

# Redescription of two species of *Microcyclops* (Copepoda, Cyclopoida) and use of ordination models to classify American species

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## Abstract

Two species of the freshwater copepod genus *Microcyclops* are redescribed, *M. finitimus* Dussart, 1984, and *M. minor* Dussart, 1984 from type specimens. Redescription includes the microstructure of intercoxal sclerites and the basipodites of thoracic appendages, as well as the urosomal microstructure. According to the cluster (UPGMA and Euclidean distance) and PCA analyses performed, it was possible to improve the resolution between the American *Microcyclops* species by considering characters such as the distal region of antennal basis, the maxillary ornamentation, and the thoracic appendages, especially the intercoxal sclerites and medial margin of the basipodite of the first to fourth trunk limbs. Considering a set of 28 morphological characters in adult females, traditional features such as the length ratio of caudal rami, the length: width ratio of the third endopod of the fourth leg, or the length ratios between apical setae of the same segment, appear to be less important for defining differences between very similar species of American *Microcyclops*. In these analyses, the redescription of the Palearctic *M. varicans* was considered, and this species was clearly separated from the American *M. dubitabilis* Kiefer, 1934 and *M. inarmatus* Gutiérrez-Aguirre and Cervantes-Martínez, 2016.

**Key words:** Classification, diversity, freshwater, species richness, taxonomy



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## Introduction

Deep taxonomic revisions of some freshwater zooplankton Neotropical groups have been carried out in recent decades. These revisions supported that the species richness is still underestimated and the geographic distribution is poorly understood in freshwater zooplankton taxa. For instance, several species considered cosmopolitan, with high phenotypic plasticity and genetic variability, are in fact species complex (usually grouping, five or more species) based upon deep, long-term and wide scale geographical studies (see Kotov et al. 2009; Mercado-Salas et al. 2018; Montoliu-Elena et al. 2019; Mercado-Salas and Suárez-Morales 2021).

Even though a high level of resolution has been reached with some taxonomically problematic groups, incomplete descriptions and lack of designated type (type series) hamper a systematic revision in many Neotropical freshwater zooplankton species, which limits the improvement of the systematic of many

taxonomic groups. This kind of taxonomical problem is magnified because of the gaps in knowledge related to taxonomic studies of zooplankton. Either gaps in time, or the interest in faunistic studies are focused on a few groups (Kotov 2016), or because the availability of some techniques, in several regions, is limited.

Some examples of Nearctic, Neotropical, or Pantropical freshwater genera that have recently been reviewed are *Mastigodiptomus* (Mercado-Salas et al. 2018; Gutiérrez-Aguirre et al. 2020), *Leptodiptomus* (Silva-Briano and Suárez-Morales 2010), *Mesocyclops* (Hołyńska et al. 2003), *Eucyclops* (Mercado-Salas and Suárez-Morales 2014), *Alona* (Sinev et al. 2005), and *Bosmina* (Kotov et al. 2009). It is notable that in all these cases, new species were described, or new taxonomical arrangements were proposed, based upon a deep taxonomic revision.

In addition, these reviews reveal morphological characters never previously considered or the re-evaluation of refuted characters that facilitate the systematic and faunistic studies of the high diversity in tropical freshwater (Gutiérrez-Aguirre and Cervantes-Martínez 2016). Even with this important progress over the last decades, some genera need further analysis.

In this work, we explore the possibilities of several morphological characters both used and not used in identification keys of *Microcyclops* under the assumption that through classification and ordering models, it is possible to define the species diagnostic characters verifiable by light microscopy observations (in adult females). In addition, the exploration of these characters helped with the redescription of *M. finitimus* Dussart, 1984, and *M. minor* Dussart, 1984, based on type material.

## Materials and methods

### Taxonomic analysis

Detailed redescriptions of *Microcyclops finitimus* and *M. minor* were based on the morphological and morphometric analyses of adult females recorded as the original material from the type localities. The evaluation included analyses of holotypes deposited in the Copepoda collection of the Muséum national d'Histoire naturelle, Paris (MNHN).

### Data analysis

To normalize the data, meristic magnitudes were square-root transformed and examined to perform two multivariate analyses with the software Multi Variate Statistical Package MVSP 3.1 (Anglesey, UK). A cluster analysis (with UPGMA as a clustering method and Euclidean distance measurement) that grouped specimens with similar morphology and one principal component analysis (PCA) was performed to identify traits that produced the most distinct groups between species (Legendre and Legendre 1998). Only adult females from different populations were considered in both analyses.

The terminology for each appendage follows Huys and Boxshall (1991):

- A1** antennule;
- A2** antenna;

<b>Md</b>	mandible;
<b>Mxl</b>	maxillule;
<b>Mx</b>	maxillae;
<b>Mxp</b>	maxilliped;
<b>Bsp</b>	basipodite of swimming legs;
<b>Enp</b>	endopodal segment;
<b>Exp</b>	exopodal segment;
<b>P1–P5</b>	first to fifth swimming legs;
<b>II</b>	lateral;
<b>III</b>	outermost;
<b>IV</b>	outer median;
<b>V</b>	inner median;
<b>VI</b>	innermost terminal; and
<b>VII</b>	dorsal caudal setae.

Biological material deposited in Smithsonian Institution (**USNM**), Staatliches Museum für Naturkunde, Karlsruhe (**SMNK**), Muséum national d'Histoire naturelle, Paris (**MNHN**), and Collection of Zooplankton of El Colegio de la Frontera Sur, Chetumal, Mexico (**ECOCH-CH-Z**) was analyzed. The following morphological characters were considered in the cluster analysis and PCA. When coding was applicable, this is in brackets; abbreviation of each character is presented after a comma. Abbreviations refer to morphological structures listed above:

1. Distal region of antennal basis caudal, A2\_DistalCaudal: without spinules on the distal region (1); with spinules on the distal region (2)
2. Distal region of antennal basis frontal, A2\_DistalFrontal: without spinules on the distal region (1); with spinules on the distal region (2)
3. Basal seta on maxillary basipodite, MxBsp\_BasalSeta: biserially ornamented (1); ornamented on medial margin (2); naked (3)
4. Claw-like projection of maxillary basipodite, MxBsp\_Claw: spines arranged on a bump (1); spines arranged on a continuous row (2)
5. Maxillary distal coxal endite, proximal seta, MxEnd\_ProxSeta: biserially ornamented (1); one margin ornamented (2)
6. Maxillary distal coxal endite, distal seta, MxEnd\_DistSeta: ornamented on medial margin (1); naked (2)
7. Bsp of P1, medial margin of basipodite, BspP1\_Medial: with hair-like setae (1); naked (2)
8. Bsp of P1, medial margin, spine ornamentation, BspP1\_SpineOrnament: spine with homonomous ornamentation (1); spine with heteronomous ornamentation (2); not apply (3)
9. Second Enp of P1, pores on lateral surface, Enp2P1\_pores: without pores (1); one pore (2); two pores (3)
10. The length (L) to width (W) ratio of Enp2P4, Enp2P4\_L:W
11. Bsp of P4, medial margin, BspP4\_Medial: naked (1); short spine-like setae (2); long hair-like setae (3)
12. The ratio between the lengths of the medial and lateral apical spines of Enp2P4, P4\_LMedSpn:LLatSpn

13. The ratio between the lengths of the medial apical spine and Enp2P4, P4\_LMedSpn:LEnp2
14. Surface of intercoxal sclerite of P4, P4\_IntcxlSclrt: with rows of spinules (1); naked (2); with rows of hair-like setules (3)
15. L to W ratio of the free segment of P5, FSP5\_L:W
16. Free segment of P5, medial margin, FSP5\_Medial: without spinule (1); with a tiny spinule (2); with a spinule enlarged beyond the apical margin of the free segment (3)
17. The ratio between the lengths of the free segment of the P5 and P5 terminal seta, P5\_L-FS:ApclSta
18. L to W ratio of genital double somite, Genital\_L:W
19. Presence of spines along the anal somite, Spns\_Anal: ventral and dorsal (1); ventral (2)
20. Caudal ramus, the ratio between the lengths of the outer median terminal seta (IV) and outermost terminal seta (III), CR\_L-IV:L-III
21. Caudal ramus, the ratio between the lengths of the medial median terminal seta (V) and outermost terminal seta (III), CR\_L-V:L-III
22. Caudal ramus, the ratio between the lengths of the innermost terminal seta (VI) and outermost terminal seta (III), CR\_L-VI:L-III
23. Caudal ramus, the ratio between the lengths of the innermost terminal seta (VI) and caudal ramus, L-VI:L-CR
24. The ratio between the lengths of the dorsal caudal seta (VII) and caudal ramus, L-VII:L-CR
25. L to W ratio of caudal ramus, CR\_L:W
26. Caudal ramus, base of lateral caudal seta (II), CR\_Base-II: without spinules (1); with spinules (2)
27. Caudal ramus, the base of outermost terminal seta (III), CR\_Base-III: without spinules (1); with spinules (2)
28. Caudal ramus, proportion between point of insertion (measured from anterior of the caudal ramus) of lateral caudal seta (II) and length of lateral margin, Position-II:CR

The sources for the morphological data considered in the multivariate analyses were the type, paratype(s), and other museum specimens (Suppl. material 1). The original descriptions of 11 named species and three named subspecies were also considered, bringing the total to 54 adult females of species recorded in America (Suppl. material 2).

In lack of material, the character states were verified in the original description of the next species: *Microcyclops varicans* (G.O. Sars, 1863); *M. anceps pauxensis* (Herbst, 1962); *M. mediasetosus* (Dussart & Frutos, 1985); *M. pumilis* (Pennak & Ward, 1985); and *M. medius* (Dussart & Frutos, 1986).

The matrix showing the distribution of the 28 characters for each species is shown in Table 1. Total likeness between the analyzed specimens was calculated by cluster analyses using Euclidean distance as a similarity index and UP-GMA as a linkage method after normalization of data, and performed in a Multi Variate Statistical Package (v. 3.1). After that, principal component analysis (Table 2) was performed to define which of the normalized characters better explain the variability between the species.

**Table 1.** Averages (Av), maximums (Max), and minimums (Min) of the characters analyzed. The abbreviation and state of each character, as noted in Methods.

		<i>M. pumilis</i>	<i>M. anceps pauxensis</i>	<i>M. minor</i>	<i>M. mediasetosus</i>	<i>M. medius</i>	<i>M. ceibaensis</i>	<i>M. dubitabilis</i>	<i>M. inarmatus</i>	<i>M. echinatus</i>	<i>M. finitimus</i>	<i>M. anceps anceps</i>	<i>M. varicans</i>	<i>M. elongatus</i>	<i>M. furcatus</i>
A2_ DistalCaudal	Av						1	1	1	2	1	1	2		
	Max						1	1	1	2	1	1	2		
	Min						1	1	1	2	1	1	2		
A2_ DistalFrontal	Av						1	1	1	1	2	2	1		
	Max						1	1	1	1	2	2	1		
	Min						1	1	1	1	2	2	1		
MxBsp_ BasalSeta	Av						3	1	1	2	3	3	2		
	Max						3	1	1	2	3	3	2		
	Min						3	1	1	2	3	3	2		
MxBsp_Claw	Av						2	2	2	2	1	1	2		
	Max						2	2	2	2	1	1	2		
	Min						2	2	2	2	1	1	2		
MxEnd_ ProxSeta	Av						2	2	1	1	2	2	2		
	Max						2	2	1	1	2	2	2		
	Min						2	2	1	1	2	2	2		
MxEnd_ DistSeta	Av						2	1	1	2	1	1	2		
	Max						2	1	1	2	1	1	2		
	Min						2	1	1	2	1	1	2		
BspP1_ Medial	Av		2	1			2	1	1	2	1	1	1	2	
	Max						2	1	1	2	1	1	1		
	Min						2	1	1	2	1	1	1		
BspP1_Spine Ornament	Av	3	3	3	3	1	2	1	2	2	3	3	1	1	1
	Max						2	1	2	2	3	3	1		
	Min						2	1	2	2	3	3	1		
Enp2P1_ pores	Av				3		3	1	2	3	2	2	2		
	Max				3		3	1	2	3	2	2	2		
	Min				3		3	1	2	3	2	2	2		
Enp2P4_L:W	Av	2.11	2.71	2.46	2.33	1.83	2.25	1.94	2.18	2.56	2.36	2.52	2.44	2.59	
	Max						2.43	2.18	2.64	2.75	2.5	2.75	2.7		
	Min						2.1	1.75	1.9	2.33	2.22	2.25	2.22		
BspP4_ Medial	Av	1	2	3		1	2	2	3	3.2	3	2	2		
	Max						2	2	3	4	3	2	2		
	Min						2	2	3	2	3	2	2		
P4_ LMedSpn: LLatSpn	Av	1.37	1.52	1.95	1.22	1.55	1.45	1.90	1.98	2.07	1.39	1.33	1.40	1.75	
	Max						1.7	2.5	2.19	2.26	1.39	1.5	1.50		
	Min						1.45	1.1	1.58	1.9	1.38	1.16	1.25		
P4_ LMedSpn: LEnp2	Av	0.57	0.76	0.73	0.76	0.7	0.64	0.85	0.91	0.81	0.78	0.76	0.88	0.49	
	Max						0.74	1.02	0.97	1.02	0.8	0.82	1		
	Min						0.6	0.71	0.86	0.69	0.75	0.7	0.80		

