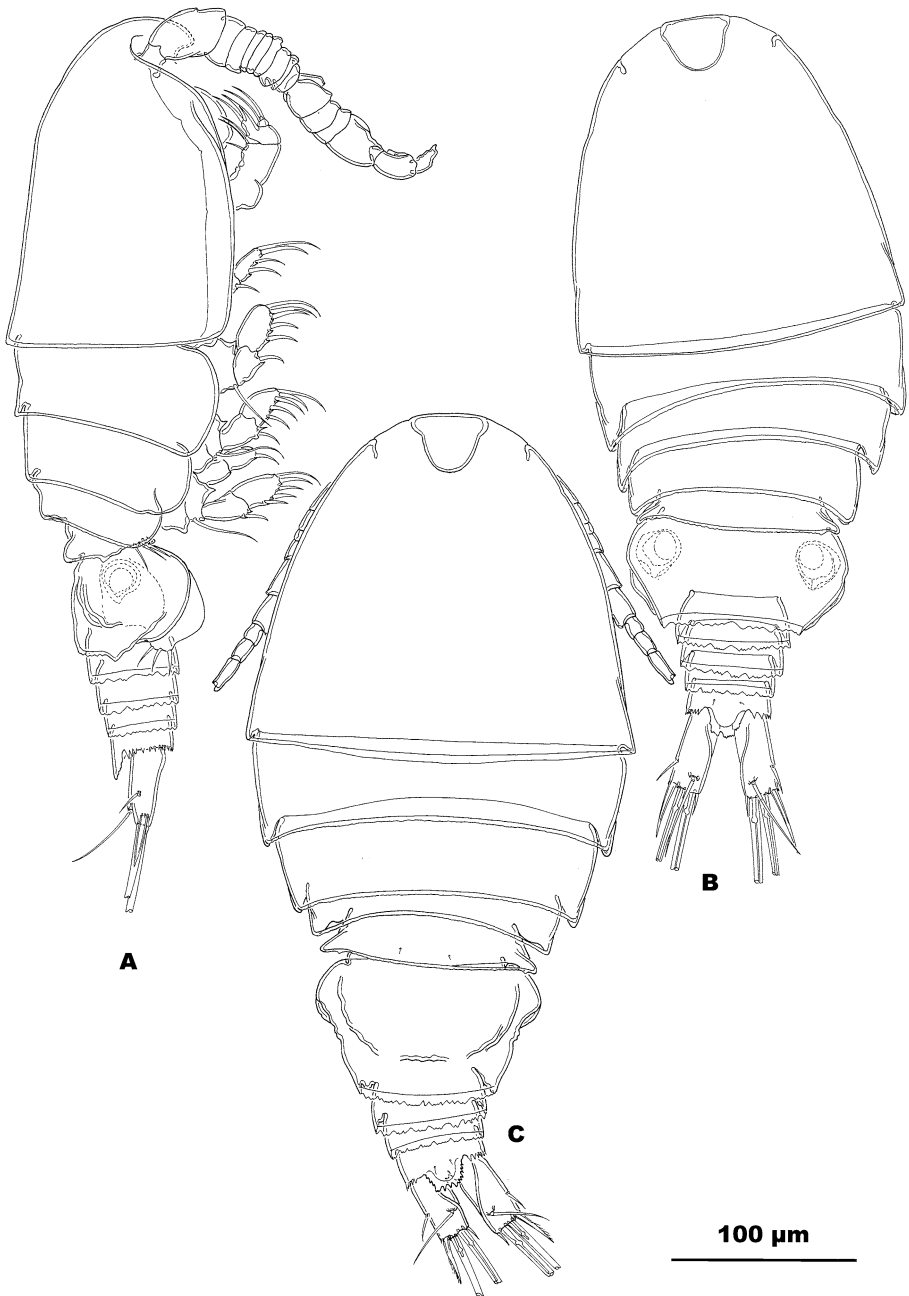


Fig. 1. *Apalachocyclops minotaurus* gen. n., sp. n. A, male habitus, lateral; B, male habitus, dorsal; C, female habitus, dorsal (A, B: RBINSc COP 9199; C: RBINSc COP 9200).

