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Review of the types of *Palola* (Eunicidae: Polychaeta)

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As part of a review of the types of all currently known species of eunicid polychaetes, the genus *Palola* is reviewed. Nineteen named taxa are here accounted for; of these 12 are tentatively considered valid; the other species are incompletely known, or are considered synonyms of other species or are indeterminable. The number of species suggested in this paper may change once variability and allometric patterns have become better understood.

KEYWORDS: Annelida, Polychaeta, Eunicidae, *Palola.*

Introduction

The palolo-worms* live in burrows in coral or coralline substrata and are largely limited to tropical or subtropical waters. A few species are present at temperate latitudes: *Palola paloloides* (Moore, 1904) is found off southern California (Hartman, 1968) in very shallow water, and the most frequently recorded species, *P. siciliensis* (Grube 1840) was first described from the Mediterranean and has been widely reported in warm-temperate waters (cf. Fauvel, 1923, 1953).

The palolos are best known for their spawning habits. The posterior part of each individual, filled with gametes, breaks off and swarms at the water surface, while the anterior end survives in its coral burrow. Timing of the swarming is closely tied to lunar cycles and the swarming of thousands of individuals in shallow reef areas has attracted a great deal of both popular and scientific attention. A considerable literature discusses the relation of spawning to lunar cycles (e.g. Hauenschild *et al.*, 1968) and the morphological changes that take place, including the development of a set of ventral eyes on each segment of the epitokous part of the body, presumably responsible for the reaction of the worms to moonlight. The early literature especially contains notes on the use of the swarming posterior ends of the worms as food (e.g. Stair, 1847; Macdonald, 1858).

Two additional, unrelated, species of polychaetes have been called palolos, probably because they show a similarly close coordination of spawning and lunar cycles. The Atlantic palolo is a member of the same family as *Palola,* but belongs to the genus *Eunice,* it is currently called *E. fucata* Ehlers 1887 (see Fauchald, 1992). The

* The generic name *Palola* is spelled with a terminal a, the common name, at least in Samoa, is palolo, with a terminal o. Other names used for these worms are cognates of the Samoan name.

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Japanese palolo is a brackish-water nereidid, *Tylorhynchus heterochaetus* Quatrefages 1866 (cf. Imajima and Hartman, 1964).

Distinctively scoop-shaped (deeply U-shaped) mandibles are present in the genera *Nematonereis, Lysidice* and *Palola;* other eunicids have shallowly V-shaped lower jaws. Members of *Nematonereis* have a single median antenna and species of *Lysidice* have three antennae. Subacicular hooks and pectinate setae are present in both. Members of *Palola* have five antennae and lack subacicular hooks and pectinate setae.

Problems were caused by the different life-stages of the specimens examined by early scientists. The first recognizably described species was *Eunice siciliensis* Grube 1840 from Palermo, Sicily; Grube based his description on sexually immature anterior ends and he had no hesitation in assigning his new species to the genus *Eunice.* In 1847 Gray described a new genus and species, *Palola viridis,* from Samoa, based on material collected by J. B. Stair. All specimens reported by Gray were swarming posterior ends, making the relationship to *Eunice* far less obvious, since all characteristic prostomial and peristomial features were missing. Macdonald (1858), after quoting Gray's description *in toto,* described the anterior end of a single specimen from Fiji. He mentioned that the head-end was small in relation to the rest of the body and that it had three antennae, as do members of the genus *Lysidice;* however, during regeneration, all species of eunicids with five occipital antennae, go through a stage in which they have only three antennae. Macdonald's illustration shows that the anterior end must have been translucent with the jaws showing through the body-wall, suggesting that Macdonald had a regenerating specimen. Macdonald's illustration of the parapodia shows that subacicular hooks are absent, showing that it must have been a *Palola.*

Macdonald's report, however, led Quatrefages (1866: 379) to transfer Macdonald's species to *Lysidice;* a genus he included among the Lumbrineridae rather than in the Eunicidae. Quatrefages also renamed the species, *Lysidice palolo.* Ehlers (1898) examined specimens sent to him from Samoa and Fiji; he established very firmly that the 'true' palolos were closely related to Grube's *Eunice siciliensis.* He agreed with Quatrefages that Macdonald had described the anterior end of a *Lysidice,* not that of a 'true' palolo, and proceeded to name this species, based on material sent to him from Fiji, *Lysidice fallax.* Ehlers (1898: 415) noted that the jaws as illustrated by Macdonald appeared to contain traits from both genera.

The genus name *Nereidonta* Blainville 1828 appears to threaten the validity of the name *Palola.* Blainville (1828: 476) briefly described his genus, without illustrations. He described a new species, *N. paretti;* and listed other species, all of which are taxa included by Cuvier (1817), Lamarck (1818) and Savigny (1820) in *Eunice* (or *Leodice*); thus there can be no doubt that Blainville considered the species a member of the family Eunicidae. Blainville (1828: 477) stated that his name would replace generic names previously erected by Cuvier, Lamarck and Savigny, including *Eunice* and *Leodice.* Such replacement is not necessary, *Eunice* has been established as a valid generic name for the taxon (see discussion in Fauchald, 1992). Ehlers (1868: 353 and 358) suggested that *Nereidonta paretti* was a synonym *Eunice siciliensis.* Blainville's description matches any number of polychaetes and Ehlers' proposed synonymy must be rejected. The genus is here considered a junior synonym of *Eunice.*

Identifying species of *Palola* is difficult. The characters commonly used to characterize eunicids are either absent (subacicular hooks and pectinate setae) or are present erratically (branchiae) and tend to be uniform in structure (again the branchiae). Most authors have referred to their specimens by any combination of the generic names

Eunice or *Palola* and the specific names *viridis* or *siciliensis,* and have listed other described species as synonyms of these taxa. The large, calcified scoop-shaped mandibles are so unusual that few early zoologists went beyond mentioning this feature to describe in any detail other characters, such as setal structures and branchial distribution. None of the roughly 20 species can be identified from the original descriptions; a re-description of the types represents a first step towards a better understanding of the relationship among the circumtropical populations.

Abbreviations used in the text

A-I, Outer lateral antennae; A-II, inner lateral antennae; A-III, median antenna.

The jaws are conventionally observed as *in situ* from the dorsal side and are numbered from the posterior and dorsal side, towards the anterior and ventral side. Mx-I, First maxillae (fang); Mx-II, second maxillae; Mx-III, unpaired, third maxilla present on left side only; Mx-IV, fourth maxillae; Mx-V, fifth maxillae; Mx-VI, sixth maxillae.

Palola Gray, in Stair, 1847

Eunicids with slender cylindrical bodies made up of many, short segments. Dorsum expanded and convex; ventrum short and slightly flattened. Prostomium short, anteriorly truncate with short, cylindrical or tapering antennae. Antennae without articulations. Peristomium cylindrical, consisting of two rings, with a pair of peristomial cirri located dorsally on the second ring. Jaws with paired Mx-I, II, IV and V; unpaired Mx-III present on left side only as viewed from dorsal side. Small, paired Mx-VI present in some species. Mandibles usually heavily calcified; always forming a deep scoop enclosing maxillae. Branchiae present from mid-body (often from about setiger 100); always single filaments; often missing on long stretches of body; absent in some species. Parapodia located below midline of body. Notopodia represented by single, tapering or digitiform cirri. Neuropodial presetal lobes usually lower than acicular lobes; distally truncate or rounded; neuropodial postsetal lobes similar, but usually about as high as setal lobes. Ventral cirri basally inflated in median or median and posterior setigers. Inflated bases strictly ventral in position; forming paired ventral scutes where well developed. One setal bundle with geniculate or straight, limbate or capillary setae. The other setal fascicle with compound simple falcate, or bidentate falcigers. Compound spinigers, pseudocompound falcigers, subacicular hooks and pectinate setae absent.

Type-species, by monotypy, *Palola viridis* Gray in Stair, 1847.

Systematic characters

I attempted to expand the number of characters used to characterize species of *Palola.* The morphological structures which I have examined are common to all eunicids, and are potentially usable in all eunicid genera. I report here not only positive results but also the negative results, since especially in the study of the setae, the demonstrable pattern of setal lengths etc., may be of use in other genera.

All new characters were tested against the size of the specimens to show possible allometric relationships. Measurements taken on all specimens included a count of numbers of setigers, total length and maximum width. Since most specimens were incomplete, the size of the specimens was also measured as the length of the anterior end through setiger 10 (L-10) and the width at setiger 10 (W-10). Multiplying the two measures for setiger 10 gives a measure of size that has elsewhere been demonstrated to bear a good relation to the total size of the specimens (Fauchald, 1991) and has the

advantage of making it possible to characterize the size of incomplete specimens. Other authors have measured the length of the first five setigers; I prefer the larger measure since this decreases the relative measurement error.

Of the traditionally used characters in eunicid taxonomy applicable to *Palolo,* only the dentition of the maxillae and the distribution of the branchiae remain. Both features are known to be subject to variation (Fauchald, 1991). However, other morphological features are present; these features (or their counterparts) have been used for taxonomic purposes in other polychaete families, if not for closely related forms.

Occipital antennae. The character or character-set derivable from measuring the length of the occipital antennae may be valuable in grouping species at the generic level (Fauchald, in preparation), but show no usable patterns in the material examined in this study.

Maxillae. The presence of a small distal denticle on Mx-II has been used as a major character to separate *P. paloloides* from *P. siciliensis* (Hartman, 1944: 131). This denticle is predictably present in material in intertidal areas of the northwestern coast of Mexico and southern California. Two new characters, the location and structure of Mx-III and the structure of Mx-IV, characterize different species in this study (see the key below and the descriptions). The reduction of Mx-III in some species is unique in the family.

Notopodial cirri. The notopodial cirri of setiger 1 are usually longer than those of setiger 2. In some species they appear to be longer than in other taxa, but with the limited material this could not be statistically demonstrated. Notopodial cirri in branchial region (at about setiger 150) are either long, slender and digitiform or short and sharply tapering. I suspect that when more specimens have been examined, the shape of the median and posterior notopodial cirri will be useful to identify different populations.

Branchiae. Branchiae are present from setiger 100 or beyond in most species examined. All branchiae are single, usually flattened filaments; the lengths of the filaments appear to vary systematically; however, this has not been demonstrated statistically. Some species lack branchiae; such absence must be documented on complete specimens since the first branchiae may not be present before setiger 250. Characterizing a species as abranchiate after examining incomplete specimens with 100 or less setigers should never be attempted.

Compound falcigers. Setal measurements have been used in describing syllids (e.g. Russell, 1990) so I attempted to measure the compound falcigers in these taxa as well. The length of the emergent region of a seta may vary with varying muscular contraction at fixation, so a measurement of setal length *per se* is difficult to interpret.

The length of the appendage in a compound seta is independent of fixation. In types of *Palola* the length of the appendage is related in part to the size of the specimens. In addition, length of the appendages varies with position in the body. It increases in the first 100 setigers by about 100 μm thereafter it drops to less than 100 μm over the next 300 setigers. Three species have consistently shorter appendages than the other seven studied, but the separation between the two groups is not statistically significant ($P > 0{\cdot}05$).

The lengths of the appendages are strongly correlated to the length of the shafts ($r = 0{\cdot}86$, $n = 150$). This demonstrates that the length of the setae in preserved animals is a good representation of the normal length of the setae. Thus, I have documentation to show that length measurements of setae change in a predictable pattern. Unfortunately, in this genus, the absolute length of the setae does not vary greatly from one

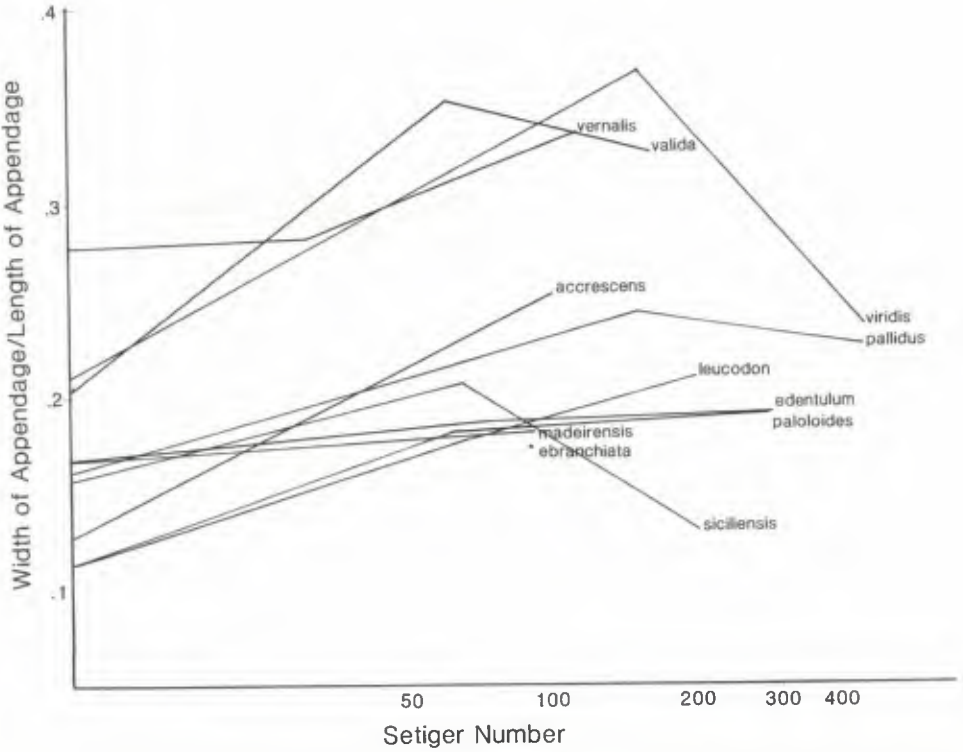

FIG. 1. Distribution of width versus length of appendages of compound falcigers along the body for species of *Palola.* Note that this is a semilog plot. Further explanation in the text.

species to the next, so in this genus these measurements have no value as systematic characters.

The ratio between width and length of the appendages shows an interesting pattern (Fig. 1, note the semilog scale). Three species, *valida, vernalis* and *viridis,* have, at least through the first 300 + setigers, considerably 'chunkier' appendages than the other species. Two of these species, *vernalis* and *viridis,* also have shorter appendages than other species at corresponding setigers. The third species, *valida,* has appendages of approximately mean length compared to other species in the genus. In one species with short appendages, *edentulum,* the appendages are also very slender. The distribution of the ratios appears to be independent of the size of the specimens: one species with very large type-specimens, *accrescens,* falls in the middle of the range of width/length ratios; and *valida,* also with large types, is grouped with two species with small type specimens. Note that measurements of setal patterns in the genus were based mostly, but not exclusively, on type specimens; additional measurements done on non-type specimens of *Palola viridis* from the central Pacific and *P. siciliensis* from the Caribbean Sea demonstrated patterns similar to the ones mentioned above (Fauchald, in preparation).

This new character has been scored for all species; slim appendages are by far the most common state in the genus *Eunice,* the most likely outgroup for *Palola.* The character states are defined in the character list (character 83).

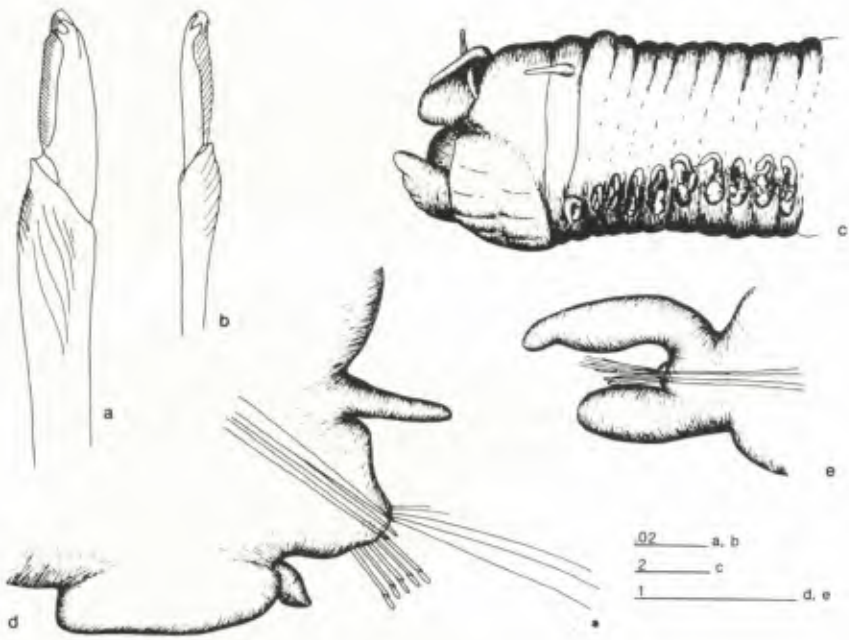

FIG. 2. *Palola accrescens* (syntype, USNM 19020); **a**, compound falciger, setiger 100; **b**, compound falciger, setiger 1; **c**, anterior end, lateral view; **d**, parapodium 100, anterior view; **e**, parapodium 1, anterior view.

List of species

accrescens Hoagland 1920 as *Leodice,* referred to *Palola,* previously also listed in *Eunice.*
adriatica Schmarda 1861 as *Eunice;* referred to *Palola siciliensis.*
bitorquata Grube 1870 as *Eunice;* referred to *Palola siciliensis.*
dubia Woodworth 1907 as *Eunice;* indeterminable.
ebranchiata Quatrefages 1866 as *Eunice;* referred to *Palola siciliensis.*
edentulum Ehlers 1901, as *Nicidion.*
gallapagensis Kinberg 1865 as *Nicidion,* indeterminable.
leucodon Ehlers 1901 as *Eunice;* referred to *Palola siciliensis.*
longicirrata Kinberg 1865 as *Nicidion,* indeterminable, see below.
madeirensis Baird 1869 as *Eunice;* referred to *Palola.*
pallidus Hartman 1938 as *Palola.*
palola Quatrefages 1866 as *Lysidice;* referred to *Palola viridis.*
paloloides Moore 1909 as *Eunice* (*Eriphyle*); referred to *Palola.*
paretti Blainville 1828, as *Nereidonta;* indeterminable.
siciliensis Grube 1840 as *Eunice;* referred to *Palola.*
simplex Peters 1855 as *Eunice* (*Palola*) referred to *Palola siciliensis.*
taenia Claparède 1864 as *Eunice;* referred to *Palola siciliensis.*
valida Gravier 1900 as *Eunice;* referred to *Palola siciliensis.*
vernalis Treadwell 1922 as *Leodice viridis vernalis.*
viridis Gray 1847 as *Palola.*
viridis vernalis Treadwell 1922 as *Leodice;* referred to *Palola vernalis.*
worsleyi, Stewart 1881 as *Lithognatha;* indeterminable.

