

The distribution of species of the genus *Thermocyclops* (Copepoda, Cyclopoida) in the western hemisphere, with description of *T. parvus*, new species

Janet W. Reid

Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

Received 30 September 1987; in revised form 18 February 1988; accepted 21 March 1988

Key words: *Thermocyclops*, Copepoda Cyclopoida, neotropical limnology, biogeography, ecology

Abstract

The distribution and ecology of species of cyclopoid copepods of the genus *Thermocyclops* in the western hemisphere are reviewed. These are: *Thermocyclops brehmi* (Kiefer), *T. crassus* (Fischer), *T. decipiens* (Kiefer), *T. hastatus antillensis* Herbst, *T. inversus* (Kiefer), *T. minutus* (Lowndes), *T. tenuis* (Marsh), *T. tenuis longifurcatus* Pesce, and *T. parvus*, new species. *T. brehmi* is known from microlimnotopes in a restricted region in northern Argentina and Uruguay, while *T. crassus* has been reliably recorded only from small ponds in Costa Rica. *T. decipiens*, with many records from northern Argentina to Costa Rica, Guatemala and the Antilles, is often numerous in mesotrophic and eutrophic lakes and reservoirs. The range of *T. minutus* extends over tropical and subtropical lowlands of South America from northern Argentina to Venezuela; this species prefers oligotrophic and mesotrophic conditions in larger lakes. *T. inversus* may prefer mildly carbonate waters and inhabits large and small reservoirs, natural lakes, ponds, wells and caves from northeastern Brazil to Mexico and the Antilles. *T. tenuis* ranges from northern Argentina to the Antilles and the southern United States, inhabiting large and small, natural and artificial bodies of water. *T. tenuis longifurcatus* is known only from two wells on Bonaire, *T. hastatus antillensis* from a well on the island of Guadeloupe, and *T. parvus* only from plankton samples from the Florida Everglades. Knowledge of population dynamics, feeding and reproductive biology of several planktonic species is reviewed.

Introduction

More than 51 species and subspecies have been distinguished within the cyclopoid copepod genus *Thermocyclops* Kiefer, 1927. Herbst (1986) has recently reviewed world records, compared morphology of several species, and furnished a key to females. Although a few species of *Thermocyclops* occur in temperate Eurasia, most inhabit the tropical belt: Africa south of the Sahara, Australia and

tropical and subtropical regions of Asia and the Americas. Several species, such as *T. crassus* (= *T. hyalinus*) and *T. decipiens* are often the dominant crustacean zooplankters in large mesotrophic and eutrophic lakes and reservoirs; therefore an understanding of their geographical and ecological distribution is of particular significance to limnologists. Nevertheless, such studies are frequently impeded by taxonomic confusion among closely related species. Errors of identification

sometimes have been corrected in the literature (Burgis, 1970); many have not. The need exists for reviews of species records, so that the ranges, habitats and ecological preferences of individual species can be accurately characterized.

Nine species or subspecies of *Thermocyclops* are now known to occur in the western hemisphere; of these, seven occur primarily as plankters: *Thermocyclops brehmi* (Kiefer, 1927), *T. crassus* (Fischer, 1853), *T. decipiens* (Kiefer, 1929), *T. inversus* (Kiefer, 1936), *T. minutus* (Lowndes, 1934), *T. tenuis* (Marsh, 1910), and *T. parvus*, new species. The remaining two species have been described from groundwater habitats: *T. tenuis longifurcatus* Pesce (1985) from two wells in Bonaire, and *T. hastatus antillensis* Herbst (1986) from a well on Guadeloupe (Fig. 17). An additional species, *T. orghidani* was described by Pleša (1981) from several caves in Cuba. Unfortunately, Pleša's description is seriously incomplete and may refer to a species of *Mesocyclops* (Herbst, 1986). The groundwater species are not treated further in this article.

The discrimination of most species of *Thermocyclops* (by some authors still treated as a subgenus of *Mesocyclops*) is based on a series of microcharacters which until recently have not been well-defined in the literature generally available to the non-specialist. Compounding the problem has been the lack of identification keys and comprehensive species lists for neotropical aquatic invertebrate fauna, a lacuna only recently begun to be filled (for example Collado, Fernando & Sephton, 1984; Dussart *et al.*, 1984; Hurlbert, 1978; Hurlbert & Villalobos-Figueroa, 1982; Hurlbert *et al.*, 1981; Reid, 1985; Smith & Fernando, 1978, 1980). In many cases, workers in neotropical areas have perforce relied on keys to European and North American faunas, resulting in 'a literature that contains innumerable gross mistakes and often cannot be trusted' (Dumont & Tundisi, 1984).

Records of *Thermocyclops* obtained from personal collections as well as additional information and specimens made available to me by colleagues are summarized here, in order to correct numerous erroneous records and to collate present

knowledge of the distributions and preferred habitats of the species of *Thermocyclops* in the western hemisphere. A new species is described.

Thermocyclops parvus, new species

Material. – ♀ holotype, United States National Museum – USNM 234135; ♂ allotype, USNM 234136; 1♂ paratype, USNM 234137, all from undated sample; 2♀ 2♂ paratypes, Site 06C, April 1986, USNM 234138; 16♀ 1♂ paratypes, Site 23, May 1986, USNM 234139; other paratype material in collections of Everglades National Park. All from Shark River Slough, Everglades National Park, Florida, USA; undated sample from *Eleocharis* sp. marshes, northeast section of slough; Site 06C at 25° 37.2' N 80° 43.9' W; Site 23 at 25° 40.0' N 80° 36.9' W. Coll. R. Conrow.

Female. – Length of holotype 480 µm; lengths of 10 paratypes 450–490 µm. Prosoma (Fig. 1) oval, much broader than urosome; sides of fourth prosomite rounded, expanded posteriorly, reaching middle of fifth prosomite; fifth prosomite lacking ornamentation. Genital segment (Figs. 1, 2) about 1.3 X longer than broad. Seminal receptacle (Figs. 2, 2a) with narrow, posteriorly recurved lateral arms and almost equally narrow posterior extension, and with broad lateral cuticular frame. Posterior margin of anal somite with fine spinules; anal operculum convex. Caudal rami 2.5 X longer than broad; measurements of caudal setae of holotype as follows: lateral 17, dorsal 35, outermost to innermost terminal 32, 112, 135, 43 µm. Lateral seta plumose, or in some specimens with 1 setule as illustrated. Outermost terminal caudal seta stout, more than 3 X width of innermost terminal seta. Next innermost terminal caudal seta with tip bent anteriorly.

Antennule (Fig. 3) of 17 articles, extending past posterior margin of first prosomite; article 12 with slender esthetasc. Article 1 of antenna (Fig. 4) with only 2 setae and lacking ornamentation on surface; article 3 with 4 setae. Remaining mouthparts as in Figs. 5–8.

Legs 1–4 (Figs. 9–12) each with rami of 3 articles. Spine formula 2,3,3,3; legs 2 and 3 with

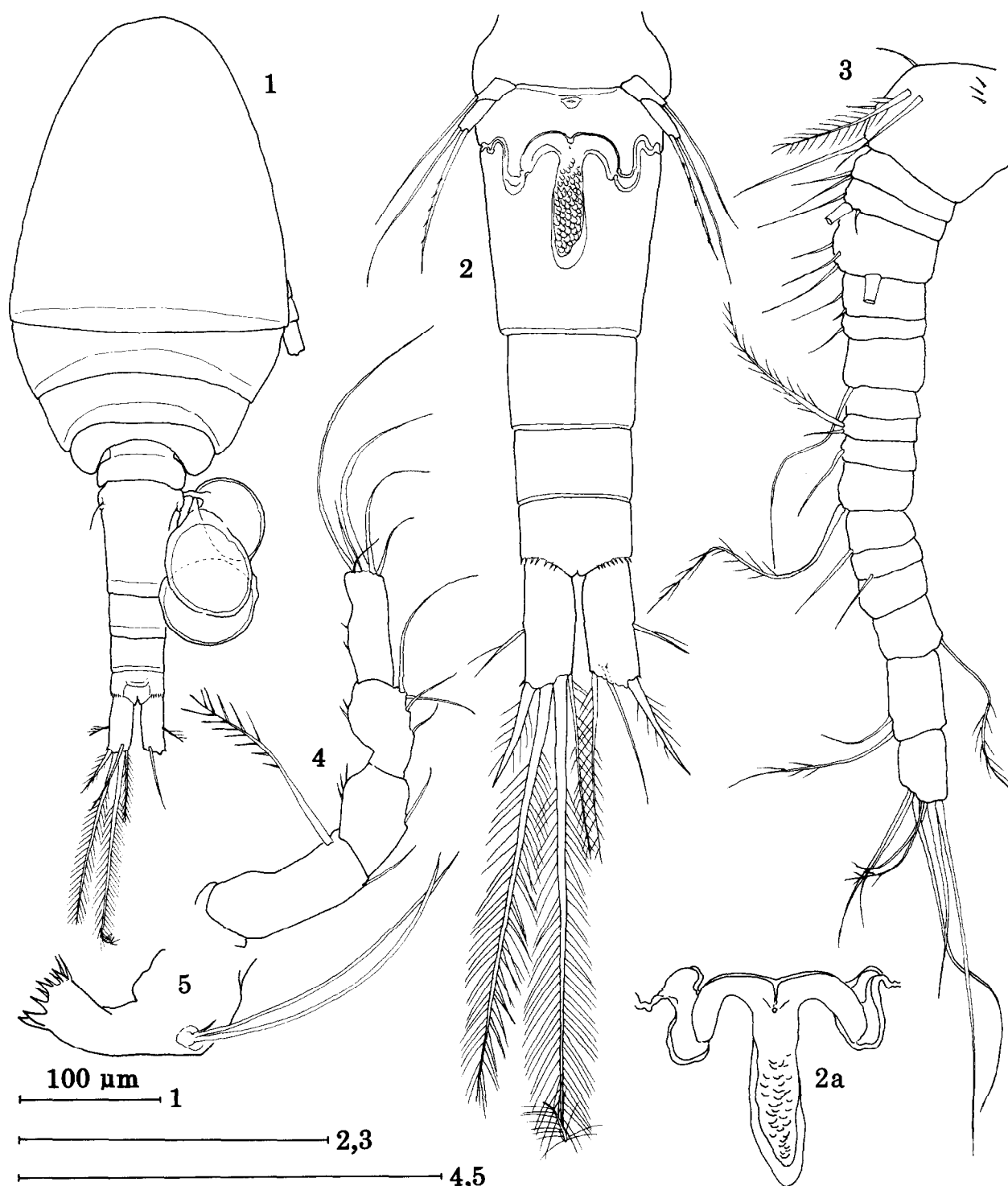


Fig. 1–5. *Thermocyclops parvus*, new species, female: 1, habitus; 2, urosome, ventral; 2a, seminal receptacle of a second specimen, slightly enlarged; 3, antennule; 4, antenna; 5, mandible.

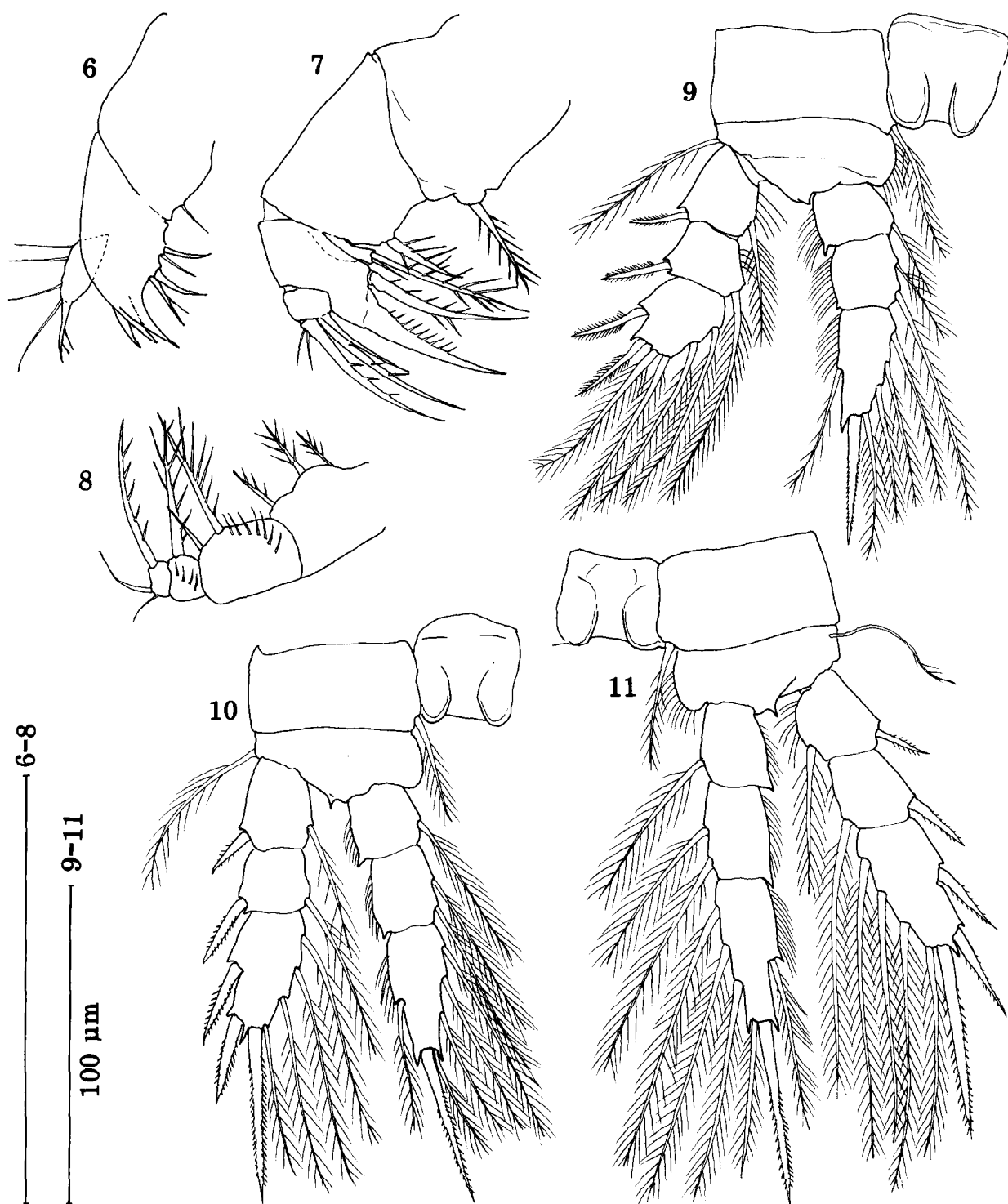


Fig. 6-11. *Thermocyclops parvus*, new species, female: 6, maxillule; 7, maxilla; 8, maxilliped; 9, leg 1; 10, leg 2; 11, leg 3.

stouter exopodal spines, and with longer spines on exopod 3 than those of legs 1 and 4. Basipod of leg 1 lacking spine on inner distal margin. Connecting plate of basipod of leg 4 without ornamentation and with convex margin. Leg 4 endopod 3, length 31 μm , breadth 12 μm , thus about 2.6X longer than broad; lengths of outer and inner terminal spines 12 and 34 μm respectively.

