METACYCLOPS (COPEPODA, CYCLOPIDAE) FROM AYYALON CAVE, ISRAEL

BY

DANIELLE DEFAYE[1,3]) and FRANCIS DOV POR[2,4])

[1]) Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques UMR 7208, CP 53, 61, rue de Buffon, F-75005 Paris, France

[2]) Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Edmund Safra Campus, Jerusalem 91904, Israel

ABSTRACT

A new species of Cyclopidae (Copepoda, Cyclopoida) is described from Ayyalon Cave, Israel, as *Metacyclops longimaxillis* n. sp. The description is based on specimens collected in a small, brackish, warm and sulfidic water pool, recently described from this cave that belongs to the Yarqon-Tanninim aquifer. The new taxon is distinguished by specific morphological traits, but in particular by the remarkable maxillae, the large size of which may be related to the specific environmental conditions in which these crustaceans are living. Its closest similar congener is *M. stammeri* Kiefer, 1938, with which it mainly shares the terminal seta and spine on endopodal segment 2 of P4 in both male and female, the armature of two setae and the strong exopodal seta on the basipodite of the antenna, the spine formula of the exopodites of the swimming legs (3.4.4.3), the general shape and setation of the furca with the inner median seta enlarged at its base; the 11-segmented female antennule, and the segmentation pattern of the antennule. They principally differ by their body size, the shape of the seminal receptacle, the setation of the antenna, the structure of the male antennule, the ornamentation of the intercoxal plates of the swimming legs, and the structure of the male P6. Some information and a description of the only other cyclopid found at this site, attributed to *Metacyclops subdolus* Kiefer, 1938, is given in addition.

RÉSUMÉ

Une espèce nouvelle de Cyclopidae (Copepoda, Cyclopoida) est décrite de la grotte d'Ayyalon, Israel, *Metacyclops longimaxillis* n. sp., à partir de spécimens collectés dans une petite mare d'eau saline chaude, riche en sulfites, récemment découverte dans cette grotte appartenant au réseau aquifère Yarqon-Tanninim. La nouvelle espèce se distingue par des caractères morphologiques spécifiques, mais surtout par sa maxille, remarquable, dont la grande taille pourrait être en rapport avec les conditions environnementales particulières dans lesquelles vivent ces crustacés. L'espèce la plus proche est *M. stammeri* Kiefer, 1938 avec laquelle elle partage la soie et l'épine terminales de

[3]) e-mail: ddefaye@mnhn.fr

[4]) e-mail: fdpor@netvision.net.il

Also available online: www.brill.nl/cr

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l'endopodite 2 de P4, présentes dans les deux sexes, l'armature du basipodite de l'antenne composée de deux soies et d'une forte soie exopodale, la formule des épines des exopodites des pattes natatoires (3.4.4.3), la forme générale de la furca, avec la soie furcale interne élargie à sa base, le modèle de segmentation de l'antennule à 11 segments de la femelle. Elles diffèrent principalement par leur taille, la forme du réceptacle séminal, la structure de l'antennule mâle, l'ornementation des plaques intercoxales des pattes natatoires et la structure de la P6 mâle. Une nouvelle description ainsi que des informations complémentaires sont également données sur l'autre espèce de cyclopide présent dans le site, *Metacyclops subdolus* Kiefer, 1938.

INTRODUCTION

The Ayyalon Cave in Israel was discovered in March 2006, as an "accidental opening" in a quarry in the inner coastal plain of the country, near Ramla. The pool in the cave had brackish and sulfidic waters, of 30°C. This subterranean ecosystem, characterized by chemoautotrophic resources, was described and named "Ophel" by Por (2007). The crustacean fauna of the pool revealed populations of *Tethysbaena* n. sp. (H. P. Wagner, in litt.) and of *Typhlocaris ayyaloni* Tsurnamal, 2008, as well as two cyclopid copepods belonging to the genus *Metacyclops*, namely *M. subdolus* Kiefer, 1938 and a new species described in the present paper. This new species is distinguished by specific morphological traits, first of all by the remarkable maxillae, the large size of which might be related to the mode of feeding in the particular sulfidic environment in which these crustaceans are living.

MATERIAL AND METHODS

The specimens were dissected and mounted in glycerol. Some were mounted in lactic acid and/or stained with chlorazol black E on a slide in lactic acid. Measurements and dissections were made in glycerol. The observations were done with a compound microscope (Leica DMLB) and the drawings made with a camera lucida at resolutions up to 1000×. Permanent preparations have been mounted in glycerol and sealed with Eukitt (O. Kindler GmbH & Co, Freiburg, Germany). Drawings were made in part from the holotype and allotype, and also from paratypes and whole specimens in glycerol, using an oil immersion lens. The description is based on the holotype female. The terminology follows Dussart & Defaye (2001).

For scanning electron microscopy (SEM), copepods were dehydrated through graded series of ethanol concentrations, critical point dried, mounted on aluminium stubs, coated with gold, and examined in a JEOL 840 scanning electron microscope. Observations were made and photographs taken at the Service commun des Sciences de la Vie du Muséum national d'Histoire naturelle (Paris, France).

The holotype, allotype, and paratypes, as well as the other material examined have been deposited in the Section of Invertebrates of the Hebrew University of Jerusalem Biological Collections (HUJINV). A few paratypes of the new species and some specimens of *M. subdolus* are deposited in the Museum national d'Histoire naturelle, Paris (MNHN).

SYSTEMATICS

Family CYCLOPIDAE Rafinesque, 1815

Subfamily CYCLOPINAE Rafinesque, 1815

Genus *Metacyclops* Kiefer, 1927

Metacyclops longimaxillis n. sp. (figs. 1-5)

Material examined. — Holotype: ♀ dissected and mounted on two slides (HUJINVCOP139). Allotype: ♂, dissected and mounted on one slide (HUJINVCOP140). Paratypes: 6 ♀♀ each dissected on one slide (HUJINVCOP141 to 146), 8 ♂♂ each dissected on one slide (HUJINVCOP147 to 154), numerous ♂♂, ♀♀ and copepodites, ethanol-preserved (HUJINVCOP155); 3 ♀♀ each dissected on one slide (MNHN-Cp2500 to 2502), 2 ♂♂ each dissected on one slide (MNHN-Cp2503 and 2504); and approx. 20 ♂♂, ♀♀ and copepodites, ethanol-preserved (MNHN-Cp2505).

Type locality. — Pool in Ayyalon Cave, Israel, coll. Ch. Dimentman, April-May 2006, 31°54′37.48″N 34°55′39.33″E.

Etymology. — The species name refers to the large maxillae that characterize this species.

Description of female (figs. 1-4). — Holotype. Body length excluding furcal setae, 0.74 mm. Small cyclopid of compact shape, widest at the posterior part of the cephalothorax in dorsal view (fig. 1A). Cephalothorax almost 1.5 times as long as the following pedigerous somites. Prosome/urosome length ratio 1.35; body length/width ratio 2.4; cephalothorax/genital double somite width ratio about 2.5. Urosome with somite bearing P5 about same width as genital double-somite and devoid of lateral hairs. Genital double-somite (fig. 1A, C), about 1.15 times as wide as long, broader in its anterior part and in this part as wide as the fifth pedigerous somite, and 4 times as long as each of the two following urosomites. In ventral view, seminal receptacle appearing elliptical, consisting of two parts, anterior part the smallest, and posterior part with margin reaching two thirds of the somite's length (fig. 1A), different from the usual structure in *Metacyclops*. Copulatory pore located in the centre of the somite. Gonopores located in lateral position, protected by the reduced legs 6 (fig. 1H). Anal somite (fig. 1B) about twice as long as the preceding somite, anal operculum hardly curved and located halfway the somite, with smooth margin and without ornamentation. No ornamentation at the distal margins of any of the somites.