Description of species

Palola accrescens (Hoagland 1920)
(Fig. 2, Table 1)

Leodice accrescens Hoagland 1920: 616.

Eunice accrescens Hartman (1959: 308, 316).
Palola accrescens Fauchald (1992: 24).

Material examined. HOLOTYPE, USNM 18956; Philippine Islands, *Albatross.* 2 specimens, USNM 19020, Philippine Islands, coll. *Albatross.* 2 specimens (dried out), USNM 19021, *Albatross* st. D5148, 5°35'40"N, 120°47'30"E, 16 February 1908, 38 m, coarse sand and shells, Agassiz trawl. 2 specimens USNM 18990, *Albatross* st. D5142, 6°06'10"N, 121°02'40"E, 15 February 1908, 38–53 m, coarse sand and shell, Agassiz trawl.

Comments on material examined. The syntype from USNM 18956 is specifically listed by Hoagland (1920) as her type, thus taking the status of holotype. No additional information is available about this specimen, or about the specimens from USNM 19020. The other specimens, characterized as juveniles by Hoagland, are from specified *Albatross* stations. The illustration of the anterior end is of the specimen from USNM 19020.

Description. Type from USNM 18956 incomplete, of unknown sex (possibly immature female), consisting of 317 setigers. Total length 144 mm, maximum width 12 mm at setiger 10. Length through setiger 10, 11 mm. Body abruptly tapering anteriorly; otherwise without taper. Dorsum highly convex; ventrum flattened; with a pronounced median groove; cross-sections nearly hemispherical. Ventral groove increasingly indistinct posteriorly; ventrum slightly convex in last setigers present. Parapodia located at intersection between dorsum and ventrum with inflated bases of ventral cirri forming the lowermost edge of each cross-section. Body light evenly tan-coloured without colour patterns.

Prostomial and peristomial features. Prostomium (Fig. 2c) frontally rounded; dorsally inflated, prostomial halves hemispherical in appearance. Median sulcus deep. Prostomium distinctly shorter than peristomium; about as wide as peristomium; as

Table 1. Summary of selected characters in the types of *Palola accrescens* (Hoagland 1920).

USNM no.	18956	19020	18990	
Specimen no.			1	2
Variable characters				
Complete	no	no	no	no
Number of setigers	317	242	115	173
Total length	144	115	53	77
Maximum width	6	6	2·5	3
at setiger	10	30	60	20
Length through setiger 10	11	10	7·5	7
Width at setiger 10	12	5	2	2·75
Start of branchiae	98	114	?	?
Last branchiae on setiger	?	?	?	?
Number of anterior cirriform ventral cirri	5	5	4	4
Ventral cirri inflated to setiger	?	191	?	?
Invariable characters				
Teeth in left Mx-II	3	3	3	3
Teeth in right Mx-II	4	4	4	4
Teeth in Mx-III	0	0	0	0
Teeth in left Mx-IV	4	4	4	4
Teeth in right Mx-IV	4	4	4	4

deep as half the peristomium or deeper. Eyes between bases of A-I and A-II. Antennae arranged in a horseshoe shape; evenly spaced; similar in thickness. Ceratophores ring-shaped in all antennae; without articulations. Ceratostyles digitiform; without articulations. A-I to middle of anterior peristomial ring; A-II and III to middle of posterior peristomial ring. Median three antennae outreaching prostomium when stretched forwards. Length of A-II and III similar with A-I shorter. Peristomium with muscular lower lip marked off by a groove. Separation between peristomial rings distinct on all sides. Anterior ring two-thirds of total peristomial length. Peristomial cirri to middle of anterior peristomial ring; digitiform; without articulations.

Jaws. Maxillae strongly calcified; maxillary formula 3 + 4, 1 + 0, 4 + 4 and 1 + 1. Mx-II convex; fitting closely inside expanded bases of Mx-I. Mx-III short, located behind left Mx-II as a short, sharp-edged ridge. Mx-IV short, straight ridges with four very small teeth. Mx-V short, straight ridges. Mandibles missing in specimen from USNM 18956; in other specimens curved to enclose maxillae; strongly calcified with oblique cutting edge; high edge laterally.

Branchiae. Present from setiger 98 through the end of the fragment; initially as short, scattered filaments; later on all setigers. Each branchia a single, slender, cylindrical filament; about as long as one-half of body width. Branchiae emerging from body wall distinctly above notopodial cirri.

Parapodial structures. Neuropodial acicular lobes truncate in anterior setigers; becoming increasingly rounded in median and posterior setigers (Fig. 2d, e). Anterior presetal lobes slightly shorter than acicular lobes; truncate; other presetal lobes and all postsetal lobes follow outline of acicular lobes closely. Ventral cirri thick, cylindrical; nearly ovoid in first setigers; becoming basally inflated from about setiger 5. All other ventral cirri with inflated bases forming transverse ridges. Distal tips distinct; strongly tapering and attached slightly posterior to upper edge of base. Notopodial cirri of parapodium 1 about twice as long as in next following parapodia; terete; about twice as long as ventral cirri of same setiger. Next following notopodial cirri slender, cylindrical, becoming increasingly tapering from about setiger 5; without articulations.

Setae. Limbate setae at least twice as long as compound falcigers; slender; straight. Limbation very narrow; marginally serrated. Pectinate setae absent. Appendages of compound falcigers distally bidentate; guards distally without mucro, rounded. In anterior compound falcigers (Fig. 2b) shafts subdistally distinctly inflated; marginally serrated; with distinct internal striations. Appendages slender, with nearly parallel sides; heads distinct. Proximal teeth larger than distal teeth; directed obliquely distally and uptilted. Distal teeth erect; with straight taper. In median compound falcigers (Fig. 2a) shafts distally distinctly inflated and marginally serrated. Appendages distinctly tapering. Proximal teeth larger than distal teeth; directed laterally; uptilted. Distal teeth directed obliquely distally; with straight taper. Ratio of length to width of median appendages 0·25 or less. Compound spinigers and pseudocompound falcigers absent. Aciculae dark honey-coloured to brown with round transverse section. Separation of acicular cores and sheaths distinct. Aciculae distally pointed; straight. Anterior parapodia usually with paired aciculae. Median and posterior parapodia usually with three or more aciculae in each parapodium. Subacicular hooks absent.

Remarks. The holotype and the specimen from USNM 19020 are very similar; the two specimens from USNM 18990 differ from the others in that they lack branchiae

throughout (115 and 173 setigers respectively); in the other two specimens branchiae are present from setiger 98 and 114 respectively.

[***Eunice adriatica*** Schmarda 1861

Eunice adriatica Schmarda 1861: 124.
Eunice siciliensis Ehlers (1863: 353).

Remarks. There appears to be no disagreement about the synonymy proposed by Ehlers (1868). The name is listed here for the sake of completeness; as far as is known, it has never been considered a separate species in the genus *Palolo.*]

Palola bitorquata (Grube 1870)

Eunice bitorquata Grube 1870: 55; Fauchald (1992: 25, see also page 86).
?Eunice siciliensis Grube (1878: 101).
Eunice siciliensis Augener (1913: 279–281).

Remarks. No material is available. The original description was very brief, in updated terminology it contained the following information.

The species is brown with golden to brown cross-bars on the peristomium. Branchiae are present from setiger 104; always as single filaments, far outreaching the notopodial cirri. Segments are remarkably short and the median antenna is as long as four segments. Maxillae with coarse teeth; Mx-II with 4 teeth.

Augener (1913: 280) re-described the type. The specimen was posteriorly incomplete and at that time in two pieces, including in all about 185 setigers. The colour pattern at that time had faded to a dull greyish-red, with indistinct brown cross-bars on the posterior half of the 'buccal segment' and on setiger 1. Augener believed that this colour pattern must have been the only cause for the separation of the species from *P. siciliensis* since no other differences could be perceived. He added that the jaws resembled those of *P. siciliensis* in shape and colour, including the presence of the scoop-shaped mandible, except that the jaws were light brown rather than the usual dark brown to nearly black present in that species.

Grube (1878: 101) referred his species, apparently under some doubt, to his own *Eunice siciliensis* without comment. Augener (1913: 279) formalized this proposed synonymy.

The original description is wholly inadequate to characterize the species; the information given is consistent with the synonymy indicated.

Palola dubia (Woodworth 1907)

Eunice dubia Woodworth 1907: 11-12, pl. 1, figs 4–6, pl. 2, fig. 15.
Lysidice falax Woodworth (1903: 878).

Remarks. The name *Eunice dubia* was proposed for the epitokous spawning ends of a palola Woodworth had previously called *Lysidice falax.* The illustration indicates that the specimen seen by Woodworth belongs to *Palola.* No material is available. The species is indeterminable.

Palola ebranchiata (Quatrefages 1866)
(Fig. 3)

Eunice ebranchiata Quatrefages, 1866: 316–317. Fauchald (1992: 126).
Eunice siciliensis Ehlers (1868: 353), Grube (1870: 296), Fauvel (1911: 18).

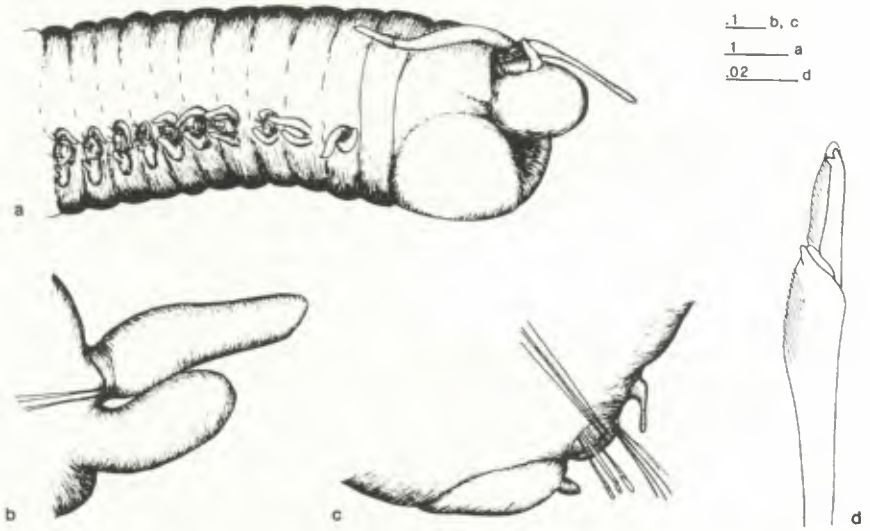

FIG. 3. *Palola ebranchiata* (type, MNHN, Paris); **a**, anterior end, lateral view; **b**, parapodium 1, anterior view; **c**, parapodium 51, anterior view; **d**, compound falciger, parapodium 51.

Material. Type, MNHN, A[1] (R.)–1868–No. 51, Palermo.

Comments on material examined. It is unclear if more than one specimen was examined by Quatrefages; the specimen here examined may represent only part of Quatrefages' material.

Description. Specimen examined incomplete, of unknown sex, with 130 setigers. Total length 52 mm; maximal width 2·5 mm; length through setiger 10, 8 mm; width at setiger 10, 2·2 mm. Anterior end cylindrical; medially ventrally flattened with inflated bases of ventral cirri located wholly ventrally. Segments short and crowded.

Prostomial and peristomial features. Prostomial lobes (Fig. 3a) frontally rounded; dorsally slightly inflated; median sulcus deep. Prostomium distinctly shorter and narrower than peristomium; about half as deep as peristomium. Eyes between bases of A-I and A-II; faded. Antennae in a very shallow horseshoe shape; A-I separated from A-II and A-III by a distinct gap; similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles tapering; without articulations. A-I to middle of second peristomial ring; A-II and A-III to setiger; A-III slightly longer than A-II. Peristomium with distinct, inflated muscular lower lip; otherwise cylindrical. Separation between peristomial rings distinct on all sides. Anterior ring nearly three-quarters of total peristomial length. Peristomial cirri barely reaching middle of anterior ring; tapering; without articulations.

Jaws. Dissected out; currently missing.

Branchiae. Absent throughout fragment.

Parapodial structures. First few acicular lobes barely distinguishable; forming a low swelling near base of notopodial lobes (Fig. 3b). Median acicular lobes (Fig. 3c) low, gently rounded ridges. Aciculae emerging dorsal to midline near upper edge of neuropodium. Pre- and postsetal lobes follow acicular lobes closely in first few parapodia. Thereafter, all presetal lobes low, excavate folds, covering bases of setae. Postsetal lobes rounded; slightly higher than acicular lobes in most setigers. First 10

ventral cirri tapering; thereafter becoming basally inflated. Inflated bases transverse ridges; present in all remaining setigers. Distal free tip present in all setigers; rounded or conical. First notopodial cirri twice as long as those in next setiger; digitiform. Other notopodial cirri strongly tapering from wide base. Distinct separation between cirrophore and style present in all setigers. Articulations of notopodial cirrostyles absent.

Setae. Not emergent in first setiger; visible inside acicular lobe; including limbate setae and compound falcigers. Limbate setae otherwise distinctly longer than all other setae; slender, tapering; with smooth or slightly dentate margins. Pectinate setae absent. All appendages of compound falcigers bidentate; guards without mucros, distally bluntly rounded. Anterior compound falcigers with shafts with long, gently inflated distal ends; marginally distinctly serrated; distal beak present. Appendages shorter than inflated shaft; only slightly tapering with nearly parallel sides. Proximal teeth larger than distal teeth; triangular, directed laterally; with straight taper. Distal teeth erect; with straight taper. Median compound falcigers (Fig. 3d) with shafts distinctly inflated; marginally serrated. Appendages distinctly tapering. Proximal teeth larger than distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Compound spinigers and pseudocompound falcigers absent. Aciculae paired; brown; separation into core and sheath indistinct. Aciculae distally tapering; straight. Subacicular hooks absent.

Remarks. The original description is brief, but includes the information that branchiae are missing; that the mandibles are very large and enclose the other jaws and that the antennae are short. Grube (1870: 296) examined the type and declared it completely in agreement with many specimens which he had seen of *Eunice siciliensis*. The species is currently characterized by a combination of features including the shape of the prostomium, the insertion of the occipital antennae and the shape of the presetal parapodial lobes.

Palola edentulum (Ehlers 1901)
(Fig. 4)

Nicidion edentulum Ehlers 1901: 261–262.

Material examined. Holotype, ZMB 3730 Juan Fernandez Island, coll. Plate.

Description. Holotype of unknown sex; incomplete; with 111 setigers. Total length 42 mm, maximum width 1·75 mm at setiger 3. Length through setiger 10, 5·5 mm, width at setiger 10, 1·5 mm. Anterior body slightly inflated dorsally; flattened ventrally; remainder of fragment less distinctly ventrally flattened.

Prostomial and peristomial features. Prostomium (Fig. 4c) about as wide and as long as peristomium; distinctly deeper than one-half of depth of peristomium. Prostomial lobes frontally rounded; dorsally slightly inflated; median sulcus shallow. Eyes between bases of A-I and A-II; black. Antennae in a transverse row; A-I separated from A-II and III by distinct gap; similar in thickness. Ceratophores short, distinct cylinders in all antennae; without articulations. Ceratostyles digitiform, abruptly tapering distally; without articulations. A-I to posterior edge of anterior peristomial ring; A-II and III to setiger 1; A-III slightly longer than A-II. Peristomium cylindrical; with distinctly muscular lower lip. Separation between rings distinct on all sides. Anterior ring slightly longer than posterior ring on dorsal side and about twice as

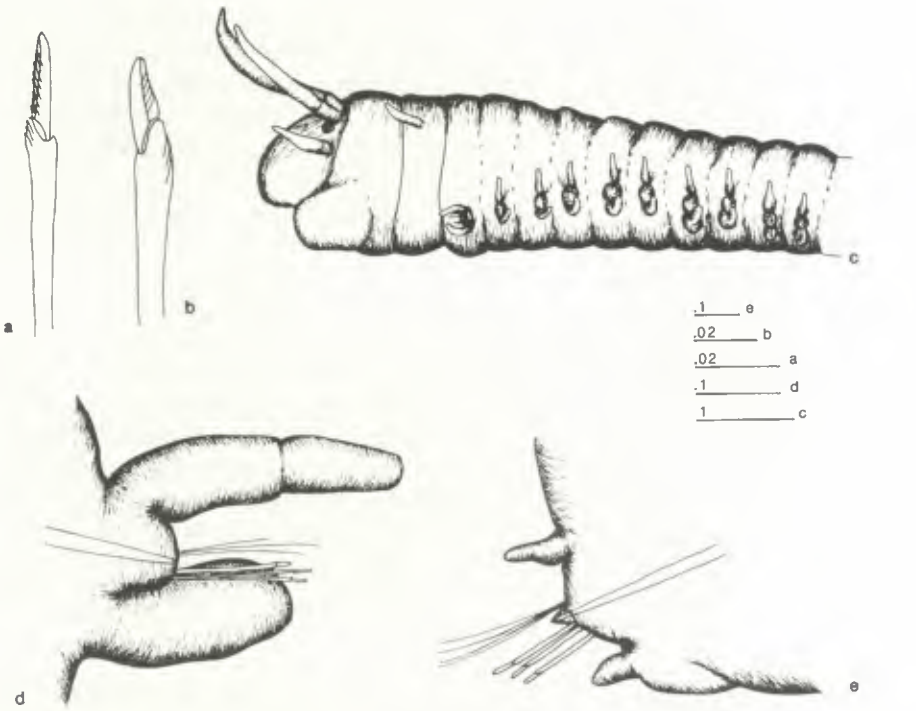

FIG. 4. *Palola edentulum* (holotype, ZMB 3730); **a**, compound falciger, setiger 1; **b**, compound falciger, setiger 1; **b**, compound falciger, setiger 97; **c**, anterior end, lateral view; **d**, parapodium 1, anterior view; **e**, parapodium 97, anterior view.

long as posterior ring on ventral side. Peristomial cirri reaching middle of anterior peristomial ring; digitiform; without articulations.