Leg 5 (Fig. 2) normal for genus; outer terminal seta slightly longer than inner subterminal spine. Leg 6 (Fig. 1) inserted somewhat dorsally on genital segment, consisting of small prominence bearing single seta. Holotype and other egg-bearing females with 3 eggs each side.

Male. – Length of allotype 470 μm ; of paratypes 430–470 μm . Habitus, caudal rami and caudal setae (Fig. 14) much as female. Antennule (Fig. 15) geniculate, article 1 with 3 esthetascs and articles 4 and 9 each with 1 esthetasc; esthetasc of article 9 longer and broader than those of other articles. Mouthparts, swimming legs and leg 5 as in female, except terminal seta and subterminal spine of leg 5 (Fig. 16) subequal. Lengths of inner spine, middle and outer setae of leg 6 (Fig. 16) 17, 5 and 24 μm respectively; outer seta reaching past posterior margin of succeeding somite.

Etymology. – From the Latin for ‘small’, since this is one of the smallest known species of the genus.

Remarks. – Because of the shared characters of a straight, unornamented connecting plate of leg 4 basipod and an antennule of 17 articles, *Thermocyclops parvus* keys to *T. dalmaticus* Petkovski (1956) in the key of Herbst (1986). However, *T. parvus* differs from *T. dalmaticus* in having a relatively stouter caudal ramus, with thick outermost terminal seta; also, the genital segment of the female of *T. parvus* is relatively more slender and the forms of the seminal receptacles differ, that of *T. parvus* being slightly emarginate anteriorly while that of *T. dalmaticus* is convex. The longest caudal setae of *T. parvus* are curved anteriorly at the tips, while those of *T. dalmaticus* are straight. *T. parvus* differs from most congeners

in lacking a spine on the inner distal margin of the basipod of leg 1, as far as this character has been described.

The specimens of *T. parvus* were obtained in plankton samples from a freshwater slough in the Florida Everglades (Fig. 17). Water depths were 14–23 cm at Site 06 and 14–29 cm at Site 23 (R. Conrow, in litt.). In Everglades sloughs, conductance, dissolved oxygen, turbidity and other physical and chemical parameters are highly variable, both diurnally and seasonally; pH remains moderately basic at 7.0–8.5 (Loftus & Kushlan, 1987).

Distribution records

The following section includes distribution records for the planktonic species of *Thermocyclops* reported from the western hemisphere. Records listed as ‘confirmed and probable’ include those verified personally by the author, or else those for which some taxonomic information was given or the taxonomist named. Records classified as ‘possible’, which are in most cases older, in general are discussed following the listing. If a species was listed under an older classification (i.e. the genera *Cyclops* or *Mesocyclops*), that listing is given. Information regarding type of water body and ambient conditions, where available, has been included in summary form.

Thermocyclops crassus

The only confirmed record of this species in the western hemisphere is that of Collado, Defaye *et al.* (1984) from three small ponds in San José Province, Costa Rica (Fig. 17). B. H. Dussart, C. H. Fernando (in litt.) and co-workers (Collado, Fernando & Sephton, 1984) agree that most published records of *T. crassus* in South and Central America and the Caribbean region refer to *T. decipiens* (discussed below).

Thermocyclops tenuis

Confirmed and probable records:

Argentina:

- Ringuelet (1958a): Chaco, unnamed charcas in Makallé (27° 13' S, 59° 17' W); Santa Fé,

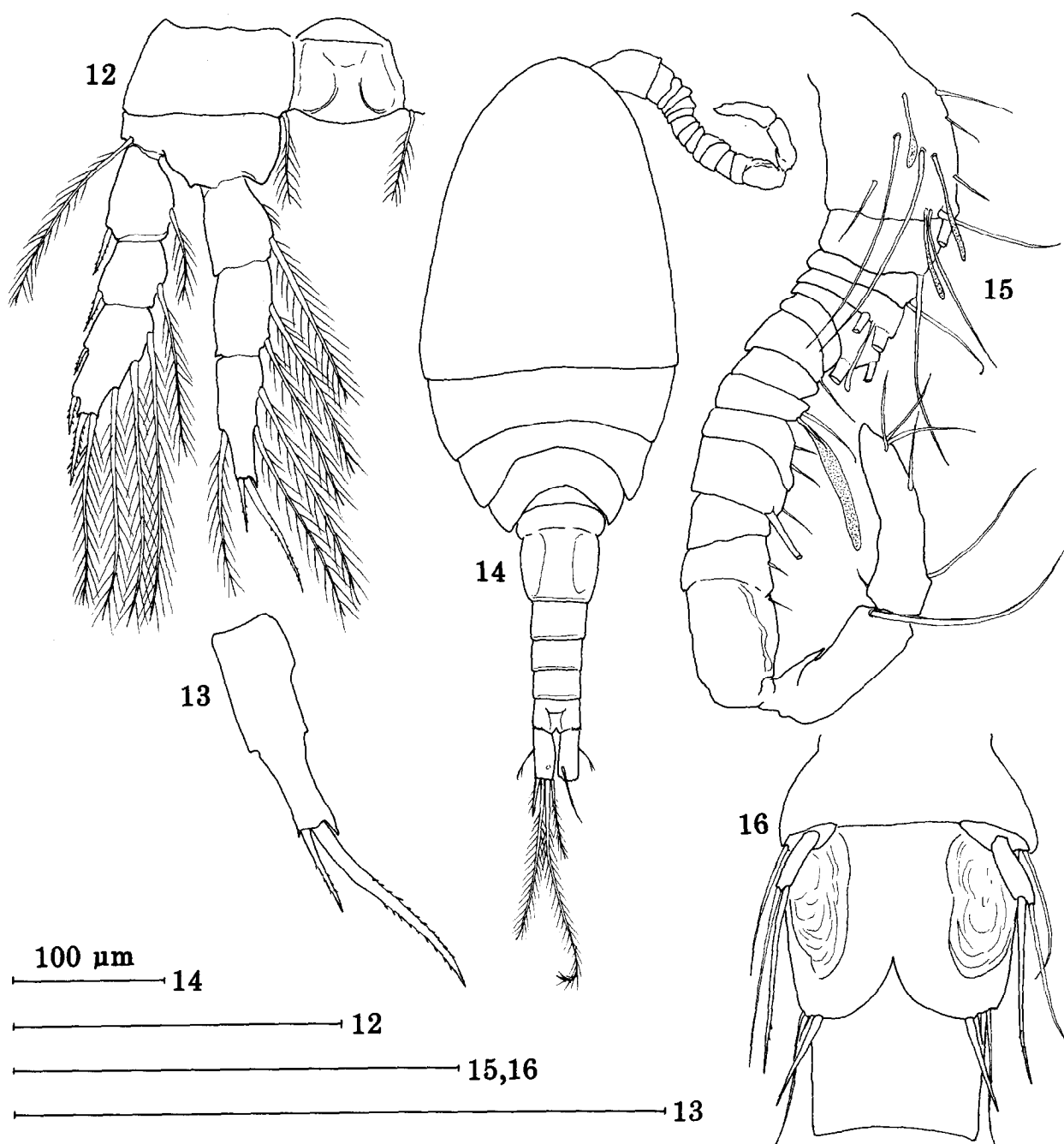


Fig. 12, 13. *Thermocyclops parvus*, new species, female: 12, leg 4; 13, leg 4, endopod 3. Figs. 14–16. *T. parvus*, male: 14, habitus; 15, antennule; 16, anterior urosomites, ventral.

charcas in Firmat ($33^{\circ} 27' S$, $61^{\circ} 29' W$), San Justo ($34^{\circ} 40' S$, $58^{\circ} 33' W$), Crespo ($32^{\circ} 02' S$, $60^{\circ} 19' W$) and Calchaquí ($29^{\circ} 54' S$, $60^{\circ} 18' W$).

Brazil:

- Kiefer (1936b), Schubart (1938): several unspecified locations, State of Pernambuco.
- Reid (unpublished): cowpond 17 km east of

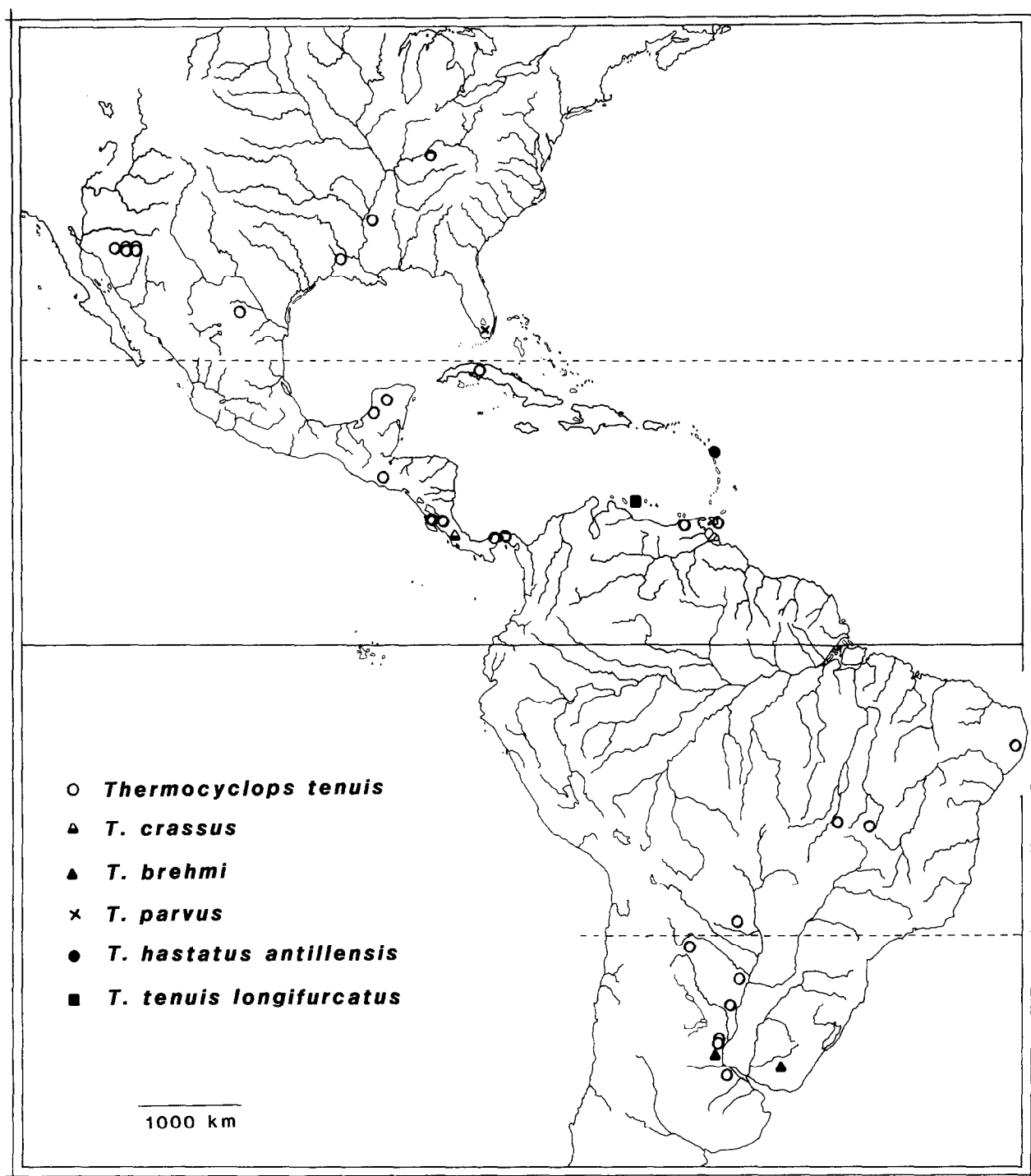


Fig. 17. Locations in the western hemisphere of confirmed and probable records of *Thermocyclops tenuis*, *T. tenuis longifurcatus*, *T. crassus*, *T. brehmi*, *T. hastatus antillensis* and *T. parvus*.

