

LYCASTILLA CAVERNICOLA, A NEW FRESHWATER
NEREIDID FROM AN INLAND MEXICAN CAVE
(POLYCHAETA: NEREIDIDAE: NAMANEREIDINAE)

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Abstract.—A new genus and species of nereidid (*Lycastilla cavernicola*) is described from a freshwater pond within a cave found in Mexico. Its affinities with the other five genera of the subfamily are discussed with comments on the genus *Namanereis*. The new genus has more affinities with *Lycastoides* Johnson than with other genera in the subfamily despite the difference in the structure and number of tentacular cirri, and is presumably a relict species. The habitat is described and some remarks on the biology of the species are given.

In the course of a survey of a Mexican cave, a freshwater pool was found to contain a population of a previously undescribed species of Nereididae. The available material is of particular interest, not only on account of its extraordinary freshwater habitat, an elevated cave 1650 m above sea level and 176 km from the Pacific ocean, but also because it belongs to a new genus more related to *Lycastoides* than to the other genera of the subfamily that occur in freshwater and euryhaline habitats.

Study Area

The material was collected by one of us (L.E.) in the "Polychaete Pond" (after Espinasa 1989) of Isote cave (Guerrero State, Taxco de Alarcón Municipality, Mexico, 18°36'40"N, 99°33'25"W) at a distance of 176 km from the Pacific Ocean and at an altitude of 1650 m. The cave is 1567 m long and 197 m deep below ground level. The pool where the nereidids were found is 500 m from the cave entrance, at a depth of 70 m below ground level in a completely dark section of the cave. The pool is maintained by water falling from a second, smaller, more elevated pool devoid of organisms, which in turn receives its waters through perco-

lation from the surface soil. The overflow goes to the main river at a lower level from which the pool is permanently disconnected (for a detailed description of the cave topography, see Espinasa 1989).

The pool, 80 m in length and 1-2 m in width, has a mean depth of 1-1.5 m. The cave is accessible only during the dry season (November through April). The nereidids were concentrated at a section where there was little flow (approximately 1 l/sec). The sediment was mud on the surface (about 1/2 cm) and sandy below.

Cave formation.—The limestone rock was formed during the lower Cretaceous period (Albian, Cenomanian and Turonian). Elevation occurred at the end of the Cretaceous (Maastrichtian) when erosion began. The presence of an igneous rock (Riolite tilzapotla) overlaying the limestone from which the water that formed the cave comes, seems to indicate that the cave was not formed until the late Oligocene (López-Ramos 1974). It is also known that the cave was already formed in the Quaternary because there is evidence (in the cave sediments) of climatic changes related to this period (Espinasa R., pers. comm.).

Thus, if the cave was formed at some point between the Oligocene and the Quaternary,

there is reason to suppose that the worms were separated from the outside communities more or less at the same period.

Materials and Methods

Sampling was done in November, during the dry season, the only period of the year when access to the cave is possible. The organisms that were seen crawling on the bottom of the pond were placed directly into a vial and fixed with 6% formalin, except for 6 of them which were placed alive into a vial with some water and sediment. After a few days in the fixative, the polychaetes were transferred to 70% alcohol. The live specimens were kept in an aquarium in the dark, occasionally adding tap water to compensate for evaporation.

Granulometric characterization of the sediment was done by sorting analysis by mesh. Organic matter content in the sediment was calculated as percent of carbon following the method of Gaudette et al. (1974).

All illustrations were made with the aid of a camera lucida attached to a stereo or a compound microscope.

The morphological terminology is derived from Hartman (1959) and Pettibone (1963).

The types are deposited in the following collections: ICML-MEX (Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico); USNM (Smithsonian Institution, Washington, D.C., U.S.A.); BMNH (British Museum of Natural History, London, England); AM (Australian Museum, Sydney, Australia); and HZM (Zoologisches Museum, Hamburg, Germany).