		<i>M. pumilis</i>	<i>M. anceps pauxensis</i>	<i>M. minor</i>	<i>M. mediasetosus</i>	<i>M. medius</i>	<i>M. ceibaensis</i>	<i>M. dubitabilis</i>	<i>M. inarmatus</i>	<i>M. echinatus</i>	<i>M. finitimus</i>	<i>M. anceps anceps</i>	<i>M. varicans</i>	<i>M. elongatus</i>	<i>M. furcatus</i>
P4_ IntcxISclrt	Av		1	3			1	2	2	1	1	1	2	2	2
	Max						1	2	2	1	1	1	2		
	Min						1	2	2	1	1	1	2		
FSP5_L:W	Av	2.33	3	2	2.66	2.5	3	3.51	3.11	3.77	2.75	2.58	3.6	3.5	2
	Max						3	4.28	4	4	3	2.85	4.2		
	Min						2.6	2.8	2.75	3.66	2.5	2	3.2		
FSP5_Medial	Av	1	2	3	2	1	2	1	2	2	2	3	2	2	1
	Max						2	1	2	2	2	3	2		
	Min						2	1	2	2	2	3	2		
P5_L- FS:ApclSta	Av	0.29	0.18	0.34	0.21	0.33	0.26	0.42	0.28	0.45	0.48	0.41	0.38	0.46	0.40
	Max						0.34	0.58	0.30	0.46	0.53	0.50			
	Min						0.23	0.27	0.26	0.44	0.44	0.23			
Genital_L:W	Av	0.6	1.1	1.06	1.8		0.95	1.02	0.87	1.12	0.94	1.13	1.2		1.41
	Max						1.0	1.2	1	1.22	1.1	1.31			
	Min						0.92	0.9	0.8	1.04	0.78	0.96			
Spns_Anal	Av	1	1	2	1	1	1	1	2	1	1.5	1	2	2	2
	Max						1	1	2	1	2	1	2		
	Min						1	1	2	1	1	1	2		
CR_L-IV:L-III	Av		4.83	6.2	7.3	8.5	5.71	4.59	4.82	6.52	6.05	4.92	5.3	0.54	2.37
	Max						6.24	5.5	5.64	7.26	6.06	5.67	5.4		
	Min						4.67	4.17	3.86	5.52	6.03	4.17	5.2		
CR_L-V:L-III	Av		8.33	8.1	9	13.25	9.95	6.57	7.15	10.48	8.95	7.09	7.14		2.37
	Max						10.4	7.38	7.8	12.52	8.97	8.42	7.14		
	Min						9.63	5.58	6.22	8.54	8.94	6.11	7.14		
CR_L-VI:L-III	Av	0.92	1.81	2.33	3	1	1.82	1.54	1.62	1.96	1.92	1.35	1.64		1
	Max						2.12	1.72	1.88	2.31	2.125	1.74	1.80		
	Min						1.5	1.26	1.29	1.71	1.72	0.96	1.40		
L-VI:L-CR	Av	0.44	1.44	1.16	2.7	0.28	0.81	1.35	1.46	0.56	1.05	0.80	0.93	0.25	0.4
	Max						0.9	1.68	1.51	0.65	1.26	1.08	1		
	Min						0.85	1.1	1.4	0.51	0.85	0.58	0.85		
L-VII:L-CR	Av	0.48	1.55	0.6	0.95	0.58	0.75	1.02	0.89	0.50	0.65	0.55	0.53	0.37	0.2
	Max						1.0	1.22	1.17	0.71	0.78	0.9			
	Min						0.56	0.7	0.71	0.36	0.53	0.4			
CR_L:W	Av	2.9	2.4	3.15	2.29	4.35	3.37	2.51	2.51	5.97	3.40	3.78	3.39	5	6.66
	Max						3.8	3	2.93	6.3	4.1	4.25	3.68		
	Min						3.1	1.88	1.78	5.3	2.7	3	3		
CR_Base-II	Av	1	1	1	2	2	2	1.08	1	2	1	1.08	1	2	1
	Max						2	2	1	2	1	2	1		
	Min						2	1	1	2	1	1	1		
CR_Base-III	Av	1	2	2	2	2	2	2	1	2	2	2	1	1	1
	Max						2	2	1	2	2	2	1		
	Min						2	2	1	2	2	2	1		
Position-II:CR	Av	65.5	68	78	56.25	68.96	69.55	70.12	58.92	73.26	74.70	71.12	68.11	62.5	80
	Max						72.5	76.2	63.15	76.54	75.56	73.33			
	Min						65	61.54	54.00	70.13	73.85	69.12			

**Table 2.** Principal components analysis, variable loadings in bold (analyzing 28 variables for 54 specimens). Data square-root transformed.

	<b>Axis 1</b>	<b>Axis 2</b>	<b>Axis 3</b>
Eigenvalues	1.61	0.46	0.361
Percentage	48.523	13.878	10.886
Cum. Percentage	<b>48.523</b>	<b>62.401</b>	<b>73.287</b>
Genital_L:W	0.078	-0.029	0.011
Enp2P4_L:W	0.074	-0.024	0.06
BspP4_Medial	<b>0.222</b>	0.005	-0.14
P4_IntcxISclrt	0.065	<b>0.271</b>	<b>-0.294</b>
P4_LMedSpn:LLatSpn	0.059	0.033	<b>-0.166</b>
P4_LMedSpn:LEnp2	0.055	0.012	-0.077
CR_L-IV:L-III	<b>0.25</b>	<b>-0.482</b>	<b>-0.204</b>
CR_L-V:L-III	<b>0.335</b>	<b>-0.609</b>	<b>-0.237</b>
CR_L-VI:L-III	0.048	-0.116	-0.093
L-VII:L-CR	0.008	0.01	<b>-0.184</b>
L-VI:L-CR	0.022	-0.002	<b>-0.231</b>
CR_L:W	0.007	-0.089	<b>0.275</b>
CR_Base-II	0.006	-0.1	0.038
CR_Base-III	0.042	-0.104	0.054
Position-II:CR	0.036	-0.071	0.197
Spns_Anal	-0.028	0.054	-0.078
FSP5_L:W	0.038	0.075	<b>-0.138</b>
FSP5_Medial	0.064	-0.097	<b>0.303</b>
P5_L-FS:ApclSta	0.012	0.02	0.042
BspP1_SpineOrnament	0.024	<b>-0.174</b>	<b>0.35</b>
BspP1_Medial	<b>0.16</b>	0.09	-0.015
MxBsp_BasalSeta	<b>0.385</b>	0.097	<b>0.405</b>
MxBsp_Claw	<b>0.311</b>	<b>0.261</b>	-0.278
MxEnd_ProxSeta	<b>0.318</b>	<b>0.26</b>	0.027
MxEnd_DistSeta	<b>0.304</b>	<b>0.142</b>	-0.019
A2_DistalCaudal	<b>0.285</b>	<b>0.159</b>	-0.035
A2_DistalFrontal	<b>0.284</b>	<b>0.153</b>	0.202
Enp2P1-Pores	<b>0.339</b>	-0.05	0.137

## Results

According to Dussart and Defaye (1995), the morphological characters listed below are diagnostic for *Microcyclops*, and they were present in all the specimens analyzed here:

- a. A1 10–12-segmented.
- b. Caudal ramus with seta VI as long as, shorter, or longer than seta III.
- c. Thoracic limbs (P1–P4) biramous; each ramus 2-segmented. Enp2P4 has two well-developed apical spines, and coxa of P4 has a long-feathered seta on the medial margin.
- d. Fifth urosome with fifth leg represented by a lateral seta and a free segment, elongated. The latter bearing one apical seta and with or without one medial spine.

## Taxonomic account

**Order Cyclopoida Burmeister, 1835**

**Family Cyclopidae Rafinesque, 1815**

**Subfamily Cyclopinae Rafinesque, 1815**

**Genus *Microcyclops* Claus, 1893**

***Microcyclops finitimus* Dussart, 1984**

Figs 1, 2

*Microcyclops finitimus* Dussart, 1984: 57, 58, fig. 19A; Dussart 1983: 325, fig. 2B; da Rocha and Por 1998: 2138; da Rocha 1998: 426–431, figs 6, 7, 12, 18; Gutiérrez-Aguirre and Cervantes-Martínez 2016: 54, fig. 14A–E.

**Material examined. Holotype.** One dissected adult female on a slide labelled as *Microcyclops finitimus* female nov. sp. 'Lagoon' with *Trapa* between Coporito and Barrancas, Venezuela 24.X.1981, 8h40. Collector Bernard Dussart, and det. B. Dussart (MNHN Cp-678).

**Other material.** One dissected, adult female on a slide labelled as *Microcyclops finitimus* female. Rorota, prés Guyane 21.X.1985. GUYANE. Collector Bernard Dussart, and det. B. Dussart (MNHN Cp-7294).

**Redescription based on the holotype. Female:** body length excluding furcal setae = 0.89 mm (as described by Dussart 1984). Labral plate distally toothed: eight central teeth are flanked by lateral, basally widened teeth, which are followed by two low teeth on each side; medial labral plate with two groups of long, wide setulae; lateral lobes rounded (Fig. 1A).

Antennule 12-segmented: each segment was armed with setae (s), spines (sp) or aesthetascs (ae) in the following order: (1) 8 s; (2) 4 s; (3) 2 s; (4) 6 s; (5) 3 s; (6) 1 s + 1 sp; (7) 2 s; (8) 3 s; (9) 2 s + 1ae; (10) 2 s; (11) 2 s + 1 ae; (12) 7 s + 1 ae.

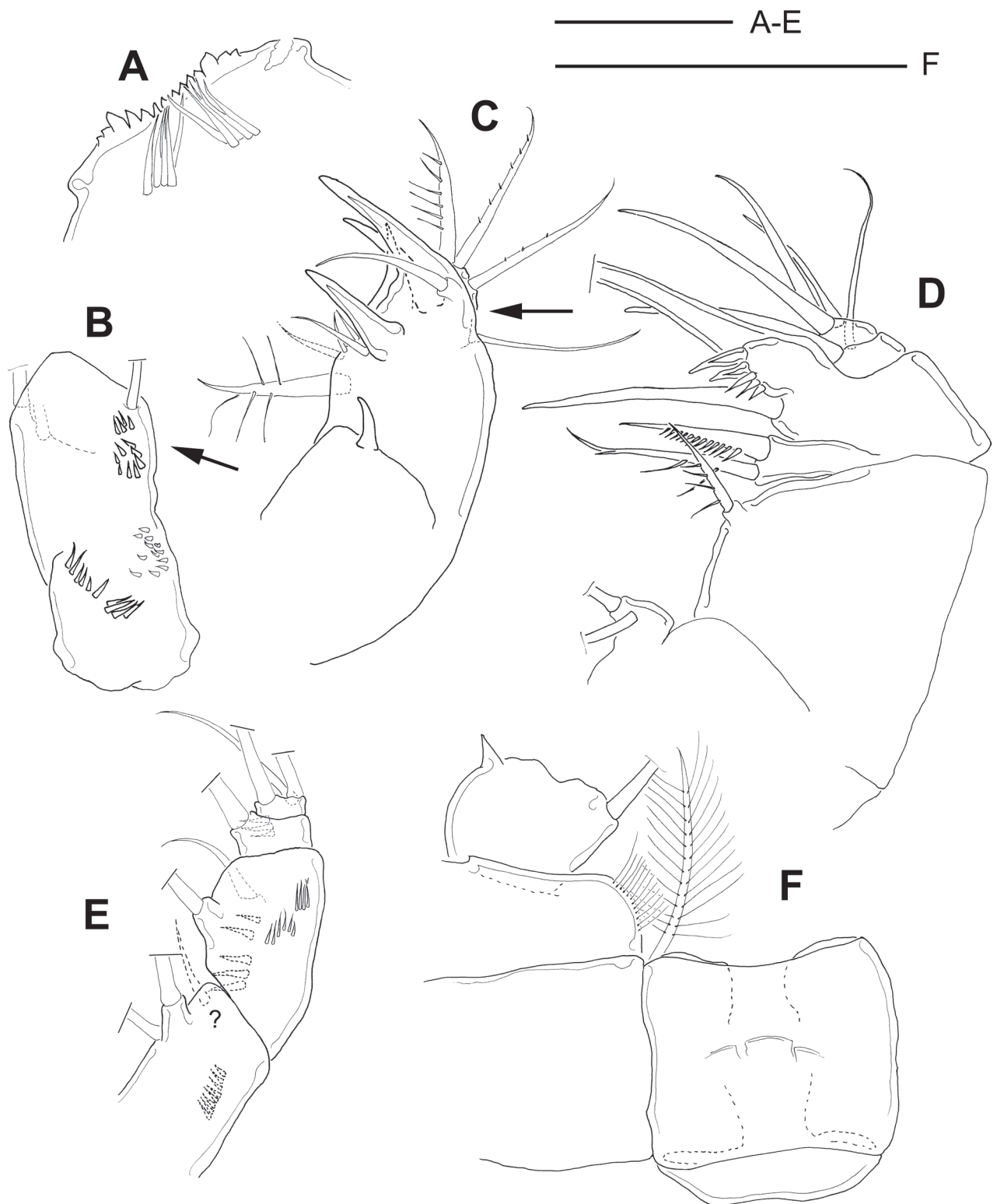
Antenna with two groups of spinules on the basal margin of the basis in caudal view. In the frontal view antennal basis with two groups of spinules: one next to the exopodal seta, on the distal region (arrowed in Fig. 1B) and one is along the lateral margin.