- city of Goiás Velho, State of Goiás, Amazon drainage basin, approximately 16° 00' S, 50° 02' W, 13 Jan 1980.
- Reid (unpublished): temporary puddle by Rio Cana Brava, State of Goiás, Amazon drainage basin, approximately 15° 00' S, 47° 04' W, 1 Dec 1983; depth 0–20 cm, temp. 29.8 °C, cond. 90 μ S cm⁻¹.
- Costa Rica:
- Collado, Defaye *et al.* (1984): small artificial pond at Residential los Arcos, Alejuela Province (10° 30' N, 84° 30' W); Nuñez *Tilapia* ponds, Guanacaste Province (10° 30' N, 85° 15' W).
 - Collado, Fernando & Sephton (1984): localities unspecified.
- Cuba:
- Smith & Fernando (1978, 1980): Habana Province, a lagoon near Havana.
 - Collado, Fernando & Sephton (1984): localities unspecified.
- Mexico:
- Rioja (1942): Laguna de San Felipe, Xochiltepec.
 - Cole (1966): cenotes, Yucatán; as *Mesocyclops tenuis*.
 - H. C. Yeatman (unpublished, in litt.): Cenote Bocchen, Campeche, 30 Oct 1974. Coll. J. Reddell.
 - Reid (unpublished): ephemeral pond, Municipio de Villa Aldama, Nuevo León, 2 Aug 1987. Coll. J. A. Zamudio V.
- Paraguay:
- Lowndes (1934): ponds and rain pools in Makthlawaiya and Nanahua; as *M. tenuis*.
- Trinidad:
- Collado, Fernando & Sephton (1984): localities unspecified.
- United States:
- Marsh (1910), original description, unspecified ponds in 'Calabresas' (possibly Calabasas – 31° 29' N, 110° 58' W), southern Arizona; as *Cyclops tenuis*.
 - Reed & McQuaid (1966): shallow pond in stream bed 16 km east of Leesville, Louisiana (31° 10' N, 93° 19' W); also a sinkhole pond near Louisville, Kentucky (H. C. Yeatman in litt. to Reed & McQuaid); as *M. tenuis*.
 - Harris (1978): 'taken once... during late summer... in a large oxbow lake near the Mississippi River in northwestern Mississippi'; as *M. tenuis*.
 - L. H. Carpelan & G. A. Cole (unpublished, in litt.): two 'tanks' (cowponds) near Portal, southeastern Arizona, and a tank and a roadside ditch near Animas, southwestern New Mexico; all in July and August 1969. (Copepods identified by G. Cole).
- Possible records:
- Argentina:
- Wierzejski (1892): Jujuy Province ('about under 24° S lat. '); as *Cyclops oithonoides*.
- El Salvador:
- Marsh (1931): Lake Ahuachapan (shallow) and Lakes Chalchuapa, Coatepeque and Guija (deep); as *C. tenuis*.
- Mexico:
- Wilson (1936) and Pearse (1938): Yucatán cenotes; as *M. tenuis*.
- Panama:
- Marsh (1913): Miraflores, pond by dump; Bolino Pond; savannas near Panama; Gatun Lake; Rio Trinidad; Agua Clara, Calabraras, Nindi, Camacho, Cocoli, Cambali and Gorgona Reservoirs (detailed records from Marsh's unpublished records in the Marsh Collection, Division of Crustacea, National Museum of Natural History); as *C. tenuis*.
 - Dodds (1926): Gatun and Miraflores Lakes, also four reservoirs and 36 ponds in the Canal Zone; as *C. tenuis*.
- Puerto Rico:
- Candelas & Candelas (1966): unspecified lakes; as *M. tenuis*.
- Venezuela:
- Margalef (1961): rarely in ephemeral ponds in northeastern Venezuela; as *T. brehmi*.
- Some of the records of Marsh from El Salvador (1931) and Panama (1913), and of Dodds (1926)

from Panama must be considered dubious (Reed & McQuaid, 1966); Kiefer (1931) thought that Marsh was probably dealing with several species, and Coker (1943) found *T. inversus*, but not *tenuis*, among some of Marsh's material. As Yeatman (1977) observed, Wilson's identification of Pearse's material from cenotes of Yucatán might refer either to *T. tenuis* or to *T. inversus*. The determinations of Candelas & Candelas (1966) of *M. tenuis* from Puerto Rico were likewise made before the presence in this area of other species of *Thermocyclops* was known. Margalef (1961) identified specimens from Venezuela as *T. brehmi*, but the species which he illustrated is most probably *T. tenuis*; E. Zoppi de Roa (in litt.) has never recorded *T. brehmi* in the Venezuelan fauna.

Ringuet (1958b, 1959, 1968) considered all three species of *Thermocyclops* (*T. tenuis*, *T. brehmi* and *T. minutus*) then known to occur in Argentina to be subtropical; all were found only in the northern provinces. J. C. Paggi (in litt.) agrees that this genus is not abundantly represented in the Argentine fauna (see record under *T. decipiens*). As regards the northern boundary of its distribution, *T. tenuis* seems to occur sporadically in the southern and central United States, but has been collected more regularly in Central and tropical South America east of the Andes, and in the Antilles (Fig. 17).

T. tenuis is exclusively an American species. The report of *Mesocyclops tenuis* in Pakistan by Mahoon & Zia (1985) is obviously an error, underscoring once more the dangers of relying on identification keys which were developed for another part of the world.

Thermocyclops brehmi

Confirmed records:

Argentina:

- Ringuelet (1958a): charca in Santa Fé de la Esquina.

Uruguay:

- Kiefer (1927): original description, locality unspecified.

Ringuet (1958b, 1959, 1968) considered *T. brehmi* a 'heliobiont', subtropical species, typi-

cal of microlimnotopes. Its distribution is the most restricted of the limnetic species (Fig. 17).

Thermocyclops decipiens

Confirmed records:

Argentina:

- Menu Marque (1982): Río Hondo reservoir, Santiago del Estero Province; pH 7.0, Secchi depth 0.33–0.37 m, conductivity $2.9 \times 10^2 \mu\text{S cm}^{-1}$.
- J. C. Paggi (in litt.): unnamed ox-bow (madrejón) lake near Madrejón Don Felipe, in floodplain of Río Paraná near city of Santa Fé; March, 1970.

Aruba:

- Pesce (1985): shallow well in limestone, Pos Chiquito near San Nicholas ($12^\circ 27' 56'' \text{N}$ $69^\circ 57' 24'' \text{W}$), chlorinity 2772 mg l^{-1} , May 1980. (Pesce gives very complete hydrological data, which I have abstracted.)

Bonaire:

- Kiefer (1933a): Tanki Onima, oligohaline reservoir; as *M. (T.) decipiens*.
- Pesce (1985): shallow wells on Estate Washikemba ($12^\circ 10' 24'' \text{N}$ $68^\circ 13' 08'' \text{W}$), June 1976, and Pos di Salina Chikita, near Estate Pourier ($12^\circ 14' 50'' \text{N}$ $68^\circ 21' 35'' \text{W}$), chlorinity 632 mg l^{-1} , 28 May 1980.

Brazil:

- Arcifa (1984): Americana, Atibainha, Cabucu, Cachoeira, Félix Guisard, Jaguarí, Paraibuna, Paraitinga, Santa Branca and Taiaçupeba Reservoirs, State of São Paulo; as *T. crassus*.
- M. A. J. Carvalho (1975): Represa Americana, large mesotrophic reservoir, State of São Paulo; as *T. crassus*.
- Matsumura-Tundisi *et al.* (1981): unspecified reservoirs, State of São Paulo; as *T. crassus*.
- Sendacz & Kubo (1982) and Sendacz *et al.* (1985): Águas Claras, Guarapiranga, Itapeva, Itupararanga, Juqueri, Pedreira, Riacho Grande, Rio das Pedras and Serraria Reservoirs, State of São Paulo; as *T. crassus*.
- Sendacz (1984) and Sendacz *et al.* (1984): Billings Complex, large mesotrophic to eutrophic reservoir, State of São Paulo; as *T. crassus*.

Freitas (1983), Giani (1984), Pinto-Coelho (1983, 1987) and Reid (unpublished): Lago Paranoá, large eutrophic reservoir in Distrito Federal (basin of Paraná River); 15° 45' S, 47° 50' W.

Reid (unpublished): Lagoa da Península Norte, mesotrophic pond connected to Lago Paranoá, Distrito Federal; 1979–1982.

Reid (unpublished): cattle ponds 1 and 2, Fazenda Taquarí, Distrito Federal (basin of Amazon River), about 15° 31' S 47° 44' W; 6 Nov 1979, 4 Jul 1982.

Reid *et al.* (in press): Pampulha (19° 53' S 43° 59' W) and Vargem das Flores (19° 55' S 44° 02' W) Reservoirs, large mesotrophic to eutrophic reservoirs in Belo Horizonte, State of Minas Gerais, 1984–1985; and Lagoa Santa (19° 38' S 43° 53' W), small mesotrophic doline lake in Minas Gerais, 1 Sep 1985.

Freire & Pinto-Coelho (1986): Vargem das Flores Reservoir, Minas Gerais.

Neumann-Leitão & Nogueira (1987) and Nogueira (1987): shrimp culture ponds at Nova Cruz (Igarassu, 7° 51' 57" S 35° 01' 20" W) and at Cabo, State of Pernambuco; as *T. neglectus decipiens*.

Reid (unpublished): Açude de Apipucos and Tanque de Casa Forte, small reservoirs in Recife, State of Pernambuco, about 8° S 35° W; 4 Mar 1981. Coll. L. Elmoor-Loureiro.

Reid (unpublished): Lago 2, seasonally flooded lake on Ilha de Marchantaria, Rio Solimões near Manaus, State of Amazonas, about 60° 2' W 3° 35' S, 2 May 1984. Coll. B. Robertson.

Reid (unpublished): Inlet ('Bay') of Rio Paraguai near Corumbá, State of Mato Grosso do Sul, 1986. Coll. I. H. Moreno.

C. E. F. Rocha (pers. commun.): Dique (dike) Tororó, Salvador, State of Bahia, about 13° 00' S 38° 27' W, 26 Oct 1983. Coll. J. J. Santos. Açude (reservoir) de Itabaiana, city of Itabaiana, about 10° 43' S 37° 27' W; and lake in floodplain of Rio São Francisco, city of Neópolis, about 10° 19' S 36° 35' W, State of Sergipe.

Colombia:

- Kiefer (1956): Barranquilla; as *T. neglectus decipiens*.
- Reid (1988): permanent rain-fed breeding site of anopheline mosquitoes, Localidad Bucheli, Municipio Tumaco, about 1° 49' N 78° 45' W, 1986. Coll. M. F. Suarez.

Costa Rica:

- Collado, Fernando & Sephton (1984): localities unspecified.

Cuba:

- Smith & Fernando (1978, 1980): Cuban lakes in Habana, Las Villas, Oriente and Pinar del Río Provinces; as *T. crassus*.
- Collado, Fernando & Sephton (1984): localities unspecified: as *T. crassus*.

Curaçao:

- Pesce (1985): shallow well on Estate Leliënberg (12° 17' 55" N 69° 05' 43" W), chlorinity 155 mg l⁻¹, Apr 1974.

El Salvador:

- Collado, Fernando & Sephton (1984): localities unspecified (as *T. crassus*).

French Antilles:

- Dussart (1982): Guadeloupe: Mare Anse Bertrand, Mare Dubisquet (stockpond), Ravine des Coudes (canal), Ravine Cassis, Damencourt Laboratory, three unnamed ponds and a small pool; Martinique: 'Station 2'; and Marie-Galante: unnamed pond with Characea at Locomobile.

Haiti:

- Collado, Fernando & Sephton (1984): localities unspecified; as *T. crassus*.
- Pesce 1985: records from 12 wells in Departments de Artibonete, Nord, Ouest, and Sud; chlorinities 17–2330 mg l⁻¹, Oct–Dec 1979.

St. Croix, U. S. Virgin Islands:

- Pesce 1985: large well on Longford Estate (17° 43' 02" N 64° 41' 47" W), Nov 1975.

Trinidad:

- Collado, Fernando & Sephton (1984): localities unspecified; as *T. crassus*.

Venezuela:

- Kiefer (1956): Lagunillas, Venezuelan Andes; as *T. neglectus decipiens*.
- Montiel & Zoppi de Roa (1979): Edo. Apure, temporary ponds; as *T. n. decipiens*.
- E. Zoppi de Roa (in litt.): unspecified localities.
- Epp & Lewis (1980), Infante (1978a,b, 1981), Infante & Riehl (1984) and Infante *et al.* (1979): Lago de Valencia, a large mesotrophic lake; as *M. (T.) crassus* or *T. hyalinus*.
- Dussart (1984): Lago de Valencia; Zuata Reservoir, near Cagua (Aragua); Guárico Reservoir, near Calabozo (Guárico); Caño Falcón, Río Portuguesa near San Fernando de Apure (Guárico); Río Portuguesa at Camaguán (Guárico); unnamed pool near Camaguán; man-made lake at Camatagua (Aragua); unnamed natural pond near El Sombrero (Guárico), with extensive littoral macrophytes; Río Orinoco at Ciudad Bolívar and at Soledad; two charcas near Río Unare at Clarines.
- Reid (unpublished): Laguna La Orsinera, floodplain lake near Río Orinoco in Bolívar State, 8° 10' N, 63° 34' W, 22 Aug, 19 Sep and 1 Oct 1984. Coll. S. Twombly.

Probable records:

Argentina:

- Bonetto & Martínez de Ferrato (1966) and Martínez de Ferrato (1967): Madrejón Don Felipe and other ponds in island area of middle Río Paraná; as *T. hyalinus*.

Cuba:

- Straškraba *et al.* (1969): Lagunas de Alcatraz Chico, Santa Bárbara, La Luisa, Eduardo, del Tesoro; Presas Río Mosquito, Hanabanilla, Charco Mono; Acueducto de Holguín; as *T. cf. oithonoides*.

Guatemala:

- Deevey *et al.* (1980): Lake Quexil, Petén Lake District; as *M. hyalinus*.

Haiti:

- Richard (1895): Lake Florian near Port-au-Prince; as *C. oithonoides* var. *hyalina*.

Venezuela:

- Margalef (1961): ephemeral ponds on Margarita and Cubagua Islands; as *T. hyalinus*.
- Zoppi de Roa (1972): Laguna de Campoma, large littoral freshwater lagoon in Edo. Sucre; as *T. crassus*.

Broadly distributed in Africa south of the Sahara as well as Egypt, *T. decipiens* is also common in tropical and subtropical Asia (Kiefer, 1978) and has been recorded as well from Australia (Tait *et al.*, 1984). For 45 years after the first registry in the neotropics by Kiefer (1933a), from Bonaire, it was recorded only once, from Venezuela and Colombia (Kiefer, 1956), though the earlier record was listed by Lindberg (1954) and Kiefer himself (1938b, 1952) called attention to its occurrence in this region. Montiel and Zoppi de Roa (1979) discussed its ecology in temporary waters in Venezuela. More recently, Dussart (1982, 1984) has published numerous records from the French Antilles and Venezuela, and Pesce (1985) reported numerous records from groundwater habitats in the Antilles.

