Morphological variability and distribution of the exotic Asian *Mesocyclops thermocyclopoides* (Copepoda: Cyclopoida) in the Neotropical region

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ABSTRACT. From a series of biological samples collected from different freshwater environments in Costa Rica, Central America, the exotic Asian cyclopoid *Mesocyclops thermocyclopoides* Harada, 1931 was identified. We analyzed the morphology and appendage ornamentation of different Neotropical populations of this species, including specimens from Honduras, southeastern Mexico, and Costa Rica. We also examined Asian specimens from Taiwan, Indonesia, Vietnam, and Thailand, and performed a comparison of the Neotropical and Asian populations including a Principal Component Analysis (PCA). The Neotropical and Asian specimens show subtle morphological variations in the antennules, antennae, mandibles, swimming legs 1-4, and fifth legs. Some characters in the Neotropical group appear to diverge from the Asian pattern and the PCA indicated that intercontinental populations of *M. thermocyclopoides* are far from being homogeneous. These intra-specific differences are described to expand the known morphological range of this species and to provide the first comparative analysis of an exotic copepod in the Americas. Our analysis suggests that the geographic isolation of the American populations and the subtle morphological divergences with respect to the Asian patterns could be related to speciation processes in the Neotropical region, but also intra-Asian differences are reported. In the Neotropical region this species appears to be restricted to southeastern Mexico, Central America, and one Caribbean island; its potential as biological control of mosquito might enhance its spread in the region.

KEY WORDS. Crustacean taxonomy; freshwater crustaceans; copepods; exotic species; morphometrics.

The copepod order Cyclopoida includes many species with complex taxonomic problems stemming from their morphological variability (MIRABDULLAYEV & DEFAYE 2004, ALEKSEEV *et al.* 2006). Several cyclopoid copepod species among the genus *Mesocyclops* have invaded the Americas from Africa or Asia, each showing distinct distributional patterns (REID & SANDERS 1986, REID & PINTO-COELHO 1994, SUÁREZ-MORALES *et al.* 1999, HRIBAR & REID 2008). The knowledge of the freshwater copepod fauna, including the occurrence and distribution of exotic species, is still lacking for extensive areas of the Neotropical region, and detailed taxonomical and morphological data are needed to distinguish the non-indigenous species (OKOLODKOV *et al.* 2007). One of these poorly known areas is Central America, which is known to have a key role in the biogeographical history of the cyclopoid copepod fauna in the Neotropical region (SUÁREZ-MORALES *et al.* 2004).

From a series of biological samples collected from different freshwater environments in the area of El Arenal, of Costa Rica, Central America, copepods were taxonomically examined. The exotic Asian cyclopoid *Mesocyclops thermocyclopoides* Harada, 1931, was recorded. The specimens examined showed some interesting morphological variations with respect to other known populations of the species, motivating us to perform a deeper morphological analysis of *M. thermocyclopoides*. These

variations are presented here in order to expand the knowledge of the morphological range of the species through a comparative analysis of different populations. We compared the morphology of the Neotropical populations, also including specimens from Honduras and Mexico, with published descriptions and museum specimens from different zones of Asia. Specimens were borrowed from the collection of the National Museum of Natural History, Smithsonian Institution (USNM) and from the Collection of Zooplankton at El Colegio de la Frontera Sur, Chetumal, Mexico (ECO-CHZ). The current distribution of the exotic *M. thermocyclopoides* in the Neotropical region is also assessed and discussed.

