Redescription of *Microdiaptomus cokeri* (Crustacea: Copepoda: Diaptomidae) from caves in central Mexico, with the description of a new diaptomid subfamily

M. Elías-Gutiérrez and E. Suárez-Morales

(ME-G) Universidad Nacional Autónoma de México, Campus Iztacala. Av. De los Barrios s/n.
Los Reyes Iztacala, Tlalnepantla 54000, Edo. de México. Mexico;
(ES-M) El Colegio de la Frontera Sur (ECOSUR)—Chetumal. A.P. 424. Chetumal,
Quintana Roo 77000. Mexico

Abstract.—Microdiaptomus cokeri, the only true troglobitic copepod from Mexico, is redescribed on the basis of new material collected from the type locality, Cueva Chica cave, state of San Luis Potosi, Mexico. This species bears a unique combination of features not present in any other subfamily of Diaptomidae: legs 1–4 with two-segmented exopods, one-segmented endopods, one seta on the inner margin of the first exopodal segment of legs 1–4, a right male fifth leg with a 1-segmented endopod, and absence of sensillae on pediger 5 and on genital somite. Therefore, the erection of the new subfamily Microdiaptominae is appropriate. The genus Troglodiaptomus, previously accomodated in the subfamily Speodiaptominae, was found to be closely related to Microdiaptomus and is reallocated to the Microdiaptominae. Because of its apparent limited distribution in a system related to a highly polluted basin, it is necessary to follow this species closely to assess its true distributional range and to establish its conservation status.

The aquatic fauna of Mexican caves has been surveyed for decades, and some checklists are available (Reddell & Mitchell 1971, Reddell 1977); however, several taxonomic groups remain practically unknown. Particularly, the troglobitic copepod fauna of Mexico needs revision, because several of the earlier identifications of these crustaceans seem to be unaccurate (Reid 1990, Suárez-Morales et al. 1996).

The troglobitic copepod genus *Microdiaptomus* was originally described as a subgenus of *Diaptomus* by Osorio-Tafall (1942), from specimens collected at caves located in the area of Sierra de El Abra, state of San Luis Potosí, central Mexico. The genus can be separated from all other diaptomid genera by several features, but mainly by legs 1–4 with 2-segmented exopods and 1-segmented endopods, a male right antennula with segments 13 to 18 un-

dilated, female fifth leg without a third exopodal segment, and by the presence of one pad on the second exopodal segment of the male left fifth leg (Osorio-Tafall 1942, Dussart & Defaye 1995). The type species (by monotypy) of this genus is *Microdiaptomus cokeri*. With a size of ca. 0.7 mm, it is one of the smallest diaptomids known.

According to Osorio-Tafall (1942) data, and our own records, this species has been collected exclusively in caves along the Sierra de El Abra mountain system (Cueva Chica, Cueva de los Sabinos, Sótano de Montecillos), San Luis Potosí, Mexico. The type locality (Cueva Chica) has not been sampled for its planktonic fauna since 1940 (Reddell & Mitchell 1971). The type material was deposited in the collection of the Escuela Nacional de Ciencias Biológicas of the Mexican Instituto Politécnico Nacional, but was lost decades ago. Since this loss,

preserved specimens of *M. cokeri* were not available until late 1995, when Janet W. Reid identified this species from material collected by Thomas M. Iliffe in May, 1991 at Sotano de Montecillos, a non-type locality (USNM 264171). A recent survey of the type locality yielded several adult male and female specimens of *Microdiaptomus cokeri*. In this work the species is redescribed based on this new material. Additional morphological data, including a description of mouthparts and thoracic legs, are also provided.

Methods

Specimens of Microdiaptomus cokeri were collected during a zooplankton survey carried out on 28 February 1996 at Cueva Chica cave, state of San Luis Potosí, Mexico. Samples were collected using a plankton net with a 0.05 mm mesh. The material was fixed in a 4% sugar-formalin solution. All copepods were sorted and preserved in 70% ethanol with a drop of glycerin. Male and female specimens of M. cokeri were sorted from the samples under a stereomicroscope and then processed for examination. Descriptions were made based on observations of whole and dissected specimens mounted in glycerin. Drawings were made with the aid of a camera lucida. A Student's "t" test was performed to detect length differences in both males and females from the two localities surveyed. Abbreviations used for descriptions are: Exp = Exopod, Enp = Endopod, P1-P4 = legs 1-4.