In reality, *T. decipiens* is one of the most commonly encountered species of the genus in broad areas of the neotropics. The absence of this species from many commonly available keys to European and North American Cyclopoida has led, apparently, to numerous misidentifications as the closely related species *T. (or M.) crassus* (syn. *T. hyalinus*). Reid (in press) has reviewed these records as well as morphological similarities among *T. decipiens* and several other species. In addition, some nomenclatural confusion has been caused by the fact that Kiefer (1952) for a time considered *T. decipiens* to be a subspecies of *T. neglectus*; but he later (Kiefer, 1978) restored the taxon to species status.

The southernmost records of *T. decipiens* are the probable finds of Bonetto & Martínez de Ferrato (1966) and of Martínez de Ferrato (1967) from the island region of the middle Paraná River. J. C. Paggi (in litt.) was not able to find the sample used by Martínez de Ferrato, but Paggi's own records (see above) and that of Menu Marque (1982) from northern Argentina comprise con-

vincing evidence that Martínez de Ferrato's specimens were *T. decipiens*. This species apparently does not occur in more southern parts of Argentina and was omitted from Ringuelet's (1958a) taxonomic synopsis of Argentine Crustacea. Ringuelet (1972:64) noted that several species collected by Martínez de Ferrato do not occur farther south in the valley of the Plate River, and characterized them as subtropical. Indeed, *T. decipiens*, like its congeners, is restricted to the warm lowlands of eastern South America, Central America and the Caribbean (Fig. 18). It is the only species of the genus recorded west of the Andes (Tumaco, Colombia).

Thermocyclops minutus

Confirmed records:

Argentina

- Ringuelet (1958a): Chaco, charca in Makallé.

Brazil

- Herbst (1967): Lago Joanico, State of Amazonas.
- Hardy (1978, 1980): Lagos Castanho and Jacaretinga, várzea lakes near Manaus; and Tarumã-Mirim, a blackwater tributary of the Rio Negro; State of Amazonas.
- Brandorff (1977, 1978): Lago Castanho.
- Brandorff (1978): Tarumã-Mirim.
- Brandorff & Andrade (1978): Lago Jacaretinga.
- Brandorff *et al.* (1982): several localities on the lower Rio Nhamundá including Lago da Terra Santa and Rio Maracanã, the mouth of the Rio Xingú, and lakes near Maracanã and Nhamundá villages; States of Amazonas and Pará.
- M. L. Carvalho (1983): Lago Grande, Amazonas.
- Reid (unpublished): Lago 2, Ilha de Marchantaria, Rio Solimões near Manaus, about 3° 35' S 60° 2' W, 2 May 1984, State of Amazonas; and Represa Curuá-Una, 25 Mar and 25 Apr 1978, State of Pará. Coll. B. Robertson.
- Barbosa & Matsumura-Tundisi (1984), Matsumura-Tundisi & Rocha (1983), Matsumura-

Tundisi & Tundisi (1976), Rocha & Matsumura-Tundisi (1976): Represa da Broa (Lobo), a large oligotrophic to mesotrophic reservoir; State of São Paulo.

- Matsumura-Tundisi *et al.* (1981): unspecified reservoirs; State of São Paulo.
- Sendacz & Kubo (1982) and Sendacz *et al.* (1985): Águas Claras, Alecrim, França, Fumaça, Funil, Itupararanga and Serraria Reservoirs; State of São Paulo.
- Reid (unpublished): Lagoa Feia, a small mesotrophic lake, State of Goiás (Amazon drainage basin), 15° 34' 20" S, 46° 18' 30" W; 16 Jan 1980, coll. L. Elmoor-Loureiro; 23 Apr 1982, coll. J. W. Reid.
- Reid (unpublished): inlet ('bay') of Rio Paraguai near Corumbá, State of Mato Grosso do Sul, 1986. Coll. I. H. Moreno.
- Gouvêa (1978): Lagoa do Abaeté, a small mesotrophic coastal lake near Salvador, State of Bahia.
- Matsumura-Tundisi & Okano (1983) and Okano (1980): Lago Dom Helvécio, a large oligotrophic lake, 19° 10' S 42° 1' W; State of Minas Gerais.
- Reid *et al.* (in press): Vargem das Flores Reservoir, Belo Horizonte, State of Minas Gerais, 1984-85; Lagoa Santa and Lagoinha, natural doline lakes in the Municipality of Lagoa Santa near Belo Horizonte, both about 19° 38' S 43° 53' W, 1 Sep 1985; and Lago Sumidouro, a doline lake near Belo Horizonte, 1 Sep 1985; State of Minas Gerais.
- Freire & Pinto-Coelho (1986): Vargem das Flores Reservoir, Minas Gerais.
- Reid & Turner (in press): canal from Lago Viana to Rio Pindaré, State of Maranhão, about 3° 30' S 45° 19' W; 2 Oct 1985.
- Reid & Esteves (1984): Lagoas Cima (21° 45' S 41° 30' W), Feia (21° 58' S 41° 21' W) and Saudade (21° 42' S 41° 20' W), large freshwater coastal lakes; State of Rio de Janeiro.
- Kiefer (1936b) and Schubart (1938): pool in dried streambed of Riacho Doce, Município Caruarú; and unspecified water body in Carapatos; State of Pernambuco.

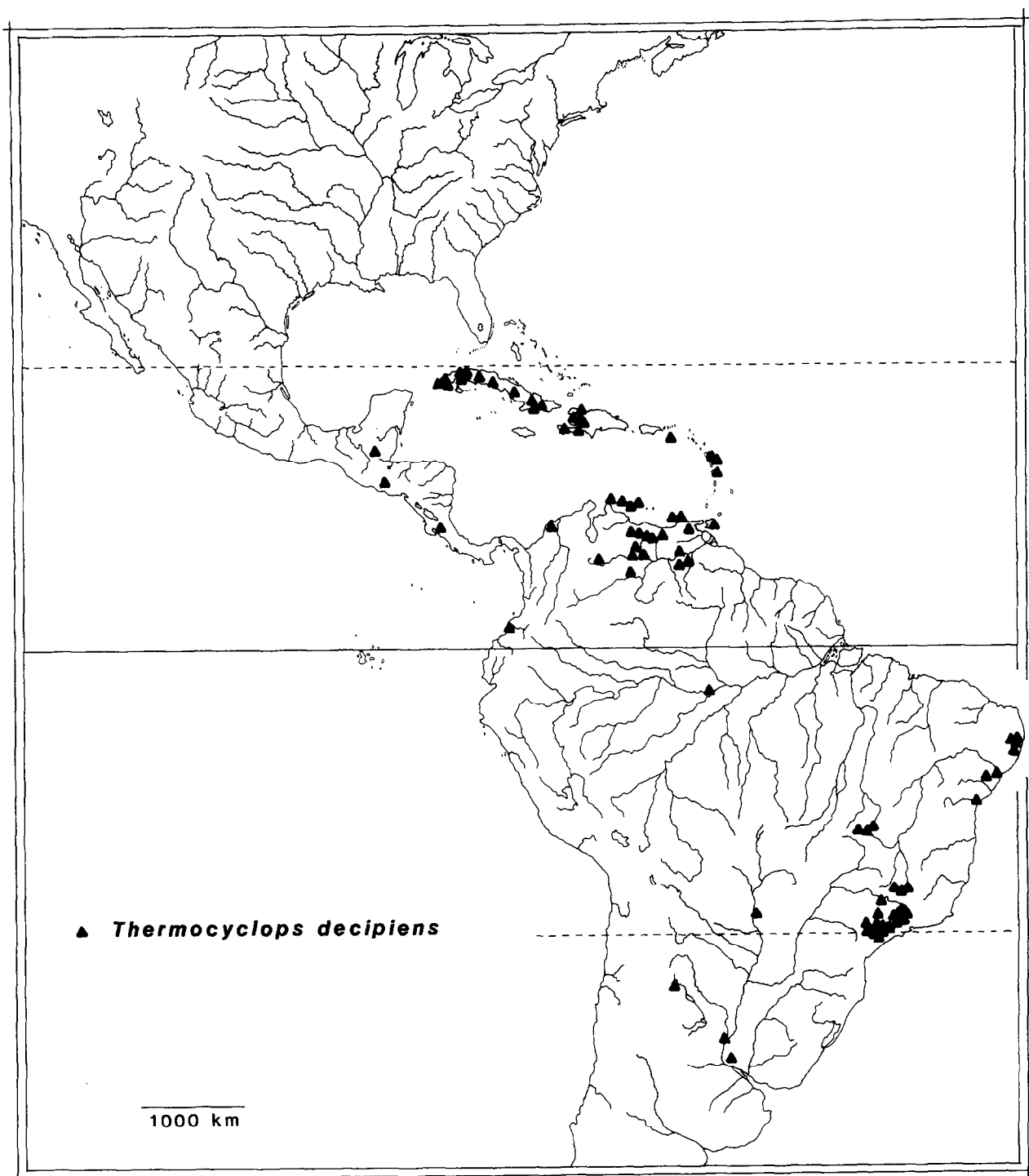


Fig. 18. Locations in the western hemisphere of confirmed and probable records of *Thermocyclops decipiens*.

Paraguay:

- Lowndes 1934: original description, from swamp 32 km west of Makthlawaiya; as *Mesocyclops minutus*.

Venezuela:

- Dussart (1984): estero (backwater of river) at Camaguán (Guárico); unnamed pool near Camaguán; unnamed natural pond with extensive littoral macrophytes, near El Sombrero (Guárico); unnamed pond near Río Orinoco at Barrancas; Guri Lake, a man-made lake near Río Caroní.
- E. Zoppi de Roa (in litt.): unspecified localities.

Figure 19 shows the known distribution of *T. minutus*, which appears to be confined to tropical and subtropical lowlands of continental South America east of the Andes; most records are from Brazil. Ringuelet (1958a, 1959, 1968) considered *T. minutus*, like *T. brehmi* and *T. tenuis*, a subtropical species in Argentina. In central Amazonian lakes influenced by 'white water', i.e. relatively high in nutrients, this species is often numerically important (Brandorff *et al.*, 1982).

Thermocyclops inversus

Confirmed and probable records:

Brazil:

- Kiefer (1936a) and Schubart (1938): original description; Rio Branco, a recently constructed reservoir near Campo da Criação; and Brejo (marsh) de São José (Município Buique); State of Pernambuco.
- Reid (unpublished): well at Forte Pau Amarelo, near Olinda, about 8° 0' S, 34° 50', 9 April 1981; State of Pernambuco.
- Reid *et al.* (in press): pool in Brejo do Hipódromo 'Serra Verde', Belo Horizonte, 1 Sep 1985; State of Minas Gerais.

Costa Rica:

- Collado, Fernando & Sephton (1984): localities unspecified.
- Collado, Defaye *et al.* (1984): Cachi Reservoir and Dona Ana Pond, a small natural reservoir (Cartago Province); Arenal Reservoir (Guanacaste Province); Aguilar Pond, a small natural pond (province unspecified).

Cuba:

- Straškraba *et al.* (1969): Laguna del Valle de San Juan (pH = 7.0); and Laguna de Alcatraz Grande (pH = 8.4).
- Smith & Fernando (1978, 1980): 3 unspecified lakes in Habana and Las Villas Provinces.
- Collado, Fernando & Sephton (1984): localities unspecified.

El Salvador:

- Coker (1943): San Salvador, localities unspecified; as *M. inversus*.
- Collado, Fernando & Sephton (1984): localities unspecified.

Guatemala:

- Peckham & Dineen (1953): Lake Amatitlan, 14° 25' N 90° 30' W, altitude 1175 m; as *M. inversus*.
- Brinson & Nordlie (1975) and H. C. Yeatman (in litt.): Lake Izabal, a large, low-altitude, hard-water, mesotrophic lake; as *M. (T.) inversus*.
- Deevey *et al.* (1980): Lakes Petén Itza, Yaxha, Sacnob, Quexil, Macanche, Monifata I, Oquevix, and Petenxil in Petén Lake District; as *M. inversus*.

Mexico:

- Coker (1943), Kiefer (1938a), Osorio Tafall (1941, 1944), Rioja (1940a,b), Uéno (1939): Lake Pátzcuaro, Michoacán Province; as *M. inversus* or *T. inversus*.
- Osorio Tafall (1943): 2 caves in Valles, San Luis Potosí; mildly carbonate waters, pH = 8. Osorio Tafall commented that these copepods were transported into the caves in stream water.

Nicaragua:

- Cole (1976, in litt.): Lake Nicaragua, a shallow, turbid, well-oxygenated, somewhat saline, highly productive lake; copepods identified by H. C. Yeatman.
- H. C. Yeatman (in litt.): Rio Grande at Capalar, 23 May 1977.

Possible record:

Panama:

- Marsh (1913): see comments under *T. tenuis*.