Jaws. Jaw apparatus dissected out. Mandibular wings enclosing remainder; not calcified; no teeth visible. Mx-I falcate; Mx-II with 4 teeth on each side. Mx-III–V not visible.

Branchiae. Absent in fragment.

Parapodial structures. Anterior neuropodial acicular lobes (Fig. 4d) distally rounded; aciculae emerging at midline. Median acicular lobes (Fig. 4e) distally conically pointed with aciculae emerging at midline. Anterior pre- and postsetal lobes follow outline of acicular lobes closely; median pre- and postsetal lobes low transverse folds. First four ventral cirri thick, digitiform. Ventral cirri inflated from setiger 5 through remainder of fragment. Inflated bases elongated transverse welts; increasing in size through about setiger 60; thereafter decreasing, but distinct on last setigers present. Distal tip of ventral cirri distinct in all setigers; tapering. Inflated bases located wholly on ventral surface of each segment. Anterior notopodial cirri digitiform; tapering in median setigers. Notopodial cirri of setiger 1 no longer than those in next following setigers.

Setae. Limbate setae slender, tapering; distinctly longer than other setae in all setigers. Pectinate setae, compound spinigers and pseudocompound falcigers absent. Appendages of compound falcigers simple and falcate; guards distally bluntly rounded; marginally serrated. Anterior compound falcigers (Fig. 4a) with shafts slightly inflated; marginally serrated; distal beak indistinct. Appendages slender; with nearly parallel sides, tapering only gently distally to simple, nearly erect tips. Median

compound falcigers (Fig. 4b) with shafts distinctly inflated; marginally serrated; marginal teeth less distinct than in anterior setigers. Ratio of length width of median setigers less than 0·25. Compound spinigers and pseudocompound falcigers absent. Aciculae single in all setigers; brown; separation into core and sheath indistinct. Aciculae straight; tapering to blunt tips. Subacicular hooks absent.

Remarks. The distally falcate (unidentate) tips of the appendages of the compound falcigers in both anterior and median setigers are unusual. The appendages are weakly bidentate or nearly falcate appendages in anterior setigers in several species, but in all other species examined to date, distinctly bidentate falcigers are present in median and posterior setigers.

Palola gallapagensis (Kinberg 1865)

Nicidion gallapagensis Kinberg 1865: 564. Kinberg (1910: 43).
Palola edentulum Hartman (1948: 81), not Ehlers (1901).

Materials examined. Syntypes (remnants of perhaps 2 specimens), RM 346, Chatham Island, Galapagos Islands, *Eugenie* Expedition.

Remarks. As noted by Hartman (1948: 81) the original material of this species is unsatisfactory. One anterior end, badly distorted by removal of the maxillary apparatus, and some short, poorly preserved fragments are not present. The fragments lack subacicular hooks and pectinate setae and thus agree with species of *Palola,* but without examination of the jaws the species cannot be identified. *Palola gallapagensis* is here considered unidentifiable.

The synonymy proposed by Hartman (1948) cannot be sustained; the compound falcigers of the fragments are distinctly bidentate; in *P. edentulum* the falcigers are distally falcate at least through median setigers.

Palolo leucodon (Ehlers 1901)
(Fig. 5)

Eunice leucodon Ehlers 1901: 261; Ehlers (1901: 128–130, pl. 16, figs 1–10).
Eunice siciliensis Fauvel (1911: 18), not Grube (1840).

Material examined. Four syntypes, ZMB 3729, Juan Fernandez Islands, 27 m, coll. Plate.

Comments on material examined. One complete specimen, three long anterior fragments and many median and posterior fragments are present in the type lot.

Description. Complete syntype of unknown sex; with 308 setigers. Total length 83 mm; maximal width 2·2 mm at setiger 65. Length through setiger 10, 6 mm; width at setiger 10, 2 mm. Other, incomplete, syntypes with 81 (18 mm length), 109 (30 mm) and 140 (45 mm) anterior setigers. Anterior end cylindrical becoming strongly flattened ventrally in median and posterior part of body. Inflated bases of ventral cirri located strictly ventrally. Segments short and crowded.

Prostomial and peristomial features. Prostomium (Fig. 5a) shorter and distinctly narrower than peristomium; about as deep as half of peristomium. Prostomium frontally rounded; distinctly inflated; median sulcus deep. Eyes located between bases of A-I and A-II. Antennae in very shallow horseshoe, or in a nearly straight line; A-I separated from A-II and A-III by distinct gap; similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles digitiform; without articulations.

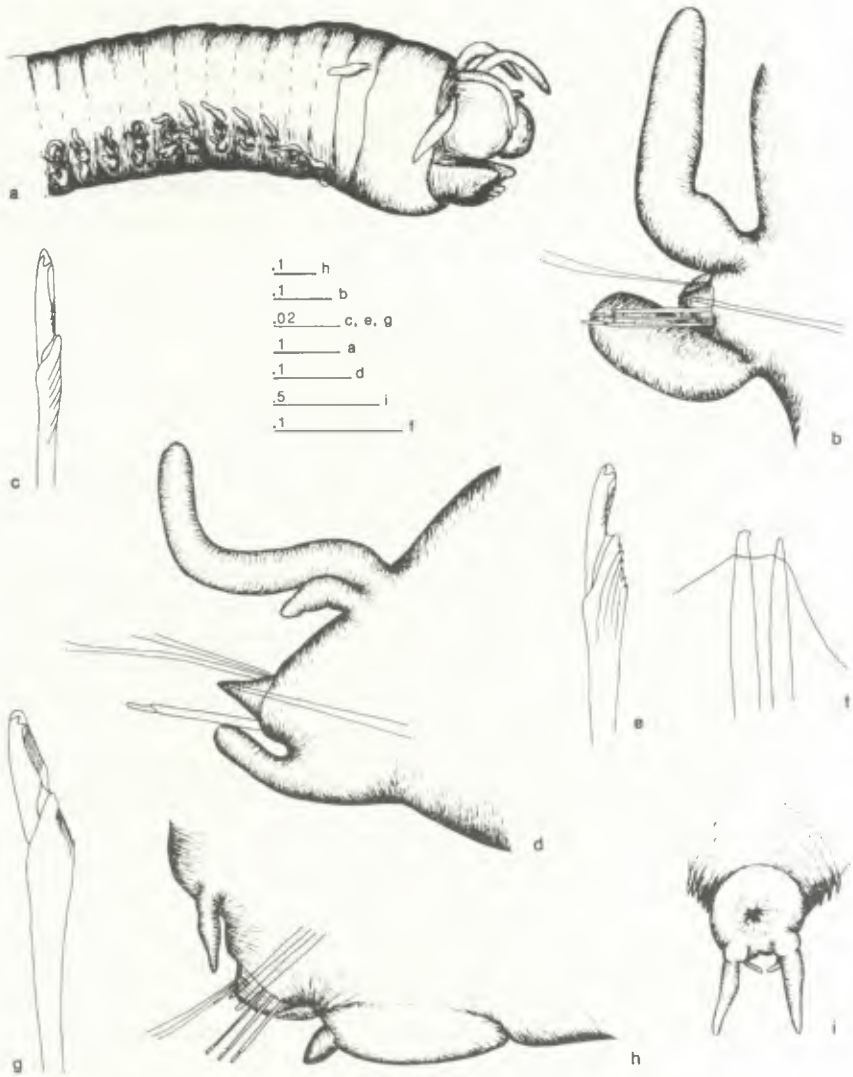

FIG. 5. *Palola leucodon* (syntype, ZMB 3729); **a**, anterior end, lateral view; **b**, parapodium 1, anterior view; **c**, compound falciger, setiger 1; **d**, parapodium 200, anterior view; **e**, compound falciger, parapodium 200; **f**, aciculae, setiger 65; **g**, compound falciger, setiger 65; **h**, parapodium 65, anterior view; **i**, pygidium, dorsal view.

A-I top posterior edge of anterior peristomial ring; ceratostyles of A-II and A-III to middle of posterior peristomial ring. Peristomium cylindrical; lower lip with distinct muscular inflated region. Separation between peristomial rings distinct on all sides; anterior ring two-thirds of total peristomial length. Peristomial cirri barely outreaching posterior peristomial ring; digitiform; without articulations.

Jaws. Maxillary formula 1 + 1, 3 + 3, 2 + 0, 2 + 2, 1 + 1. Teeth short, blunt; now decalcified. Mandibles scoop-shaped, enclosing maxillae completely. Mandibles with five or six teeth distally.

Branchiae. From setigers 121 in longest incomplete specimen; from setiger 126 to setiger 302 in complete specimen. Branchiae present on more than 65% of setigers.

All branchiae single filaments; distinctly longer than notopodial cirri; digitiform. Where best developed, branchiae distinctly shorter than one-half of body width.

Parapodial structures. Anterior acicular lobes (Fig. 5b) conical, becoming increasingly rounded in posterior setigers (Fig. 5d, h); aciculae emerging medially. Presetal lobes low, transverse folds. Postsetal lobes about as high as acicular lobes; rounded; displaced ventrally in relation to acicular lobes and visible behind acicular lobes in anterior view. First five ventral cirri digitiform; becoming distinctly basally inflated. Inflated bases transverse ridges with distinct, tapering distal tips. Inflated bases decreasing in size from about setiger 100, and completely reduced by setiger 120. Notopodial cirri of first setiger twice as long as those in next following setigers; digitiform. Notopodial cirri increasingly tapering; retaining about same length in all setigers.

Setae. Limbate setae distinctly longer than all other setae; slender, straight; without marginal serrations. Pectinate setae absent. Appendages of compound falcigers bidentate; guards without mucros; rounded. Anterior compound falcigers (Fig. 5c) with shafts of compound falcigers tapering; marginally finely serrated; with distinct distal beak. Appendages slender, with nearly parallel sides. Proximal teeth about as large as distal teeth; directed obliquely distally; with nearly straight taper. Distal teeth erect; with straight taper. Median compound falcigers (Fig. 5g) with shafts distally distinctly inflated; marginally serrated. Appendages distinctly tapering. Proximal teeth about as large as distal teeth; directed laterally; distally downturned (curved to nearly parrot-beaked). Distal teeth directed obliquely distally; curved. Ratio of length to width in median appendages less than 0·25. Posterior compound falcigers (Fig. 5e) with shafts distally inflated; marginally serrated. Appendages slender with nearly parallel sides. Proximal teeth distinctly larger than distal teeth; directed obliquely distally; with straight taper. Distal teeth directed obliquely distally; with straight taper. Compound spinigers and pseudocompound falcigers absent. Aciculae paired in all setigers; with distinct dark cores and clear sheaths. Aciculae distally blunt or tapering to fine tips (Fig. 5f). Subacicular hooks absent.

Pygidium. Pygidium (Fig. 5i) with a pair of long and a pair of short anal cirri. All cirri digitiform. Long cirri about as long as last 10 setigers. Anus dorsal without distinct single lobes.

Remarks. Palola edentulum and *P. leucodon* were both described from the same collection from Juan Fernandez Island in the eastern Pacific Ocean. Ehlers originally placed the former in *Nicidion,* at that time recognized for abranchiate species otherwise referable to *Eunice. Palola leucodon* was originally described in *Eunice.* Apart from the (apparent) lack of branchiae in *P. edentulum,* the most striking difference between the two species is the absence of secondary teeth in the appendages of the compound falcigers in *P. edentulum.* The appendages of *P. leucodon* are bidentate.

?Palola longicirrata (Kinberg 1865)

Nicidion longicirrata Kinberg 1865: 564; Kinberg (1910: 43, pl. 16, fig. 20).
Eunice (*Nicidion*) *cariboea* Hartman (1948: 80), not Grube (1856).
Eunice longicirrata Fauchald (1969: 14); Fauchald (1992: 198).

Material examined. Holotype, RM 415, Honolulu, Hawaii, *Eugenie* Expedition.

Comments on material examined. Kinberg (1865: 564) gave locality information as: 'Mare pacificum juxta urbem Honolulu insulae Oahu, inter corallia, summa aqua,' The

type lot includes a very poorly preserved anterior end and a median fragment. The anterior end has been ripped apart and the whole jaw apparatus is missing.

Description. A-III distinctly longer than A-I and A-II. Separation between peristomial rings distinct dorsally, but probably not laterally; unknown for ventral side. Peristomial cirri to frontal margin of peristomium.

Branchial distribution indeterminable. Median fragment with long, digitiform single branchial filaments.

Shape of parapodial structures indeterminable. Notopodial cirri short; slender in median fragment.

Limbate setae marginally serrated. Pectinate setae absent.

Appendages of compound falcigers bidentate; guards without mucro and marginally serrated. Median compound falcigers with shafts strongly inflated. Appendages short; both teeth directed laterally. Compound spinigers and pseudocompound falcigers absent. Aciculae brown; distally bent. Subacicular hooks absent.

Remarks. Hartman (1948: 80) referred *Nicidion longicirrata* to Grube's species, *Eunice cariboea,* originally described from Caribbean. This synonymy is incorrect. In *E. cariboea* all antennae are similar in size and digitiform, in the type of *?P. longicirrata* A-III is distinctly longer than other antennae and all antennae tapering. The absence not only of subacicular hooks, but also of pectinate setae points to an affiliation with *Palola* rather than with *Eunice,* but the specimen is in such poor shape that the affiliation with *Palola* is somewhat dubious. The species is here considered indeterminable.

Palolo madeirensis Baird 1869
(Fig. 6)

Eunice madeirensis Baird 1869: 344–345.

Material examined. Holotype, BM(NH) ZH 1857.7.27.66, Madeira, purchased Mr Masson.

Description. Holotype incomplete; of unknown sex; with 297 setigers. Total length 160 mm; maximum width 5·5 mm at setiger 50. Length through setiger 10, 13 mm; width at setiger 10, 4·5 mm. Anterior slightly inflated; body dorsally strongly convex with flattened ventrum from about setiger 5 through rest of specimen. Inflated bases of ventral cirri located wholly ventrally, forming paired transverse cushions on ventral side. Segments short and crowded.

Prostomial and peristomial features. Prostomium (Fig. 6d) distinctly shorter and narrower than peristomium; about as deep as half of peristomium. Prostomium frontally rounded; dorsally depressed around bases of A-I with thickened rim; dorsal sulcus deep. Eyes black; located between bases of A-I and A-II. Antennae in straight line; A-I separated from A-II and A-III by distinct gap; similar in thickness. Ceratophores short and ring-shaped in all antennae; slightly more prominent in A-I than in other antennae; without articulations. Ceratostyles tapering; articulations absent. A-I and A-II to middle of first peristomial ring; A-III to second ring; A-III nearly twice as long as A-II. Peristomium medially inflated, barrel-shaped; lower lip not distinctly inflated or muscularized. Separation between peristomial rings distinct dorsally and ventrally. Anterior ring about half of total peristomial length. Peristomial cirri not outreaching posterior peristomial ring; digitiform; without articulations.

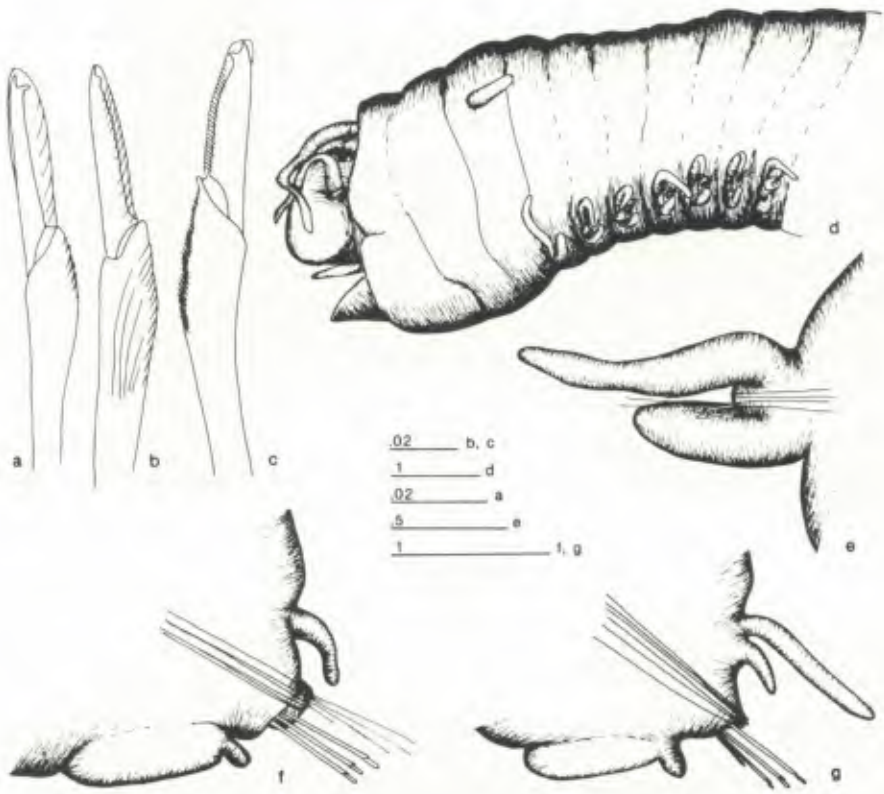

FIG. 6. *Palola madeirensis* (holotype, BM(NH) ZH 1857.7.27.66); **a**, compound falciger, setiger 1; **b**, compound falciger, setiger 61; **c**, compound falciger, setiger 283; **d**, anterior end, lateral view; **e**, parapodium 1, anterior view; **f**, parapodium 61, anterior view; **g**, parapodium 283, anterior view.