Material Examined

Cueva Chica: two adult males, one adult female deposited in the National Museum of Natural History at Washington, D.C., under catalog number USNM-285516; eight adult males, three adult females deposited in the Zooplankton Reference Collection of UNAM, Campus Iztacala, Tlalnepantla, Mexico, catalog numbers COP-197 and 198. One male and one female deposited in

the Zooplankton Collection of El Colegio de la Frontera Sur, Chetumal, Mexico, under number ECO-CH-Z00223.

Sótano de Montecillos: three adult males, three adult females deposited at the Museum National d'Histoire Naturelle (Paris), catalog numbers MNHN-Cp1131 and MNHN-Cp1132, respectively. Additional material at El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico, and Zooplankton Reference Collection at UNAM, Campus Iztacala, Mexico (COP-199 and 200).

Croatia: Two male and three female specimens of *Troglodiaptomus sketi* Petkovski, 1978 from the type locality, near Rovigno (=Rovinj).

Slovenia: A female specimen of *T. sketi* from Kompoljska cave, collected in August 18, 1996.

Family Diaptomidae Baird, 1850 Microdiaptominae, new subfamily

Diagnosis.—Legs 1–4 with 2-segmented exopods, 1-segmented endopods, with or without a seta on inner margin of the first segment of exopod. One or two setae on inner margin of second exopodal segment of legs 1–4. One outer distal spine on first exopodal segment of leg 1 and on second exopodal segments of legs 2–4. Endopod of male right leg 5 absent or 1-segmented, of left leg, 1 or 2-segmented. Endopods of female leg 5 reduced to a small bulb or 1-segmented. In both sexes, sensillae absent on pediger 5 and on female genital somite.

Remarks.—Previous assignment of M. cokeri to Diaptominae (e.g., Dussart & Defaye 1995) was based on the original description of Osorio-Tafall. However, in that work, no information was given on segmentation or setation patterns of the swimming legs or of most cephalic appendages.

Borutzky (1962) erected the subfamily Speodiaptominae to allocate the troglobitic *Speodiaptomus birsteini* Borutzky, 1962. This taxon is featured mainly by a 2/1, 2/2, 2/2, 3/2 segmentation pattern in legs 1–4.

The original diagnosis of this subfamily was later changed by Petkovski (1978) to accomodate the new genus Troglodiaptomus. The new definition of the Speodiaptominae included characters such as a variable segmentation pattern of legs 1-4 with exopods and endopods as: 2/1; 2/1-2; 2/1-2; 2-3/1-2, first exopod of first legs without inner seta, no dilated segments 13-18 on male right antennule, and endopod of the male right fifth leg absent (Troglodiaptomus) or 2-segmented (Speodiaptomus). This expanded scheme allowed both genera to be included within the Speodiaptominae; according to this diagnosis, M. cokeri should be included in this subfamily.

The main criterion used by Petkovski (1978) to include Troglodiaptomus in the Speodiaptominae was the reduction of the swimming legs as an adaptation to troglobious life. From the comparison of this taxon with other troglobitic genera such as Spelaeodiaptomus Dussart, 1970 and Speodiaptomus, he concluded that Troglodiaptomus represented the cave-adapted extreme while Spelaeodiaptomus with fewer reductions and a member of the Diaptominae, showed the least adapted pattern. He considered that these reductions related Speodiaptomus and Troglodiaptomus, and included both genera in the Speodiaptominae. However, he recognized the possibility that Troglodiaptomus could be a representative of a new subfamily.