Lycastilla, new genus

Diagnosis.—Antennae, tentacular cirri and anal cirri articulate, well developed. Prostomium cleft anteriorly; with paired antennae, biarticulate palps. Tentacular segment with 3 pairs of tentacular cirri.

Eversible pharynx without chitinous paragnaths or soft papillae; jaws with few teeth.

Parapodia uniramous, with neuropodial ligule only, dorsal and ventral cirri; notoaciculum and neuroaciculum present. Notoaciculum distally recurved. Setae include heterogomph spinigers and falcigers. Two anal cirri.

Etymology.—The name is a free derivation of *Lycastopsis* and *Lycastoides*, close genera, Gender: feminine.

Type species.—*Lycastilla cavernicola*, new species.

Lycastilla cavernicola, new species

Figs. 1A–E, 2A–F

Material examined.—Mexico, Guerrero State, Taxco de Alarcón municipality, Isote cavern, 18°36'40"N, 99°33'25"W.; altitude 1650 m; collected by L. Espinasa, 20 Nov 1988. (ICML POH-39001), complete with 78 setigers, 32 mm length, 1 mm width, without parapodia. 7 Paratypes (ICML POP-39001, 2; USNM 136559, 2; BMNH ZB1991.7, 1; AM W20588, 1; HZM P-20658, 1), 50–70 setigers, 24–34 mm length, 0.7–1.3 mm width.

The description is based on the holotype unless specified otherwise. Measurements were done to the closest millimeter. None were gravid.

Description.—Color in life: off-white. Dorsal blood vessel conspicuous. Color in alcohol: off-white. Prostomium quadrangular, cleft anteriorly, short, approximately $\frac{1}{3}$ of width; deep medial groove extending from anterior margin of prostomium to middle part (Fig. 1A); without eyes; biarticulate palps shorter than frontal antennae. Antennae articulated with 5 joints (Fig. 1A). Tentacular segment shorter than following, with three pairs of tentacular cirri, articulated; posterior-medial cirri longest (Fig. 1B), extending to setiger 5, with 12 joints; jaws amber (yellow brown), each with 2 teeth (Fig. 1C).

Parapodia all uniramous, with neuropodial ligule only, similar in shape throughout