Jaws. Maxillary formula not determinable without damaging specimen. Mandibles large and scoop-shaped; containing all maxillae.

Branchiae. Sporadically from setiger 231; in every segment from setiger 248. Where best developed branchiae single, distinctly shorter than one-half body width; cylindrical; tapering or digitiform and longer than notopodial cirri.

Parapodial structures. Anterior acicular lobes truncate (Fig. 6e); becoming increasingly bluntly conical in posterior setigers (Fig. 6f, g). All pre- and postsetal lobes low, transverse folds. First nine ventral cirri thick and tapering; becoming basally strongly inflated from about setiger 10. Where best developed, inflated bases thick, transverse welts, located entirely on ventral side of body; inflated bases distinct in all setigers, becoming relatively shorter in posterior setigers. All ventral cirri with short, digitiform free tips. Notopodial cirri of first setiger about twice as long as those in next following setigers; slightly tapering or nearly digitiform. Other pre-branchial notopodial cirri strongly tapering with slender tips. Notopodial cirri in branchial setigers less distinctly tapering, but otherwise similar in shape to those in median setigers. Notopodial cirri without articulations.

Setae. Limbate setae nearly straight with narrow, distinctly frayed limbations. Pectinate setae, compound spinigers and pseudocompound falcigers absent. Appendages of compound falcigers bidentate; guards without mucro; marginally serrated. Anterior compound falcigers (Fig. 6a) with shafts slightly inflated with

distinct distal beak; marginally serrated. Appendages slender, with nearly parallel sides. Proximal teeth of same size as distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Median compound falcigers (Fig. 6b) with shafts inflated; marginally strongly serrated. Appendages distinctly tapering. Proximal teeth larger than distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Ratio of length to width of median appendages not exceeding 0·25. Posterior compound falcigers (Fig. 6c) with shafts slender, but distinctly inflated; marginally strongly serrated. Appendages slender, with nearly parallel sides. Proximal teeth of same size as distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Aciculae paired in anterior setigers; numbering three in median and posterior setigers. Aciculae brown; with indistinct core and sheath construction; tapering, distally straight and blunt. Subacicular hooks absent.

Remarks. *Palola madeirensis* has gone unreported since it was first described. It is characterized by the late start of the branchiae and by the unusually long middle antenna.

Palola pallidus Hartman 1938
(Fig. 7)

Palolo pallidus Hartman 1938: 99, figs 24–35.
Palola paloloides Hartman (1944: 131) in part, not Moore (1904).

Material examined. Holotype and two paratypes, USNM 20362 and 20399, Laguna Beach, California, coll. Olga Hartman ('common in vermetid colonies and kelp holdfasts in low-tide region' according to Hartman, 1938: 99).

Comments on material examined. The description is based on the holotype with comments on the paratype where necessary.

Description. Holotype complete; of unknown sex; with 565 setigers. Total length 200 mm; maximum width 3 mm. Length through setiger 10, 6·5 mm; width at setiger 10, 2·5 mm. Both paratypes incomplete; with 365 and 121 setigers respectively; total length 130 and 27 mm; maximal width 3 mm at setiger 50 for both; length through setiger 10, 7 and 5 mm; width at 10, 2 mm in both. Anterior end including prostomium, peristomium and first three setigers cylindrical; body thereafter ventrally flattened with dorsum highly convex and parapodia oriented laterally at junction of dorsum and ventrum with inflated bases of ventral cirri strictly ventral. Posterior half of body increasingly dorsoventrally flattened, becoming ovate in cross-section with parapodia strictly lateral. Posterior end abruptly tapering.

Prostomial and peristomial features. Prostomium (Fig. 7a) about as wide as peristomium; distinctly shorter than peristomium; about as deep as half peristomial depth. Prostomial lobes frontally rounded; dorsally inflated with depressions at base of A-I; median sulcus shallow and very wide. Eyes between bases of A-I and A-II; dark purple. Antennae in a very shallow horseshoe; A-I separated from A-II and A-III by distinct gap; similar in thickness. Ceratophores short and ring-shaped. Ceratostyles slightly tapering; nearly digitiform; with irregular wrinkles; articulations absent. A-I to front edge of second peristomial ring; A-II and III to posterior edge of peristomium. Peristomium cylindrical with slightly inflated, muscular lower lip. Separation between peristomial rings distinct on all sides; anterior ring two-thirds of total peristomial length. Anterior ring ventrally separated by shallow groove into two sections of similar

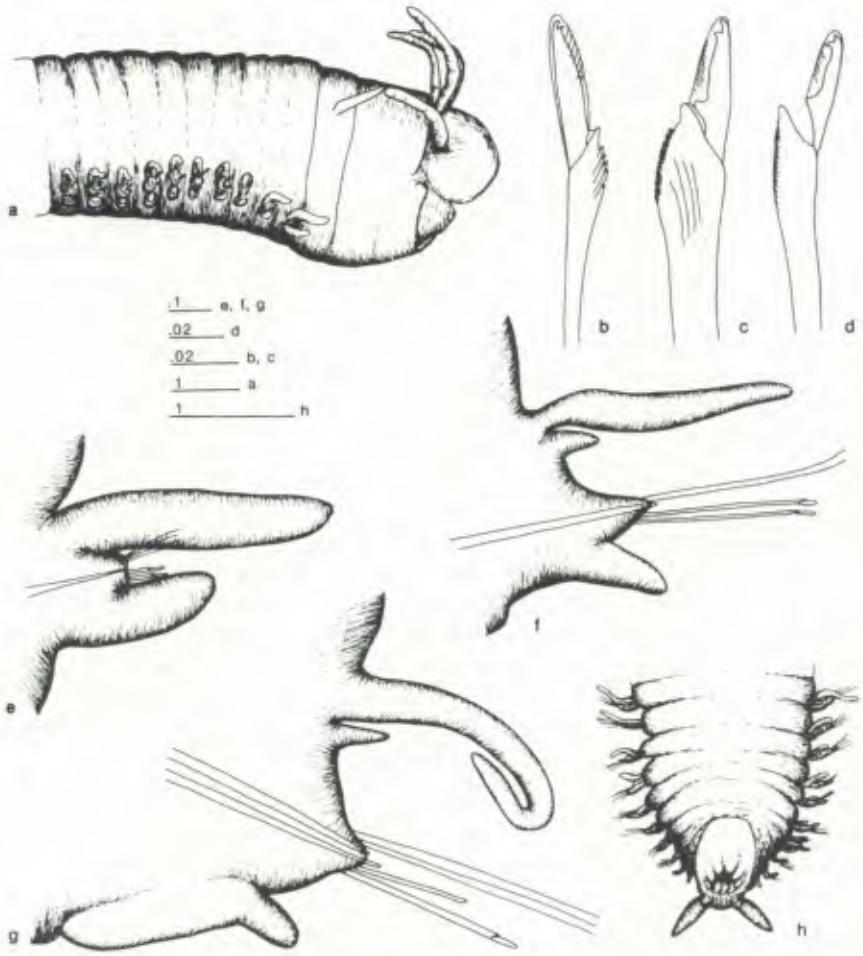

FIG. 7. *Palola pallidus* (holotype, USNM 20362); **a**, anterior end, lateral view; **b**, compound falciger, setiger 1; **c**, compound falciger, setiger 150; **d**, compound falciger, setiger 450; **e**, parapodium 1, anterior view; **f**, parapodium 450, anterior view; **g**, parapodium 150, anterior view; **h**, pygidium, dorsal view.

length. Peristomial cirri tapering; without articulation; peristomial cirri to middle of anterior peristomial ring.

Jaws. Maxillary formula of longer paratype 1 + 1, 3 + 3, 1 + 0, 1 + 1, 1 + 1. Distal jaws ridges without distinct teeth; Mx-III + IV on left side forming a distal arc corresponding in length to right Mx-IV.

Branchiae. First branchiae on setiger 133 in holotype; continuously present from setiger 137; absent only on last three setigers. Branchiae present from setiger 120 in longer paratype and absent in shorter paratype (consisting of 121 setigers). All branchiae single, flattened, contractile filaments. Branchiae longer than notopodial cirri; distinctly shorter than one-half of body width.

Parapodial structures. Acicular lobes of first few setigers (Fig. 7e) truncate; becoming conical in middle parapodia (Fig. 7g) and retaining that shape through rest of body. Pre- and postacicular lobes follow outline of acicular lobes in all setigers. Ventral cirri of first eight or nine setigers digitiform. Ventral cirri ventrally inflated from setiger 10 through setiger 195 in holotype and 197 in long paratype. Inflated

bases transverse welts. Free tips short and tapering. Posterior ventral cirri increasingly tapering; located midway along ventral edge of neuropodium; distinctly outreaching neuropodium in posterior setigers. Notopodial cirri of first three setigers about twice as long as corresponding ventral cirri; digitiform. Notopodial cirri decreasing in length from about setiger 4; from about setiger 10 short, sharply tapering and conical in all remaining setigers. Articulations absent.

Setae. All setae distinctly gold-shafted in median and posterior setigers. Limbate setae slender; very long; nearly straight with a short distal curved end. Pectinate setae absent. Appendages of compound falcigers bidentate; guards without mucro, marginally serrated. Anterior compound falcigers (Fig. 7b) with shafts tapering; marginally deeply serrated; distal beak distinct. Appendages slender with only slight taper and very small heads; proximal teeth of same size as distal teeth; directed obliquely distally with straight taper. Distal teeth directed obliquely distally; with straight taper. Median compound falcigers (Fig. 7c) with shafts inflated; marginally finely serrated; distal beak distinct. Appendages tapering; head distinct. Proximal teeth of same size as distal teeth; directed laterally; curved, nearly parrot-beaked. Distal teeth erect; slender; curved. Ratio of length to width in median appendages less than 0·25. Posterior compound falcigers (Fig. 7d) with shafts slightly inflated; distinctly serrated; distal beak distinct. Appendages barely tapering with large distal head. Proximal teeth larger than distal teeth; directed laterally; curved, nearly 'parrot-beaked'. Distal teeth directed obliquely distally; curved. Pseudocompound falcigers and compound spinigers absent. Aciculae single in anterior and posterior setigers; paired in median setigers; brown; tapering; distally pointed. Separation of acicular cores and sheaths indistinct. Subacicular hooks absent.

Pygidium. Pygidium (Fig. 7h) elongate, inflated; anus dorsal; dorsal lip crenulated; ventrolateral lip smooth. One pair of anal cirri; anal cirri do not reach beyond setiger 5 from the posterior end; tapering; articulations absent. Anus without distinct, large lobes.

Remarks. *Palola pallidus* was considered a synonym of *P. paloloides* by Hartman (1944); the two forms are very similar, but appear to differ in some details, such as the relative length of the branchiae, the size and shape of the notopodial cirri in median and posterior setigers and possibly in the length of the appendages of median and posterior compound falcigers.

[***Lysidice palola*** Quatrefages 1866

Lysidice palola Quatrefages 1866: 379.

Remarks. This name was proposed to replace *Palolo viridis sensu* Macdonald (1858). Quatrefages must have assumed that the specimens described by Macdonald differed at the species level from those described by Gray, in Stair (1847). Macdonald probably had the same species as Gray, and his use of Gray's name is here considered valid, making replacement of the species name unnecessary. Macdonald described the head of his specimen as having three antennae (regeneration?), thus leading Quatrefages to move the species to *Lysidice.*]

Palola paloloides (Moore 1904)

(Fig. 8)

Eunice (*Eriphyle*) *paloloides* Moore 1904: 246–249, pl. 7, figs 5–7.
Palolo paloloides Hartman (1944: 131–132) in part.

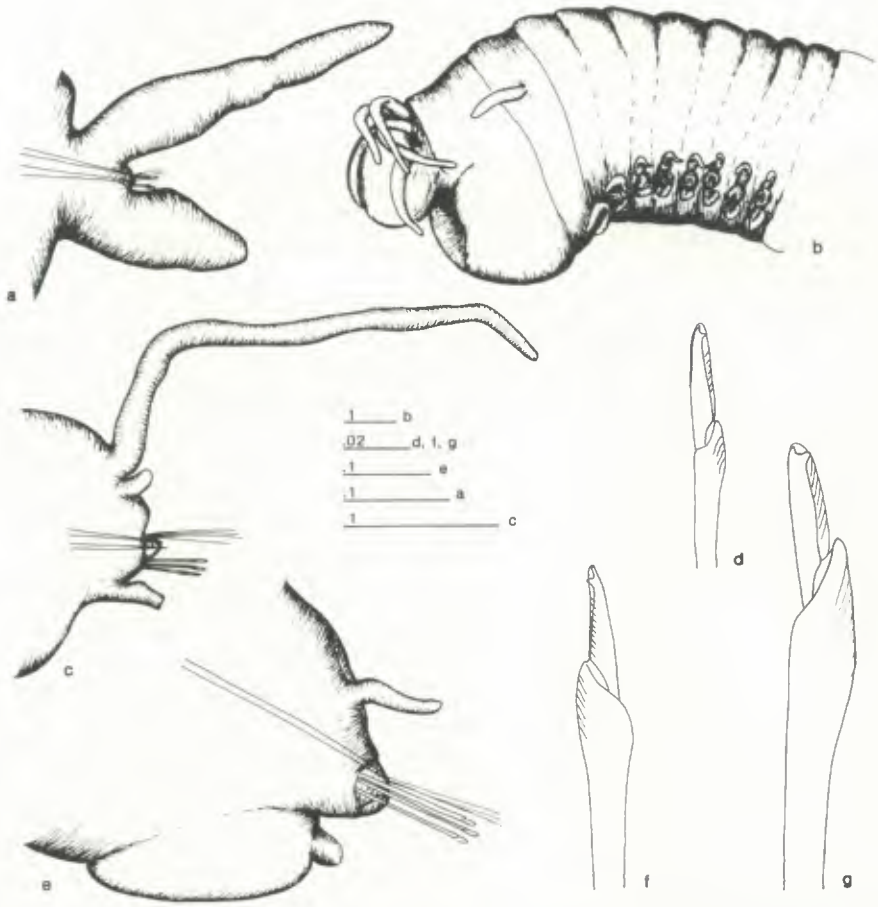

FIG. 8. *Palola paloloides* (holotype, CAS TY58); **a**, parapodium 1, anterior view; **b**, anterior end, lateral view; **c**, parapodium 226, anterior view; **d**, compound falciger, setiger 1; **e**, parapodium 74, anterior view; **f**, compound falciger, setiger 74; **g**, compound falciger, setiger 226.

Material examined. CAS TY58 (also numbered as Cat no. 020554), holotype, San Diego, California, coll. E. C. Starks.

Description. Holotype incomplete, of unknown sex, with 230 setigers. Total length 130 mm; maximal width 5 mm at setiger 10. Length through setiger 10, 10 mm. Anterior body cylindrical, becoming ventrally flattened medially. Segments short and crowded.

Prostomial and peristomial features. Prostomium (Fig. 8b) shorter and distinctly narrower than peristomium; less than half as deep as peristomium. Prostomial lobes frontally rounded; dorsally only slightly inflated; median sulcus deep. Eyes between bases of A-I and A-II. Antennae in nearly a straight line; A-I isolated from A-II and III by a distinct gap; similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles slender, tapering; without articulations. A-I to middle of anterior peristomial ring; A-II and III to posterior peristomial ring. Three median

antennae similar in length. Peristomium anteriorly inflated with thick, muscular lowe lip. Separation between peristomial rings distinct on all sides; anterior ring two-third: of total peristomial length. Peristomial cirri slender, digitiform; without articulations

Jaws. Maxillae not examined; maxillary formula 1 + 1, 4 + 3, 1 + 0, 1 + 2 an< 1 + 1 according to Moore (1904: 248, and pl. 7, fig. 7). Mandibles with large oute wings.

Branchiae. Present from setiger 103 to last setigers present. First branchiae shor and button-shaped, increasing in length posteriorly to very long, slender filaments about as long as width of body in least few setigers; distinctly longer than notopodia cirri in most branchiated segments.

Parapodial structures. All parapodia short, distally appearing truncate. Anterio acicular lobes (Fig. 8a) distally truncate; becoming triangular in last setigers presen (Fig. 8c, e). Aciculae emerging medially in anterior setigers; emerging distinctly dorsa to midline in posterior setigers. Presetal lobes low transverse folds; postsetal lobe following acicular lobes closely; becoming low, transverse folds in median and poste rior setigers. First four or five ventral cirri tapering; thereafter becoming increasingl inflated basally. All ventral cirri with distinct, free tips; free tips in median setigers short, triangular. Inflated bases forming transverse ridges in median setigers. Inflate bases decreasing from about setiger 150; not distinguishable in last setigers present Last ventral cirri digitiform. First notopodial cirri slender; tapering; about twice a long as ventral cirrus. Median notopodial cirri digitiform; posterior notopodial cirr digitiform, very short. Notopodial cirri without articulations.

Setae. Limbate setae slender, marginally smooth and distinctly longer than al other setae. Pectinate setae absent. Appendages of compound falcigers bidentate guards distally without a mucro; marginally serrated. Anterior compound falciger (Fig. 8d) with shafts of compound setae distally slightly inflated; marginally coarsel serrated; distinct distal beaks present. Appendages slender, with nearly parallel sides Proximal teeth about same size as distal teeth; triangular and blunt; directed laterally with straight taper. Distal teeth nearly erect, slender; with straight taper. Media compound falcigers (Fig. 8f) with shafts distinctly inflated and marginally serrated Appendages distinctly tapering. Proximal teeth shorter than distal teeth; triangular directed laterally; with straight taper. Distal teeth erect; with straight taper. Ratio o length to width in median appendages less than 0·25. Posterior compound falciger (Fig. 8g) with shafts inflated; marginally serrated. Appendages with nearly paralle sides. Proximal teeth larger than distal teeth; triangular; directed laterally; with straigh taper. Distal teeth erect; with straight taper. Compound spinigers and pseudo compound falcigers absent. Aciculae at least paired in all parapodia. Aciculae witl dark cores and clear sheaths; distally tapering; straight. Subacicular hooks absent

Remarks. The branchiae are unusually long in this species. Hartman (1944) sepa rated this species from *P. siciliensis* based on the dentition of Mx-II; left Mx-II has fou teeth in *P. paloloides* and three teeth in *P. siciliensis.*

[***Nereidonta paretti*** Blainville 1828

Nereidonta paretti Blainville 1828: 476.
?Eunice siciliensis Ehlers (1868: 353, 358) in part, not Grube (1840).
Palolo siciliensis Hartman (1959: 324) in part, not Grube (1840).