Borutzky (1962) and Borutzky et al. (1991) emphasized the taxonomic relevance of the segmentation pattern of swimming legs within the Calanoida at the subfamily level. This is the main criterion we used herein to justify the creation of the new subfamily Microdiaptominae. Following this criterion, both, *Troglodiaptomus* and *Microdiaptomus* should be included in the new subfamily. The new subfamily includes the only two diaptomids bearing this unique segmentation pattern of 2/1 in exopods/endopods of legs 1–4. Moreover, *Troglodiaptomus sketi* Petkovski, 1978, which is an hypogean form (Brancelj 1987, 1991; Dus-

sart & Defaye 1995), and is the type species of Troglodiaptomus, shares some relevant additional characters with M. cokeri. Such characters include the structure of the male right antennule with undilated segments (in both only segment 14 is slightly wider than the others), the absence of sensilla on fifth pedigerous or genital somites, and the structure of other appendages such as the antennae and the maxillipeds. The male and female fifth legs of both Troglodiaptomus and Microdiaptomus have strong similarities between them (see Table 1). These legs differ from Speodiaptomus in the general structure but particularly in the endopods, which are 2-segmented in the right male and female P5 of the latter (see Petkovski 1978, Brancelj 1987, Dussart & Defaye 1995). The original Borutzky's diagnosis of the Speodiaptominae should then be retained.

The information available does not allow us to conclude if a common ancestor existed for both, the European *Troglodiaptomus* and the American *Microdiaptomus* or if they evolved independently in a similar environment from epigean forms. Considering the peculiar characters they share, it is evident that both forms are related. *Microdiaptomus cokeri* is distributed in caves located in one of the geologically oldest zones of Mexico (Padilla y-Sánchez & Aceves-Quesada 1990).

Microdiaptomus cokeri (Osorio-Tafall 1942)

Microdiaptomus cokeri Osorio-Tafall, 1942:206–210, figs. 1–17 (Diaptomus (Microdiaptomus) cokeri); Osorio-Tafall, 1943:49–53, 56 (Diaptomus (Microdiaptomus) cokeri); Wilson, 1959:780, fig. 29.67 (Diaptomus cokeri); Reddell & Mitchell, 1971:141 (Diaptomus (Microdiaptomus) cokeri); Reid, 1990:179; Dussart & Defaye, 1995:180–181, fig. L73.

Figs. 1-23

Description.—Male: Mean body length of Cueva Chica specimens: 0.723 mm;

| Table 1.—Comparison of | characters among | Microdiaptomus | cokeri, | Stygodiaptomus | birsteini and | Troglo- |
|------------------------|------------------|----------------|---------|----------------|---------------|---------|
| diaptomus sketi. | | | | | | |

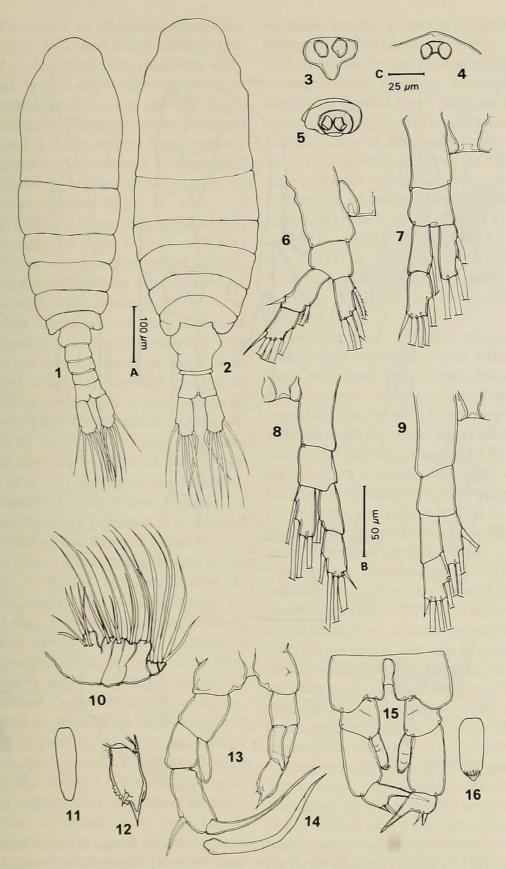
| Character | M. cokeri | S. birsteini | T. sketi |
|---------------------------------------|-----------------|-----------------|-----------------|
| Segments on P1-P4 | | | |
| (exp/end) | 2/1;2/1;2/1 | 2/1;2/2;2/2;3/2 | 2/1;2/1;2/1;2/1 |
| Inner setae on exp 1 | | | |
| P1-P4 | 1;1;1;1 | 0;0;0;0 | 0;0;0;0 |
| Outer spines on exp 1 | | | |
| P1-P4 | 1;0;0;0 | 1;1;1;1 | 1;0;0;0 |
| Setae on exp 2 P1-P4 | | | |
| inner/apical | 1/3;2/2;2/2;2/2 | 2/3;2/3;2/3;1/0 | 2/3;2/3;2/3;2/3 |
| Outer spine on exp 2 | | | |
| P1-P4 | 1;1;1;1 | 1;1;1;1 | 1;1;1;1 |
| Setae on terminal segment of endopods | | | |
| P1-P4 inner/apical | 1/3;2/2;2/2;2/2 | 1/3;2/3;2/3;2/3 | 0/3;0/3;0/3;0/3 |
| 2-segmented endopod(s) | | | 0,0,0,0,0,0,0 |
| in male P5 | No | Yes | Yes |
| 2-segmented endopod(s) | | | |
| in female P5 | No | Yes | No |
| Reduced endopod in | | | |
| female P5 | No | No | Yes |