TAXONOMY

Cyclopinae Rafinesque, 1815
Mesocyclops thermocyclopoides Harada, 1931
Figs 1-12

Material examined. Ten females from Charco Pulsar, Tabasco, Mexico, M.A. Gutiérrez-Aguirre *leg.*, 31-I-1999 (ECO-CHZ-1212), female from Laguna Popalillo, Tabasco, Mexico, M.A. Gutiérrez-Aguirre *leg.*, 31-I-1999 (ECO-CHZ-1218), 10 females
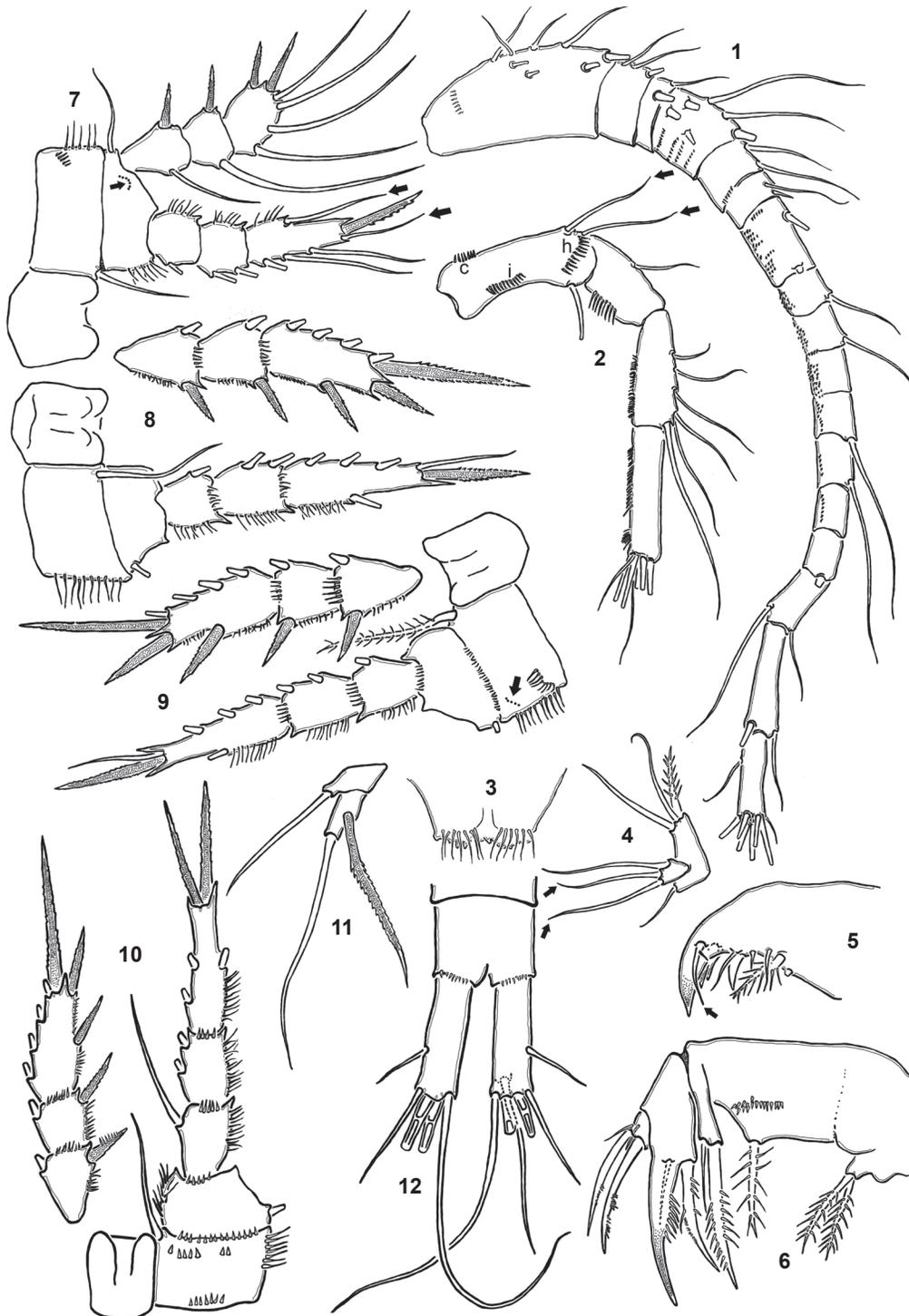
Figures 1-12. *Mesocyclops thermocyclopoides*, adult female from El Arenal, Costa Rica: (1) antennule; (2) antenna, showing spinal rows *c*, *h*, *i* and medial basipodal setae; (3) labrum, anterior view; (4) maxillule palp (medial and outer seta arrowed); (5) maxillule; (6) maxilla; (7) first swimming leg (P1), frontal view, curved row of basipodal spinules arrowed; (8) second swimming leg (P2); (9) third swimming leg (P3); (10) fourth swimming leg (P4); (11) fifth leg; (12) anal somite and caudal rami, ventral view.

from Charco Báscula, Tabasco, Mexico, M.A. Gutiérrez-Aguirre *leg.*, 01-II-1999 (ECO-CHZ-1219). Ten females from El Progreso, Honduras, 27-VIII-1991 (ECO-CHZ-1181). Eight adult females from reservoir El Arenal, Costa Rica, collected 2-XI-2007, ethanol-preserved, vial (ECO-CHZ-06595), 2 adult females from same locality and date, semi-permanent slides, sealed with nail varnish (ECO-CHZ-06596). Asian specimens: One female from Bao-Shan Reservoir, Hsin-chu, Taiwan,G. Wyngaard *leg.*, VII-2002 (USNM 1083794); two females from Chachoengsao, Thailand, G. Marten *leg.*, XI-1994 (USNM 271905, USNM 271904); three females from Hai Hung, Phan Boi Village, Vietnam, Mr. Phich *leg.*, 11-II-1994 (USNM 271930); two females from Sword Lake, Hanoi, Vietnam, B.H. Kay *leg.*,13-VI-1990 (USNM 251632); and two females from undetermined locality in Indonesia, G. Marten *leg.*, I-1994 (USNM 264006).

