

Review of Oweniidae Rioja, 1917
(Annelida, Palaeoannelida) from Malaysia,
with a description of two new species
and a key to South China Sea species

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COUVERTURE / COVER:

Galathowenia minuta n. sp. holotype, UMTAnn 2184, hooked uncini in oblique position mid body.

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Review of Oweniidae Rioja, 1917 (Annelida, Palaeoannelida) from Malaysia, with a description of two new species and a key to South China Sea species

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ABSTRACT

Several species of the family Oweniidae Rioja, 1917 (Annelida) are believed to be responsible for sediment stabilisation, therefore the taxonomic identification and description of species from this family is crucial. Nevertheless, few oweniids have been identified in the South China Sea (SCS), whereas none were reported from the east coast of Peninsular Malaysia. Two new oweniid species are described here: *Galathowenia minuta* n. sp. and *Owenia unipinnata* n. sp., both stemming from the coastal defense structure area of Kuala Nerus, Terengganu, east coast of Peninsular Malaysia. These two species represent the smallest one ever recorded in their genera; *G. minuta* n. sp. is unique among all species of *Galathowenia* Kirkegaard, 1959 because of the following combination of features: brownish eyespots at head, first and second segments twice as long as the third, pigmentation encircling the fourth segment, seventh segment longest, and two blunt pygidial lobes. Conversely, *O. unipinnata* n. sp. is different from its congeners because of the presence of three pairs of tentacles on the branchial crown with three minor and simple ramifications, one of the pairs located solitary at the midventral side. Detailed descriptions and illustrations, as well as several comments on the biological and ecological traits of these two new species are included. Furthermore, identification keys to the species of oweniids recorded in the South China Sea (SCS) region are also provided.

KEY WORDS

Galathowenia,
Owenia,
Kuala Nerus,
South China Sea,
coastal defense structure,
new species.

RÉSUMÉ

Révision des Oweniidae Rioja, 1917 (Annelida, Palaeoannelida) de Malaisie, avec la description de deux nouvelles espèces et une clé des espèces de la mer de Chine méridionale.

On pense que plusieurs espèces de la famille des Oweniidae Rioja, 1917 (Annelida) sont responsables de la stabilisation des sédiments. L'identification et la description des espèces de cette famille sont donc cruciales. Néanmoins, peu d'oweniidés ont été identifiés dans la mer de Chine méridionale (SCS), alors qu'aucun n'a été signalé sur la côte est de la péninsule malaisienne. Deux nouvelles espèces d'oweniidés sont décrites ici : *Galathowenia minuta* n. sp. et *Owenia unipinnata* n. sp., toutes deux originaires de la zone des structures de défense côtière de Kuala Nerus, Terengganu, côte est de la Malaisie péninsulaire. Ces deux espèces représentent la plus petite espèce jamais signalée dans leur genre respectif ; *Galathowenia minuta* n. sp. est unique parmi toutes les espèces de *Galathowenia* Kirkegaard, 1959 en raison de la combinaison de caractéristiques suivante : ocelles brunâtres sur la tête, premier et deuxième segments deux fois plus longs que le troisième, pigmentation entourant le quatrième segment, le septième segment le plus long et deux lobes pygidiens obtus. À l'inverse, *O. unipinnata* n. sp. se distingue de ses congénères par la présence de trois paires de tentacules sur la couronne branchiale avec trois ramifications mineures et simples, l'une des paires étant située solitaire du côté médio-ventral. Des descriptions et illustrations détaillées, ainsi que plusieurs commentaires sur les caractéristiques biologiques et écologiques de ces deux nouvelles espèces sont inclus. En outre, des clés d'identification des espèces d'oweniidés signalées dans la région de la mer de Chine méridionale (SCS) sont également fournies.

MOTS CLÉS

Galathowenia,
Owenia,
Kuala Nerus,
mer de Chine méridionale,
structure de défense côtière,
espèces nouvelles.

INTRODUCTION

Oweniidae Rioja, 1917 is a monophyletic family (Sene-Silva 2002; Capa *et al.* 2012) of sessile tubicolous marine annelids with a body segmentation barely indicated by the presence of chaetal fascicles (Villalobos-Guerrero 2021). These soft-bodied permanent tube dwellers are frequently reported in continental shelves, in addition to shallow depths and deep-sea environments (Capa *et al.* 2012). They are commonly found in soft bottoms, form dense patchy populations, and are capable of moving around within the tube (Silva & Lana 2017; Parapar *et al.* 2021). In turn, the tubes exhibit varying consistencies and are mainly composed of interlocking sand grains, shell fragments, foraminifera tests, and sponge spicules (Capa *et al.* 2019). Moreover, these surficial modifiers have a relatively small size, with most of the species measuring 20–30 mm, and have a life span of up to four years (Villalobos-Guerrero 2021; Parapar *et al.* 2021).