Remarks. Blainville (1828: 476) described this species in the following words:

> 'Nouvelle espèce, des côtes de Gênes, remarquable par la brièveté et le grand nombre de ses anneaux, ainsi que par la petitesse de ses appendices'. (New species, from the coast of Genoa, remarkable for the narrowness and the large number of its segments and also for the smallness of its appendages. K.Fd, translation.)

Blainville did not illustrate his new species. Audouin and Milne Edwards (1833: 145) remarked that they had not seen Blainville's species and proceeded to quote Blainville's description *in toto*. I interpret this to mean that Audouin and Milne Edwards considered the species to be incompletely known. The species was not mentioned by Quatrefages (1866), who considered *Nereidonta* as a synonym of *Eunice*. All other species listed by Blainville were considered by Quatrefages.

Nereidonta paretti was listed as a possible synonym of *Eunice siciliensis* by Ehlers (1868: 353, 358). After paraphrasing Blainville's original description, Ehlers stated (p. 358):

> 'es würde nach den Gesetzen der Priorität dieser Name (*Nereidonta paretti*) vor dem Grube'schen (*Eunice siciliensis*) den Vorzug verdienen, wenn Blainville seine damals neue Art mit einer kennzeichnenden Diagnose versehen hätte' (according to the law of priority, this name (*Nereidonta paretti*) should have priority over Grube's name (*Eunice siciliensis*), if Blainville had given his, at that time new species a recognizable diagnosis. K.Fd. translation; parentheses added.)

Blainville's description matches many species of polychaetes. *Nereidonta paretti* is here considered to be an indeterminable eunicid and the genus is considered a junior synonym of *Eunice*.]

Palola siciliensis (Grube 1840)
(Fig. 9d–j)

Eunice siciliensis Grube 1840: 83.
Eunice adriatica Schmarda (1861: 124–125, pl. 32, fig. 257, 12 text-figs); Grube (1864: 79); Grube (1867): 67–68).
Eunice taenia Claparède (1864: 580–581, pl. 4, fig. 11); Quatrefages (1866: 653–654).

Material. Five syntypes, Palermo, Sicily, coll. Grube, ZMB F1989; 4 syntypes, Palermo and Triest, ZMB F2008.

Comments on material examined. All types are incomplete; the description is based on the largest.

Description. Syntype described incomplete, of unknown sex; with 229 setigers. Total length 90 mm; maximal width 4 mm at setiger 10. Length through setiger 10, 9 mm. Three other syntypes with 104, 121 and 144 setigers. Segments short and crowded. Anterior body cylindrical, becoming ventrally flattened posteriorly.

Prostomial and peristomial features. Prostomium (Fig. 9d) nearly as long as peristomium; distinctly narrower than peristomium; about one-half as deep as peristomium. Peristomial lobes frontally rounded; dorsally slightly inflated; median sulcus deep. Eyes absent. Antennae in a transverse line; A-I separated from A-II and A-III by distinct gap; similar in thickness. Ceratophores short and ring-shaped; without

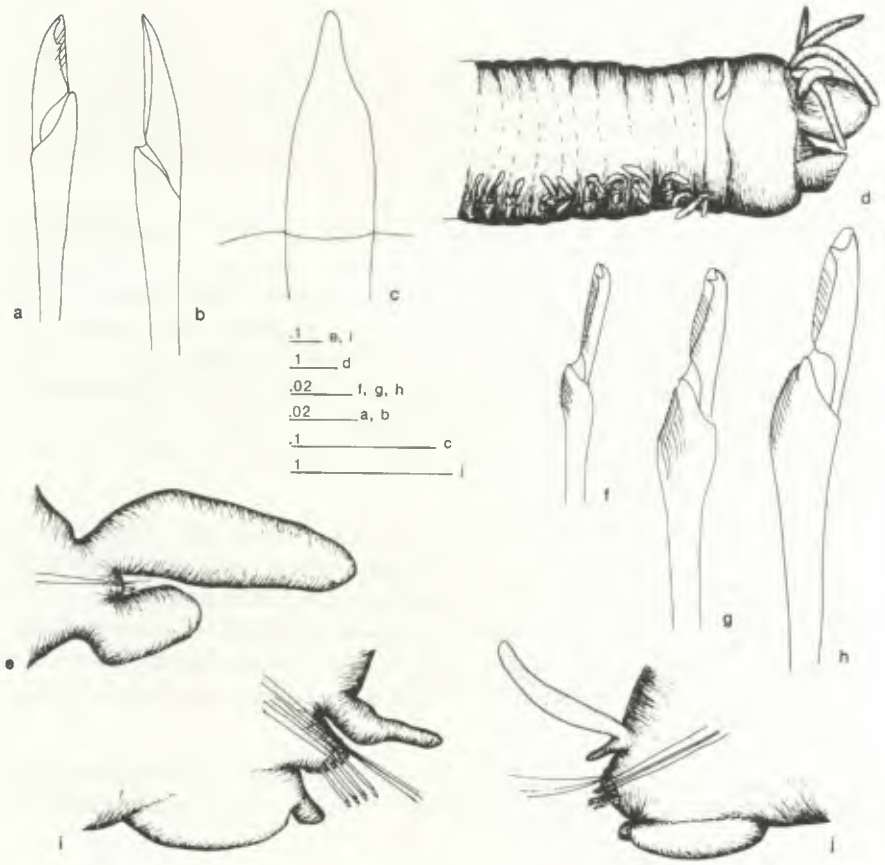

FIG. 9. *Palola simplex* (slide of holotype, BM(NH) ZB 1984.73); **a**, compound falciger; **b**, compound spiniger, anterior parapodium; **c**, acicula, anterior parapodium; *Palola siciliensis* (syntype, ZMB F2008), **d**, anterior end, lateral view; **e**, parapodium 1, anterior view; **f**, compound falciger, setiger 1; **g**, compound falciger, setiger 65; **h**, compound falciger, setiger 200; **i**, parapodium 65, anterior view; **j**, parapodium 200, anterior view.

articulations. Ceratostyles digitiform with very little taper; without articulations. A-I to posterior peristomial ring; A-II to setiger 1 and A-III to setiger 2; in another syntype, A-II and III to setiger 3. A-III longer than A-II. Peristomium slightly inflated ventrally; with distinct, muscular lower lip. Separation between peristomial rings distinct on all sides; anterior ring two-thirds of total peristomial length. Peristomial cirri to middle of anterior peristomial ring; tapering; without articulations.

Jaws. Maxillae of longest specimens absent on left-hand side; right-hand formula I, 3, 0, 2, I; in other specimens formula 1 + 1, 3 + 3, ridge + 0, 2 + 2 and I + I. Mx-III located behind left Mx-II. Mandibles scoop-shaped, calcified; with three or four blunt teeth anteriorly; enclosing maxillae entirely.

Branchiae. From setiger 180 in largest specimen; absent in one specimen (121 setigers); present from setiger 92 in other two specimens. Branchiae single, strap-like; distinctly longer than notopodial cirri; as long as one-half of body-width where best developed.

Parapodial structures. Anterior acicular lobes (Fig. 9e) distally truncate; becoming low and rounded in median and posterior setigers (Fig. 9i, j). Aciculae

emerging medially in anterior setigers and distinctly dorsal to midline in median setigers. Presetal lobes low transverse folds; postsetal lobes follow outline of acicular lobes closely. First eight or nine ventral cirri tapering; becoming basally inflated from about setiger 10. Inflated bases where best developed, transverse ventral ridges; distal tip distinct in all setigers; slightly conical. First notopodial cirri twice as long as the next following ones; anterior notopodial cirri digitiform; median and posterior notopodial cirri increasingly tapering; flattened and triangular in last setigers examined.

Setae. Limbate setae very much longer than all other setae; marginally smooth; straight. Pectinate setae absent. Appendages of compound falcigers bidentate; guards without mucro, marginally serrated. Anterior compound falcigers (Fig. 9f) with shafts distinctly inflated; marginally coarsely serrated; distal beak distinct. Appendage longer than inflated end of shaft; slender, with nearly parallel sides and with relatively large head. Proximal teeth smaller than distal teeth; directed obliquely distally with straight taper. Distal teeth directed obliquely distally; with straight taper. Median compound falcigers (Fig. 9g) with shafts distinctly inflated; marginally serrated. Appendages distinctly tapering. Proximal teeth smaller than distal teeth; directed laterally; with straight taper. Distal teeth directed obliquely distally; with straight taper. Ratio of length to width of median appendages less than 0·25. Posterior compound falcigers (Fig. 9h) with shafts distinctly inflated; marginally serrated; beaks distinct. Proximal teeth about same size as distal teeth; directed obliquely distally; with straight taper. Distal teeth erect; with straight taper. Compound spinigers and pseudocompound falcigers absent. Aciculae single in anterior setigers; paired in median and posterior setigers; with distinct brown cores and clear sheaths. Aciculae distally tapering; straight. Subacicular hooks absent.

Remarks. *Eunice adriatica* was referred to *P. siciliensis* by Grube (1864: 79 and 1867: 68, see also Ehlers, 1868: 358, all as *Eunice*). Nothing in Schmarda's description and illustrations argues against this conclusion and the synonymy is here accepted.

Claparède described *E. taenia* from Port-Vendres, France. No original material is available; nothing in the description or illustrations argues against the synonomy first proposed by Grube (1867).

This species has been reported from shallow-water hard-bottom environments in all warm-water areas. How many of these records match the species as described here, and how many belong to similar species, is unknown.

Palolo simplex Peters 1854

(Fig. 9a–c)

Eunice simplex Peters 1854: 611; Fauchald (1992: 307).
Eunice siciliensis (?) Grube (1878: 101).
Palola siciliensis (?) Hartman (1959: 315).

Material examined. Holotype, ZMB 45, Mossambique, coll. Peters, also slide marked TYPE, BM(NH) ZB 1984.73 containing 4 parapodia.

Comments on material examined. The holotype has been badly dissected anteriorly and is very soft so no meaningful illustrations of the soft parts can be made.

Description. Holotype nearly complete; of unknown sex; with 110 setigers. Total length 34 mm long; maximum width at setiger 10, 2 mm. Length through setiger 10, 6 mm.

Prostomial and peristomial features. Prostomium frontally rounded; dorsally flattened; median sulcus deep. Eyes between bases of A-I and A-II. Antennae arranged in a horseshoe; with A-I isolated by a gap; similar in thickness. Ceratophores ring-shaped in all antennae; without articulations. Ceratostyles digitiform; without articulations. Length of antennae increasing from A-I to A-III; A-I to second peristomial ring; A-II to setiger 1 and A-III to setiger 3. Separation between peristomial rings distinct on all sides; anterior ring makes up two-thirds of total peristomial length. Peristomial cirri reach middle or anterior end of peristomium; slender and digitiform; without articulations.

Jaws. Jaw apparatus detached, but still present. Maxillary formula 1 + 1, 3 + 3, 0 + 0, 2 + 2 and 1 + 1. Mx-III a small edentate plate behind left Mx-II. Mx-IV with one large and one very small, nearly rudimentary tooth. Mx-V small and very poorly sclerotinized. Mandibles completely decalcified; consisting of paired, shallowly angled major plates with erect, very thin lateral wings.

Branchiae. Absent.

Parapodial structures. Anterior acicular lobes distally rounded, becoming triangular in last setigers present; with aciculae emerging at midline. Pre- and postsetal lobes low transverse folds in all setigers. Ventral cirri thick and tapering in the first four setigers, becoming basally inflated to thick, ventrolateral ridges in all later setigers; distal tip missing in anterior and median setigers, becoming distinct as a short, button-shaped distal tip in posterior setigers. First notopodial cirri of setiger 1 about twice as long as those in next following setigers; basally inflated and tapering to slender tips. Notopodial cirri becoming reduced over the next 20–30 setigers; missing between setigers 40 and 90. From about setiger 90, notopodial cirri again distinct as digitiform, thick projections, increasing in length posteriorly. Articulations absent.

Setae. Slender limbate setae present in all fascicles. pectinate setae absent. Appendages of compound falcigers distally bidentate; guards distally amucronate; marginally serrated. Anterior compound falcigers (Fig. 9a) with shafts subdistally tapering; marginally smooth. Appendages distinctly tapering. Proximal teeth much smaller than distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Median compound falcigers with shafts tapering; marginally smooth. Appendages distinctly tapering. Proximal teeth smaller than distal teeth; directed laterally; with straight taper. Distal teeth erect; with straight taper. Ratio of length to width of median appendages 0·25 or less. Compound spinigers (Fig. 9b) present in first setigers. Shafts tapering; marginally smooth. Appendages triangular; slightly curved. Pseudocompound falcigers absent. Aciculae (Fig. 9c) light brown anteriorly, becoming darker posteriorly. Separation of acicular cores and sheaths indistinct. Cross-section round. Aciculae distally pointed; straight (shown compressed by coverslip in illustration). Subacicular hooks absent.

Remarks. Grube (1878: 101) referred this species to *Palola* (=*Eunice*) *siciliensis* under some doubt. There is nothing in Peters's original description to contradict such a conclusion; however, the specimen has some rather unusual features.

Compound spinigers are present in some anterior setigers, becoming replaced by compound bidentate falcigers in median setigers. The shafts of the compound setae are smooth, rather than serrated, and the shape of the appendage of the compound falcigers is unusually triangular.

The species is here considered distinct.

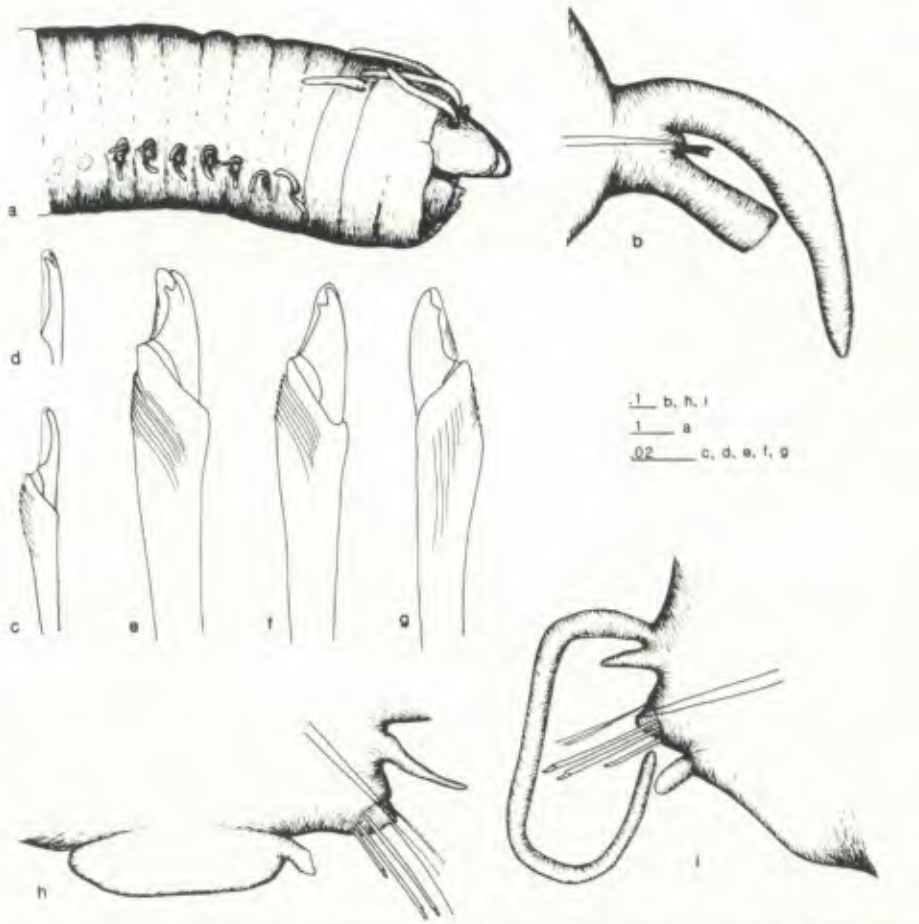

FIG. 10. *Palola valida* (syntype, MNHN, Paris); **a**, anterior end, lateral view; **b**, parapodium 1, anterior view; **c**, compound falciger, setiger 1; **d**, appendage of compound falciger, setiger 1; **e**, compound falciger, setiger 60; **f**, compound falciger, setiger 60; **g**, compound falciger, setiger 160; **h**, parapodium 60, anterior view; **i**, parapodium 160, anterior view.

Eunice taenia Claparède 1864

Eunice taenia Claparède 1864: 580–581, pl. 4, fig. 11; Quatrefages (1866: 653–654).
Eunice siciliensis Grube (1866b: 68); Ehlers (1868: 353–358).

Remarks. No material is available; nothing in the description or illustrations argues against the synonymy proposed first by Grube (1866). As far as known, the species name has never been used in combination with the generic name *Palola.*

Palolo valida (Gravier 1900)
(Fig. 10, Table 2)

Eunice valida Gravier 1900: 264–267.
Eunice siciliensis Crossland (1904: 323) in part, not Grube (1840).

Material examined. The syntypes, MNHN, Djibouti, Mission Jousseaume et Coutière, No. 29, 1897, Bocal A136.

Table 2. Summary of selected characters of syntypes of *Palola valida* (Gravier).

