Prehendocyclops, a new genus of the subfamily Halicyclopinae (Copepoda, Cyclopoida, Cyclopidae) from cenotes of the Yucatan Peninsula, Mexico

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SARSIA

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Prehendocyclops, a new genus of Halicyclopinae, is described from cenotes of the Yucatan Peninsula, Mexico. Within the subfamily, the new genus resembles *Halicyclops*, *Colpocyclops*, and *Smirnoviella* in body shape as well as structure of the antennule and legs 1 to 5. In addition, *Prehendocyclops* shares with the latter two genera modifications in the antenna and mouth parts, which are here interpreted as structures used to hold onto some external part of a host. The possible host for the genus remains unknown. *Prehendocyclops* is characterized mainly in having an antennal prehensile device formed by a stout curved spine on the third segment, and the three proximalmost appendages of the terminal segment modified into stout, heavily serrate spines; the distalmost spine of these is claw-shaped. In addition, on the praecoxal arthrite of the maxillule the two outermost apical spines are curved towards a strong, straight, pointed spine inserted on the inner surface of the arthrite. The three species of *Prehendocyclops* described here (*P. monchenkoi*, *P. boxshalli*, and *P. abbreviatus*) can be separated from each other by a combination of characters found in the integumental pore pattern of the body surface and legs 1-4, the number of tergal integumental windows, the shape of the seminal receptacle, and the armament of the caudal ramus, antenna, mouth parts, and legs 1, 4, and 5 of both sexes, as well as legs 5 and 6 of males.

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INTRODUCTION

To date, Halicyclopinae includes five valid genera of cyclopids. *Halicyclops* Norman, 1903 is the most diversified genus, with more than 70 taxa inhabiting estuaries, coastal lagoons, anchialine caves, and interstitial water of beaches around the world from 60°N to 45°S, approximately. *Neocyclops* Gurney, 1927 is represented by 7 species allocated to the subgenus *Protoneocyclops* Petkovski, 1986, 6 in the subgenus *Neocyclops,* and 3 species not yet ascribed to any of the 2 mentioned subgenera, because their males remain unknown (Petkovski, 1986). *Colpocyclops* Monchenko, 1977, as well as *Smirnoviella* Monchenko, 1977, each with 2 species, are restricted to the coastal area of the Ponto-Caspian region. More recently, Rocha & Iliffe (1994) proposed the genus *Troglocyclops* to accommodate a very primitive halicyclopine from an anchialine cave on Eleuthera Island, Bahamas.

Knowledge of the copepod fauna of Yucatan Peninsula was summarized by Suárez-Morales & al. (1996). The new genus described here, represented by 3 species, was found living together with *Halicyclops cenoticola* Rocha (Rocha & al. 1998) in several cenotes from the peninsula, as well as individuals of the family Speleoithonidae, the latter to be dealt with in another paper.

MATERIAL AND METHODS

Whole specimens were examined in temporary lactic acid mounts in different positions (see Rocha 1995b). After examination the specimens were preserved in 70 % ethanol.

The figures were made using an oil immersion lens and a camera lucida on a Leitz Laborlux D phase-contrast microscope.

Material is deposited in the National Museum of Natural History (NMNH), Washington, USA.; Museu de Zoologia of the University of São Paulo (MZUSP), São Paulo, Brazil; and El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico.

Habitat description

The cenote Grutas de Santa Maria is located on the northwest edge of the village of Homun, State of Yucatán. The entrance consists of a 2 m deep, 4 m diameter sinkhole with a breakdown slope descending into a chamber about 15 m in diameter. Two passages extend off from this room. One is partially blocked by a flowstone-encrusted Mayan wall, while the other leads to 2 deep clear pools. The first of these pools is 15 m long by 5 m wide and more than 10 m deep where it opens into a large underwater chamber. The floor of the pool consists of sunken calcite rafts and breakdown at time of collection. The water was very clear. Mysids (*Antromysis cenotensis* Creuser, 1936), juvenile amphipods (*Mayaweckelia cenoticola* Holsinger, 1977), cladocerans and ostracods were also collected from the pool. The cyclopoid copepod *Halicyclops cenoticola* Rocha, 1998 was recently described from this cave (Rocha & al. 1998).

The cenote Grutas de Tzab-Nah is located 2 km south of the village of Tecoh on the road to Telchaquillo, State of Yucatán. The 1.8 m high by 3 m wide entrance is in a gently sloping sink, 100 m east of the road. To the left, a walking passage in the cave leads to a bridge across a 7 m deep chasm with a lake at the bottom. Across the bridge and to the right, the main passage of the cave continues past several deep fissure pools and 2 crawlways to a 30 m diameter lake. Two artificial well shafts enter this large chamber at opposite ends of the lake. Underwater, the sandy bottom of the lake slopes down to a 20 m wide submerged cave entrance at 15 m depth. This underwater passage of solutional origin continues for 130 m to 33 m depth where it abruptly ends. While the water in this section of the cave is exceptionally clear, other pools in the cave are murky and have a thick scum at the surface. This pollution apparently arises from liquid wastes from a heniquen sisal processing plant located above the cave. Aquatic fauna reported from the cave by Reddell (1977) included mysids (*Antromysis cenotensis*), amphipods (*Mayaweckelia cenoticola*), atyid shrimps (*Typhlatya mitchelli* Hobbs & Hobbs, 1976; *T. pearsei* Creaser, 1936), palaemonid shrimps (*Creaseria morleyi* Creaser, 1936), blind eels (*Ophisternon infernale* Hubbs, 1938) and brotulids (*Typhliasina pearsei* Hubbs, 1938). Copepods collected from this cave include the cyclopoids *Macrocyclops albidus* (Jurine, 1820), *Thermocyclops inversus* Kiefer, 1936, *Mesocyclops chaci* Fiers, 1996, *M. yutsil* Reid, 1996, *M. longisetus* (Thiébaud, 1914), *M. reidae* Petkovski, 1986, and *Halicyclops cenoticola* (Suárez-Morales & al. 1996; Fiers & al. 1996; Rocha & al. 1998). In addition, ostracods, isopods (*Creaseriella anops* Creaser, 1936; *Haptolana bowmani* Botosaneanu & Iliffe, 1997) and thermosbaenaceans were also collected from the last lake.

Cenote Kambul (= Cenote Noc Ac) is located 1 km south of the village of Noc Ac, State of Yucatán. The circular, 4 m diameter sinkhole entrance lies directly above a clear deep pool. The depth from the surface of the ground to water level is 3 m. Below the entrance, water depths are 3 m. The rock surrounding the entrance sinkhole is undercut so that a room 22 m long by 14 m wide is present at water level. Directly beneath the entrance, the floor of the pool consists of gravel. Detrital organic matter and large breakdown boulders cover the bottom in areas under the ledge. The water is very clear. At opposite ends of the pool, segments of the cave continue down over breakdown to 35 and 21 m depths but no passage development was found. Numerous fish are present in all sections of the entrance pool. Isopods (*Creaseriella anops* and *Haptolana bowmani*) and shrimp (*Typhlatya* sp.) were collected from the deeper waters in darkness. Copepods collected from this cave include the cyclopoids *Macrocyclops albidus*, *Tropocyclops prasinus* aff. *aztequei* Lindberg, 1955, *Mesocyclops yutsil*, and *Halicyclops cenoticola* (Suárez-Morales & al. 1996; Fiers & al. 1996; Rocha & al. 1998).

Cenote Yuncú is located about 1.5 km west of Yuncú, State of Yucatán, on the west side of an abandoned railroad right-of-way running north to south. The entrance consists of a vertical pit, 7 m in diameter and 10 m deep, descended by a ladder made from railroad track. At the bottom of the ladder, a breakdown slope descends to the edge of a U-shaped pool that continues 3/4 of the way around the northern side of the 40 m long by 37 m wide entrance chamber. Large, 1-3 m diameter stalagmitic columns are present in the rear of this chamber. The pool on the east side of the chamber is very shallow, averaging about 1 m deep. However, on the west side, the pool extends down to over 30 m depth where it pinches out between breakdown and the bedrock wall. Large stalactites and stalagmites are present in the submerged parts of the cave. Copepods collected from this cave include the calanoid *Mastigodiaptomus nesus* Bowman, 1986, and the cyclopoids *Macrocyclops albidus*, *Tropocyclops prasinus* aff. *aztequei*, *Diacyclops chakan* Fiers & Reid, 1996, *Mesocyclops yutsil*, *Paracyclops fimbriatus chiltoni* (Thompson, 1882), and *Halicyclops cenoticola* (Suárez-Morales & al. 1996; Fiers & al. 1996; Rocha & al. 1998). Mysids (*Antromysis cenotensis*), ostracods, thermosbaenaceans, amphipods, and isopods (*Creaseriella anops* and *Haptolana bowmani*) were also collected from the pool.

Cenote Chan-Hoch is located on a small ranch at the southeast edge of the village of Homun, State of Yucatán. The cenote consists of a 15 m diameter, 13 m deep sinkhole reaching a very clear, deep pool. Using roots, it is possible to free-climb down to the edge of the 12 m long by 6 m wide pool. Maximum depth was 12 m at the entrance to a large underwater cave entrance leading into a huge black room. A smaller underwater entrance and an alcove in darkness were also present. Visibility was 15 m or more. A large root mass hung down into the water on one side of the pool. Copepods collected from this cave include *Mesocyclops longisetus curvatus* Dussart, 1987, *Diacyclops chakan*, and *Tropocyclops extensus* (Kiefer, 1931) (Suárez-Morales & al. 1996; Fiers & al. 1996). Also collected from the pool were ostracods, mysids (*Antromysis cenotensis*), thermosbaenaceans, aquatic mites, and shrimp (*Typhlatya* sp.).

Cenote Tos Virlol is located 0.5 km east of Kilometer 129 on the highway from Señor to Felipe Carrillo Puerto and about 13 km south of Señor, State of Quintana Roo. The entrance consists of a 4.2 m diameter circular opening. From this point, the cave drops vertically for 12 m to a deep pool about 25 m in diameter. Large numbers of cirolanid isopods (*Creaseriella anops*), atyid shrimp (*Typhlatya pearsei*), and palaemonid shrimp (*Creaseria morleyi*) were reported from the pool by Reddell (1977). Ostracods, thermosbaenaceans and mysids (*Antromysis cenotensis*) were also collected from the cave along with other copepods including *Mesocyclops longisetus curvatus*, *M. reidae*, and *Tropocyclops prasinus* (Suárez-Morales & al. 1996).

TAXONOMY

Order Cyclopoida

Family Cyclopidae

Subfamily Halicyclopinae

Prehendocyclops gen. nov.

Diagnosis. Urosomal somites 3 and 4 without integumental sensilla on dorsal surface. Implantation area of middle apical setae on caudal ramus expanded forward reaching insertion site of dorsal seta. Inner middle apical caudal seta much stouter and longer than outer seta. No breaking planes in middle apical caudal setae. Seminal receptacle conspicuous, consisting of short copulatory duct connecting copulatory pore to lobed anterior expansion, and pair of convoluted receptacle ducts leading to genital antra; normally present pair of transverse ducts leading the copulatory duct directly to each genital antrum absent. Anal somite shorter than half of length of precedent urosomal somite. Anal pseudoperculum absent. Antennule of 6 segments in female and 14 in male; male antennule with only 1 and 2 aesthetascs on penultimate and terminal segments respectively. Antenna of 4 segments, with prehensile device formed by stout spinulose spiniform seta located on inner corner of third segment and curved toward set of 2 spinulose spines and 1 claw located on proximal expansion of inner margin of last antennal segment. Maxillular arthrite bearing 6 setae on inner surface and 4 spines at apex, innermost spine much more developed than others. Maxillular palp with spinulose short spine on basis. Maxilla armed with thick setae; basal endite with 3 articulated setae. Maxilliped of 2 segments; proximal segment unarmed. Leg 1 with 1 inner seta on endopod 2. Leg 5 exopod with 3 spines and 1 or 2 setae in female; 3 spines and 2 setae in male.