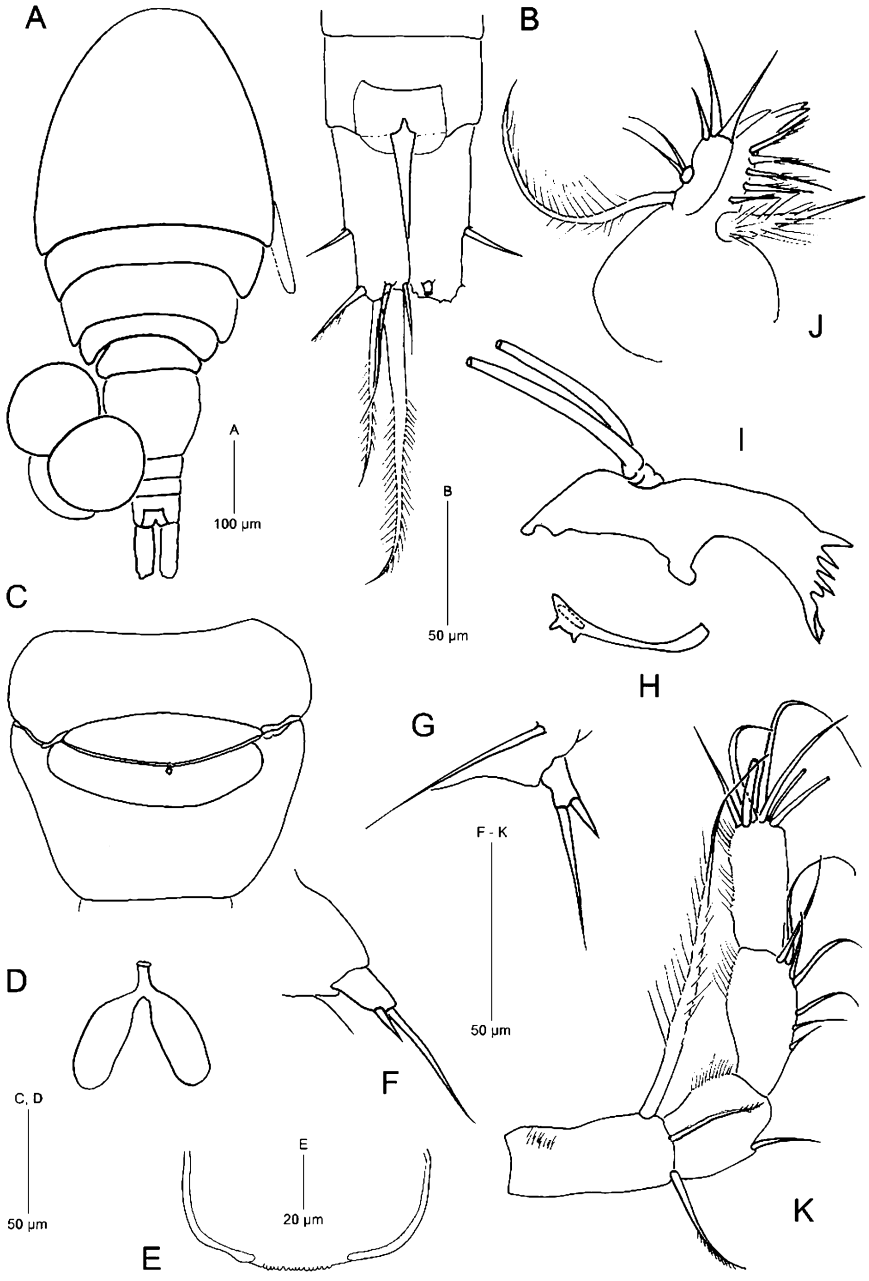

Fig. 1. *Metacyclops longimaxillis* n. sp., ♀. A, habitus, dorsal; B, anal somite and furca, dorsal; C, genital double-somite, showing seminal receptacle (internal), ventral; D, aspect of spermatophore (♂) when fixed on the copulatory pore of the genital double-somite of the ♀; E, labrum; F-G, P5 (different views); H, P6; I, mandible; J, maxillule; K, antenna (caudal).

Furcal rami (figs. 1A, B, 5E) rather short, 2.9 times as long as broad, with the usual 6 setae. Furcal setae: median external (lateral) seta inserted at 60% from the base of the furcal ramus; externalmost terminal seta slightly longer than internalmost (ratio: 1.1) and half as short as the dorsal seta (ratio 0.52); internal median terminal seta strong and enlarged at its base, 1.75 times as long as furcal rami and 1.65 times as long as external median terminal seta, which is itself 1.3 times as long as the dorsal seta no breaking planes in the median setae. All furcal setae plumose (not all figured). Some denticles at the insertion of the median external (lateral) seta and of the externalmost terminal setae.

Antennule 11-segmented (fig. 2A), short, reaching the posterior margin of the somite bearing the second swimming legs; setation from proximalmost to distalmost segments (numbers of setae in parentheses; a, aesthetasc): 1(8), 2(4), 3(5), 4(1), 5(1 + a), 6(2), 7(3), 8(2 + a), 9(2), 10(2), and 11(7 + a). Segment 1 without ornamentation; on segment 4, the seta is a small spine; aesthetasc of segment 5 very short, of same length as seta; segments 7 and 8 very long. The segmental fusion pattern of the antennule is: I-V, VI-VII, VIII-XI, XII-XIII, XIV, XV-XVI, XVII-XX, XXI-XXIII, XXIV, XXV, XXVI-XXVIII.

Antenna (fig. 1K) 4-segmented, composed of basipodite and tri-segmented endopodite. Basipodite with two internal distal setae, one inserted antero-distally, the other inserted more medially (fig. 1K), and externally the long and strong exopodal seta, inserted distally and bearing long spinules. Ornamentation on the basipodite as an oblique group of about 10 hair-like setae, inserted at the external basal part of the segment. Endopodite on its three segments bearing, respectively, 1, 7 (with a space between the group of three lateral and the group of 4 externo-distal setae), and 7 setae; all three segments ornamented with a row of hairs on the outer margin, which is discontinuous on the distal segment.

Labrum (fig. 1E) of rectangular shape, with straight cutting edge, equipped with 16 tiny teeth, occupying the median third of the anterior margin, and with very long hairs on the external side (not figured).

Mandible (fig. 1I) with gnathobase ending in 5/6 strong teeth and the usual barbed spinule, ornamented with a kind of denticulated membrane; palp consisting of two strong, long plumose setae inserted on a short but distinct vestigial segment.

Maxillule (fig. 1J) with well-developed precoxopodite ending in strong terminal spines, laterally five other spines, and the strong hairy spine. Maxillulary palp ending in three slender, spiniform setae, and with a small, rounded endopodite bearing two setae, and also a well developed exopodal seta ornamented with long setules.

Maxilla (fig. 2C) of particularly large size, exceeding the size of the other buccal appendages and hiding the maxilliped when the animal is observed in profile or in ventral view. Five-segmented, composed of precoxopodite, coxopodite, basipodite,

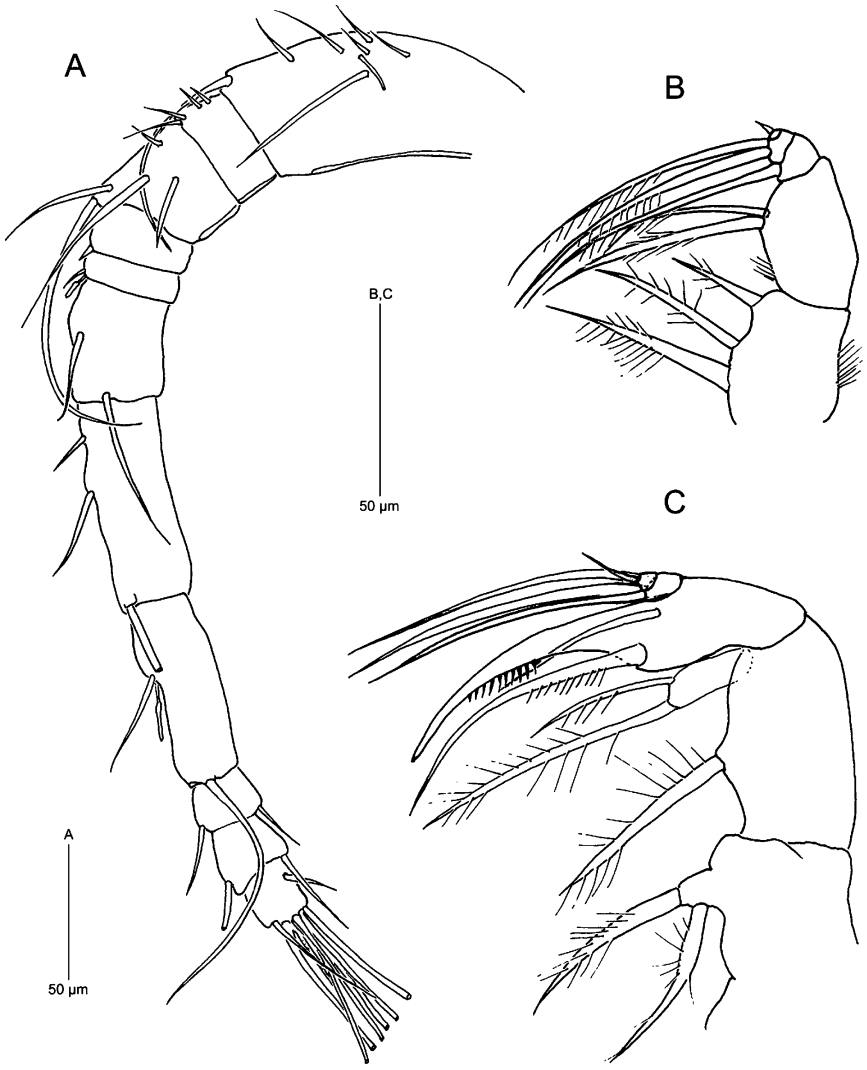

Fig. 2. *Metacyclops longimaxillis* n. sp., ♀. A, antennule; B, maxilliped; C, maxilla.

and bi-segmented endopodite. Precoxopodite with the lobate distal endite armed with two strong, bipinnate setae. Coxopodite with a strong, long barbed seta, as long as the coxopodite, distal endite with two unequal spines, the proximal one the longest, longer than the coxopodite and bipinnate, the distal spine short, half as long as the other. Basipodite with the endite armed with three elements, the distal-most forming a characteristic, very strong and large claw, moderately curved and bearing 10 sharp spines on its interior face. Endopodite bi-segmented, first segment bearing two robust setae and second segment ending in a long, slender seta and a thin subapical seta.