Maxillule (Fig. 1C): praecoxal arthrite with seven setae. Apical region of maxillary palp with two setae armed with tiny spinules, plus a third seta with long setules. Lateral lobe lost (area arrowed in Fig. 1C). One smooth proximal seta.

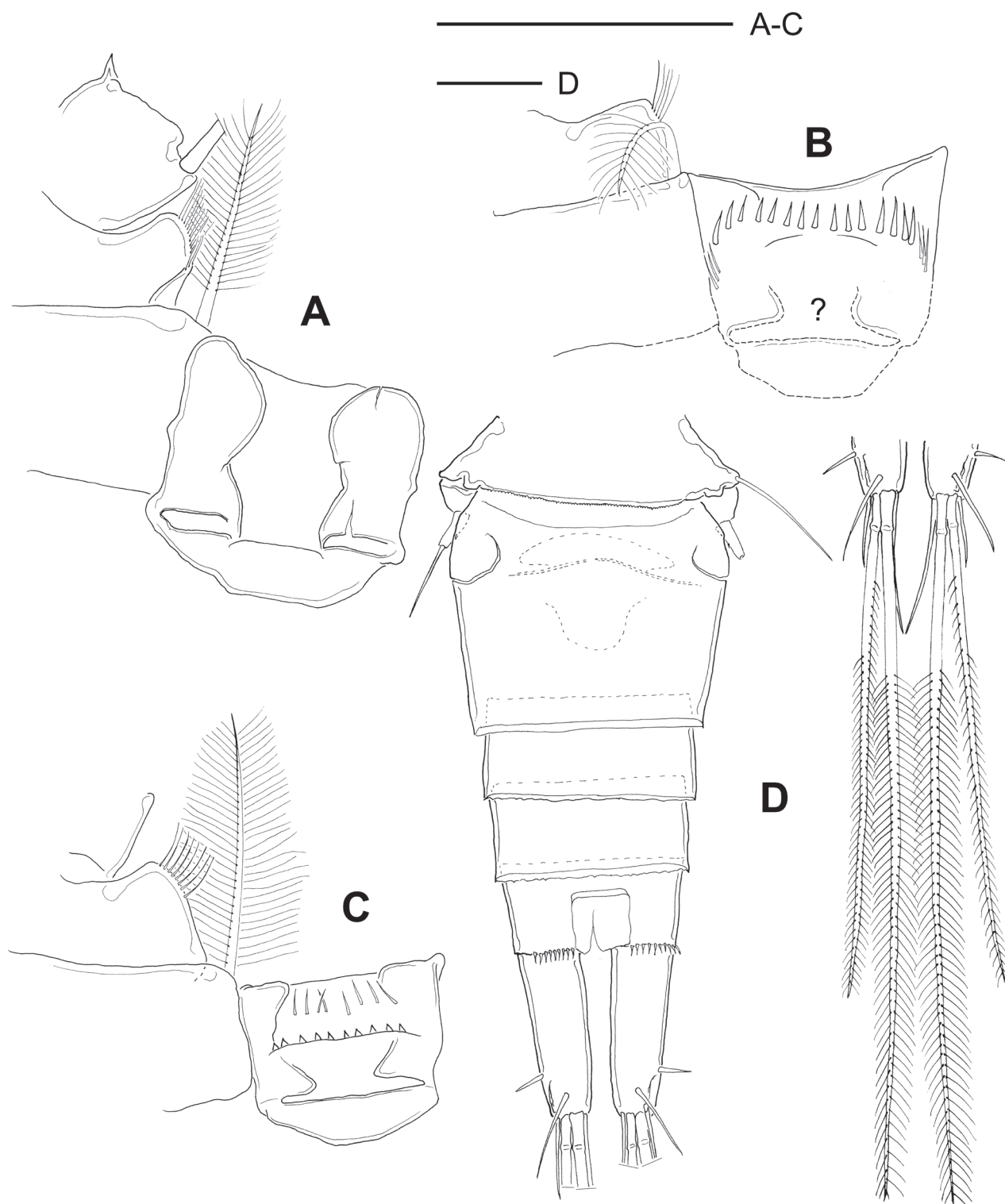
Maxillary syncoxal surface smooth (Fig. 1D). Distal coxal endite with two setae: proximal seta distally bifurcated, with long spinules; distal seta with an elongated row of spine-like setules. Basipodite with a bump bearing robust, engrossed spines on the concave margin and one long, bare seta on its base. Enp1 and Enp2 bearing two and three naked and long setae, respectively.

Maxilliped with syncoxa (3 setae, one broken off), basis (2 setae), and two-segmented Enp bearing one and three setae, respectively. Syncoxa, basis, and Enp1 with rows of spinae: basis on frontal and caudal surfaces; syncoxa and Enp1 only on the frontal surface (Fig. 1E).





**Figure 1.** *Microcyclops finitimus*. Adult female (MNHN-Cp678) **A** labrum **B** antenna, note that the distal group of spines is arrowed in this caudal-frontal view **C** maxillule, note that the lateral lobe of maxillular palp is missing (area arrowed) **D** maxilla **E** maxilliped, note that the insertion of broken off seta is suggested (indicated by ?) **F** first leg, medial area: intercoxal sclerite, Bsp, and Enp1. Scale bars: 50  $\mu$ m.



**Figure 2.** *Microcyclops finitimus*. Adult female (MNHN-Cp678) **A** second leg, medial area: intercoxal sclerite, Bsp, and Enp1 **B** third leg, medial area: intercoxal sclerite, and Bsp: the basal area of intercoxal sclerite was not verified (indicated by ?) **C** fourth leg, medial area: intercoxal sclerite, and Bsp **D** urosome, note the separate terminal caudal setae. Scale bars: 50  $\mu$ m.

Medial margin of basipodites of P1–P4 with long hair-like setae. There is no medial spine on the margin of BspP1 (Fig. 1F). Intercoxal sclerite of P1, and P2 quadrangular, naked (Figs 1F, 2A). Intercoxal sclerite of P3 rectangular with long and robust spinules arranged laterally along the distal margin of the plate

(Fig. 2B). Proximal region of the intercoxal sclerite of P3 not observable (indicated by ? in Fig. 2B).

P4 as illustrated and described by Dussart (1984: 57, 58, fig. 19A): intercoxal sclerite rectangular, with two rows of spinules; distal row with elongated spinules, proximal row with short spinules (Fig. 2C). Ratio between the lengths to width of Enp2P4 is 2.2–2.5; the medial spine of Enp2P4 is 1.3× as long as lateral spine and 0.7× as long as the segment.

Fifth pediger bare, with dorsal hyaline membrane serrated posteriorly (Fig. 2D); length to width ratio of genital double somite 0.78. Free segment of P5 3.0× as long as wide, bearing one tiny medial spinule, and 0.4× as long as distal seta. Hyaline fringes of prosomal somites smooth, except the fourth which is serrated; urosomal somites with hyaline fringes slightly serrated. As described by Dussart (1984), length to width ratio of the caudal ramus is 4.1, the inner margin naked; no spinules at the base of the lateral caudal (II) but spines at the base of the outermost terminal (III) caudal setae (spines verified in MHN-Cp7294). Spinae along dorsal and ventral margins of anal somite. Lateral caudal seta (II) inserted 73.0–75.5% of the caudal ramus.

Dorsal caudal seta (VII) 0.5–0.7× as long as caudal ramus, innermost terminal caudal seta (VI) 1.05× as long as caudal ramus. Length ratio between outer median (IV) and outermost terminal seta (III) is 6.0; and between medial median (V) and outermost terminal seta (III) is 8.9 (Fig. 2D).

#### ***Microcyclops minor* Dussart, 1984**

Fig. 3

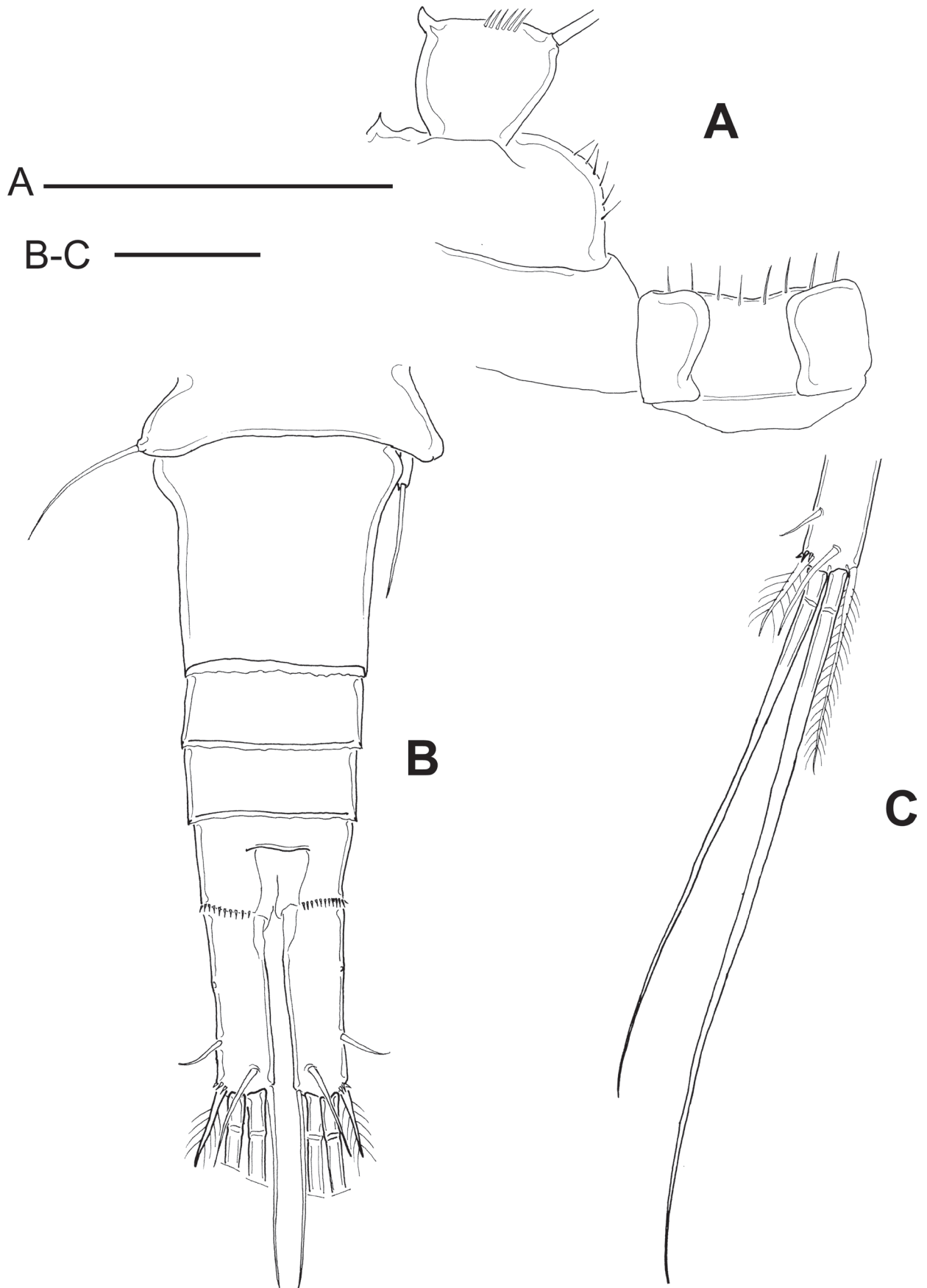
*Microcyclops anceps* var. *minor* Dussart, 1984: 57, fig. 17.

**Material examined. Holotype.** Dissected, adult female on slide labelled as: *Microcyclops anceps* var. *minor* [nov. var.]. Charca I, near Unaré river at Clarines (Venezuela), 13.4.1981, Collector Bernard Dussart, and det. B. Dussart (MNHN Cp-673).

**Redescription based on the holotype.** Dorsal margin of prosomal somites smooth (unfigured). Because of the position of the specimen, it was not possible to observe the buccal appendages.

As per the illustration by Dussart (1984), basipodites of P1 with short hair-like setules but without spine on medial margins; coxa with one row of short setules along lateral margins. Basipodite of P4 with short hair-like setules on medial margin (Fig. 3A); P4 intercoxal sclerite rectangular with long setules along distal margin. As illustrated by Dussart (1984) Enp2P4 is 2.46× as long as wide; medial spine 1.95× as long as lateral spine and 0.73× as long as the segment.

Fifth pediger bare, with dorsal hyaline membrane smooth posteriorly; P5 is a cylindrical free segment that bears one apical seta and one projected medial spinule (Fig. 3B). Free segment of P5, 2.0× as long as wide and 0.34× as long as apical seta. Length to width ratio of caudal ramus is 3.15, medial margin naked; no spinules at base of lateral caudal setae, but spinules present at base of outermost terminal caudal setae (Fig. 3B). Short spinules along all the posterior margin of anal somite; lateral caudal seta inserted at 78% of caudal ramus.



**Figure 3.** *Microcyclops minor*. Adult female (MNHN-Cp673) **A** fourth leg, medial area: intercoxal sclerite, Bsp, and Enp1 **B** urosome, dorsal **C** terminal caudal setae. Scale bars 50  $\mu$ m.