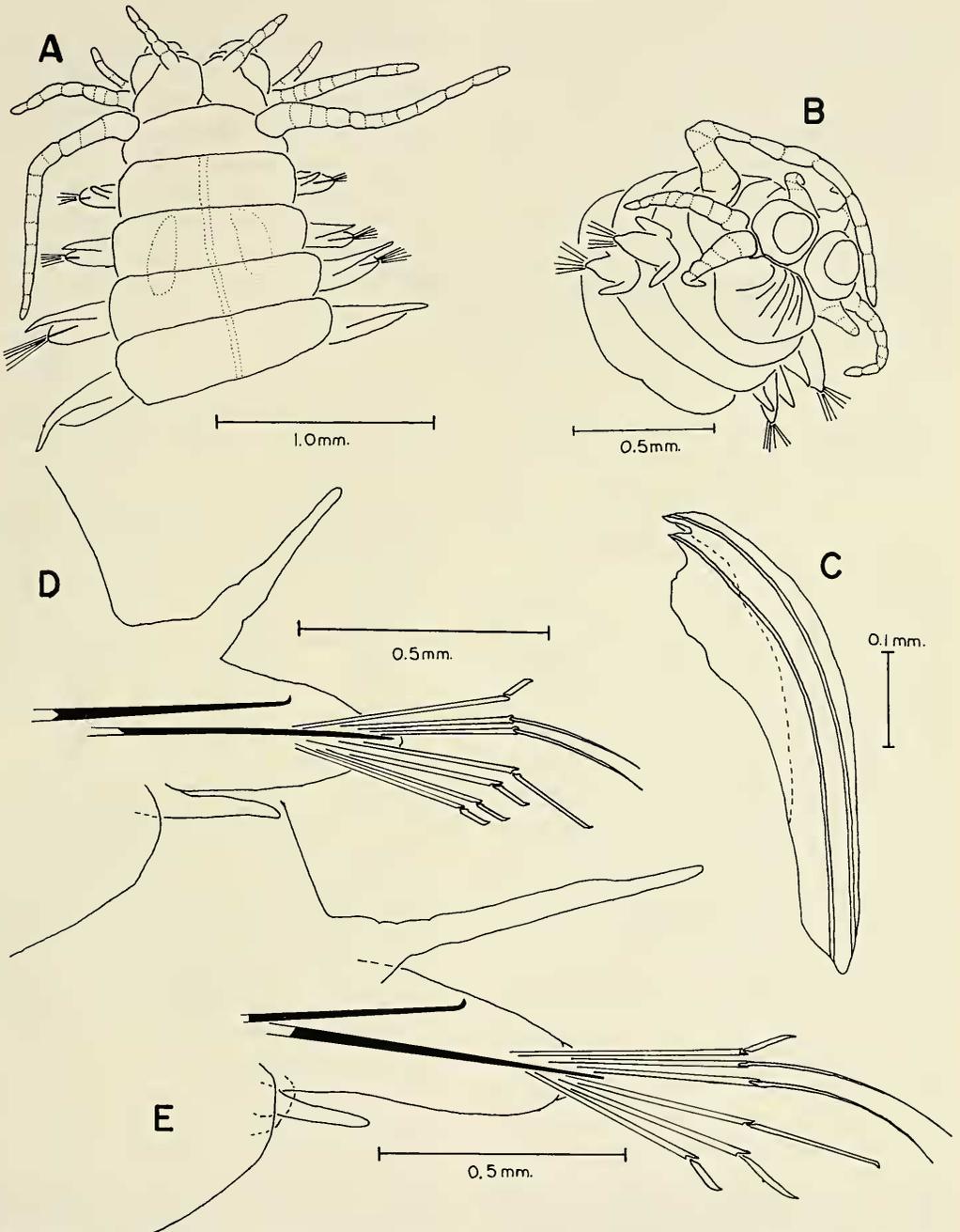


Fig. 1. *Lycastilla cavernicola*: A, Anterior end, dorsal view, dorsal longitudinal blood vessel and jaws dotted; B, Anterior end, 3/4 ventral view; C, Jaw; D, Setiger 5, anterior view; E, Setiger 34, anterior view; A, C-E: holotype (ICML-POH-39-001), B: paratype (ICML-POP-39-001).