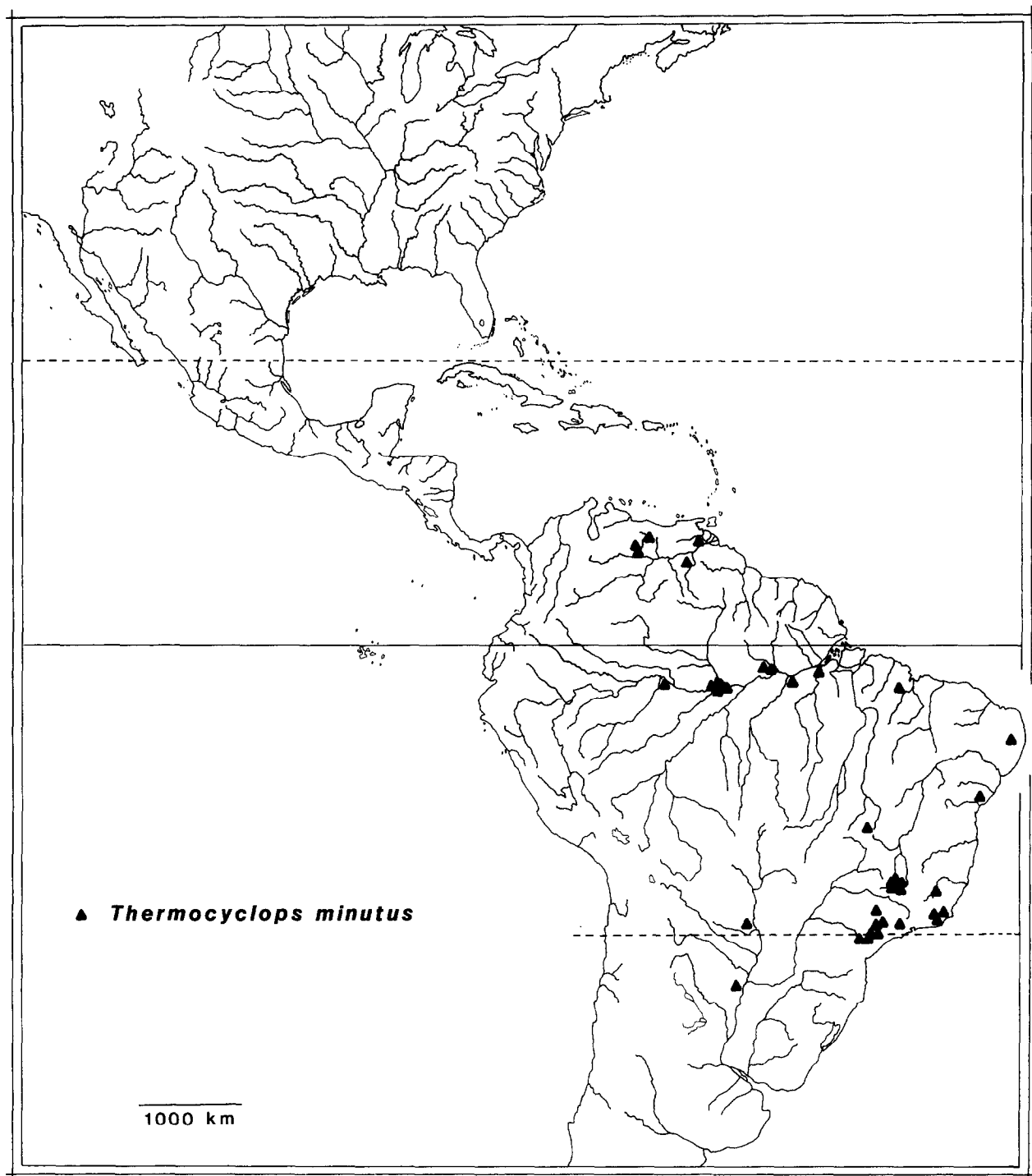


Fig. 19. Locations in the western hemisphere of confirmed and probable records of *Thermocyclops minutus*.

Although Yeatman (1959) included *T. inversus* in his key to North American Cyclopoida, based on records in Mexico, no recent find of this species in North America seems to have been made. In the opinion of Yeatman (1977), C. B. Wilson's report of *T. tenuis* from cenotes in Yucatán may refer to that species or to *T. inversus*. *T. inversus* probably occurs sporadically in Mexico as well as in Cuba. The four records from Brazil represent the only continental South American finds (Fig. 20).

Some questionable records

Thermocyclops dybowskii (Landé, 1890)

Yeatman (1959) and Pennak (1953, 1978) included *T. dybowskii* in their keys to North American *Mesocyclops* s. l. on the basis of E. B. Forbes' records from Wyoming and Illinois (Forbes, 1897). These records are unaccompanied by figures, and Coker (1943) considered them doubtful. Since in spite of its presence in these widely used keys, no further record of a species of *Thermocyclops* has been published from the North American Midwest, I concur with Coker's opinion. The record of *T. dybowskii* from Louisiana (southern United States) by Nasci *et al.* (1987) refers in actuality to *Diacyclops navus* (Herrick). Daday's record of *C. dybowskii* from Paraguay was judged by Lindberg (1954) to refer to *M. longisetus*. Collado, Fernando & Sephton (1984) recorded '*M. dybowskii*' from Trinidad; since these authors did distinguish the genera *Thermocyclops* and *Mesocyclops*, it is possible that this record also refers to a species of *Mesocyclops* s. str.

Thermocyclops oithonoides (Sars, 1863)

This species has several times been recorded from the western hemisphere; unfortunately no record has been accompanied by good figures. Probably for this reason, Lindberg (1954) listed the record of Daday (1905) from Paraguay as species incerta sedis, and considered that the record of Wierzejski (1892) from Argentina probably referred to *T. tenuis*. Meek (1901) reported

T. oithonoides from Lake Atitlán, Mexico; the copepods were identified in this case by C. Juday. Coker (1943) considered all records from North America dubious. Yeatman (1959) included *M. oithonoides* in his key, based on Herrick's record from Minnesota (1884, repeated 1895). Herrick's figures from the 1884 report clearly show a species of *Mesocyclops*, most likely the common *M. edax*; this was also the opinion of Kiefer (1931). The identification by Straškraba *et al.* (1969) from Cuba very likely refers to *T. decipiens*, which is the common planktonic species there (Smith & Fernando, 1978, 1980). Collado, Fernando & Sephton (1984) mentioned a record by 'others' of *T. oithonoides* from Haiti, but gave no attribution. Therefore *T. oithonoides* as well as *T. dybowskii* are probably not present in the western hemisphere.

Discussion

Ranges and biogeographical considerations

In the western hemisphere, members of the genus *Thermocyclops* inhabit warm lowland regions in continental South America east of the Andes Mountains (except for the single record of *T. decipiens* from western Colombia) and southwards to northern Argentina, where occurrence is sporadic. Northwards they extend into several islands of the Antilles and through Central America, Mexico and the southern United States. Aside from *T. tenuis longifurcatus*, *T. hastatus antillensis* and *T. parvus*, the species with the most restricted range is *T. brehmi*, from northern Argentina and Uruguay. While *T. crassus* has been reliably recorded only from ponds in Costa Rica, in Africa and southern Europe it is quite common and should be looked for in future Central American and Antillean collections. *T. minutus* is restricted to eastern continental South America, from northern Argentina to Venezuela. The ranges of the remaining three species extend throughout the neotropics. Reliable records of *T. decipiens* extend from Argentina northwards only to Costa Rica, Guatemala and the Antilles, though the species is probably present in Mexico

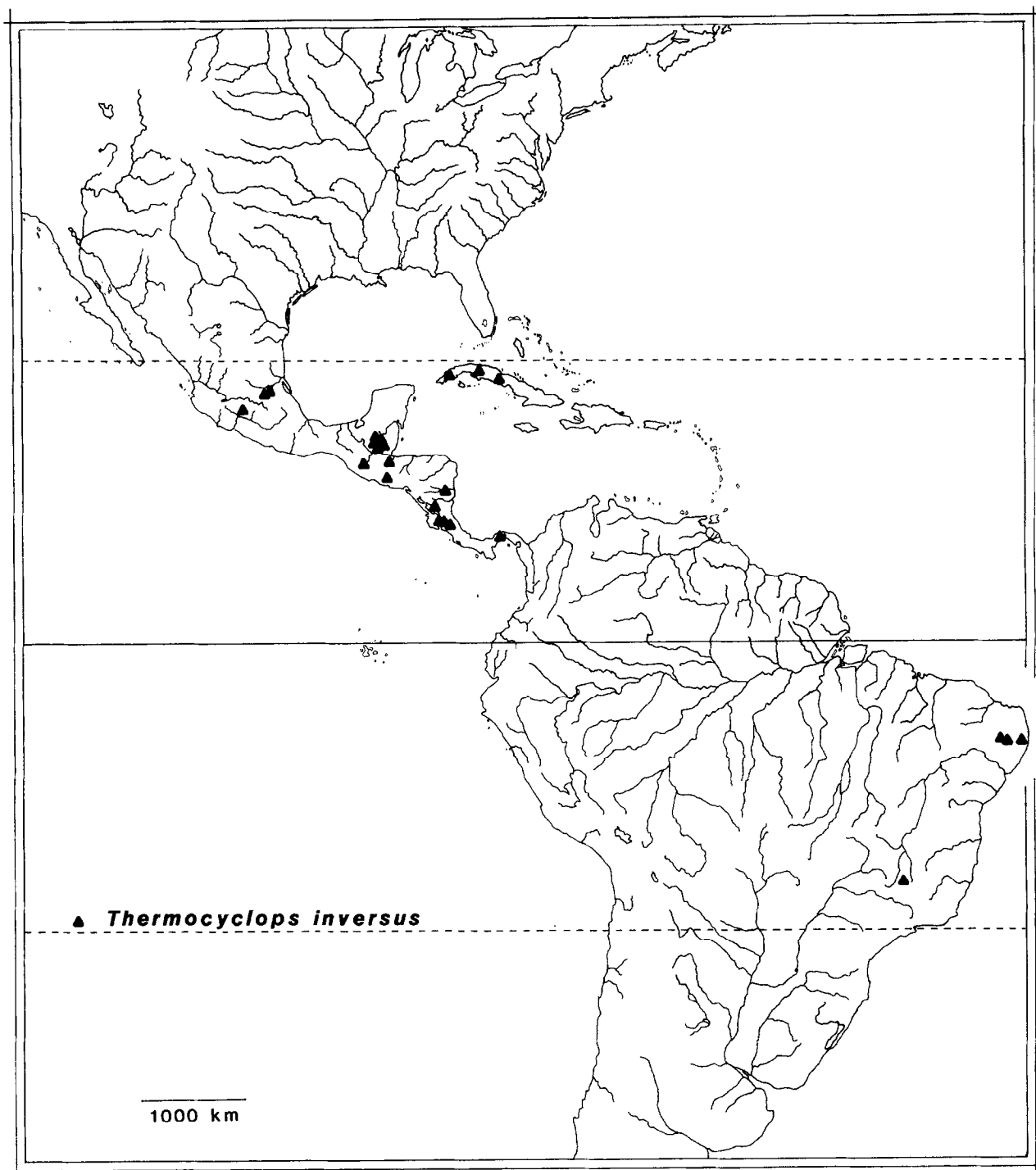


Fig. 20. Locations in the western hemisphere of confirmed and probable records of *Thermocyclops inversus*.

also. *T. inversus* occurs from northeastern Brazil to Mexico and the Antilles. *T. tenuis* ranges from northern Argentina to the Antilles and the southern United States.

To both north and south, then, *T. tenuis* and *T. brehmi* are the only species which seem to occur consistently outside the tropics. Surprisingly, *T. parvus* seems to be the only member of the genus to inhabit the peninsula of Florida. No congener has yet been recorded from lakes in the middle and upper peninsula, where numerous lakes and other aquatic habitats have been investigated. In most Florida lakes, even in highly productive phosphate pit lakes, *Mesocyclops edax* is the common planktonic cyclopoid species (Blancher, 1984; Dickinson, 1949; Elmore *et al.*, 1984; G. K. Reid & Blake, 1969; J. Elmore and G. Wyngaard, pers. commun.). In waters of the central and southwestern United States, *T. tenuis* occurs extremely rarely, and then only in summer (Cole, 1966; L. H. Carpelan, in litt.). Similarly, the apparent absence of the genus from coastal states of Brazil south of São Paulo, where *T. decipiens* and *T. minutus* are common, does not result from lack of collecting effort, since collections in that area from the time of Richard (1897) down to a recent, thorough study of the Lagoa Negra in the State of Rio Grande do Sul by Fallavena (1985) have failed to record these species. Species of *Thermocyclops* were also absent from an extensive series of samples from ponds and reservoirs in the region of Porto Alegre, made by Kleerekoper in 1941 (Reid, unpublished).

The known ranges of most western hemisphere species of *Thermocyclops* except for *tenuis*, therefore, coincide strikingly with the 'South American-Caribbean track' for faunal distribution described by Rosen (1975), which includes South America, the Antilles, Bahamas, Central America and the Mexican lowlands. If one accepts Rosen's argument that the sequence of vicariant events dividing populations and thus permitting speciation can be reconstructed from the present distribution of species, species of greater age would be the most broadly distributed (*T. decipiens* in this case), with the most recently evolved species

having the most restricted distribution (*T. brehmi*, *T. hastatus antillensis* and *T. parvus*). *T. crassus* may have existed longer than *T. decipiens* in other parts of the tropics, but have recently arrived in the western hemisphere. A debatable assumption in Rosen's theory as applied to these copepods is that their vagility is not so great as to permit them to reach all possible habitats within relatively short periods after speciation occurs. However, a high degree of vagility is inferable from the spatial distribution of *T. tenuis*, which in the New World is actually greater than that of *T. decipiens*. Small aquatic crustaceans are well suited to passive dispersal by birds and semiaquatic mammals (Maguire, 1971). Such great vagility would imply that the speciation events of *T. brehmi*, *T. hastatus antillensis* and *T. parvus* are recent indeed.

The other striking aspect of the recorded distributions of *T. decipiens*, *T. tenuis* and *T. inversus* is their apparent rarity or complete absence from the central Amazon basin, where *T. minutus* is common in lakes and rivers. Copepods from many kinds of Amazonian habitats including rivers, side channels, floodplain (várzea) lakes, ponds and puddles have been examined by Cipólli & Carvalho (1973), Herbst (1962, 1967), Brandorff (1978), Brandorff *et al.* (1982), Reid (unpublished) and others. The only records within the greater basin are those of the author for *T. decipiens* and *T. tenuis* in some puddles and cattle ponds in the north of the Federal District, and the single record of *T. decipiens* from a lake on Marchantaria Island near Manaus (see above). On the other hand, *T. decipiens* is common in the basin of the Orinoco River, which has now and has historically had numerous connections to the Amazon. It is probable that the apparent absence of some species from the Amazon lowlands is due to biological and ecological rather than geographical causes; as pointed out by Dumont (1980), passive dispersal is successful only if suitable niches are encountered. Besch (1969) explained a similar disjunction in the distribution of the cold-stenothermal rheophilic Hydrachnellae (Arachnida) by postulating a lack of suitable environmental conditions in the warm lowlands. Since no environ-

mental factors in the Amazon basin suggest themselves as similarly likely to inhibit species of *Thermocyclops*, an explanation for their apparent absence might be sought in their biology, competition from non-congeneric cyclopoids, or predation factors.