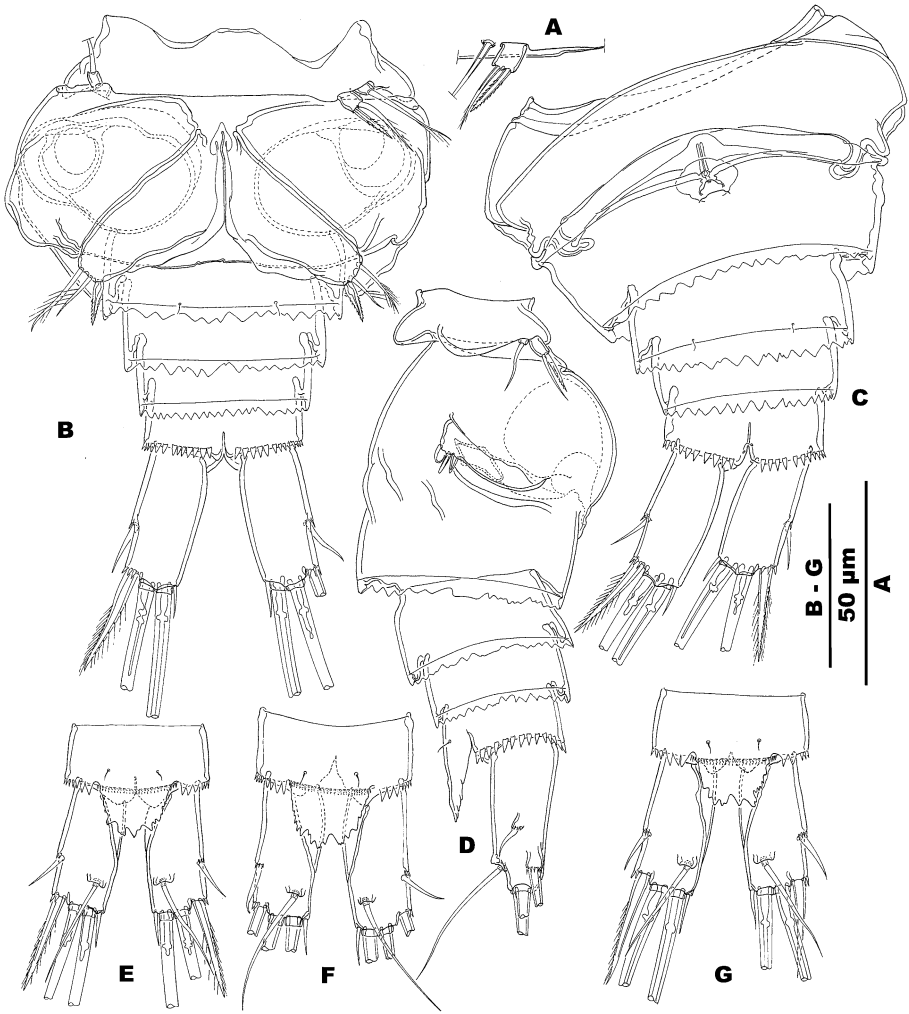


Fig. 2. *Apalachocyclops minotaurus* gen. n., sp. n. A, female left leg 5; B, male urosome, ventral; C, female abdominal somites, ventral; D, female urosome, lateral; E–G, anal somite and caudal rami of paratype specimens, dorsal (A, C, D: RBINSc COP 9200; B: RBINSc COP 9199; F–G: 2 males, 1 female from RBINSc COP 9201).

following somites; ventral surface inflated anteriorly, flat in posterior half (visible in lateral view); leg 6 vestiges located laterally, copulatory pore situated in middle of ventral surface at caudal side of inflated anterior half; posterior margin with wide, irregularly incised fringe; urosomites 4 and 5 narrow, parallel-sided with wide, irregularly incised posterior fringe; anal somite short, with large and broad caudally expanded anal operculum having

an irregular, sinuate border; posterior margin of somite completely set with distinct spinules.

Caudal rami cylindrical, twice as long as wide, divergent; anterolateral seta in distal half of margin with minute spinules at insertion; posterolateral element robust, slightly shorter than ramus, ornamented with fragile setules; with set of obvious spinules at insertion; medial terminal seta short, less than 1/4 of ramus length, setiform; median setae rigid, pinnate, with irregularly shaped breaking plane and short and narrow lumen; full lengths unknown (broken off in all specimens); dorsal seta arising from small socket, articulating on short quadrate basal part, and as long as ramus.

Antennule (fig. 3A, B) 11-segmented, not reaching proximal end of cephalothorax; first segment lacking ornament; armament (Roman numerals refer to segment number, Arabic numerals to number of setae, aesth. means aesthetasc): I(8)–II(4)–III(8)–IV(4)–V(1 + spine)–VI(2)–VII(3)–VIII(2 + aesth)–IX(2)–X(2 + aesth)–XI(7 + aesth); aesthetascs: narrow linguiform (segment VIII), filiform and short (on segment X) and short, tubiliform, fused at base forming terminal bithek (on segment XII); all setae short, rather stout, sparsely feathered; spiniform process on segment V prominent, blunt, with hyaline appearance.

Antenna (fig. 3C) lacking exopodal element and bearing single abexopodal seta on coxo-basis; endopodite segments with 1, 6, and 7 setae, respectively; no spinule pattern discernable on coxo-basis; outer margin of penultimate and ultimate segments set with spinules.