Relative lengths of terminal caudal setae from outermost to innermost caudal seta are 1: 6.2: 8.1: 2.33 (Fig. 3C). Due to the differential morphological characteristics previously described, we propose to elevate the status of *M. minor* to the species level.

### Cluster and PCA analyses

In Fig. 4, the cluster analyses show the grouped specimens according to the total likeness of the 28 considered characters (Table 1). *Microcyclops medius* Dussart & Frutos, 1985, *M. mediasetosus* Dussart & Frutos, 1985, *M. minor*, *M. anceps pauxensis* Herbst, 1962, *M. furcatus* (Daday, 1905), *M. elongatus* (Lowndes, 1934), and *M. pumilis* Pennak & Ward, 1985 were observable as isolated entities, because of the lack of information on the buccal appendages in these taxa.

In all species from various geographical regions (Suppl. material 1) *M. inarmatus* Gutiérrez-Aguirre & Cervantes-Martínez, 2016, *M. varicans* (G.O. Sars, 1863), *M. dubitabilis* (Kiefer, 1934), *M. anceps anceps* (Richard, 1897), *M. finitimus*, *M. echinatus* Fiers, Ghenne & Suárez-Morales, 2000, and *M. ceibaensis* (Marsh, 1919), specimens belonging to the same putative species formed single clusters that were clearly separated from those of other species.

The three groups with the least distance between specimens (the more compact groups in Fig. 4), even though the analyzed specimens were recorded in a wider latitudinal range (Suppl. material 1), were *M. ceibaensis*, *M. varicans*, and *M. anceps anceps*, but the group with the highest inter- and intrapopulation variability in morphological characters was *M. dubitabilis*. Even though the records are in a more limited latitudinal range (compared to the three previously mentioned species), it is possible to observe discontinuities within the group *M. dubitabilis*.

According to the PCA, all features related to maxilla ornamentation are important characters that explain the model variability in the first axis (Table 2), followed by the presence/absence of cuticular pores on lateral area of Enp2P1, and the ornamentation of the distal region of the antennal basis (with or without a group of spinules on caudal or frontal views). Following the order of importance, the presence or absence of hair-like seta (or another ornament) on the medial margin of BspP4 is also essential, followed by the length ratio between median caudal setae, IV, and V, with the outermost terminal seta (III), and finally, the presence/absence of a hair-like seta on the medial margin of BspP1.

In addition to the characters mentioned before, in Axis 2, the model points that are important characters the ornamentation of the spine on the inner basis of BspP1 (when it is present) and the ornamentation of the intercoxal sclerite of P4 (Table 2).

Axes 1 and 2 together explain 62.4% of the variability, and Axis 3 adds 10% more. In this third axis with values of importance lower than 0.41 (Table 2), the following morphological characters are important according to the model: length ratios between the innermost and dorsal caudal setae with caudal rami length, as well as the length ratio of the medial spine and lateral apical spines of Enp3P4. However, this last character is in a penultimate place (in order of importance), after all other features mentioned before.

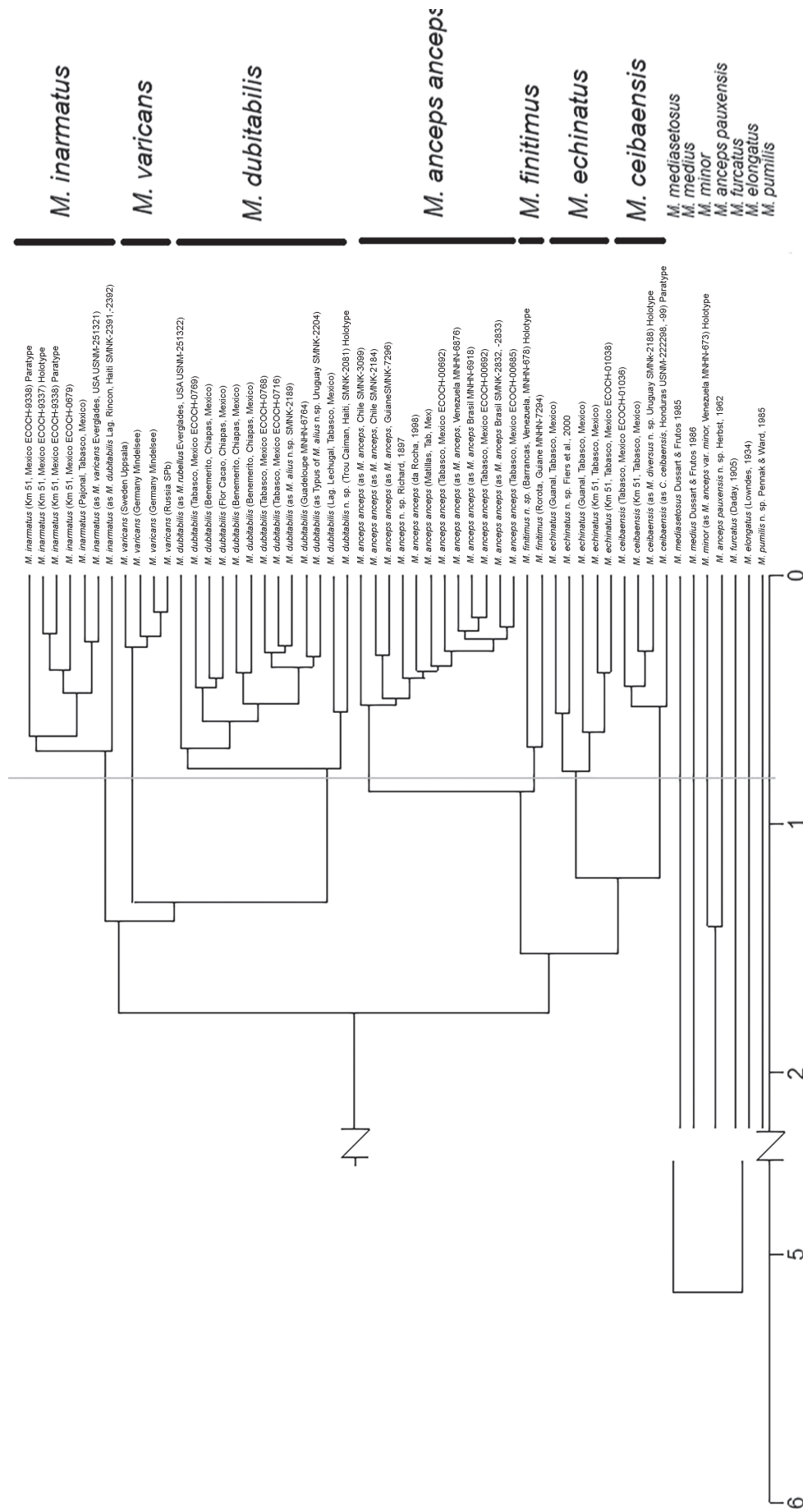


Figure 4. Dendrogram: total morphology likeness between specimens representing the Neotropical species, and *Microcyclops varicans*. UPGMA as clustering method and Euclidean distance.

## Discussion

With the analyses performed here, it was clear that the American species *M. inarmatus* and *M. dubitabilis* are not morphologically similar to *M. varicans* (recently redescribed by Mirabdullayev and Defaye 2022), and that the cluster analysis exposes them as different groups.

Some differential morphological characteristics between *M. anceps pauxensis* and *M. minor* had already been previously described in Gutiérrez-Aguirre and Cervantes-Martínez (2016). However, after the analysis of the type material of *M. minor*, the differences between the medial margin of BspP1 and BspP4 are clear, as well as in the ornamentation of the intercoxal sclerite of P4, in the length of the apical seta of P5, and in the length ratio displayed by the terminal furcal setae (see Suppl. material 2). These characters are of importance to delineate between the American species, based on the PCA performed here. Although the evaluation of the buccal appendages of *M. anceps pauxensis* and *M. minor* is still pending, we suggest them as separate species (even distinct from the species *M. anceps anceps*). To the best of our knowledge, *M. minor* and *M. anceps pauxensis* have only been recorded as original descriptions. Probably the information included herein will encourage the finding of these species in their actual distribution areas.

The majority of *Microcyclops* species occur in the Neotropical region (Suárez-Morales et al. 2020). In addition to the records presented in Suppl. material 1, *Microcyclops furcatus* was recorded in São Jose do Norte, Brazil (Cardozo et al. 2007) and Paraguay (Reid 1985). *Microcyclops finitimus* and *M. mediasetosus* together with *M. anceps anceps* and *M. dubitabilis* were recorded in Mato Grosso do Sul, Brazil (da Rocha and Por 1998).

*Microcyclops anceps anceps* appears to be a Neotropical species with a large geographic range including southeastern Mexico, Guatemala, Venezuela, Guyana, Uruguay, Brazil, and Chile. *Microcyclops dubitabilis* is also widely distributed in the Neotropics (southeastern Mexico, Florida, Haiti, Guadeloupe, Uruguay, Brazil, and Venezuela).

*Microcyclops ceibaensis* occurs in southeastern Mexico, Central America, and Brazil. *Microcyclops elongatus* was recorded in Brazil and Paraguay, and *M. inarmatus* appears to be distributed in Florida, Haiti, and southeastern Mexico (Gutiérrez-Aguirre and Cervantes-Martínez 2016). To our knowledge, the next species have been recorded exclusively in a single locality: *M. medius* in Argentina (Dussart and Frutos 1986), *M. minor* in Venezuela (Dussart 1984), *M. pumilis* in United States (Pennak and Ward 1985), and *M. anceps pauxensis* in Brazil (Herbst 1962).

*Microcyclops inarmatus*, *M. varicans*, and *M. dubitabilis* share the character of an armed seta on the maxillary basipodite. In contrast, in *M. anceps anceps*, *M. finitimus*, *M. echinatus*, and *M. ceibaensis*, the ornamentation of this seta is absent or reduced (in *M. echinatus*). The maxilla has some special features in these four species, such as the row of strong spines on a bump on the concave side of the claw-like seta (in *M. finitimus* or *M. anceps anceps*); the proximal seta of the maxillary distal coxal endite only ornamented on one side (in *M. ceibaensis*, *M. finitimus*, and *M. anceps anceps*); the smooth distal seta of the maxillary distal coxal endite (in *M. ceibaensis* and *M. echinatus*). The distribution of these features explains the arrangements in the cluster analysis.

*Microcyclops finitimus*, *M. minor*, *M. anceps pauxensis*, *M. pumilis*, *M. mediasetosus*, and *M. anceps anceps* are the American species that share the absence of spine on the medial margin of the basipodite of first leg. Except for *M. finitimus*, we were not able to observe the buccal structures of most of these species. However, they appear as independent entities (see Fig. 4) because of the clear differences (between species) in the ornamentation of the medial margins of BspP1 and BspP4 (see Table 1), which were of the most important characters to delineate the *Microcyclops* species analyzed here.

Recently, the maxillary and antennal basis microstructure, as well as the structure of swimming legs, especially the ornamentation of intercoxal sclerites and medial margin of basipodite, have been suggested by Einsle (1993), Mirabdullayev (2007), and Gutiérrez-Aguirre and Cervantes-Martínez (2016) as species diagnostic characteristics in *Microcyclops*. Previously da Rocha (1998) pointed out the importance of considering the presence/absence and number of pores on the lateral margin of Enp2P1 as a diagnostic character to recognize Neotropical *Microcyclops* species. The ordination analysis performed here allowed us to distinguish them as the most important characters to be considered in the classification of American *Microcyclops* species.

With this work, it was determined that, indeed, the length ratios (ranges and average) between terminal caudal setae IV:III and V:III are very informative for distinguishing species. These characters are also relatively easy to distinguish using light microscopy; fortunately, they have been illustrated/described in most original descriptions (see Herbst 1962; Dussart 1984) and were observed in the type material examined here.

For the American *Microcyclops* species the statistical analysis also improves the definition that can be achieved in combination with morphological analysis for species resolution, as has been tested with other aquatic species (Lajus et al. 2015; Bradford-Grieve et al. 2017).

Other characteristics that have traditionally been used to differentiate some cyclopoid species are the length ratio of caudal rami, the length ratios in structures on distal endopod of the fourth leg, or the length ratio between dorsal caudal seta and caudal ramus. However, similar to other genera such as *Mesocyclops* or *Eucyclops*, after the analysis surveyed here, these characters can be considered as not informative for differentiating the American *Microcyclops* species because they are shared or have overlapping features (see Table 1).

Additionally, the species *M. echinatus* (in caudal view), *M. finitimus*, *M. anceps anceps*, and *M. varicans* (in frontal view) share the presence of a group of spines on the distal region of the antennal basis, whereas in *M. inarmatus*, *M. dubitabilis*, and *M. ceibaensis*, this region is bare. The importance of species-specific patterns of teeth and spines on BspA2 has been widely reported in the genera *Macrocyclops*, *Eucyclops*, and *Ectocyclops* in Eucyclopinae (Fiers and Van de Velde 1984; Mercado-Salas and Suárez-Morales 2014) and *Cyclops*, *Mesocyclops*, and *Thermocyclops* in Cyclopinae (Fiers and Van de Velde 1984; Holyńska 2006; Karanovic et al. 2017). However, for *Microcyclops* species, this pattern has been qualified as remarkably simple, with doubts about its taxonomic value (Fiers and Van de Velde 1984). After this analysis, we confirm that it is possible to differentiate the American *Microcyclops* species when the microstructure (features and position) of teeth and spinules on the caudal or frontal surfaces of A2 are also observed.