Biological and ecological considerations

Most records of these species are accompanied by fragmentary or no description of the habitat, but most species, like their congeners in other parts of the world, appear facultatively eurytopic. The least known species is *T. brehmi*, which Ringuelet characterized as an inhabitant of 'microlimnotopes'. *T. crassus*, known in the western hemisphere only from a few ponds in Costa Rica, is otherwise present throughout the Palearctic, Australia, South and Southeast Asia, occurring most commonly in tropical Africa. It typically inhabits large natural and artificial lakes, but also occurs occasionally in more restricted habitats such as pools and ditches (Dussart, 1969; Kiefer, 1978). *T. minutus* has been recorded most often in larger oligotrophic to mesotrophic lakes, as well as some Amazonian rivers. *T. decipiens* is commonly found in and frequently numerous in large and small mesotrophic and eutrophic lakes and reservoirs, as well as in open shallow wells. *T. tenuis*, also extremely eurytopic, inhabits large and small lakes, reservoirs, ponds, roadside ditches and puddles. In Arizona and New Mexico, this species was collected by L. H. Carpelan (pers. commun.) in cowponds and a roadside ditch shortly after the first filling by seasonal rains in July, and did not appear in collections made 3–4 months later. Similarly, in the arid central Brazilian highlands *T. tenuis* was found only in a temporary puddle and an ephemeral cowpond, though in extremely high numbers. Many other records of *T. tenuis* seem to be from ephemeral waters, though some are from large lakes. *T. inversus* may prefer mildly carbonate waters and its records include large and small reservoirs, natural lakes, ponds, wells and caves. In lakes it is often abundant (Deevey *et al.*, 1980; Peckham & Dineen, 1953).

Where two or more of these species have been

recorded in the same lake or reservoir district, there is some evidence of separation according to environmental conditions. In the Guatemalan lake system examined by Deevey *et al.* (1980), *T. decipiens* occurred only in Lake Quexil, one of three lakes undergoing anthropogenic disturbance in modern times. *T. inversus* inhabited eight of the lakes, co-occurring with *T. decipiens* only in Lake Quexil. In the Vargem das Flores Reservoir in southeastern Brazil, *T. decipiens* co-occurred with *T. minutus* (Freire & Pinto-Coelho, 1986; Reid *et al.*, in press). *T. minutus* is a common inhabitant of the natural (oligotrophic to mesotrophic) waters of the region, though populations of *T. decipiens* are high in both Vargem das Flores and Pampulha, the other large reservoir in the city of Belo Horizonte. Both reservoirs have in recent years undergone severe siltation and loading of urban pollutants (Freire & Pinto-Coelho, 1986). Of 17 Cuban lakes investigated by Straškraba *et al.* (1969), *T. inversus* occurred in two and *T. decipiens* (= '*T. oithonoides*') in 11; the two species never occurred together. The two lakes inhabited by *T. inversus* were a deep lake with calcareous rock basin and a shallow basin on fine siliceous sand; lakes inhabited by *T. decipiens* included two of the latter type as well as large and small reservoirs, a small lake with vegetation, and a large natural lake. In or near the Federal District in the central Brazilian highlands, three species occurred (see above). *T. tenuis* was found only in a rain-fed cowpond and a puddle during the rainy season. *T. decipiens* was the dominant crustacean zooplankton in a large eutrophic reservoir (Lake Paranoá), in a closely associated mesotrophic pond, subject to erosion and flooding from nearby construction (Lagoa da Península Norte); and in two perennial cowponds. *T. minutus* occurred in small numbers together with calanoids in Lagoa Feia, a natural mesotrophic lake somewhat modified by damming and drainage from a nearby town. *T. decipiens* and *T. minutus* co-occurred in an inlet of Rio Paraguai near Corumbá; these inlets are subject to great seasonal alterations in depth, primary productivity and coverage by *Eichhornia crassipes* and other macrophytes (I. H. Moreno, pers. commun.). Data from several

studies of reservoirs in São Paulo indicate that *T. decipiens* tends to dominate the crustacean zooplankton in mesotrophic to eutrophic reservoirs, while *T. minutus*, though it occurs in large populations in some eutrophic systems, tends to be more numerous in mesotrophic to oligotrophic reservoirs (Arcifa, 1984; Matsumura-Tundisi & Tundisi, 1976; Matsumura-Tundisi *et al.*, 1981; Sendacz & Kubo, 1982; Sendacz *et al.*, 1984, 1985). Co-occurrences of any two species of *Thermocyclops*, therefore, seem to indicate a system in which environmental conditions are changing.

T. minutus, while frequently abundant in waters of low productivity, is successful in more productive waters up to a certain point. In the natural Lake Dom Helvécio as well as Broa (Lobo) Reservoir, population peaks of *T. minutus* are strongly associated with entry of nutrients into the system through overturn or in the rainy season, with consequent increased phytoplankton production (Matsumura-Tundisi & Tundisi, 1976; Matsumura-Tundisi & Okano, 1983). In Lago Castanho, a white-water Amazonian floodplain (várzea) lake, populations of *T. minutus*, the dominant crustacean zooplankton, fluctuated by about an order of magnitude, showing no clear relationship to water level in the lake (Brandorff, 1977, 1978b). Since highest egg numbers followed periods of total circulation and consequent increases in (non-blue-green) phytoplankton populations, while egg production decreased during and after blooms of blue-green and filamentous algae and volvocines, Brandorff (1977) attributed these periods of increased egg production to increases in small 'filterable' algae. In the Amazon system, *T. minutus* seems not to occur in black (humic) waters, but frequently attains high population sizes in whitewater lakes or rivers (Brandorff, 1977; Brandorff *et al.*, 1982). These latter systems have been considered more productive than the nutrient-poor blackwaters, though this opinion is debatable (Brandorff, 1977). In the mesotrophic Lagoa do Abaeté, *T. minutus* remained abundant year-round (Gouvêa, 1978).

Although cyanophytes are usually considered unavailable as food for zooplankters (Junk, 1984), much evidence exists that

T. decipiens and some congeners can exploit them. *T. decipiens* is a dominant or quantitatively important zooplankton in several well-studied eutrophic neotropical lakes and reservoirs in which the phytoplankton tends to be dominated by one of several species of Cyanophyceae. In these systems, populations of *T. decipiens* tend to remain stable or at least numerous year-round; fluctuations whether positive or negative are usually associated with the rainy season. In the Venezuelan Laguna de Campoma, numbers of most zooplankters including *T. decipiens* decreased during the rainy season (Zoppi de Roa, 1972); a similar cycle was observed in the Brazilian Lake Paranoá, though *T. decipiens* populations tended to vary less than other crustacean plankters (Freitas, 1983; Giani, 1984; Pinto-Coelho, 1984, 1987). Populations of *T. decipiens* remain more or less stable throughout the year in Rio Grande (Billings Complex), an eutrophic reservoir in São Paulo (Sendacz *et al.*, 1984). In Billings Reservoir itself, *T. decipiens* is dominant in the rainy season but supplanted by *Metacyclops mendocinus* during the dry season, a period of extreme eutrophication (Sendacz, 1984). In Lake Valencia, high densities of copepods, primarily *T. decipiens*, corresponded with maxima of *Lyngbya limnetica*, *Oscillatoria limnetica* and sometimes *Microcystis aeruginosa* (Infante & Riehl, 1984). The positive relationship between these copepods and blue-green algae is substantiated by the history of gradual displacement of the calanoid *Notodiaptomus venezolanus* by *T. decipiens* as the dominant crustacean zooplankton in Lake Valencia in the 1970's; during this decade cyanophytes became the predominant phytoplankters as the lake's pollution levels increased (Infante, 1978a). A similar sequence of events has occurred in Paranoá, where an unidentified diaptomid calanoid copepod occurred during the early period of reservoir formation but has been apparently absent in recent years. Experimental reduction of zooplankton numbers in enclosures in Lake Paranoá resulted in virtual elimination of the blue-green *Raphidiopsis brooki* from the phytoplankton and its substitution by several species of *Chlorella*, *Scenedes-*

mus, *Closterium* and another species of *Raphidiopsis* (Pinto-Coelho, 1983). In the Philippine Lake Lanao the production of *T. crassus*, closely related to *T. decipiens*, also showed a strong positive statistical relationship to the abundance of blue-greens, as well as to diatoms, and particularly to filamentous or elongate unicellular forms (Lewis, 1979). On the other hand, in the Cuban lakes studied by Straškraba *et al.* (1969), there was no obvious correlation between the presence of *T. decipiens* and dominance of a particular lake by blue-greens.

Aside from such observations of coincidental occurrence, several studies have shown directly that adults and copepodites, and probably nauplii as well, of some species of *Thermocyclops* do feed raptorially upon blue-green algae as well as on other phytoplankton groups. Infante (1978b) has shown by examination of stomach contents of some zooplankters in Lake Valencia that *T. decipiens* ingests but may not efficiently assimilate the colonial *M. aeruginosa*; while the filamentous *L. limnetica* is both ingested and 83% assimilated. However, in Lake Valencia blue-greens and Bacillariophyceae dominated the recognizable gut contents during much of the year, cyanophycean species mostly being ingested from September through February when these species were also most abundant in the plankton. A species better adapted to utilize *Microcystis* may be *T. crassus*, which in Lake George not only ingested the colonies but broke up cells and efficiently assimilated their carbon; nauplii apparently ingested and assimilated the less numerous single cells (Burgis *et al.*, 1973; Moriarty *et al.*, 1973). Such differences in capability to utilize various species of blue-green algae may account for the virtually complete separation of *T. decipiens* and *T. crassus* in plankton records of the Sunda-Expedition (Heberer & Kiefer, 1932; Kiefer, 1933b, 1938b) noted by Hutchinson (1951). *Thermocyclops minutus* is so much smaller than either *T. decipiens* or *T. crassus* that it may be dependent upon, or at least more restricted to relatively palatable green algae and diatoms, proportionately more available in less highly productive waters. Much of the explanation for the com-

parative success of these species in different water bodies may, therefore, lie in the nature of the available phytoplankton assemblages. Hutchinson's (1951) characterization of *T. decipiens* as a 'fugitive species', that is a species forever on the move from competition with any other species capable of entering the same niche, is probably incorrect, since the success of *T. decipiens* seems to depend upon the availability of cyanophycean food, a resource which few other species seem adapted to utilize. Unfortunately, understanding of the biology of most of these interesting cyclopoids, which are frequently quantitatively important in disturbed and eutrophic waters, has advanced little since Hutchinson wrote. Further investigation would yield valuable insights into zooplankton-phytoplankton relationships and population dynamics.

In lacustrine systems the species richness of zooplankters is frequently low when compared to that of the phytoplankton community; Colinvaux & Steinitz (1980) have called this the 'paradox of the zooplankton'. Low species richness is even more striking in tropical lakes (Colinvaux & Steinitz, 1980; Deevey *et al.*, 1980; Lewis, 1979; Ruttner, 1952). In tropical waters, zooplankters generally maintain breeding populations year-round, and these populations must adapt to changes in the availability of food organisms. At least in mesotrophic and eutrophic systems, some species of *Thermocyclops* may be able to maintain high populations relative to those of other herbivorous copepods by gaining a significant portion of their nutrition from blooms of blue-green algae which most other cyclopoid as well as calanoid copepods are unable to exploit effectively. Several species of temperate cyclopoids have been shown to take blue-green algae unselectively, even in the presence of supposedly more palatable greens (McNaught *et al.*, 1980); however, blue-greens may not be assimilated efficiently (Schindler, 1971). By maintaining relatively high numbers during periods of blooms of the less palatable algal species, then, these species can, in the aggregate, outcompete calanoids and other herbivorous cyclopoids for more desirable algal species during periods when these algae are

increasing. This hypothesis is advanced as one possible mechanism for the frequently observed decline or disappearance of filter-feeders from many lakes and reservoirs undergoing eutrophication (Infante & Riehl, 1984; Sendacz, 1984; Sendacz *et al.*, 1984). It might also partially account for the low species richness of planktonic copepod communities in tropical lakes, since copepods which are able to survive on less desirable phytoplankters may outcompete more specialized feeders.

Acknowledgments

I am very grateful to these colleagues for their kind assistance with collecting, checking species identifications and records, lending specimens, manuscripts, and unpublished data, and for helpful conversations and general improvement of the manuscript: Lars H. Carpelan, Gerald A. Cole, Roxanne Conrow, Charles C. Davis, Kristin Smith Day, Edward S. Deevey, Jr., Bernard H. Dussart, Lourdes Elmoor-Loureiro, James L. Elmore, Francisco de A. Esteves, C. Herbert Fernando, June Springer de Freitas, Alessandra Giani, Loren R. Haury, Maria Socorro R. Ibañez, Aida de Infante, Gerald G. Marten, Takako Matsumura-Tundisi, Ivã de Haro Moreno, Juan César Paggi, Guido Pereira, Ricardo M. Pinto-Coelho, Edward B. Reed, Barbara Robertson, Carlos E. F. da Rocha, James F. Saunders III, Suzana Sendacz, Marco F. Suarez, Stephen Threlkeld, Saran Twombly, Grace Wyngaard, Harry C. Yeatman, Jesús Andrés Zamudio Valdés, Evelyn Zoppi de Roa, and two anonymous reviewers. These organizations provided funds for travel to Brazil: National Science Foundation, Organization of American States, Companhia de Amparo a Pesquisa (CAPES), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). I thank the Department of Invertebrate Zoology, National Museum of Natural History for providing laboratory and library facilities.