Mandible (fig. 3G) with slender gnathobasis; biting edge with sharp teeth and single accessory seta; palp with 3 elements: 2 long plumose ones, one short and smooth. Labrum (fig. 3K) with wide masticatory margin formed by 12 blunt teeth between 2 crescentic processes; surface sparsely furnished with hairs. Paragnath (fig. 3D) with 3 medial elements; subdistal inner process with a row of slender hairs. Maxillulary arthrite (fig. 3F) with 4 medial elements: 3 confluent and blunt smooth claws, and 1 spiniform articulating element; lateral margin with 4 spiniform uni-dentate teeth and 1 plumose stout seta. Maxillulary palp (fig. 3E) with 3 medial setae (2 pinnate, 1 smooth), one (pinnate?) outer lateral seta, and 3 long and sparsely plumed setae on uni-segmented endopodite; proximal half of stem of endopodal elements stout; surface of maxillulary palp devoid of ornamentation. Maxilla (fig. 3H) typically cyclopid; pre-coxa and coxa separated; elements on prae-coxal endite short, plumose (not illustrated); proximal element on distal coxal endite (fig. 3I) partially serrate and flagellated, accompanying seta smooth; claw



Fig. 3. *Apalachocyclops minotaurus* gen. n., sp. n. A, female antennule contour, dorsal view; B, first antennular segment of female antennule, ventral view; C, antenna; D, paragnath; E, maxillary palp; F, maxillary arthrite; G, mandible (setae on palp partially broken); H, maxilla; I, maxillary distal endite; J, maxilliped; K, labrum (A–K: RBINSc COP 9200).

with equal-sized minute teeth along inner margin; accessory basal claw stout, serrate on both sides; endopodite clearly 2-segmented, armed with 3 stout (2 serrate, 1 smooth) and two slender (naked?) setae; surfaces of components smooth. Maxilliped (fig. 3J) 4-segmented with (from proximal to distal) 2, 2, 1 and 2 setae, all furnished with few, widely spaced slender setules, except for smooth distalmost element.

Legs 1-4 (fig. 4A, B from male; C, D of female). Intercoxal plates with rounded distolateral edges and smooth surfaces; medial coxal element present in all legs, robust and pinnate; outer half of distal margin of coxae set with minute spinules, frontal and caudal surfaces smooth, except for a short median spinule row on caudal surface of leg 4; basis of leg 1 with medial spine reaching towards middle of second endopodite segment, serrate in proximal half, smooth distally; mediolateral margin of basis produced in triangular process; surface smooth, except in leg 1 and leg 3, both having a short spinule row near articulation with endopodite; medial edge of leg 1 basis crescentic, of legs 2-4 angular; outer seta on leg 1 basis long, on legs 2-3 moderately long, equal-sized; exopodites and endopodites 2-segmented; second endopodite segment with triangular outgrowth in middle of outer margin, reminiscent of outer distal edge of ancestral median segment; setal armament short, rather rigid, having a sturdy appearance; exopodite spine formula: 3.4.4.4, and seta formula: 5.4.5.5; complete armament listed in table I; leg 4 second endopodite segment 1.33 times as long as wide, bearing 2 sub-equal terminal spines: inner one longest, about 0.75 times the segment length; outer subdistal seta absent.

Leg 5 (fig. 2A) with obsolete basal segment, represented by a minute cylindrical socket bearing outer seta; distal segment inserted directly on posteroventral margin of somite, nearly quadrate, bearing an outer seta (2.5 times the segment length) and a long (2 times as long as segment) subdistal robust inner spine; basal segment remnant and distal segment nestled up against each other. Leg 6 (fig. 2D) represented as a long ovate transverse plate positioned in middle of lateral side of genital double-somite; bearing 3 appendages: a short seta (outmost) and 2 well developed blunt spiniform elements (middle and median ones); surface of valves smooth; seminal receptacle narrow, ribbon-shaped in fixed animals (probably expandable anterior region in inflated anterior part of genital double-somite: see dashed contour line in fig. 2D); copulatory pore and duct embedded in ovate area of tissue; duct rather long and straight; lateral arms distinct, slightly curved frontally.

Male. Habitus (fig. 1A, B) with same appearance as the female, but with separated urosomites 2 and 3; former one barrel-shaped, half as long as wide,



Fig. 4. *Apalachocyclops minotaurus* gen. n., sp. n. A, leg 1; B, leg 2 (second exopodite segment detached); C, leg 3, female (exopodite detached); D, leg 4, female (second exopodite segment detached) (A–B: RBINSc COP 9199; C–D: RBINSc COP 9200; A–C in frontal view; D, in caudal view).

TABLE I

Leg armament of female and male of *Apalachocyclops minotaurus* gen. n., sp. n.

