

Revision of *Pseudexogone* Augener, 1922 (Annelida, Polychaeta, Syllidae), and its transfer to Pilargidae

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ABSTRACT

Pseudexogone Augener, 1922, with *P. backstromi* Augener, 1922 as the type and only species, has been regarded as a member of the family Syllidae. It was questionably placed in the Syllidae in the description and apparently some morphological features were confused. The type material is lost. In this contribution: 1) *Pseudexogone* is redefined with the apparent autapomorphy of having curved, bidentate notospines; 2) *Pseudexogone* is transferred to the Pilargidae, closely allied to *Synelmis* Chamberlin, 1919; 3) those species described or identified as *Synelmis dineti* Katzmann, Laubier & Ramos, 1974 are regarded as members of *Pseudexogone*; and 4) additional species from several localities are described. Specimens were studied by using light and scanning electron microscopy. Besides the type species, four other species are distinguished by using the presence of eyes and type of furcated chaetae: *P. dineti* n. comb., from the Mediterranean and northeastern Atlantic Ocean; *P. helmuti* n. sp. from the southern Indian Ocean; *P. imajimai* n. sp., from the western Pacific Ocean; and *P. williamsae* n. sp., from the eastern Pacific Ocean. A key is included to identify all species in the genus.

KEY WORDS

Annelida,
Polychaeta,
Pseudexogone,
Synelmis dineti,
distribution,
new species.

RÉSUMÉ

Révision de *Pseudexogone Augener, 1922* (Annelida, Polychaeta, Syllidae) et son transfert dans les Pilargidae.

Pseudexogone Augener, 1922, avec *P. backstromi Augener, 1922* comme espèce type et seule espèce, a été considéré comme appartenant aux Syllidae. Dans la description originale, ce genre a été placé avec hésitation dans les Syllidae et il semble que quelques traits morphologiques ont été mal interprétés. Le matériel type est perdu. Dans cette contribution : 1) *Pseudexogone* est redéfini avec l'autapomorphie apparente de la présence de noto-épines bidentées courbées ; 2) *Pseudexogone* est transféré dans les Pilargidae, apparentés à *Synelmis Chamberlin, 1919* ; 3) des espèces déjà décrites ou identifiées comme *Synelmis dineti Katzmann, Laubier & Ramos, 1974* sont considérées comme appartenant à *Pseudexogone* ; et 4) quelques espèces supplémentaires de plusieurs localités sont décrites. Les spécimens ont été étudiés en microscopie optique et électronique à balayage. Exceptée l'espèce type, quatre autres espèces sont distinguées par la présence d'yeux et le type de soies bifurquées : *P. dineti* n. comb., de l'océan Atlantique, de la Méditerranée et de l'Atlantique nord-est ; *P. helmuti* n. sp., du sud de l'océan Indien ; *P. imajimai* n. sp., de l'ouest de l'océan Pacifique ; et *P. williamsae* n. sp., de l'est de l'océan Pacifique. Une clé des espèces du genre est incluse.

MOTS CLÉS

Annelida,
Polychaeta,
Pseudexogone,
Synelmis dineti,
distribution,
nouvelles espèces.

INTRODUCTION

The proposal of *Pseudexogone Augener, 1922*, with *Pseudexogone backstromi Augener, 1922* as the type and only species, was based on a single specimen collected sublitorally from a dead hydroid theca in Másatierra (= Robinson Crusoe) Island, Juan Fernández Archipelago, Chile. As for its taxonomic affinities, Augener (1922) questionably regarded it as a syllid polychaete, stressing that its nematode-like body and anterior end resembled *Exogone Ørsted, 1845*. However, he found it was different because of the presence of bidentate spines in median and posterior chaetigers, and because of its longer gut. Hartman (1959: 220) and Fauchald (1977: 84) regarded it as a syllid, but it is a pilargid that belongs in the Synelminae Salazar-Vallejo, 1987, as has been briefly commented elsewhere (Ruíz-Ramírez & Salazar-Vallejo 2001: 119), and as will be more extensively shown below. Further, one species formerly described in *Synelmis Chamberlin, 1919*, provided with bidentate notospines (*S. dineti Katzmann, Laubier & Ramos, 1974*), is also transferred to this genus.

METHODS

Type and non-type material was borrowed from several institutions listed below. Specimens were studied and photographed using light and scanning electron microscopy. Morphological variation was evaluated by standardizing the length and width measurements to the chaetiger 10 if specimens were not complete, and by noting the start of notospines or accounting external features. All specimens for SEM were washed in a 50:50 mixture of commercial vinegar and 70% ethanol, and then brushed carefully to remove excessive adsorbed materials, so as not to damage body cilia.

ABBREVIATIONS

Abbreviations used in the illustrations

ac	anal cirrus;
cb	ciliated band;
dc	dorsal cirrus;
dt	dorsal tentacular cirrus;
fs	furcate chaeta;
la	lateral antenna;
ma	median antenna;
no	nuchal organ;

ns	notospine;
ph	pharynx;
pp	palp papilla;
vc	ventral cirrus;
vt	ventral tentacular cirrus.

Museums and collections acronyms

ECOSUR	Colección de Referencia, El Colegio de la Frontera Sur, Chetumal, México;
LACM-AHF	Los Angeles County Museum of Natural History, Allan Hancock Foundation Polychaete Collection, Los Angeles;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMW	Naturhistorisches Museum, Wien;
NSMT	National Science Museum, Tokyo;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC;
WRRC	Water Resources Research Center, University of Hawaii, Honolulu.

RESULTS

MORPHOLOGY

Body

The species in *Pseudexogone* have very small, cylindrical bodies, with the integument thin, transparent, smooth, and each segment multiannulated. The body wall is muscular but thin, making the organism resemble a large nematode.

Prostomium

The prostomium has a blunt triangular shape, which can be more or less elongate depending on the relative length of the palps. The palps are simple, blunt, and more or less fused along their length; each palp is provided with a ventrolateral papilla. These papillae were regarded as palpostyles by Darbyshire & Mackie (2003: 64), but palpostyles are the distal article in biarticulated palps and, if present, as in *Synelmis* or other pilargid genera, they are always distal. However, the palp papillae that can be seen in members of *Synelmis*, *Litocorsa* Pearson, 1970, and in *Pseudexogone*, are subdistal and ventral. There are three antennae of about equal length, the two laterals are placed anterior to the median one, which is attached on the posterior prostomial margin. Further, over the external side of the lateral antennae bases, there are two rounded

ciliated depressions, the nuchal organs. Compound eyes may be present just behind the lateral antennae; they are provided with lenses and are only present in *Pseudexogone* and in *Synelmis*.

Peristomium

The peristomium is presegmental, but it is difficult to delineate from adjacent regions. The prostomium might be projected posteriorly and thus the median antenna appears located on the peristomium; further, the first segment is completely fused to the peristomium but it has no chaetae, but two pairs of cirri, the tentacular cirri. These modifications mean that the peristomium is a body part surrounding the mouth, somehow projected dorsally, and often carrying tentacular cirri. Therefore, it is not a single segment, and it results from the partial or complete fusion of adjacent regions. In the species of *Pseudexogone* the first body segment carries the paired tentacular cirri and it is cephalised, forming the peristomial region; its lateral and dorsal surfaces have some pairs of bundles of cilia running laterally; the cilia may be abundant giving the impression of a continuous band (Fig. 7A-D), but there are four or five discrete groups per side. Cilia are fragile, however, and if they are eroded, the reminders are oval depressions which are only seen by using SEM, and the corresponding surface appears smooth (Fig. 2B).

Parapodia and chaetae

The parapodia are often uniramous along few (1-6) anterior chaetigers, and biramous along the rest of the body. Dorsal cirri are digitate, or cirriform; the chaetal lobe may be globose or truncate, and the ventral cirri may be cirriform or basally swollen. Notochaetae are reduced to bidentate sigmoid spines, with a single one per bundle. The chaetiger where notospines first occur can be useful to separate similar species because its start has been shown to be a stable feature by Katzmann *et al.* (1974; see below). Neurochaetae are present in three different types, although the "limbate chaetae" *ex auctore* have been regarded as present in two distinct types by Katzmann *et al.* (1974: 30). By using SEM, neurochaetae may be seen to have a double longitudinal row of denticles; the shorter chaetae might be called

pectinates (Fig. 7F), while the longer ones might be called denticulate capillaries (Fig. 7E, F). There are furcate chaetae in several anterior chaetigers. The tines of furcates are very different in size and relative thickness; the larger is slightly or markedly curved, while the smaller tine is often straight (Figs 2E; 4D; 5D; 7E, F). The larger tine is provided with a variously developed blade, expanded towards the inner space; it is often straight, but it can be curved. Despite their shorter length, furcates are more easily seen when the specimen is mounted in side view; this works better in thin, transparent worms. Furcates shape is characteristic for different species; however, because of their small size, they must be observed with SEM. Light microscopy may be enough for identifications because the species might be more or less widespread in a large geographic region.

Posterior end

The posterior end has one achaetous segment, or none at all, and a pygidium provided with two ventrolateral anal cirri; the anus is generally dorsal or dorso-terminal.

Pharynx

The pharynx is rarely exposed; it is unarmed, eversible, made by two barrel-shaped lobes.

SYSTEMATICS

Order PHYLLODOCIDA Dales, 1962

Suborder NEREIDIFORMIA Glasby, 1993

Family PILARGIDAE de Saint-Joseph, 1899

Subfamily SYNELMINAE Salazar-Vallejo, 1987

Genus *Pseudexogone* Augener, 1922

Pseudexogone Augener, 1922: 191. — Fauchald 1977: 84.