The specimens from Costa Rica were identified following the keys and illustrations by Suárez-Morales & Gutiérrez-Aguirre (2001), Gutiérrez-Aguirre *et al.* (2003), and Holynska *et al.* (2003). The morphological analysis of these specimens revealed some differences with respect to specimens from other Neotropical populations, and from the Asian pattern, as described below.

Morphological remarks and comparisons. The main differences between populations from Asia (cf. Holynska 1994, Holynska *et al.* 2003; museum specimens from different geographic areas in Asia), southeastern Mexico (two localities at the state of Tabasco, southeastern Mexico), Honduras (cf. Gutiérrez-Aguirre *et al.* 2003; specimens from El Progreso), and Costa Rica (specimens from El Arenal) are presented in detail in Table I and summarized in Table II. The size of the body of individuals in these populations (excluding caudal rami) differ among the Neotropical populations examined: specimens from Costa Rica are the smallest (0.78-0.80 mm), those from Honduras are the largest (0.97-1.0 mm); specimens from two localities in southeastern Mexico have intermediate size ranges (Báscula: 0.74-0.89 mm; Pulsar 0.90-1.0 mm). Overall, the Asian specimens tend to be larger than the Neotropical forms; the smallest sizes were found in Vietnam II (0.73-0.88) and the largest were from Thailand (0.95-1.26 mm) and Indonesia (1.01-1.30 mm).

Additional differences among the Neotropical populations include the ornamentation of the antennular segments 4 and 7, as follows: the specimens from Costa Rica and Asia bear four rows of spinules on the fourth antennular segment vs. two in both the Honduran and Mexican populations (Fig. 1). On the seventh antennular segment, the Asian specimen has six groups of tiny spinules, vs. five such groups in both Mexico and Honduras and nine in the Costa Rican specimens.

The ornamentation of the antennal basis includes several rows of spines which have been marked and denominated by their position following Gutiérrez-Aguirre *et al.* (2003). The range of the number of spines per row is different in all groups of specimens examined (Tabs I and II). None of the Neotropical populations have less than seven and more than 11 spines in row *h*. Only the Asian populations examined have less than

six spines in row *i*. We did not consider the number of spinules in row *c* because it often continues on the anterior surface, making counting difficult. We observed, however, that the specimens from Costa Rica (Fig. 2) have clearly larger and stronger spinules in this row when compared with the Asian, Mexican, and Honduran populations (Gutiérrez-Aguirre *et al.* 2003, Holynska *et al.* 2003). The length ratio of the medial basipodal setae (arrowed in Fig. 2) is alike in the Neotropical populations (Mexico, Honduras, Costa Rica) (1:1) and differs from the Asian figure: 1.2-1.47:1 (n = 12).

The mandible gnathobase and the teeth number show clear interspecific variation in *Mesocyclops* (Suárez-Morales *et al.* 2003). In line with that prediction, we found some differences among the Neotropical populations investigated (Figs 13-16). Specimens from Báscula (Tabasco, Mexico) have nine teeth vs. eight in the Costar Rican, Honduran and Pulsar (Tabasco, Mexico) populations (Figs 13-16); among the latter populations, only the Costar Rican specimens do not bear accessory spines. The mandibular size relative to the body size (MSI index, Suárez-Morales *et al.* 2003) was measured; the Costar Rican (3.17) and Báscula (3.11) populations showed the highest MSI values. Lower values were found in the Honduran specimens (2.79) and in the population from Pulsar (Tabasco) (2.67). These mandibular characters were not evaluated in the Asian specimens.
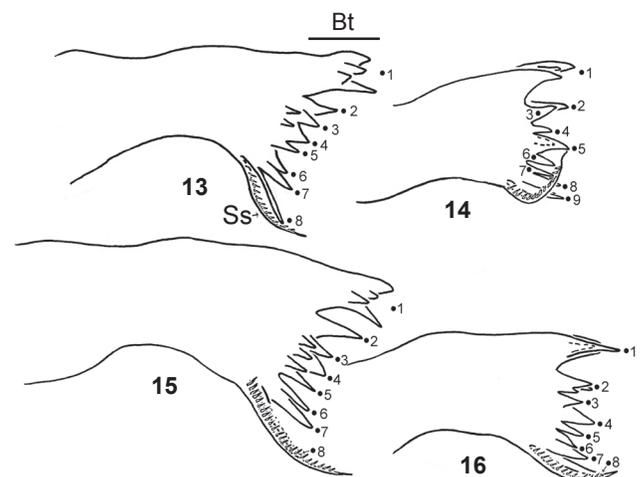
Figures 13-16. Morphology of mandible edge in Neotropical populations of *Mesocyclops thermocyclopoides*: (13) female from Pulsar (Tabasco, Mexico); (14) female from Báscula (Tabasco, Mexico); (15) female from El Progreso, Honduras; (16) female form El Arenal, Costa Rica. (Bt) Blade tooth, (Ss) outer dorsal seta.