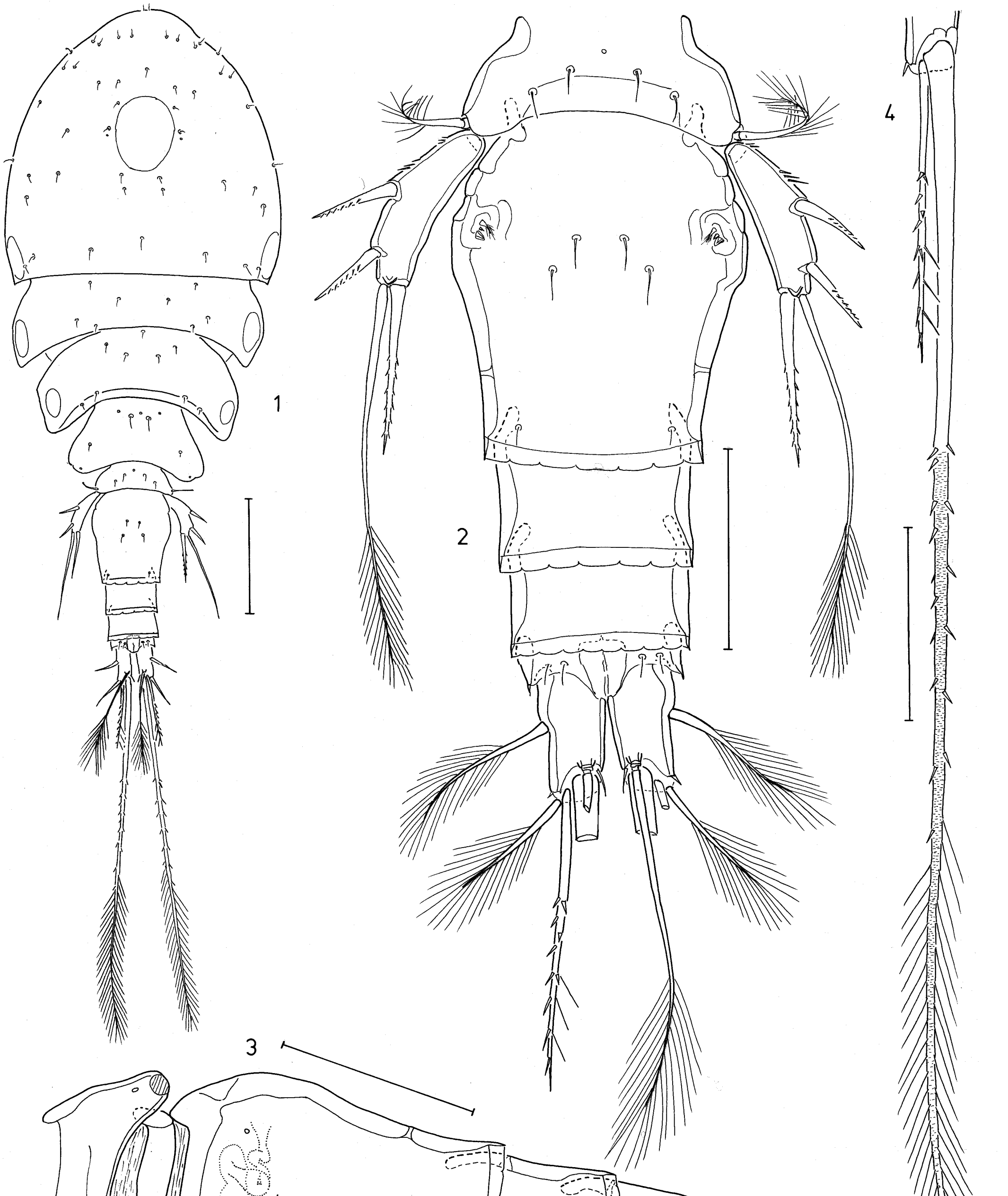
Type species: *Prehendocyclops monchenkoi* Rocha.

Etymology. The generic name (from the Latin *prehendere*, to grasp) alludes to the prehensile device on the antenna.

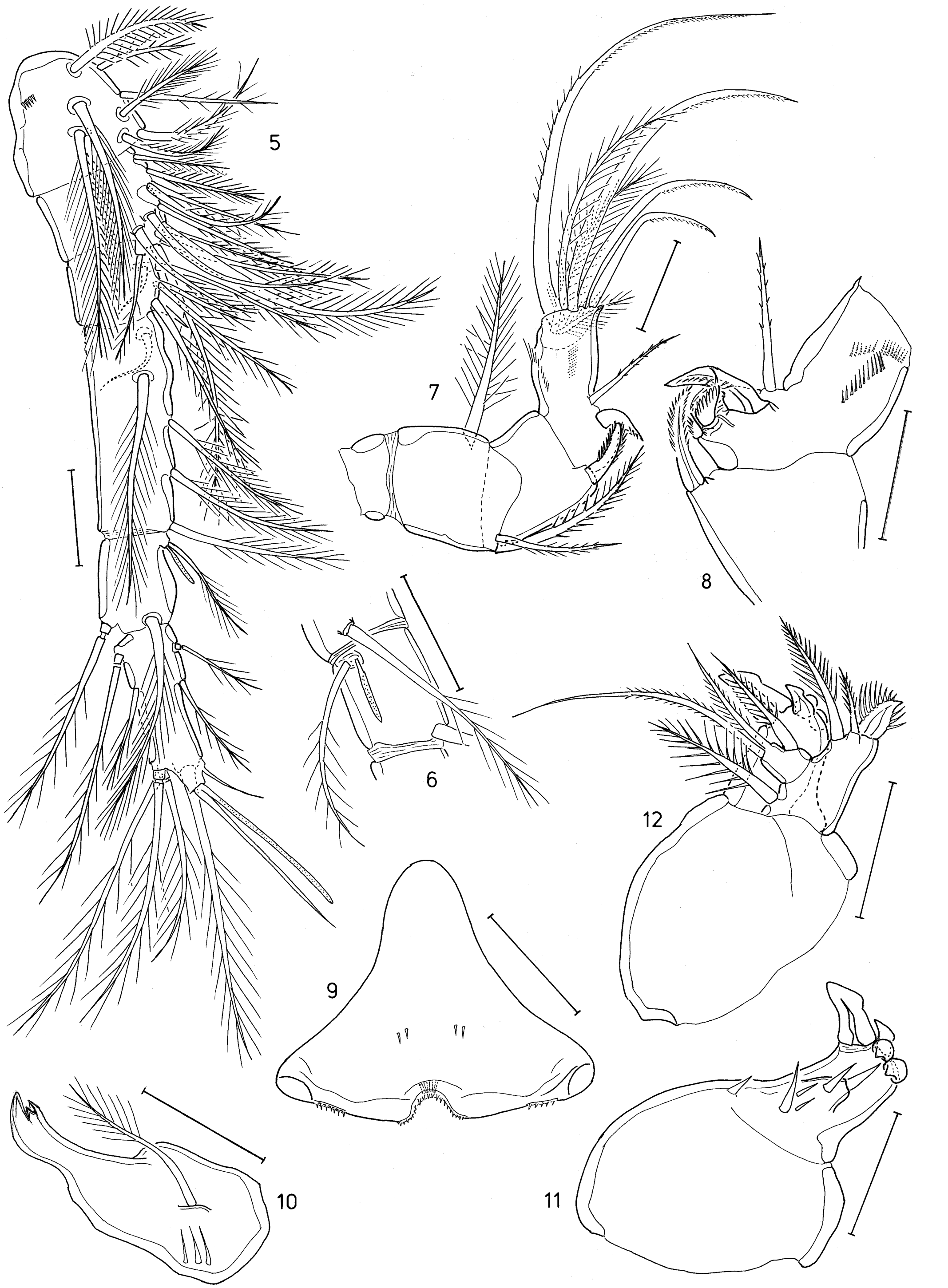
Prehendocyclops monchenkoi Rocha, sp. nov.
(Figs 1-22)

Material examined. Mexico, Yucatán: Grutas de Santa Maria, Homun (20°44'29"N, 89°17'28"W) 21 June 1991, 1 male from sample #91-016 collected with 93 µm mesh plankton net from water column and sand bottom of cave pool in 0-6 m water depths; Grutas de Tzab-Nah, Tecoh, (20°44'08"N, 89°28'23"W), 27 June 1991, 5 females and 1 male from sample #91-021 collected with 93 µm mesh plankton net from water column and sand bottom of cave pool in 0-8 m water depths; Cenote Yuncú (20°34'51"N, 89°36'46"W), 13 August 1994, 1 female and 3 males from sample #94-023 collected with 93 µm mesh plankton net from water column of cave pool in 0-5 m water depths. Quintana Roo: Cenote Tos Virlol, Felipe Carrilo Puerto, (19°41'10"N, 88°4'00"W), 16 June 1992, 1 female from sample #92-003 collected with 93 µm mesh plankton net from water column of cave pool in 0-8 m water depths. All material collected by T.M. Iliffe. Female holotype (USNM 287094) and 8 paratypes (USNM 287095, 287096) in NMNH; 2 paratypes (ECO-CHZ 00498) in ECOSUR; and 2 paratypes in MZUSP (13060).

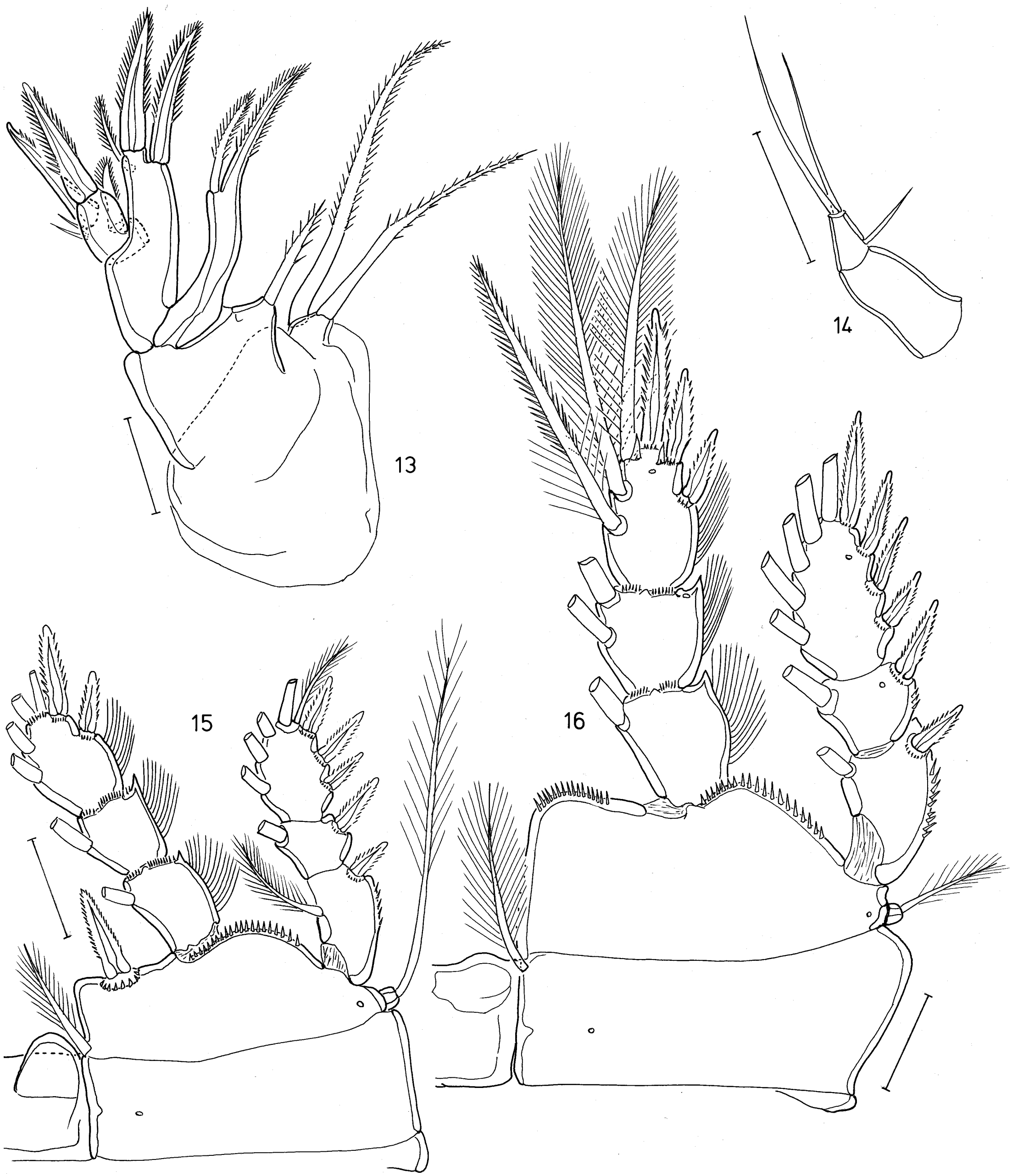
Female. Body length, excluding caudal setae, ranging from 505 µm in very contracted specimen to 650 µm in extended specimen. Prosome: urosome ratio 1.94-2.32 : 1. Prosome with integumental sensilla pattern as shown in Fig. 1. Cephalothorax (Fig. 1) bearing dorsal middle integumental window and pair of lateral integumental windows at posterior corners; 2 subsequent prosomites each with pair of lateral integumental windows. Urosome with following arrangement of integumental sensilla (Figs 2 and 3): 5 dorsal and 2 ventral on first somite; genital double somite with 4 sensilla at level of genital pores and posterior pair on dorsal surface, 2 ventral pores