	Female		Male	
	Exo	End	Exo	End
Leg 1	I.1–III.2.3	0.1–I.1 + 1.2	idem	idem
Leg 2	I.1–III.I + 1.3	0.1–I.1 + 1.2	idem	idem
Leg 3	I.1–III.I + 1.4	0.1–I.1 + 1.3	I.1–I.1–II.I + 1.3	0.1–0.1–I.1 + 1.2
Leg 4	I.1–III.I + 1.4	0.1–0.II.3	I.1–I.1–II.I + 1.3	0.1–0.1–0.II.2

equalling width of pediger 4; urosomite 3 narrow, parallel-sided, slightly wider than following somites; anal somite and operculum, caudal rami and armament, integument of somites and distribution and shape of hyaline fringes as in female; mean body length 440 μm , ranging from 400 to 478 μm ($n = 4$); principal terminal setae on caudal rami 180 μm and 290 μm (outer and inner one, respectively).

Antennule (fig. 5A) bigenulate, 16-segmented with conventional armature: I(8 + 2 aesth)–II(4)–III(2)–IV(2 + 1 aesth)–V(2)–VI(2)–VII(2)–VIII(2)–IX(2 + 1 aesth)–X(2)–XI(2)–XII(2)–XIII(2 + 1 aesth)–XIV(2 + 1 T-plate)–XV(1 + 2 T-plates)–XVI(11 + 2 aesth); aesthetascs on segments I, IV, IX linguiform (fig. 5B) and proportionally short; aesthetascs on segment XVI filiform (proximal one) and tubiliform (distal one).

Mouthparts and legs 1 and 2 (fig. 4A, B) as in female, see description above. Leg 3 (fig. 5C) prae-coxa, coxa, and basis as in female, but coxal medial element more inflated; exopodite and endopodite 3; armature formula in table I; medial setae on endopodite and exopodite inflated, lengths comparable with those of female; spines on exopodite longer and more robust than in female; inner subdistal seta short, half as long as segment at the most; densely plumose in distal half; medial terminal segment naked, half as long as previous element; outer distal segment hook-shaped, serrate along outer border; outer subdistal seta as in female.

Leg 4 (fig. 5D) with protopodal components as in female, except for the inflated appearance of the coxal medial seta; rami 3-segmented (armature formula in table I) with medial setae and outer spines equally modified as in leg 3; terminal spines on endopodite longer and more robust than in female; proportional lengths (inner/outer): 1/1.8 larger.

Leg 5 (fig. 2B) as in female. Leg 6 (fig. 2B) robust and represented as a large triangular plate with anterior angle situated close to anterior limits of somite; surface unornamented, but posterior border with distinct, sclerotized