Maxilliped (fig. 2B) 5-segmented, characterized by very long setae ornamented with long spinules (not all figured, but as in male, see fig. 5D). Armature formula: 3.2.1.2.1 as 3 strong setae on syncoxopodite, the distal one shorter, 2 on basipodite; endopodite of 3 segments, the first with a long seta, the second bearing two long slender setae, and a very small distal segment bearing a much reduced seta. Syncoxopodite and basipodite bearing some long setae on the external margin.

Swimming legs P1-P4 (fig. 3A-D) with bi-segmented rami. Spine and setal formula of the distal segments of the exopodites 3.4.4.3 and 5.5.5.5, respectively. Intercoxal plates of P1-P4 with distal margin straight, and with only slightly rounded prominences on P1. No ornamentation observed on coxopodites. All inner setae on the inner distal corners of coxopodites bearing setules or spines, plumose on P1, plumose at the base and barbed apically on P2 and P3, with spines only on the distal half on P4. Basipodite of P1 with spine on the inner corner longer than the first endopodal segment. Outer basipodal seta very long on P1. Hairs observed on the inner sides of basipodites on P1, setules on P2, absent on P3, tiny spinules on P4. First segment of endopodite of P4 with margin markedly thickened (fig. 3D). Endopodite of P4 ending in an external spine and a longer seta, about as long as the segment itself.

Spine and setal formula as follows (spines in Roman numerals, setae in Arabic numerals; legend: outer/inner spine or seta; outer/terminal/inner):

	Coxopodite	Basipodite	Exopodite	Endopodite
P1	0-1	1-I	I-1; III, 2, 3	0-1; 1, 1-I, 3
P2	0-1	1-0	I-1; III, I-1, 4	0-1; 1, I-1, 4
P3	0-1	1-0	I-1; III, I-1, 4	0-1; 1, I-1, 4
P4	0-1	1-0	I-0; II, I-1, 4	0-1; 1-I, 3

P5 (fig. 1F, G) composed of a seta, inserted on a tiny plate directly on the somite, and of one segment twice as long as wide, bearing 2 unequal elements. Spiniform setae clearly separated, a long external one, 3.2 times as long as the internal short, robust spine.

P6 (fig. 1H) located dorsolaterally, composed of two small, short, external spine-like processes inserted on the outer corner of the gonoporal plate.

No colour observed.

Egg-sacs paired, each bearing three large eggs.

Description of male (fig. 4A). — Body length (excluding furcal setae): 0.62 mm. Anterior part of body of the same general shape as in female, slightly more slender. Greatest width at the posterior part of the cephalothorax. Prosome/urosome length ratio: 1.6. Cephalothorax 2.6 times as wide as genital somite, which is itself a little wider than the somite bearing P5, and 1.4 times as wide as long, and about twice as wide as the following urosomites. No ornamentation at the posterior margins of any somite or on the their lateral margins, except for the two symmetrical, arcuate

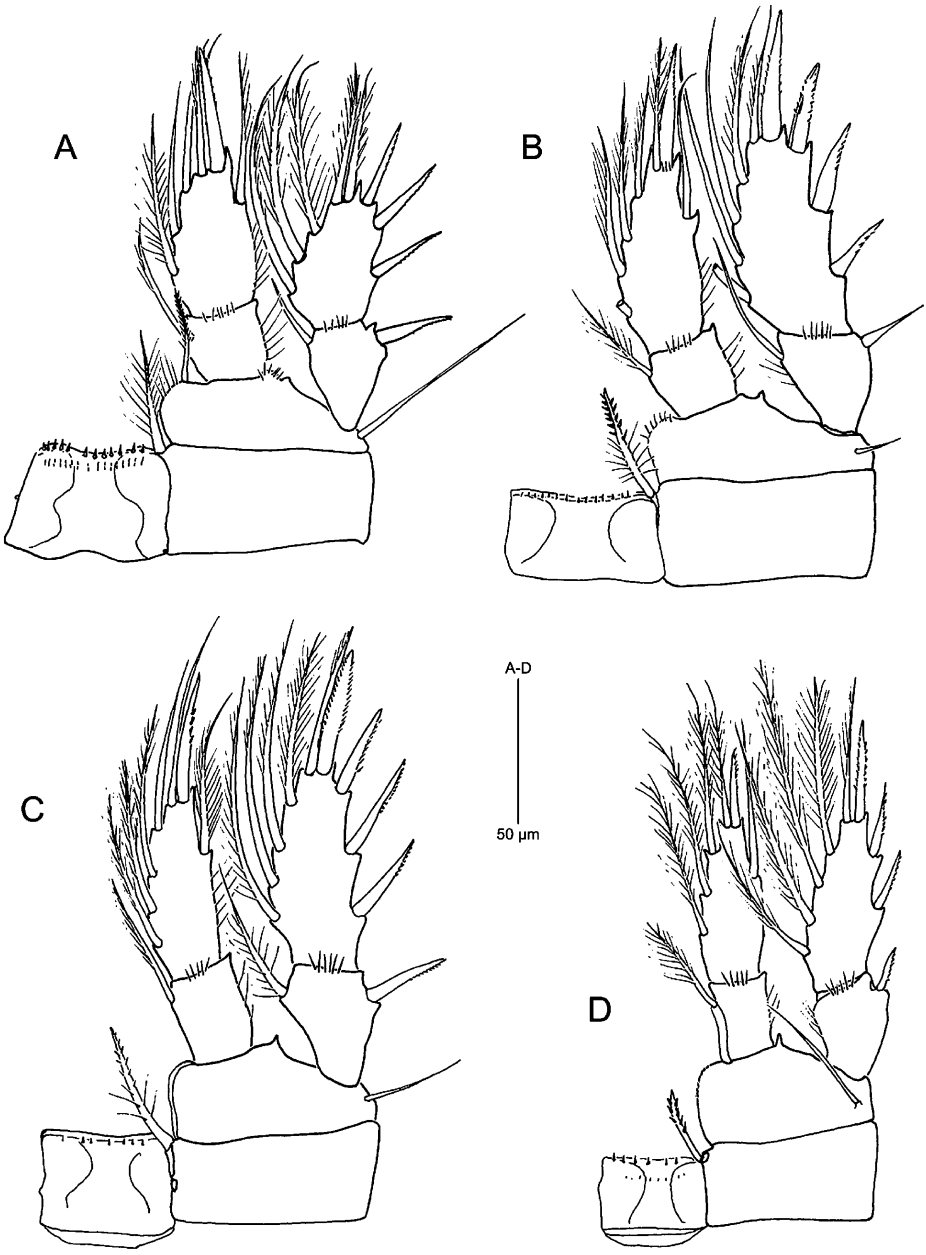

Fig. 3. *Metacyclops longimaxillis* n. sp., ♀. A, P1; B, P2; C, P3; D, P4.

rows of spinules on the proximal ventral part of the genital somite (fig. 5C, arrow). Anal somite of same width as the last three urosomites, anal operculum located in the middle of the somite, with smooth margin, slightly convex as in female,