TYPE SPECIES. — *Pseudexogone backstromi* Augener, 1922, by original designation.

POTENTIAL APOMORPHY BASED DEFINITION. — Bidentate curved notospines.

SPECIES INCLUDED. — *Pseudexogone backstromi* Augener, 1922, *P. dineti* (Katzmann, Laubier & Ramos, 1974) n. comb., *P. helmuti* n. sp., *P. imajimai* n. sp. and *P. williamsae* n. sp.

DISTRIBUTION. — Cosmopolitan.

EMENDED DIAGNOSIS. — Synelminae with palps simple, each with a ventrolateral papilla. Three antennae. Eyes present or absent. Two pairs of tentacular cirri. Parapodia with bidentate curved notospines, neurochaetae include pectinate and denticulate capillaries and furcate chaetae.

REMARKS

Although the anterior end of *P. backstromi* resembles species of *Exogone* Ørsted, 1845, its general appearance is very similar to some pilargids that have been included in *Synelmis* Chamberlin, 1919 (Salazar-Vallejo 2003); besides, the differences in the structure of the alimentary canal, especially the presence of a proventricle in syllids, are so important that Augener had some doubts about its placement among syllids. *Synelmis* is usually defined by having biarticulate palps and straight notospines, but its perceived similarity to syllids is depicted by the generic placement that some species received in the past, e.g., *Ancistrostylis albinii* Langerhans, 1881 and *A. rigida* Fauvel, 1919. *Synelmis* is the type genus for Synelminae, which has been defined by having a smooth integument, body cylindrical, and straight or curved notospines (Salazar-Vallejo 2003). *Pseudexogone* belongs to this subfamily and differs from *Synelmis* especially by having simple palps, and bidentate sigmoid notospines. These two pilargid synelmin genera are apparently closely allied. Further, *Pseudexogone* is closely allied to *Litocorsa* Pearson, 1970; they share a thin transparent body and simple palps. However, they differ because *Litocorsa* has straight emergent notospines with tapering tips, instead of having notospines with bidentate tips. Further, *Litocorsa* has the potential autapomorphy of having neurospines (Darbyshire & Mackie 2003).

In the original diagnosis, Augener (1922: 191) indicated that *Pseudexogone* was syllid-like, had a nematoid body with simple palps, simple hooks in median and posterior chaetigers, and an unarmed pharynx. After the description of *P. backstromi*, he tentatively placed the animal close to syllids (Augener 1922: 194). Augener (1922: 193) confused the position of the bidentate notospines, since he regarded them as ventral (neuropodial). This could

be explained because of either the polychaete body was too transparent, or because he confused the typical morphology of the pygidium; i.e. anal cirri are generally ventral or ventrolateral, which is shown in his original drawings, but if the specimen was twisted, then there would be some confusion about which surface was dorsal or ventral in the posterior end. An important missing detail in the original description is the start of notospines; since this is a rather conservative useful feature (see below), this species could be separated by using additional materials or by employing other morphological features.

Further delay in recognizing this genus as a member of the Pilargidae resulted because *Pseudexogone* was regarded as a syllid in two major reviews (Hartman 1959: 220; Fauchald 1977: 84). However, the same morphological features such as body pattern and structures (nematoid body, simple palps, bidentate emergent spines) were recognized in a pilargid by Katzmann *et al.* (1974), when they described *Synelmis dineti* (see below). As herein defined, *Pseudexogone* includes species living in subtidal depths and rarely from deeper waters (*c.* 1000 m depth). Besides the type species, it includes *P. dineti* n. comb., *P. helmuti* n. sp., *P. imajimai* n. sp., and *P. williamsae* n. sp.

Pseudexogone backstromi Augener, 1922
(Figs 1; 2)

Pseudexogone backstromi Augener, 1922: 192-194, textfig. 7a-c, only pl. 4-4b. — Rozbaczyllo 1985: 75 (ref., distr.).

TYPE MATERIAL. — The type specimen of the type species was not deposited in Sweden, although it was collected during a Swedish expedition, nor in Hamburg, where Augener lived. Museum curators were unable to find it, therefore the type and only specimen is being regarded as lost.

TYPE LOCALITY. — Másatierra (Robinson Crusoe) Island, Juan Fernández Archipelago, Chile. It was collected from a dead hydroid theca in a sample of calcareous algae, dredged in 30-45 m depth.

MATERIAL EXAMINED. — **Hawaii.** Oahu, Off Barber's Point, stn ZR1, 21°16'53.5"N, 158°01'30.3"W, I.2001, 63.7 m, 1 specimen (WRRC unnumb.). — Off Mamala, stn 26, 21°17.35'N, 157°56'49.0"W, 32.9 m, VIII.2001, 1 specimen (WRRC unnumb.). — Stn 27, 21°17'38.2"N,

157°55'31.8"W, 20.1 m, VIII.2001, 2 specimens (WRRC unnumb.). — Off Mokapu, stn B2R2 (no coordinates), 32.3 m, III.1998, 2 specimens (WRRC unnumb.). — Stn B2R3 (no coordinates), 32.3 m, III.1998, 2 specimens (WRRC unnumb.). — Off Waianae, stn ZWR6 (no coordinates), 36.6 m, X.1996, 1 specimen (WRRC unnumb.). — Stn ZWR2 (no coordinates), 33 m, V.1998, 2 specimens (one WRRC unnumb., 1 gold-coated in ECOSUR). — Stn ZWR1 (no coordinates), 36.3 m, V.2001, 1 specimen (WRRC unnumb.).

DISTRIBUTION. — Previously only known from the type locality in sublittoral rocky bottoms; the additional specimens were collected in Hawaii. They are regarded as belonging to *P. backstromi*, which implies a very wide distribution from the southeastern Pacific to the central north Pacific. The tiny size of *P. backstromi* and the presence of this species with sessile invertebrates, which may be widely distributed as foulers or as members of drifting communities, may explain this wide distribution.

DESCRIPTION OF THE TYPE SPECIMEN

(based on the original description and drawings)
Body smooth, cylindrical, tapering towards anterior and posterior ends (Fig. 1A); 9 mm long, 0.05 mm wide, *c.* 64 chaetigers. Prostomium subtriangular; palps simple, almost completely free from each other; one pair of large dorsal eyes; three antennae, the right lateral one placed ahead of the right eye. Two pairs of tentacular cirri, apparently the dorsal one longer than the ventral one (Fig. 1B). Parapodia with dorsal and ventral cirri similar to each other. Median and posterior chaetigers with a single bidentate sigmoid notospine; each spine with large proximal tooth and smaller distal tooth (Fig. 1C). Neurochaetae include finely denticulate capillaries (Fig. 1D). Posterior end with one achaetous segment; pygidium with two ventrolateral anal cirri, each as long as pygidium plus achaetous segment (Fig. 1E). Pharynx everted with margin smooth.

DESCRIPTION OF NON-TYPE SPECIMENS

Complete non-type specimens transparent, long, cylindrical, rarely yellowish, slightly wider anteriorly, tapering posteriorly (Fig. 2A), 5.0-7.5 mm long, 0.12-0.30 mm wide, with 41-61 chaetigers.

Prostomium subtriangular, about as long as wide, slightly narrower than peristomium. Three cirriform antennae of about the same size; lateral antennae located in the center of prostomium,

