

Description of three new species of *Ninoe* and *Cenogenus* (Polychaeta: Lumbrineridae) from the Mexican Pacific

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SUMMARY: In this study, 169 lumbrinerids of the genera *Ninoe* and *Cenogenus* from the sublittoral zone of the Gulf of California and Gulf of Tehuantepec were analysed. Previous records in these regions of the Mexican Pacific included five species of *Ninoe* (*N. chilensis*, *N. foliosa*, *N. gemma*, *N. longibranchia* and *N. moorei*) and two of *Cenogenus* (originally identified as *Ninoe fusca* and *N. fuscoides*). *Ninoe jessicae* and *N. marthae* are newly described. They are characterized by the presence of multidentate hooded hooks from chaetiger 1 and at least 7 branchial filaments in the best developed branchiae. *N. marthae* n. sp. differs not only from *N. jessicae* n. sp. but also from the other species of the Genus *Ninoe*, because only four teeth are present in maxilla II, while in all the other described species, 6-8 teeth are present there. The new species *Cenogenus eliae* is characterized by the presence of branchiae starting at chaetigers 32-51 and simple multidentate hooded hooks in all parapodia.

Keywords: Polychaete, new species, Lumbrineridae, *Ninoe*, *Cenogenus*, Mexican Pacific.

RESUMEN: DESCRIPCIÓN DE TRES NUEVAS ESPECIES DE *NINOE* Y *CENOGENUS* (POLYCHAETA: LUMBRINERIDAE) DEL PACÍFICO MEXICANO. – Se analizaron 169 lumbrinéridos de los géneros *Ninoe* y *Cenogenus* de la zona sublitoral del Golfo de California y Golfo de Tehuantepec. Los registros previos en esta zona del Pacífico Mexicano incluyen cinco especies de *Ninoe* (*N. chilensis*, *N. foliosa*, *N. gemma*, *N. longibranchia* y *N. moorei*) y dos de *Cenogenus* (originalmente identificadas como *Ninoe fusca* y *N. fuscoides*). *Ninoe jessicae* y *N. marthae* se describen por primera vez, y se caracterizan por presentar ganchos simples cubiertos multidentados a partir del quetígtero 1 y al menos 7 filamentos cuando las branquias están mejor desarrolladas. *N. marthae* n. sp. difiere de *N. jessicae* n. sp. y de las otras especies del Género *Ninoe* por la presencia de cuatro dientes en la maxila II, ya que las especies descritas previamente tienen 6-8 dientes. La nueva especie *Cenogenus eliae* se caracteriza por la presencia de branquias a partir de los chaetigeros 32-51 y ganchos simples cubiertos multidentados en todos los parapodios.

Palabras clave: Poliquetos, nuevas especies, Lumbrineridae, *Ninoe*, *Cenogenus*, Pacífico Mexicano.

INTRODUCTION

The family Lumbrineridae is characterized by long, cylindrical, free-living burrowing polychaetes, with essentially identical chaetigers. Their morphological homogeneity and the reduced number of external characteristics make it difficult to separate the genera taxonomically (Oug, 2002).

In 1865 Kinberg established the Genus *Ninoe* to include the eunicemorphs with no prostomial appendices or tentacular cirri and with branchiae arising from the postchaetal lobes in anterior parapodia. Initially, he included three species from Chile and Brazil: *N. chilensis*, *N. brasiliensis* and *N. oculata*. Much later, Fauchald (1970) emended the genus to include all lumbrinerids with branchial

processes whatever their origin, structure or position and no other characters considered. However, this amendment was rejected by Orensanz (1973, 1990) who considered that the lumbrinerids' "branchiae" are represented by two types of different structures that are not homologous. He differentiated the branchiae of *Ninoe sensu stricto* (which are unique in their position, shape and distribution), from the other "branchial" structures found in some lumbrinerids (constituted by branchial lobes such as those found in "*Ninoe*" *dolichognatha* Rioja, 1941). With this distinction, the species of the genus *Ninoe sensu stricto* can be clearly separated from the others, but the structure and origin of the branchial lobes still constitutes an unsolved problem, so that all species in which they are present have been grouped in genera such as *Cenogenus* or *Paraninoe* whose position is not yet universally accepted.

Initially, Chamberlin (1919) established the genus *Cenogenus* based on the presence of a conical nuchal process, four maxillae (III and IV with no teeth), limbate chaetae, simple multidentate hooded hooks and the presence in anterior parapodia of a cylindrical, slender, finger-like, and short, postchaetal process. In 1970, Fauchald considered this genus as a junior synonym of *Lumbrineris sensu stricto*; however, currently, *Lumbrineris* is considered a heterogenous taxon, which includes only lumbrinerids with no branchiae (Frame, 1992).

Levenstein (1977) named the genus *Paraninoe* to include all species with a nuchal organ and simple digitate branchiae, stating that the difference with *Ninoe* was in the number of branchial filaments and the shape of maxillae III and IV, which in the former lack teeth. However, Carrera-Parra (2001) in his revision of type material of *Cenogenus descendens* Chamberlin, 1919 and *Ninoe fusca* Moore, 1911 (type species of *Paraninoe*), concluded that the genus *Cenogenus* is valid and that *Paraninoe* is a junior synonym.