The spine-like seta on the frontal surface of the maxillules of both the Mexican and the Honduran specimens reaches half the length of the chitinized spine, whereas in the Asian and the Costar Rican populations this seta almost reaches the dis-

tal end of the spine (arrow in Fig. 5). Also, the inner and outer endopodal setae of the maxillular palp are subequal in the Asian, Mexican, and Honduran populations, but the medial seta is clearly shorter than the other setae in specimens from Costa Rica (arrowed in Fig. 4). Ornamentation and elements of the maxilla are practically the same in all specimens (Fig. 6).

The coxal ornamentation of P1 is similar in all groups examined. The populations from Honduras, Mexico, and Asia all have a semi-circular row of spines on the anterior surface of the distal margin of the basipodite, near the insertion of the exopodite (arrowed in Fig. 7). Furthermore, specimens from Mexico and Honduras also have a row of tiny spinules near the insertion of the endopodite. In the Costa Rican specimens (Fig. 7), the inner coxal seta reaches the distal margin of the first endopodal segment, whereas this seta is distinctly longer in the Asian, Mexican, and Honduran populations, reaching the distal margin of the second endopodal segment (see Holynska *et al.* 2003). The length ratio of the apical endopodal seta/segment length is 0.71 in Asian specimens vs. 1.04 in Costa Rican specimens (Fig. 7). The inner apical seta of this segment also differs between populations; in Asian specimens this seta is clearly longer than the inner spine, being relatively shorter in the Costa Rican specimens. The seta on the lateral margin of the same segment is longer than the apical spine in Asian specimens, whereas this spine barely exceeds half of the length of the spine in specimens from Costa Rica (arrowed in Fig. 7).

The ornamentation of both the coxopodite and basipodite of the second swimming leg differs among the examined populations. Specimens from Costa Rica bear only a single row of hair-like setae on the outer coxal margin (Fig. 8), whereas specimens from Mexico and Honduras have three additional transverse rows of setal elements on the frontal surface (Gutiérrez-Aguirre *et al.* 2003). The ornamentation of the third swimming leg also differs among the three Neotropical groups of specimens; all populations bear a row of hair-like setae on the outer coxal margin, but the Mexican and Hondu-

ran specimens have a second row of shorter hair-like setae on the proximal surface of same inner margin (see Gutiérrez-Aguirre *et al.* 2003: fig. 3b). Another difference is the position and size of a transverse row of hair-like setae along the distal margin of the coxopodite. In both the Mexican and Honduran specimens this row is located medially near the insertion of the coxopodite, whereas in the Costa Rican specimens the position of this row is on the middle coxal surface and closer to the outer margin (arrowed in Fig. 9).

The coxal ornamentation of the fourth swimming leg is almost the same in all populations examined (Fig. 10). The four groups of specimens have a group of hair-like setae on the inner margin of the basipodite, including a transverse row of hair-like setae close to the insertion of the inner coxal seta. Differences in P4 ornamentation and proportions include the ranges of length ratio of the apical spine/third endopodal segment, length/width ratio of the same segment, and inner spine/ outer spine ratio (Tabs I and II). Only in the Asian populations less than six spines on the basal margin of coxopodite have been observed. Additionally, specimens from Mexico and Honduras have a unique pattern of ornamentation of tiny spinules on the anterior surface of the three endopodal segments. This pattern was not observed in the Costa Rican or in the Asian populations.

The length ratio of the inner spine/outer seta of the fifth leg was also evaluated; all populations examined have variable ratios (Fig. 11, Tabs I and II). The proportion and relative lengths of the setal elements and the ornamentations of the caudal rami of specimens from Costa Rica, Mexico, Honduras and specimens from Asia are within the range known from the type Asian population (Holynska 1994, Holynska *et al.* 2003).