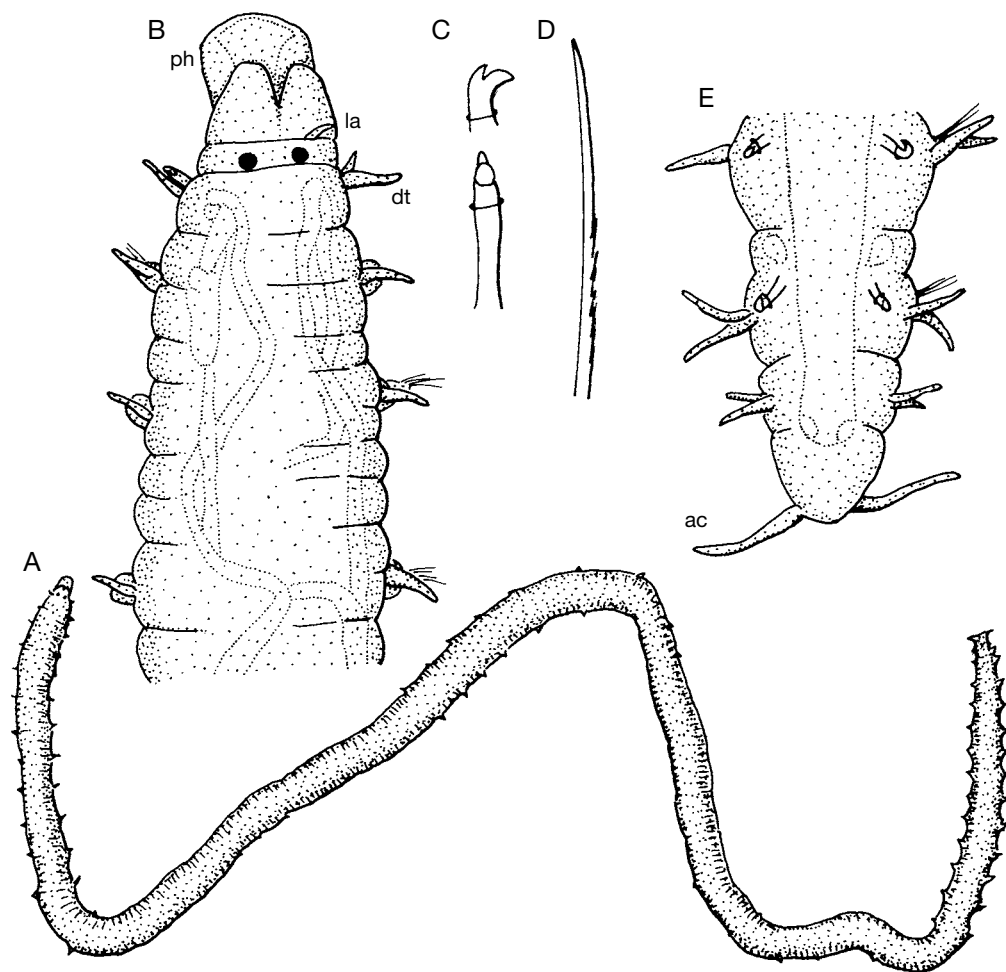


FIG. 1. — *Pseudexogone backstromi* Augener, 1922: **A**, entire worm in dorsal view (c. 9 mm long); **B**, anterior end in dorsal view (0.05 mm wide), median and left lateral antennae missing; **C**, bidentate notospines in frontal and side view; **D**, tip of finely spinulose capillary; **E**, posterior end in dorsal view (redrawn and rearranged from the original illustrations by Augener 1922). Abbreviations: see p. 536.

median antenna placed on the posterior prostomial margin. Eyes dark brown, visible in all specimens. Palps anteriorly rounded, tapering, free from each other distally (Fig. 2B); ventrolateral papillae cirriform, as long as antennae, placed half way along the palp length. Two pairs of cirriform tentacular cirri, equal-sized, most specimens with dorsal cirri longer, few with dorsal cirri slightly shorter, with a small median knob; ventral pair placed ventrally, appear smaller than dorsal one (Fig. 2C). Ciliary bundles eroded.

Parapodia uniramous in chaetigers 1-6, thereafter biramous. Parapodial cirri cirriform throughout body. Anterior parapodia with slightly emergent bidentate notospines, denticulate capillaries and furcates (Fig. 2D). Dorsal cirri digitate, ventral cirri cirriform; dorsal ones slightly longer. Notopodia with large sigmoid bidentate spines starting on chaetiger 7 (in smaller specimens on chaetiger 5, rarely on chaetiger 8), continued to the last chaetiger. Neuropodia include furcates in anterior chaetigers, pectinates and denticu-

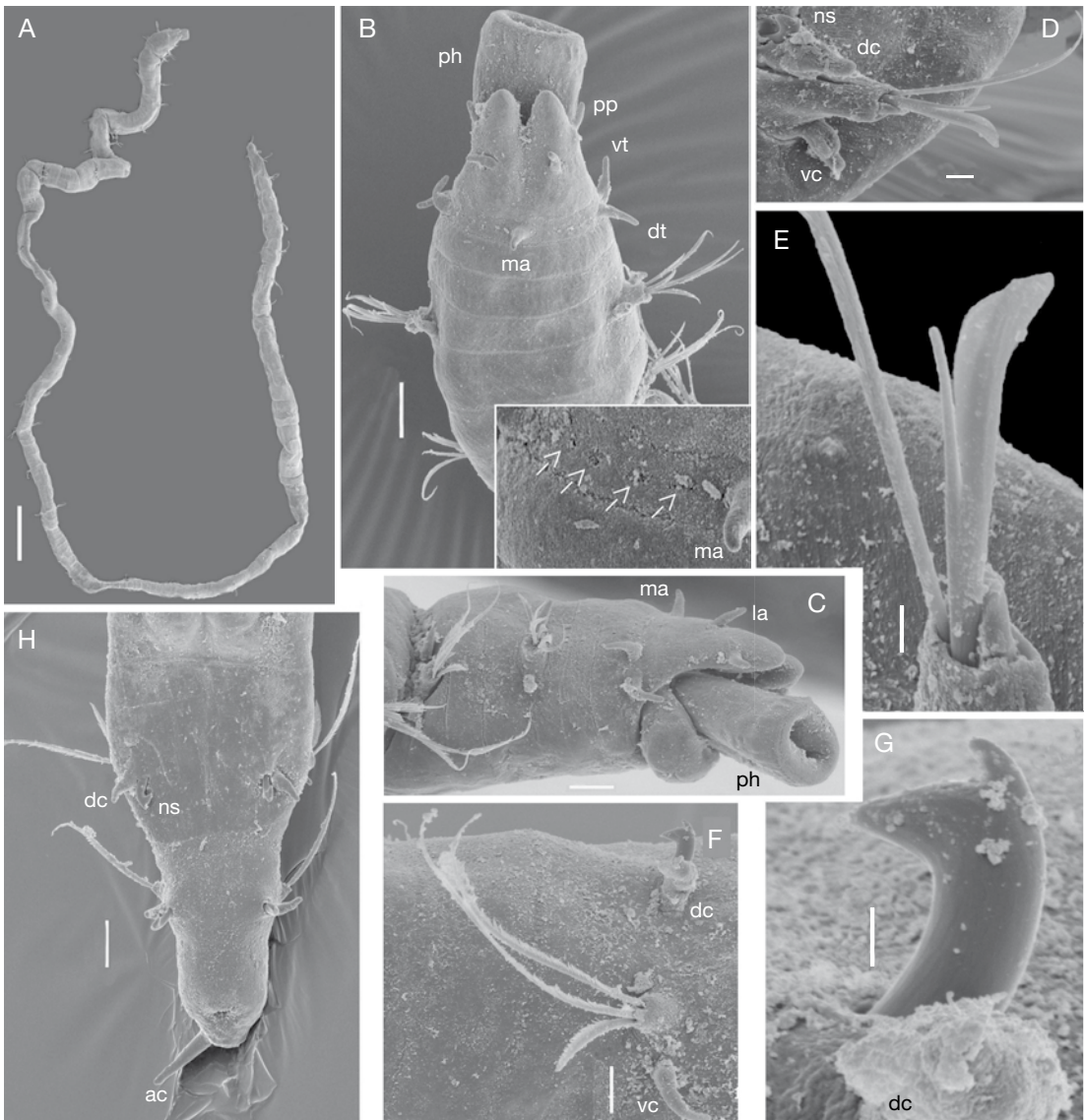


FIG. 2. — *Pseudexogone backstromi* Augener, 1922: **A**, complete specimen, anterior end over the left upper corner; **B**, same, anterior end in dorsal view, notice smooth integument (inset: close-up of ciliary bundles area; arrows point their bases); **C**, same, seen from the right, notice the everted pharynx and the ventrolateral papilla; **D**, anterior parapodium showing furcates and denticulates; **E**, same, close-up to show details of furcates; **F**, median parapodium; **G**, same, notospine; **H**, posterior end in dorsal view showing dorsal anus and ventrolateral anal cirrus (right one lost). Abbreviations: see p. 536. Scale bars: A, 333 μ m; B, 33.3 μ m; C, H, 25.0 μ m, D, 7.14 μ m; E, 3.22 μ m; F, 11.7 μ m; G, 2.50 μ m.

late capillaries, mostly broken. In median and posterior chaetigers, about two pectinates and two denticulate capillaries per bundle. Furcates (Fig. 2E) with unequal tines, longer tine with

a short flange, smaller tine cylindrical. Median chaetigers (Fig. 2F) without furcates; notospines emerge slightly. Notospines with larger subdistal tooth (Fig. 2G).

Posterior end tapering (Fig. 2H), one achaetous segment visible in about half the specimens. Pygidium conical, rounded, with two lateral anal cirri (right cirrus lost). Anus terminal. Pharynx everted in few specimens, as long as the prostomium and palps, tubular, with smooth margin; ventral pharyngeal organ enlarged (Fig. 2C). Brain lobes extended posteriorly to chaetiger 4. Oocytes present in larger specimens in chaetigers 15-40, measure 40-45 μm in diameter.

VARIATION

Notospines start on chaetigers 6-8 (5 in small specimens). Undamaged parapodia had one furcate, and two of each: pectinates and denticulate capillaries.

REMARKS

Pseudexogone backstromi resembles *P. imajimai* n. sp. and *P. williamsae* n. sp. by having well-defined eyes; they differ because of the type of furcates. In *P. williamsae* n. sp., they have a thicker, smaller tine while in the other two, they are thinner. The main differences between *P. backstromi* and *P. imajimai* n. sp. are on the relative shape of both prostomia and the larger tine of furcates. Thus, in *P. backstromi* the prostomium is about as long as wide, and the larger tine in furcates has a dorsal keel straight with a subdistal hump. On the contrary, in *P. imajimai* n. sp. the prostomium is markedly wider than long, and the larger tine in furcates has a dorsal keel curved with a subdistal notch. Furcates are very short and thus would be barely exposed to sediment abrasion or fractures, rendering their shape useful as a diagnostic feature.