Figs 1-4. *Prehendocyclops monchenkoi* Rocha, sp. nov., female. 1. Habitus, dorsal. 2. Urosome, dorsal. 3. Urosome, ventral. 4. Middle apical caudal setae, dorsal. Scale bars = 100 µm (Fig. 1); 50 µm (Figs 2-4).



Figs 5-12. *Prehendocyclops monchenkoi* Rocha, sp. nov., female. 5. Antennule, ventral. 6. Fifth segment of antennule, showing bithek composed of seta and aesthetasc, frontal. 7. Antenna, posterior. 8. Endopod of antenna, showing prehensile device, anterior. 9. Labrum, ventral. 10. Mandible, posterior. 11. Maxillular arthrite, inner. 12. Maxillule, outer posterior. Scale bars = 20 μm.



Figs 13-16. *Prehendocyclops monchenkoi* Rocha, sp. nov., female. 13. Maxilla, posterior. 14. Maxilliped, outer posterior. 15. Leg 1, anterior. 16. Leg 2, anterior. Scale bars = 20 µm.

beside seminal receptacle, and pair of slits laterally; urosomal somite 3 and 4 bearing 1 pair of lateral slits each; anal somite with 2 pairs beside anal area and another pair ventrally; caudal ramus with ventral pore at level of insertion of lateral caudal seta. Posterior borders of all prosomites and first urosomite smooth (Fig. 1). Hyaline frills of genital double somite and 2 subsequent somites (Figs 2 and 3) with wide flat indentations. Genital double somite (Figs 2 and 3) about 1.2 times longer than wide. Seminal receptacle as shown in Fig. 3. Copulatory pore located in external depressed area posterior to seminal receptacle. Copulatory duct straight.

Anterior portion of receptacle expanded into 4 lobes and connected to lateral genital antra by coiled receptacle ducts. Posterior expansion of seminal receptacle as well as transverse ducts commonly found in family Cyclopidae absent. Anal somite about 2.5 times wider than long and little shorter than half of length of precedent urosomal somite.

Caudal rami (Figs 2 and 3) 2 times longer than wide. Lateral seta little longer than ramus (1.15 : 1). Outermost apical seta as long as ramus and 5.7 times longer than innermost apical seta. Dorsal seta inserted on protuberance placed halfway between level of insertion of lateral caudal seta and distal ventral end of ramus, and reaching slightly beyond tip of outer middle apical seta. Inner middle apical seta (Fig. 4) about 3.5 times thicker near base and 4.5 times longer than outer middle apical seta; armament as follows: proximal 1/3 smooth; middle 1/3 sparsely spinulose and terminal 1/3 plumose. Outer middle apical seta (Fig. 4) sparsely spinulose on outer margin and with 3 setules on inner margin of terminal part.

Antennule (Figs 5 and 6) of 6 segments, and armed as follows: 8 + short comb of spinules, 12, 5 + spine, 5, 3 + aesthetasc, 10 + aesthetasc. Segment 4 about 2.5 times longer than wide.

Antenna (Figs 7 and 8) consisting of 4 segments. Coxa reduced and unarmed. Inner corner of basis bearing 2 setae armed with stiff setules; longest seta 1.5 times longer than shortest seta and almost reaching tip of spiniform seta located on inner corner of proximal endopod segment. Seta representing exopod armed with stiff setules. Proximal endopod segment bearing heavily serrate curved spiniform seta directed toward spinulose claw on inner margin of terminal segment. Terminal endopod segment bearing 7 setae around apex and 2 spinulose spines, 1 spinulose claw, and 1 sparsely setulose seta on expanded portion of inner margin; seta about 1.4 times longer than claw. Distal portion of terminal segment beyond insertion site of seta on inner margin about 1.3 times longer than broad.

Labrum (Fig. 9) with group of spinules on each side of posterior rim and spinulose medial depression; ventral surface bearing 2 pairs of setules.

Mandible (Fig. 10) composed of gnathobase and palp represented by seta implanted directly on coxa. Gnathobasic armament consisting of strong acute spine and 2 short spines.

Maxillule (Figs 11 and 12) comprised of praecoxa and 2-segmented palp. Praecoxal arthrite with 3 spines fused to segment (2 of them curved inward) and 1 articulated spine on apex; inner surface armament consisting of 6 setae; distalmost seta stiff, implanted on protuberance, and directed toward 2 curved apical spines of arthrite. Palp composed of basis bearing stout pectinate spine and 2 setulose setae on inner margin, and 1 proximal outer seta representing exopod; endopod 1-segmented, with 3 setae.

Maxilla (Fig. 13) 4-segmented. Praecoxa fused to coxa on posterior surface and with 2 setae on endite similar in length and ornamentation. Coxa armament consisting of 1 seta inserted on proximal endite and 2 distal setae on well developed distal endite, one of the latter setae fused to endite. Basis expanded and armed with 3 setae; 2 strong setae similar in length. Endopod carrying 2 short outer naked setae, 1 inner seta of intermediary size, and 2 apical setae.

Maxilliped (Fig. 14) 2-segmented. Basal segment unarmed. Terminal segment with 1 inner proximal seta and 2 apical setae.

Legs 1-4 (Figs 15-17) armed as in Table 1. Leg 1 basis with spine inserted at inner corner (Fig. 15) reaching distal edge of proximal endopodal segment, and outer seta extending beyond end of exopod. Endopod 3 of legs 2 and 3 (Fig. 16) with proximalmost seta spiniform, plumose basally and with stiff setules distally. Both inner setae of leg 4 endopod 2 plumose (Fig. 17). Leg 4 endopod 3 (Fig. 17) about 1.6 times longer than wide; inner apical spine as long as or little longer than segment, and 1.65 times longer than outer apical spine. Inner proximal seta stiff, armed with sparse long flexible setules basally and stiff setules terminally. Inner distal seta plumose, 1.2 times longer than inner proximal seta.

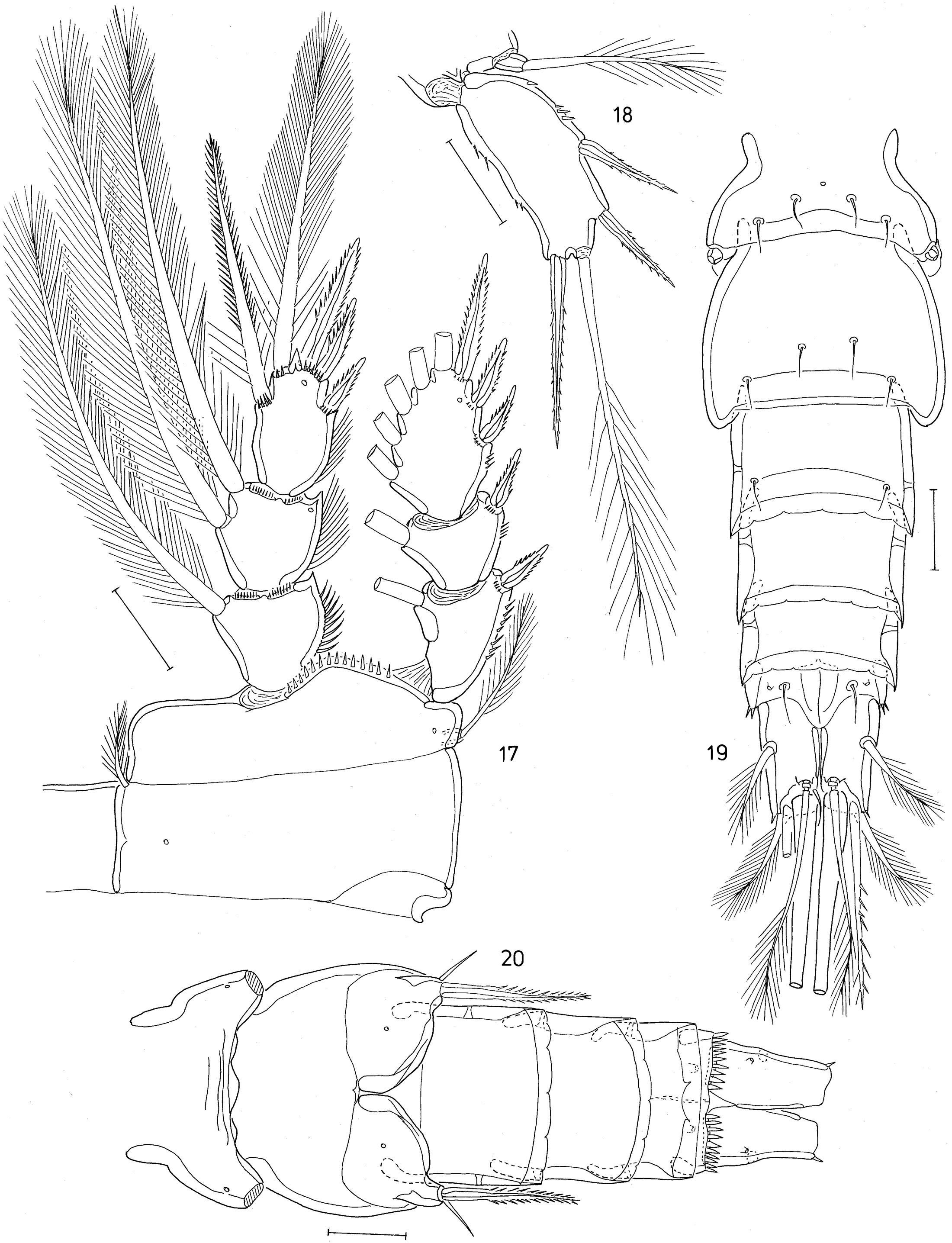
Legs 1-4 bearing the following arrangement of integumental pores on anterior surface. All legs with pore on coxa near articulation of intercoxal sclerite, and another on basis near insertion of outer seta. Leg 1 without pores on exopod and endopod. Legs 2-4 with pore at outer terminal corner of endopod 2 and another pore located on terminal endopodal segment between both apical spines. Exopod of legs 2 and 3 carrying pore on intermediary segment, and pore at insertion level of subterminal spine of distal segment. Exopod of leg 4 differing from those of legs 2 and 3 by absence of pore on intermediary segment.

Intercoxal sclerite of leg 1 with 2 well developed smooth humps. Legs 2 and 3 with humps slightly produced. Sclerite of leg 4 without humps.