range = 0.69–0.74 mm. Sótano de Montecillos, mean: 0.752 mm; range 0.70–0.79 mm. Body slender, with a typical diaptomid shape (Fig. 1). Eyes or eye-related structures absent or quite reduced, body unpigmented. Rostral filaments absent, rostrum represented by two rounded, heavily chitinized projections (Fig. 4).

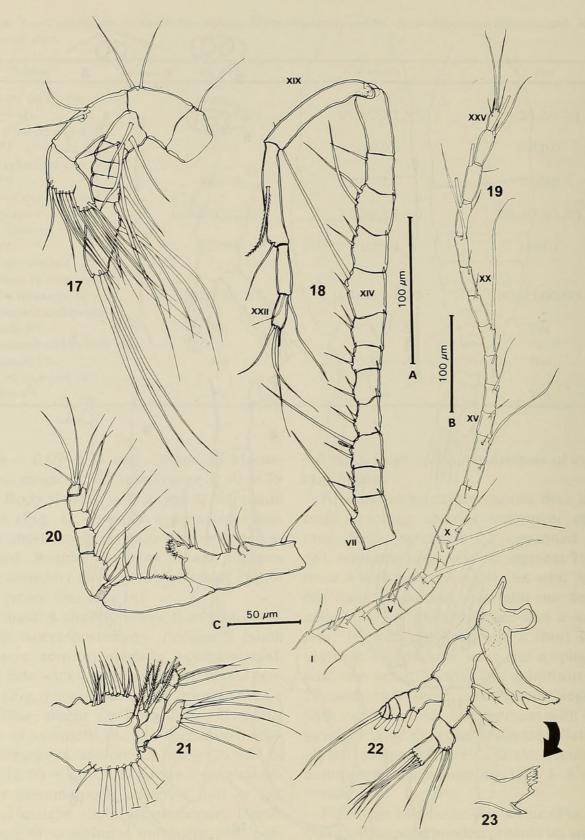
Pediger 4 slightly wider than pediger 5, which tapers posteriorly. Pediger 5 (sixth thoracic somite) slightly asymmetrical, right side with a more evident rounded process (Fig. 1), without dorsal ornamentation. Sensillae absent on both sides. Urosome (Fig. 1) symmetrical, five-segmented, relative lengths of urosomites being: 26.6:21.6: 16.8:15:20 = 100. Urosomite 1 (genital somite) asymmetrical, posterior half of left lateral margin slightly protuberant. Dorsal surface of urosomites unornamented, posterior margins smooth. Caudal rami nearly two times longer than wide, inner and outer margins smooth, with 5 terminal caudal setae subequal in length and width, plus the dorsal one, subterminally inserted. Caudal setae finely plumose, non-articulated, relatively short, about 2.0 times length of caudal rami. Inner and outer margins of caudal rami naked.