Variable characters					
Complete	no	no	no	no	no
Number of setigers	134	123	274	267	215
Total length	40	37	86	70	85
Maximum width	4	3·75	3	2·5	4·5
at setiger number	50	50	50	60	65
Length through setiger 10	7	8	7	5	15
Width at setiger 10	3·2	3·5	2·75	2·25	4
Start of branchiae	118	121	99	75	112
Number of anterior cirriform ventral cirri	10	10	10	8	10
Teeth in left Mx-IV	4	3	3	3	2
Teeth in right Mx-IV	4	3	3	3	2
Invariable characters					
Teeth in left Mx-II	3	3	3	3	3
Teeth in right Mx-II	2	2	2	2	2
Teeth in Mx-III	0	0	0	0	0

Comments on material examined. One syntype had been dissected, for the jaws and parapodia have been removed. This specimen is described in detail; variability is noted where appropriate and is demonstrated in Table 2.

Description. Large syntype incomplete, of unknown sex with 215 setigers. Total length 85 mm; maximum width 4·5 mm at setiger 65. Length through setiger 10, 15 mm; width at setiger 10, 4 mm. Body cylindrical; abruptly tapering anteriorly. Anterior end ventrally flattened with distinct ventral groove; median body dorsally strongly inflated; posteriormost parts of body ovate in cross-section with parapodia as far apart as possible and directed laterally. Anterior body with faded olive base colour and faded white dots; remainder of body grey.

Prostomial and peristomial features. Prostomium (Fig. 10a) distinctly shorter, but about as wide as peristomium; depth distinctly less than one-half of peristomial depth. Prostomial lobes anteriorly obliquely truncate; dorsal surface flattened; median sulcus wide but shallow. Eyes black; located between A-I and A-II, close to bases of A-I. Antennae in a shallow horseshoe; A-I separated from three other antennae by distinct gap; antennae similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles digitiform; without articulations. A-I to anterior peristomial ring; A-II to posterior peristomial ring; A-III to setiger 1. Peristomium tapering towards anterior end; without distinctly thickened lower lip. Separation between peristomial rings distinct on all sides; anterior ring two-thirds of total peristomial length. Anterior ring divided ventrally in two equal parts by shallow groove. Peristomial cirri to middle of anterior peristomial ring; tapering; without articulations.

Jaws. Maxillary formula 1 + 1, 2 + 3, ridge + 0, 4 + 4, 1 + 1; small sclerotinized patches may represent Mx-VI. Mx-III located behind left Mx-II; without distinct teeth. Mx-IV with two large and two very small teeth. Mandibles forming an open scoop; with about 10 distal teeth along the edge. Jaws currently decalcified.

Branchiae. Single rounded or slightly flattened from setiger 112 through rest of incomplete specimen. All branchiae longer than notopodial cirri; towards posterior end of fragment about as long as one-half of body width.

Parapodial structures. Anterior parapodia (Fig. 10b) with very small acicular lobes in relation to ventral and dorsal cirri. Anterior acicular lobes visible as short

papillae between bases of notopodial and ventral cirri. Median and posterior acicular lobes (Fig. 10h, i) more prominent; distally rounded in median setigers; becoming increasingly conical posteriorly. Aciculae emerging centrally in anterior setigers; dorsally in median and posterior setigers. Anterior pre- and postsetal lobes follow outline of acicular lobes closely. Median and posterior pre- and postsetal lobes low, transverse folds. Ventral cirri without basal inflation through setiger 10; digitiform and distally distinctly truncate. Median ventral cirri basally inflated; inflated region a thick welt along the ventral edge of each parapodium; free distal tip tapering. Parapodium oriented with inflated bases strictly ventral. Inflated bases decrease from about setiger 100; posterior ventral cirri without inflated bases; short and digitiform. First notopodial cirri distinctly longer than next following ones; tapering; next notopodial cirri slender, digitiform. Notopodial cirri sharply tapering in median and posterior setigers. All notopodial cirri without articulations.

Setae. Slender, nearly capillary limbate setae in all setigers. Pectinate setae absent. Anterior compound falcigers (Fig. 10c) with shafts inflated and marginally serrated. Appendages either slender with nearly parallel sides and bidentate (Fig. 10d) or tapering with simple falcate tips (Fig. 10c). In bidentate appendages, proximal teeth larger than distal teeth; directed obliquely distally; with straight taper. Distal teeth erect; with straight taper. Median falcigers (Fig. 10e, f) with shafts inflated and marginally finely serrated with distinct internal striation. Appendages very short, chunky and strongly tapering; all bidentate. Proximal teeth smaller than distal teeth; directed obliquely distally and distinctly upturned. Distal teeth directed obliquely distally; curved. Ratio between length and width in median appendages larger than 0·35. Posterior falcigers (Fig. 10g) with shafts distinctly inflated and marginally serrated. Appendages distinctly tapering. Proximal teeth very short; distinctly smaller than distal teeth; triangular; directed laterally; with straight taper. Distal teeth triangular and nearly erect with straight taper. Guards in all compound falcigers distally narrowly rounded; marginally with very fine serrations; without mucros. Compound spinigers and pseudocompound falcigers absent. Aciculae brown; separation between sheath and core indistinct; straight; tapering and distally blunt. Aciculae single in all setigers. Subacicular hooks absent.

Remarks. The species was considered a synonym of *Eunice siciliensis* by Crossland (1904). Crossland did not examine the types of Gravier's species, nor those of Grube's species. The two species can be separated on the shape of the appendages of the compound falcigers in median and posterior setigers; short and strongly tapering in *P. valida* and long with nearly parallel sides in *P. siciliensis.*

Palolo vernalis (Treadwell 1922)
(Fig. 11)

Leodice viridis vernalis Treadwell 1922: 133–134, pl. 1, figs 8–11.

Material examined. Holotype, AMNH 1539 , Suva, Fiji, April 1920.

Description. Holotype incomplete; of unknown sex; with 233 setigers. Total length 100 mm; maximum width 1·5 mm. Length through setigers 10, 5·5 mm.

Prostomial and peristomial features. Prostomial lobes (Fig. 11c) frontally truncate; dorsally flattened; median sulcus deep. Prostomium distinctly shorter and narrower than peristomium; as deep as one-half of depth of peristomium. Eyes between bases of A-I and A-II. Antennae in a horseshoe; A-I separated from A-II and

FIG. 11. *Palola vernalis* (holotype, AMNH 1539); **a**, parapodium 1, anterior view; **b**, compound falciger, setiger 1; **c**, anterior end, lateral view; **d**, parapodium 31, anterior view; **e**, acicula, setiger 31; **f**, parapodium 110, posterior view; **g**, compound falciger, setiger 130; **h**, compound falciger, setiger 110.

III by a distinct gap; similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles slender, cylindrical, tapering only slightly towards the tip; articulations absent. A-I to second peristomial ring; A-II and III to setiger 1; A-II slightly longer than A-III. Peristomium cylindrical; lower lip distinctly muscular, but not inflated. Separation between peristomial rings distinct on all sides; anterior ring about two-thirds of total peristomial length. Peristomial cirri to middle of anterior peristomial ring; slender; without articulations.

Jaws. Not dissected in the single specimen available.

Branchiae. From setiger 88 to end of fragment; all single, slender, tapering filaments emerging from body wall above notopodial cirri; very much longer than notopodial cirri; where best developed as long as one-half of body width.

Parapodial structures. First three neuropodia with truncate acicular lobes (Fig. 11a). Pre- and postsetal lobes oblique folds, sloping from upper high end to base of ventral cirri. Neuropodial acicular lobes obliquely triangular in median setigers (Fig. 11d); becoming symmetrically triangular in posterior setigers (Fig. 11f); aciculae emerging dorsal to midline. Presetal lobes retaining shape through median setigers;

becoming low, transverse folds in posteriormost setigers present. Median postsetal lobes free, rounded folds, becoming low, transverse folds in posteriormost setigers present. First three ventral cirri tapering. Ventral cirri distinctly inflated from setiger 4. Inflated region increasing in size to about setiger 30; forming very large transverse welts along ventral edge of neuropodia; distinct free tip present in all setigers; tapering. Inflated region decreasing from about setiger 60; glandular material retracted into lower edge of neuropodia in posteriormost setigers present. Ventral cirri moving on to anterior face of parapodia; slightly tapering, about as long as ventral cirri in first three parapodia. Notopodial cirri tapering, slender; increasing in length to about setiger 5; thereafter decreasing in length. Posterior notopodial cirri slender, cylindrical; about half as thick as corresponding ventral cirri; without articulations.

Setae. Limbate setae slender, narrowly limbate, smooth-edged. Pectinate setae absent. Appendages of compound falcigers bidentate; guards without mucros and marginally serrated. Anterior compound falcigers (Fig. 11b) with shafts inflated and marginally serrated. Appendages distinctly tapering. Proximal teeth about as large as distal teeth; directed obliquely distally; with straight taper. Distal teeth directed obliquely distally; curved. Median compound falcigers (Fig. 11g, h) with shafts distinctly inflated and marginally serrated. Appendages distinctly tapering. Proximal teeth about as large as distal teeth; directed obliquely distally; with straight taper. Distal teeth directed obliquely distally; with straight taper. Ratio of length to width of median appendages greater than 0·35. Compound spinigers and pseudocompound falcigers absent. Aciculae dark brown, distinctly separated into a clear sheath and a dark coloured core; single, slender, distally geniculate (Fig. 11e) in some setigers, otherwise straight and pointed. Aciculae round in transverse section. Subacicular hooks absent.

Remarks. The subspecies was named by Treadwell for a spring-breeding form present in Fiji. Treadwell recognized the strong similarities between his subspecies and the main form, but also demonstrated a series of minor characters in which the two forms differ, including the relative length of the antennae and the peristomial cirri, and the shape of the parapodial lobes.

Palolo viridis Gray, in Stair 1847
(Fig. 12)

Palola viridis Gray, in Stair 1847: 18. Macdonald (1858: 237–239, pl. 41).
Lysidice palola Quatrefages (1866: 379).
Eunice viridis auctores.

Material examined. LACM-AHF, 4 specimens, Fag'aituta bay, Tutuila Islands, American Samoa, 22 October and 9 November, 1966, coll. D. K. Hofmann *et al.*

Comments on material examined. One of two specimens collected 22 October 1966 is illustrated and described.

Description. Specimen complete; immature (female); with about 550 setigers. Total length about 80 mm; maximum width 3 mm and setiger 15. Length through setiger 10, 4·5 mm: width at setiger 10, 2·5 mm. Prostomium, peristomium and first setiger dorsally brown with scattered white spots; rest of anterior dorsum strongly faded brown through about setiger 20. Body otherwise light tan without distinct colour patterns. Body tapering very slowly posteriorly; dorsum strongly convex; ventrum

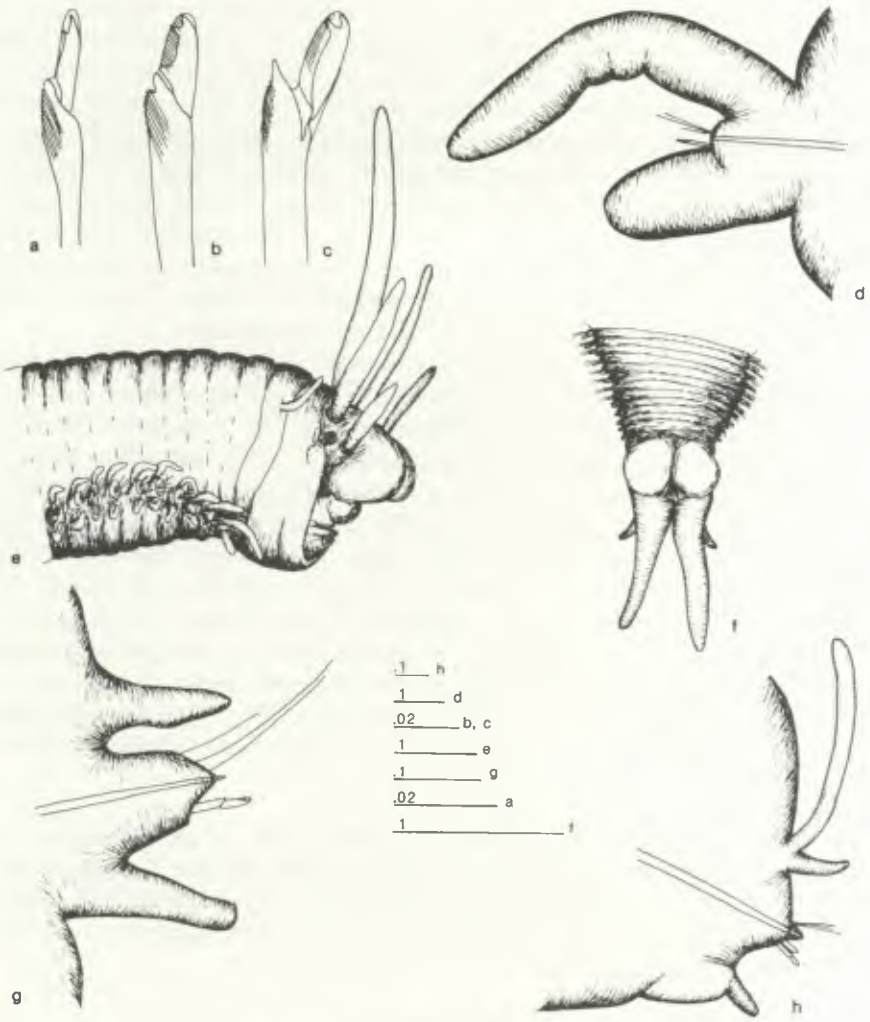

FIG. 12. *Palola viridis* (Fag'aituta Bay, Samoa, AHF); **a**, compound falciger, setiger 1; **b**, compound falciger, setiger 149; **c**, compound falciger, setiger 450; **d**, parapodium 1, anterior view; **e**, anterior end, lateral view; **f**, pygidium, dorsal view; **g**, parapodium 450, anterior view; **h**, parapodium 149, anterior view.

flattened throughout; inflated bases of ventral cirri, where present, strictly ventral in position.

Prostomial and peristomial features. Prostomium (Fig. 12e) longer than, and about as wide as, peristomium; about one-half as deep as peristomium (jaws partially extruded). Prostomial lobes frontally rounded; strongly flaring; dorsum excavate around bases of A-I, with thickened rim; median sulcus short. Eyes between bases of A-I and A-II; dark brownish-purple. Antennae in a horseshoe; A-I separated from other three antennae by distinct gap; all antennae similar in thickness. Ceratophores short and ring-shaped; without articulations. Ceratostyles slightly tapering; digitiform; without distinct articulations, but distinctly wrinkled. A-I to posterior edge of peristomium; A-II to setiger 4 and A-III to setiger 10. Peristomium cylindrical; anterior ring ventrally flaring (jaws partially extruded) without distinct muscular lower lip. Separation

Table 3. Summary of selected characters of *Palola viridis*.

Variable characters			
Complete specimens	yes	yes	no
Number of setigers	550	645	366
Total length	80	153	65
Maximum width	3	3	2
at setiger	15	50	10
Length through setiger 10	4·5	6	5
Width at setiger 10	2·5	2·5	2
Start of branchiae	110	145	118
End of branchiae	440	364	280
Number of cirriform anterior ventral cirri	15	15	15
Ventral cirri inflated to setiger number	160	200	168
Invariable characters			
Left Mx-II	3	3	3
Right Mx-II	3	2	2
Mx-III	0	0	0
Left Mx-IV	2	2	2
Right Mx-IV	2	2	2

between peristomial rings distinct on all sides. Anterior ring about one-half of total peristomial length on dorsal side; about two-thirds of total length on ventral side. Anterior ring subdivided ventrally by distinct groove. Peristomial cirri reaching front edge of peristomium; digitiform; without articulations.

Jaws. Heavily decalcified; maxillary formula 1 + 1, 3 + 3, 2 + 0, 2 + 2, 1 + 1. Mx-III located behind left Mx-II. Mx-V poorly sclerotinized, nearly clear; all other jaws heavily sclerotinized, dark-brown to black. Mandibles forming open scoop enclosing maxillae.

Branchiae. First present from setiger 110; present on every segment from setiger 115; absent from about last 100 segments. All branchiae single, flattened, distally truncate filaments. Where best developed (from about setiger 135 through setiger 175), filaments distinctly shorter than one-half of body width.

Parapodial structures. Anterior acicular lobes rounded (Fig. 12d); becoming triangular in median setigers (Fig. 12h). Posterior acicular lobes (Fig. 12g) distinctly raised above the body surface; distally bluntly triangular. Anterior pre- and postsetal lobes follow outline of acicular lobes closely; median pre- and postsetal lobes low, transverse folds; posterior pre- and postsetal lobes follow outline of acicular lobes closely. Anterior ventral cirri digitiform; less than one-half as long as notopodial cirri. Ventral cirri basally inflated from about setiger 15; inflated region a thick welt with distinct, digitiform free tops. Basal inflated region gradually reduced posteriorly and absent posterior to setiger 300; far posterior ventral cirri digitiform; distinctly longer than corresponding notopodial cirri. Notopodial cirri of setiger 1 long and digitiform; notopodial cirri decreasing in length to about one-half of that of the first setiger by setiger 4; retaining same length through rest of body. Notopodial cirri sharply tapering; nearly triangular in branchial region; without articulations.

Setae. Limbate setae curved, nearly geniculate; short; strongly tapering; cutting edge frayed. Pectinate setae absent. Anterior compound falcigers (Fig. 12a) with shafts inflated and marginally serrated; distal beak present. Appendages slender, with nearly parallel sides. Proximal teeth smaller than distal teeth; directed obliquely distally; with

straight taper. Distal teeth erect; with straight taper. Median compound falcigers (Fig. 12b) with shafts inflated; marginally very strongly serrated with serrations continued as internal striations. Appendages tapering. Proximal teeth about same size as distal teeth; directed obliquely distally; uptilted at tips. Distal teeth directed obliquely distally; with straight taper. Ratio of length to width of median appendages more than 0·35. Posterior compound falcigers (Fig. 12c) with shafts distally tapering; marginally serrated. Appendages with nearly parallel sides. Proximal teeth about same size as distal teeth; directed obliquely distally; slender; uptilted distally. Distal teeth directed obliquely distally; curved. Anterior guards narrow; distally blunt; marginally smooth. Median and posterior guards distally rounded; marginally serrated. Pseudocompound falcigers and compound spinigers absent. Aciculae single in anterior and posterior setigers; up to three aciculae present in median setigers. All aciculae brown; tapering and distally blunt; separation between sheath and core indistinct. Subacicular hooks absent.