Traditionally, the identification of the genera and species in this family has been based on the external morphological characters. However, more recently, the trend in systematics of the lumbrinerids has been to include characters such as the maxillary apparatus, even if they are more difficult to observe. This is why the posterior region in most genera and species is not considered critical. However, when descriptions are carried out from incomplete material, caution should be the norm, since, as happens with *Cenogenus eliae* n. sp. the digitate branchiae,

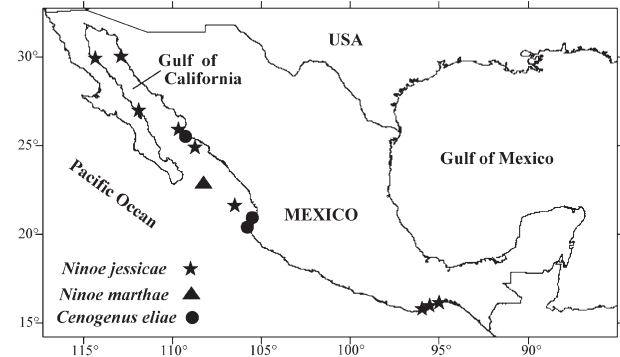


FIG. 1. – Distribution of the three new species described from the study area (Mexican Pacific).

one of the most important character, for species designation are not present before chaetigers 32-51.

In the Mexican Pacific Ocean (from sublittoral habitats to deep waters), reports of lumbrinerids with branchiae are sparse and only eight species have been recorded so far (Rioja, 1941; Fauchald, 1970, 1972; Salazar-Vallejo, 1981; Arias-González, 1984; López-Hernández, 1986; Sarti-Martínez and Solís-Weiss, 1987; Lezcano-Bustamante, 1989; Padilla-Galicia and Solís-Weiss, 1992; Hernández-Alcántara, 1992; Varela-Hernández, 1993; González-Ortiz, 1994): one corresponds to the genus *Kuwaita*, originally identified as *Ninoe dolichognatha* (Rioja, 1941), five to *Ninoe* (*N. chilensis* (Kinberg, 1865), *N. foliosa* Fauchald, 1972, *N. gemmea* Moore, 1911, *N. longibranchia* Fauchald, 1972 and *N. moorei* Rioja, 1941) and two to *Cenogenus* (originally identified as *Ninoe fusca* (Moore, 1911) and *N. fuscoides* (Fauchald, 1972)).

The aim of this study is to describe three new species of lumbrinerids, two from the genus *Ninoe* and one from *Cenogenus*, which were collected as part of different expeditions to the Gulf of California, Gulf of Tehuantepec and Mexican Pacific littoral regions. The area covered can be seen in Figure 1.

MATERIALS AND METHODS

The specimens were collected by personnel of the Instituto de Ciencias del Mar y Limnología (ICML), Universidad Nacional Autónoma de México (UNAM) on board R/V "El Puma" during the oceanographic expeditions "CORTES II", "MIMAR III", "MAZCAB II" and "SEDIMENTO I". The study area included the coasts of the Mexican Pacific (Fig. 1). Stations' position was determined by Global Positioning System (GPS).

Samples were taken with a Smith-McIntyre grab (0.1 m²) or a US-NEL box corer (0.25 m²). The biological material was fixed in 10% formalin and preserved in 70% ethanol.

The holotypes and paratypes are deposited at the Polychaete Collection ICML-UNAM (CP-ICML). Additional paratypes are deposited at the Los Angeles County Natural History Museum (LACM), the Australian Museum (AM), The Natural History Museum, London (NHM).

The habitat data for each species are abbreviated as follows: D = depth in meters; T = temperature in °C; S = salinity in ppt; DO = dissolved oxygen in ml/l (determined by the Winkler method (Strickland and Parsons, 1977)); OM = organic matter content in the sediments in %C (determined by the Walkley-Black method (1934) modified by Jackson (1958)).

The diagnostic differences among the species described here were assessed by comparing selected morphological characters in the specimens coming from different localities (Population Aggregation Analysis) (Davis and Nixon, 1992). Fifteen variables were used to quantify the morphological differences among the populations of the species *Ninoe jessicae*, *Ninoe marthae* and *Cenogenus eliae*. The samples (n = 47) of 11 populations, representative of the areas where the described species are distributed, were analysed. In Table 1, the characters evaluated are listed and correspond to the characters routinely used to diagnose lumbrinerid species (Uebelacker, 1984; Orensanz, 1990; Hilbig, 1995). The selected attributes can be coded as discrete alternative states; attributes 1-4 are binary, whereas 5-15 are multistate. Numbers designate individuals sampled from the same locality (A-K), and these individuals are taken to be members of the same interbreeding group.

RESULTS

For this study, 169 lumbrinerids with branchial processes were identified: two new species of the genus *Ninoe* and one new species of *Cenogenus*.

Ninoe jessicae n. sp. (Fig. 2)

Material examined. 26 specimens: Holotype (CP-ICML: POH-54-002), Expedition MIMAR III, Station 212, 15°57.2'N, 95°20.1'W, 01 June 1987, 70 m; 5 paratypes (CP-ICML: POP-54-001), Expedition MIMAR III, sta. 212, 15°57.2'N, 95°20.1'W, 01 June 1987, 70 m; 5 paratypes (LACM-AHF POLY 2171), Expedition

MIMAR III, sta. 241, 15°47.5'N, 95°55.4'W, 01 June 1987, 76 m; 5 paratypes (NHM: 2005.1517.1521), Expedition MIMAR III, sta. 212, 15°57.2'N, 95°20.1'W, 01 June 1987, 70 m; 5 paratypes (AM: XXXXXX), Expedition MIMAR III, sta. 241, 15°47.5'N, 95°55.4'W, 01 June 1987, 76 m.