Because the specimens were collected in Hawaii, far away from the type locality, they should not be employed for establishing a neotype. Further, the specimens from Hawaii have faintly pigmented eyes, whereas in the type specimen they were very large. This difference may be due to sexual maturity since the type specimen was about 9 mm long, while these specimens were up to 7.5 mm long, or alternatively due to preservation and storing in ethanol. The start of bidentate notospines was not specified in the original description, but they start in chaetigers 6-8 in all *Pseudexogone* species, so

that this feature is of very little use. A comparison between the original illustrations, the specimens and the SEM photos indicates a very close resemblance. Although the distribution is very wide, these pilargids may occupy a large geographic area with the same ecological conditions.

Pseudexogone dineti

(Katzmann, Laubier & Ramos, 1974) n. comb.
(Figs 3; 4)

Synelmis dineti Katzmann, Laubier & Ramos, 1974: 28-31, fig. 11. — Amoureux 1982a: 41; 1982b: 211.

Litocorsa dineti – Darbyshire & Mackie 2003: 65, table 1.

TYPE MATERIAL. — **Adriatic Sea.** Holotype presumably lost.

Croatia. Adriatic Sea, off Dubronik, sandy bottom, RV Jean Charcot, 42°27'N, 17°01.8'E, no date, 275 m, 3 paratypes (NHMW-13078).

TYPE LOCALITY. — Adriatic Sea, off Dubrovnik, Croatia, 42°27'N, 17°01.8'E, sandy bottom, 275 m.

ADDITIONAL MATERIAL. — **Northeastern Atlantic Ocean.** *Thalassa*, stn Z-414, 48°05'00"N, 08°20'08"W, off Brest, France, gravel, 650 m, 11 specimens (complete specimen 11 mm long, 0.15 mm wide, 52 chaetigers; notospines from chaetiger 6) (MNHN-A488, As418; one gold-coated in ECOSUR).

DISTRIBUTION. — Northeastern Atlantic Ocean to the Adriatic Sea, in sandy bottoms in 275-650 m depth.

REDESCRIPTION

Paratypes (NHMW-13078) three anterior fragments (one beheaded); larger anterior fragment with 38 chaetigers, notospines from chaetiger 7; smaller one with 16 chaetigers, notospines from chaetiger 6; head-less fragment with 11 chaetigers.

Prostomium subtriangular (corrugated in SEM specimen, Fig. 4A), about as long as wide, narrower than peristomium (Fig. 3A). Three cirriform antennae of about the same size; lateral antennae placed in the middle of prostomium, over a low elevation, slightly ahead of median antenna, do not reach palp tips; median antenna on posterior prostomial margin. No eyes. Palps anteriorly rounded, distally separated, with one pair of ventrolateral papillae (Fig. 3B, C), cirriform, as long as antennae

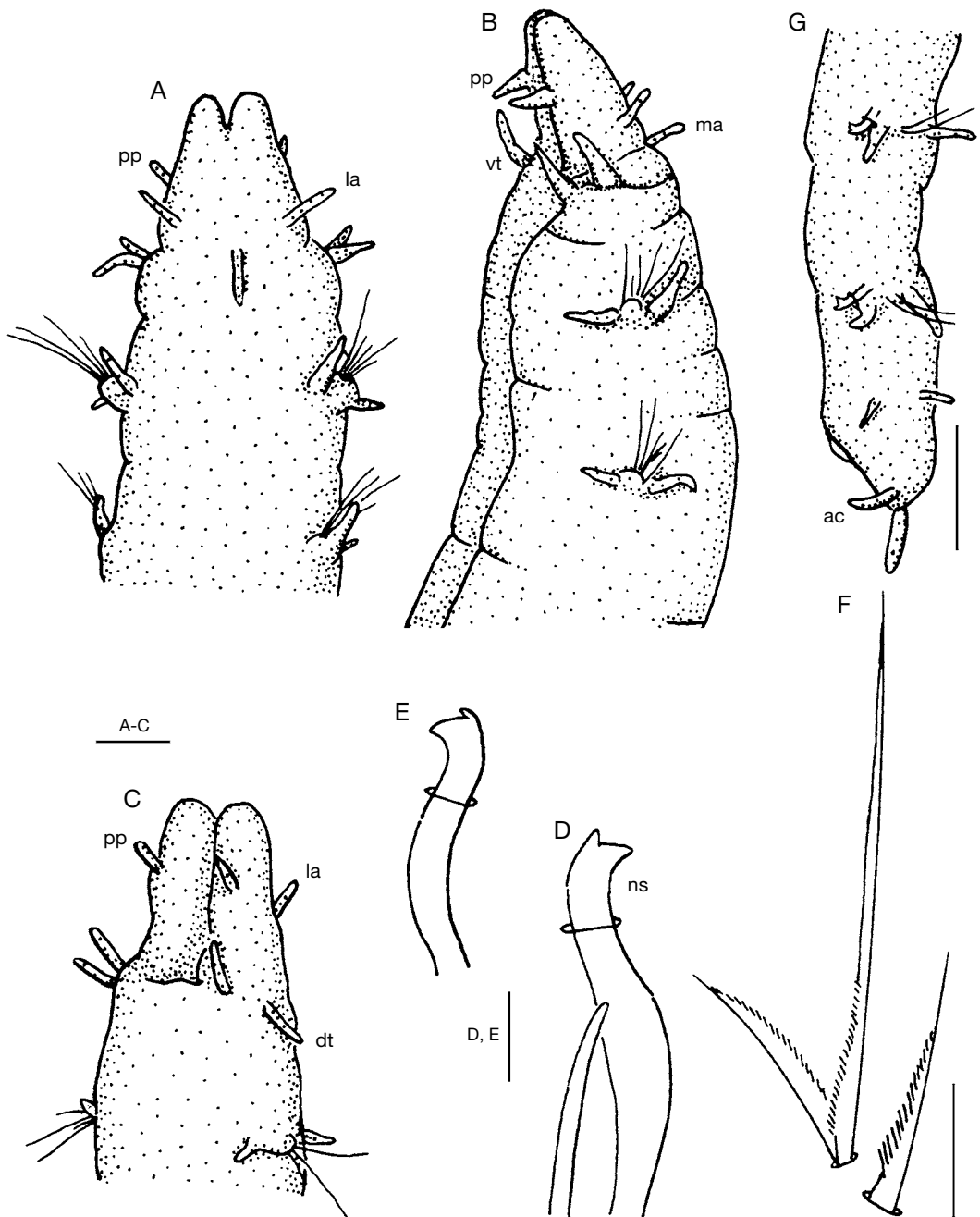


FIG. 3. — *Pseudexogone dineti* (Katzmann, Laubier & Ramos, 1974) n. comb.: **A**, anterior end in dorsal view; **B**, same, seen from the left; **C**, same, ventral view showing the ventrolateral papillae; **D**, **E**, notospines and notaculacae, in side view; **F**, denticulate capillary and pectinate chaetae; **G**, posterior end in right lateral view (redrawn and rearranged from the original illustration by Katzmann *et al.* 1974). Abbreviations: see p. 536. Scale bars: A-C, 40 µm; D-F, 20 µm; G, 100 µm.

(collapsed in SEM specimen). Two pairs of cirriform tentacular cirri, dorsal pair slightly longer (Fig. 4B). Ciliary bundles eroded.

Parapodia uniramous in chaetigers 1-6(7), thereafter biramous. Parapodial cirri cirriform throughout body; dorsal cirri twice as long, and three times wider than ventral ones. Anterior parapodia (Fig. 4C) with notospines slightly exposed. Chaetae include an emergent, brittle, sigmoid bidentate notospine (Fig. 3D, E), first present in chaetigers 6-7, continued to posterior end; each notospine slightly curved (not sigmoid), with proximal tooth larger than distal one; neurochaetae 3-4 denticulate capillaries, some pectinates in a few anterior chaetigers, one smooth straight capillary (Fig. 3F), and one furcate chaeta remaining in a few anterior chaetigers. Furcates (Fig. 4D) with unequal tines, longer tine with a flaring curved blade not reaching the smaller, tapering tine. Posterior parapodia with notospines more exposed (Fig. 4E), with 2 denticulate capillaries and one pectinate neurochaeta; dorsal cirri cirriform, longer than ventral cirri. Bidentate notospines from median chaetigers (Fig. 4F) slightly exposed, with larger subdistal tooth and blunt distal tooth.

Pygidium not seen in paratypes. The original description stated that it has two ventrolateral cirriform cirri (Fig. 3G), about as long as the last achaetous segment. Brain with posterior lobes separated and passing the level of chaetal lobes in chaetiger 3. Pharynx 4.5 chaetigers long.

VARIATION

Specimens from northeastern Atlantic Ocean mostly anterior fragments; complete specimen was 9.5 mm long, with 51 chaetigers; others were eight anterior fragments, and two median fragments. Most had two brown eyespots external to the lateral antennae bases. Furcates were mostly broken but they seem to appear in chaetigers 1-2, and there are two furcates per bundle in chaetigers 1-3, then only one until chaetiger 5 or 6, thereafter they apparently disappear. One anterior fragment had its pharynx everted, it is distally smooth, barely surpassing palps.

REMARKS

Pseudexogone dineti n. comb. resembles *P. helmuti* n. sp. by lacking eyes. They differ in the relative devel-

opment of the furcates blade; in *P. dineti* n. comb. the blade is curved, and straight in *P. helmuti*. Katzmann *et al.* (1974: 28) stated that the holotype was a complete specimen with 29 segments and that it had been formally deposited (and catalogued as NHMW-13078). However, none of the specimens (labeled as paratypes in a small paper tag) were complete, so the holotype might be regarded as missing. On the other hand, Katzmann *et al.* (1974: 30) made an interesting discovery regarding the variation in the start of the notospines, since they found that in 13 out of 16 specimens, bidentate notospines started in chaetiger 6; in the other three specimens they started in chaetiger 7. Thus, it is a rather conservative feature. On the other hand, Darbyshire & Mackie (2003: 65) included *S. dineti* as a member of *Litocorsa*, despite the fact it has bidentate notospines and lacks neurospines. This inclusion prompted them to modify the generic definition. However, *S. dineti* belongs in *Pseudexogone*, not in *Litocorsa*, and the latter genus should be restricted as to include only those similar species provided with straight simple notospines, and neurospines.