Pygidium (Fig. 12f). Nearly twice as deep as long; dorsal edge formed by paired rounded lobes; bases of long anal cirri forming lateral sides. Long anal cirri about as long as last five setigers. Short anal cirri emerging from bases of long anal cirri; less than one-quarter as long as long anal cirri.

Remarks. The original material from Samoa examined by Gray consisted of swarming individuals only; Macdonald (1858) examined a large number of individuals from Fiji and found a single specimen with a (regenerating?) head. He described and illustrated this specimen as having three antennae; however, his illustration of the mandible shows a distinct *Palola/Lysidice* shape. Quatrefages did not quote Gray's original description and may not have seen it; he cited Macdonald and moved what he considered Macdonald's species to *Lysidice* based on the absence of outer lateral antennae; why he proceeded to rename Macdonald's species is unknown. Quatrefages referred *Lysidice* to the lumbrinerids. Quatrefages did not examine any material of this species as far as I can determine.

[*Lithognatha worsleyi* Stewart 1881

Lithognatha worsleyi Stewart 1881: 717; McIntosh (1885: 262).

Remarks. McIntosh (1885: 262) quoted Stewart's surmise that this species might be responsible for drilling into telegraph cables near Singapore without making any comments about the taxonomic position of the species. Fauchald (1970: 7) suggested that this species might be a member of *Palolo,* but that there were problems with both description and illustration. There are no specimen of Stewart's species available in BM(NH) (A. Muir, in litt.) and the species is here considered an indeterminable *Palolo.*]

Key to species of *Palola*

Only 12 species are well enough characterized to be included in the key. The key was written using the KEY program available as part of the DELTA package. The data files can be found in Appendix A and B.

1a A-I and II similar in length; A-III much longer (Fig. 6d) . . . . . *madeirensis*
b Three median antennae similar in length; A-I shorter (Fig. 5a) 2
c Length of antennae increasing from A-I through A-III (Fig. 11e) 3
d A-II longer than both A-I and I-III (Fig. 11c) . . . . . *vernalis*

2a Maxilla IV with a single sharp ridge on each side; posterior ventral cirri without inflated bases, tapering . . . . . *pallidus*
b Maxilla IV with one tooth on left side and two teeth on right side; posterior ventral cirri without inflated bases, digitiform, distally truncate . . . . . *paloloides*
c Maxilla IV with two teeth on either side; posterior ventral cirri without inflated bases, digitiform, distally tapering . . . . . *leucodon*
d Maxilla IV with four teeth on either side; posterior ventral cirri with inflated bases forming thick, transverse welts . . . . . *accrescens*

3a Prostomium dorsally inflated 4
b Prostomium dorsally flattened 5
c Prostomium dorsally excavate with a thickened rim . . . . . *viridis*

4a Median postsetal lobes follow outline of acicular lobes closely . . . *siciliensis*
b Median postsetal lobes form low transverse lobes . . . . . *edentulum*
c Median postsetal lobes project as free lobes . . . . . *ebranchiata*

5a Maxilla IV with two teeth on either side; prostomium frontally rounded; peristomial cirri digitiform . . . . . *simplex*
b Maxilla IV with four teeth on either side; prostomium frontally obliquely truncate; peristomial cirri tapering . . . . . *valida*

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Appendix A

Character list for *Palola* formated for use with DELTA (CHARS file). The various marks (in, rn, etc.) are abbreviations used in working with DELTA files, punctuation and the use of / also reflect usage in that program.

1.01	#1. specimen/
1.02	1. complete/
1.03	2. incomplete/
2.01	#2. ⟨specimen, um⟩/
2.02	1. male/
2.03	2. female/
2.04	3. of unknown sex/
2.05	4. juvenile/
3.01	#3. setigers numbering ⟨in⟩/
4.01	#4. total length ⟨rn⟩/ mm/
5.01	#5. maximum width ⟨rn⟩/ mm, first reached at setiger/

6.01 #6. ⟨maximum width first reached at setiger⟩ ⟨in⟩/

7.01 #7. length through setiger 10 ⟨rn⟩/
mm/

8.01 #8. width at setiger 10 ⟨rn⟩/
mm/

9.01 #9. Prostomium ⟨um⟩/
9.02 1. frontally truncate/
9.03 2. frontally obliquely truncate/
9.04 3. frontally rounded/

10.01 #10. ⟨prostomium, um⟩/
10.02 1. dorsally inflated/
10.03 2. dorsally flattened/
10.04 3. dorsally excavate with a thickened rim/

11.01 #11. median sulcus ⟨um⟩/
11.02 1. invisible dorsally/
11.03 2. shallow/
11.04 3. deep/

12.01 #12. prostomium ⟨um⟩/
12.02 1. distinctly shorter than peristomium/
12.03 2. about as long as peristomium/
12.04 3. distinctly longer than peristomium/

13.01 #13. ⟨prostomium⟩/
13.02 1. about as wide as peristomium/
13.03 2. distinctly narrower than peristomium/

14.01 #14. ⟨prostomium⟩/
14.02 1. less than 1/2 as deep as peristomium/
14.03 2. as deep as 1/2 the peristomium or deeper/

15.01 #15. eyes ⟨um⟩/
15.02 1. absent/
15.03 2. lateral to the bases of A-I/
15.04 3. behind bases of A-I/
15.05 4. between bases of A-I and A-II/
15.06 5. behind bases of A-II/
15.07 6. on ceratophores of A-I/
15.08 7. on ceratophores of A-II/

16.01 #16. antennae arranged in a ⟨um⟩/
16.02 1. horseshoe/
16.03 2. semicircle/
16.04 3. straight line/

17.01 #17. ⟨antennae, um⟩/
17.02 1. evenly spaced/
17.03 2. with A-I isolated by a gap/
17.04 3. with A-III isolated by a gap/

18.01 #18. ⟨antennae, um⟩/
18.02 1. similar in thickness/
18.03 2. with A-I slimmer than other three/
18.04 3. with A-III slimmer than other four/
18.05 4. with A-I thicker than other three/
18.06 5. with A-II thicker than other three/
18.07 6. with A-III thicker than other four/

19.01 #19. ceratophores ⟨um⟩/
19.02 1. long in all antennae/
19.03 2. long in A-I and ring-shaped in other three/
19.04 3. ring-shaped in all antennae/

20.01 #20. ⟨ceratophores⟩/
20.02 1. articulated/
20.03 2. without articulations/

21.01 #21. ceratostyles ⟨um⟩/
21.02 1. tapering/
21.03 2. medially inflated/
21.04 3. digitiform/
21.05 4. club-shaped/

22.01 #22. ⟨ceratostyles, um⟩/
22.02 1. without articulations/
22.03 2. with long or short cylindrical articulations/
22.04 3. with basally cylindrical and distally moniliform
22.05 or drop-shaped articulations/
22.06 4. with all articulations (except the basal one)
22.07 moniliform/

23.01 #23. length of ⟨um⟩/
23.02 1. A-I and II similar with A-III much longer/
23.03 2. A-II and III similar with A-I shorter/
23.04 3. antennae increasing from A-I to A-III/
23.05 4. A-II greater than A-I and A-III/
23.06 5. all antennae similar (short)/

24.01 #24. peristomium/
24.02 1. with muscular lower lip marked off by a groove/
24.03 2. without muscular lower lip/

25.01 #25. separation between peristomial rings ⟨um⟩/
25.02 1. absent/
25.03 2. visible dorsally only/
25.04 3. visible ventrally only/
25.05 4. visible both dorsally and ventrally/
25.06 5. distinct on all sides/

26.01 #26. anterior ring makes up ⟨um⟩/
26.02 1. 1/2 of total peristomial length/
26.03 2. 2/3 of total peristomial length/
26.04 3. 3/4 of total peristomial length/
26.05 4. 4/5 of total peristomial length/
26.06 5. 5/6 of total peristomial length/
26.07 6. 6/7 of total peristomial length/
26.08 7. 7/8 of total peristomial length/
26.09 8. 8/9 of total peristomial length/
26.10 9. 9/10 of total peristomial length/

27.01 #27. peristomial cirri ⟨um⟩/
27.02 1. absent/
27.03 2. reach middle of anterior end of peristomium/
27.04 3. reach middle or front of prostomium/
27.05 4. reach beyond prostomium/

28.01 #28. ⟨peristomial cirri, um⟩/
28.02 1. tapering/
28.03 2. digitiform/

28.04 3. medially inflated/
28.05 4. basally inflated/
28.06 5. ovate/

29.01 #29. ⟨peristomial cirri⟩/
29.02 1. without articulations/
29.03 2. articulated/

30.01 #30. Maxilla II with ⟨um⟩/
30.02 1. 2 + 3/
30.03 2. 3 + 3/
30.04 3. 3 + 4/
30.05 4. 4 + 3/
30.06 5. 4 + 4/
30.07 6. 5 + 4/
30.08 7. 5 + 3/

31.01 #31. Mx-III ⟨um⟩/
31.02 1. without teeth/
31.03 2. with a single distinct tooth/
31.04 3. with two distinct teeth/
31.05 4. with a sharp continuous ridge/

32.01 #32. ⟨Mx-III⟩/
32.02 1. located behind left Mx-II/
32.03 2. part of distal arc with Mx-IV/

33.01 #33. Maxilla IV with ⟨um⟩/
33.02 1. no teeth, rounded/
33.03 2. a single sharp ridge on each side/
33.04 3. 1 + 1/
33.05 4. 1 + 2/
33.06 5. 2 + 2/
33.07 6. 4 + 4/

34.01 #34. branchiae ⟨um⟩/
34.02 1. absent/
34.03 2. single filaments/
34.04 3. palmate/
34.05 4. pectinate/

35.01 #35. ⟨branchiae, um⟩/
35.02 1. distinctly longer than notopodial cirri/
35.03 2. about as long as notopodial cirri/
35.04 3. distinctly shorter than notopodial cirri/

36.01 #36. ⟨branchiae⟩/
36.02 1. reduced in mid-body region/
36.03 2. not reduced in mid-body region/

37.01 #37. branchial stems ⟨um⟩/
37.02 1. absent or rudimentary/
37.03 2. erect/
37.04 3. flexible/

38.01 #38. branchiae from setiger ⟨in⟩/

39.01 #39. to setiger ⟨in⟩/

40.01 #40. branchiae/
40.02 1. present to near posterior end/
40.03 2. terminating well before posterior end/

41.01 #41. ⟨branchiae⟩ present on/

41.02 1. more than 65% of total number of setigers/
41.03 2. on less than 55% of total number of setigers/

42.01 #42. anterior setigers with single filaments number ⟨in⟩/

43.01 #43. posterior setigers with single filaments number ⟨in⟩/

44.01 #44. maximum number of filaments ⟨in⟩/

45.01 #45. ⟨maximum number of filaments⟩ first reached in
45.02 setiger ⟨in⟩/

46.01 #46. where best developed branchiae/
46.02 1. as long as, or longer than 1/2 of body-width/
46.03 2. distinctly shorter than 1/2 of body-width/

47.01 #47. median acicular lobes ⟨um⟩/
47.02 1. distally truncate/
47.03 2. distally rounded/
47.04 3. triangular or conical/
47.05 4. withdrawn into body-wall/
47.06 5. bilobed/

48.01 #48. ⟨median acicular lobes⟩ with ⟨um⟩/
48.02 1. aciculae emerging ventral to midline/
48.03 2. aciculae emerging at midline/
48.04 3. aciculae emerging dorsal to midline/

49.01 #49. anterior presetal lobes ⟨um⟩/
49.02 1. follow outline of acicular lobes closely/
49.03 2. form low, transverse lobes/
49.04 3. project as free lobes/
49.05 4. form low, oblique lobes/

50.01 #50. median presetal lobes ⟨um⟩/
50.02 1. follow outline of acicular lobes closely/
50.03 2. form low transverse lobes/
50.04 3. project as free lobes/
50.05 4. form low, oblique lobes/

51.01 #51. posterior presetal lobes ⟨um⟩/
51.02 1. follow outline of acicular lobes closely/
51.03 2. form low transverse lobes/
51.04 3. project as free lobes/
51.05 4. form low, oblique lobes/

52.01 #52. anterior postsetal lobes ⟨um⟩/
52.02 1. follow outline of acicular lobes closely/
52.03 2. form low transverse lobes/
52.04 3. project as free lobes/

53.01 #53. median postsetal lobes ⟨um⟩/
53.02 1. follow outline of acicular lobes closely/
53.03 2. form low transverse lobes/
53.04 3. project as free lobes/

54.01 #54. posterior postsetal lobes ⟨um⟩/
54.02 1. follow outline of acicular lobes closely/
54.03 2. form low transverse lobes/
54.04 3. project as free lobes/

55.01 #55. anterior setigers without basally inflated ventral
55.02 cirri number ⟨in⟩/

56.01 #56. anterior ventral cirri ⟨um⟩/
56.02 1. tapering from narrow bases/
56.03 2. tapering from wide, triangular bases/
56.04 3. digitiform/

57.01 #57. median ventral cirri ⟨um⟩/
57.02 1. without inflated bases, tapering/
57.03 2. without inflated bases, digitiform/
57.04 3. with ovate or spherical inflated bases/
57.05 4. with inflated bases forming thick, transverse welts/
56.06 5. with scoop-shaped inflated bases/

58.01 #58. ⟨median inflated ventral cirri with⟩ narrow tips
58.02 ⟨um⟩/
58.03 1. short and button-shaped/
58.04 2. tapering/
58.05 3. digitiform/
58.06 4. truncate/
58.07 5. absent/

59.01 #59. posterior ventral cirri ⟨um⟩/
59.02 1. without inflated bases, tapering/
59.03 2. without inflated bases, digitiform, distally
59.04 tapering/
59.05 3. without inflated bases, digitiform, distally
59.06 truncate/
59.07 4. without inflated bases, short, nearly tubercular/
59.08 5. without inflated bases, broadly triangular, nearly
59.09 scoop-shaped/
59.10 6. with ovate or spherical inflated bases/
59.11 7. with inflated bases forming thick, transverse welts/
59.12 8. with inflated bases forming triangular welts/
59.13 9. with scoop-shaped inflated bases/

60.01 #60. posterior inflated ventral cirri with narrow tips
60.02 ⟨um⟩/
60.03 1. short and button-shaped/
60.04 2. tapering/
60.05 3. digitiform/
60.06 4. absent/

61.01 #61. anterior notopodial cirri ⟨um⟩/
61.02 1. basally inflated/
61.03 2. medially inflated/
61.04 3. tapering/
61.05 4. digitiform/
61.06 5. clavate/

62.01 #62. median notopodial cirri ⟨um⟩/
62.02 1. basally inflated/
62.03 2. medially inflated/
62.04 3. tapering/
62.05 4. digitiform/
62.06 5. clavate/
62.07 6. strongly tapered/
62.08 7. absent/

63.01 #63. posterior notopodial cirri ⟨um⟩/
63.02 1. basally inflated/
63.03 2. medially inflated/
63.04 3. tapering/

63.05 4. digitiform/
63.06 5. clavate/
63.07 6. strongly tapered/

64.01 #64. notopodial cirri ⟨um⟩/
64.02 1. articulated throughout body/
64.03 2. articulated in anterior setigers/
64.04 3. without articulations/

65.01 #65. appendages of compound falcigers distally ⟨um⟩/
65.02 1. simple, falcate/
65.03 2. bidentate/
65.04 3. tridentate/

66.01 #66. guards distally/
66.02 1. mucronate/
66.03 2. without mucro/

67.01 #67. shafts of anterior compound falcigers subdistally/
67.02 1. distinctly inflated/
67.03 2. tapering/

68.01 #68. ⟨shafts of anterior compound falcigers⟩ marginally/
68.02 1. appearing serrated or dentate/
68.03 2. appearing smooth/

69.01 #69. appendages of anterior compound falcigers/
69.02 1. slender, with nearly parallel sides/
69.03 2. distinctly tapering/

70.01 #70. proximal teeth of appendages of anterior compound
70.02 falcigers ⟨um⟩/
70.03 1. smaller than distal teeth/
70.04 2. about the same size as distal teeth/
70.05 3. larger than distal teeth/

71.01 #71 ⟨proximal teeth⟩/
71.02 1. directed obliquely distally/
71.03 2. directed laterally/

72.01 #72. ⟨proximal teeth, um⟩/
72.02 1. uptilted distally/
72.03 2. with straight taper/
72.04 3. downturned distally (curved to parrot-beaked)/

73.01 #73. distal teeth/
73.02 1. erect/
73.03 2. directed obliquely distally/

74.01 #74. ⟨distal teeth⟩/
74.02 1. with straight taper/
74.03 2. curved-parrot-beaked/

75.01 #75. shafts of median compound falcigers distally/
75.02 1. distinctly inflated/
75.03 2. tapering/

76.01 #76. ⟨shafts of median compound falcigers⟩ marginally/
76.02 1. appearing serrated or dentate/
76.03 2. appearing smooth/

77.01 #77. appendages of median compound falcigers/
77.02 1. slender, with nearly parallel sides/
77.03 2. distinctly tapering/

78.01 #78. proximal teeth of appendages of median compound
78.02 falcigers ⟨um⟩/
78.03 1. smaller than distal teeth/
78.04 2. about the same size as distal teeth/
78.05 3. larger than distal teeth/

79.01 #79. ⟨proximal teeth⟩/
79.02 1. directed obliquely distally/
79.03 2. directed laterally/