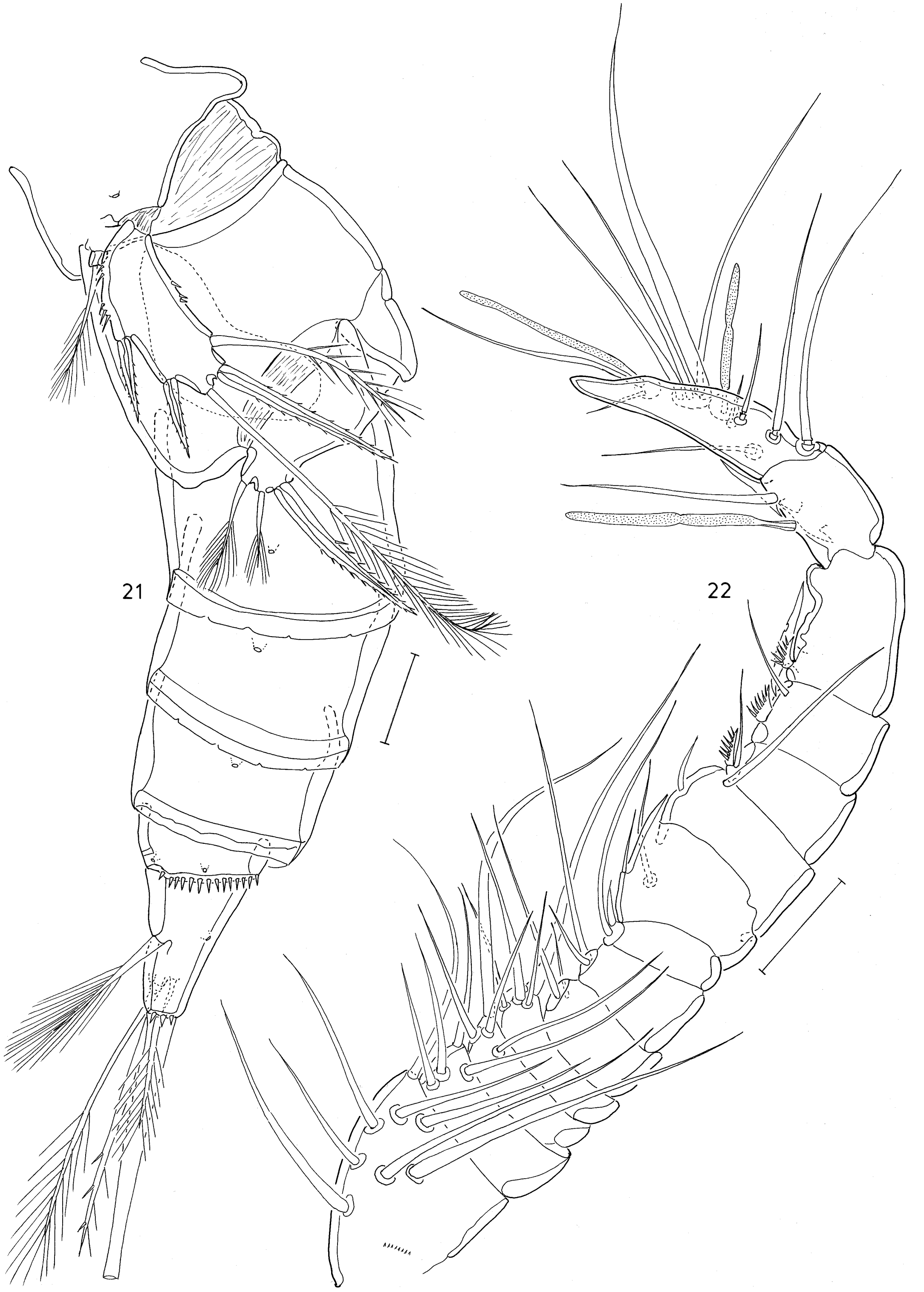
Leg 5 exopod (Fig. 18) elongate, 2.3 times longer than broad. Both outer spines similar in length and correspond-

Table 1. Numbers of spines (Roman numerals) and setae (Arabic numerals) per segment of the swimming legs 1 to 4 of *Prehendocyclops monchenkoi* sp. nov.

	Coxa	Basis	Exopod 1 2 3	Endopod 1 2 3
Leg 1	0-1	1-I	I-1; I-1; III,2,3	0-1; 0-1; I,I+1,3
Leg 2	0-1	1-0	I-1; I-1; III,I+1,4	0-1; 0-2; I,II,3
Leg 3	0-1	1-0	I-1; I-1; III,I+1,4	0-1; 0-2; I,II,3
Leg 4	0-1	1-0	I-1; I-1; II,I+1,4	0-1; 0-2; I,II,2



Figs 17-20. *Prehendocyclops monchenkoi* Rocha, sp. nov., female. 17. Leg 4, anterior. 18. Leg 5, outer. Male: 19. Urosome, dorsal. 20. Urosome, ventral. Scale bars = 20 µm.



Figs 21-22. *Prehendocyclops monchenkoi* Rocha, sp. nov., male. 21. Urosome, lateral. 22. Antennule, ventral. Scale bars = 20 µm.

ing to about half of length of segment. Inner apical spine as long as exopod. Apical seta about 2 times longer than segment.

Male. Body length, excluding caudal setae, ranging from 500 to 550 µm (n = 3). Prosome : urosome ratio 1.89-1.94 : 1. Urosome (Figs 19-21) with 6 somites. Genital somite with 2 pairs of integumental sensilla on dorsal surface and pore on each flap closing off genital aperture; number and position of integumental pores of other urosomal somites as in female. Antennule (Fig. 22) of 14 segments, armed as follows: 8 + row of spinules, 4, 4, 4, 2, 2, 1 + spine, 2, 2, 1 + spine, 1 + spine, 1 spine + anvil-shaped process, 1 + aesthetasc + 2 anvil-shaped processes, 11 + 2 aesthetascs. Leg 5 exopod (Fig. 21) elongate, about 2.3 times longer than wide, with 2 outer spines similar in length to each other, 1 apical seta, 1 inner serrate spine 2.4 times longer than outer spines, and 1 inner seta armed with setules little stouter than those of apical seta. Leg 6 (Fig. 21) represented by inner spine 2.5 and 2.1 longer than middle and outer seta, respectively.

The male is identical to the female in all other respects.

Etymology. The specific name honours Dr Vladislav I. Monchenko, eminent Ukranian copepodologist, who has contributed significantly to knowledge of the cyclopoid copepods.

Prehendocyclops boxshalli Rocha, sp. nov.
(Figs 23 - 40)

Material examined. Mexico, Yucatán: Grutas de Santa Maria, Homun (20°44'29"N, 89°17'28"W) 21 June 1991, 1 male from sample #91-016 collected with 93 µm mesh plankton net from water column and sand bottom of cave pool in 0-6 m water depths; Grutas de Tzab-Nah, Tecoh, (20°44'08"N, 89°28'23"W), 27 June 1991, 2 females from sample #91-021 collected with 93 µm mesh plankton net from water column and sand bottom of cave pool in 0-8 m water depths; Cenote Kambul, Noc Ac (21°04' 27"N, 89°43'16"W), 7 July 1993, 1 female from sample #93-044 collected with 93 µm mesh plankton net from water column of cave pool in 10-15 m water depths. All material collected by T.M. Iliffe. Female holotype (USNM 287097) and 2 paratypes (USNM 287098-287099) in NMNH; 1 paratype in MZUSP (13061).

Female. Body length, excluding caudal setae, measuring 515, 570, and 610 µm in 3 specimens. Prosome : urosome ratio varying from 1.85 to 1.94 : 1. Except for anal somite bearing row of spinules along ventral posterior edge (Fig. 25), posterior borders of all body somites smooth (Figs 23 and 24). Cephalothorax (Fig. 23) with dorsal middle integumental window and pair of lateral integumental windows at posterior corners; 2 subsequent prosomal somites each with pair of lateral integumental windows. Integumental sensilla pattern of cephalothorax not visible in any preparation. Tergal plates of pedigerous somites 2 to 4 with number and position of integumental sensilla as shown in Fig. 24. Integumental pore pattern of urosome (Figs 24 and 25) differing from that of previously described species by absence of middle dorsal pore on first somite, and outer pair of pores located dorsally at level of genital openings. Genital double somite about 1.1 times longer than wide. Seminal receptacle as shown in Fig. 25. Copulatory duct slightly curved. Lobes of anterior portion of receptacle little expanded. Receptacle ducts leading to lateral genital antra narrower and more stretched than those ducts in *P. monchenkoi*. Anal somite approximately 2.7 times broader than long and about half of length of precedent urosomal somite.

Caudal rami (Figs 23-25) 2.1-2.2 times longer than wide. Outermost apical seta as long as lateral seta and about 1.45 times longer than innermost apical seta. Dorsal seta 4.2 times longer than outermost apical seta. Inner middle apical seta (Fig. 26) 7.4 times longer than outer middle apical seta, and armed as follows: proximal half naked basally and sparsely spinulose distally; terminal half entirely plumose. Outer middle apical seta (Fig. 26) sparsely spinulose on outer margin and with 3 setules on inner margin of terminal part.

Antennule of 6 segments, armed as in *P. monchenkoi*. Segment 4 about 2.5 times longer than wide.

Antenna (Figs 27 and 28) consisting of 4 segments, all shorter and wider than antennular segments of *P. monchenkoi*. Coxa reduced and unarmed. Basis with 2 spinulose setae of different lengths at inner corner; seta representing exopod also spinulose. Spiniform seta of proximal endopod segment 1.6 times longer than wide, excluding marginal spinules. Terminal endopod segment with 2 spinulose spines, and serrate claw 1.35 times longer than setulose seta on expanded part of inner margin; apex of segment bearing 7 setae.

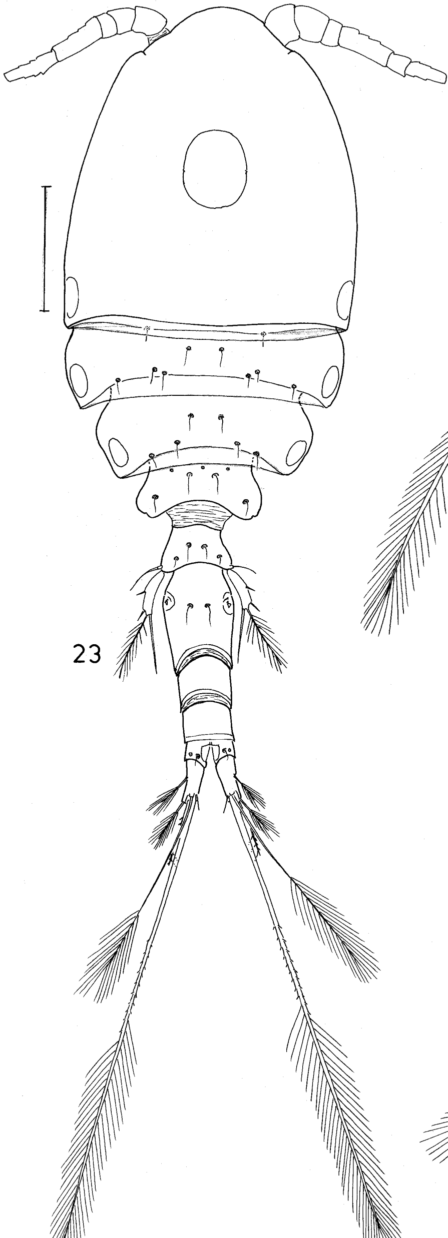
Labrum (Fig. 29) with medial spinulose depression and 2 lateral groups of teeth; ventral surface bearing transverse row of setules.

Mandible (Figs 30 and 31) with 2 separate rows of spinules and seta representing palp implanted on ventral surface of coxa. Gnathobasic armament consisting of long wide bifid spine and 2 short spines.