In order to define the extent and relevance of the differences found among the different populations of *M. thermocyclopoides* examined, we performed a Principal Component Analysis (PCA), which is a statistical tool commonly used to evaluate the morphometric and meristic characters among populations

Table I. Variation of the appendage ornamentation and other morphological characters among different populations of *Mesocyclops thermocylopoides*. Characters of Asian Lit. based on Harada (1931), Holynski & Fiers (1994), and Holynski *et al.* (2003). Mexico and Honduras specimens from Gutiérrez-Aguirre & Suárez-Morales (2001), Suárez-Morales & Gutiérrez-Aguirre (2001) and ECO-CHZ-1181, Costa Rican specimens from Collado *et al.* (1984), and specimens from El Arenal. Vietnam I from Hai Hung, Vietnam (USNM 271930). Vietnam II from Sword Lake, Hanoi, Vietnam (USNM 251632). Thailand I and Thailand II from Chachoengsao, Thailand (USNM 271905, USNM 271904). Indonesia from undetermined locality in Indonesia (USNM 264006), Taiwan from Bao-Shan Reservoir, Hsin-chu, Taiwan (USNM 1083794). (P4) Fourth swimming leg, (End3P4) third endopodal segment of fourth swimming leg.

Number of spines in rows/proportion	Mexico and Honduras	Costa Rica	Asian Lit.	Vietnam I	Thailand I	Thailand II	Indonesia	Taiwan	Vietnam II
Antennal basis, row *h*	11	11	5	8	13		13	7	8
Antennal basis, row *i*	11	12	10	7	11	10	15	8	9
Spines on basal margin of coxa P4	9	7	5-8 (6-7)	6		7			7
Apical spine/length of End3P4	0.71	0.86	0.76	0.84	0.92	1.06	1.02	0.97	0.73
Length/width End3P4	3.2-3.6	3.2-3.6	4.1	4	3.57	3.61	4.08	3.58	3.81
Inner spine/outer spine End3P4	0.76	0.86	0.95	1.03	1.15	1.25	1.25	1.07	0.83
Inner spine/outer seta of P5	0.6-0.7	0.6-0.7	0.44	0.81	0.87	0.96	0.97		0.98

Table II. Summarized data of the variation of appendage ornamentation and other morphological characters among three different groups of populations of *Mesocyclops thermocylopoides*. (P4) Fourth swimming leg, (End3P4) third endopodal segment of fourth swimming leg.

Number of spines in rows/proportion	Asian specimens (n = 12)	Mexico (n = 21)	Honduras (n = 3)	Costa Rica (n = 6)
Antennal basis, row *h*	5-13	7-11	10	8-10
Antennal basis, row *i*	6-15	8-13	14	10-13
Spines basal margin of coxa P4	5-9	6-8	7-9	7
Apical inner spine/length of End3P4	0.76-1.06	0.75-0.88	0.74-0.85	0.82-0.86
Length/width of End3P4	3.57-4.1	3.5-4.6	2.85-4.6	3.2-5.0
Inner spine/outer spine of End3P4	0.86-1.25	0.82-1.02	0.90-1.17	0.86-0.88
Inner spine/outer seta of P5	0.44-0.98	0.71-0.90	0.74-0.80	0.6-0.7

of invertebrates (Costa-Paiva & Paiva 2007). We used the PRIMER 6 software with $\log_{10}$-transformed meristic and morphometrical data. The resulting plot (Fig. 17) included all individuals of the different populations examined. The first principal component (PC1) accounted for 42.2% of the variation, the second (PC2) for 20% among the samples (Tab. III). The plot of the component variants PC1 and PC2 (Fig. 17) shows a discrimination of population scores of different groups along PC1, including the Asian populations from Indonesia (marked as "In" in Fig. 17) with highest scores and also the two Thailand populations (TA and TB) with lower ones. Also, the Mexican populations are aligned along the PC2, thus forming a uniform group. The Honduran specimens clearly diverge in character 2, number of spines on row "*i*" of the antennal basis. The other Central America specimens, from Costa Rica, appear to be more closely related to the Mexican pattern that to the Honduran or Asian ones. Among the Asian populations, there is a divergence between the Indonesia and Thailand forms and the Vietnam (Vi1, Vi2) and Taiwan (Tw) populations (Fig. 17). Examination of the distance of variables from the origin revealed that the main observed differences (characters 1 and 2) were related to the number of spines on the rows of the antennal basis. Characters 6 and 7, the ratios of length/width of the third endopodal segment of the fourth leg and the inner/outer spines of the same segment, respectively, were also important. Characters 8 and 9 (inner spine of the fifth leg and ratio of the outer apical spines of the third endopodal segment of the fourth leg) have no detectable variations.