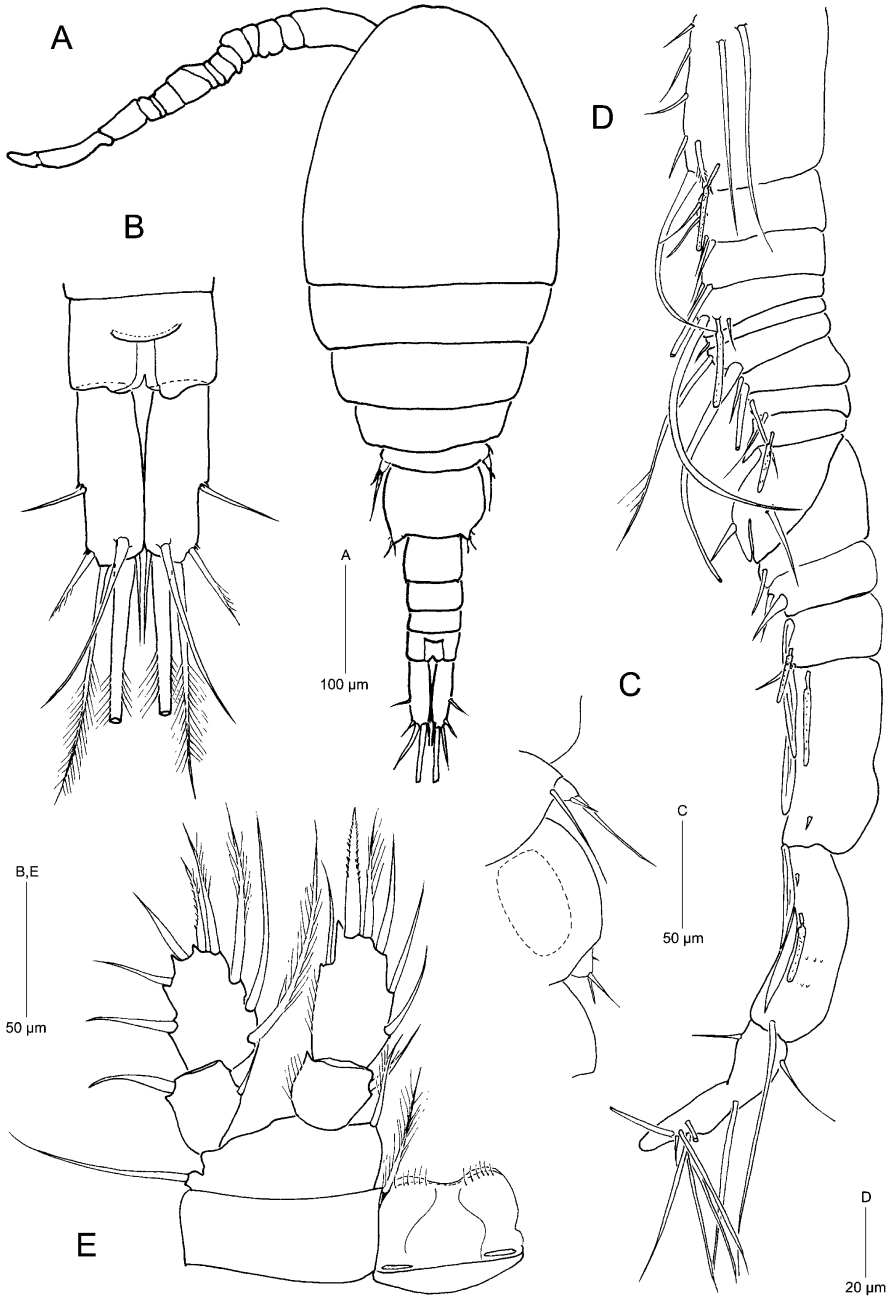

Fig. 4. *Metacyclops longimaxillis* n. sp., ♂. A, habitus, dorsal; B, anal somite and furca, dorsal; C, P5 and P6, dorsal (dotted line, internal spermatophore); D, antennule; E, P1.

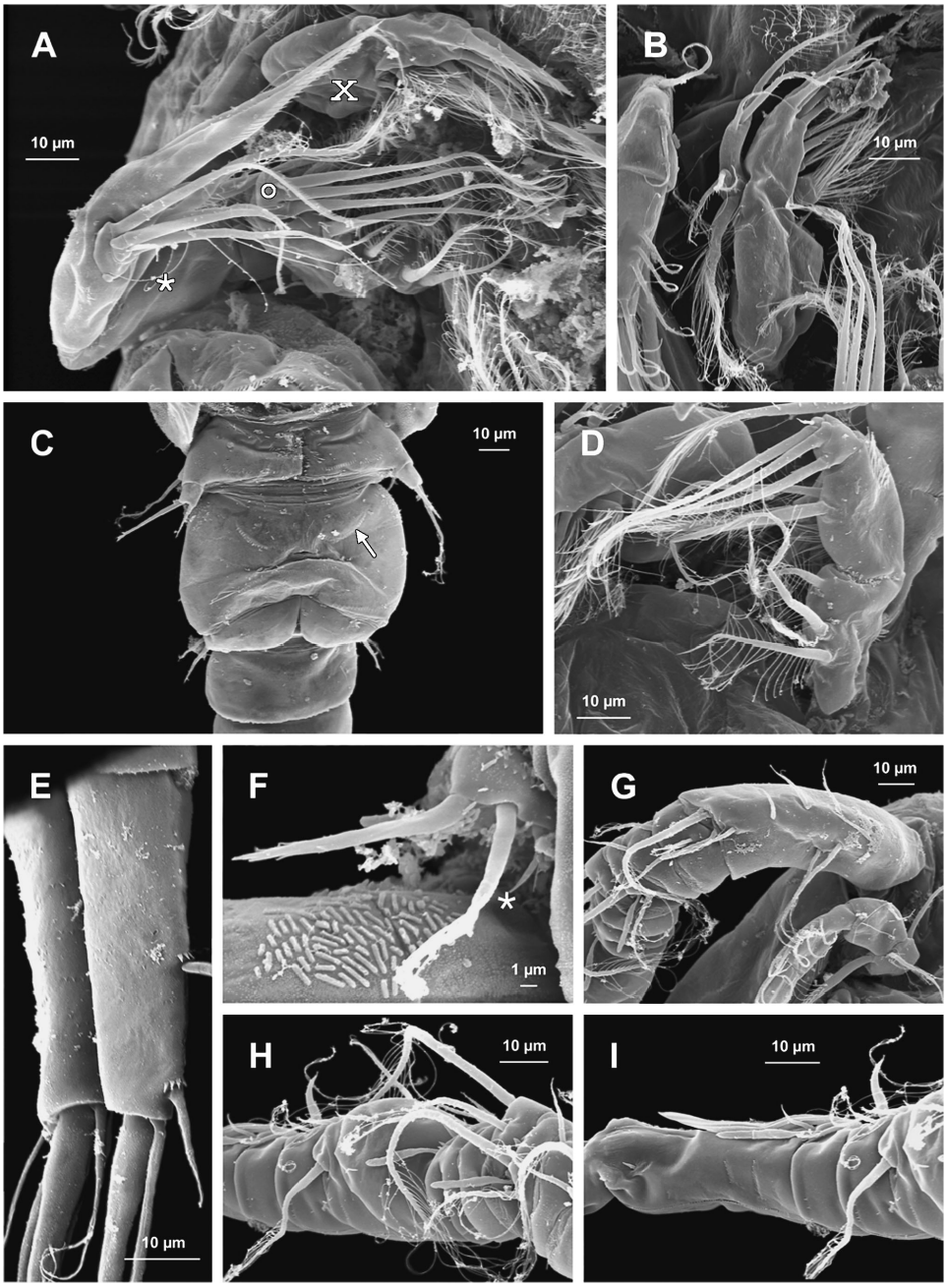

Fig. 5. *Metacyclops longimaxillis* n. sp., ♂, SEM photographs. A, maxilla (*), maxilliped (°), and maxillule (×) in situ: note the size of the maxilla, enveloping the maxilliped; B, maxillule and, at left, part of the antennule; C, part of the urosome, ventral, with somite bearing P5, and genital somite with arcuate rows of spinules (arrow); D, maxilliped; E, furca: ventral, profile, note the spinules at the insertion of externalmost and lateral setae, and ornamentation of tiny denticles on the furca; F, P6, with the small external spine (at right, *); G-H-I, antennule: G, segments 1-9; H, segments 10-13; I, segments 11-15.

and without other ornamentation. Rostrum large, with straight margin expanding ventrally.

Furcal rami (figs. 4A, B, 5E) rather short, 2.9 times as long as broad, with the usual 6 setae. Furcal setae: external lateral seta inserted at 60% from the base of the furcal ramus; outermost terminal seta shorter than the innermost (ratio: 0.64) and than the dorsal seta (ratio: 0.44); external median terminal seta almost as long as the dorsal seta (ratio: 1.09), internal median terminal seta 3.5 times as long as furcal rami, and 2 times as long as the external median terminal seta. All furcal setae plumose (not all figured). Some spinules at the insertion of the outermost terminal and lateral setae, small denticles present on the surface of the furcal rami (fig. 5E).

Antennule (fig. 4D, 5G-I), 16-segmented, with double geniculation, one between 7^{th}-9^{th} segments and the other, as usual, between 14^{th} and 15^{th} segments. Setal formula: 1(8), 2(4), 3(2), 4(2), 5(1), 6(2), 7(2), 8(2), 9(1), 10(2), 11(1), 12(1), 13(0), 14(0), 15(1), 16(10), the long setae plumose. Aesthetascs present on segments 1(1), 4(1), 9(1), 13(1), 14(1), 15(1), all long and linguiform. Modified, leaf-shaped setae present on segments 13(1), 14(2), 15(1). Two short transversal, rows of tiny spinules on segment 15.

Antenna (fig. 5G), mandible (not figured), maxillule (fig. 5A, B), maxilla (fig. 5A), and maxilliped (fig. 5D) without significant differences from those of the female, and with the same large maxilla enveloping the maxilliped (fig. 5A).

Segmentation of swimming legs P1-P4 (P1 figured only, fig. 4E) identical to those of the female. P5 (figs. 4A, C, 5C), of same structure as in the female, with two spiniform setae, the external 3.6 times as long as the internal, and about 0.6 times as long as the genital somite. P6 (figs. 4A, C, 5F), composed of two short, spiniform elements and a very small one, the former inserted close to each other on a rounded prominence on each lateral side of the genital somite, better visible dorsally, and partly hidden by the genital plates in ventral view.

Spermatophore (fig. 1D) as two elongated sacs joined in a small duct, shorter than the genital double somite, and observed deposited on the copulatory pore of the female.

Variability. — Body length of female varies from 0.71 to 0.76 mm, average 0.74 mm, n = 9. Body length of male varies from 0.65 to 0.68 mm, average 0.67 mm, n = 5.

Sexual dimorphism. — The males differ from the females in the relative lengths of the furcal setae: dorsal seta and median terminal seta longer than in female, absence of dorsal spines at the base of the furcal rami in the male. Concerning swimming legs P1-P4, the setae appear slightly longer in the male than in the

female, and the cuticular thickening on the inner side of the first endopodal segment of P4 has not been observed in the male.