References

- Arcifa, M. S., 1984. Zooplankton composition of ten reservoirs in southern Brazil. *Hydrobiologia* 113: 137–145.
- Barbosa, P. M. M. & T. Matsumura-Tundisi, 1984. Consumption of zooplanktonic organisms by *Astyanax fasciatus* Cuvier, 1819 (Osteichthyes, Characidae) in Lobo (Broa) Reservoir, São Carlos, SP, Brazil. *Hydrobiologia* 113: 171–181.
- Besch, W., 1969. South America Arachnida. In E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe & H. Sioli (eds.). *Biogeography and Ecology in South America*. Vol. 2. Dr. W. Junk N. V., The Hague: 723–740.
- Blancher, E. C. II, 1984. Zooplankton-trophic state relationships in some north and central Florida lakes. *Hydrobiologia* 109: 251–263.
- Bonetto, A. A. & A. Martínez de Ferrato, 1966. Introducción al estudio del zooplancton de las cuencas isleñas del Paraná Medio. *Physis*, B. Aires, A 26: 385–396.
- Brandorff, G. -O., 1977. Untersuchungen zur Populationsdynamik des Crustaceenplanktons im tropischen Lago Castanho (Amazonas, Brasilien). Dissertation, Christian-Albrechts-Univ., Kiel. 108 pp.
- Brandorff, G. -O., 1978. Preliminary comparison of the crustacean plankton of a white water and a black water lake in central Amazonia. *Verh. int. Ver. Limnol.* 20: 1198–1202.
- Brandorff, G. -O. & E. R. Andrade, 1978. The relationship between the water level of the Amazon River and the fate of the zooplankton population in Lago Jacaretinga, a Varzea lake in the central Amazon. *Stud. neotrop. Fauna Environ.* 13: 63–70.
- Brandorff, G. -O., W. Koste & N. N. Smirnov, 1982. The composition and structure of rotiferan and crustacean communities of the lower Rio Nhamundá, Amazonas, Brazil. *Stud. neotrop. Fauna Environ.* 17: 69–121.
- Brinson, M. M. & F. G. Nordlie, 1975. Lake Izabal, Guatemala. *Verh. int. Ver. Limnol.* 19: 1468–1479.
- Burgis, M. J., 1970. The effect of temperature on the development of eggs of *Thermocyclops* sp., a tropical cyclopoid copepod from Lake George, Uganda. *Limnol. Oceanogr.* 15: 742–747.
- Burgis, M. J., P. E. C. Darlington, I. G. Dunn, G. G. Ganf, J. J. Gwahaba & L. M. McGowan, 1973. The biomass and distribution of organisms in Lake George, Uganda. *Proc. Roy. Soc. London*, B. 184: 271–298.
- Candelas, G. A. & G. C. Candelas, 1966. The West Indies. In D. G. Frey (ed.). *Limnology in North America*. Univ. Wisconsin Press. Madison: 435–450.
- Carvalho, M. A. J., 1975. A Represa de Americana: Aspectos físico-químicos e a variação das populações de Copepoda, Cyclopoida de vida livre. Dissertation, Instituto de Biociências, Univ. S. Paulo. 157 pp.
- Carvalho, M. L., 1983. Efeitos da flutuação do nível da água sobre a densidade e composição do zooplâncton em um lago de várzea da Amazônia, Brasil. *Acta Amazon.* 13: 715–724.

- Cipólli, M. N. & M. A. J. Carvalho, 1973. Levantamento de Calanoida e Cyclopoida (Copepoda, Crustacea) das águas da região do Guamá, Capim e Tocantins, com nota sobre a fauna acompanhante. *Papéis Avulsos Zool.*, S. Paulo 27: 95–110.
- Coker, R. E., 1943. *Mesocyclops edax* (S. A. Forbes), *M. leuckarti* (Claus) and related species in America. *J. Elisha Mitchell sci. Soc.* 59: 181–200.
- Cole, G. A., 1966. The American Southwest and Middle America. In D. G. Frey (ed.). *Limnology in North America*. Univ. Wisconsin Press. Madison: 393–434.
- Cole, G. A., 1976. Limnology of the great lakes of Nicaragua. In T. B. Thorson (ed.). *Investigations of the Ichthyology of Nicaraguan Lakes*. School of Life Sciences, Univ. Nebraska. Lincoln: 9–15.
- Colinvaux, P. & M. Steinitz, 1980. Species richness and area in Galapagos and Andean lakes: equilibrium phytoplankton communities and a paradox of the zooplankton. In W. C. Kerfoot (ed.). *Evolution and Ecology of Zooplankton Communities*. The University Press of New England. Hanover (NH); Lond.: 697–711.
- Collado, C., D. Defaye, B. H. Dussart & C. H. Fernando, 1984. The freshwater Copepoda (Crustacea) of Costa Rica with notes on some species. *Hydrobiologia* 119: 89–99.
- Collado, C., C. H. Fernando & D. Sephton, 1984. The freshwater zooplankton of Central America and the Caribbean. *Hydrobiologia* 113: 105–119.
- Daday, E. von, 1905. Untersuchungen über die Süßwasser-Mikrofauna Paraguays. *Zoologica*, Stuttg. 18: 1–374 + 23 plates.
- Deevey, E. S., G. B. Deevey & M. Brenner, 1980. Structure of zooplankton communities in the Petén Lake District, Guatemala. In W. C. Kerfoot (ed.). *Evolution and Ecology of Zooplankton Communities*. The University Press of New England. Hanover (NH); Lond.: 669–678.
- Dickinson, J. C. Jr., 1949. An ecological reconnaissance of the biota of some ponds and ditches in northern Florida. *Quart. J. Fla. Acad. Sci.* 11: 1–28.
- Dodds, G. S., 1926. Entomostraca from the Panama Canal Zone with description of one new species. *Occ. Pap. Mus. Zool. Univ. Michigan* 8: 1–27.
- Dumont, H. J., 1980. Zooplankton and the science of biogeography: The example of Africa. In W. C. Kerfoot (ed.). *Evolution and Ecology of Zooplankton Communities*. The University Press of New England. Hanover (NH); Lond.: 685–696.
- Dumont, H. J. & J. G. Tundisi, 1984. The future of tropical zooplankton studies. Epilogue to International Workshop on Tropical Zooplankton. *Hydrobiologia* 113: 331–333.
- Dussart, B. H., 1969. Les Copépodes des Eaux Continentales d'Europe Occidentale. Tome II: Cyclopoides et Biologie. Editions N. Boubée & Cie., Paris, 292 pp.
- Dussart, B. H., 1982. Copépodes des Antilles françaises. *Revue Hydrobiol. trop.* 15: 313–324.
- Dussart, B. H., 1984. Some Crustacea Copepoda from Venezuela. *Hydrobiologia* 113: 25–67.
- Dussart, B. H., C. H. Fernando, T. Matsumura-Tundisi & R. J. Shiel, 1984. A review of systematics, distribution and ecology of tropical freshwater zooplankton. *Hydrobiologia* 113: 77–91.
- Elmore, J. L., B. C. Cowell & D. S. Vodopich, 1984. Biological communities of three subtropical Florida lakes of different trophic character. *Arch. Hydrobiol.* 100: 455–478.
- Epp, R. W. & W. M. Lewis, Jr., 1980. The nature and ecological significance of metabolic changes during the life history of copepods. *Ecology* 61: 259–264.
- Fallavena, M. A. B., 1985. Composição e variações sazonal e espacial dos copépodes planctônicos (Crustacea, Copepoda) na Lagoa Negra, Município de Viamão, Rio Grande do Sul, Brasil. *Iheringia, Zool.* 65: 3–30.
- Forbes, E. B., 1897. A contribution to a knowledge of North American fresh-water Cyclopidae. *Bull. Ill. State Lab. nat. Hist.* 5: 27–83 + Plates VIII–XX.
- Freire, B. M. & R. M. Pinto-Coelho, 1986. Composição e distribuição horizontal do zooplâncton no Reservatório de Vargem das Flores, Betim/Contagem, Minas Gerais. *Ciênc. Cult.* 38: 919–927.
- Freitas, J. S., 1983. Variação sazonal e distribuição vertical de microcrustáceos planctônicos no lago Paranoá, DF. Thesis, Univ. Brasília. 110 pp.
- Giani, A., 1984. Distribuição horizontal do fitoplâncton e zooplâncton no lago Paranoá, Brasília, DF, Brasil. Thesis, Univ. Brasília. 148 pp.
- Gouvêa, E. P., 1978. Estágios de desenvolvimento pos-embriônico de *Thermocyclops minutus* (Lowndes) e de *Notodiaptomus confier* (Sars) (Crustacea, Copepoda) da Lagoa do Abaeté (Salvador – BA). Dissertation, Univ. S. Paulo. 131 pp.
- Hardy, E. R., 1978. Composição do zooplâncton em cinco lagos da Amazônia Central. Thesis, Univ. S. Carlos. 149 pp.
- Hardy, E. R., 1980. Composição do zooplâncton em cinco lagos da Amazônia Central. *Acta Amazon.* 10: 577–609.
- Harris, M. J., 1978. Copepoda of northern Mississippi with a description of a new subspecies. *Tulane Stud. Zool. Bot.* 20: 27–34.
- Heberer, G. & F. Kiefer, 1932. Zur Kenntnis der Copepod-enfauna der Sunda-Inseln. *Arch. naturgesch.*, N. F. 1: 225–274.
- Herbst, H. V., 1962. Crustacea aus dem Amazonasgebiet, gesammelt von Professor Dr. H. Sioli und Dr. R. Braun. 1. Litorale und substratgebundene Cyclopoida Gnathostoma (Copepoda). *Crustaceana* 3: 259–278.
- Herbst, H. V., 1967. Copepoda und Cladocera aus Südamerika. *Gewäss. Abwäss.* 44/45: 96–108.
- Herbst, H. V., 1986. Beschreibung des *Thermocyclops hastatus antillensis* n. ssp. mit einem Bestimmungsschlüssel für die Gattung *Thermocyclops* Kiefer, 1927. *Bijdr. Dierk.* 56: 165–180.
- Herrick, C. L., 1884. Part V. A final report on the Crustacea of Minnesota included in the Orders Cladocera and Copepoda. In N. H. Winchell (ed.). *The Geological and*

- Natural History Survey of Minnesota, The Twelfth Annual Report for the Year 1883. Johnson, Smith & Harrison. Minneapolis: 1-192 + Plates A-V.
- Herrick, C. L., 1895. Part I. Copepoda of Minnesota. In H. F. Nachtrieb (ed.). Second Report of the State Zoologist Including a Synopsis of the Entomotraca of Minnesota. Geological and Natural History Survey of Minnesota, Zoological Series II. The Pioneer Press Company. St. Paul: 39-138 + Plates 1-26.
- Hurlbert, S. H., ed. 1978. Aquatic Biota of Southern South America. San Diego State Univ., San Diego, California, 342 pp.
- Hurlbert, S. H., G. Rodriguez & N. D. Dos Santos, eds., 1981. Aquatic Biota of Tropical South America. Part 1. Arthropoda. San Diego State Univ., San Diego, California, 323 pp.
- Hurlbert, S. H. & A. Villalobos-Figueroa, eds. 1982. Aquatic Biota of Mexico, Central America and the West Indies. San Diego State Univ., San Diego, California, 529 pp.
- Hutchinson, G. E., 1951. Copepodology for the ornithologist. Ecology 32: 571-576.
- Infante, A., 1978a. The zooplankton of Lake Valencia (Venezuela). I. Species composition and abundance. Verh. int. Ver. Limnol. 20: 1186-1191.
- Infante, A., 1978b. Natural food of herbivorous zooplankton of Lake Valencia (Venezuela). Arch. Hydrobiol. 82: 347-358.
- Infante, A., 1981. Natural food of copepod larvae from Lake Valencia, Venezuela. Verh. int. Ver. Limnol. 21: 709-714.
- Infante, A. & W. Riehl, 1984. The effect of Cyanophyta upon zooplankton in a eutrophic tropical lake (Lake Valencia, Venezuela). Hydrobiologia 113: 293-298.
- Infante, A., W. Riehl & J. F. Saunders, 1979. Los copepodos del Lago de Valencia, Venezuela. Acta cient. venez. 30: 224-233.
- Junk, W. J., 1984. Ecology of the várzea, floodplain of Amazonian white-water rivers. In H. Sioli (ed.). The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dr. W. Junk N. V., The Hague: 215-243.
- Kiefer, F., 1927. Beiträge zur Copepodenkunde (VI). Zool. Anz. 74: 116-122.
- Kiefer, F., 1929. Crustacea Copepoda. 2. Cyclopoida Gnathostoma. Tierreich 53: 1-102.
- Kiefer, F., 1931. Zur Kenntnis der freilebenden Süßwasser-copepoden, insbesondere der Cyclopiden Nordamerikas. Zool. Jb., Syst. 61: 579-620.
- Kiefer, F., 1933a. Süß- und Brackwasser-Copepoden von Bonaire, Curaçao und Aruba. II. Cyclopoida. Zool. Jb., Syst. 64: 405-414.
- Kiefer, F., 1933b. Die freilebenden Copepoden der Binnengewässer von Insulinde. Arch. Hydrobiol., Suppl. 12: 519-621.
- Kiefer, F., 1936a. Brasilianische Ruderfusskrebse (Crustacea Copepoda), gesammelt von Herrn Dr. Otto Schubart. II. Mitteilung. Zool. Anz. 114: 129-133.
- Kiefer, F., 1936b. Brasilianische Ruderfusskrebse (Crust. Copepoda), gesammelt von Herrn Dr. Otto Schubart. V. Mitteilung. Zool. Anz. 116: 31-35.
- Kiefer, F., 1938a. Ruderfusskrebse (Crust. Cop.) aus Mexico. Zool. Anz. 123: 274-280.
- Kiefer, F., 1938b. Die von Wallacea-Expedition gesammelten Arten der Gattung *Thermocyclops* Kiefer. Int. Revue ges. Hydrobiol. 38: 54-74.
- Kiefer, F., 1952. Copepoda Calanoida und Cyclopoida. Explor. Parc Natn. Albert Miss. H. Damas 1935-1936, 21: 1-136 + 21 tables + 5 plates.
- Kiefer, F., 1956. Freilebende Ruderfusskrebse (Crustacea Copepoda). I. Calanoida und Cyclopoida. Ergebn. deutsch. limnol. Venezuela-Exped. 1952, 1: 233-268 + 2 tables.
- Kiefer, F., 1978. Freilebende Copepoda. Binnengewässer 26: 1-343.
- Lewis, W. H., Jr., 1979. Zooplankton Community Analysis: Studies on a Tropical System. Springer-Verlag, NY, 163 pp.
- Lindberg, K., 1954. Cyclopoïdes (Crustacés copépodes) du Mexique. Ark. Zool. 7: 459-489.
- Loftus, W. F. & J. A. Kushlan, 1987. Freshwater fishes of southern Florida. Bull. Fla. State Mus., Biol. Sci. 31: 147-344.
- Lowndes, A. G., 1934. Reports of an expedition to Brazil and Paraguay in 1926-7 supported by the trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland. Copepoda. J. linn. Soc., Zool. 39: 83-131.
- Maguire, B., Jr., 1971. Phytotelmata: biota and community structure determination in plant-held waters. Ann. Rev. Ecol. Syst. 2: 435-464.
- Mahoon, M. S. & Z. Zia, 1985. Taxonomic studies in Copepoda (Calanoida and Cyclopoida). Biologia 31: 251-292.
- Margalef, R., 1961. La vida en los charcos de agua dulce en Nueva Esparta (Venezuela). Mems Soc. Cient. nat. 'La Salle' 21: 75-110.
- Marsh, C. D., 1910. A revision of North American species of *Cyclops*. Trans. Wisc. Acad. Sci. Arts Lett. 26: 1067-1135.
- Marsh, C. D., 1913. Report on the freshwater copepods from Panama, with descriptions of new species. Smithsonian. misc. Collns 61: 1-31.
- Marsh, C. D., 1931. On a collection of Copepoda made in El Salvador by Samuel F. Hildebrand and Fred J. Foster of the U.S. Bureau of Fisheries. J. Washington Acad. Sci. 21: 207-209.
- Martínez de Ferrato, A., 1967. Notas preliminares sobre migraciones del zooplancton en cuencas isleñas del Paraná Medio. Acta zool. lilloana 23: 173-188.
- Matsumura-Tundisi, T., K. Hino & S. M. Claro, 1981. Limnological studies at 23 reservoirs in southern Brazil. Verh. int. Ver. Limnol. 21: 1040-1047.
- Matsumura-Tundisi, T. & W. Y. Okano, 1983. Seasonal fluctuations of copepod populations in lake Dom Helvécio