Additional material examined: 68 specimens: Expedition MIMAR III, sta. 241, 15°47.5' N, 95°55.4' W, 01 June 1987, 76 m, (11 specimens); Expedition MIMAR III, sta. 230, 15°52.4' N, 95°40.0' W, 01 June 1987, 94 m (2 specimens); Expedition MIMAR III, Station 223, 15°56.0' N, 95°30.3' W, 01 June 1987, 78 m (3 specimens); Expedition MIMAR III, sta. 222, 15°53.4' N, 95°30.2' W, 01 June 1987, 94 m (3 specimens); Expedition MIMAR III, sta. 212, 15°57.2' N, 95°20.1' W, 01 June 1987, 70 m (21 specimens); Expedition MIMAR III, sta. 202, 16°06.5' N, 95°10.5' W, 31 May 1987, 20 m (4 specimens); Expedition MIMAR III, sta. 187, 15°58.1' N, 94°59.9' W, 31 May 1987, 97 m (6 specimens); Expedition CORTES II, sta. 5, 24°54.6' N, 108°45.3' W, 10 March 1985, 120 m (1 specimen); Expedition CORTES II, sta. 33, 29°55.4' N, 114°19.3' W, 15 March 1985, 82 m (7 specimens); Expedition CORTES II, sta. 44, 30°02.4' N, 112°55.4' W, 17 March 1985, 104 m (3 specimens); Expedition CORTES II, sta. 49B, 26°59.4' N, 111°53.5' W, 19 March 1985, 69 m (1 specimen); Expedition CORTES II, sta. 51, 25°42.1' N, 109°30.6' W, 21 March 1985, 46 m (1 specimen); Expedition CORTES II, sta. 62D, 21°38.4' N, 106°31.9' W, 22 March 1985, 132 m (5 specimens).

Description. The description is based on the holotype unless specified otherwise. Holotype complete with 139 chaetigers: 28.9 mm long and 1.3 mm wide. Some fixed paratypes with reddish coloration along the body, covering 3 to 8 chaetigers. Prostomium conical, as long as wide, with blunt end. Peristomium formed by a pair of rings (Fig. 2a). Nuchal organs like small furrows. No eyes. Maxillary apparatus: MI unidentate curved and forceps-like; MII with six teeth; MIII and MIV unidentate, with irregularly serrated cutting edges (Fig. 2b); mandibles slender, with anterior ends flared.

Branchiae present from first or second chaetiger (Fig. 2c) as far as chaetigers 19-33; first branchial pairs with only one filament, in following pairs the number increases, to a maximum of 12 filaments. Dorsal filament is longer and thicker than the others (Figs. d, e).

Body sturdy, cylindrical; chaetigers short with similar thickness along body. In the postbranchial region, chaetigers short with short digitiform dorsal postchaetal lobe, shorter than hooks.

Chaetae limbate, distally pointed (Fig. 2g), 1-5 per chaetiger. In postbranchial chaetigers, limbate chaetae diminish in number, only 1 or 2 per parapodium in the posterior region; with 1-2 yellowish brown aciculae. Chaetae also include 1-4 multidentate hooded hooks present from first chaetiger; with one tooth and four or five apical denticles (Fig. 2h).

Pygidium with two anal cirri.

Etymology. The species is named after Perla Jessica Pérez Mendoza, sister of one of us (AYPM).