Discussion. — The genus *Metacyclops* is currently represented by 61 species and subspecies (Dussart & Defaye, 2006). This large genus is in need of revision and might be divided in several separate genera in the future, when all species will have their morphology known in detail. Its validity has been discussed since Lindberg (1961), and successively mainly by Pleşa (1981), Reid (1987), and Karanovic (2004, 2004a). The species of the genus basically share the structure of P5 and of the swimming legs with bi-segmented rami, and the shape of the female seminal receptacle with the distal part more developed and blister-shaped. They differ mainly in the segmentation of the antennule, with from 9 to 12, even 17 segments (only in *Metacyclops grandis* (Kiefer, 1935)); by the setal ornamentation of the antenna; the segmentation of the maxilliped; the spine formula of the second exopodal segment of the swimming legs, and the terminal armature of the second endopodal segment of P4: these elements are either two spines (plesiomorphic state), or one single spine (about half of the species for each state), or one spine and one seta (only *M. stammeri* until now, since *M. postojnae* Brancelj, 1987 has been rightfully transferred to the genus *Microcyclops* by Karanovic, 2004). Various attempts at grouping have been proposed: according to the presence of one or two terminal spines on the terminal segment of the endopodite of the fourth swimming leg; according to the spine formula of the second exopodal segment of P1 to P4; or according to the armature of the male P6, composed of two or three spines (used in keys by Lindberg, 1961; Reid, 1987; Herbst, 1988; Defaye, 1992). Karanovic (2004, 2004a) defined a "*trispinosus*-group" on the basis of the spine formula 3.3.3.3 of the second segment of the exopodites of the swimming legs.

M. longimaxillis n. sp. conforms to the genus *Metacyclops* mainly by the following characters: the antennule segmentation, the antenna with the basipodite bearing two internal setae and an exopodal one, the bi-segmented swimming legs, and the structure of P5. The 11-segmented antennule and the spine formula for Exp2 of P1 to P4: 3.4.4.3 (except *M. mortoni* Pesce, De Laurentiis & Humphreys, 1996, which has 3.4.4.2 and *M. arnaudi* 3.3.3.3) are shared (without any consideration of phylogenetic closeness) by about half of the species of *Metacyclops*, so by at least 28 other species*) (of which 12 have two terminal

*) These species are: *Metacyclops communis* (Lindberg, 1938); *M. aequatorialis* Dussart, 1977 §; *M. agnitus* Herbst, 1988; *M. chelazzi* Dumont, 1981 §; *M. campestris* Reid, 1987 §; *M. curtispinosus* Dussart, 1984; *M. cushae* Reid, 1991; *M. denticulatus* Dussart & Frutos, 1985; *M. dianae* Pesce, 1985 §; *M. gasparoi* Stoch, 1987; *M. geltrudae* Galassi & Pesce, 1994 §; *M. gracilis* (Lilljeborg, 1853) §; *M. grandispinifer* (Lindberg, 1940); *M. hannensis* Defaye, 1992; *M. lusitanus* Lindberg, 1961; *M. minutus* (Claus, 1863); *M. mutatus* Herbst, 1988; *M. oraemaris* Rocha, 1994 §; *M. palu-*

spines on Exp2 of P4). Among these species, only one has also the Exp2 of P4 ending in a seta and a spine: *Metacyclops stammeri*, described by Kiefer in 1938 from Italy (La Zinzulusa Cave and passim, Salento, Apulia). This species appears to be the closest similar to *M. longimaxillis* n. sp. *M. stammeri* was found again in Salento (Pesce et al., 1978), and then in Montenegro (two males, Karanovic, 1999). *M. stammeri* and *M. longimaxillis* have various morphological traits in common, in addition to the setation of Enp2 of P4: in both male and female, the presence of two setae and the strong exopodal seta on the basipodite of the antenna, the setal formula of the exopodites of the swimming legs (3.4.4.3), the general shape and setation of the furca, with the inner median seta enlarged at the base; in the female, the 11-segmented antennule, the globular genital double-somite; and the segmentation pattern of the antennule. They first of all differ by their size: the female of the new species is larger, 0.71 to 0.76 mm and the male 0.65 to 0.68 mm (in *M. stammeri*: 0.62 to 0.64 mm in the female and 0.50 to 0.59 mm in the male). They also differ by traits of the antennule: in the female, the aesthetasc on the 8th segment is shorter than in *M. stammeri*; the male antennule is 16-segmented in the new species, with 6 asthetascs, while in *M. stammeri*, Karanovic (1999) described a 14-segmented antennule with only 2 aesthetascs. The species also have a different setal formula of the antenna: 1.7.7 in the new species, 1.8.7 in *M. stammeri*. The structure of mandible and maxilliped is not known for *M. stammeri*; however, the maxilla figured by Karanovic (1999) shows a comparable shape of the basipodite claw. Differences can be noted also in the intercoxal plates of the swimming legs: without ornamentation in *M. stammeri*, unlike the new species. Other differences concern the endopodite of P4, particularly the relative lengths of the terminal seta and spine: the seta is very long in *M. stammeri*, 2.5 times as long as the spine and 1.9 times as long as the segment, while these ratios are, respectively, 1.9 and 0.86 in the new species (for females). The furcal rami are relatively shorter in the new species: length/width ratio: 2.9 (n. sp.) and 3.8 for *M. stammeri* (females); the internal median seta is twice as long as the external median seta in *M. stammeri* (female) while it is 1.65 in the new species. Other main differences are in the shape of the seminal receptacle, in which the posterior part is not blister-shaped in the new species; and in the structure of the male P6, consisting of two setae in *M. stammeri* and three in the new species.

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dicola (Herbst, 1959) §; *M. pectiniatus* Shen & Tai, 1964; *M. pseudoanceps* (Green, 1962) §; *M. rudis* Pleşa, 1981 §; *M. stammeri* Kiefer, 1938; *M. somalicus* Dumont, 1981 §; *M. subaequalis* Dussart, 1984 §; *M. subdolus* Kiefer, 1938; *M. superincidentis* Karanovic, 2004 §; *M. trisetosus* (Herbst, 1957).

(The § sign stands for species with two terminal spines on exopodal segment 2 of P4.)

Metacyclops subdolus Kiefer, 1938 (figs. 6-9)

Material examined. — Eight ♀♀, dissected and mounted on one or two slides (HUJINVCOP129, HUJIMVCOP131 to 135; MNHN-Cp2497, MNHN-Cp2498), 3 ♂♂, dissected and each mounted on one slide (HUJINVCOP130, HUJINVCOP136-137; MNHN-Cp2499), numerous ♂♂, ♀♀ and copepodites, ethanol-preserved (HUJINVCOP138), all from pool in Ayyalon Cave, Israel, coll. Ch. Dimentman, April-May 2006.

For comparison, slides from the Kiefer collection. N°s: 03873, *Metacyclops subdolus* n. sp., Typus, 3 ♂♂ A1-P4, Italien Abisso Höhle Tümpel im Gang, Stammer leg., 24.9.37; id Kiefer 31.3.38; – 03874, *Metacyclops subdolus* n. sp., Typus, 3 ♂♂ Abd + P5 wie 3873; – 03875, *Metacyclops subdolus* n. sp., Typus ♀♀ A1-P4, Italien Höhle Abisso Tümpel, Stammer leg., 24.9.37; – 03876, *Metacyclops subdolus* n. sp., Typus, 3 ♀♀, Italien, Abisso Höhle Tümpel, Stammer leg., 24.9.37, id Kiefer 31.3.38; – 03879, *Metacyclops subdolus* 2 ♂♂, A1-P4, Italien, La Zinzulusa, Kl. Tümpel, Stammer leg., 25.9.37, id. Kiefer 2.4.38; – 3880, idem; 03879, Abd + P5.

The specimens from Ayyalon cave present the main diagnostic characters of *M. subdolus*, as in the female, the 11-segmented antennule and the general shape of the seminal receptacle, and in both sexes, the spine and setal formulae of the last exopodal segments of the four legs as, respectively, 3.4.4.3 and 5.5.5.5; the second endopodal segment of the fourth leg ending in a single spine as long as the segment itself; the fifth leg composed of a seta, inserted on a tiny plate directly on the somite and of one segment 1.2 times as long as wide, bearing 2 unequal elements clearly separated, an external long seta, 3.3 as long as the internal, short, robust spine. Only some slight differences could be observed in comparing our material with the type-material from Kiefer's collections. In the female as in male, the swimming legs appear more slender in the Israelian material and the intercoxal plates all show an ornamentation of hairs and spinules in their distal half. The Ayyalon specimens are generally larger, with body lengths of the females from 0.76 to 0.95 (average 0.91, n = 10) instead of 0.60 to 0.65 in Kiefer (1938), and of the males from 0.61 to 0.66 (average 0.63, n = 4) instead of 500 μm. The ratio length/width of the furca is, on average, slightly less than 3 (from 2.8 to 3.2, average 2.97, n = 5). This ratio, however, is similar to that observed in specimens of *M. subdolus* from Greece studied by Pesce (1978). The P5 sometimes shows the inner spine separated from the seta by an either more, or less pronounced space, and is clearly visible when the specimen is observed from its dorsal side. Thus, it appears to be differently positioned than in the type specimens of *M. subdolus*, in which it is only visible when the animal is observed from ventral (as in Kiefer's slides). No comparison could be made about the morphology of the antennae and the buccal appendages, which are not accurately visible in Kiefer's type slides. The differences observed, in the absence of a complete redescription of *M. subdolus* from its type-locality, can be considered a consequence of the saline conditions in which the specimens have been found. *M. subdolus* has already been identified from Israel by Dimentman & Por (1991) from springs near the Dead Sea. The

species was also reported from the northern Negev by Defaye & Dussart (1995), who noted especially long dorsal and internalmost terminal furcal setae. These observations have been checked from the specimens studied by these authors; the dorsal and internalmost terminal setae have the same length and are 1.38 times as long as the furcal rami. Also, the P5 have a very long terminal seta, 6.4 times as long as the spine, both elements being well separated at their insertion on the terminal segment. *M. subdolus* has a European Mediterranean distribution (no record from North Africa); it has first been reported by Kiefer (1938) from southern Italy (La Zinzulusa, Abysso caves), then from Sardinia (Lindberg, 1956), Italy (Pesce et al., 1978; Pesce, 1985), Greece (Peloponnesos, Attica, Crete: Pesce, 1978; Pesce & Maggi, 1981, 1983), Mallorca (Can Pastilla: Lescher-Moutoué, 1981), Dragonera (Jaume, 1990).