DISCUSSION

Because of the rarity of cosmopolitan forms in *Mesocyclops*, earlier Neotropical records of *M. thermocyclopoides* were suspected to represent undescribed taxa, but Gutiérrez-Aguirre *et al.* (2003) confirmed the presence of the strict form of this species in the Neotropics. Our survey provides detailed morphological information about subtle differences among Neotropical and Asian populations of this species. Intraspecific morphological variations among some cyclopoids have been related to seasonal
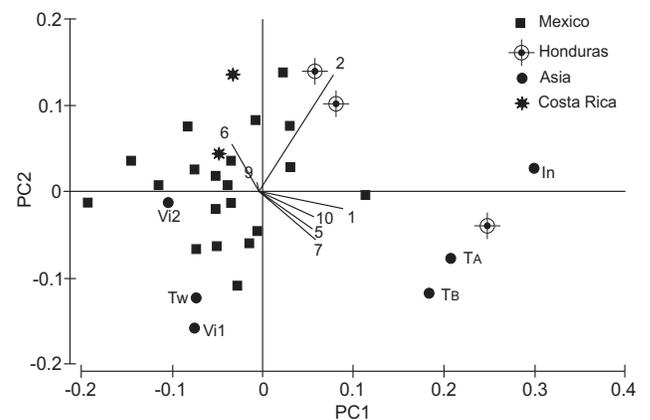

Figure 17. Principal Component Analysis (PCA) of meristic and morphometric data of specimens from different populations of *M. thermocyclopoides*. Vi1=Vietnam I from Hai Hung, Vietnam (USNM 271930); Vi2= Vietnam II from Sword Lake, Hanoi, Vietnam (USNM 251632). TA, TB= Thailand I and Thailand II from Chachoengsao, Thailand (USNM 271905, USNM 271904). In= Indonesia from undetermined locality in Indonesia (USNM 264006); Tw=Taiwan from Bao-Shan Reservoir, Hsin-chu, Taiwan (USNM 1083794).

Table III. Results of the PCA, including eigenvalues and percentages of variability explained for PC's of populations of *Mesocyclops thermocyclopoides*.

PC	Eigenvalues	%Variation	Cumm.%Variation
1	1,22E-2	42.2	42.2
2	5,79E-3	20.0	62.2
3	5E-3	17.3	79.5
4	2,98E-3	10.3	89.8
5	1,62E-3	5.6	95.4
6	6,93E-4	2.4	97.8
7	6,23E-4	2.2	100.0
8	6,29E-6	0.0	100.0

changes, but such variations in presumably cosmopolitan species are, in many species, related to the formation of species complexes (Lee 2000, Mirabdullayev & Defaye 2003).

Overall, the morphological differences described herein are not consistently related to either the Neotropical or the Asian populations groups of *M. thermocyclopoides*. Our analysis showed that the characters evaluated, which are usually those used to distinguish species within the genus, show subtle but detectable intra-specific differences among the populations examined; it is clear that these meristic and morphometric characters are not uniform throughout the species range. There is some indication that the American populations are diverging from the Asian ones and that even among the Asian forms there is some degree of differentiation, particularly between the Indonesia-Thailand and Taiwan-Vietnam groups. Among the Neotropical groups, the Honduran diverges at least in one of the most variable characters, and the Mexican and Costa Rican specimens are more closely related to each other than to most of the other groups examined. Overall, the geographic isolation and the presumed reproductive isolation of the immigrant Neotropical populations, and also the subtle but consistent morphological divergence with respect to the Asian populations, suggest that a process of speciation could be occurring among the American populations of *M. thermocyclopoides*, particularly in Central America and southern Mexico. This isolation is expressed in subtle differences not only between the continents but also within them.

Originally described from Taiwan, the known distributional range of *M. thermocyclopoides* in Asia includes Japan, southern China, Burma, Vietnam, Thailand, Indochina, Malaysia, Indonesia, and Java (Holynska 1994, Guo 2000, Holynska *et al.* 2003). American records from Central America and the Caribbean most probably represent introduced populations (Gutiérrez-Aguirre *et al.* 2003, Holynska *et al.* 2003). In Central America *M. thermocyclopoides* was first recorded from Costa Rica by Collado *et al.* (1984), from 14 localities, and later on by Hernández-Chavarría & Schaper (2000). It has also been recorded from Puerto Rico (Marten, 1994), Honduras (Marten *et al.* 1994) and southeastern Mexico (Gutiérrez-Aguirre & Suárez-Morales 2001, Suárez-Morales & Gutiérrez-Aguirre 2001, Gutiérrez-Aguirre *et al.* 2006), together with other exotic species (Suárez-Morales *et al.* 2011), thus confirming the growing occurrence of populations of exotic copepods in the neotropics (Fig. 18).