Maxillule consisting of praecoxa and 2-segmented palp armed as in Figs 32 and 33. Outer seta of terminal segment of palp stout and without row of spinules.

Maxilla as in *P. monchenkoi*.

Maxilliped (Figs 34 and 35) 2-segmented. Basal segment unarmed. Terminal segment with 1 or 2 apical setae.



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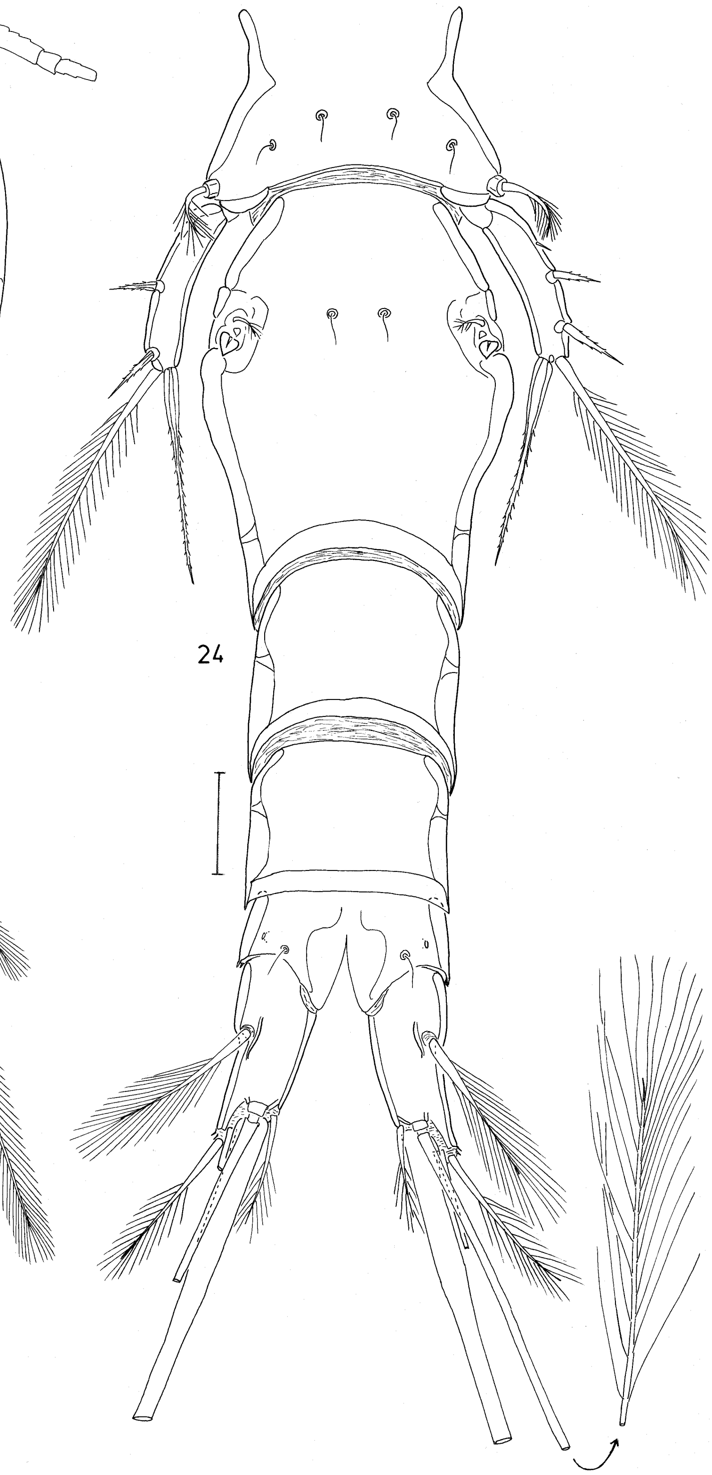

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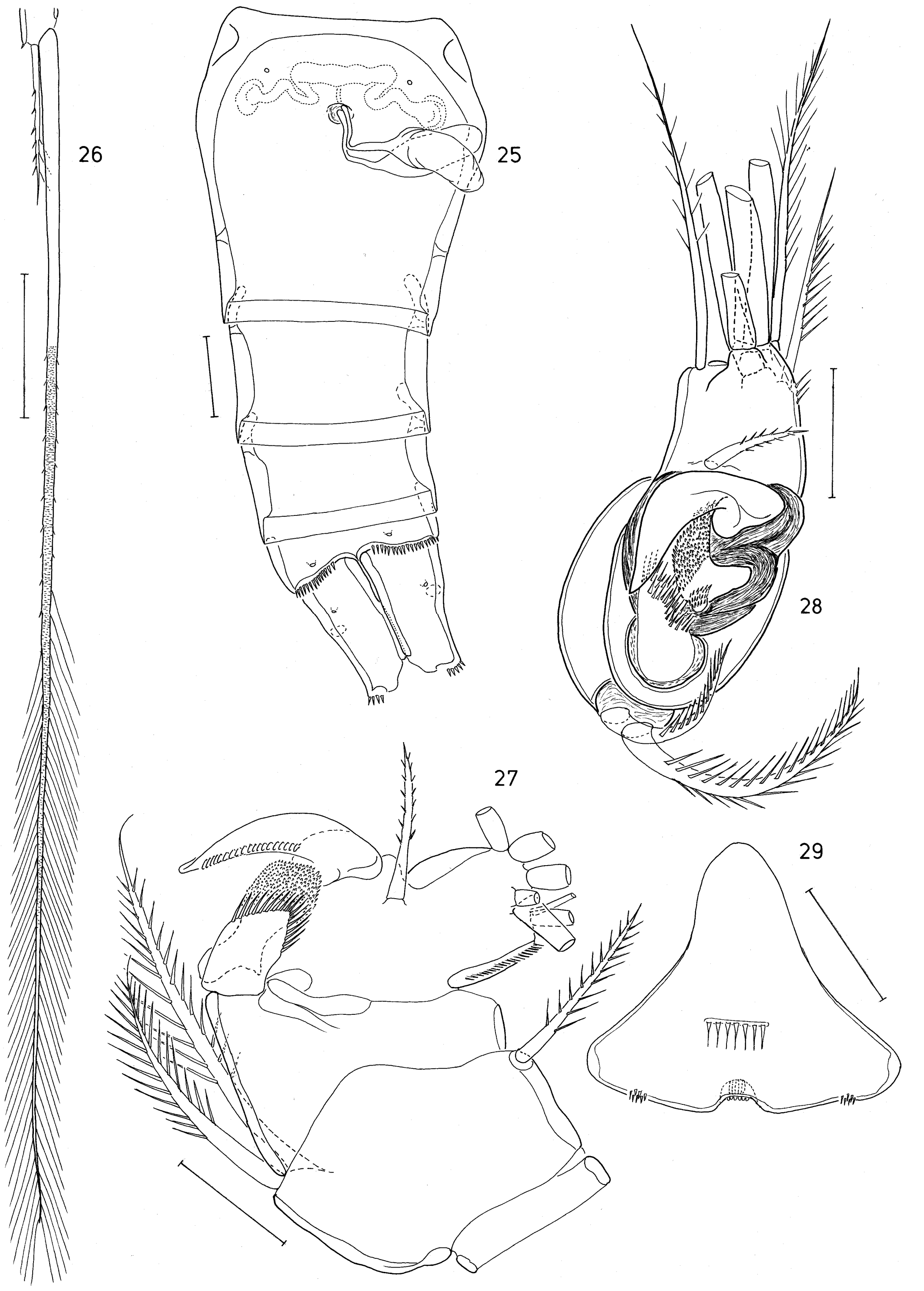
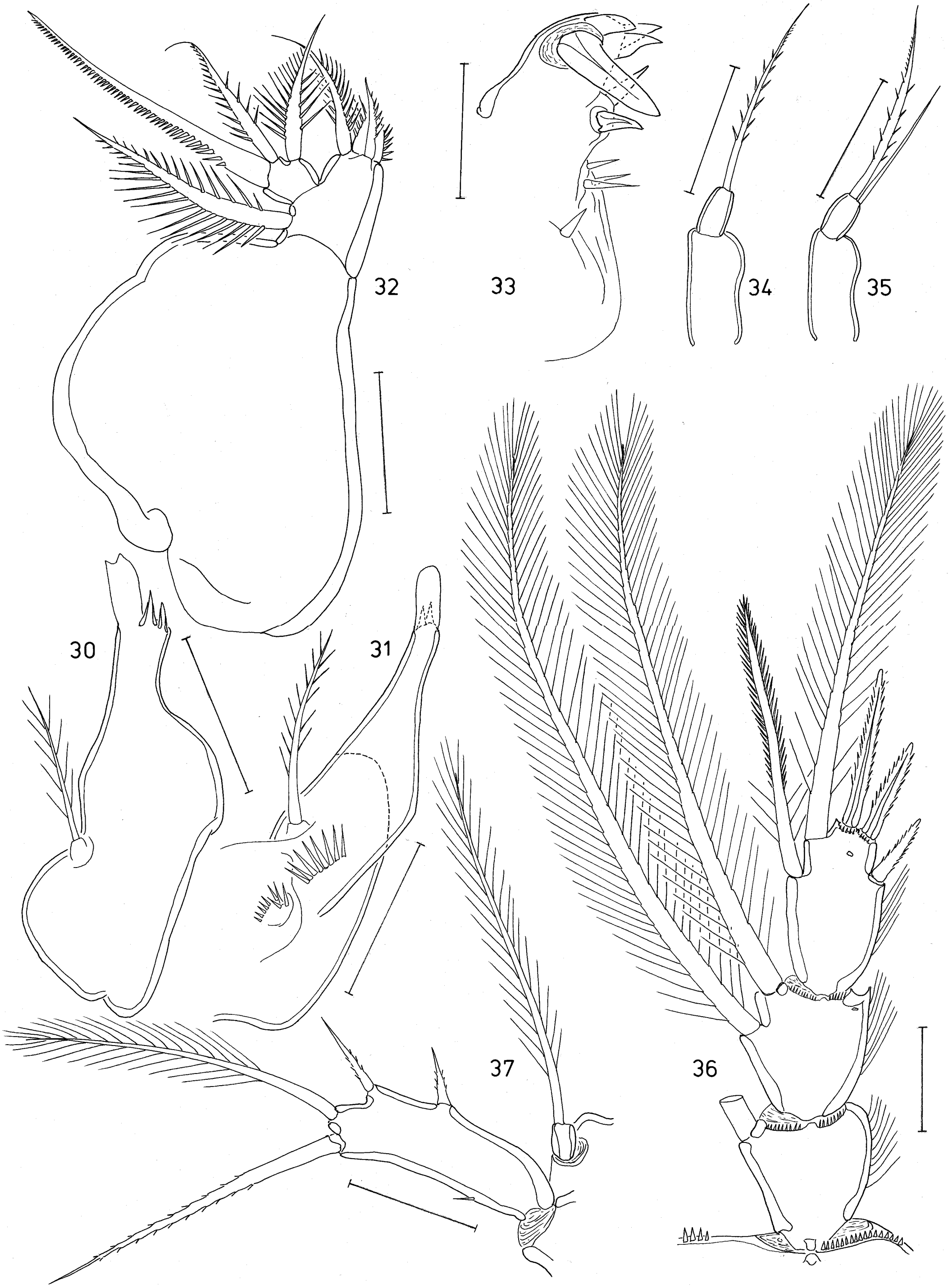
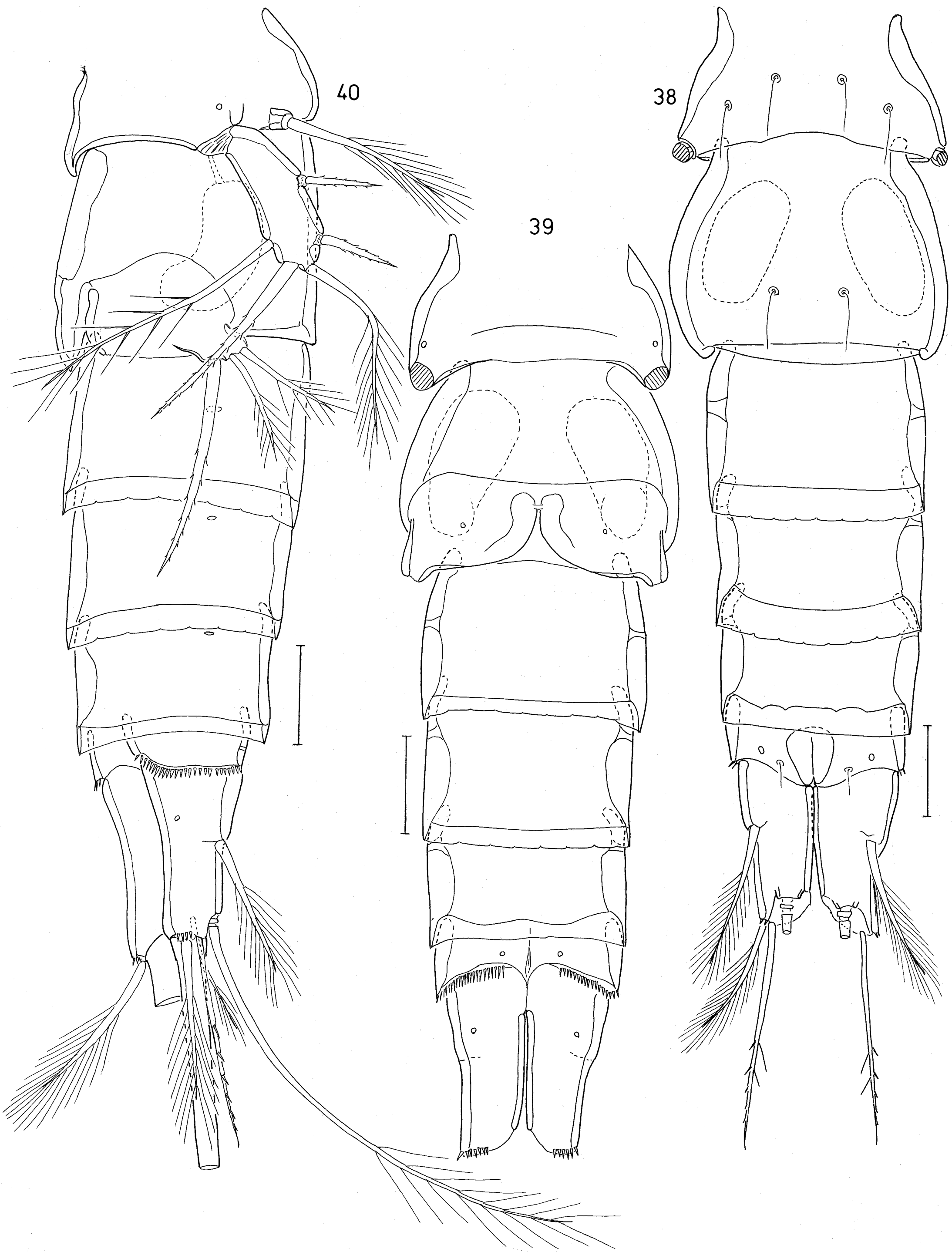
Figs 23-24. *Prehendocyclops boxshalli* Rocha, sp. nov., female. 23. Habitus, dorsal. 24. Urosome, dorsal. Scale bars = 100 µm (Fig. 23); 20 µm (Fig. 24).