However, new findings and a redescription of *M. subdolus* from the type locality will be necessary to clearly establish the species' variability, both morphological and ecological, as well as its systematic position in the genus *Metacyclops*. We here give the description of the Ayyalon specimens (figs. 6-9).

Description of female (figs. 6-8). — Body length excluding furcal setae, from 0.76 to 0.95 mm, average 0.91 mm, n = 8. Habitus slender, widest at the posterior part of the cephalothorax in dorsal view (fig. 6A). Cephalothorax almost 1.6 times as long as the following pedigerous somites. Prosome/urosome ratio 1.6; body length/width ratio 2.7; cephalothorax/genital double-somite width ratio about 2.5. Somite bearing the P5 slightly wider than genital double-somite and devoid of lateral hairs. Genital double-somite (fig. 6A, C), about 1 to 1.2 times as long as wide. In ventral view, seminal receptacle consisting of two parts, with anterior part flattened, and a small, bulbous posterior part (fig. 6A), and of a structure common for *Metacyclops*. Copulatory pore located at about 0.40 of the length of the somite from the anterior margin. Gonopores located in lateral position, protected by the reduced legs 6. The two following urosomites (fig. 6A) almost of the same length, 0.4 and 0.3 times (respectively) as long as the genital somite, and slightly narrowing toward the anal somite (fig. 6B). Anal somite a little shorter than the preceding somite, bearing a short anal operculum with smooth margin, convex and located in the anterior half of the somite, and which is without other ornamentation on the anal sinus. No ornamentation at the distal margin of any somite, only four small ventral spinules on the distal margin of the anal somite, at the base of each of the furcal rami.

Furcal rami (fig. 6A, B) 3.2 times as long as broad. Furcal setae: median external (lateral) seta inserted at 70% from the base of the furcal ramus; outermost terminal seta shorter than the innermost (ratio: 0.68) and than the dorsal seta (ratio: 0.80); external median terminal seta 3.5 as long as the dorsal seta,

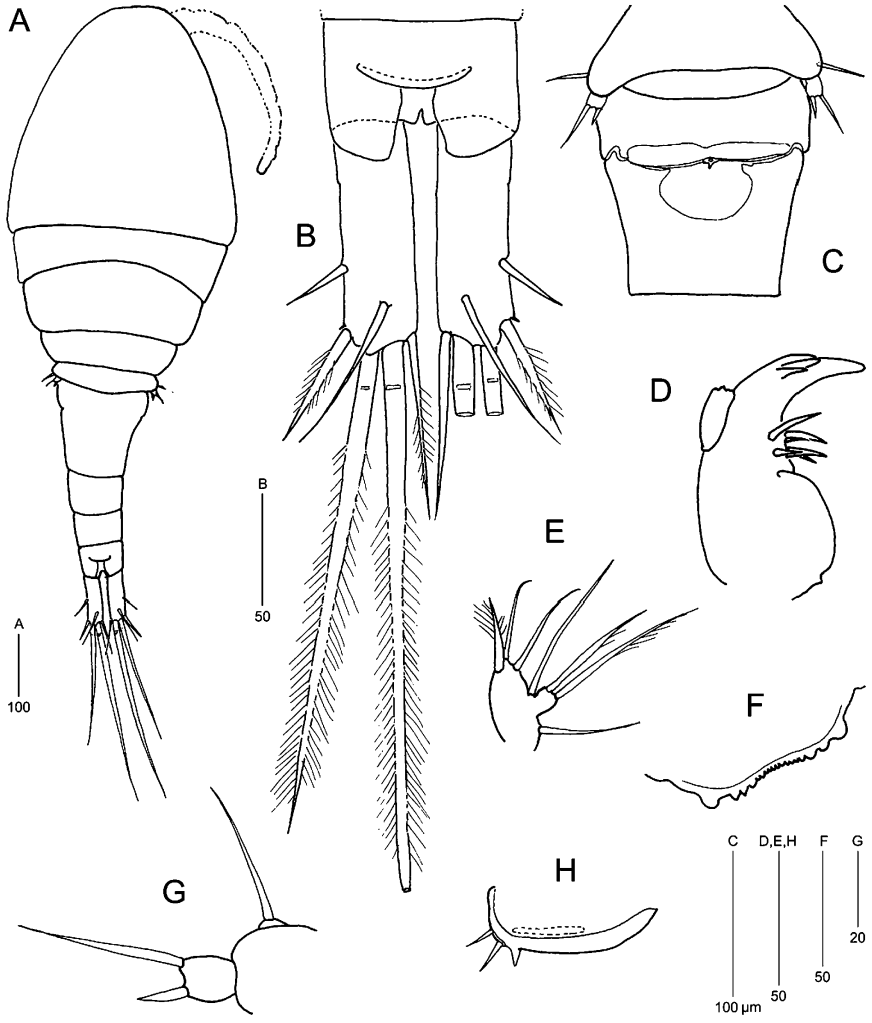

Fig. 6. *Metacyclops subdolus* Kiefer, 1938, ♀. A, habitus, dorsal; B, anal somite and furca, dorsal; C, somite bearing P5 and genital double-somite, showing seminal receptacle (internal), ventral; D-E, maxillule, palp separated; F, labrum; G, P5; H, P6 (gonopore represented in dotted line).

internal median terminal seta 3.8 times as long as furcal rami, and 1.4 times as long as the external median terminal seta. All furcal setae plumose (not all figured). A denticle is present at the insertion of the outermost terminal furcal setae.

Antennule 11-segmented (fig 7A), short, not reaching posterior margin of cephalothorax, setation from proximal to distalmost segments (number of setae in parentheses; a, aesthetasc; s, spine): 1(8), 2(4), 3(6), 4(2), 5(2), 6(1 + s), 7(3), 8(2 + a), 9(2), 10(2 + a), and 11(7 + 1a). Segment 1 ornamented with spinules

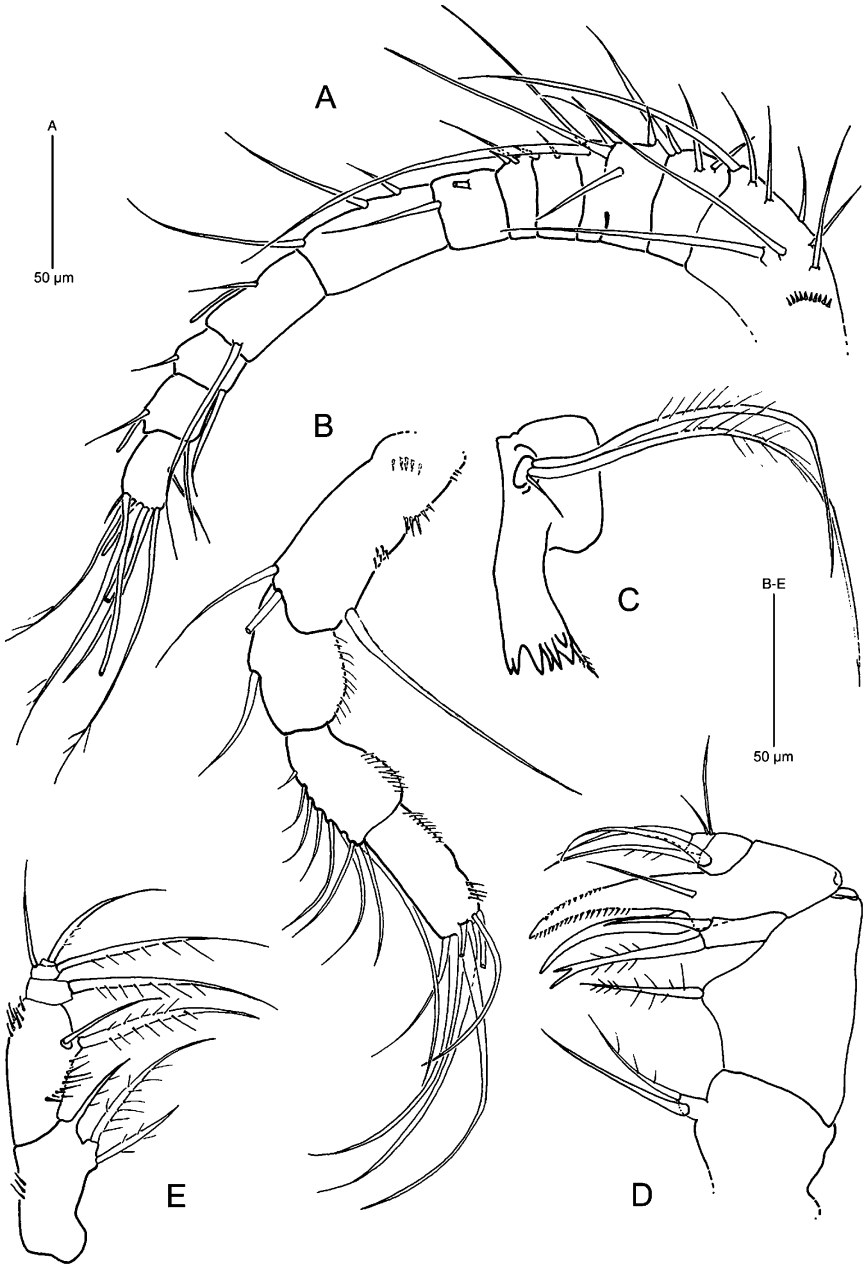

Fig. 7. *Metacyclops subdolus* Kiefer, 1938, ♀. A, antennule; B, antenna; C, mandible; D, maxilla; E, maxilliped.