- (Parque Florestal, Rio Doce, Minas Gerais, Brazil). Rev. Hydrobiol. trop. 16: 35-39.
- Matsumura-Tundisi, T. & O. Rocha, 1983. Occurrence of copepod (Calanoida Cyclopoida and Harpacticoida) from 'Broa' Reservoir (São Carlos, São Paulo, Brazil). Revta bras. Biol. 43: 1-17.
- Matsumura-Tundisi, T. & J. G. Tundisi, 1976. Plankton studies in a lacustrine environment. I. Preliminary data on zooplankton ecology of Broa Reservoir. Oecologia (Berl.) 25: 265-270.
- McNaught, D. C., D. Griesmer & M. Kennedy, 1980. Resource characteristics modifying selective grazing by copepods. In W. C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. The University Press of New England. Hanover (NH); Lond.: 292-298.
- Menu Marque, S. A., 1982. *Thermocyclops decipiens* (Kiefer, 1929) una nueva especie para la fauna argentina (Copepoda, Cyclopoida). Physis, B. Aires, B. 41: 41-46.
- Montiel, E. & E. Zoppi de Roa, 1979. Notas sobre la disposición horizontal de copepodos en un cuerpo de agua temporal en el Alto Apure, Venezuela. Acta biol. venez. 10: 109-128.
- Moriarty, D. J. W., J. P. E. C. Darlington, I. G. Dunn, C. M. Moriarty & M. P. Tevlin, 1973. Feeding and grazing in Lake George, Uganda. Proc. roy. Soc. Lond., B. 184: 299-319.
- Nasci, R. S., S. G. F. Hare & M. Vecchione, 1987. Habitat associations of mosquito and copepod species. J. am. Mosquito Control Ass. 3: 593-600.
- Neumann-Leitão, S. & J. D. C. Nogueira, 1987. Rotíferos, cladóceros e copépodos de Pernambuco. I. Algumas espécies que ocorrem em viveiros de cultivo de camarões de Nova Cruz. Anais Soc. nordestina Zool., Teresina 2: 87-118.
- Nogueira, J. D. C., 1987. Ocorrência de copépodos nos viveiros de camarões do Cabo - Pernambuco - Brasil. Anais Soc. nordestina Zool., Teresina 2: 77-86.
- Okano, W. Y., 1980. Padrão de migração vertical e flutuação sazonal das principais espécies de Copepoda (Crustacea) do Lago Dom Helvécio, Parque Florestal do Rio Doce - MG. Thesis, Univ. S. Carlos. 168 pp.
- Osorio Tafall, B. F., 1941. Materiales para el estudio del microplancton del Lago de Pátzcuaro (México). I. Generalidades y fitoplancton. An. Esc. nac. Cienc. biol., México 2: 331-383.
- Osorio Tafall, B. F., 1943. Observaciones sobre la fauna acuática de las cuevas de la region de Valles, San Luis Potosí (México). Revta Soc. mexicana Hist. nat. 4: 43-71.
- Osorio Tafall, B. F., 1944. Biodinámico del lago de Pátzcuaro. I. Ensayo de interpretación de sus relaciones tróficas. Revta Soc. mexicana Hist. nat. 5: 197-227.
- Pearse, A. S., 1938. Fauna of the caves of Yucatán. Chapt. 11. Copepoda from Yucatán caves. Publs Carnegie Instn Washington 491: 153-154.
- Peckham, R. S. & C. F. Dineen, 1953. Summer plankton of Lake Amatitlan, Guatemala. Am. midl. Nat. 50: 377-381.
- Pennak, R. W., 1953. Fresh-water Invertebrates of the United States. The Ronald Press Company, NY, 769 pp.
- Pennak, R. W., 1978. Fresh-water Invertebrates of the United States. 2nd edition. J. Wiley & Sons, Inc., NY, 803 pp.
- Pesce, G. L., 1985. Cyclopids (Crustacea, Copepoda) from West Indian groundwater habitats. Bijdr. Dierk. 55: 295-323.
- Petkovski, T. K., 1956. Über einige Copepoden aus Höhlen- und Grundgewässern Jugoslaviens. Izdanija, Inst. Pisc. Rep. Macedoine 1: 185-208.
- Pinto-Coelho, R. M., 1983. Efeitos do zooplâncton na composição qualitativa e quantitativa do fitoplâncton no lago Paranoá, Brasília, DF, Brasil. Thesis, Univ. Brasília. 163 pp.
- Pinto-Coelho, R. M., 1987. Flutuações sazonais e de curta duração na comunidade zooplancônica do Lago Paranoá, Brasília-DF, Brasil. Revta bras. Biol. 47: 17-29.
- Pleša, C., 1981. Cyclopides (Crustacea, Copepoda) de Cuba. Result. Exped. biospeol. cubano-roumaines à Cuba 3: 17-34.
- Reed, E. B. & M. A. McQuaid, 1966. A new record of *Mesocyclops tenuis* (Marsh) with a description of the male (Copepoda: Cyclopoida). Proc. biol. Soc. Washington 79: 153-164.
- Reid, G. K. & N. J. Blake, 1969. Diurnal zooplankton ecology in a phosphate pit lake. Quart. J. Fla. Acad. Sci. 32: 275-284.
- Reid, J. W., 1985. Chave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da ordem Cyclopoida (Crustacea, Copepoda). Bolm Zool., S. Paulo 9: 17-143.
- Reid, J. W., 1988. Cyclopoid and harpacticoid copepods (Crustacea) from Mexico, Guatemala and Colombia. Trans. am. microsc. Soc. 107: 190-202.
- Reid, J. W., in press. *Thermocyclops decipiens* (Copepoda Cyclopoida): exemplo de confusão taxonômica. Acta limnol. bras. 2.
- Reid, J. W. & F. A. Esteves, 1984. Considerações ecológicas e biogeográficas sobre a fauna de copépodos (Crustacea) planctônicos e bentônicos de 14 lagoas costeiras do Estado do Rio de Janeiro. In L. D. Lacerda, D. S. D. Araújo, R. Cerqueira & B. Turcq (orgs.). Restingas: Origem, Estrutura, Processos. Univ. Federal Fluminense. Niterói, Brazil: 305-326.
- Reid, J. W., R. M. Pinto-Coelho & A. Giani, in press. Uma apreciação da fauna de copépodos (Crustacea) na região de Belo Horizonte, com comentários sobre espécies habitantes de Minas Gerais. Acta limnol. bras. 2.
- Reid, J. W. & P. N. Turner, in press. Planktonic Rotifera, Copepoda and Cladocera from Lakes Açú and Viana, State of Maranhão, Brazil. Revta bras. Biol. 48.
- Richard, J., 1895. Sur quelques entomostracés d'eau douce d'Haiti. Mem. Soc. zool. Fr. 8: 189-199.
- Richard, J., 1897. Entomostracés de l'Amerique du Sud, recueillis par Mm. U. Deiters, H. von Ihering, G. W. Müller et C. O. Poppe. Mem. Soc. Zool. Fr. 10: 263-301.

- Ringuelet, R. A., 1958a. Los crustáceos copépodos de las aguas continentales de la República Argentina. Sinopsis sistemática. Contrones cient. Fac. Cienc. exact. fis. nat. Univ. B. Aires, Zool., 1: 35–126.
- Ringuelet, R. A., 1958b. Primeros datos ecológicos sobre copépodos dulciacuícolas de la República Argentina. Physis, B. Aires 21: 14–31.
- Ringuelet, R. A., 1959. Novedades sobre copépodos de agua dulce de la Argentina. Physis, B. Aires 21: 314 (abstract).
- Ringuelet, R. A., 1968. Biogéographie des copépodes d'eau douce de l'Argentine. Biol. Am. austr. 4: 261–267.
- Ringuelet, R. A., 1972. Ecología y biocenología del habitat lagunar o lago de tercer orden de la región neotropical templada (Pampasia sudoriental de la Argentina). Physis, B. Aires 31: 55–75.
- Rioja, E., 1940a. Observaciones acerca del plancton del lago de Pátzcuaro. An. Inst. Biol. Univ. México 11: 417–425.
- Rioja, E., 1940b. Notas acerca de los crustáceos del lago de Pátzcuaro. An. Inst. Biol. Univ. México 11: 469–475.
- Rioja, E., 1942. Observaciones acerca del plancton de la laguna de San Felipe Xochiltepec (Puebla). An. Inst. Biol. Univ. México 13: 519–526.
- Rocha, O. & T. Matsumura-Tundisi, 1976. Atlas do Zooplâncton (Represa do Broa, São Carlos). Vol. I. Copepoda. Univ. S. Carlos, 68 pp.
- Rosen, D. E., 1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431–464.
- Ruttner, F., 1952. Planktonstudien der deutschen Limnologischen Sunda-Expedition. Arch. Hydrobiol. 21: 1–274.
- Schindler, J. E., 1971. Food quality and zooplankton nutrition. J. anim. Ecol. 40: 589–595.
- Schubart, O., 1938. Considerações sobre as investigações nas águas de Pernambuco. Archos Inst. Pesq. agron., Pernambuco 1: 26–57.
- Sendacz, S., 1984. A study of the zooplankton community of Billings Reservoir – São Paulo. Hydrobiologia 113: 121–127.
- Sendacz, S. & E. Kubo, 1982. Copepoda (Calanoida e Cyclopoida) de reservatórios do Estado de São Paulo. Bolm Inst. Pesca 9: 51–89.
- Sendacz, S., E. Kubo & M. A. Cestaroli, 1985. Limnologia de reservatórios do sudeste do Estado de São Paulo, Brasil. VIII. Zooplâncton. Bolm Inst. Pesca 12: 187–207.
- Sendacz, S., E. Kubo & L. P. Fujiara, 1984. Further studies on the zooplankton community of an eutrophic reservoir in southern Brazil. Verh. int. Ver. Limnol. 22: 1625–1630.
- Smith, K. E. & C. H. Fernando, 1978. The freshwater calanoid and cyclopoid Crustacea of Cuba. Can. J. Zool. 56: 2015–2023.
- Smith, K. E. & C. H. Fernando, 1980. Guía para los copépodos (Calanoida y Cyclopoida) de Cuba. Editorial Academia, Academia de Ciencias de Cuba, Havana, 28 pp.
- Straškraba, M., M. Legner, J. Fott, J. Holčík, M. Komarkova-Legnerova, K. Holčíkova & M. Perez Eirez, 1969. Primera contribución al conocimiento limnológico de las lagunas y embalses de Cuba. Acad. Cienc. Cuba, Biol. 4: 1–44.
- Tait, R. D., R. J. Shiel & W. Koste, 1984. Structure and dynamics of zooplankton communities, Alligator Rivers Region, N. T., Australia. Hydrobiologia 113: 1–13.
- Uéno, M., 1939. Zooplankton of Lago de Pátzcuaro, Mexico. Annotnes zool. jap. 18: 105–114.
- Wierzejski, A., 1892. Skorupiaki i wrotki (Rotatoria) slodkowodnie zebrane u Argentynie. Anz. Akad. Wiss. Krakau 24: 229–246 + 3 plates.
- Wilson, C. B., 1936. Copepods from the cenotes and caves of the Yucatán Peninsula, with notes on Cladocerans. Publ. Carnegie Instn Washington 457: 77–88.
- Yeatman, H. C., 1959. Free-living Copepoda: Cyclopoida. In W. T. Edmondson (ed.). Ward & Whipple's Fresh-water Biology, 2nd edition. J. Wiley & Sons, Inc. NY: 795–815.
- Yeatman, H. C., 1977. *Mesocyclops ellipticus* Kiefer from a Mexican cave. In J. R. Reddell (ed.), Studies on the Caves and Cave Fauna of the Yucatán Peninsula. Bull. Assoc. Mex. Cave Stud. 6: 5–7.
- Zoppi de Roa, E., 1972. Zooplankton de la Laguna de Campona, Edo. Sucre, Venezuela. Cuad. oceanogr., Univ. Oriente 3: 49–53.

Notes added in proof:

1. The author has recorded *Thermocyclops inversus* in material from several ephemeral ponds and cemetery pits in greater New Orleans, State of Louisiana, U.S.A., collected in spring 1988 by G. Marten.
2. M. A. J. Carvalho has observed adults of *Thermocyclops decipiens* (reported as *T. crassus*) preying upon their own nauplii, cladocerans, and larvae of Chironomidae; she also noted declines of populations of *T. decipiens* during blooms of cyanophycean algae (*Anabaena spiralis* and *Microcystis* sp.) in Americana Reservoir, São Paulo, Brazil.
Reference: Carvalho, M. A. J., 1984. On the feeding behaviour of *Thermocyclops crassus*. Crustaceana, Suppl. 7: 122–125.