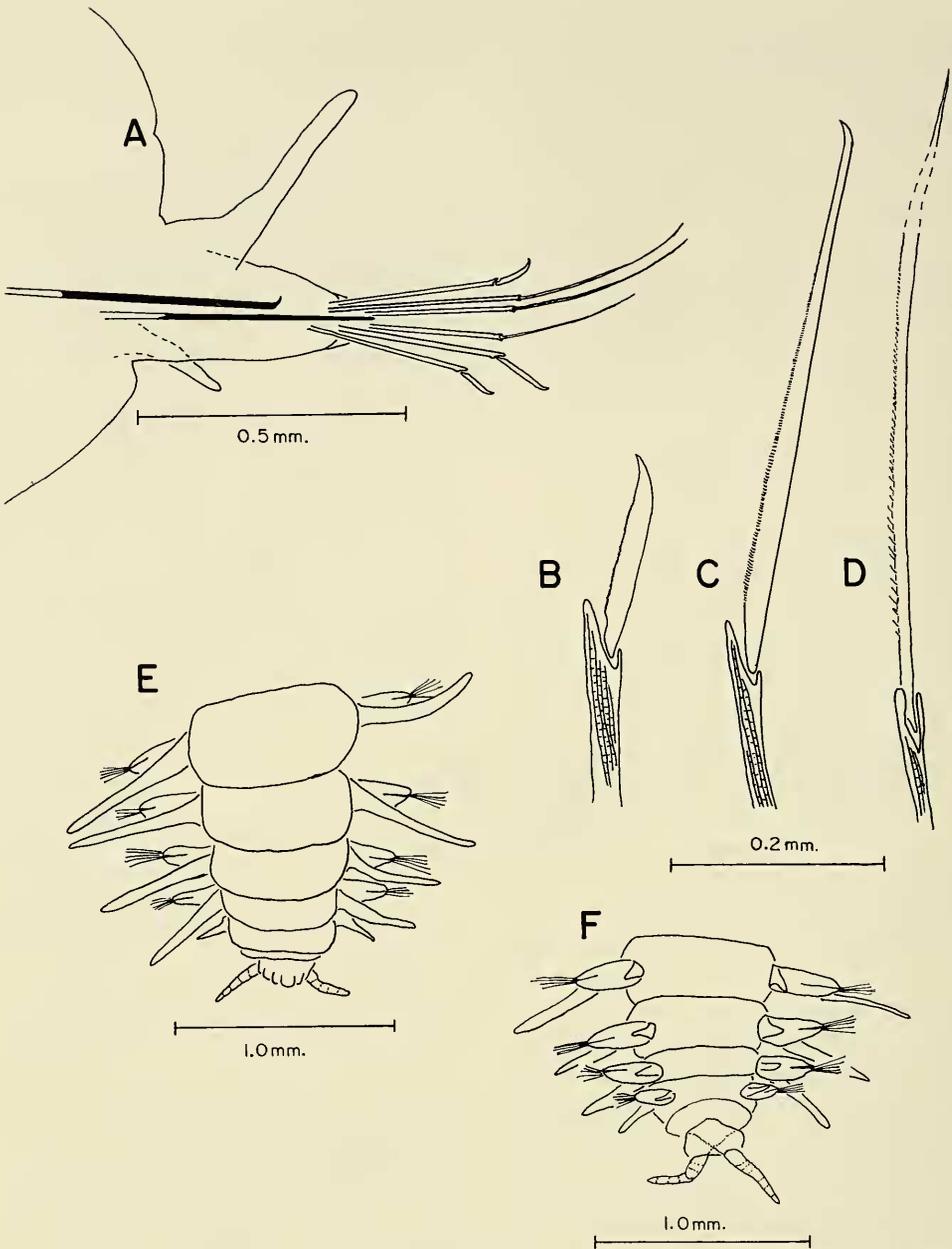


Fig. 2. *Lycastilla cavernicola*; holotype (ICML-POH-39-001) : A, Setiger 63, anterior view; B, Heterogomph falciger; C, Long bladed heterogomph pseudospiniger; D, Heterogomph spiniger; E, Posterior end, dorsal view; F, Same, ventral view.

body; first parapodium slightly smaller than following. Notopodium reduced to dorsal cirrus and notoaciculum. Dorsal cirrus digitiform, subequal in length to neuropodial ligule in anterior setigers (Fig. 1D); length-

ening and surpassing neuropodial ligule slightly at midbody (Fig. 1E); decreasing in length but extending beyond neuropodial ligule posteriorly (Fig. 2A, E, F).

Pygidium terminal, with papillae. Anal

cirri ventrally produced, articulated, with ca. 5 joints, short, length equal to 2–3 posterior setigers (Fig. 2E, F).

Acicula dark brown; notoaciclulum with recurved tip, shorter than neuroaciculum.

Setae. — Dorsal neuropodium with slight-ly heterogomph spinigers (appear homo-gomph when viewed frontally) with long blades (2–3) (Fig. 2D) and with a hetero-gomph falciger with short rather straight blade with tapered tip (Fig. 2B, also, Fig. 1D, E).