Figs 25-29. *Prehendocyclops boxshalli* Rocha, sp. nov., female. 25. Urosome, ventral. 26. Middle apical caudal setae, dorsal. 27. Antenna, anterior. 28. Antenna, top. 29. Labrum, ventral. Scale bars = 50 µm (Fig. 26); 20 µm (Figs 25 and 27-29).



Figs 30-37. *Prehendocyclops boxshalli* Rocha, sp. nov., female. 30. Mandible, inner lateral. 31. Mandible, ventral. 32. Maxillule, outer posterior. 33. Maxillular arthrite, inner. 34. Maxilliped, ventro-lateral. 35. Abnormal maxilliped, ventro-lateral. 36. Leg 4 endopod, anterior. 37. leg 5, anterior. Scale bars = 20 µm.



Figs 38-40. *Prehendocyclops boxshalli* Rocha, sp. nov., male. 38. Urosome, dorsal. 39. Urosome, ventral. 40. Urosome with legs 5 and 6, lateral. Scale bars = 20 µm.

Legs 1-4 armed as in *P. monchenkoi*. Leg 1 basis with inner spine slightly more slender than that of *P. monchenkoi*; outer seta short, reaching only posterior border of leg 1 exopod 1. Endopod 3 of legs 2 and 3 with proximalmost seta stiff, plumose basally and spinulose distally. Leg 4 with outer basal seta reaching posterior margin of exopod 2. Leg 4 endopod 3 (Fig. 36) about 1.6 times longer than wide; inner apical spine as long as or slightly longer than segment, and 1.5 times longer than outer apical spine. Inner proximal seta stiff, slightly curved, 1.8 times longer than inner apical spine, armed with few long weak setules basally and stiff setules terminally. Inner distal seta plumose, 1.45 times longer than inner proximal seta.

Integumental pore pattern on anterior surface of legs 1-4 as follows: all legs with pore on coxa near articulation of intercoxal sclerite, and another pore on basis close to insertion of outer seta; leg 1 with pore on endopod segment 3 between both apical setae, and another pore at outer corner of exopod segment 2; legs 2-4 endopod with pore at outer terminal corner of middle segment, and pore on terminal segment between both terminal spines; legs 2-4 exopod carrying pore at outer distal corner of middle and terminal segments.

Intercoxal sclerite of legs 1-4 as in *P. monchenkoi*.

Leg 5 exopod (Fig. 37) elongate, 3.2 times longer than wide. Distal outer spine about 1.5 times longer than outer proximal spine. Inner apical spine 1.4 times longer than segment and 3.5 times longer than outer distal spine. Apical seta as long as inner apical spine.

Male. Body length, excluding caudal setae, 500 µm. Prosome : urosome ratio 1.94 : 1. Urosome with 6 somites and integumental sensilla pattern as shown in Figs 38-40. Antennule as in *P. monchenkoi*. Maxilliped with only 1 apical spinulose seta. Leg 5 exopod (Fig. 40) elongate, 2.6 longer than wide, with 2 outer spines similar in length to each other, 1 apical seta, 1 inner serrate spine 2.7 times longer than outer spines, and 1 inner seta. Leg 6 (Fig. 40) represented by 2 setae similar in length, and inner spine twice longer than setae.

The male is identical to the female in all other respects.

Etymology. The species is named after Prof. Geoffrey A. Boxshall, distinguished copepodologist of The Natural History Museum, London.

Prehendocyclops abbreviatus Rocha, sp. nov.
(Figs 41-57)

Material examined. Mexico, Yucatan: Cenote Chan-Hoch, Homun, (20°44'02"N, 89°16'16"W), 24 June 1991, 1 female holotype (USNM 287100) from sample #91-020 collected with 93 µm mesh plankton net from water column and submerged tree roots in 0-8 m water depths.

Female. Body length, excluding caudal setae, 665 µm. Prosome : urosome ratio 1.43: 1. Body (Fig. 41) more elongate than in 2 previous species. Cephalothorax about 1.25 times longer than wide and with dorsal middle integumental window only. Tergal plate of pedigerous somite 2 with pair of lateral integumental windows. Integumental sensilla pattern of prosome as shown in Fig. 41. Urosome with following arrangement of integumental sensilla: first somite with 4 dorsal sensilla; genital double somite as well as 2 subsequent somites without sensilla; anal somite bearing 2 pairs of dorsal sensilla; each caudal ramus with ventral pore at level of insertion of lateral caudal seta. Posterior borders of all prosomal somites and first urosomal somite smooth (Fig. 41). Genital double somite (Figs 41 and 42) as long as wide. Seminal receptacle as shown in Fig. 42. Copulatory duct short and wide. Anterior portion of receptacle slightly expanded into 4 lobes. Receptacle ducts almost straight and tapering towards genital antra. Hyaline frills of genital double somite and 2 subsequent somites (Fig. 43) irregularly serrate laterally and ventrally. Anal somite 3.2 times wider than long and about half of length of precedent urosomal somite.

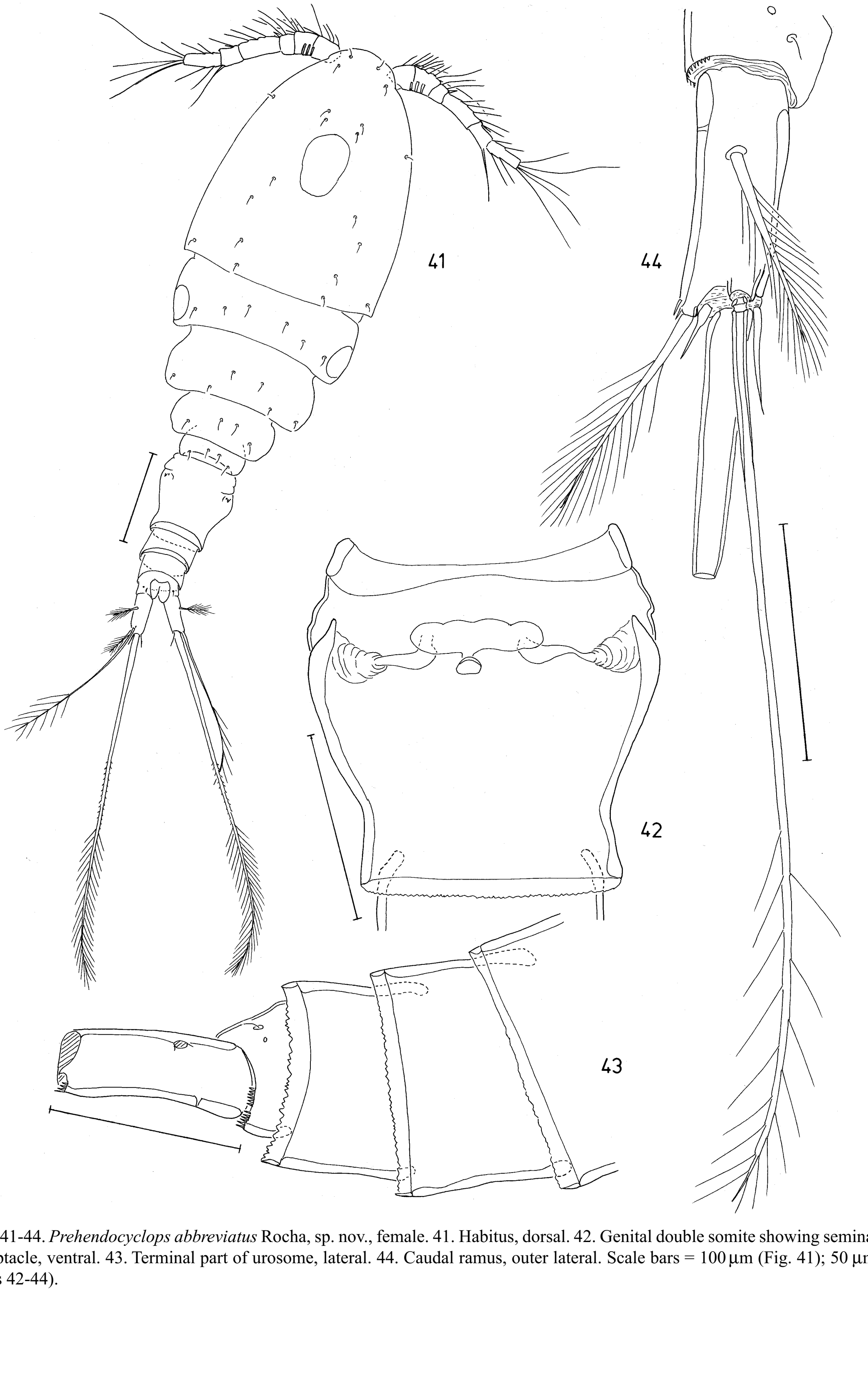
Caudal rami (Fig. 44) 2.6 times longer than wide. Ramus 1.2 times longer than lateral seta. Outermost apical seta similar in length to ramus and 2.1 times longer than innermost apical seta. Dorsal seta 4 times longer than outermost apical seta. Outer middle apical seta remarkably reduced (half length of innermost apical seta, approximately), dilated at base and smooth. Inner middle apical seta (Fig. 45) having proximal portion smooth followed by sparsely spinulose middle area and terminal portion plumose.