Pseudexogone helmuti n. sp. (Fig. 5)

TYPE MATERIAL. — Southern Indian Ocean. Off Saint-Paul Island, *Marion Dufresne*, campagne MD50 JASUS, stn 20-DC91, 38°47'67"S, 77°27'11"E, 17.VII.1986, 975 m, very compacted fine sand, holotype (MNHN-1482); paratypes (12 in MNHN, 6 in ECOSUR, including SEM specimen).

TYPE LOCALITY. — Off Saint-Paul Island, southern Indian Ocean, in deep water.

ETYMOLOGY. — This species is named after Helmut Zibrowius, author of many important publications on serpulid polychaetes, and who participated in several cruises, including the one on which the specimens of this new species were collected.

DISTRIBUTION. — Only known from the type locality, off the Saint-Paul Island, southern Indian Ocean, in about 1000 m depth.

DESCRIPTION

Holotype complete, transparent; body tapering posteriorly, 7.5 mm long, 0.25 mm wide, with 42

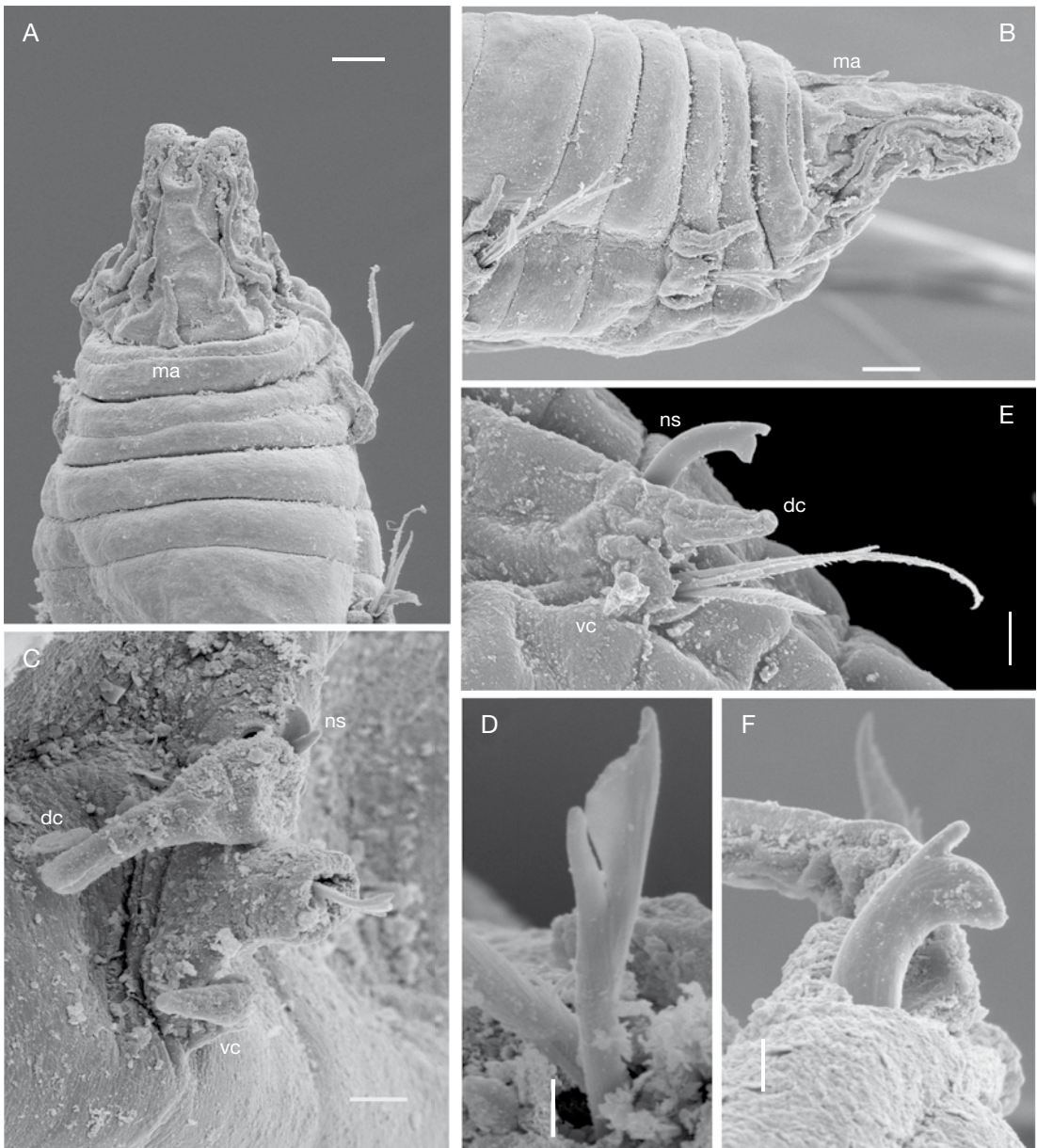


FIG. 4. — *Pseudexogone dineti* (Katzmann, Laubier & Ramos, 1974) n. comb.: **A**, anterior end in dorsal view; **B**, same, seen from the right; **C**, anterior parapodium showing larger dorsal cirrus; **D**, furcate from an anterior chaetiger; **E**, posterior parapodium; **F**, notospine from a median chaetiger. Abbreviations: see p. 536. Scale bars: A, B, 25.0 μm ; C, 6.66 μm ; D, 2.5 μm ; E, 10.0 μm ; F, 3.33 μm .

chaetigers. Prostomium subtriangular, about as long as wide, slightly narrower than peristomium (corrugated in SEM specimens). Three antennae, all cirriform of about the same size; laterals placed

by the prostomial middle, median placed over the posterior prostomial margin. Eyes not visible. Palps tapering, separated distally, in SEM specimens distorted, free from each other (Fig. 5A-C), each

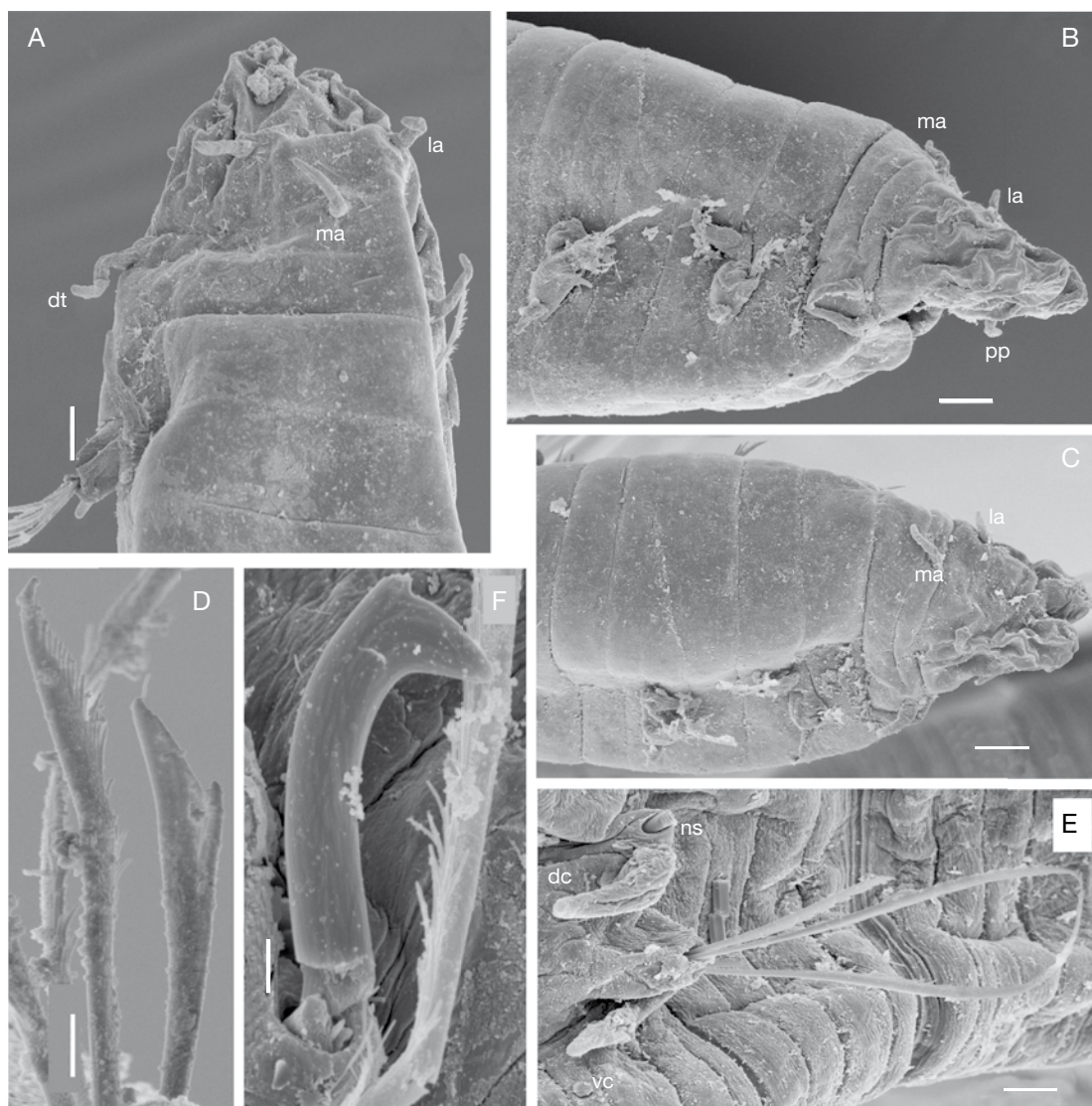


FIG. 5. — *Pseudexogone helmuti* n. sp.: **A**, anterior end in dorsal view; **B**, another specimen, anterior end in lateral view; **C**, same, showing antennae; **D**, furcate and pectinate chaetae from an anterior chaetiger; **E**, median chaetiger, showing a notospine slightly exposed; **F**, notospine broken, from a posterior chaetiger. Abbreviations: see p. 536. Scale bars: A, 20.0 μ m; B, 20.5 μ m; C, 33.3 μ m; D, 4.0 μ m; E, 11.1 μ m; F, 2.05 μ m.