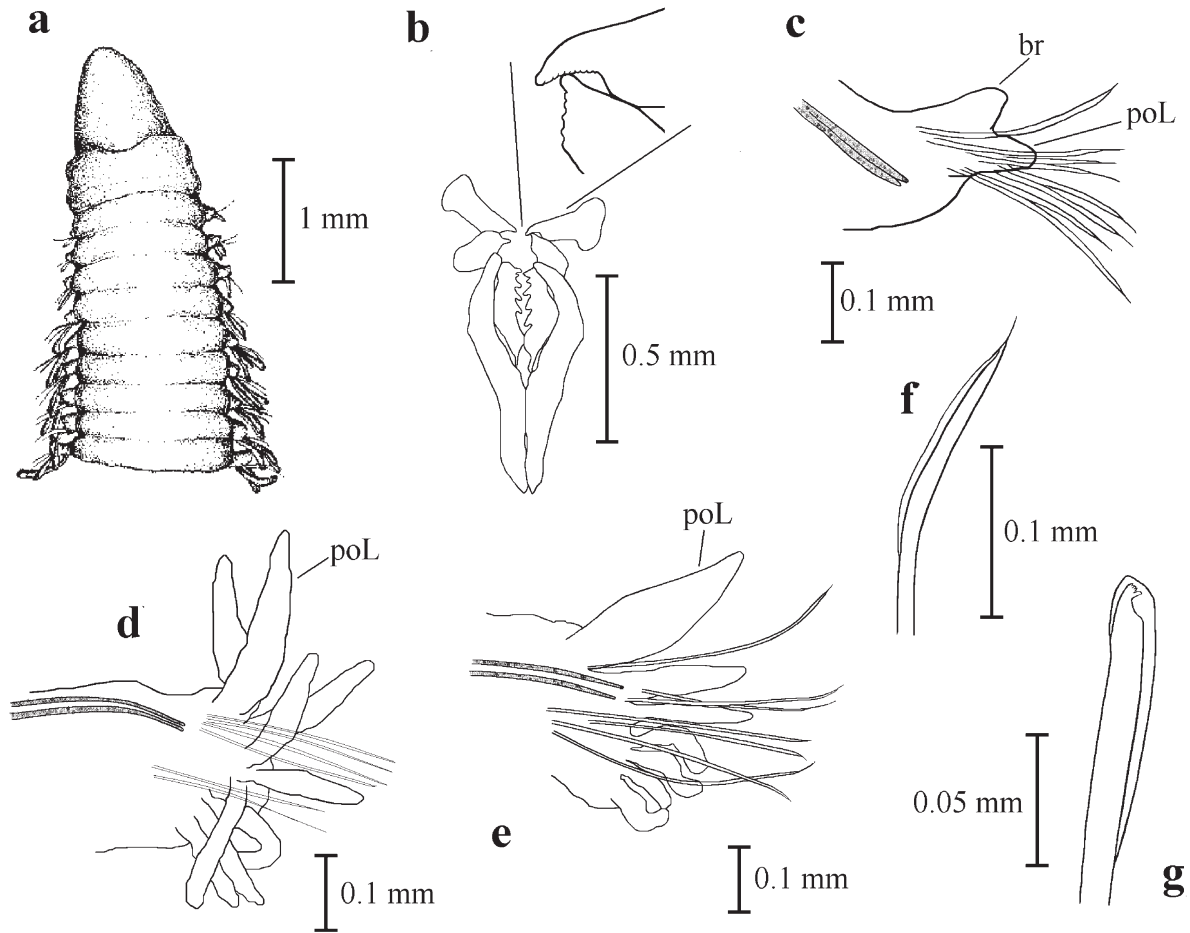


FIG. 2. – *Ninoe jessicae* n. sp.: a, anterior end, dorsal view; b, maxillae; c, parapodium from chaetiger 1; d, parapodium from chaetiger 18; e, parapodium from midbody region; f, limbate chaetae; g, hooded hook (poL = postchaetal lobe; br = branchiae).

Remarks. The branchial distribution and the maximum number of branchial filaments of the new species *N. jessicae*, only resemble *N. foliosa* Fauchald, 1972 (branchiae from chaetiger 2 to 36, with up to 12-13 filaments), recorded for Sal si Puedes Basin in the Gulf of California and in San Cristobal Bay (Pacific side of Baja California), and *N. chilensis* Kinberg, 1865 (branchiae from chaetigers 1 or 2 to 28-41, with 12 filaments), originally recorded from shallow waters of the central part of Chile, but widely distributed in the warm-temperate waters of the south American Pacific coasts. According to Orensanz (1990), who examined the type material of *N. chilensis* and an extensive topotypic collection of the same species from Valparaiso Bay (Chile), *N. foliosa* is so similar morphologically to *N. chilensis* that it could well be a junior synonym of the latter. Although these two species are very similar to *N. jessicae* n. sp., in the distribution and development of their branchiae

and their maxillary apparatus, they can be clearly differentiated from the latter by the simple multi-dentate hooded hooks, which are present after chaetiger 25 in *N. foliosa* and *N. chilensis*. So, *N. jessicae* n. sp. belongs to the set of species in the genus *Ninoe* which have not lost their anterior hooks in the course of lumbrinerid evolution (Orensanz, 1990), which is why the simple multi-dentate hooded hooks are present from chaetiger 1, as in *N. palmata* Moore, 1903, *N. gemma* Moore, 1911 and *N. longibranchia* Fauchald, 1972. However, there are also other differences between these species and *N. jessicae* n. sp., especially a lower number of branchial filaments in the former group of species (6 at most).

Habitat. 20-120 m depth, in silty sands, muddy sands and muds, T = 12.9-30°C, S = 34.98-35.33, DO = 0.20-2.40 ml/l, OM = 0.28-7.2%.

Distribution. Gulf of California and Gulf of Tehuantepec, Mexican Pacific (Fig. 1).