Antennules relatively shorter than in female, reaching anterior margin of caudal rami. Right antennule 22-segmented (Fig. 18), with one large seta on segment 7; segment 8 with one spine and one seta; 9 with one long and a short setae plus one aesthetasc; 10-13 each with spine and a longer seta; 14 with one long and a short setae; segment 15 with one setae and a spine; 16 with two setae; 17 with one spiniform seta; 20 with two setae, penultimate segment with two long seta; last segment with three terminal setae plus one aesthetasc. Setation of left antennule as in female. Antennae, mouthparts and swimming legs 1-4 as in female.

Fifth legs biramous: Right one (Fig. 13): Coxa with small rounded process on anterolateral margin tipped with short sensilla. Basis 1.2 times as long as first exopodal segment and larger than that of left leg. Outer margin of exopod 1 almost straight, inner margin smooth. Exopod 2 ca. 1.7 times length of exopod 1. Lateral spine curved and borne at distal $\frac{2}{3}$ of segment,



Figs. 1–16. *Microdiaptomus cokeri* Osorio-Tafall, 1942. 1. Habitus, male. 2. Habitus, female. 3. Rostral area, female. 4. Rostral area, male. 5. Genital opening, female. 6. First leg, female. 7. Second leg, female. 8. Third leg, female. 9. Fourth leg, female. 10. Second maxilla, female. 11. Right fifth endopod, male. 12. Close view of second segment, fifth left exopod, male. 13. Fifth leg, frontal view, male. 14. Variation in the shape of terminal claw, right exopod, male. 15. Fifth leg, anterior, female. 16. Fifth left endopod, female. Scale bar A: Figs. 1,2; B: Figs. 6–16; C: Figs. 3–5.



Figs. 17–23. *Microdiaptomus cokeri* Osorio-Tafall, 1942. 17. Antenna, female. 18. Right antennule, male, segments VII–XXII. 19. Left antennule, female. 20. Maxilliped, female. 21. First maxilla, female. 22. Mandible, female. 23. Mandibular blade, female. Scale bar A: Fig. 18; B: Fig. 19; C: Figs. 17,20–23.

about half as thick as endopod, almost 0.7 length of exopod 2, and about same length as exopod 1. Terminal claw relatively slender, curved, with a slight sigmoid shape in some animals, inner margin smooth (Figs. 13, 14), tapering gradually from enlarged base, about 1.4 times longer than exopods 1 and 2 combined. Endopod 1-segmented reaching about ½ beyond distal margin of first exopodal segment (Figs. 11, 13).

Left leg 5 (Fig. 13) reaching proximal \(\frac{1}{2} \) of inner margin of right second exopodal segment. Coxa with small rounded process tipped with short sensillum near outer margin. Basis with short lateral seta on outer margin. First exopodal segment almost as long as segment 2, in some specimens with short hairs on distal portion of inner margin. Second exopodal segment ending in acute distal process with a stout, smooth subterminal spiniform structure. Along inner margin of distal pad in exopod 2, there are several rows of 8-10 small vesicle-like structures (Fig. 12). Endopod one-segmented, asymmetrical, narrowing abruptly at distal 1/3 and reaching proximal 1/3 of exopod 2. Tip of endopod with short hairs.

Female: Cueva Chica, mean length 0.723 mm; range = 0.64-0.78 mm. Sótano de Montecillos, mean 0.814 mm; range = 0.74-0.89 mm. Prosome relatively wide in dorsal view, symmetrical, first pedigerous somite separated from cephalic area (Fig. 2). Pedigers 4 and 5 separated, pediger 5 with rounded posterolateral margins, smooth, with no sensilla on them. Urosome with three segments, relative lengths of each being: 61.5:13.4:25.1 = 100. Genital double somite about 1.6 times as long as remaining urosomites together, slightly asymmetrical in dorsal view, with lateral rounded protuberances, and no lateral sensillas present. Genital double somite ventrally expanded, with genital openings as shown in Fig. 5; posterior margin slender. Second somite very short, partially telescoped into the genital double somite. Anal somite large. Furca and caudal setae similar to male. Rostral points represented by two strong, rounded projections (Fig. 3).