provided with a ventrolateral papilla (Fig. 5B, C), as long as antennae, placed about the half of the palp length. Tentacular cirri cirriform, dorsal cirri slightly longer; ciliary bundles eroded (Fig. 5B).

Parapodia uniramous in chaetigers 1-6, thereafter biramous. Parapodial cirri cirriform throughout body. Anterior parapodia with two denticulate capil-

laries, one pectinate, and one furcate neurochaetae (Fig. 5D). Notopodia with large sigmoid bidentate spines starting in chaetiger 7, continued to last chaetiger. Neuropodia includes furcates in anterior chaetigers, pectinates and denticulate capillaries, most broken. Furcates with unequal tines, longer tine with a flaring blade not reaching the blunt digitate

smaller tine. Median chaetigers (Fig. 5E) with slightly emergent notospines, parapodial cirri digitate, dorsal cirri larger than ventral cirri. Chaetal lobe conical, with 2 denticulate capillaries and 1 or 2 pectinates. Bidentate curved notospines more exposed in posterior chaetigers (Fig. 5F), each with rounded larger subdistal tooth, and a smaller, probably eroded, apical tooth. In median and posterior chaetigers, broken pectinates resemble furcates but they differ.

Posterior end tapering. No achaetous segments. Pygidium conical, blunt, with two lateral anal cirri. Anus terminal. Pharynx not everted, as long as first 4 chaetigers in length.

VARIATION

The complete paratypes were 5.0–5.8 mm long, 0.15–0.25 mm wide, with 34–40 chaetigers. The start of notospines was in chaetiger 7. One with unbroken chaetae had two of each: furcates, pectinates and denticulate capillaries. There were no prepygidial achaetous segments. One paratype had its pharynx everted; it is made of two muscular rings with an apparently smooth margin.

REMARKS

Pseudexogone helmuti n. sp. is the only described species of the genus living in almost 1000 m depth. It resembles *P. dineti* n. comb. by lacking eyes but they differ in the relative development of the blade of furcates; it is straight in *P. helmuti* n. sp. while it is curved in *P. dineti* n. comb.

Pseudexogone imajimai n. sp.

(Figs 6; 7)

Synelmis dineti – Imajima 1987: 158, fig. 5a–h (*non* Katzmann *et al.* 1974).

TYPE MATERIAL. — **Northwestern Pacific Ocean.** Japan, off Tanega-shima, 30°37.8'N, 13°054.2'E, 45 m, VI.1975, M. Imajima coll., holotype (NSMT-85251).

Guam. Off Tanguisson, stn WWRCT-NE-R3, 13.5523°N, 144.8072°E, 43 m, 2001, 5 paratypes (USNM). — Stn WRRC T-NW-R1, 13.5537°N, 144.8072°E, 50.3 m, 2001, 4 paratypes (MNHN).

ADDITIONAL MATERIAL. — **Guam.** Off Tanguisson, stn WWRC T-NE-R3, 13.5523°N, 144.8072°E, 43 m (no date available), 1 specimen (gold-coated,

ECOSUR). — Stn WRRC T-NW-R1, 13.5537°N, 144.8072°E, 50.3 m, 2001, 1 specimen (gold-coated, ECOSUR).

TYPE LOCALITY. — Off Tanega-shima, Kyūshū, Japan, in 45 m.

ETYMOLOGY. — The specific name is a modest homage to Dr. Minoru Imajima, in recognition of his very productive career in polychaete systematics, who has concentrated his efforts in Japanese fauna, and especially because of his publication on pilargids.

DESCRIPTION

Holotype complete, damaged, 5.5 mm long, 0.2 mm wide, 38 chaetigers. Because of the removal of chaetigers 1, 15, and 32, body breaking apart in those segments. Prostomium subtriangular (Fig. 6A), wider than long, with three similar medially constricted antennae; lateral antennae placed in the middle of prostomium, on the base of palps, not reaching palp tips; median antenna on posterior prostomial margin. Palps free from base, rounded, each with subdistal ventral papillae (Figs 6B; 7A, C). Eyes not visible, but two large globular colourless structures present just behind lateral antennae. Nuchal organs placed in the outer external base of lateral antennae (Fig. 7D). Peristomium with two pairs of similar tentacular cirri, as long as median antenna, because they are lateroventral, dorsal cirri looks longer than ventral one. Ciliary bundles extended laterally from the median antenna insertion, and two others extend over the dorsal surface of peristomium (Fig. 7A–C).

Anterior parapodia uniramous. Median and posterior parapodia biramous. Dorsal cirri digitate throughout the body, ventral cirri basally swollen in anterior and median chaetigers. Anterior parapodia (Fig. 6C) with dorsal and ventral cirri with median constriction, of about same size; median (Fig. 6D) and posterior chaetigers, with dorsal cirri larger, digitate, ventral cirri basally swollen. Anterior parapodia with two denticulate capillaries, two pectinates, and a furcate chaeta (Fig. 7E). Following chaetigers with an emergent, brittle, sigmoid bidentate notospine (Fig. 6F, G), first present from chaetiger 6, continued to posterior end, more exposed in posterior chaetigers (Fig. 7G), each notospine with larger subdistal tooth; 1 or

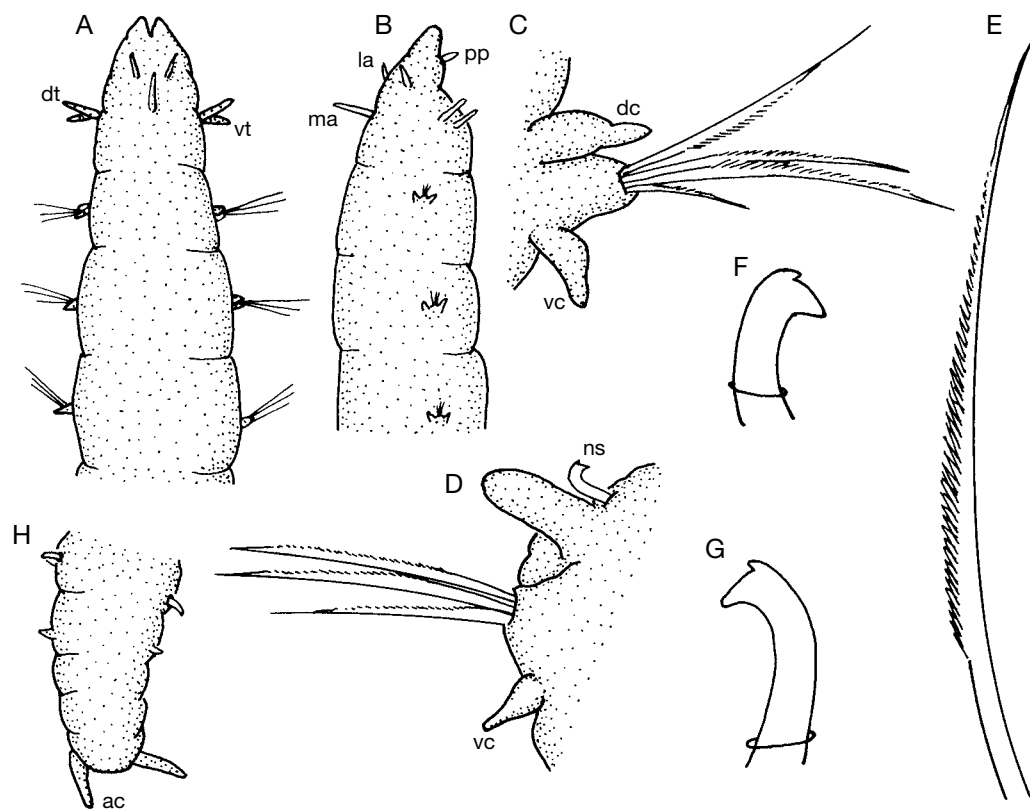


FIG. 6. — *Pseudexogone imajimai* n. sp.: **A**, anterior end in dorsal view; **B**, anterior end in lateral view; **C**, first parapodium, anterior view; **D**, 25th parapodium, anterior view; **E**, same, pectinate chaetae; **F**, **G**, notospines; **H**, posterior end in dorsal view (redrawn and rearranged from the original illustrations by Imajima 1987; without scale bars in the original). Abbreviations: see p. 536.