Antennule armed as in *P. monchenkoi*. Segment 4 about 2.4 times longer than wide.

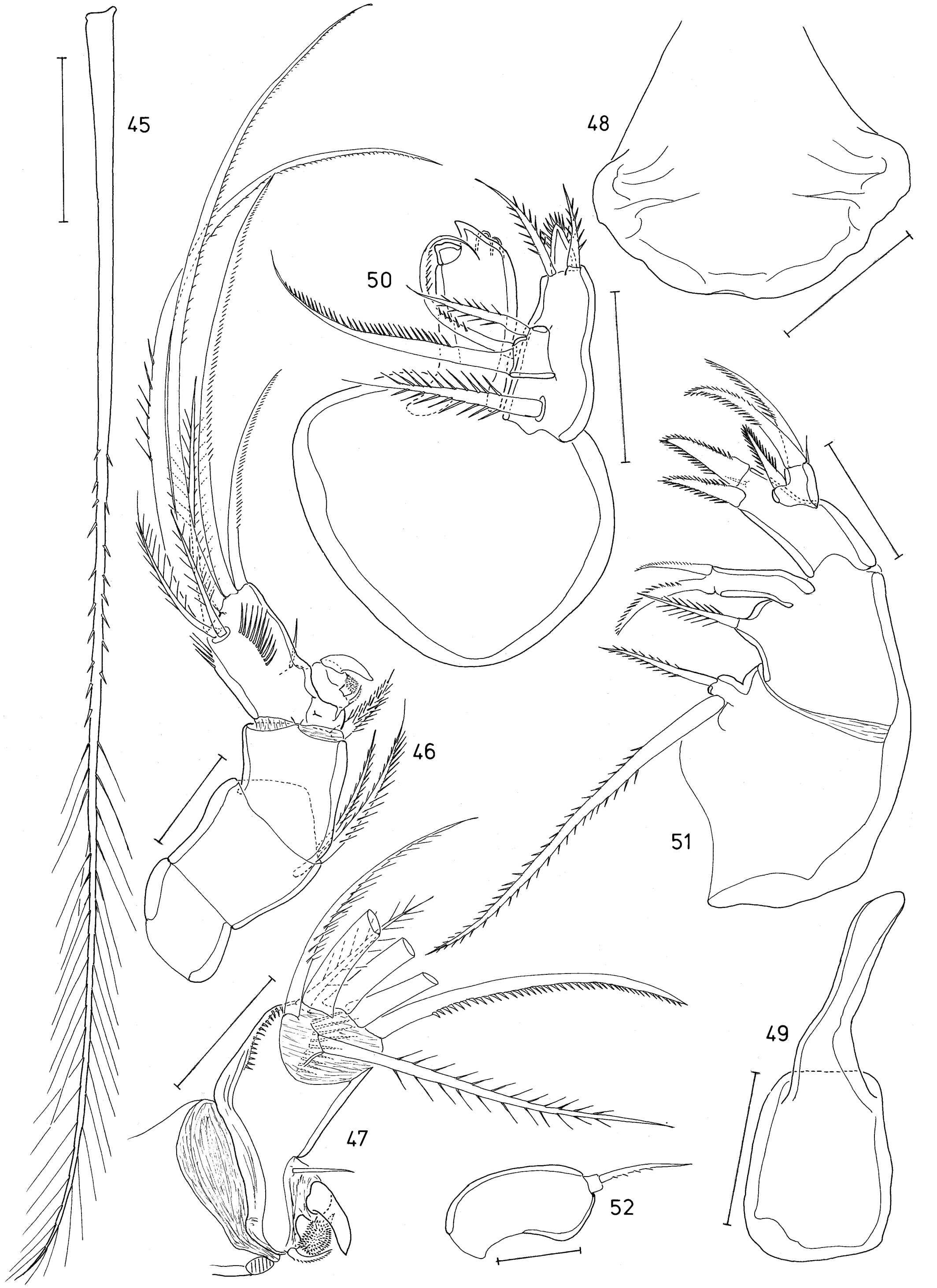
Antenna (Figs 46 and 47) of 4 segments. Coxa unarmed. Basis with 2 inner setae at inner corner, armed with stiff setules; longer seta 1.5 times longer than shorter seta and almost reaching tip of spiniform seta located on inner corner of proximal endopod segment. Seta representing exopod absent. Inner seta of third segment stiff, curved and densely spinulose. Terminal endopod segment bearing 7 setae around apex. Prehensile device consisting of spinulose broad spine, curved short spine, smooth claw, and slender smooth seta; claw about 1.3 times longer than slender seta. Distal part of terminal segment beyond insertion site of seta about 1.15 times longer than broad.

Labrum (Fig. 48) with posterior rim and ventral surface smooth.

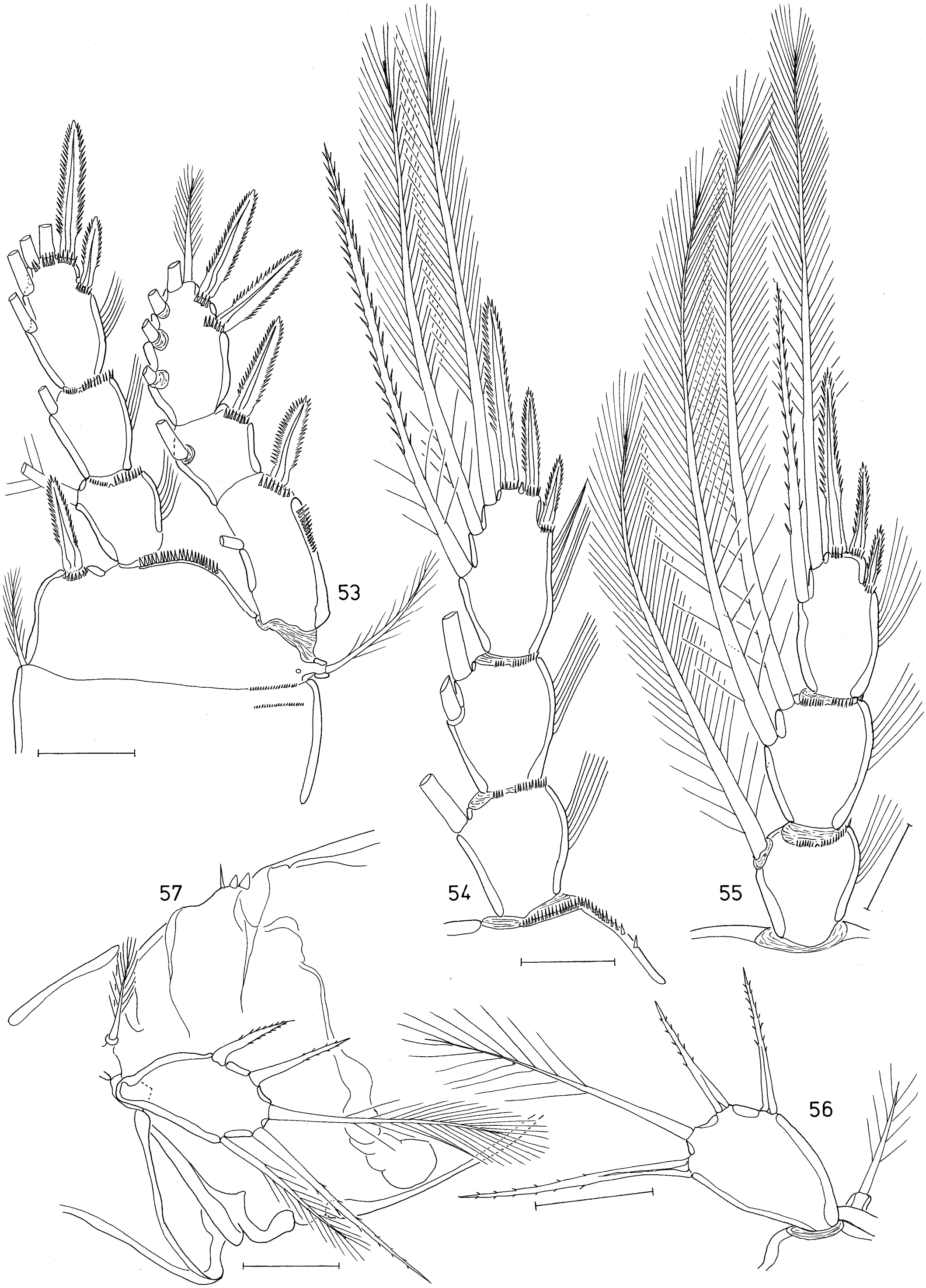
Mandibular coxa (Fig. 49) unarmed. Gnathobasic armament not visible in preparation.



Figs 41-44. *Prehendocyclops abbreviatus* Rocha, sp. nov., female. 41. Habitus, dorsal. 42. Genital double somite showing seminal receptacle, ventral. 43. Terminal part of urosome, lateral. 44. Caudal ramus, outer lateral. Scale bars = 100 µm (Fig. 41); 50 µm (Figs 42-44).



Figs 45-52. *Prehendocyclops abbreviatus* Rocha, sp. nov., female. 45. Inner middle apical caudal seta, dorsal. 46. Antenna, anterior. 47. Terminal part of antenna, posterior from top. 48. Labrum, ventral. 49. Mandible, ventral. 50. Maxillule, outer posterior 51. Maxilla, posterior. 52. Maxilliped, inner ventral. Scale bars = 50 μm (Fig. 45); 20 μm (Figs 46-51); 10 μm (Fig. 52).



Figs 53-57. *Prehendocyclops abbreviatus* Rocha, sp. nov., female. 53. Leg 1, anterior. 54. Leg 3 endopod, anterior. 55. Leg 4 endopod, anterior. 56. Right leg 5 of holotype, anterior. 57. Left leg 5 of holotype. Scale bars = 20 µm.

Maxillule (Fig. 50) consisting of praecoxa and 2-segmented palp. Articulated spine of apex of praecoxal arthrite reduced, being shorter than adjacent spine; other 2 apical spines of praecoxal arthrite curved inward; inner surface armament of arthrite not visible in preparation. Palp composed of basis bearing stout pectinate spine and 2 setulose setae on inner margin, and 1 proximal outer seta representing exopod; endopod 1-segmented and with 3 setae ornamented as shown in Fig. 50.

Maxilla (Fig. 51) 4-segmented, with 2, 3, 3, 4 setae. Proximalmost seta of praecoxal endite about 3.2 times longer than distalmost seta.

Maxilliped (Fig. 52) 2-segmented. Basal segment inflated and unarmed. Terminal segment reduced to short knob with seta.

Legs 1-4 (Figs 53-55) in general with spines and setae more elongated than in 2 previous species and armed as in Table 2. Coxae of all legs with 2 transverse rows of spinules on anterior surface near outer corner. Outer corners of proximal and intermediary segments of endopods of all legs rounded.

Leg 1 basis with inner spine (Fig. 53) reaching slightly beyond distal edge of proximal endopod segment; outer seta not reaching distal edge of exopod 1. Apical spine of leg 1 endopod 3 twice longer than outer spine. Endopod 3 of legs 2 and 3 Fig. 54) with proximalmost seta stiff, serrate distally and plumose basally. Both inner setae of leg 4 endopod 2 plumose. Leg 4 endopod 3 (Fig. 55) about 1.85 times longer than wide; inner apical spine 1.25 times longer than segment, and twice longer than outer apical spine. Inner proximal seta stiff, spinulose, and 1.7 times longer than inner apical spine.