Superior ventral neuropodium having an heterogomph falciger with long blade, the blade elongating from anterior to posterior setigers (Fig. 2C, also Fig. 1D, E; Fig. 2A), becoming spinigerous towards midbody (ca. 40th setiger). Inferior neuropodium with heterogomph falcigers showing moderate dorso ventral gradation of blade length (2–3).

Etymology. — *cavernicola* is the Latin term for cave dweller.

Discussion

Discussion of the genera and species in this subfamily is difficult because, as pointed out by Hutchings & Glasby (1985), the characters usually used to separate the nereidids at the specific level are lacking. These pertain mainly to the pharyngeal structures, complex parapodial lobes and types of notosetae present (Day 1967).

Hartman (1959), indicating that such parts are much reduced or altogether lacking in these genera, separated them as a new subfamily, the Namanereinae (sic) and used the following as generic characters: the number of pairs of tentacular cirri (three or four); the degree of middorsal cleavage of the prostomium; overall size; the number of teeth on the jaws; the relative length of the cirri; and the distribution of setae. The presence or absence of eyes was controversial.

Fitzhugh (1987), in his revision of the phylogenetic relationships within the Nereididae, recognized five genera in the sub-

family Namanereidinae: *Namanereis* Chamberlin, 1919; *Cryptonereis* Gibbs, 1971; and *Lycastopsis* Augener, 1922 in one clade with *Lycastoides* Johnson, 1903 and *Namalycastis* Hartman, 1959 as a sister group. The two groups are separated by having three and four pairs of tentacular cirri respectively.

Lycastilla belongs to the first group, because of its three pairs of tentacular cirri, but has more affinities with *Lycastoides* than with the other genera as shown below in the analysis of its affinities with the other five genera.

Lycastilla is easily separated from *Cryptonereis* Gibbs, which lacks antennae, and has at maturity biramous parapodia with capillary setae (Gibbs 1971).

The main differences with *Namanereis* Chamberlin are that in *Namanereis* antennae and cirri are smooth, there is no cleft prostomium, the teeth on the jaws number from 4 to 20 (Johnson 1903), and, except in *N. kartaboensis* Treadwell, there are one to a few setae in the reduced notopodium. There are three recognized species of *Namanereis*: *N. quadriceps* (Gay 1849), *N. kartaboensis* Treadwell, 1926 and *N. littoralis* Hutchings & Turvey, 1982. No type material appears to have been deposited for *N. quadriceps* (Hutchings & Glasby, 1985) and the type of *N. kartaboensis* has dried (Hartman 1956). The fundamental question of the number of tentacular cirri present seems here to be controversial. When they designated the neotype of *N. quadriceps*, Hutchings & Glasby (1985) clearly indicated in their redescription of that species, four pairs of tentacular cirri, whereas Hartman's (1959) synonymy of five species of *Lycastopsis* (*L. beumeri* Augener, 1922, *L. cataractarum* Feuerborn, 1932, *L. amboinensis* Pflugfelder, 1933, *L. hummelincki* Augener, 1933, *L. augeneri* Okuda, 1937 and *L. te-colutlensis* Rioja, 1946) with *N. quadriceps*, as well as Fitzhugh's (1987) cladograms, indicate equally clearly three pairs. Day (1967) also remarks on the discrepancy

between Chamberlin's (1919) definition of the genus inferring 4 pairs and Hartman's definition of 3 pairs.