2 finely denticulate capillaries and 1 or 2 pectinates per bundle (Fig. 6E). Furcates with a flaring rounded blade, slightly longer than the tapering smaller tine, with dorsal keel curved, with a subdistal notch (Fig. 7E, F).

Posterior end with two prepygidial achaetous segments; pygidium with two ventrolateral anal cirri as long as last achaetous segment and pygidium (Figs 6H; 7H). Pharynx not everted.

VARIATION

Complete specimens were 3.0–5.5 mm long, about 0.15 mm wide, with 30–45 chaetigers, often with an achaetous prepygidial segment. Oocytes visible in chaetigers 13–23, along a line, each of about 25–30 μm in length.

DISTRIBUTION

Japan to Guam, in shallow sublittoral depths. This is a new record for the polychaete fauna of Guam, Mariana Islands (Bailey-Brock 2003).

REMARKS

Pseudexogone imajimai n. sp. resembles *P. backstromi* by having furcates with a thin smaller tine. These two species differ in the relative shape of both prostomia and in the blade in furcates. Thus, in *P. imajimai* n. sp. the prostomium is wider than long, and the dorsal keel of furcates blade is curved with a subdistal notch. In *P. backstromi*, on the contrary, the prostomium is longer than wide, and the dorsal keel of furcates is straight with a subdistal hump. Since furcates are very short, it would make them barely

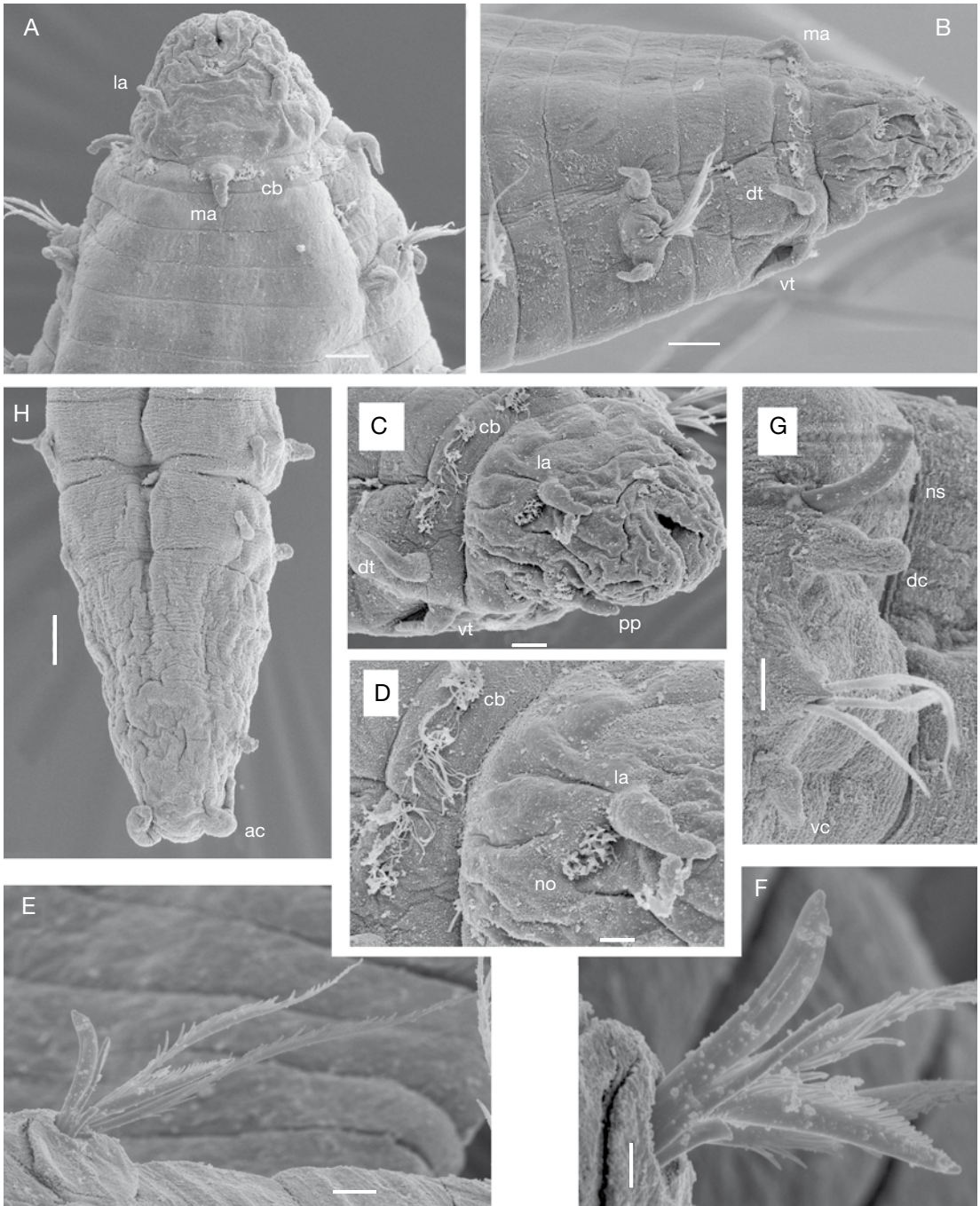


FIG. 7. — *Pseudexogone imajimai* n. sp.: **A**, anterior end in dorsal view, palps are free but collapsed after dehydration; **B**, same, lateral view; **C**, same in oblique view, showing ciliated bands; **D**, same, close up to show nuchal organ; **E**, anterior chaetiger with furcates; **F**, same, close up of furcate, pectinate, and base of denticulate capillary; **G**, posterior parapodium; **H**, posterior end, dorsal view. Abbreviations: see p. 536. Scale bars: A, B, H, 20 μ m; C, 11.1 μ m; D, 5.5 μ m; E, 6.66 μ m; F, 2.85 μ m; G, 9.09 μ m.

exposed to fractures, and their shape is diagnostic. In the holotype of *P. imajimai* n. sp., there are bifid curved notospines from chaetiger 6 (on the right side) though over the left side, most are broken and there is one left on chaetiger 9. This could explain the finding by Imajima (1987: 158).

Pseudexogone williamsae n. sp.
(Fig. 8)

TYPE MATERIAL. — **Eastern Pacific Ocean.** USA, Bureau of Land Management Southern California Baseline Studies, off Southern California, Allan Hancock Foundation cruise 1341, RV *Velero IV*, stn 22979, 33°50.88'N, 119°59.91'W, 6.1 miles, 13° T to East Point, Santa Rosa Island, 78 m, box core, coarse biogenic sand with occasional pebbles, 15.X.1975, holotype (LACM-AHF POLY 2184) and paratype (LACM-AHF POLY 2185). — Allan Hancock Foundation cruise 1341, RV *Velero IV*, stn 23039, 33°52.97'N, 120°01.05'W, 4.5 miles, 34° T to East Point, Santa Rosa Island, 57 m, box core, muddy fine sand with shell, 17.X.1975, 1 paratype (23039 ECOSUR). — RV *Thomas G. Thompson*, stn 80901, 33°46.2'N, 119°50.9'W, NW slope Santa Cruz Basin, 22 km SSW of Gull Island, Santa Cruz Island, BLM 80, 222-271 m, sand, 21.VIII.1977, 2 paratypes (LACM-AHF POLY 2186, another one ECOSUR).

ADDITIONAL MATERIAL. — **Eastern Pacific Ocean.** California, Allan Hancock Foundation cruise 1341, RV *Velero IV*, stn 22943, 32°44.05'N, 119°06.17'W, 35.7 miles, 83.5° T to China Point, San Clemente Island, 319 m, box core, indurated mud and fine sand with rocks, 12.X.1975, 1 specimen (LACM-AHF). — RV *Thomas G. Thompson*, stn 818-10, 32°53.3'N, 119°23.4'W, 34 km NW of pinnacle, Tanner Bank, California Channel Islands, 113 m, box core, shell and coarse sand, 24.VIII.1977, anterior fragment (LACM-AHF).

Western Mexico. Seamount studies (see Levin *et al.* 1994 for details; most in LACM-AHF), Alvin Dive 2318, Fieberling Guyot, 992 km W of San Diego, Sea Pen Rim, on northeast perimeter of top, box 1, Rep. 6, 0-1 cm, SPR, 32°27.631'N, 127°49.489'W, 636 m, basaltic and calcareous sands, 4.XII.1990, 3 specimens (LACM-AHF). — Alvin dive 2318, box 1, Rep. C, 5-10 cm, SPR, 32°27.631'N, 127°49.489'W, 636 m, basaltic and calcareous sands, 4.XII.1990, 1 specimen (LACM-AHF). — Alvin dive 2327, box 1, Rep. 8, 5-10 cm, 32°27.631'N, 127°49.489'W, 636 m, basaltic and calcareous sands, 13.XII.1990, 1 specimen (LACM-AHF). — Alvin dive 2401, box 3, 1-2 cm, SPR, 32°27.631'N, 127°49.489'W, 636 m, basaltic and calcareous sands, 23.X.1991, 1 specimen (LACM-

AHF). — Alvin dive 2401, box 1, Rep. 8, 0-1 cm, SPR, 32°27.631'N, 127°49.489'W, 636 m, basaltic and calcareous sands, 27.X.1991, 2 specimens (one gold-coated, ECOSUR, the other LACM-AHF). — Alvin dive 2322, White Sand Swale, 32 box 2, Rep. 1, 2-5 cm, WSS, 32°27.581'N, 127°47.839'W, 579 m, nearly white foraminiferal and calcareous sands, 8.XII.1990, 1 specimen (LACM-AHF). — Alvin dive 2326, White Sand Swale, 32 box 2, Rep. C, 1-2 cm, 32°27.581'N, 127°47.839'W, 582 m, nearly white foraminiferal and calcareous sands, 12.XII.1990, anterior fragment (LACM-AHF). — Alvin dive 2322, White Sand Swale, 32 box 5, Rep. A, 2-5 cm, WSS, 32°27.581'N, 127°47.839'W, 579 m, nearly white foraminiferal and calcareous sands, 8.XII.1990, 2 specimens (LACM-AHF).