## Conclusions

Two insufficiently known South American species, *M. finitimus* and *M. minor* were redescribed based on type material. According to the classification and ordination models, the microstructure of cephalic appendages, the medial area of thoracic appendages, and the caudal setae of caudal rami (identifiable with light microscopy) were strongly supported as morphological characters that improves resolution between the American *Microcyclops* as well as in species with wide geographic distribution.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: MAGA. Data curation: MAGA, ACM. Formal analysis: ACM. Funding acquisition: MAGA, ACM.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Biological material examined

Authors: Martha Angélica Gutiérrez-Aguirre, Adrián Cervantes-Martínez

Data type: Morphological

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## Supplementary material 2

### Distribution of characters by specimen; abbreviation is explained in data analysis

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Data type: Morphological






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Review

# Freshwater Diversity of Zooplankton from Mexico: Historical Review of Some of the Main Groups †

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**Abstract:** In this review, we include rotifers, copepods, and cladocerans, including other groups not usually deemed as zooplankters: i.e., protists, acari, and large branchiopods. The objectives of this study were to integrate the dispersed literature on the taxonomy and diversity of these freshwater zooplankton groups and to explain (1) how these contributions can be arranged in distinct historical periods and (2) how this knowledge has allowed the detection of exotic and threatened species. We divided the freshwater zooplankton studies in Mexico into three historical periods: the first one comprised the 1840s to the 1940s when foreign researchers carried out most studies during several expeditions. Spanish researchers promoted surveys on different zooplankton taxa at the end of this first period. The second period, from the early 1950s to the end of the 1990s of the XX century, showed a remarkably increased research activity in its last ten years only (that is, during the 1990s to 2000), represented by contributions of a new generation of Mexican zooplanktologists. This period yielded more complete zooplankton listings and detailed morphological descriptions of rotifers, cladocerans, copepods, and large branchiopods. The third period started from the year 2000 to date. During this time, listings and online faunistic baselines based on integrative taxonomy have been the primary trend. An account of exotic zooplankters and conservation issues of several native species are discussed. The results of this review show that the knowledge of the freshwater zooplankton of this country has increased significantly over the last 40 years, with at least 408 first records of species for Mexico. Currently, the knowledge of Mexican freshwater zooplankton is among the most complete in the world. However, it is estimated that only a small fraction of the true diversity has been documented.

**Keywords:** zooplankton; taxa; regional; microcrustaceans; macrocrustaceans; continental waters; Mexico

## 1. Introduction

In this revision of the Mexican freshwater zooplankton, we include data on rotifers, copepods, cladocerans, protists, acari, and large branchiopods. Ostracods, chironomids, and fish larvae were excluded.

Protists have been recognized as a group since Haeckel's early system of classification (1866) [1]. They are recognized as polyphyletic, which is used as a functional and operational term. For example, "protozooplankton" is commonly used for predominantly non-filamentous heterotrophic species that belong to the zooplankton, although many species can be mixotrophic [2]. Protists are a crucial link to higher trophic levels in the freshwater plankton food webs, but they also contribute to recycling organic carbon and energy in the microbial loop [3]. They occupy various trophic levels within the plankton community. In addition, their capacity to either live with symbiotic zoochlorellae or sequester chloroplasts makes them the most diverse feeding-behavior planktonic group. This functional protist overlapping explains their occurrence in the same niches, but more observations are necessary to discover their actual richness, which should be higher than the apparent one [4–7]. The protozooplankton is present in most freshwater habitats but has been largely neglected in plankton studies [7]. Morphologically, ciliates, flagellates, and heliozoans are among the main groups of heterotrophic zooplankton protists.

Rotifers are chiefly parthenogenetic zooplankters, mainly represented by females, but the group also comprises benthic or periphytic forms. A complex mandible, the mastax, characterizes them. They are eutelic blastocoelomates with an anterior ciliated corona, their main locomotion structure, for which they are also known as "wheel animals."

Water mites include thousands of acari species that are true permanent residents of many freshwater habitats [8]. They are grouped into eight superfamilies [8,9], three of which include members with adaptations to living in the plankton [10–13]. Furthermore, water mites can prey on other zooplankters [12,14,15]. More than 7,500 water mite species have been described worldwide [9,16,17].

Cladocerans and rotifers have been traditionally considered part of the zooplankton communities, but they include bottom-living or phytal forms. Like rotifers, cladocerans reproduce mainly with a parthenogenetic cycle [18]. Up to 850 cladoceran species are known worldwide [19]. The taxonomic identity of several species recorded in Mexico has been confirmed with molecular tools, but groups of cryptic species have also been recognized [20].

The large branchiopods, i.e., fairy and brine shrimps of the order Anostraca, tadpole shrimps of the order Notostraca, and clam shrimps of the orders Cychletherida, Laevicaudata, and Spinicaudata, live mostly in ephemeral freshwater bodies with extreme physical and chemical conditions. The Anostraca is represented in Mexico by species of four families [21] (Supplementary Table S1). The brine shrimp *Artemia* is limited to brine water habitats (TDS > 35 g L). The Notostraca is represented by two genera: *Triops* and *Lepidurus* [22]. The clam shrimp order Cycletherida is represented in Mexico by the Cycletheriidae, the Laevicaudata by the Lynceidae, and the Spinicaudata by the Cyzicidae, Leptestheriidae, and Limnadiidae [23] (Supplementary Table S1). They have not been considered true zooplankters.

The free-living planktonic Copepoda is represented by three orders in Mexico: Calanoida, Cyclopoida, and Harpacticoida; the latter, largely benthic, is represented by 21 species in this country [24] (Supplementary Table S1), but their diversity is probably underestimated. Among the cyclopoids, 19 genera of the highly diverse and widespread family Cyclopidae have been recorded; also, four families of the order Calanoida are known to occur in Mexico: Diaptomidae, Centropagidae, Temoridae, and Pseudodiaptomidae.

A single member of each of the chiefly euryhaline families Centropagidae, Temoridae, and Pseudodiaptomidae has been recorded in Mexico (Supplementary Table S1) [18,25,26].

The family Diaptomidae is the most diverse in Mexico, with members of eight genera [27–29] (Supplementary Table S1). Many freshwater calanoid copepods appear to have limited distributional patterns in the Neotropical region [30,31]. The two Mexican regions with the most records and potential endemisms of Cladocera and Copepoda are the Neovolcanic Axis of the central-eastern region and the Yucatan Peninsula [30,32].

The objectives of this review are to integrate the dispersed literature on the taxonomy and diversity of these freshwater zooplankton groups in Mexico and to explain (1) how these contributions can be arranged into distinct historical periods and (2) how this knowledge has allowed a general estimation of the national biodiversity of the freshwater zooplankton and the detection of exotic and threatened species to support the conservation of this largely ignored community. The results of the review show that the knowledge of the freshwater zooplankton of this country has increased significantly over the last 40 years, with at least 408 first records of zooplankton species for Mexico.

## 2. Methods

We surveyed all published papers on the taxonomy of Mexican epicontinental zooplankton, including visits to institutional libraries (i.e., the Royal Belgian Institute of Natural Sciences, University of Ghent, National Autonomous University of Mexico, and the National Polytechnic Institute, Mexico), theses, and project reports performed in Mexico. We also performed multiple searches of specialized literature, including keywords for each group from different academic databases, including Web of Knowledge, SCOPUS, and Google Scholar, among others. All consultations were made until 30 November 2022 and included searches as “Calanoid”, “Freshwater”, and “Mexic\*” not “New Mexico”, for example, for calanoid copepods.

## 3. Results

Following the comprehensive analysis of the available specialized literature, we divided the zooplankton studies in Mexico into three historical periods: the first comprised the XIX century to the 1940s decade in the XX century, the second period was from the early 1950s to the end of the 1990s of the XX century, the third period started from the year 2000 to date. The rise in publications coverage and the increased number of species reported (Figures 1–5) are markers of the progress in discovering the Mexican zooplankton biodiversity. In the following paragraphs, we provide details of each phase. Additionally, in the Supplementary Table S1, we include the number of species for each group and further bibliographic information regarding them.

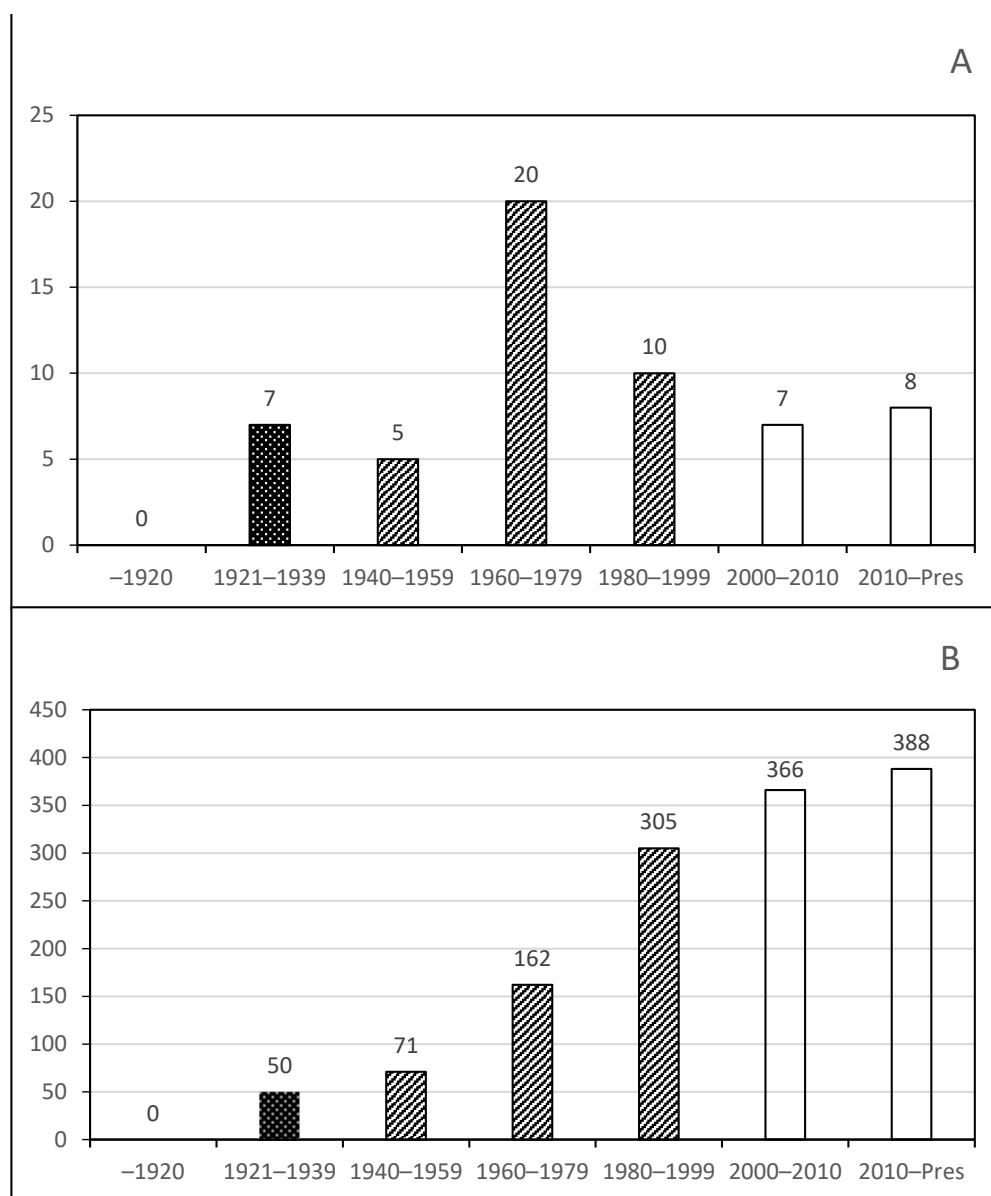
### 3.1. Phase 1: Early Studies Dominated by Foreign Researchers (Second Half of XIX Century to 1940s of XX Century)

In this phase, foreign scientists or scientific expeditions worked in Mexico; for example, the studies of Pearse et al. 1936 in the Yucatan Peninsula [33]. All of them intended to discover the diversity of different groups. Subsequently, the arrival of the Spanish zoologists E. Rioja and B. Osorio Tafall promoted new studies on zooplankton crustaceans also on protists and rotifers.

#### 3.1.1. Protists

Formal studies on planktonic protists started in this phase with works by Bravo-Hollis [34] in Central Mexico [35]. In that same period, Sámano and Sokoloff [36], Ancona et al. (see 39), and Osorio-Tafall [37,38] also contributed to the knowledge of this group [39].