Hutchings & Glasby (1985) noted this difference, and, based on Fauchald's (1977) definition of the genus as having 3 or 4 pairs of tentacular cirri and on the fact that the notopodium is poorly developed, presume that material from southern California examined by them and identified as *N. quadraticeps* by Hartman (1968) is another species of the same genus. This is supported by the fact that there is a notoseta present in the neotype of *N. quadraticeps*. We consider, however, that the number of tentacular cirri is a character important enough to consider separating groups of genera, as did Fitzhugh (1987). In that case, if *N. quadraticeps*, as redescribed by Hutchings & Glasby, prevails, *Namanereis* should be moved to the sister group with *Lycastoides* and *Namalycastis*. *N. littoralis* will remain in the same genus, and *N. kartaboensis* remains problematic because the type has dried (Hartman 1956). Moreover, the material referred to *N. quadraticeps* by Hartman (1968) from California, and the material examined by Hutchings & Glasby in 1985 (from the same area, from Chile (collected by Straughan) and Ehler's material) should be moved to another genus considering they have four pairs of tentacular cirri and lack notosetae.

Lycastopsis and *Lycastilla*, on the other hand, share the following characters: three pairs of tentacular cirri, uniramous parapodia, similar small size. *Lycastopsis* differs from the new genus in having an entire (rather than a cleft) prostomium, reduced and unarticulate antennae, tentacular and anal cirri, and a straight notoaciculum. The presence of eyes is controversial: Wesenberg-Lund (1958) and Marcus (1960) considered *Lycastopsis hummelincki* Augener, 1933 as the only species of the genus lacking eyes; not recognizing that Hartman (1959) had transferred the species to the genus *Namanereis* Chamberlin, based on the presence of eyes and the jaw structure.

Its affinities with *Namalycastis* are few because besides the number of tentacular cirri (four in the latter) there are differences in the shape of the parapodial lobes (significantly enlarged at the posterior end in *Namalycastis*); the presence of eyes; no articulations in antennae and cirri (peristomial and anal); a straight notoaciculum; and the occasional presence of notosetae. Fauvel (1923) indicated that *Lycastis* (now *Namalycastis*) *brevicornis* has homogomph spinigers which would be an important difference, but it is the only species of the six genera that would have those setae reported. Rioja (1946) indicates that for *Lycastoides tecolotlensis* some superior neurosetae can easily be confused for homogomph spinigers especially if viewed frontally. This is certainly the case in *Lycastilla*, so that Fauvel's observation of this character should be taken with caution. Fitzhugh (1987), following Hartman (1959) and Gibbs (1971), indicates only heterogomph spinigers in the whole subfamily.

Lycastoides and *Lycastilla* share several characters: a cleft prostomium; articulated and well-developed antennae; tentacular and anal cirri; uniramous parapodia; distally recurved notoaciculum; eyes lacking; jaws with few teeth; and small size. *Lycastoides* differs from the new genus in having four pairs of tentacular cirri and having a greatly enlarged first basal joint of the posterior peristomial cirri (Johnson 1903). Both were collected in freshwater and elevated habitats far from the sea.

Attempts were made to collect material of *Lycastoides alticola* in the type area as indicted by Johnson (1903). A thorough exploration of the area at the altitude indicated in the literature was undertaken by one of us (L.E.) recently (Nov 1990) and no polychaetes could be found. Because the area has undergone considerable man-made changes since the first collection was done, before 1903, we conclude that it is most unlikely that this species will be found again, at least in the type area.

If we follow Hartman (1959) and Fitz-

hugh (1987), the new genus would be placed in a cladogram in the same sister group with *Cryptonereis*, *Lycastopsis* and the species currently assigned to *Namanereis* which have three pairs of tentacular cirri as discussed above.

Nevertheless, this genus appears to be much closer to *Lycastoides* than to the other four previously described genera, its main differences with that genus being the number of tentacular cirri and the remarkable elongation of the first joint in the peristomial cirri noted by Johnson (1903). The annulation of the antennae and cirri in only found in *Lycastilla* and *Lycastoides*.

Both *Lycastilla* and *Lycastoides* were found in strictly freshwater, rather high altitude habitats in Mexico. *Lycastoides* comes from an elevated stream (ca. 2300 m above sea level) in Sierra Laguna at the southern end of the Baja California peninsula. The state of Guerrero, where *Lycastilla* is found, borders on the Pacific ocean.