Legs 1-4 bearing integumental pore on outer corner of basis only.

Intercoxal sclerite of leg 1 with 2 well developed smooth humps; humps of leg 2 and 3 slightly produced; sclerite of leg 4 without humps.

Leg 5 exopod (Figs 56) 1.7 times longer than broad. Outer proximal spine 1.12 times longer than outer apical spine, both shorter than segment. Inner apical spine 1.3 times longer than segment. Apical seta about 1.2 times longer than inner apical spine. Anomalous leg 5 as shown in Fig. 57.

Male. Unknown.

Etymology. The specific name (from the Latin *abbreviatus*, shortened) refers to the remarkably reduced outer middle apical caudal seta.

REMARKS

Within the subfamily Halicyclopinae, *Prehendocyclops* can be grouped with the genera *Halicyclops*, *Colpocyclops*, and *Smirnoviella* by shared characteristics in the body segmentation, as well as in the structure of the antennule, antenna and legs 1 to 5. Their flattened body bears the first pedigerous somite completely amalgamated to the cephalosome, forming a cephalothorax; the other two halicyclopine genera (*Troglocyclops* and *Neocyclops*) have the first pedigerous somite still distinct, although partially hidden laterally and dorsally by a carapace-like extension of the posterior margin of the cephalic shield (Rocha & Iliffe 1994, Rocha 1995b).

The antennules of the females of these 4 genera are 6-segmented and identically armed. It is important to point out that the proximal bithek is inserted proximally on the fifth antennular segment and not terminally on the fourth segment as commonly referred to for many species of *Halicyclops* and *Smirnoviella reducta* Monchenko, 1977. Fiers (1995) was the first author indicating the right position of that bithek. Posteriorly, Schutze (1997) corroborated Fiers's findings, investigating the antennular development of copepodids of *Halicyclops aberrans* Rocha, 1983.

The antenna consists of 4 segments formed by fusion of the last 2 endopodal segments to each other; these segments are separated in *Troglocyclops* and *Neocyclops,* making their antennae 5-segmented.

Legs 1 to 4 of the 4 genera of the group have 3-segmented exopods and endopods. The middle segment of the endopod of leg 1 bears only one plumose seta, an apomorphic character state in relation to the plesiomorphic condition (2 setae) commonly found in the family Cyclopidae. Except for *Colpocyclops*, the proximalmost seta of the terminal endopodal segment of legs 2 and 3 is stiff and heterogeneously ornamented (plumose basally and spinulose distally). It is necessary to mention that the armament of the third endopodal segment of leg 4 varies slightly or not at all among the species of *Colpocyclops*, *Smirnoviella*, and *Prehendocyclops*; and this armament is diagnostic for the great majority of *Halicyclops* species.

Leg 5 of the female is composed of a basal seta implanted on the dorsal surface of the first urosomal somite, and an unisegmented exopod bearing 3 spines and 1 seta. Such a condition is also a synapomorphy grouping

Table 2. Numbers of spines (Roman numerals) and setae (Arabic numerals) per segment of the swimming legs 1 to 4 of *Prehendocyclops abbreviatus* Rocha sp. nov.

	Coxa	Basis	Exopod 1 2 3	Endopod 1 2 3
Leg 1	0-1	1-I	I-1; I-1; II,2,3	0-1; 0-1; I,I+1,3
Leg 2	0-1	1-0	I-1; I-1; III,I+1,4	0-1; 0-2; I,II,3
Leg 3	0-1	1-0	I-1; I-1; III,I+1,4	0-1; 0-2; I,II,3
Leg 4	0-1	1-0	I-1; I-1; II,I+1,4	0-1; 0-2; I,II,2

Prehendocyclops and its allies, in opposition to the 3-segmented leg 5 of *Troglocyclops* and *Neocyclops*. The sexual dimorphism observed in leg 5 of *Prehendocyclops* (addition of 1 seta on the inner margin of the exopod) has also been recorded in *Colpocyclops*, *Neocyclops* s.s. and the majority of the species of *Halicyclops*. Males of the only species of *Troglocyclops,* as well as of 3 species of *Halicyclops*, namely *H. caridophilus* Humes, 1947, *H. tetracanthus* Rocha, 1995, and *H. cenoticola* Rocha, 1998 bear 2 setae on the inner margin of leg 5 exopod (Humes 1947; Rocha & Iliffe 1994; Rocha 1995a; Rocha & al. 1998). Nothing can be said about *Smirnoviella,* as the male of this genus remains unknown.

Although the specimens of *Prehendocyclops* have all been collected from plankton, it is assumed here that these copepods live associated with other organisms. Such a presumption is based on modifications of the basic structure of the antennae and mouthparts observed in the subfamily. Free-living halicyclopines such as *Troglocyclops*, *Neocyclops*, and *Halicyclops* and even *H. caridophilus*, which was found in the gill chambers of *Thalassina anomala* (Herbst), show the following arrangement of setae on the inner margin of the antennal endopod: endopod 1 with a seta at midlength of the first segment; endopod 2 with an isolated proximal seta, 2 distal setae, a somewhat stout and curved seta at the distal corner, and an adjacent apical seta. This basic pattern changes very little in *Smirnoviella* and in *Colpocyclops longispinosus* (Monchenko, 1974), in which the seta at the distal corner is modified into a basally inflated pointed hook. The corresponding seta is thick and sigmoid in *Colpocyclops dulcis* Monchenko, 1977. Nevertheless, in *Prehendocyclops* the aforedescribed arrangement changes drastically: the seta on the endopod 1 was moved to the distal corner of the segment and modified as a thick, outward-curved spinulose seta; concerning the 5 setae of the second endopodal segment, it is considered here that the proximal seta is lost, the 2 distal setae transformed into serrate spines, the stiff curved seta at the distal corner is homologous with the claw and, finally, the adjacent seta has persisted as a slender seta.

In comparison with other Halicyclopinae the mandible of *Prehendocyclops* is quite simplified in the armament of the gnathobase, consisting of only 3 elements: a large outer tooth and 2 shorter inner teeth. All other halicyclopines, including *H. caridophilus*, possess gnathobase with approximately ten teeth plus a serrate seta along the apical rim, and a row of spinules subterminally on the inner surface. Mandibular palp represented by 1 seta implanted directly on the coxa as in *Prehendocyclops* has also been observed in *H. caridophilus*.

The structure of the maxillule of *Prehendocyclops* is also characteristic. The 2 innermost apical teeth of the arthrite are turned toward the medial axis of the body, whereas the 2 outermost apical teeth are curved toward the most distal spines of the inner surface of the arthrite. These 4 spines of the arthrite have the same orientation in the other halicyclopine genera, i. e. slightly turned toward the longitudinal axis of the body. The maxillular palp of *Prehendocyclops* differs from that of *Troglocyclops* and *Neocyclops* only in having the apical middle seta of the basis modified as a short broad spinulose spine. Among the Halicyclopinae, the maximum specialization of the maxillular palp was achieved in *Smirnoviella reducta* and *Colpocyclops longispinosus* (Monchenko, 1974). In these species the palp has become unisegmented by complete fusion of the endopod to the basis. Additionally, the armament was reduced from 7 to 5 setae, the middle apical seta of the basis being modified into a long strong articulated spine (Monchenko 1974, 1977, 1978).

The maxilla of the new genus closely resembles those of *Neocyclops* and *Halicyclops*. The 3 genera possess unisegmented endopods as well as similar setal formulae on the entire appendage. However, the maxilla of *Prehendocyclops* bear stronger and shorter setae. The new genus shares with *H. caridophilus* the presence of 3 setae articulated on the basal endite; all other halicyclopine taxa for which the maxilla has been described bear the distalmost apical seta claw-shaped and fused to the endite. The most specialized maxillae are found in *Smirnoviella* and *Colpocyclops*. Both genera have the basis enlarged and drawn out into a well developed claw, whereas the unisegmented endopod is reduced or even absent, as in *Smirnoviella unisetosa*, described by Monchenko (1982).

Prehendocyclops approximates *Halicyclops* in having a bisegmented maxilliped. However, the genera differ in the number of setae. The 3 known species of *Prehendocyclops* have no seta on the first segment and 1 to 3 setae on the terminal segment. In *Halicyclops* the setal formula is 3 setae on the basal and 5 setae on the terminal segment. According to Monchenko (1977, 1982) both species of *Smirnoviella* have an unisegmented maxilliped with 2 apical setae. The maxilliped is absent in *Colpocyclops.*

Males of *Prehendocyclops* bear aesthetascs on the last 2 segments of the antennule only. In comparison with *Halicyclops*, all 7 aesthetascs found on male antennular segments 1 to 12 (see Rocha 1995a; Rocha & al. 1998) were lost in the new genus. Monchenko (1978) illustrated the male antennule of *Colpocyclops longispinosus* as consisting of 13 segments (12, according to the text) and without any aesthetascs. Monchenko may have neglected elements of the antennular armament, since some setae and spines widely found on male antennules within the family Cyclopidae are not represented in the figure provided by him.

Prehendocyclops species are similar to each other concerning some aspects of the caudal rami. The ramus is at least twice longer than wide, with the apex inclined by extension of the ventral surface of the ramus; the outermost apical seta and the lateral seta are plumose and similar in length; the inner middle apical seta is remarkably stouter than the other setae and similarly ornamented in the 3 species. However, the species differ concerning the length of some caudal setae. The dorsal seta corresponds to 1/4 of the length of the outer middle apical seta in *P. monchenkoi*, but approximately half the length of that seta in *P. boxshalli* and *P. abbreviatus*. In addition, the latter species has an inconspicuous outer middle apical seta, which is well developed and ornamented similarly in both *P. monchenkoi* and *P. boxshalli*. An extremely reduced outer middle apical seta was described for *Smirnoviella unisetosa* by Monchenko (1982).

Of the 3 species of *Prehendocyclops*, *P. monchenkoi* is closer to *P. boxshalli*. Both species have the same arrangement of integumental windows on the prosome, whereas the labrum has the posterior rim medially notched, and the inner spine of the praecoxal arthrite of the maxillule is long and strong. They also share a similar structure of the maxilla and male antennule. Differences between them exist in the number of integumental sensilla on the first urosomal somite, and genital double somite in both sexes; shape and size of elements composing the prehensile device of the antenna; armament of labrum and mandible; ornamentation of some setae on the maxillular endopod; and in the structure of leg 5 in both sexes. On the other hand, *P. abbreviatus* can be easily separated from its congeners in having a more elongated prosome, a pair of integumental windows only on the pedigerous somite 2, a genital double somite as well as the 2 subsequent somites without integumental sensilla, a seminal receptacle with almost straight ducts leading to the genital antra, a remarkably reduced outer middle apical caudal seta (even shorter than the inner apical seta), a short inner apical spine of the praecoxal arthrite, the ventral surface of the labrum smooth, the setae of the praecoxal endite of the maxilla very different in length, the maxilliped with the terminal segment reduced to a small knob, 2 outer spines on exopod 3 leg 1, and legs 1-4 with only 1 integumental pore on the outer corner of the basis.

Judging from all the morphological aspects discussed, the close relationship of *Halicyclops* with the more derived genera *Prehendocyclops*, *Smirnoviella*, and *Colpocyclops* seems undeniable. The development of some kind of prehensile device on the antenna of the latter three genera, allied to the characteristic modifications in the structure of their mouthparts, allow the assumption that these genera are able to exploit some hosts. It is proposed here that attempts towards some level of ectoparasitism in Halicyclopinae have occurred from one or more *Halicyclops*-like ancestral forms, leading to the differentiation of the 3 genera now known: *Prehendocyclops*, with 3 species, nowadays apparently confined to Mexican cenotes, whereas *Smirnoviella* and *Colpocyclops*, with 2 species each would have evolved in estuaries connected to the Caspian and Black Sea. It is noteworthy that these areas were linked in the past, forming part of the ancient Tethys Sea.

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