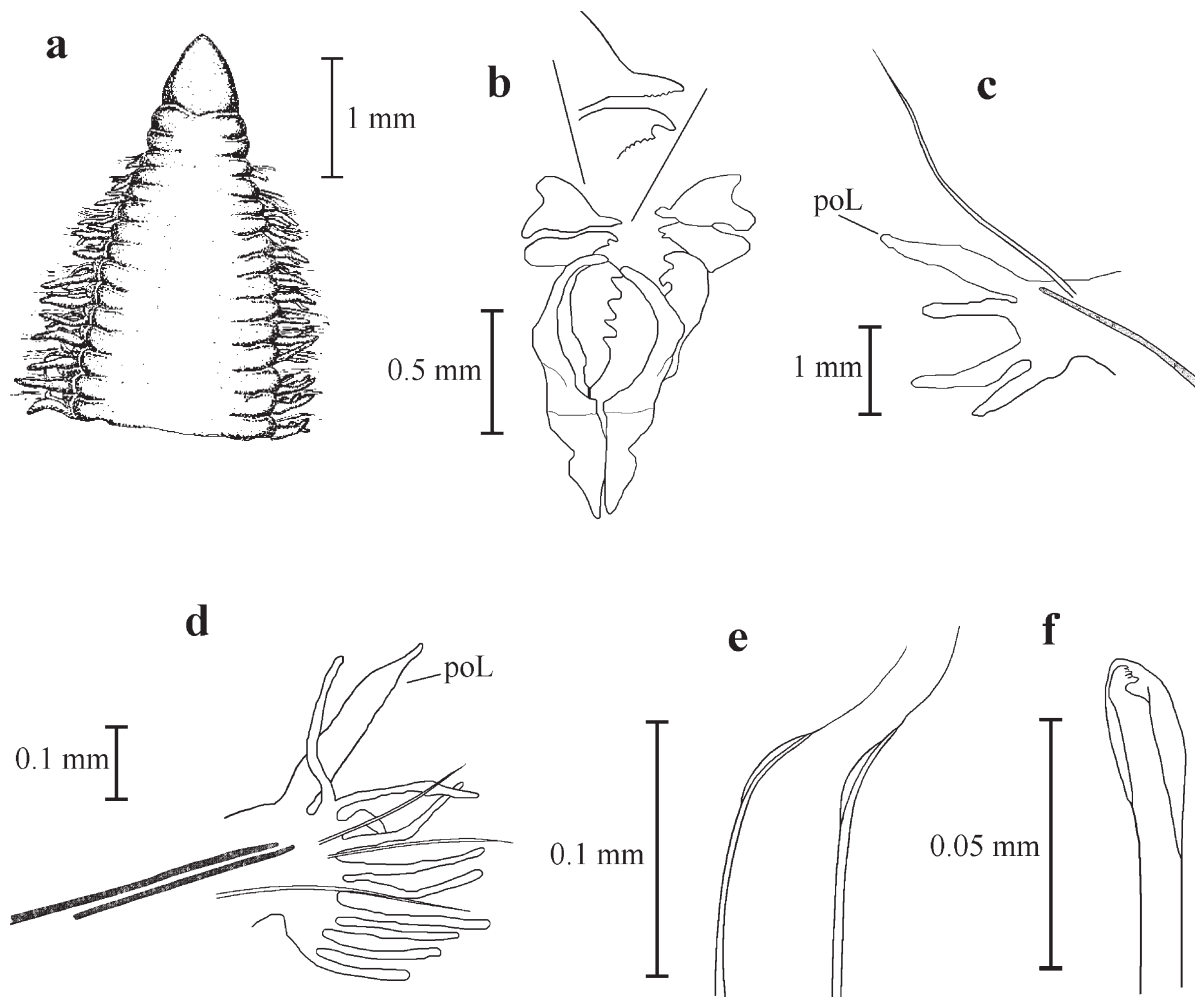


FIG. 3. – *Ninoe marthae* n. sp.: a, anterior end, dorsal view; b, maxillae; c, parapodium from chaetiger 3; d, parapodium from chaetiger 19; e, limbate chaetae; f, hooded hook (poL = postchaetal lobe).

Ninoe marthae n. sp.
(Fig. 3)

Material examined. 2 specimens: Holotype (CP-ICML: POH-54-001), Expedition MAZCAB II, sta. 3, 22°58.1'N, 108°15.5'W, 16 May 1998, 2950 m; 1 paratypes (CP-ICML: POP-54-002), Expedition MAZCAB II, sta. 3, 22°58.1'N, 108°15.5'W, 16 May 1998, 2950 m.

Description. Holotype incomplete with 55 chaetigers, 15.8 mm long and 0.7 mm wide. Prostomium conical, as long as wide, nuchal organs formed by two small furrows in the occipital region, with a protuberance in the central portion of the prostomium. No eyes. Prostomium and peristomium dorsally smooth (Fig. 3a). Peristomium formed by two rings dorsally and laterally visible, fused in the ventral part to form a rim around the mouth. Maxilla and maxillary carriers long, scarcely pigmented. MI forceps-like, unidentate and curved; MII with four teeth; MIII bidentate and MIV unidentate (3b), with

finely serrated cutting edge; mandibles fused along proximal half.

Parapodia rounded. Prechaetal lobes short and rounded, postchaetal lobes longer and conical. Branchiae present from chaetigers 1 or 2 to 17 (Fig. 3c); with up to 7-9 filaments, dorsal filament larger and thicker (Fig. 3d); a few first and last branchial pairs with two to three filaments.

Capillary chaetae limbate, with one of the wings wider in one margin and long filiform tip; length of the wide wing located at the distal part of the chaeta approximately one fifth of total chaetal length (Fig. 3e). Multidentate simple hooded hooks from chaetiger 1, present in all following chaetigers of the incomplete organism; with four to five distal denticles (Fig. 3f). First hooks with distal part poorly developed, posterior hooks thicker, with a larger basal tooth than those located in anterior chaetigers. Each anterior parapodium with 4-5 limbate chaetae

and 1-2 simple hooks, in posterior chaetigers, 1-2 limbate chaetae and 3-4 simple hooks. With one or two dark amber-coloured aciculae (darker than the chaetae, but not black).

Etymology. The species is named after Martha del Rocio Pérez Mendoza, sister of one of us (AYPM).

Remarks. As in *N. jessicae* n. sp. described above, in *N. marthae* n. sp. simple multidentate hooded hooks are present in anterior chaetigers with a relatively large number of branchial filaments (up to 7-9). This is the main difference from other similar species which have numerous branchial filaments such as *N. foliosa* Fauchald, 1972 and *N. chilensis* Kinberg, 1865, where the simple hooks are found after chaetiger 25. In addition, *N. marthae* n. sp. differs not only from *N. jessicae* n. sp. but also from the other species of the Genus *Ninoe*, because only four teeth are present in maxilla II, while in all the other described species, 6-8 teeth are present there.

Habitat. Continental shelf (85 m) and deep-sea (600-2700 m), in muddy sands and muds.

Distribution. Southern Gulf of California, Mexican Pacific (Fig. 1).

***Cenogenus eliae* n. sp.**
(Fig. 4)

Material examined. 7 specimens: Holotype (CP-ICML: POH-54-003), Expedition CORTES II, sta. 60, 20°51.6'N, 105°33.5'W, 23 March 1985, 76 m; 6 paratypes, Expedition CORTES II, sta. 60 20°51.6'N, 105°33.5'W, 23 March 1985, 76 m; 2 specimens (LACM-AHF POLY 2172); 4 specimens (CP-ICML: POP-54-003).