80.01 #80. ⟨proximal teeth, um⟩/
80.02 1. uptilted distally/
80.03 2. with straight taper/
80.04 3. downturned distally (curved to parrot-beaked)/

81.01 #81. distal teeth/
81.02 1. erect/
81.03 2. directed obliquely distally/

82.02 #82. ⟨distal teeth⟩/
82.02 1. with straight taper/
82.03 2. curved to parrot-beaked/

83.01 #83. ratio of width to length of median appendages/
83.02 1. 0·25 or less/
83.03 2. 0·35 or more/

84.01 #84. shafts of posterior compound falcigers distally ⟨um⟩/
84.02 1. slender, distinctly inflated/
84.03 2. slender, tapering/
84.04 3. thick, tapering/

85.01 #85. ⟨shafts of posterior compound falcigers⟩ marginally/
85.02 1. appearing serrated or dentate/
85.03 2. appearing smooth/

86.01 #86. appendages of posterior compound falcigers/
86.02 1. slender, with nearly parallel sides/
86.03 2. distinctly tapering/

87.01 #87. proximal teeth of appendages of posterior compound
87.02 falcigers ⟨um⟩/
87.03 1. smaller than distal teeth/
87.04 2. about the same size as distal teeth/
87.05 3. larger than distal teeth/

88.01 #88. ⟨proximal teeth⟩/
88.02 1. directed obliquely distally/
88.03 2. directed laterally/

89.01 #89. ⟨proximal teeth, um⟩/
89.02 1. uptilted distally/
89.03 2. with straight taper/
89.04 3. downturned distally (curved to parrot-beaked)/

90.01 #90. distal teeth ⟨um⟩/
90.02 1. erect/
90.03 2. directed obliquely distally/
90.04 3. directed laterally/

91.01 #91. ⟨distal teeth⟩/
91.02 1. with straight taper/
91.03 2. curved to parrot-beaked/

92.01 #92. compound spinigers/
92.02 1. absent/
92.03 2. present/

93.01 #93. pseudocompound falcigers/
93.02 1. absent/
93.03 2. present/

94.01 #94. aciculae/
94.02 1. light yellow or translucent/
94.03 2. dark honey-coloured to black/

95.01 #95. separation of acicular cores and sheaths/
95.02 1. distinct/
95.03 2. indistinct/

96.01 #96. cross-section ⟨of aciculae⟩/
96.02 1. round/
96.03 2. flattened and knife-edged/

97.01 #97. aciculae distally ⟨um⟩/
97.02 1. pointed ⟨sharp or blunt⟩/
97.03 2. flattened with rounded tabs/
97.04 3. expanded, knurled and knobbed/
97.05 4. hammer-headed/
97.06 5. bifid ⟨bidentate⟩/

98.01 #98. ⟨aciculae distally⟩/
98.02 1. straight/
98.03 2. bent or curved/

99.01 #99. anterior parapodia usually with ⟨um⟩/
99.02 1. single acicula/
99.03 2. paired aciculae/
99.04 3. three or more aciculae/

100.01 #100. median parapodia usually with ⟨um⟩/
100.02 1. single acicula/
100.03 2. paired aciculae/
100.04 3. three or more aciculae/

101.01 #101. posterior parapodia usually with ⟨um⟩/
101.02 1. single acicula/
101.03 2. paired aciculae/
101.04 3. three or more aciculae/

102.01 #102. pygidium with/
102.02 1. a single pair of ventrolateral anal cirri/
102.03 2. two pairs of ventrolateral anal cirri/

103.01 #103. anus/
103.02 1. without distinct, single lobes ⟨usually folded or
103.03 wrinkled⟩/
103.04 2. with paired hemispherical dorsal lobes and in addition bases of anal cirri
103.05 forming ventral edge/

Appendix B

Description of species of *Palola* in DELTA format (ITEMS file) using the character list in Appendix A. Each feature is represented by two numbers; the first

number, the character number is followed by a comma and the character-state number. U indicates that the state for that character is unknown; – indicates that the character is inappropriate (for example if branchiae are absent (34,1) all characters used to describe the branchiae (35–46) become inappropriate.

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*SHOW: Species of *Palola* Scored 1 March 1991

*ITEM DESCRIPTIONS

1.01 # *Palola accrescens* (Hoagland, 1920)/
1.02 1,2 2,3 3,317 4,144 5,12 6,10 7,11 8,12 9,3 10,1 11,3 12,1
1.03 13,1 14,2 15,4 16,1 17,1 18,1 19,3 20,2 21,3 22,1 23,2 24,1
1.04 25,5 26,2 27,1 28,2 29,1 30,3 31,4 32,1 33,6 34,2 35,1 36,2
1.05 37,1 38,98 39,U 40,U 41,U 42,– 43,– 44,1 45,– 46,1 47,2
1.06 48,2 49,2 50,1 51,1 52,1 53,1 54,1 55,4 56,3 57,4 58,2 59,7
1.07 60,2 61,2 62,3 63,U 64,3 65,2 66,2 67,1 68,1 69,1 70,3 71,1
1.08 72,1 73,1 74,1 75,1 76,1 77,2 78,3 79,2 80,1 81,2 82,1 83,1
1.09 84,U 85,U 86,U 87,U 88,U 89,U 90,U 91,U 92,1 93,1 94,2 95,1
1.10 96,1 97,1 98,1 99,2 100,3 101,3 102,U 103,U

2.01 # *Palola ebranchiata* (Quatrefages, 1866)/
2.02 1,2 2,3 3,130 4,52 5,2.5 6,50 7,8 8,2.2 9,3 10,1 11,3 12,1
2.03 13,2 14,2 15,4 16,1 17,2 18,1 19,3 20,2 21,1 22,1 23,3 24,1
2.04 25,5 26,3 27,2 28,1 29,1 30,U 31,U 32,U 33,U 34,1 35,– 36,–
2.05 37,– 38,– 39,– 40,– 41,– 42,– 43,– 44,– 45,– 46,– 47,2 48,3
2.06 49,1 50,2 51,U 52,1 53,3 54,U 55,10 56,3 57,4 58,2 59,U
2.07 60,U 61,4 62,6 63,U 64,3 65,2 66,2 67,1 68,1 69,1 70,3 71,2
2.08 72,2 73,1 74,1 75,1 76,1 77,2 78,3 79,2 80,2 81,1 82,1 83,1
2.09 84,U 85,U 86,U 87,U 88,U 89,U 90,U 91,U 92,1 93,1 94,2 95,2
2.10 96,1 97,1 98,1 99,2 100,2 101,U 102,U 103,U

3.01 # *Palola edentulum* (Ehlers, 1901)/
3.02 1,2 2,3 3,111 4,42 5,1.75 6,3 7,5.5 8,1.5 9,3 10,1 11,2
3.03 12,1 13,1 14,2 15,4 16,3 17,2 18,1 19,1 20,2 21,3 22,1 23,3
3.04 24,1 25,5 26,1 27,2 28,2 29,1 30,5 31,U 32,U 33,U 34,1 35,–
3.05 36,– 37,– 38,– 39,– 40,– 41,– 42,– 43,– 44,– 45,– 46,– 47,3
3.06 48,2 49,1 50,2 51,U 53,2 54,U 55,4 56,3 57,4 58,2 59,U
3.07 60,U 61,4 62,3 63,U 64,2 65,1 66,2 67,1 68,1 69,1 70,– 71,–
3.08 72,– 73,1 74,1 75,1 76,1 77,1 78,– 79,– 80,– 81,1 82,1 83,1
3.09 84,U 85,U 86,U 87,U 88,U 89,U 90,U 91,U 92,1 93,1 94,2 95,2
3.10 96,1 97,1 98,1 99,1 100,1 101,U 102,U 103,U

4.01 # *Palola leucodon* (Ehlers, 1901)/
4.02 1,1 2,U 3,308 4,83 5,2.2 6,65 7,6 8,2 9,3 10,1 11,3 12,1
4.03 13,2 14,2 15,4 16,1 17,2 18,1 19,3 20,2 21,3 22,1 23,2 24,1
4.04 25,5 26,2 27,2 28,2 29,1 30,2 31,3 32,U 33,5 34,2 35,1 36,2
4.05 37,1 38,126 39,302 40,1 41,1 42,– 43,– 44,1 45,– 46,2 47,2
4.06 48,1 49,2 50,2 51,2 52,3 53,3 54,3 55,5 56,3 57,4 58,2 59,2
4.07 60,– 61,4 62,3 63,3 64,3 65,2 66,2 67,2 68,1 69,1 70,2 71,1
4.08 72,2 73,1 74,1 75,1 76,1 77,2 78,2 79,2 80,3 81,2 82,2 83,1
4.09 84,1 85,1 86,1 87,3 88,1 89,2 90,2 91,1 92,1 93,1 94,2 95,1
4.10 96,1 97,1 98,1 99,2 100,2 101,1 102,2 103,1

5.01 # *Palola madeirensis* (Baird, 1869)/
5.02 1,2 2,3 3,297 4,160 5,5.5 6,50 7,13 8,4.5 9,3 10,3 11,3
5.03 12,1 13,2 14,2 15,4 16,3 17,2 18,1 19,3 20,2 21,1 22,1 23,1
5.04 24,2 25,4 26,1 27,2 28,2 29,1 30,U 31,U 32,U 33,U 34,2 35,1
5.05 36,2 37,1 38,231 39,U 40,U 41,U 42,– 43,– 44,1 45,– 46,2
5.06 47,3 48,3 49,2 50,2 51,2 52,2 53,2 54,2 55,9 56,1 57,4 58,3

5.07 59,7 60,3 61,4 62,6 63,3 64,3 65,2 66,2 67,1 68,1 69,1 70,2
5.08 71,2 72,2 73,1 74,1 75,1 76,1 77,2 78,3 79,2 80,2 81,1 82,1
5.09 83,1 84,1 85,1 86,1 87,2 88,2 89,2 90,1 91,1 92,1 93,1 94,2
5.10 95,2 96,1 97,1 98,1 99,2 100,3 101,3 102,U 103,U

6.01 # *Palola pallidus* Hartman, 1938/
6.02 1,1 2,3 3,565 4,200 5,3 6,50 7,6.5 8,2.5 9,3 10,3 11,2 12,1
6.03 13,1 14,2 15,4 16,1 17,2 18,1 19,3 20,2 21,1 22,1
6.04 23,2 24,1 25,5 26,2 27,2 28,1 29,1 30,2 31,4 32,2 33,2 34,2
6.05 35,1 36,2 37,1 38,133 39,562 40,1 41,1 42,– 43,– 44,1 45,–
6.06 46,2 47,3 48,2 49,1 50,1 51,1 52,1 53,1 54,1 55,9 56,3 57,4
6.07 58,1 59,1 60,– 61,4 62,6 63,6 64,3 65,2 66,2 67,2 68,1 69,1
6.08 70,2 71,1 72,2 73,2 74,1 75,1 76,1 77,2 78,2 79,2 80,3 81,2
6.09 82,2 83,1 84,1 85,1 86,2 87,3 88,2 89,3 90,2 91,2 92,1 93,1
6.10 94,2 95,2 96,1 97,1 98,1 99,1 100,2 101,1 102,1 103,1

7.01 # *Palola paloloides* (Moore, 1904)/
7.02 1,2 2,3 3,230 4,130 5,5 6,10 7,10 8,5 9,3 10,1 11,3 12,1
7.03 13,2 14,1 15,4 16,3 17,2 18,1 19,3 20,2 21,1 22,1 23,2 24,1
7.04 25,5 26,2 27,2 28,2 29,1 30,7 31,2 32,U 33,4 34,2 35,1 36,2
7.05 37,1 38,103 39,U 40,U 41,U 42,– 43,– 44,1 45,– 46,1 47,3
7.06 48,3 49,2 50,2 51,2 52,1 53,2 54,2 55,5 56,1 57,4 58,3 59,3
7.07 60,– 61,3 62,4 63,4 64,3 65,2 66,2 67,1 68,1 69,1 70,2 71,2
7.08 72,2 73,1 74,1 75,1 76,1 77,2 78,1 79,2 80,2 81,1 82,1 83,1
7.09 84,1 85,1 86,1 87,3 88,2 89,2 90,1 91,1 92,1 93,1 94,2 95,1
7.10 96,1 97,1 98,1 99,2 100,2 101,2 102,U 103,U

8.01 # *Palola siciliensis* (Grube, 1840)/
8.02 1,2 2,3 3,229 4,90 5,4 6,10 7,9 8,4 9,3 10,1 11,3 12,2 13,2
8.03 14,2 15,1 16,3 17,2 18,1 19,3 20,2 21,3 22,1 23,3 24,1 25,5
8.04 26,2 27,2 28,1 29,1 30,2 31,4 32,1 33,5 34,2 35,1 36,2 37,1
8.05 38,180 39,U 40,U 41,U 42,– 43,– 44,1 45,– 46,2 47,2 48,3
8.06 49,2 50,2 51,2 52,1 53,1 54,1 55,9 56,3 57,4 58,2 59,7 60,2
8.07 61,4 62,3 63,6 64,3 65,2 66,2 67,1 68,1 69,1 70,1 71,1 72,2
8.08 73,2 74,1 75,1 76,1 77,2 78,1 79,2 80,2 81,2 82,2 83,1 84,1
8.09 85,1 86,2 87,2 88,1 89,2 90,1 91,1 92,1 93,1 94,2 95,1 96,1
8.10 97,1 98,1 99,1 100,2 101,2 102,U 103,U

9.01 # *Palola simplex* (Peters, 1854)/
9.02 1,2 2,3 3,110 4,34 5,2 6,U 7,U 8,U 9,3 10,2 11,3 12,U 13,U
9.03 14,U 15,4 16,1 17,2 18,1 19,3 20,2 21,3 22,1 23,3 24,U 25,5
9.04 26,2 27,2 28,2 19,1 30,2 31,1 32,1 33,5 34,1 35,– 36,– 37,–
9.05 38,– 39,– 40,– 41,– 42,– 43,– 44,– 45,– 46,– 47,3 48,2 49,2
9.06 50,2 51,U 52,2 53,2 54,U 55,4 56,1 57,4 58,1 59,U 60,U 61,1
9.07 62,7 63,4 64,3 65,2 66,2 67,2 68,2 69,2 70,1 71,2 72,2
9.08 73,1 74,1 75,2 76,2 77,2 78,1 79,2 80,2 81,1 82,1 83,U 84,U
9.09 85,U 86,U 87,U 88,U 89,U 90,U 91,U 92,2 93,1 94,2 95,2 96,1
9.10 97,1 98,1 99,U 100,U 101,U 102,U 103,U

10.01 # *Palola valida* (Gravier, 1900)/
10.02 1,2 2,3 3,215 4,85 5,4.5 6,65 7,15 8,4 9,2 10,2 11,2 12,1
10.03 13,1 14,1 15,4 16,1 17,2 18,1 19,3 20,2 21,3 22,1 23,3
10.04 24,2 25,5 26,2 27,2 28,1 29,1 30,1 31,4 32,1 33,6 34,2
10.05 35,1 36,2 37,1 38,112 39,U 40,U 41,U 42,– 43,– 44,1 45,–
10.06 46,1 47,2 48,3 49,1 50,2 51,2 52,1 53,2 54,2 55,10 56,3
10.07 57,4 58,2 59,2 60,– 61,3 62,6 63,6 64,3 65,1–2 66,2 67,1
10.08 68,1 69,1 70,3 71,1 72,2 73,1 74,1 75,1 76,1 77,2 78,1
10.09 79,1 80,1 81,2 82,1 83,2 84,1 85,1 86,2 87,2 88,2 89,2
10.10 90,2 91,2 92,1 93,1 94,2 95,2 96,1 97,1 98,1 99,1 100,1
10.11 101,1 102,U 103,U

11.01 # *Palola vernalis* (Treadwell, 1922)/
11.02 1,2 2,3 3,233 4,100 5,1.5 6,U 7,5.5 8,U 9,1 10,2 11,3 12,1
11.03 13,2 14,2 15,4 16,1 17,2 18,1 19,3 20,2 21,3 22,1 23,4
11.04 24,1 25,5 26,2 27,2 28,2 19,1 30,U 31,U 32,U 33,U 34,2
11.05 35,1 36,2 37,1 38,88 39,U 40,U 41,U 42,– 43,– 44,1 45,–
11.06 46,1 47,2 48,3 49,4 50,4 51,2 52,3 53,3 54,2 55,3 56,1
11.07 57,4 58,2 59,1 60,– 61,3 62,3 63,3 64,3 65,2 66,2 67,1
11.08 68,1 69,2 70,2 71,1 72,2 73,2 74,2 75,1 76,1 77,2 78,2
11.09 79,1 80,2 81,2 82,1 83,2 84,1 85,1 86,U 87,U 88,U 89,U
11.10 90,U 91,U 92,1 93,1 94,2 95,1 96,1 97,1 98,1–2 99,1 100,1
11.11 101,1 102,U 103,U

12.01 # *Palola viridis* Gray, 1847/
12.02 1,1 2,2 3,550 4,80 5,3 6,15 7,4.5 8,2.5 9,3 10,3 11,2
12.03 12,3 13,1 14,2 15,4 16,1 17,2 18,1 19,3 20,2 21,3 22,1
12.04 23,3 24,2 25,5 26,1 27,2 28,1 29,1 30,2 31,3 32,1 33,5
12.05 34,2 35,1 36,2 37,1 38,110 39,U 40,2 41,2 42,– 43,– 44,1
12.06 45,– 46,2 47,3 48,1 49,1 50,2 51,1 52,1 53,2 54,1 55,14
12,07 56,3 57,4 58,3 59,2 60,– 61,4 62,3 63,4 64,3 65,2 66,2
12.08 67,2 68,1 69,1 70,1 71,1 72,2 73,1 74,1 75,1 76,1 77,2
12.09 78,2 79,1 80,1 81,2 82,1 83,2 84,2 85,1 86,1 87,2 88,1
12.10 89,1 90,2 91,2 92,1 93,1 94,2 95,2 96,1 97,1 98,1 99,1
12.11 100,3 101,1 102,2 103,2