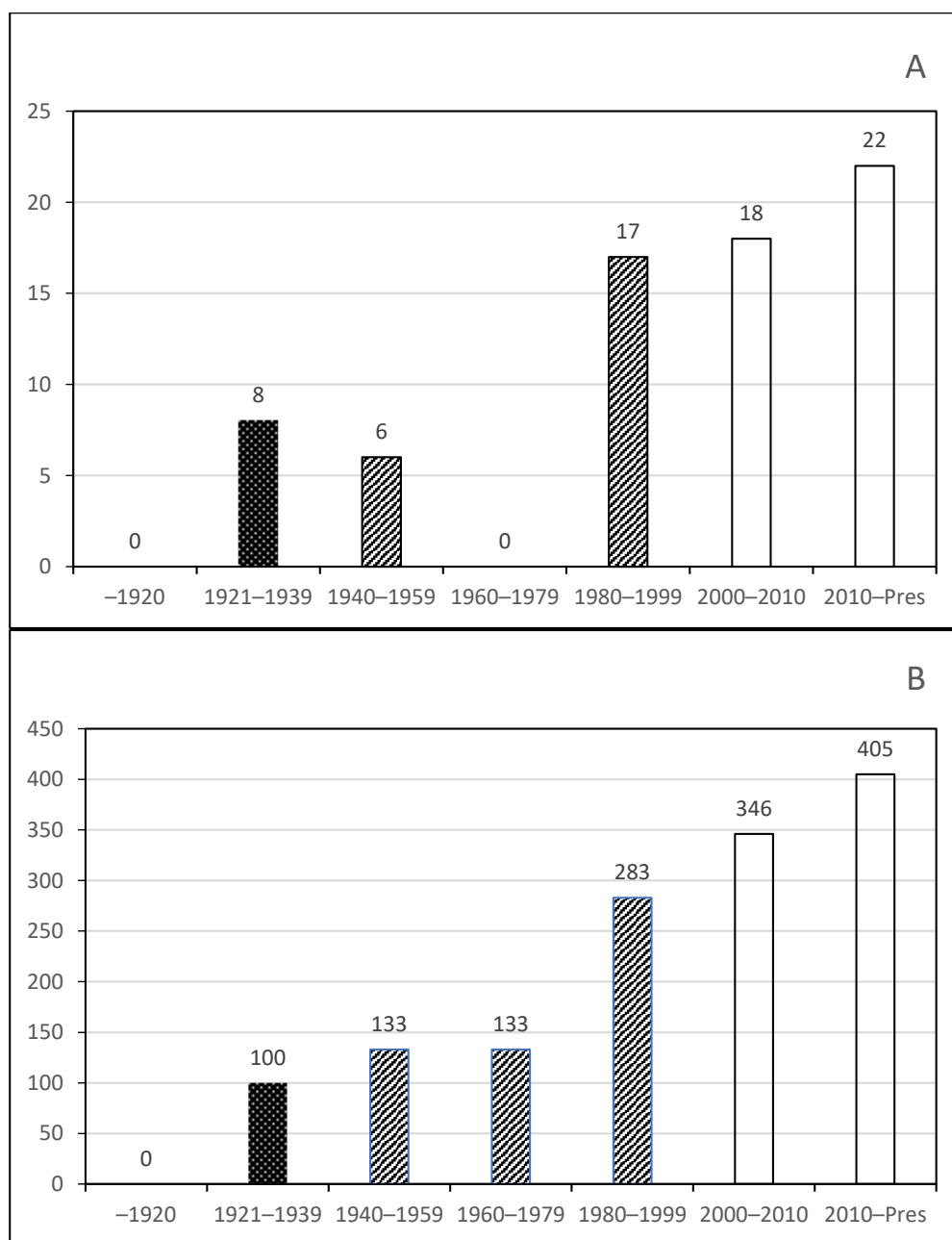




**Figure 1.** Historical progress of studies on Mexican Protists. (A) Number of publications. (B) Cumulative number of species found. ■ Phase 1. Early studies dominated by foreign visitors; ▨ Phase 2. Towards the formation of Mexican protistologists; □ Phase 3. Consolidation of Protist studies.

### 3.1.2. Rotifers

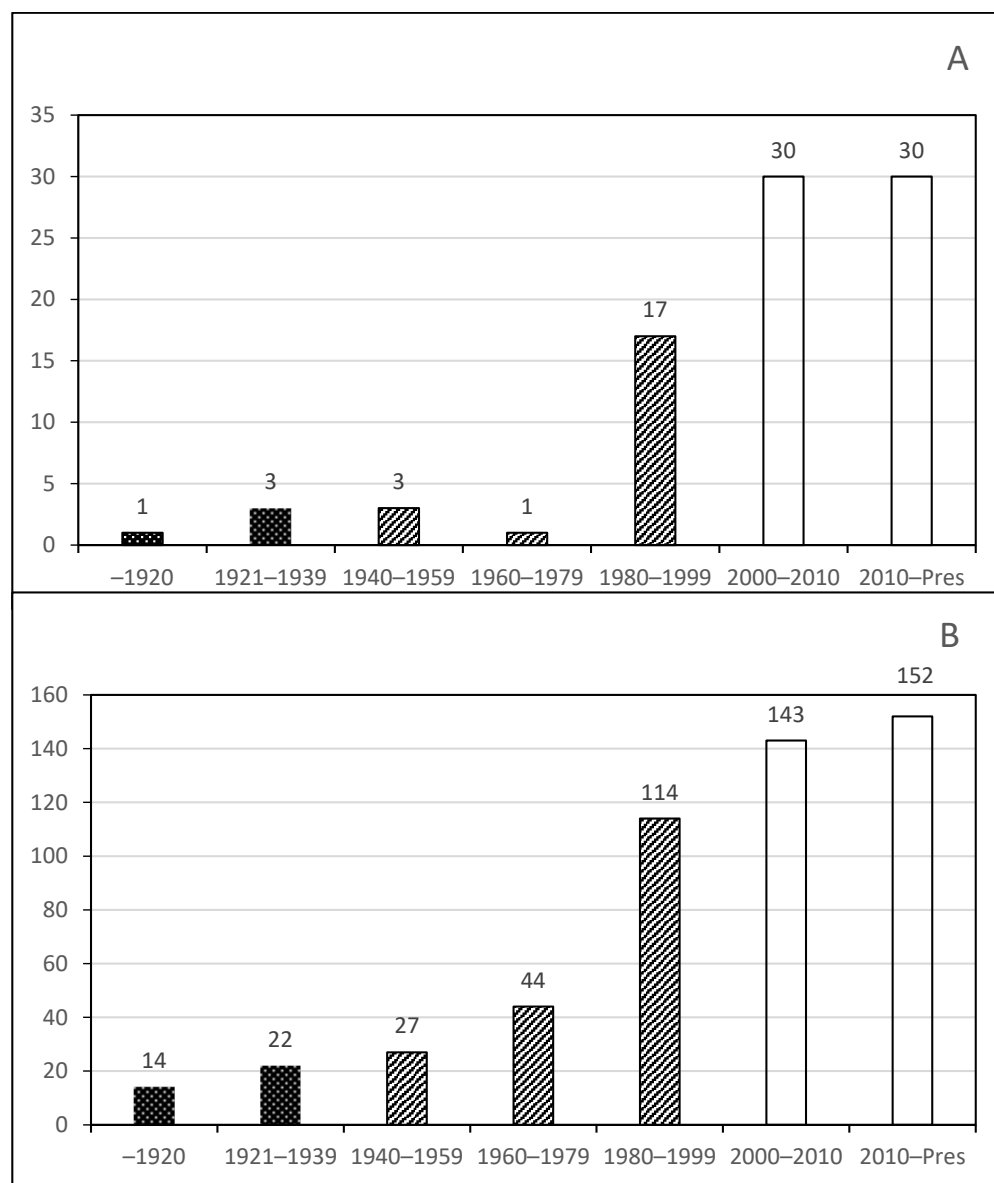
During this phase, a few Mexican researchers conducted the earliest studies on rotifers [40], and several foreign scientists conducted biological expeditions, mainly in central Mexico. Subsequently, other authors like Ahlstrom [41], Carlin-Nilson [42], Sámano [43], Hoffman and Sámano [44,45], and Uéno [46] reported on the rotifers of Lake Patzcuaro and other Mexican localities. At the end of this phase, studies on rotifers expanded to other areas in central Mexico [47–51]. After this first period, the interest in the knowledge of rotifers was paused for several years.



**Figure 2.** Historical progress of studies on Mexican Rotifers. (A) Number of publications (B) Cumulative species recorded in this region. ■ Phase 1. Early studies included Mexican researchers but were dominated by foreign visitors; ▨ Phase 2. Towards the formation of Mexican rotiferologists, working with foreign researchers, and first species descriptions; □ Phase 3. Consolidation of rotifer studies and integrative taxonomy descriptions.

### 3.1.3. Water Mites

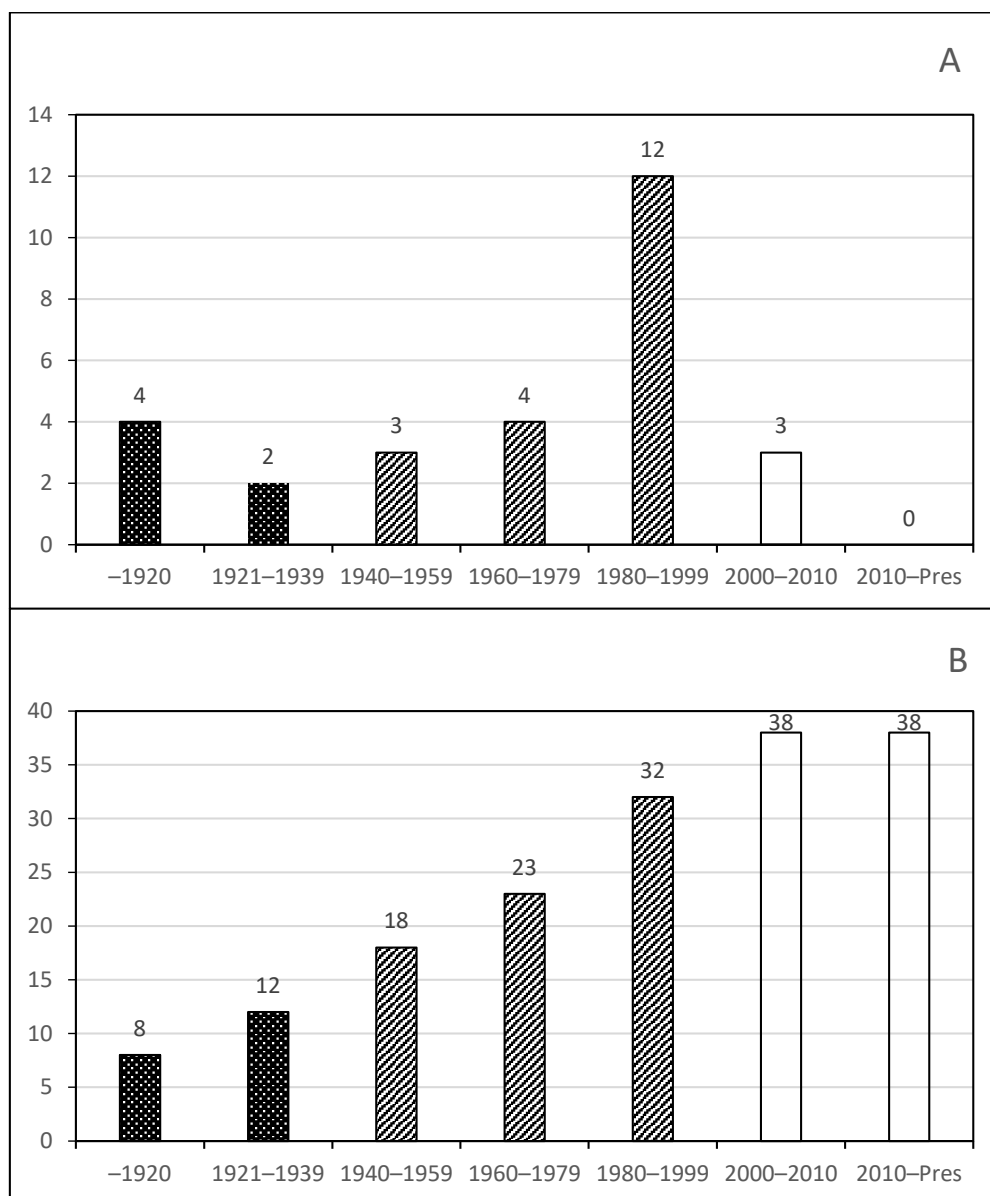
This phase also comprises the first descriptions of water mites in Mexico, contributed by the French naturalist Alfredo Dugés [52,53] (see Marshall [54]). Subsequently, Marshall [55] contributed to the first taxonomic account of Mexican water mites of the Yucatan Peninsula.



**Figure 3.** Historical progress of studies on Mexican Cladocera (Anomopoda and Ctenopoda). (A) Number of publications. (B) Cumulative number of species recorded. ■ Phase 1. Early studies by foreign visitors; ▨ Phase 2. The consolidation of Mexican cladocerologists in the last period (1980–1999); □ Phase 3. Mature period and formation of 2nd and 3rd generation of researchers on this topic, and discovery of exotic species.