Other exotic Asian or Afro-Asian *Mesocyclops* known in the Neotropical region are *M. aspericornis* (Suárez-Morales *et al.* 2011) and *M. pehpeiensis* (Suárez-Morales *et al.* 2005, Menéndez-Díaz *et al.* 2006). These exotic species have been successfully tested as biological control agents of mosquito larvae. *Mesocyclops thermocyclopoides* has been deemed an efficient biological control agent of mosquito larvae in Asia (Kumar & Rao 2003) and also in the Americas (Soto *et al.* 1999); its life cycle has important advantages over that of congeners in terms of maturation (Suárez-Morales *et al.* 2007). Other native Neotropical *Mesocyclops* have ranked low as potential mosquito control (Tranchida *et al.*

2009) agents. Despite the risks involved in the introduction and spread of biological controls (Simberloff & Stilling 1996), it is expected that the success and potential use of *M. thermocyclopoides* for the biological control of mosquitoes could favor its spread into other tropical regions of the Americas.
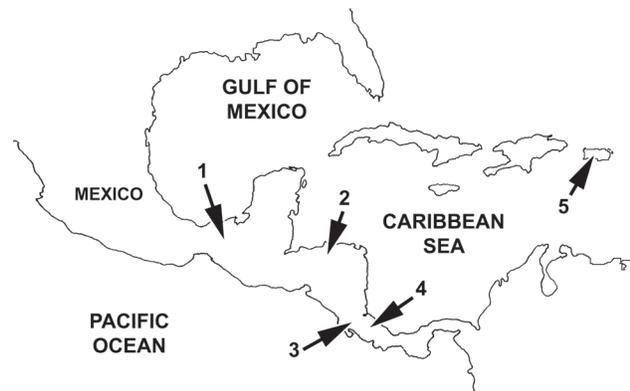

Figure 18. Distribution of the exotic cyclopoid copepod *Mesocyclops thermocyclopoides* in the Neotropical region: 1) Tabasco, Mexico (Gutiérrez-Aguirre *et al.* 2003); 2) El Progreso, Honduras (Marten *et al.*1994; Gutiérrez-Aguirre *et al.* 2003); 3) different areas of Costa Rica (Collado *et al.* 1986); 4) El Arenal, Costa Rica (this work); 5) Puerto Rico (Marten 1994).

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LITERATURE CITED

Alekseev,V.; H.J. Dumont; J. Pensaert; D. Baribwegure & J.R. Vanfleteren. 2006. A redescription of *Eucyclops serrulatus* (Fischer, 1851) (Crustacea: Copepoda: Cyclopoida) and some related taxa, with a phylogeny of the *E. serrulatus*-group. **Zoologica Scripta 35**: 123-147.

Collado, C.; D. Defaye; B.H. Dussart & C.H. Fernando. 1984. The freshwater Copepoda of Costa Rica with notes on some species. **Hydrobiologia 119**: 89-99.

Costa-Paiva, E.M. & P.C. Paiva. 2007. A morphometric analysis of *Eunice* (Annelida, Polychaeta). **Revista Brasileira de Zoologia 24**: 353-358.

Guo, X. 2000. Two new species of *Mesocyclops* from southern China and notes on the genus *Mesocyclops* in China. **Hydrobiologia 429**: 115-131.

Gutiérrez-Aguirre, M.A. & E. Suárez-Morales. 2001. Diversity and distribution of freshwater copepods (Crustacea) in southeastern Mexico. **Biodiversity and Conservation 10**: 659-672.

Gutiérrez-Aguirre, M.A.; J.W. Reid & E. Suárez-Morales. 2003. An Afro-Asian species of *Mesocyclops* (Copepoda:Cyclopoida) in Central America and Mexico. **Journal of Crustacean Biology 23** (2): 352-363.

Gutiérrez-Aguirre, M.A.; E. Suárez-Morales & A. Cervantes. 2006. Distribución de las especies de *Mesocyclops* (Copepoda: Cyclopoida) en el sureste mexicano y región norte de Guatemala. **Hidrobiológica 16**: 259-265.

Hernández-Chavarría, F. & S. Schaper. 2000. *Mesocyclops thermocyclopoides* (Copepoda: Cyclopoidea): a scanning electron microscopy study. **Revista Latinoamericana de Microbiología 42**: 53-56.

Holynska, M. 1994. A redescription of *Mesocyclops thermocyclopoides* Harada, 1931 (Copepoda, Cyclopidae). **Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 64**: 99-110.

Holynski, M. & F. Fiers. 1994. *Mesocyclops thermocyclopoides* species-group: redefinition and content. **Hydrobiologia 292/293**: 41-51.

Holynska, M.; J.W. Reid & H. Ueda. 2003. Genus *Mesocyclops* Sars, 1914, p. 12-213 *In:* H. Ueda & JW Reid (Eds). **Copepoda: Cyclopoida. Genera *Mesocyclops* and *Thermocyclops*. Guides to the Identification of the Microinvertebrates of the Contiental Waters of the world 20.** Leiden, Backhuys Publishers.

Hribar, L.J. & J.W. Reid. 2008. New records of copepods (Crustacea) from the Florida Keys. **Southeastern Naturalist 7** (2): 219-228.

Lee, C.E. 2000. Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate "populations". **Evolution 54**: 2014-2027.