(fig. 7A). Segment 3 showing remains of suture of two original segments, so probably formed by two fused segments. On segment 5, one of the two setae is

spiniform and short, but longer than that on segment 6. Segmental fusion pattern of the antennule as: I-V, VI-VII, VIII-XI, XII-XIII, XIV, XV-XVI, XVII-XX, XXI-XXIII, XXIV, XXV, XXVI-XXVIII.

Antenna (fig. 7B) 4-segmented, composed of basipodite and the 3-segmented endopodite. Basipodite bearing 2 internal setae inserted antero-distally (fig. 7B), and externally the long exopodal seta inserted distally. Ornamentation visible on the basipodite as two lateral groups of 5 spinules at the external frontal edge and a few spinules just at the base, as well as a small arc of 5 spinules in the proximal third of the frontal side. Endopodite bearing, respectively, 1, 9, and 7 setae on its three segments; all three ornamented with a row of hairs or spines on the outer margin, discontinuous on the distal segment.

Labrum with straight cutting edge, equipped with 16 small teeth, and with rounded lateral corners (fig. 6F).

Mandible (fig. 7C) with gnathobase ending in strong teeth and the usual barbed spinule, palp consisting of two long plumose setae and a thin small seta inserted on a very short vestigial segment.

Maxillule (fig. 6D, E) with well-developed precoxopodite ending in strong terminal spines, the other five spines located laterally, and a strong, hairy spine (not figured). Maxillulary palp with fused endopodite bearing three long setae, two apical and one lateral, and an exopodal seta inserted at the base of the endopodite; palp ending in two slender setae and a strong bipinnate spine.

Maxilla (fig. 7D) 5-segmented, composed of precoxopodite, coxopodite, basipodite, and bi-segmented endopodite. Precoxopodite with the lobate proximal endite armed with two strong setae. Coxopodite with a strong barbed seta, distal endite with two spines, proximal one the longest, bipinnate, and with bifid tip, and the distal one short, sharp, and curved. Basipodite with endite armed with three elements, one of these forming a strong claw, ornamented with spinules on both edges. Endopodite bi-segmented, first segment bearing two robust setae and second segment ending in a strong, spiniform seta and 2 thin subapical setae.

Maxilliped (fig. 7E) 5-segmented, with armature formula: 3.2.1.2.1, with 3 barbed setae on syncoxopodite, 2 on basipodite; endopodite of 3 segments, the first with a long, barbed seta, the second bearing two unequal setae, the external more slender and shorter, and the last endopodal segment ending in a seta. Syncoxopodite and basipodite bearing some long hairs on the external margin, an additional inner group of hairs on the basipodite in a slightly oblique line, and reaching the insertion of the barbed seta.

Swimming legs P1-P4 (fig. 8A-D) with bi-segmented rami. Spines and setal formulae of distal segments of exopodites 3.4.4.3 and 5.5.5.5, respectively. Intercoxal

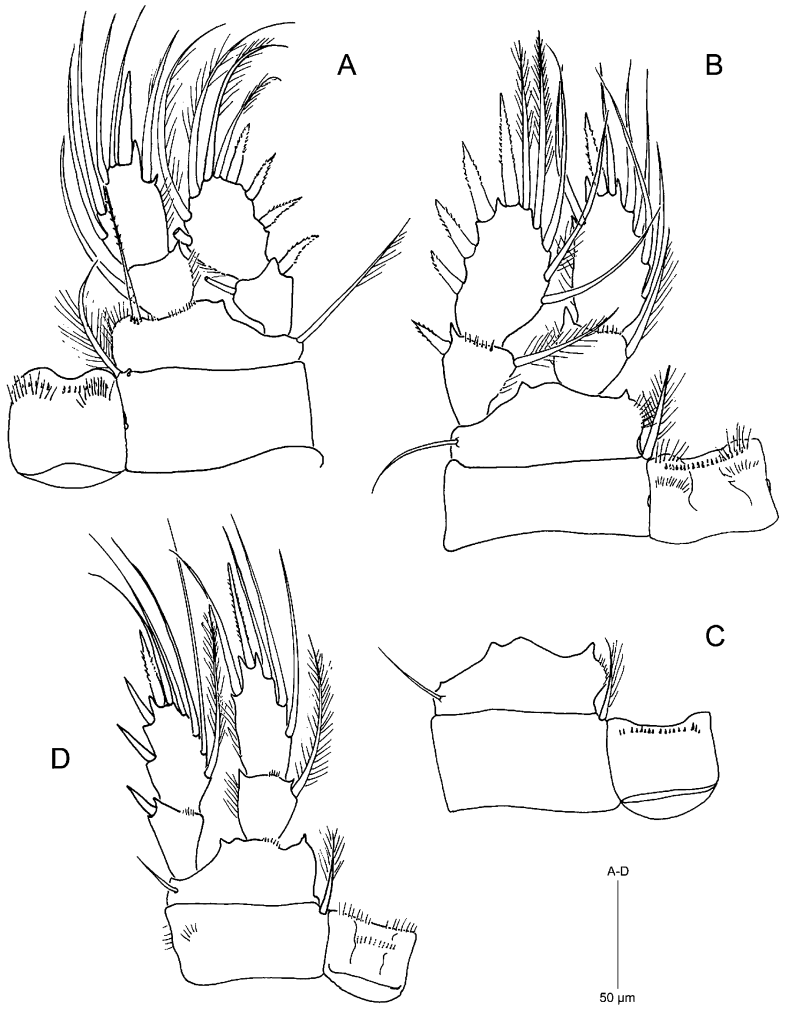

Fig. 8. *Metacyclops subdolus* Kiefer, 1938, ♀. A, P1; B, P2; C, P3: coxopodite, basipodite, and intercoxal plate; D, P4.

plates of P1-P4 with straight distal margin in P4, but with more or less rounded prominences in the other legs, with ornamentation of setae and spinules as shown in the figures. Ornamentation of coxopodites only observed in P4 and reduced to an outer group of a few spinules on the caudal side, and some lateral hairs. All inner setae on the inner distal corners of the coxopodites plumose, that of P1 the longest, and of P2 spiniform. Basipodite of P1 with a spine on the inner corner, almost reaching the tip of the second endopodal segment, bipinnate in its distal half. Outer basipodal seta very long. Hairs observed on the inner margins of basipodites of P1 to P3, but not on that of P4. Endopodite of P4 ending in a long spine, as long as the segment itself.

Spine and setal formula as follows (spines in Roman numerals, setae in Arabic numerals; legend: outer/inner spine or seta; outer/terminal/inner).

	Coxopodite	Basipodite	Exopodite	Endopodite
P1	0-1	1-I	I-1; III, 2, 3	I-1; 1, 1-I, 3
P2	0-1	1-0	I-1; III, I-1, 4	0-1; 1, I-1, 4
P3	0-1	1-0	I-1; III, I-1, 4	0-1; 1, I-1, 4
P4	0-1	1-0	I-0; II, I-1, 4	0-1; 1, I, 3

P5 (fig. 6A, C, G) composed of a seta inserted on the somite, and of a segment that is 1.2 times as long as wide, bearing 2 unequal elements, clearly separated, an external long seta, 3.3 times as long as the internal short, robust spine. Sometimes the lateral seta on the 5th thoracic somite appears not to be inserted on the tiny plate figured here, but directly on the somite instead.

P6 (fig. 6H) located dorsolaterally, composed of three small, short external spines inserted on the outer corner of the gonoporal plate.

No colour observed.

Egg-sacs paired, each bearing 6 eggs of medium size.

Description of male (fig. 9). — Body length from 0.61 to 0.66 mm, average 0.63, n = 4.

Anterior part of the body of the same shape as that of female. Urosome of 5 somites, the first one devoid of any hair laterally; genital somite the largest, twice as long as wide (fig. 9B); the three following urosomites slightly but progressively narrowing towards the anal somite. Anal somite of same width as the preceding somite. Anal operculum as in female, short, with distal margin convex and no ornamentation on sinus. A few spinules at the base of the furcal rami going laterally from the middle of the ramus. Furcal rami 2.25 times as long as broad. Furcal setae of lengths different from those in female: innermost terminal seta 2.42 times as long as outermost, 1.25 times as long as dorsal seta, and 1.54 times as long as furcal ramus; inner median terminal seta 8.1 times as long as furcal rami, and 3 times as long as outer median terminal seta. A spine is present at the insertion of the outermost terminal seta. No ornamentation at the posterior margin of any somite.