TYPE LOCALITY. — Off Santa Rosa Island, Southern California, in shallow water.

ETYMOLOGY. — This species name is made after Susan Williams who has worked during many years on Californian polychaetes, and who indicated that some of these specimens belong to an undescribed genus and species.

DESCRIPTION

Holotype complete, 32 mm long, 0.3 mm wide, 101 chaetigers. Prostomium corrugated in SEM specimens (Fig. 8A, B), with palps irregularly wrinkled, free from each other; ventrolateral papillae directed laterally, slightly shorter than lateral antennae. All antennae cirriform, median one slightly longer than laterals; lateral antennae placed medially on prostomium, slightly ahead of median, median antennae placed over projected border on posterior margin of prostomium. One pair of eyes, each one placed on the inner side of the lateral antennae; original brown pigment faded, retina and lens visible. Tentacular segment biannulate, first ring laterally reduced; tentacular cirri ventrolaterally placed, dorsal cirrus slightly longer than ventral one. Ciliary bundles eroded.

Chaetiger 1 biannulate, then mostly 3-annulated to chaetiger 10, thereafter with 6-8 rings, continued to posterior end; less clearly noticeable in elongated segments. Parapodia uniramous in chaetigers 1-5, biramous thereafter. Dorsal and ventral cirri cirriform, dorsal ones longer. Chaetal lobe rounded with 4-6 neurochaetae; two elongated denticulate capillaries, two shorter pectinates, and two shorter furcates. Anterior parapodia (Fig. 8C) with cirriform cirri, dorsal and

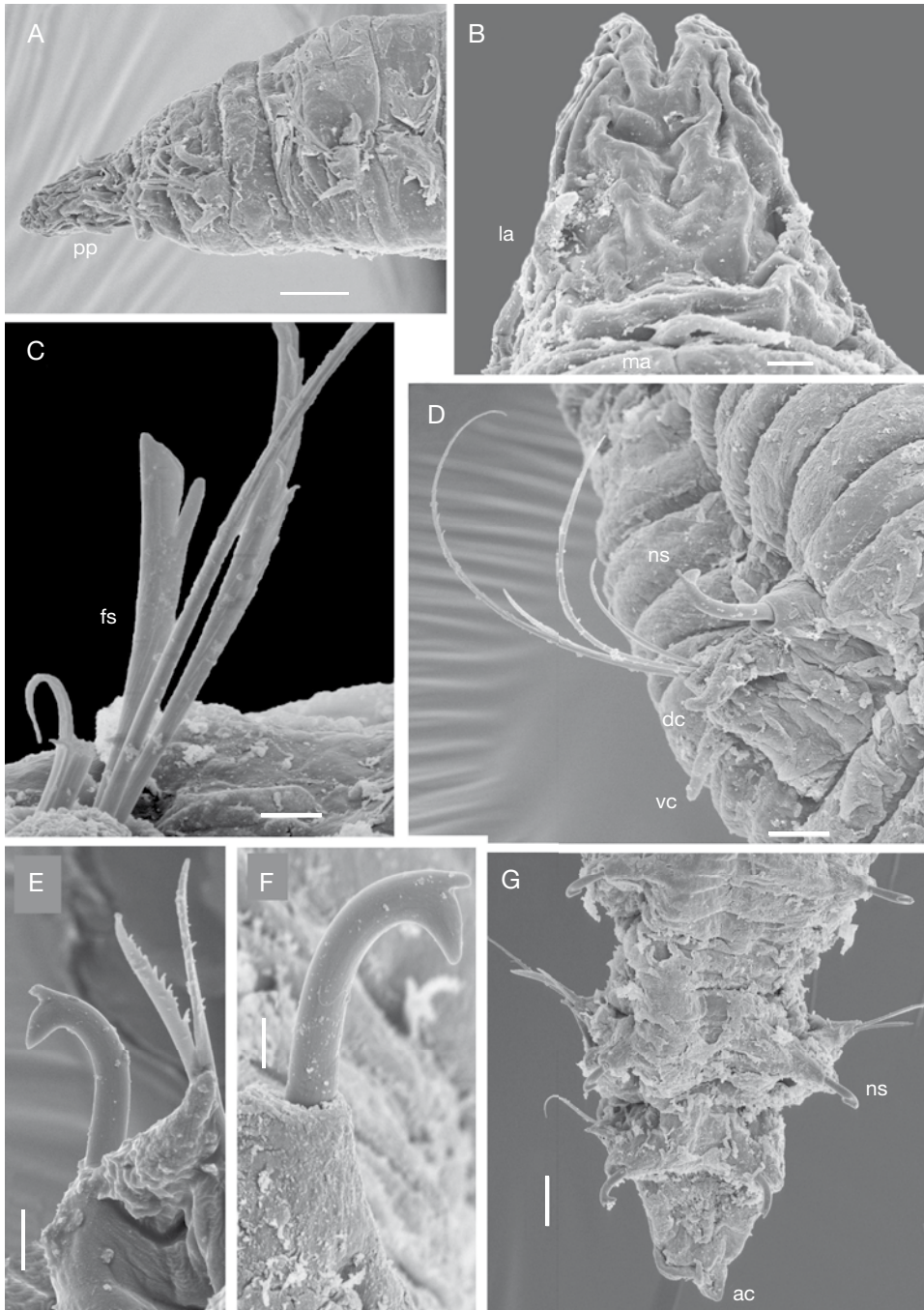


FIG. 8. — *Pseudexogone williamsae* n. sp.: **A**, anterior end, lateral view, the left ventrolateral papilla is bent posteriorly; **B**, same, dorsal view; **C**, chaetae from chaetiger 8; **D**, median chaetiger; **E**, **F**, notospines from posterior chaetigers; **G**, posterior end in dorsal view, anal cirri are bent over the pygidial posterior margin. Abbreviations: see p. 536. Scale bars: A, 50 μ m; B, 12.5 μ m; C, 5.0 μ m; D, 14.0 μ m; E, 8.33 μ m; F, 5.0 μ m; G, 25.0 μ m.

ventral cirri of about same length; 1 or 2 denticulate capillaries and 1 or 2 pectinates; single furcate per bundle, with longer tine flared, blade margin straight, not reaching smaller digitate tine. Median chaetigers (Fig. 8D) with bidentate curved notospines, clearly exposed along all body, present to last chaetiger; each notospine (Fig. 8E, F) markedly curved with larger subdistal tooth and tiny distal tooth. Furcates apparently restricted to chaetigers 3-8. From chaetiger 6, slightly exposed bidentate curved notospine, becomes more exposed in posterior chaetigers.

Posterior end with one achaetous segment (without it in SEM specimen, Fig. 8G); pygidium rounded, as long as last two segments, anus dorsal, with two ventrolateral cirriform cirri, as long as pygidium. Brain posterior lobes long, separated, reaching the level of chaetal lobes of chaetiger 3. Pharynx not everted, about 1.5 chaetigers long. Few oocytes, singly in chaetigers 65-97, each about 30 μm .

VARIATION

Type and non-type specimens were 5-32 mm long, 0.23-0.30 mm wide, with 37-110 chaetigers.

Most were thin but a few were markedly contracted showing highly annulated integument; other morphological features were unaltered. All had pale brown eyes placed at the inner side of lateral antennae, and bifid curved notospines from chaetiger 6. Mature females with large oocytes in posterior third of body; some specimens were small (AD2318, Rep. C), being only 7.5 mm long with 39 chaetigers; one paratype (BFI 23039) being 11 mm long with 55 chaetigers, had oocytes in chaetigers 37-55. Oocytes were ovoid, about 30 μm long, with a small nucleus and showing different content and size of granules, or even hyaline, but always irregularly wrinkled (probably due to preservation). There was some variation in the amount of eggs per segment and these differences could be related to the steps between maturation and spawning.

REMARKS

Pseudexogone williamsae n. sp. resembles *P. backstromi* and *P. imajimai* n. sp. It differs from them by having furcates with a thick smaller tine.

KEY TO SPECIES OF *PSEUDEXOGONE* AUGENER, 1922

1. Prostomium with dark eyes (pigment rarely faded out); furcates with larger tine slightly longer than smaller tine 2
— Prostomium without eyes; furcates with larger tine about twice as long as smaller tine ... 4
2. Furcates with smaller tine thin 3
— Furcates with smaller tine thick *P. williamsae* n. sp.
3. Furcates with larger tine blade curved, with a subdistal notch *P. imajimai* n. sp.
— Furcates with larger tine blade straight, with a subdistal hump *P. backstromi*
4. Furcates with blade straight, not curved *P. helmuti* n. sp.
— Furcates with blade curved, not straight *P. dineti* n. comb.

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