Additional material examined. 66 specimens: Expedition CORTES II, sta. 61, 20°53.9'N, 105°27.5'W, 23 March 1985, 50 m (7 specimens); Expedition CORTES II, sta. 60, 20°51.6'N, 105°33.5'W, 23 March 1985, 76 m (58 specimens); Expedition CORTES II, sta. 52, 25°39.9'N, 109°28.6'W, 20 March 1985, 28.6 m (1 specimen).

Description: Holotype incomplete with 71 chaetigers, 9.5 mm long and 0.45 mm wide. Prostomium conical, as long as wide, no eyes; the small antenna in the nuchal fold often difficult to see (Fig. 4a). Nuchal organs formed by two small furrows. Peristomium with two well developed rings, dorsally and laterally divided between them, but fused ventrally, forming a rim-like structure around the mouth. Maxillary structure: MI unidentate and curved, forceps-like; MII with three teeth; MIII and

MIV triangular edentate plates with smooth cutting edge (Fig. 4b); mandibles partially fused.

Anterior parapodia with prechaetal lobes short and rounded, postchaetal lobes approximately double the length of prechaetal ones (Figs. 4c, d). Branchiae start at chaetigers 32-51, first as small protuberances in medial-dorsal portion of postchaetal lobe, quickly increasing in size together with the postchaetal lobe; towards posterior region of body, length of branchiae can be almost equal to width of body, always depending on size of the postchaetal lobe; postchaetal lobes also increase in size towards the end of body, becoming similar in length to the branchiae so that the two structures together appear like two branchial filaments (Figs. 4e, f).

Limbate chaetae with wings long and wide (Fig. 4g); simple multidentate hooded hooks, with main fang clearly larger than the numerous distal denticles (Fig. 4h). Each of first 18 chaetigers with 3-4 limbate chaetae and one or two simple hooks; in following 10-20 chaetigers, hooks with single limbate chaeta, and in posterior chaetigers only simple hooks. Aciculae and bases of the chaetae dark amber.

Etymology. The species is named after Elia Mendoza Mendoza, mother of one of us (AYPM).

Remarks. *Cenogenus* differs from *Ninoe*, the other genus that includes lumbrinerids with branchiae, in the number of the branchiae and the structure of maxillae III and IV. In *Ninoe*, a variable number of anterior parapodia with postchaetal branchial lobes are present and maxillae III and IV are dentate along their cutting edge, while in *Cenogenus* the digitate branchiae are associated with the postchaetal lobe, and maxillae III and IV have a smooth cutting edge (Carrera-Parra, 2001). In *Cenogenus eliae* n. sp., the structure and distribution of the maxillae and the branchiae, we believe both being valid diagnostic characters, indicate it belongs to this genus; Carrera-Parra (2001) in its redescription and emendation of *Cenogenus*, states that the branchiae are present in the parapodia of the anterior region of the body. From the ten species presently included in the genus (Carrera-Parra, 2001), in *C. abyssalis* (Imajima and Higuchi, 1975) from Sagami Bay, Japan, *C. nageae* (Levenstein, 1977) from Nha Trang, South Viet Nam, and *C. simpla*