Antennules longer than in male (Fig. 19), 25-segmented, reaching beyond posterior margin of caudal rami. Seta on segment 1 short, reaching distal margin of segment 2. Largest setae on segments 7, 9, 14, 18, and 21. Armature per segment as follows (Roman numerals = segment, Arabic numerals = number of setae, a = aesthetasc, sp = spine): I(1), II(4 + a), III(1), IV(1), V(1 + a), VI(1), VIII(1), VIII(1), IX(2), X(sp), XI(1), XIII(2), XIII(1), XIV(2), XV(1), XVII(1), XVIII(1), XVIII(1), XIII(2), XXIII(2), XXIIII(2), XXIII(2), XXIII(2), XXIII(2), XXIII(2), XXIII(2), XXIIII(2

Antenna (Fig. 17) with exopod slightly longer than endopod. Coxa with one seta, basis with two long setae. Endopod with two segments, distal portion of terminal endopodal segment with two lobes, inner lobe with six anterior setae; outer lobe with one short, two medium-sized, and five long setae. Exopod 6-segmented, with 4 setae on first segment (fused original segments 1 + 2), one seta, each on segments 2–5, and terminal segment with two setae on proximal third plus three terminal setae.

Mandible (Fig. 22) with 6–7 teeth on gnathobase; outermost ventral tooth relatively high (Fig. 23). Basis with three subequal setae, two of them plumose; endopod with 2 segments, proximal segment with protuberance on inner margin, with four setae, two medium-sized, and two long; distal segment short, as long as wide, with 7 anterior and one posterior setae. Exopod 5-segmented, with 1, 1, 1, 1 and 2 setae.

First maxilla (Fig. 21) with praecoxal arthrite with 12 spiniform setae, 8 of which are apical, plus 4 posterior setae. Coxal epipodite with 8 spiniform setae, proximal two shorter than the others. Two and three setae on coxal and first basal endites, respectively. Endopod 2-segmented, articulating with basis, with two seate on first segment and four setae on second. Exopod with 6 long setae.

Second maxilla (Fig. 10) with two prae-

coxal and two coxal lobes, and well developed basal lobe carrying 5, 3, 3, 3 and 3 setae. Endopod 2-segmented, with two setae on first and three on distal segments.

Maxilliped (Fig. 20) well developed. Coxa with three coxal endites, proximal and medial with three subequal setae each, third endite represented by anterior protuberance projecting beyond next segment, with short hairs on tip and 4 simple setae inserted along process. Basis with group of three setae increasing in length distally, inserted on distal half of inner margin; proximal half hairy. Endopod 6-segmented, with first segment partially fused to basis, bearing 2 subequal setae. Second endopodal segment with three subequal setae, third and fourth with 2, fifth with two setae; terminal segment with one short and four long setae.

Legs 1–4 with 1-segmented endopods and 2-segmented exopods, coxa and basis without setae (Figs. 6–9). Armament formula for swimming legs as:

| | coxa | basis | exopod | endopod |
|-------|------|-------|--------------|-----------|
| leg 1 | 0-0 | 0-0 | I-1; I, 3, 1 | 0-0, 2, 2 |
| leg 2 | 0-0 | 0-0 | 0-1; I, 3, 1 | 0-0, 2, 2 |
| leg 3 | 0-0 | 0-0 | 0-1; I, 3, 1 | 0-0, 2, 2 |
| leg 4 | 0-0 | 0-0 | 0-1; I, 3, 1 | 0-0, 2, 2 |

Leg 5 (Fig. 15): Coxa with small protuberance tipped with short spiniform structure on the middle of inner distal margin. Basis with inner margin slightly rounded. Endopod one-segmented, relatively wide, reaching two thirds of first exopodal segment; tip protruding in a relatively acute process, partly covered with short hairs (Fig. 16). First exopodal segment about 2 times longer than exopod 2, with smooth margins. Inner margin of claw armed with short row of hairs along distal half of both margins. Exopod 3 absent, represented by two short, strong, subequal spiniform processes.