Antennule (fig. 9D), 16-segmented, with double geniculation, one between 7th-9th segments and the other, as usual, between 14th and 15th segment. Setal formula: 1(8), 2(4), 3(2), 4(2), 5(1), 6(2), 7(1), 8(2), 9(2), 10(2), 11(2), 12(1), 13(0), 14(0), 15(1), 16(10), most setae smooth. Aesthetascs present on segments 1(3), 4(1), and 9(1), all long. First segment with a proximal, oblique row of 7 spinules. Antenna and buccal appendages without significant differences from those of the female. Segmentation of swimming legs P1-P4 (last segment of endopodite of P4: fig. 9E) identical to that in the female, without sexual dimorphism. P5 (fig. 9B, C), similar to that of female, with apical external seta half as long as genital somite. P6

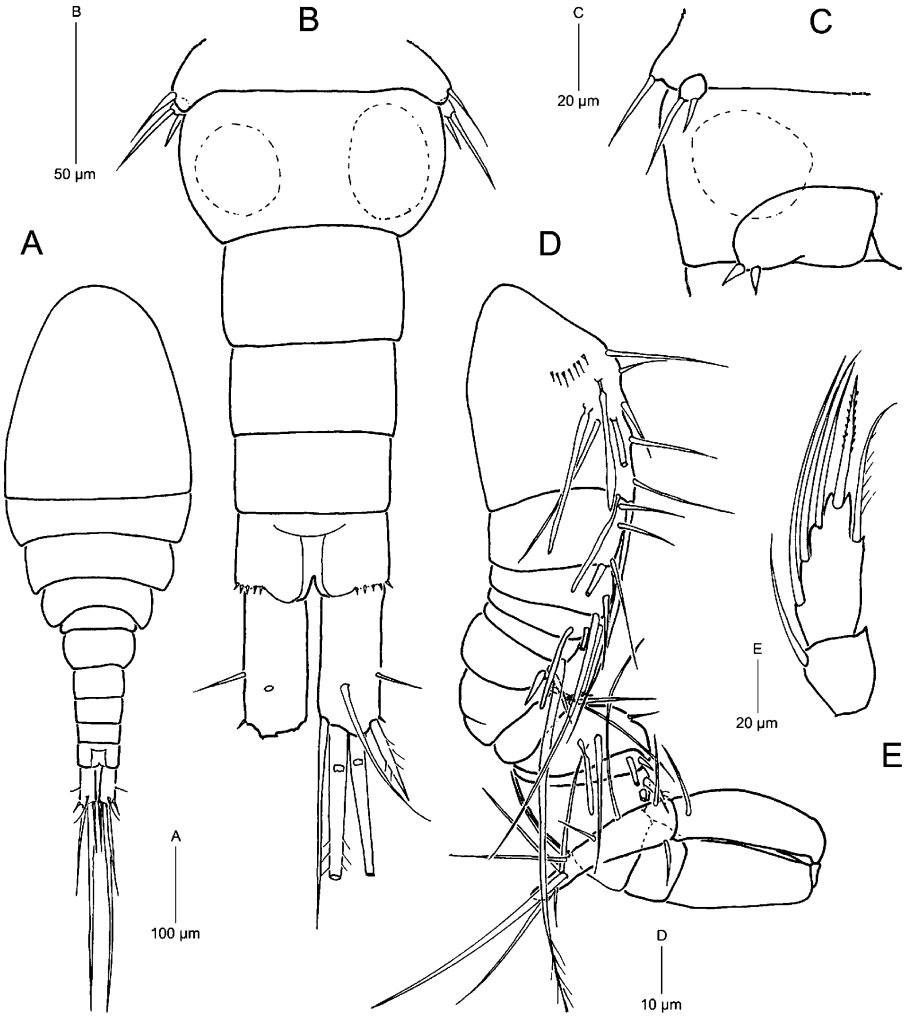

Fig. 9. *Metacyclops subdolus* Kiefer, 1938, ♂. A, habitus, dorsal; B, urosome, dorsal; C, P5 and P6, ventral (B and C showing the internal spermatophores (as dotted lines); D, antennule; E, Enp3P4.

(fig. 9C), composed of two short elements inserted close to each other at the outer corner, on a small cuticular plate.

GENERAL DISCUSSION

These two *Metacyclops* species look very different. The new species is distinguished by the segmentation of the antennule; the median insertion of the innermost seta on the antenna; the setal formula of the A2 endopodite with 7 setae on the second endopodal segment; the mandible with a peculiar gnathobase and a palp

with 2 setae; the maxillule with the particularly long exopodal seta inserted near the endopodite; the maxilliped with the much reduced seta on the third segment of the endopodite; and, especially, the extraordinary development of the maxilla with the long, specifically curved claw, enveloping the maxilliped; and the very long setae of the maxillule, maxilla, and maxilliped. Other main characteristics are: the shape of the seminal receptacle, different from the general *Metacyclops* pattern, and the Enp2P4 ending in a seta and a spine, instead of a spine as in *M. subdolus*. In the male, the geniculate antennule has a very different number of aesthetascs, one being present on segments 13, 14, and 15. The presence of the leaf-like, modified setae on these segments is also remarkable. A comparison with *M. stammeri*, phylogenetically probably its closest relative, cannot be made in the absence of a complete description, particularly of the buccal appendages and the male antennular structure of that species. The characters of the new species as mentioned here might suggest to separate it, with *M. stammeri*, from the group of 28 *Metacyclops* species having an 11-segmented antennule and a formula for the swimming leg exopodites 3.4.4.3 (most of them having 5.5.5.5 as setal formula). Its allocation, with *M. stammeri*, to a new genus appears premature, but should be carefully considered in a complete revision of the genus *Metacyclops*. Already, two new genera and a particular group have been defined, based on species first assigned to the genus *Metacyclops*: *Meridiecyclops* Fiers, 2001; *Fierscyclops* Karanovic, 2004; and the *trispinosus*-group of Karanovic (2004). Special attention should be paid to the structure of P5, because even if the general structure pattern appears identical for all the species currently belonging to *Metacyclops*, it is possible that differences can be found in the course of an objective and careful analysis of its characters. This point has been mentioned by Karanovic (2004) in his comments on the affinities of the new genus *Fierscyclops*, the characters of which to us seem very close to the current definition of the genus *Metacyclops*. Such a discussion on the genus *Metacyclops* will, however, not be developed here.

The co-occurrence of these two species is surely related to the characteristics of the biotope. The pool of Ayyalon Cave has water of a double origin: fresh groundwater, mixed with saline water. The population of *M. subdolus* in the pool is composed of a few adults and copepodids, and is small compared to that of *M. longimaxillis*. We can hypothesize that these few specimens of *M. subdolus* come from the surrounding subterranean fresh waters that arrive in the pool, since it is found in larger populations in bore holes a few meters away from the cave. *M. longimaxillis* occurs in a very large population in the cave pool, with all developmental stages represented and it seems evident that this species is better adapted to the life under the specific hydrological conditions of high temperature, and saline and sulfidic water. The long setae of the buccal appendages and, of course, the long maxillae, represent an adaptation to feeding. Gut contents would

reveal the type of nutrition of these copepods, but as the *Beggiatoa* type filamentous sulfur bacteria seem to constitute the main source of organic biomass that can be used by small crustaceans as copepods for nutrition, this may be a part of the feeding sources for *M. longimaxillis*, directly or indirectly. The growth of these bacteria is accompanied by ciliates and other protozoans (Por, 2007). These can be ingested by *M. longimaxillis*, which may use its greatly developed buccal appendages to filter or extract the protozoans or other small organisms from the *Beggiatoa* type mats.

M. subdolus comes from a habitat analogous to the habitat (bores and wells) in which *Fierscyclops fiersi* Karanovic, 2004 was found in Australia. The genus *Metacyclops* is widely distributed in the world and has been found in diverse biotopes, both epigean and hypogean. In epigean biotopes, many widespread species are frequently encountered, such as the type-species, *M. gracilis* (Lilljeborg, 1853), as well as *M. minutus* (Claus, 1863), *M. planus* (Gurney, 1909), and *M. mendocinus* (Wierzejski, 1892). In hypogean biotopes, we can cite *M. subdolus* Kiefer, 1938, recorded, for instance, from groundwaters of peri-Mediterranean countries: Greece, Italy, and the Mediterranean Islands Crete, Sardinia, Sicily, and the Balearic Islands; it has already been reported from Israel in the spring complex of 'Enot Samar', south of the Dead Sea (Dimentman & Por, 1991) and from a well in the northern Negev (Dussart & Defaye, 1995). Many other *Metacyclops* species are endemic, as the species recently described from Western Australian groundwaters (see Karanovic, 2004, 2004a). This very ancient genus has probably colonized fresh waters very early, before the break-up of Pangaea (see Boxshall & Jaume, 2000). The colonization of hypogean fresh waters occurred afterwards, and led to the speciation of numerous taxa, more or less closely related, on the different plates and continents. Further investigations in subterranean waters and a complete revision of the genus *Metacyclops* will be necessary to understand the relationships between the species of this widely distributed genus.

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