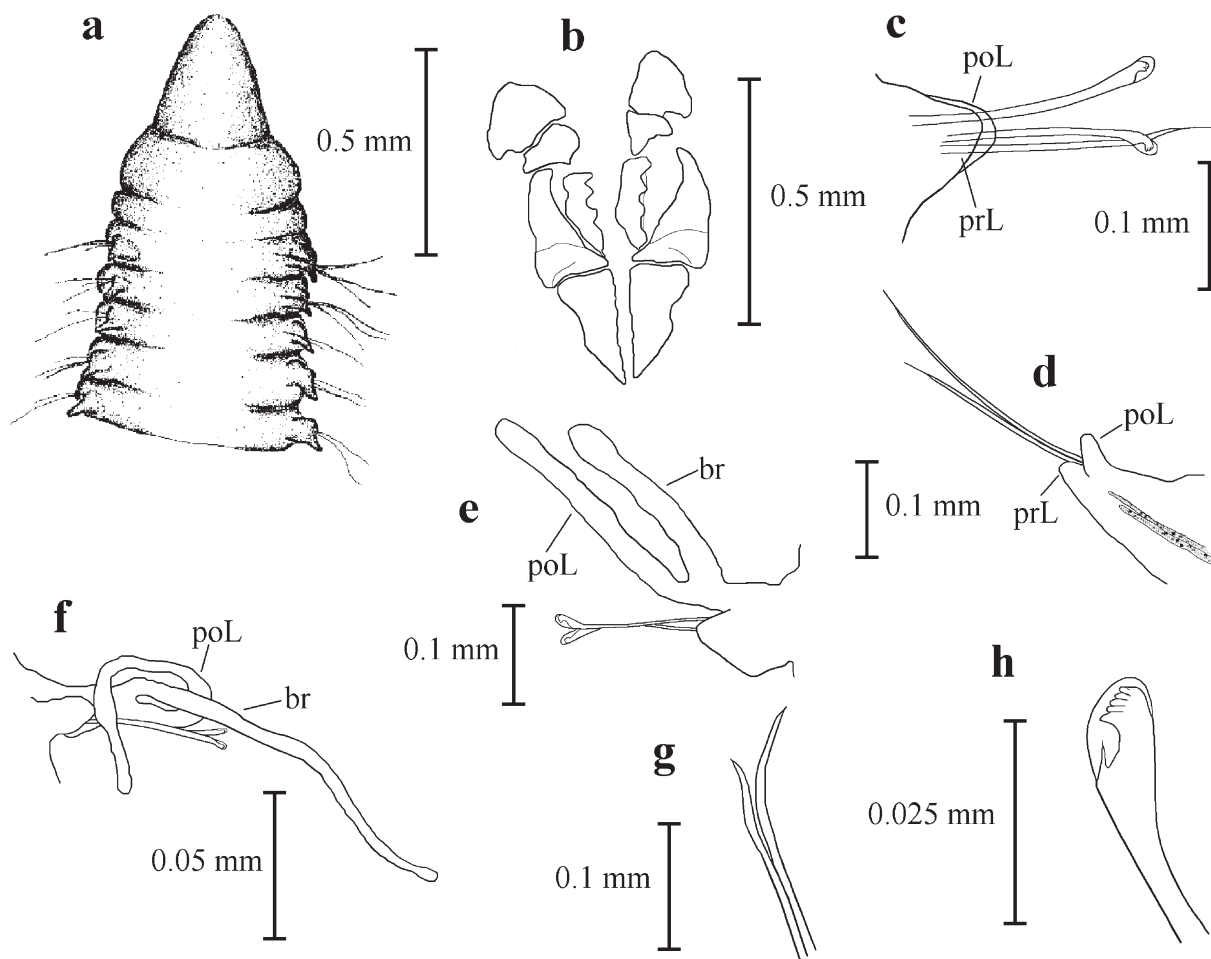


FIG. 4. – *Cenogenus eliae* n. sp.: a, anterior end, dorsal view; b, maxillae; c, parapodium from chaetiger 1; d, parapodium from chaetiger 10; e, parapodium from chaetiger 48; f, parapodium from posterior region, anterior view; g, simple chaetae; h, hooded hook (prL = prechaetal lobe; poL = postchaetal lobe; br = branchiae).

(Moore, 1905) from Alaska, the branchiae start between chaetigers 14 and 23; in the other species, the branchiae are present from chaetigers 1 or 2. In this feature, *C. eliae* clearly differs from all the other species of the genus since the branchiae start at or after chaetiger 51.

The specimens included in the “additional material examined” are anterior fragments with less than 40 segments, which makes it impossible to examine the branchial lobes. However, other diagnostic characters such as the structure of MIII and MIV enabled us to identify these specimens as *C. eliae* n. sp.

Habitat. 28-76 m depth, in fine sands and silty sands, T = 15.3-16.8, S = 34.92-35.19, DO = 0.76-5.40, OM = 3.6-5.5.

Distribution. Eastern coasts from central and southern regions of the Gulf of California (Fig. 1).

Delimiting species by the method of Population Aggregation Analysis (PAA)

The methodological aspects necessary to delimit species are not well developed, among other reasons, due to problems related to the species concept itself. The different concepts of species include a host of arguments but De Queiroz (1998) indicated that all species concepts agree fundamentally on what species are (distinct evolutionary entities), but differ in criteria for their recognition. In this sense, Davis and Nixon (1992) suggested the Population Aggregation Analysis (PAA) as a method to delimit species, based on two fundamental principles: a) all individuals from a local population are considered to belong to the same species and, b) the individuals that share identical attributes, but come from different populations constitute evidence for co-specificity. Conceptually,

TABLE 1. – Population Aggregation Analysis (PAA).

| Sample individual | Biological attributes | | | | | | | | | | | | | | |
|------------------------|-----------------------|----------|----------|----------|----------|----------|----------|----------|------------|-----------|-----------|-----------|----------|------------|------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| A (MIMAR III sta. 187) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 30 | 1 | 2-4 | 1-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 11 | 32 | 1 | 2-3 | 1-4 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 29 | 1 | 2-4 | 2-5 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 11 | 31 | 1 | 2-3 | 2-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 33 | 1 | 2-4 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | +- | +- | 1 | +- | +- |
| B (MIMAR III sta. 202) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 22 | 1 | 2-4 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 23 | 1 | 2-4 | 1-5 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 10 | 20 | 1 | 2-4 | 2-4 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 10 | 22 | 1 | 2-4 | 2-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 9 | 20 | 1 | 2-4 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | +- | +- | 1 | 2-4 | +- |
| C (MIMAR III sta. 222) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 1 | 12 | 30 | 1 | 2-4 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 10 | 29 | 1 | 2-4 | 2-4 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 29 | 1 | 2-4 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | +- | 1 | +- | +- | 1 | 2-4 | 2-4 |
| D (MIMAR III sta. 230) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 12 | 30 | 1 | 2-4 | 1-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 1 | 11 | 28 | 1 | 2-4 | 1-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | +- | +- | +- | 1 | 2-4 | 1-4 |
| E (CORTES II sta. 33) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 23 | 1 | 2-4 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 21 | 1 | 2-3 | 2-4 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 7 | 25 | 1 | 2-4 | 1-5 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 7 | 21 | 1 | 2-4 | 1-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 7 | 21 | 1 | 2-4 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | +- | +- | +- | 1 | +- | +- |
| F (CORTES II sta. 44) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 10 | 26 | 1 | 2-5 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 8 | 24 | 1 | 1-4 | 1-5 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 10 | 27 | 1 | 4-5 | 2-5 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 9 | 27 | 1 | 2-5 | 2-5 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 24 | 1 | 1-4 | 2-5 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | +- | 2 | +- | +- | 1 | +- | +- |
| G (CORTES II sta. 62D) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 8 | 23 | 1 | 2-4 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 22 | 1 | 2-4 | 2-3 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 8 | 19 | 1 | 2-4 | 2-4 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 7 | 20 | 1 | 2-3 | 2-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 8 | 22 | 1 | 1-3 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | +- | +- | +- | 1 | +- | +- |
| H (MIMAR III sta. 212) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 30 | 1 | 1-4 | 2-4 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 10 | 29 | 1 | 2-4 | 1-4 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 12 | 27 | 1 | 2-4 | 1-5 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 11 | 27 | 1 | 2-4 | 2-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 2 | 12 | 28 | 1 | 2-4 | 2-4 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | +- | +- | +- | +- | 1 | +- | +- |
| I (MIMAR III sta. 241) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 11 | 27 | 1 | 2-4 | 1-5 |
| 2 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 28 | 1 | 2-4 | 1-5 |
| 3 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 11 | 28 | 1 | 2-4 | 1-4 |
| 4 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 2 | 1 | 12 | 29 | 1 | 2-5 | 2-4 |
| 5 | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | 1-2 | 2 | 11 | 26 | 1 | 2-4 | 1-5 |
| Population profile | 1 | 1 | 1 | 0 | 1 | 6 | 1 | 1 | +- | +- | +- | +- | 1 | +- | +- |
| J (MAZCAB II sta. 3) | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 1-2 | 2 | 9 | 25 | 1 | 2-4 | 1-5 |
| 2 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 1-2 | 1 | 7 | 17 | 1 | 1-3 | 2-4 |
| Population profile | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 1-2 | +- | +- | +- | 1 | +- | +- |