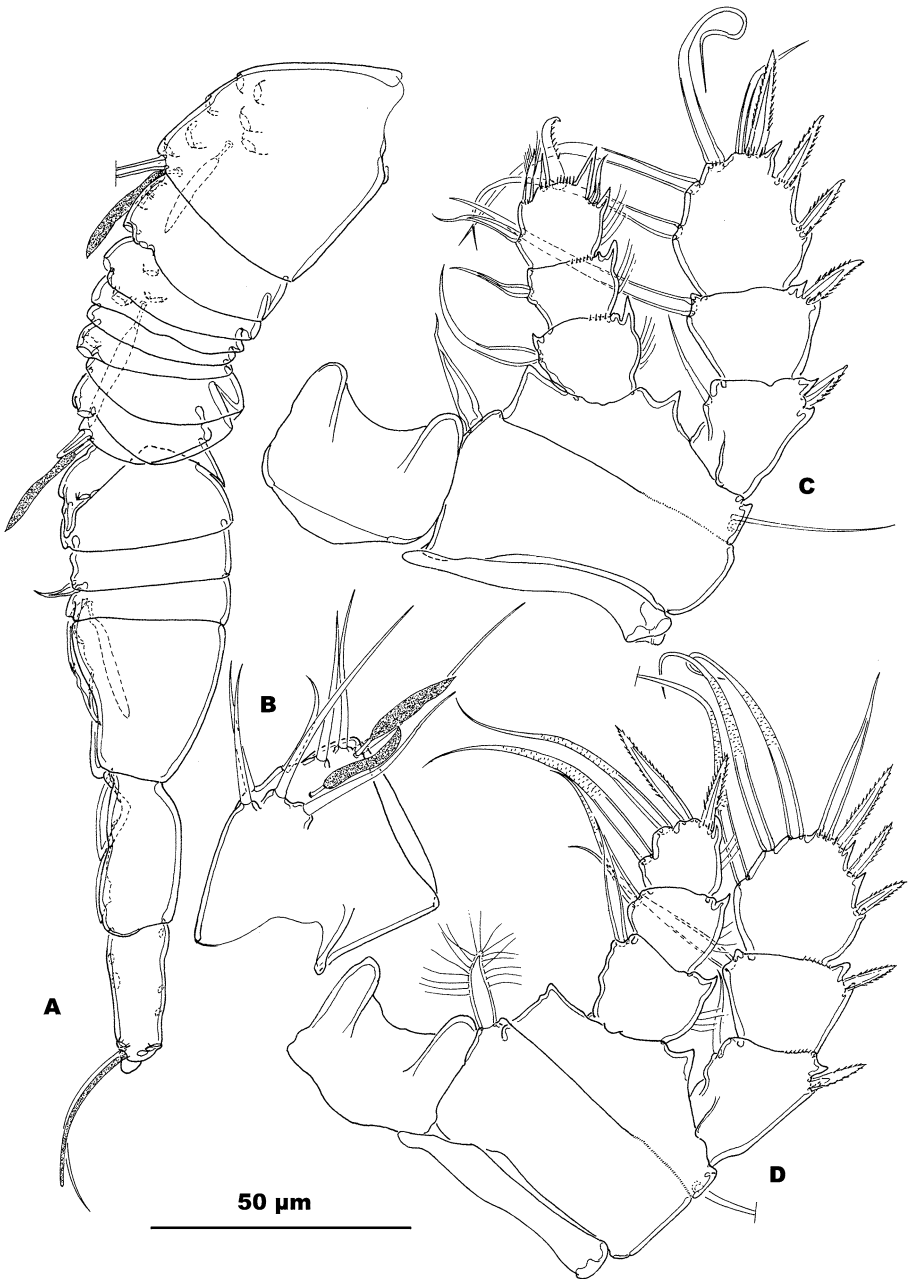


Fig. 5. *Apalachocyclops minotaurus* gen. n., sp. n. A, male antennule contour, dorsal view; B, first antennular segment of male antennule, ventral view; C, leg 3, male, frontal; D, leg 4, male, frontal (A–D: RBINSc COP 9199).

rim differentiating anterior thick part of valve from thin posterior border; armament consisting of 3 elements: an inner robust serrate spine and 2 slender pinnate setae, middle one shortest; spermatophores large and ovate, oriented with principal axis towards medial body axis.

Variability. — The rather wide range of body lengths (450-476 μm for the 2 females, 400-478 μm for the 4 males) clearly results from the expansion state of the body at fixation.

No variation is observed in body ornamentation (the irregularity of the incised fringes left aside) and appendage armature. The anal operculum appears to be variable, but is basically the same in all specimens observed. The variable aspect results solely from the irregular aspect of the incisions of the border.

Type locality. — Endless Caverns, Rockingham County, State of Virginia, U.S.A.

Etymology. — Specific epithet after the Greek mythological creature, “Minotaurus”, or the bull of King Minos of Crete, a creature with a large bull head, dwelling in the Cretan Labyrinth, chosen to make an allusion to the presence of the species in the underground labyrinth of its type locality, Endless Caverns. The name is to be treated as a noun in apposition with the generic name.

JUSTIFICATION AND DISCUSSION

In the absence of a modern systematic framework based on a sound character state analysis, the definition and positioning of a new genus among those currently recognized in the family Cyclopidae, remains provisional. For only a few is the generic definition fairly well established, for many, however, is the diagnosis vague or incomplete and rather controversial (Reid, 1993). This ambivalent situation is explicit for several cyclopine genera assembling one or more species known to occur in “marginal” habitats (see Reid, 2001 for an overview of such habitat types). The erection of a new genus, *Apalachocyclops*, to accommodate *A. minotaurus* sp. n. has to be seen within this context. In the following, a series of particular characteristics which are assumed to be relevant for the generic diagnosis are highlighted. Their importance, however, will have to be re-evaluated in view of the forthcoming revisions of several of the specialized genera.

Within the current systematic arrangement of the Cyclopidae, *Apalachocyclops* gen. n. is to be positioned in the subfamily Cyclopiniae: leg 5 with

a terminal segment bearing 2 elements and a male antennula with stalked linguiform aesthetascs, lacking particular modifications of the setae on its proximal segments. *Apalachocyclops* gen. n. lines-up with a suite of genera in which the ancestral basal segment of leg 5 is integrated within its pediger and represented by a remnant seta, and in which the (terminal) segment is a well defined article separated from the somite. Currently, up to 20 cyclopid genera possess a leg 5 morphology corresponding to this scheme. However, several of them can be ruled out as potential close relatives on the basis of the remote dorsolateral position of their basal seta (“thoraxborste”). Only a few, i.e., *Rybocyclops* Dussart, 1982, *Rheocyclops* Reid & Strayer, 1999, *Itocyclops* Reid & Ishida, 2000, and *Speocyclops* Kiefer, 1937 possess a leg 5 in which the remnant seta of the basal segment arises adherent to the terminal segment as is seen in *Apalachocyclops* gen. n. The terminal leg 5 segment in *Speocyclops* (in its type species *S. troglodytes* (Chappuis, 1923) and closest relatives) and *Rybocyclops* (in its type species, *R. pauliani* Lindberg, 1954) is far less prominent and rather compact. In some of the *Speocyclops* it appears to be coalescent with the pediger. In both other genera, the structure and appearance of the terminal segment are comparable, but the medial element is not a rigid serrate spine as in *Apalachocyclops* gen. n., but a slender, rather setiform, element.