Kumar, R. & R. Rao. 2003. Predation on Mosquito larvae by *Mesocyclops thermocyclopoides* (Copepoda: Cyclopoida) in the presence of alternate prey. **International Review of Hydrobiology 88**: 570-581.

Marten, G.G.; E.S. Bordes & M. Nguyen. 1994. Use of cyclopoid copepods for mosquito control. **Hydrobiologia 292/293**: 491-496.

Menéndez-Díaz, Z.; J.W. Reid; I. Castillo & I. Valdés-Ramos. 2006. A new record of *Mesocyclops pehpeiensis* Hu, 1943 (Copepoda: Cyclopoida) for Cuba. **Journal of Vector Ecology 31**: 193-195.

Mirabdullayev, I. & D. Defaye. 2003. On the taxonomy of the *Acanthocyclops robustus* species-complex (Copepoda, Cyclopidae): *Acanthocyclops brevispinosus* and *A. einslei* **sp. nov. Vestnik Zoologii 38** (5): 27-37.

Okolodkov, Y.B.; R. Bastida-Zavala; A.L. Ibáñez; J.W. Chapman; E. Suárez-Morales; F. Pedroche & F.J. Gutiérrez-Mendieta. 2007. Especies acuáticas no indígenas en México. **Ciencia y Mar 9**: 29-67.

Reid, J.W. & R.M. Pinto-Coelho. 1994. An Afro-Asian continental copepod, *Mesocyclops ogunnus*, found in Brazil; with a new key to the species of *Mesocyclops* in South America and a review of intercontinental introductions of copepods. **Limnologica 24**: 359-368.

Reid, J.W. & J.F. Saunders. 1986. The distribution of *Mesocyclops aspericornis* (von Daday) in South America. **Journal of Crustacean Biology 6**: 820-824.

Simberloff, D. & P. Stilling. 1996. Risks of species introduced for biological control. **Biological Conservation 78**: 185-192.

Soto, L.; S. Shaper; L. Angulo & F. Hernández. 1999. *Mesocyclops thermocyclopoides* y el control biológico de *Aedes*: ejemplo de un plan de acción comunitaria en Chacarita, Puntarenas. **Revista Costarricense de Ciencias Médicas 20**: 45-50.

Suárez-Morales, E.; M.A. Gutiérrez-Aguirre. 2001. **Morfología y taxonomía de los *Mesocyclops* (Crustacea: Copepoda: Cyclopoida) de México.** México, CONACYT/ECOSUR.

Suárez-Morales, E.; J.A. McLelland & J.W. Reid. 1999. The planktonic copepods of coastal saline ponds of the Cayman Islands with special reference to the occurrence of *Mesocyclops ogunnus* Onabamiro, an apparently introduced Afro-Asian cyclopoid. **Gulf Research Reports 11**: 51-56.

Suárez-Morales, E.; M.A. Gutiérrez-Aguirre & M. Elías-Gutiérrez. 2003. Observations on the structure of the mandible edge in some American *Mesocyclops* (Copepoda: Cyclopidae). **Proceedings of the Biological Society of Washington 116** (3): 742-753.

Suárez-Morales, E.; M.A. Gutiérrez-Aguirre & F. Mendoza. 2011. The Afro-Asian cyclopoid *Mesocyclops aspericornis* (Crustacea: Copepoda) in eastern Mexico with comments on the distribution of exotic copepods. **Revista Mexicana de Biodiversidad 81**: 109-115.

Suárez-Morales, E.; J.W. Reid; F. Fiers & T.M. Iliffe. 2004. Historical biogeography and distribution of the freshwater cyclopine copepods (Copepoda, Cyclopoida, Cyclopinae) of the Yucatan Peninsula, Mexico. **Journal of Biogeography 31**: 1051-1063.

Suárez-Morales, E.; M. A. Gutiérrez-Aguirre; J.L. Torres & F. Hernández. 2005. The Asian *Mesocyclops pehpeiensis* Hu, 1943 (Copepoda, Cyclopidae) in Southeast Mexico with comments on the distribution of the species. **Zoosystema 27**: 245-256.

Suárez-Morales, E.; G.A. Wyngaard; M.A. Gutiérrez-Aguirre & J. Costanzo. 2007. Life history traits of *Mesocyclops thermocyclopoides* Harada, 1931 (Copepoda, Cyclopoida) with observations on naupliar morphology. **Crustaceana 80**: 1205-1222.

Tranchida, M.C.; M.V. Micieli; A. Maciá & J.J. García. 2009. Native Argentinean cyclopoids (Crustacea: Copepoda) as predators of *Aedes aegypti* and *Culex pipiens* (Diptera: Culicidae) mosquitoes. **Revista de Biología Tropical 57**: 1057-1068.