#### 3.1.4. Cladocerans

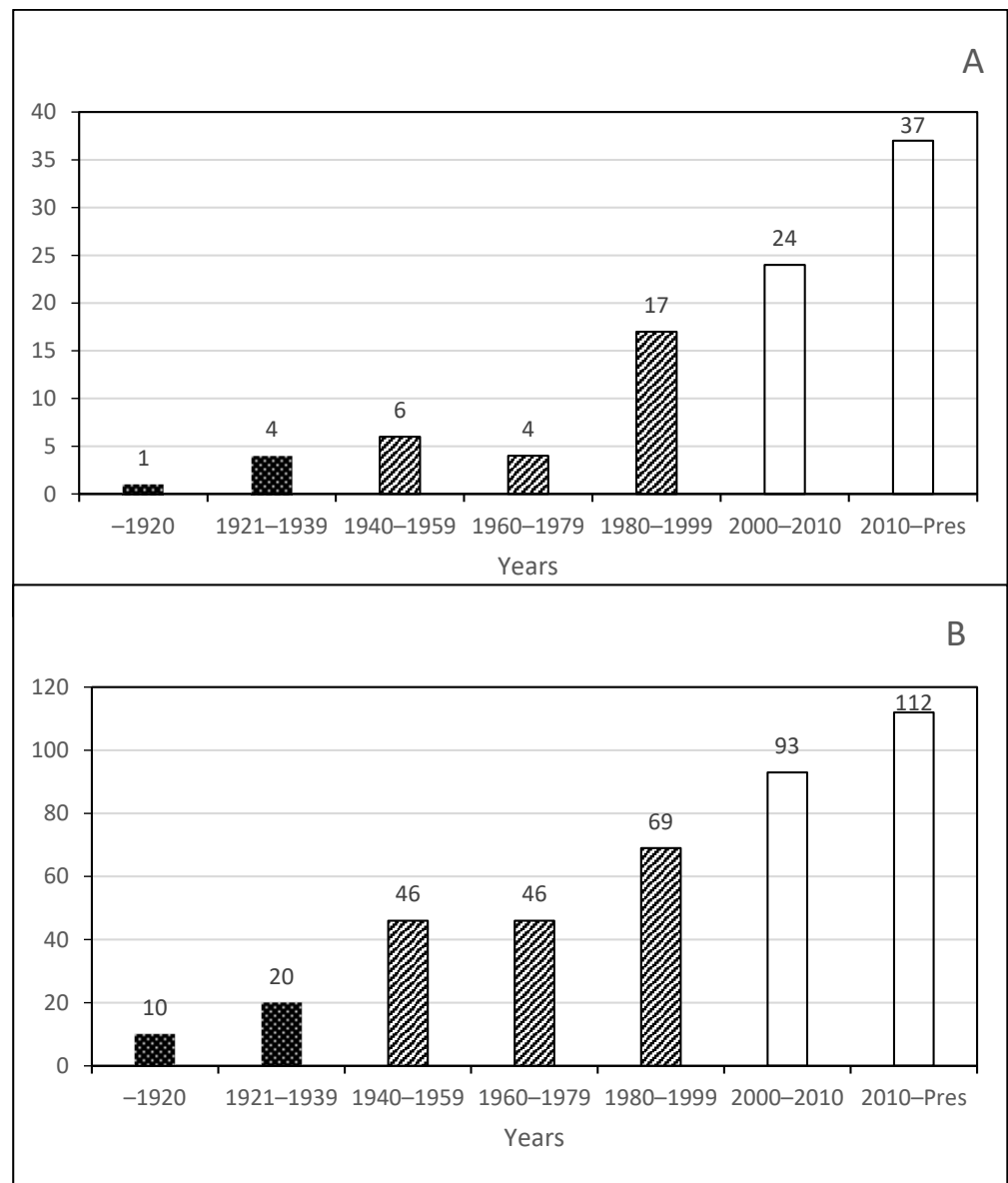
Juday [56] recorded 14 species from three locations near Mexico City about the cladoceran studies in this phase. This period ended with the creation of a hydrobiological station in Lake Pátzcuaro, Michoacán, in 1938, thus promoting additional studies like those by Brehm [57], Osorio Tafall [58], and Uéno [46].



**Figure 4.** Historical progress of studies on Large Branchiopoda: Anostraca + Notostraca + Cyclestherida + Laevicaudata + Spinicaudata in Mexico. (A) Publications. (B) Cumulative species number: ■ Phase 1. Early studies by foreign visitors; ▨ Phase 2. First publications of Mexican researchers alone or with specialists from around the world; □ Phase 3. Mature phase and discovery of unknown diversity.

### 3.1.5. Large Branchiopods

The scientific publications on large Mexican branchiopods started early in this phase, in 1860, with the description of a clam shrimp, *Cyzicus mexicanus* [59]. Three other notostracans were subsequently described by Packard [59]. Richard [60], Daday [61,62], and Linder [63] reported or described other clam shrimps and branchiopods from different localities.



**Figure 5.** Historical progress of studies on Mexican Copepoda (Cyclopoida + Calanoida). (A) Number of publications (B) Cumulative number of species ■ Phase 1. Early studies by foreign visitors; ▨ Phase 2. The first generation of Mexican copepodologists, mainly in the last two decades (1980–1999); □ Phase 3. Mature phase with integrative taxonomy and the discovery of exotic species.

### 3.1.6. Copepods

Regarding copepods, Pearse [64] described the first copepod from Mexico, soon synonymized by Marsh [65] as *Mastigodiatomus albuquerquensis*. Subsequently, Juday [56] provided a list of zooplankton crustaceans from two localities around Mexico City, and Marsh [66] described *Diatomus mexicanus*, which was later described in detail [67]. Further taxonomic work on Mexican freshwater copepods was provided by Friedrich Kiefer [68], who worked on several samples from Mexico that were sent to the Karlsruhe Natural History Museum. He described diaptomid and cyclopoid species from different areas of Mexico. Additional accounts on copepods were published by Brehm [57] and Uéno [46]. Wilson [69] and Pearse and Wilson [70] reported on the Yucatan copepods and cladocerans.

The Spanish researcher B. Osorio Tafall was active as a scientist in the 1940s. He described several species that are now deemed valid [71–73].

### 3.2. Phase 2: Towards the Formation of Mexican Limnologists (1950s to the End of XX Century)

This second phase includes works conducted by foreign scientists, closely collaborating with Mexican researchers in most cases.

#### 3.2.1. Protists

During this period, most of the protozooplankton studies in Mexico were developed under an alpha-taxonomy perspective [74]. Most Neotropical species were recorded from artificial lakes [75,76]. Examples of this phase include some contributions that were made on species from Mexico City by López-Ochoterena [77], Pérez-Reyes and Salas-Gómez [78], and Lugo-Vázquez [79].

#### 3.2.2. Rotifers

About the Rotifera, this phase started at the end of the 1980s and early 1990s, with scattered contributions [80–85]. Subsequent taxonomical studies allowed important advances in the knowledge of the Mexican rotifer diversity [86–93]. At the end of this period, Sarma [94] compiled the rotifer species recorded in Mexico at that time, an account including 283 rotifer species: Monogononta (275) and Bdelloidea (8). Two years later, Elías-Gutiérrez et al. [95] analyzed the known diversity of the Mexican freshwater zooplankton (rotifers, cladocerans, and copepods) and emphasized that the presumed cosmopolitanism of these groups should be questioned because of the discovery of species complexes with restricted geographical distributions and strong morphological affinities.

#### 3.2.3. Water Mites

The taxonomic study of water mites continued during this 2nd phase: Cook [96,97] described new Mexican species and published a book on neotropical water mites reporting 177 species for Mexico and describing 139, thus significantly increasing the country listings. Vidrine [98] and Otero-Colina [99] added more new species. In 1978, C. Cramer-Hemkes launched a large project about the taxonomy, ecology, and distribution of Mexican water mites; many species descriptions were produced from this initiative [100–109].

#### 3.2.4. Cladocerans

During this period, only three formal studies on cladocerans were published [110–112], with a few sporadic surveys remaining as gray literature.

The end of this period is characterized by the work of a rising generation of four Mexican researchers and three Indians that moved to Mexico (i.e., Roberto Rico-Martínez, Marcelo Silva-Briano, Manuel Elías-Gutiérrez, Jorge Ciros-Pérez, Singaraju Sri Subrahmanya Sarma, Nandini Sarma, Gopal Murugan), all of them influenced by a series of courses organized by Prof. Henri J. Dumont (University of Ghent, Belgium). The course (1991–1998) trained 85 students (Dumont, in litt.), and two Mexicans continued and defended their PhDs there.

So, after the 1990s, the first studies on cladocerans by this new generation of Mexican researchers started to yield publications [113–116]. In this phase, Hebert and Finston [117] discovered two new species of *Daphnia* here. The only known blind cladoceran of the Americas, *Spinalona anophthalmia*, was described by Ciros-Pérez and Elías-Gutiérrez [118]. Other new species were described during this period [119–121].

#### 3.2.5. Large Branchiopods

During the second phase, revisions of large branchiopods were conducted mainly by foreign researchers [122–125]. Additional works on the genus *Artemia* were published by Bowen [126], Abreu-Grobois, and Beardmore [127,128]. Spicer [129] described a new *Streptocephalus* from Veracruz. Martin [130] documented *Eulimnadia belki* on Cozumel Island. *Streptocephalus woottoni*, endemic to northern Baja California and southern California, USA, was described by Eng et al. [131] and is currently considered an endangered species.

Mexican researchers' first descriptions of branchiopods started during this phase with contributions by Maeda-Martínez [132–136], a former student of H. Dumont. Fugate [137] described *B. sandiegonensis*, endemic to northern Baja California (Norte) and southern California, USA.

### 3.2.6. Copepods

During the second phase, copepods were studied mainly by foreign researchers such as Comita [138], Lindberg [139], and Brehm [110], who described *Mastigodiptomus montezumae*. Fernando and Smith [140] compiled the available data on the copepods from Mexico and Central America.

In the second half of this period, Suárez-Morales et al. [80] published a brief study of the plankton of a Mexican tropical lake. Subsequently, the freshwater copepod research in Mexico was strongly encouraged by the taxonomic contributions of J.W. Reid, who provided the first comprehensive list and records of Neotropical free-living copepods [141,142]. She promoted many other taxonomic within this period [143–149].

### 3.3. Phase 3: The Mature Phase of Zooplankton Studies (21st Century)

The third phase started in the 21st century and is currently in progress when modern diversity approaches are consistently applied together with studies based on integrative taxonomy sensu Dayrat [150], as well as new paradigms and hypotheses derived from more detailed morphological studies and DNA sequencing. This phase is a mature stage of zooplankton studies in Mexico, with modern descriptions led by Mexican researchers and the training of a new generation of taxonomists, like M. Gutiérrez-Aguirre, A. Cervantes Martínez, N.F. Mercado-Salas, and A. E. García-Morales. All contribute significantly to the current knowledge of the Mexican freshwater zooplankton.

#### 3.3.1. Protists

The current and most complete list of protists includes a compilation of 197 families, 445 genera, and 1170 species of heterotrophic flagellates and ciliates recorded after more than one century of studies in Mexico [151]. Previously, 238 species of planktonic tintinnid ciliates have been recorded, chiefly in marine and brackish environments [74].

Recently, two main, partially opposed concepts to explain the biogeographical patterns of protists were proposed [152,153], one stating a continuous, ubiquitous distribution of all protists and the other declaring that 30% of their diversity is endemic.

With the aid of new sequencing technologies, a high microbial eukaryotic alpha diversity has been discovered in aquatic and terrestrial habitats. For example, the 18S gene diversity in freshwater environments has been proven to be much higher than the diversity based solely on morphological evidence [154]. Likewise, all phylogeny-oriented metabarcoding studies have discovered high eukaryotic diversity in terrestrial and aquatic environments. Thus, it is now accepted that cryptic speciation is a pervasive pattern among protist species [155]. The debate continues because neither the introduction of ecological, ethological, or molecular aspects revealed a general pattern on the species level. However, some functional diversity patterns were found using the superior categories [5,7,156,157].

Recent studies on the alpha taxonomy of protists continued in Mexico [76,158–161], and it was expanded to other areas of the country [162–164]; however, the protozooplankton biodiversity from the Mayan aquifer in Yucatan Peninsula and other interesting aquatic systems remain poorly understood.

#### 3.3.2. Rotifers

During this recent period, the studies involving rotifers became more intense, encompassing different approaches such as diversity, ecology (e.g., space-time variations, abundance, etc.), and molecular. On the diversity view, Silva-Briano et al. [165] described *Brachionus araceliae*. Later, García-Morales and Elías-Gutiérrez [166] published the first regional comprehensive list involving rotifer DNA analyses. After this study, the species

descriptions included DNA data, thus setting a new standard [167,168]. These are among the few known rotifer species described based on integrative taxonomy worldwide.

Recent studies dealing with the diversity, seasonal variation, and abundance of zooplankton, including rotifer species listings, are in work by Sarma et al. [169]. The current list of rotifer species from Mexico includes 405 species of freshwater and brackish rotifers belonging to 27 families and 75 genera. (Supplementary Table S1).

### 3.3.3. Water Mites

In this phase, many new water mite taxa were described by Cramer-Hemkes [170], Marin-Hernández and Cramer-Hemkes [171], and Ramírez-Sánchez and Rivas [172]. Currently, 258 species of water mites are recorded from Mexico, comprising 62 genera; Hygrobratoidea is the superfamily with the highest number of genera and species in Mexico, especially *Koenikea*, *Atractides*, and *Limnesia*, followed by the superfamily Arrenuroidea with the highly diverse genus *Arrenurus*.

The analysis of the genetic information and the use of new sampling methods has allowed a better overview of the water mite diversity in different microhabitats, as in Montes-Ortiz and Elías-Gutiérrez [173,174], Montes-Ortiz et al. [175,176], and Elías-Gutiérrez and Montes-Ortiz [177].