TABLE 1 (Cont.). – Population Aggregation Analysis (PAA).

| Sample individual | Biological attributes | | | | | | | | | | | | | | |
|------------------------|-----------------------|----------|----------|----------|----------|----------|----------|----------|----------|-----------|----------|----------|----------|-----------|-----------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| K (CORTES II, sta. 60) | | | | | | | | | | | | | | | |
| 1 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 44 | 1 | ? | 1 | 1-3 | 1-4 |
| 2 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 49 | 1 | ? | 1 | 1-3 | 1-4 |
| 3 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 34 | 1 | ? | 1 | 1-3 | 1-4 |
| 4 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 51 | 1 | ? | 1 | 1-2 | 1-4 |
| 5 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 40 | 1 | ? | 1 | 1-3 | 1-3 |
| Population profile | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | +- | 1 | ? | 1 | +- | +- |

1) Branchiae before chaetiger 32 (0 = no; 1 = yes); 2) Maxilla III with a finely serrated edge (0 = no; 1 = yes); 3) Maxilla IV with a finely serrated edge (0 = no; 1 = yes); 4) Aciculae (0 = yellowish; 1 = darker); 5) Maxilla I, number of teeth; 6) Maxilla II, number of teeth; 7) Maxilla III, number of teeth; 8) Maxilla IV, number of teeth; 9) Number of aciculae per parapodium; 10) Number of chaetiger at which branchiae start; 11) Maximum number of branchial lobes; 12) Number of chaetigers with branchiae; 13) Number of starting chaetiger for simple hooded hooks; 14) Number of simple hooded hooks per parapodium; 15) Number of simple capillaries per parapodium

this analysis is an adaptation of traditional methodology which delimits species based on the presence of one or more differences between the diagnostic morphological characters.

From a practical viewpoint, it is necessary to emphasize that the decision of what is a polymorphic character as opposed to a fixed one is the most relevant, since only fixed characters are suitable to delimit species (Davis and Nixon, 1992). In this respect, the populations' profile for each of the 11 populations analysed, assessed from the information taken from all specimens in each sample (Table 1), indicated that attributes 1-8 and 13, associated with the presence of branchial lobes in the anterior region of the body (before chaetiger 32), with the first chaetiger on which hooded hooks are present and the maxillary apparatus characteristics, were identical in all individuals in the samples. Therefore, these attributes were assessed as fixed and considered as the characters (invariant) in the sample that determined the differences among species. Attributes 9 and 11-15, related to the number of chaetae and hooks and to branchial development (number of lobes and number of chaetigers where they are present), were considered polymorphic (scored as "+-"). Those attributes are not crucial for delimiting species unless polymorphisms overlap.

Our results agree with the observations previously made by Hilbig (1995) i.e. that the emphasis in lumbrinerid systematics has shifted from the often rather ill-defined differences in external morphology to more reliable, although less readily accessible characters of the jaws. In particular, *Ninoe* is a well-defined taxon, based upon a set of autapomorphies, one of them being the denticles of maxilla IV or maxillae III and IV (Orensanz, 1990).

A comparison of population profiles showed that in populations A-J, attributes 1-3, 5, 8 and 13 did not vary among samples. However, in population J, in characters 4, 6 and 7 (color of aciculae, number of teeth in maxillae II and III) differences were observed with populations A-I. Therefore, two species can be recognized: one characterized by the presence of four teeth in maxilla II and two teeth in maxilla III (population K = *Ninoe marthae* n. sp.) and another (populations A-I = *Ninoe jessicae* n. sp.) defined by the presence of six teeth in maxilla II and one tooth in maxilla III (Table 1).

The Population Aggregation Analysis (PAA) also showed that in population K, the fixed attributes for alternative states 1-3 and 6-8 (branchiae appearing after chaetiger 32, maxillae II and III with smooth margins, maxilla II with three teeth and maxillae III and IV with no teeth) and attribute 11 (fixed for alternative polymorphism) are completely different from those present in populations A-J due to the presence of only one branchial lobe. These differences in the population profile result from the inclusion in this population of a species of a different genus (*Cenogenus eliae* n. sp.) from those in the previous populations.

The population profiles assessed from the 11 samples analysed, enable us to separate and validate the presence of the three species diagnosed in this study.

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