Among the European Cyclopiinae, the leg 5 morphology in *Graeteriella* Brehm, 1926 reminds of that of *Apalachocyclops* gen. n. to some extent, but lacks the basal segment remnant seta. However, *Graeteriella rouchi* Lescher-Moutoué, 1968 and *G. bertrandi* Lescher-Moutoué, 1975 are known to show variation on this scheme as some specimens have been observed with the remnant seta still present, a condition considered as atavistic (Reid & Strayer, 1994). Re-examination of the type series of both species and observations made on additional material including several closely related, yet undescribed, species revealed that the remnant seta is a normal attribute of the morphology of leg 5. In combination with other features, *G. rouchi* and *G. bertrandi* appear now to be representatives of a particular lineage, nowadays coalesced within the *Graeteriella* complex.

Similarly, the genus *Speocyclops*, with more than 40 named species and subspecies, is an artificial species assemblage unifying at least two different lineages. The typical leg 5 morphology of *Speocyclops* (cf. *S. troglodytes* (Chappuis, 1923), pers. obs.) consists of a distinct, although small and short terminal segment with 2 apical elements, and the remnant seta on a short socket located close to the free segment. Both structures are located on the ventral side of the pediger. The leg 5 morphology of other forms nowadays

assigned to *Speocyclops* is fundamentally different as there is no trace of the original segments left, and the leg is positioned laterally on the pediger. This, in combination with other features, provides sufficient arguments to remove them from *Speocyclops* and reposition them, possibly as a separate genus, among the Cyclopinae (cf. Fiers & Pandourski, in prep.). Exemplary for this lineage is *Speocyclops lindbergi* Damian, 1957 described from Banat (Romania) and reported from several localities in the Stara Planina mountain chain in Bulgaria. In order to avoid confusion, and within the context of the present contribution, comparisons with *Speocyclops* refer to the morphology of its type species, *S. troglodytes*, except when stated otherwise.

These unresolved systematic issues make positioning of *Apalachocyclops* gen. n. among the other genera more difficult. In this regard, the herein used notation “speocyclopines” refers to an undefined and loose grouping of subterranean cyclopines which share a comparable habitus with a proportionally large genital somite, short caudal rami, and a distinct, more or less produced, anal operculum, combined with oligomeric natatory appendages.

Very few cyclopoids, in so far the habitus has been depicted, have such a gracious body shape as *Apalachocyclops* gen. n. The flattened and laterally expanded body with the smooth transition between prosome and urosome resembles mostly that of *Bryocyclops* (see the outstanding illustrations of some in Reid, 1999), *Graeteriella unisetiger* (Graeter, 1908) and *Goniocyclops silvestris* Harding, 1958. This type is unmistakably an indication of the substrate-bound way of life. With only a single species in *Apalachocyclops* gen. n. known thus far, it is difficult to evaluate the importance of this body type at the genus level. In *Speocyclops*, the species related to *S. troglodytes* vary largely in the degree of flattening and accentuation of the major body articulation. To the contrary, in *Bryocyclops* (groups I & II, *sensu* Lindberg, 1956) and those *Speocyclops* species close to *S. lindbergi*, the flatness of the body and the accentuation of the major body joint are stable features and seem particularly diagnostic.

Oligomerization of natatory leg segmentation is a well known phenomenon in the Cyclopidae. The reduction of the number of armature elements on the segments is generally strongly correlated and is a character state that has been convergently acquired in the various lineages. However, the absence of the outer subdistal seta on the terminal segment of the leg 4 endopodite (and leg 3 in a few cases) is quite uncommon. Besides the here described *Apalachocyclops* gen. n., only very few other cyclopines are known in which this element is not expressed. Thus far it has been observed in: *Rybocyclops pauliani* (Lindberg, 1954), *Haplocyclops (Kiefercyclops) fiersi* Karanovic & Ranga Reddy,

2005 and some members in the genera *Goniocyclops* Kiefer, 1955 and *Bryocyclops* Kiefer, 1927. The absence of this particular element on leg 4 is undoubtedly an advanced character state, but its loss happened independently as it is observed in, at least, three distinct cyclopine lineages (*Bryocyclops*–*Rybocyclops*/*Haplocyclops*/*Goniocyclops*), and is observed in some but not all the species in *Goniocyclops*. The absence of this armament element in *Apalachocyclops* gen. n. is assumed to have been evolved independently.

Relying uniquely on the female morphology, the separate status of this subterranean copepod would have passed undetected. The short and oligomerized legs with the reduced setal armament, the 11-segmented antennule, the leg 5 morphology, combined with the particular body shape and anal operculum, would have been sufficient arguments to arrange it in *Bryocyclops* s. lat. However, the particularities of the male appendages provide a number of character state transformations which clearly demonstrate the unique position of *Apalachocyclops* gen. n. In the following paragraphs these features are discussed and compared with their homologues expressed in other cyclopines.