Habitat.—Cueva Chica cave (21°51′35″N, 98°56′07″W) is located within a private

farm near the town of El Pujal, south of Ciudad Valles, state of San Luis Potosi, central Mexico. Access to the cave is limited, but the system is well preserved, considering that it was first surveyed more than 60 years ago by Hubbs & Innes (1936), who described the blind fish currently known as *Astyanax mexicanus jordani*. Breder (1942) published a detailed synthesis of the ecology, geology, hydrology, and physiography of this cave, with an explicit account of the blind fish.

A brief description of the cave is as follows: the main entrance is a low opening which leads into a large chamber originating a partially flooded passage that opens into a small chamber with a pool; access into this secondary chamber is wide and about 1 m high. There is another larger pool at the bottom, which was not surveyed by us because the access was covered by excreta of several bat species (Atribeus jamaicensis yucatanicus Allen, Desmodus rotundus murinus Wagner, Mormoops megalophylla megalophylla Peters, Pteronotus davyi fulvus (Thomas), P. parnellii (Gray), Natalus stramineus Gray) dwelling in the cave (Reddell & Mitchell 1971). Therefore, all our sampling was made only in the first pool and flooded passage. Microdiaptomus cokeri was present only in the pool. The pool water is clear, with abundant blind fishes. It is a vase-shaped water body; its main physical and chemical characteristics are summarized in Table 2. Several cyclopoid copepods were collected. Sótano de Montecillos is also part of the Sierra de El Abra system, and is located north of Ciudad Valles.

Remarks.—Microdiaptomus cokeri has been recorded in at least three different caves of the Sierra de El Abra system, which contains 39 caves (Reddell & Mitchell 1971). Its occurrence in several other caves in this mountain system should be expected, since it could follow a similar distributional pattern to that of other local troglobionts, such as the blind fish Astyanax

Table 2.—Main physical and chemical variables from the surveyed pool in Cueva Chica. For comparison data of Breder (1942) are shown (measurements from March 11, 1940). ** Data from the adjacent pool, possibly connected to one surveyed in this work. NA = not available.

| adhla salkanta a 100 da | Data from November 28, 1996 | Data from Breder (1942) |
|--------------------------------------|-----------------------------------|----------------------------|
| Altitude above sea level (m) | 185 | NA |
| Depth (m) | 4.5 | NA |
| Temperature (°C) | 26 | 26.1-27 |
| Dissolved oxygen (mg/l) | 1.2 | NA |
| рН | 6.88 | 8.0 |
| Conductivity (µS) | 700 | NA |
| Alkalinity (mg CaCO ₃ /l) | 343 | 282** |
| Hardness (mg CaCO ₃ /l) | 205.8 | 310** |

mexicanus jordani, widely distributed in this zone (Wiley & Mitchell 1971).

Specimens from Sótano de Montecillos were larger (p > 0.95) than those collected from Cueva Chica. This observation is similar to the differences reported by Osorio-Tafall (1942, 1943), who compared material from Los Sabinos Cave and Cueva Chica. This author stated that space limitation and temperature were factors associated with this size difference. It is possible that predation, mainly from the blind fish, could be added to these factors, but further analysis is needed to support this statement.

The feeding habits of *M. cokeri* are still unknown, but the type of mandibular blade, the development of its other mouthparts, and the slender aspect of its thoracic appendages suggest that it is an epibenthic, omnivorous species feeding upon particles deposited on the walls of the pool. Most of the specimens were collected by littoral surface hauls.

The restricted distributional range of this copepod is probably shared by the fish Astyanax mexicanus jordani. Both species dwell in an ecologically fragile environment since the surveyed caves are hydrologically connected to the highly polluted Pánuco Basin (Vázquez-Gutiérrez 1994). We consider that these conditions would favor the idea of M. cokeri as a species to be

followed closely in the next years. A more intense sampling in the area would be required to assess the true distributional range and conservation status of this troglobitic copepod. In 1996 the IUCN Red List included 37 diaptomid copepod species, of which several are cavernicole (Baillie & Groombridge 1996).

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