During the Cretaceous, this region was below sea level (Santiago et al. 1984). Moreover, the separation of the Gulf of California occurred about 4 million years ago (Morán Zenteno 1984). That makes it possible, considering the probable age of the cave, to have had connections between both ancestral populations. If this is the case, we can consider them as a relict, primitive fauna. Corrêa (1948) and Banse (1977) consider the Namanereidinae as more evolved than the Gymnonereidinae for example, based on the parapodial structure and considering the uniramous parapodia as an evolutionary loss. We believe that the presence of these two genera in their secluded habitats indicate that they are more primitive. Thus, as we also agree with Pettibone's (1963) comment on *Lycastopsis* as a probably relict and primitive genus, we consider the whole subfamily as the more primitive in the Nereididae.

Environmental remarks.—The maintenance of this fauna within this pool can be explained by the physical characteristics of the river. The pond is an affluent perma-

nently disconnected from the main river that crosses the cave. The main river has a fast current that makes it impossible for silt to be deposited. The only area in the cave where there are calm waters and silt deposition is the pool containing the polychaetes. Access to the cave is impossible at other seasons of the year because of the increased river current, but the pool should not change since the river flow lies some two meters below it in the dry season.

Water temperature was 17°C measured in November 1988. The granulometric composition of the sediment was: mud (28.71%), sand (68.93%) and gravel (2.34%). The amount of organic matter present in the sediment was 1.22% of carbon (November 1988), not a very high value for marine sediments but probably high for caverns.

Biological data.—The total number of polychaetes in the pool was estimated as 2300 to 2400 organisms. Polychaetes were the largest organisms in the pool. Other organisms included copepods, trochophore larvae (about 200/ml), protozoa of at least five different species (about 10,000/ml), and bacteria (about 5×10^6 /ml).

It was observed that polychaetes from the pool could be maintained in the laboratory by adding only water, thus, presumably they feed on the microfauna. The proposed food web is as follows: *L. cavernicola* feeds on bacteria, protozoa and probably their own larvae and those of copepods. Their fecal pellets in turn make up the energy source for the development of the bacteria. The presumable small amount of energy not recycled *in situ* comes from the dripping waterfall mentioned above, mainly during the rainy season. In the laboratory, we suppose that this is replaced by the small amount of light that penetrates the shaded aquarium.