Occurrence of sexually dimorphic modifications in the natatory legs is not a general phenomenon among the Cyclopidae. Small differences between the leg armament of both sexes (viz., armature elements with a different rigidity, ornamentation, and orientation) have been mentioned (Ishida & Ohtaka in Reid & Ishida, 2000 for *Cyclops* O. F. Müller, 1785; Fiers et al., 2000 for *Diacyclops* Kiefer, 1937) and may be more common than actually acknowledged (ex. some *Microcyclops*, unpubl. pers. obs.). This type of dimorphism is not expressed in *Apalachocyclops* gen. n.

Striking structural dimorphic differences in the legs of male and female affect the ramal segmentation of the legs (more segments in the males) or are expressed as particular modifications of one or more terminal armature elements on the male leg 3 endopodite. The occurrence of a different segmentation pattern in cyclopines has been reviewed by Reid & Strayer, 1994 (considering that *D. dimorphus* has now been transferred to *Reidcyclops* Karanovic, 2000; and adding the species of the recently erected *Rheocyclops*, see below). However, none of them shows the particular pattern as seen here for *Apalachocyclops* gen. n., in which both the exopodite and the endopodite of both legs 3 and 4 are trimerous in the male, where their female counterparts are bimerous. To some extent, comparable dimorphic patterns are known for a few European subterranean cyclopines: *Graeteriella unisetiger* possesses a (exo/end) 2/2 segmentation pattern in the female leg 4, but a 3/2 combination in the male; the females of *G. brehmi* and *G. rouchi* have a 2/2 leg 4 segmentation pattern but

a 3/3 combination in the male; and the males of the two European *Reidcyclops* have legs 3 and 4 with a 3/2 ramal combination instead of the 2/2 pattern in the female. *Apalachocyclops* gen. n. can, however, not be attributed to these genera (viz., mouthpart and leg 5 morphology, male characteristics of the leg 3 endopodite armature).

The similarities of the leg 4 exopodite segmentation pattern between the present genus and the North American *Reidcyclops dimorphus* (for which the generic re-allocation to its current genus is most debatable) are considered here as a coincidence, because the latter is assumed here to be a descendant from the *jeanneli* species-group of *Diacyclops*, widely distributed in the area known as the Interior Low Plateau (Lewis & Reid, 2007). The similarities of dimorphic leg segmentation in *Rheocyclops hatchiensis* seems more relevant. Legs 3 and 4 in the *R. hatchiensis* male differ from their female counterparts in the 3-segmented nature of their exopodite, whereas the endopodites remain, however, unchanged. Thus far, males of only 2 species out of 5 attributed to *Rheocyclops* are known (Reid et al., 1999). Males of an as yet undescribed species lack, just as its closest relative, *R. virginianus*, dimorphic modifications on the legs (unpubl. pers. obs.). *R. hatchiensis* is the only representative that displays a sexually dimorphic segmentation pattern. This, in combination with the plesiomorphic leg armature (medial seta on proximal exopodite segment in legs 1-4 present), the advanced aspect of the confluent terminal segment of leg 5, and the ventrolateral position of the female leg 6 vestiges (resembling *Speocyclops*), are character states raising doubts about its position in the genus *Rheocyclops*. Although there is a certain morphological resemblance between *R. hatchiensis* and *A. minotaurus* (viz., body flatness, dimorphic ramal segmentation, mouthpart morphology), the trimerous condition of the male leg 3 and 4 endopodites and the modified armature elements in the male leg 3 endopodite of the latter, are grounds to assume both have different roots among the cyclopinas.

Sexual dimorphism that affects the structure of the terminal armature elements of the male leg 3 endopodite is, just as for the previous type, not commonly observed among cyclopinas. Such modifications have been documented to be a notoriously characteristic of *Bryocyclops* s. str. (see Reid, 1999), and have been described for the European members of *Reidcyclops* Karanovic, 2000, *Palaeocyclops* Monchenko, 1972, *Itocyclops* Reid & Ishida, 2000, *Rybocyclops pauliani* Lindberg, 1954, and *Speocyclops lindbergi* Damian, 1957 (for the last one: Fiers & Pandourski, in prep.). In *Reidcyclops* and *Rybocyclops* the dimorphic modifications affect the outer terminal element only:

this (at least in *R. pauliani* and *R. imparilis* (Monchenko, 1985)) is considerably shorter than in the female, serrate along the outer margin only, and has a rather claw-shaped aspect. The terminal inner seta and the medial setae on the segment are not affected and are identical in both males and females. The modification of the outer terminal element in the North American populations of *Itocyclops yezoensis* is comparable, but the medial armature elements are lost. Whether this is an infra-specific modification or not, this type appears to be unique (Oriental populations lack sexual modifications on leg 3, see Reid & Ishida, 2000; Lee et al., 2004). In *Bryocyclops* s. str., *Palaeocyclops*, and *S. lindbergi* both terminal elements (the inner one, often minute, has been overlooked in most cases, pers. obs.) and one or more medial elements are sexually modified. Moreover, in *Palaeocyclops* and *S. lindbergi* the outer subdistal element differs from the female homologue. In contrast, the outer subdistal armature element in the *Bryocyclops* male leg 3 displays no particular modifications. The structural modifications of the terminal elements observed for *Apalachocyclops* gen. n. coincide largely with the transformations observed in the males of *Palaeocyclops* and *S. lindbergi*. Direct affinities between these three cyclopines, based on these structural resemblances, are not envisaged. The resemblance of these modifications in the North American species and in the south-eastern part of the Palaearctic (nearly perfectly coinciding with the Ponto-Aral subregion) is considered a convergently evolved specialization in spermatophore transfer.

Most intriguing is the fact that both types of sexual modification (i.e., segmentation and armature differences) are expressed in *Apalachocyclops* gen. n. The markedly different shape of the leg 4 endopodite in male and female of certain *Bryocyclops* (and *Hesperocyclops* Herbst, 1984, which lacks modifications on the leg 3 endopodite) is not comparable and is assumed to have a different origin and function than the structural differences (trimerous) expressed in the male leg 4 endopodite of *Apalachocyclops* gen. n.

In conclusion, *Apalachocyclops minotaurus* sp. n. clearly is a specialized subterranean cyclopine characterized by a series of advanced features. Salient features are listed and compared with the homologues in other genera, summarized in table II. The present genus, however, still possesses a remarkable series of features which clearly resemble the cyclopid ground pattern. The mandible with its fully equipped palp, the presence of a medial seta on the proximal exopodite segment of each leg, the complete setation of the antennula, and the lateral position, in the same transversal plane as the copulatory pore, are traits pointing to the cyclopine basic morphology, and feeds the assumption that

TABLE II
Salient characteristics of *Apalachocyclops* gen. n., *Speocyclops*, *Itocyclops*, and *Rheocyclops* (based on personal observations; literature data are marked with *; features listed for *Speocyclops* are those of the type-species, *S. troglodytes* Chappuis)

	<i>Apalachocyclops</i>	<i>Speocyclops</i>	<i>Itocyclops</i>	<i>Rheocyclops</i>
Body appearance	Strongly depressed	Depressed, fusiform	Depressed, fusiform	Fusiform
Pro-urosome articulation	Accentuated	Not accentuated	Not accentuated	Slightly accentuated
A2 coxobasis	1 abexopodal seta	2 abexopodal setae	2 abexopodal setae	1 abexopodal seta
A2 endopodite 2	6 setae	6 setae	7 setae	6 setae
Mandible palp	Palp + 3 setae	Palp absent, 0 setae	Palp absent, 1 seta	Palp, 3 setae
Maxillar endopodite	2-segm. (3 sp + 2 setae)	2-segm. (2 sp + 3 setae)	1-segm. (2 sp + 3 setae)	2-segm. (2 sp + 3 setae)
Maxillipedal armament	2.2.1.2	1.1.1.2	2.1.1.2/2.1.1.3*	2.2.1.2/2.1.1.3*
♀ seminal receptacle, and leg 6 position	Narrow, legs 6 lateral	Central expanded, legs 6 ventral	Narrow, legs 6 dorsal	Largely expanded, legs 6 lateral
Leg 5 terminal segment	1 seta + 1 spine	2 setae**	2 setae**	2 setae**
♀ leg segm. 1-4: exo/end	2/2.2/2.2/2.2/2	2/2.2/2.2/2.2/2	2/2.2/2.3/2.3/2	Combinations of 2-3/3-2
♂ leg segm. 1-4: exo/end	2/2.2/2.3/3.3/3	2/2.2/2.2/2.2/2	2/2.2/2.3/2.3/2	Combinations of 2-3/3-2
♂ leg 3 modifications	Setae modified + hook	No transformations	Loss of setae + hook*	No transformations

* According to Reid & Ishida, 2000 (for *Itocyclops*, population dependent, see text) and Reid et al., 1999 (for *Rheocyclops*).

** The medial element has not the rigid and serrate appearance of a typical spine.

Apalachocyclops gen. n. branched off at an early stage in the evolutionary history of the Cyclopinae. These features fundamentally distinguish *Apalachocyclops* gen. n. from more advanced genera such as *Bryocyclops*, *Speocyclops* sens. lat., and *Itocyclops* to which it resembles at first glance.

Unfortunately, *Apalachocyclops* gen. n. is difficult to position among the other cyclopine genera in the absence of a coherent and well founded systematic arrangement of the group. However, the striking resemblances between this Nearctic representative and the “speocyclopines” known from the Old Continent could be an inspiring illustration of how certain morphological features convergently evolved once an ancestral lineage entered the subterranean realm at a regional scale, and got adapted to this mysterious and hidden environment.

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