### 3.3.4. Cladocerans

During this third phase, the studies on cladocerans continued, in some cases in collaboration with foreign specialists, describing new taxa, like the works by Elías-Gutiérrez and Smirnov [178], Cervantes-Martínez et al. [179], Kotov et al. [180–182], and also Elías-Gutiérrez et al. [183,184], and Garfias-Espejo and Elías-Gutiérrez [185]. In addition, Elías-Gutiérrez et al. [20] published the first large scale-study in the world involving Cladocera (61 species), and Copepoda (21 species), together with DNA sequences of the mitochondrial gene for the Cytochrome Oxidase (COI), with the key collaboration of Paul Hebert (Guelph University, Canada).

After this study, the first descriptions, including integrative taxonomy, started, being *Leberis chihuahuensis* from northern Mexico, the first cladoceran described worldwide with this method [186]. Other species described with this approach include *Scapholeberis duranguensis* by Quiroz-Vázquez and Elías-Gutiérrez [187]. Additional studies involving Mexican species of cladocerans and DNA barcodes were by Elías-Gutiérrez and Montes-Ortiz [177], Martínez-Caballero et al. [188], Montes-Ortiz and Elías-Gutiérrez [173], and Montoliu-Elena et al. [189].

### 3.3.5. Large Branchiopods

During this phase, Mexican researchers continued with descriptions of new large branchiopods, either in collaboration with foreign colleagues or alone. Maeda-Martínez et al. [21–23] published a review of the knowledge of these groups. The brine shrimp *Artemia* has been recorded in 11 Mexican states [21]. Data from genetics [190,191] and mtDNA (16S and COI) [192] support the discovery of six populations reported as *Artemia franciscana*. The rest of the population remains as *Artemia* sp. due to the lack of proper systematic characterization [21]. Based on mitogenomic analyses, Sainz-Escudero et al. [193] reported a relatively significant divergence between *Artemia* populations from Mexico and San Francisco Bay, USA (the type locality of *A. franciscana*). They suggested nuclear DNA analyses to reach a systematic conclusion. These authors proposed *Artemia monica* as the valid name for the New World *A. franciscana* group. Maeda-Martínez et al. [22] cited as *Triops* sp., all known Mexican tadpole shrimp populations and revised the existence of biochemical [194], molecular (12S mtDNA) [195], histological [196], reproductive [197], and morphological [194] differences. Studies show the existence of several species, and therefore a systematic reevaluation is needed. New species in this period include Obregón-Barboza et al. [198] and Maeda-Martínez et al. [199]. A review of *Branchinecta* species was published by Obregón-Barboza et al. [200], including the first record of *B. gigas* Lynch,



1937 for Mexico. COI data revealed two distinct clades within *B. lindahli*, but cryptic taxa are not present in the populations of the studied taxon [201].

Obregón-Barboza et al. [202] reviewed the Mexican populations of the fairy shrimps *Thamnocephalus mexicanus* and *T. platyurus*, studied their morphology, and 16S and COI haplotypes, thus confirming two separate biological lineages at the species level.

### 3.3.6. Copepods

During this period, the taxonomic work on copepods increased notably, with many descriptions and new records of species. DNA data have also been integrated with other taxonomic, ecologic, and biogeographical data.

Currently, over 30 species of the copepod order Calanoida are known in Mexico. Some genera are represented by one species (Supplementary Table S1). The diaptomid genus *Mastigodiaptomus* is the most diverse (13 species) (Supplementary Table S1); some new species of this genus have been described recently using integrative taxonomy [31,203]. *Mastigodiaptomus ha* is the second diaptomid species found on a Caribbean Island. *Leptodiaptomus* is the second most diverse diaptomid genus in Mexico (7 species), mainly recorded in the Nearctic region of this country (Supplementary Table S1). However, it is suspected that it comprises other cryptic species. *Leptodiaptomus garciai* has been recorded in the unique saline Lake Alchichica, a crater lake, by Montiel-Martínez et al. [71], in the Mexican Transition Zone (MTZ) between the Nearctic and Neotropical regions [204,205]. Several other species of this genus are known from central and western Mexico [206].

Cyclopidae can inhabit inland permanent and ephemeral freshwater systems and even high-altitude ponds or lakes. This family is the most successful and widespread group of free-living freshwater copepods. It includes over 60 genera and a record of more than 800 species worldwide [29,207]. The most updated information for Mexico includes 82 cyclopid species with members of three subfamilies: Halicyclopinae, with five species in two genera considered as endemic for the Yucatan Peninsula [208,209], Cyclopinae with 46 species in 11 genera, and Eucyclopinae with 31 species in six genera (Supplementary Table S1). The latter two subfamilies are the most widespread in Mexico, with endemic, introduced, and exotic species [206,210,211]. In this period, Suárez-Morales and Walsh [212] described two new species of *Eucyclops*, and Mercado-Salas et al. [213] described six new species of the same genus from different parts of Mexico, proposing new taxonomic characters. Some cyclopids can colonize bromeliads in the Neotropical region [214,215].

Members of the order Harpacticoida mainly inhabit the benthic habitats of the water systems. However, they can be found in the limnetic region, associated with invertebrates and vertebrates, and, recently, in bromeliads as well [214].

Harpacticoid copepods remain largely understudied in Mexico compared to the orders Calanoida and Cyclopoida; there are only a few species effectively recorded for Mexican freshwaters, like *Cletocamptus sinaloensis* by Gómez et al. [216], *Eduardonitocrella mexicana* by Suárez-Morales and Iliffe [217], and *Cletocamptus gomezi* by Suárez-Morales et al. [218]. In the last 20 years, different checklists of copepods that comprised harpacticoids allowed a better understanding of their distributional patterns and diversity [27,144]. Recently, Gómez and Morales-Serna [24] updated the inventory of this order for Mexico, including records of marine, brackish, saline, and freshwater species to assemble the current list of 21 known species for freshwater systems (Supplementary Table S1).

There is some evidence that several Mexican species exhibit different distributional patterns, i.e., *Cletocamptus sinaloensis* have been recorded in lagoons and estuarine systems of Sinaloa State [216], whereas *C. gomezi* is endemic to a high-altitude lake [219].

The increase of the knowledge of freshwater zooplankton during this last period, not only in Mexico but the rest of the world, allowed the detection of exotic or invasive species, such as the *Daphnia* (*Ctenodaphnia*) *lumholtzi*, that previously invaded the East of the USA and Canada [20]. The following section will discuss this species and other exotic or invasive zooplankters.

### 3.4. Exotic/Invasive Zooplankton Species in Mexico

This section deals with a topic that could not be properly or consistently treated in the previous phases. Our current knowledge of the Mexican zooplankton diversity has allowed us to consider an overview of this aspect. The study of the effect of exotic species on local diversity is essential, as induced changes in native communities could be of great relevance.

An account of documented exotic zooplankters in Mexico includes the cladocerans as *Daphnia curvirostris*, first reported by Nandini et al. [220], *Daphnia magna* introduced for ecotoxicological studies [221], and *Daphnia (Ctenodaphnia) lumholtzi* [20,222]. *Moina macrocopa* probably was introduced in a net by a researcher of Amphibia [189]. As for copepods, Suárez-Morales and Arroyo-Bustos [223] recorded *Skistodiaptomus pallidus* as an intra-continental exotic species in Sinaloa, north of Mexico. The Euro-Asian cyclopoid *Thermocyclops crassus* is also an introduced species [210], as are two other species of *Mesocyclops* (*M. pehpeiensis* and *M. thermocycloides*) [224–226].

### 3.5. Conservation of the Zooplankton

Aside from the large branchiopods, little is said about the conservation of endemic or endangered species [227]. Several species of Mexican zooplankton are likely to disappear together with their habitats, like the recently described rotifer *Brachionus paranguensis*, whose type locality is drying [167].

From the original descriptions, and after new fieldwork, *Spinalona anophthalma*, *Macrothrix marthae*, and *Moina hutchinsoni* have yet to be found again [118,178,228]. As for copepods, we did find *Leptodiaptomus mexicanus* once, but not *L. dodsoni* and *Mastigodiaptomus maya*. Also, several copepod species are endemic to the Yucatan Peninsula [229]. However, a common, widespread species, *Mastigodiaptomus montezumae*, is the only copepod in the IUCN red list of endangered species.

Conservation problems are also related to species and habitats threatened by human impact, including the fragile and diverse hypogean copepod fauna of the Yucatan Peninsula, currently threatened by the unregulated construction of a railway with unforeseen damages to the freshwater fauna.

## 4. Final Remarks and Conclusions

As we intended to demonstrate, there has been a progressive maturation of the zooplankton studies in Mexico, with increasing participation and leadership of Mexican researchers. In the last 40 years, the number of species known from this country has increased by 58% of protists, 67% rotifers, 71% cladocerans, 39% large branchiopods, and 59% copepods. Nevertheless, being a megadiverse country, we estimate that the species inventory of the Mexican zooplankton still needs to be completed.

Recent studies focused on some of Mexico's most important groups of freshwater biodiversity have been considered a world example by combining integrative taxonomy, DNA analyses, and their complete access to public databases [230]. However, the large territorial extension, difficult access to the study sites, progressive lack of taxonomists, reduced funds for science, and unsafe traveling conditions in different regions of the country, are the main risk factors to continuing expanding studies on Mexican zooplankton.

The group of current zooplankton taxonomists is training a third generation of active taxonomists and ecologists of zooplankton, covering different groups such as cladocerans [189], copepods [206,231], as well as additional taxa like the ostracods [232] and water mites [176].

This third generation will be able to continue expanding our knowledge of the zooplankton taxa in Mexico and help in the conservation of the freshwater ecosystems and their biota.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15050858/s1>, Table S1: Species richness of freshwater Protists, Rotifera, Cladocera and Copepoda recorded in Mexico (Aladro-Lubel et al., 2007, 2009; Albores-Celorio, 1969; Arevalo-Navarro, 1999; Bravo-Hollis, 1922, 1924; Cabral-Dorado, 2006; Elliot and Hayes, 1955; Figueroa-Torres and Moreno-Ruiz, 2003; Flores-Flores, 2012; Flores-Orta, 1983; González-Labastida, 1995; Hernández-Anaya, 1981; Kusel-Fetzmann, 1973; López-Ochoterena, 1962, 1964, 1965; López-Ochoterena and Barajas, 1964; López-Ríos, 1972; Lugo-Vázquez, 1993; Macek et al., 2022; Madrazo-Garibay and López-Ochoterena, 1973, 1985, 1986, 1990; Marrón-Aguilar and López-Ochoterena, 1969; Méndez-Sánchez, 2014, 2017; Méndez-Sánchez et al., 2018; Mendoza-González, 1973; Moreno-Ruiz, 1985; Nomdedeu and López-Ochoterena, 1988; Osorio-Tafall, 1941, 1942, 1944; Pérez-Reyes and Salas Gómez, 1960, 1961; Peštová et al., 2008; Ponce-Márquez et al., 2019; Potekhin and Mayén-Estrada, 2020; Ramírez de Guerrero, 1970; Saadi-González, 2018; Sámano and Sokoloff, 1931; Sánchez-Rodríguez et al., 2011; Sigala-Regalado, 2008; Sokoloff, 1930a, b, 1931, 1936; Tiscareño-Silva, 2008; Rico-Martínez & Silva-Briano; 1993; Dussart & Defaye 1995; Sarma et al., 1996; Suárez-Morales et al., 1996; Sarma & Elías-Gutiérrez, 1997; Sarma & Elías-Gutiérrez, 1998; Suárez-Morales & Reid, 1998; Elías-Gutiérrez et al., 1999; Sarma, 1999; Sarma & Elías-Gutiérrez, 1999a; Sarma & Elías-Gutiérrez, 1999b; Suárez-Morales et al., 2000; Elías-Gutiérrez et al., 2001; Suárez-Morales & Gutiérrez-Aguirre, 2001; Elías-Gutiérrez & Suárez-Morales, 2003; Garfías-Espejo & Elías-Gutiérrez, 2003; Suárez-Morales & Elías-Gutiérrez 2003; Suárez-Morales & Reid 2003; Suárez-Morales, 2004; García-Morales & Elías-Gutiérrez, 2004; Sinev et al., 2005; Suárez-Morales & Iliffe, 2005; Elías-Gutiérrez et al., 2006; García-Morales & Elías-Gutiérrez, 2007; Segers, 2007; Silva-Briano et al. 2007; Elías-Gutiérrez et al., 2008; Elías-Gutiérrez & Valdéz-Moreno, 2008; Mercado-Salas et al., 2009; Mercado-Salas & Suárez-Morales, 2009; Nandini et al., 2009; Suárez-Morales & Walsh, 2009; Suárez-Morales et al., 2010; Mercado-Salas & Suárez-Morales 2011; Sinev & Silva-Briano, 2012; García-Morales & Elías-Gutiérrez, 2013; Gutiérrez-Aguirre et al., 2013; Gutiérrez-Aguirre & Cervantes-Martínez, 2013; Mercado-Salas & Álvarez-Silva, 2013; Mercado-Salas et al., 2013; Sinev & Zawiska, 2013; Mercado-Salas & Suárez-Morales 2014; Gutiérrez-Aguirre et al., 2014; Mercado-Salas et al., 2015; Gutiérrez-Aguirre & Cervantes-Martínez, 2016; Mercado-Salas et al., 2018; Elías-Gutiérrez et al., 2019; Gutiérrez-Aguirre et al., 2020; Suárez-Morales et al., 2020; Sarma et al., 2021).

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