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Literature Cited

- Augener, H. 1922. Ueber littoral Polychaeten von Westindien.—Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1922:38–53.
- . 1933. Susswasser Polychaeten von Bonaire.—Zoologische Jahrbucher Abteilung fur Systematik, Okologie und Geographie der Tiere 64:351–356.
- Banse, K. 1977. Gymnonereidinae, new subfamily: The Nereididae (Polychaeta) with bifid parapodial neurocirri.—Journal of Natural History 11:609–628.
- Chamberlin, R. V. 1919. The annelida Polychaeta.—Museum of Comparative Zoology, Harvard 48: 1–514.
- Corrêa, D. 1948. A polychaete from the Amazon region.—Boletins da facultade de Filosofia Ciências e Letras. Universidade de São Paulo, Zoologia 13:245–257.
- Day, J. H. 1967. A monograph of the Polychaeta of Southern Africa, Part 1.—British Museum of Natural History Publications, London 656:1–458.
- Espinasa, R. 1989. El resumidero del Isote y la cueva de las Pozas azules.—Tepeyollotli: Gaceta de la Sociedad Mexicana de Exploraciones Subterráneas 4:24–27.
- Fauchald, K. 1977. The Polychaete Worms, Definitions and keys to the Orders, Families and Genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.
- Fauvel, P. 1923. Polychetes errantes. Faune de France Volume 5. Kraus Reprint Nendeln, Liechtenstein (1975), 488 pp.
- Feuerborn, H. J. 1932. Ein Rhizocephale und zwei Polychaeten aus dem Susswasser von Java und Sumatra.—Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie, Stuttgart. 5:618–660.
- Fitzhugh, K. 1987. Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level.—Bulletin of the Biological Society of Washington 7:174–183.
- Gay, P. C. 1849. Annelides. Historia de Chile. Zoología Paris. 52 pp.
- Gibbs, P. 1971. The polychaete fauna of the Solomon Islands.—Bulletin of the British Museum of Natural History (Zoology) 21:101–211.
- Gaudette, H. E., W. R. Flight, L. Toner, & D. W. Folger. 1974. An inexpensive titration method for the determination of organic carbon in recent sediments.—Journal of Sedimentology and Petrology 44(1):249–253.
- Hartman, O. 1956. Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology.—Bulletin of the American Museum of Natural History 109(2):245–310.
- . 1959. Capitellidae and Nereidae (Marine Annelids) from the Gulf side of Florida, with a review of freshwater Nereidae.— Bulletin of Marine Sciences of the Gulf and Caribbean 9(2): 153–168.
- . 1968. Atlas of errantiate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.
- Hutchings, P. A., & C. J. Glasby. 1985. Additional nereidids (Polychaeta) from Eastern Australia, together with a Redescription of *Namanereis quadraticeps* (Gay) and the Synonymising of *Ceratonereis pseudoerythraensis* Hutchings & Turvey with *C. aequisetis* (Augener).—Records of the Australian Museum 37(2):101–110.
- , & S. C. Turvey. 1982. The Nereididae of South Australia.—Transactions of the Royal Society of South Australia 106(3):93–144.
- Johnson, H. P. 1903. Freshwater nereids from the Pacific coast and Hawaii with remarks on freshwater Polychaeta in general.—Mark Anniversary Volume, Henry Holt & Co., New York, pp. 206–225.
- López-Ramos, E. 1974. Geología de México. Third Edition. Volume 3. Secretaría de Educación Publica, Edición Escolar, México, 453 pp.
- Marcus, E. du B.R. 1960. Notes on the freshwater polychaete *Lycastopsis* from Curacao.—Studies on the fauna of Curacao and other Caribbean Islands 10(46):58–63.
- Morán Zenteno, D. J. 1984. Geología de la República Mexicana. Instituto Nacional de Estadística

- Geografía e Informática y Facultad de Ingeniería (UNAM), México, 88 pp.
- Okuda, S. 1937. Occurrence in north Japan of a new species of an aberrant polychaete genus, *Lycastopsis*.—*Annotationes Zoologicae Japonenses* 16(4):306–309.
- Pettibone, M. 1963. Marine Polychaete Worms of the New England Region. 1. Families Aphroditidae through Trochochaetidae.—*Bulletin of the United States National Museum* 227:148–152.
- Pflugfelder, O. 1933. Landpolychaeten aus Niederlandisch-Indien. Ergebnisse der Sunda-Expedition der Notgemeinschaft der deutschen Wissenschaft 1929-30.—*Zoology Anzeiger, Leipzig* 105(Heft 3/4):65–76.
- Rioja, E. 1946. Estudios anelidológicos. XV. Nereidos de agua salobre de los esteros del litoral del Golfo de Mexico.—*Anales del Instituto de Biología, Mexico* 17:205–214.
- Santiago, J. A., J. Carrillo B., & B. Martell A. 1984. Geología Petrolera de México. In Schlumberger Offshore Services Ed. Evaluación de formaciones en México. Ediciones especiales para Petroleos Mexicanos, 1.1–1.36.
- Treadwell, A. 1926. A new polychaetous annelid from Kartobo, British Guiana, genus *Namonereis*.—*Zoologica* 7:101–104.
- Wesenberg-Lund, E. 1958. Lesser antillean Polychaetes, chiefly from brackish water with a survey and a bibliography of fresh and brackish-water Polychaetes.—*Studies on the Fauna of Curacao and other Caribbean Island* 8(30):1–41.
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