The overall external morphology of oweniids is simple, consisting of a reduced head with a distal oral cavity located at the anterior end and a smooth, elongated, and cylindrical body that is divided into short uniramous and long biramous regions with capillary notochaetae and neurochaetal uncini (Capa *et al.* 2012; Parapar & Moreira 2015). These long-shafted neurochaetae are disposed in massive patches and have parallel teeth that, among other features, differentiate the members of this family from other annelids and render them fairly difficult to remove from the tubes (Capa *et al.* 2019; Villalobos-Guerrero 2021).

The Oweniidae family consists of 55 valid species and four genera; i.e., *Galathowenia* Kirkegaard, 1959 (12 species), *Myriochele* Malmgren, 1867 (18 species), *Myriowenia* Hartman, 1960 (two species), and *Owenia* Delle Chiaje, 1844 (19 species) (Villalobos-Guerrero 2021; Parapar

et al. 2021). Historically, *Myrioglobula* Hartman, 1967 was erected by Hartman (1967). However, a subsequent study performed by Capa *et al.* (2012) relegated it to being a junior synonym of *Myriochele*. The most important taxonomic characters of these individuals at the genus level are mostly limited to their anterior region (Parapar 2006; Capa *et al.* 2019; Parapar *et al.* 2021). Overall, the presence of a tentacular crown characterises *Owenia*, a pair of palps characterises *Myriowenia*, a truncated and elongated cephalic region characterises *Galathowenia*, and a rounded anterior margin characterises *Myriochele*. The diagnostic features used to distinguish species are not restricted to a particular region of the body, rather, they are dispersed throughout the head, trunk, and pygidium regions (Villalobos-Guerrero 2021).

In the South China Sea (SCS), among all the polychaete families recorded in the available checklist (e.g. Paxton & Chou 2000; Aungtonya *et al.* 2002; Al-Hakim & Glasby 2004; Salazar-Vallejo *et al.* 2014; Jitpukdee *et al.* 2015; Glasby *et al.* 2016; Pamungkas & Glasby 2019), Oweniidae exhibits one of the lowest levels of diversity with three genera and eight species having been documented. In the southern part of the SCS, particularly in Malaysia, the taxonomy of polychaetes remains poorly understood (e.g., Idris & Arshad 2013; Ibrahim *et al.* 2017, 2019; Rosli *et al.* 2018). The records of oweniids in this country are represented exclusively through brief macrobenthos studies (e.g. Nakao *et al.* 1989; Shafie *et al.* 2021) and they were identified solely to the family and genus levels. Hence, no taxonomic description has ever been documented for this family from Malaysian waters.

The present study identified two new species of Oweniidae found in Malaysian waters, specifically in the coastal area of Kuala Nerus, Terengganu, Malaysia, which was associated with the coastal defense structure (CDS) of various types.

MATERIAL AND METHODS

As part of an ecological study aimed at understanding the effects of the different types of CDS on the macrobenthos in Kuala Nerus, Terengganu, east coast of Peninsular Malaysia, seasonal samplings were performed during March (intermonsoon), July (southwest monsoon), October (intermonsoon), and December (northeast monsoon) of 2021; and in March of 2022 (intermonsoon). Details regarding the ecology of the macrobenthic community in relation to the CDS in Kuala Nerus are available in Ibrahim *et al.* (2023). During the sampling surveys, many specimens of oweniids were retrieved from five stations (St.) with various types of CDS: St. 1, groyne + revetment; St. 2, semi-enclosed jetty type breakwater; St. 3, parallel breakwater without tombolo; St. 4, parallel breakwater with tombolo; and St. 5, control station (Fig. 1). Sediment samples were collected from the seafloor using a Ponar grab (surface area of 0.023 m²), which was operated from the “Discovery IV” boat of Universiti Malaysia Terengganu (UMT). The biological samples (macrobenthos) from the sediments were collected via the decantation method, using a sieve with a mesh size of 0.05 mm and were then preserved in 80% ethanol.

The identification of the genera and species of Oweniidae was primarily based on Capa *et al.* (2012, 2019), de León-González & Sanchez-Hernández (2012), and Parapar & Moreira (2015). Subsequently, the specimens were compared using the original descriptions, redescription or the characterisation of morphologically similar species. A total of 100 *Galathowenia* and eight *Owenia* individuals were carefully removed from the tubes via longitudinal dissection for a thorough morphological examination. Light microscopy observations were performed by an Olympus SZX7 stereoscopic microscope and a Leica DM300 compound microscope. Photographs of diagnostic features were acquired using a Zeiss Axioskop 40 transmission light microscope with ZEN 2 lite imaging software and an Olympus SZX16 stereo microscope equipped with the Rising View software. The following measurements were performed: body length of complete specimens (BL), body width at the widest uniramous region (BW), relative length of the uniramous segment (RLUS), total crown length with respect to the length of the uniramous segment (C/UL ratio), and total crown width with respect to the maximum width of the uniramous segments (C/UW ratio).

Five complete specimens of each species were prepared for scanning electron microscopy (SEM). The samples were fixed with a 4% glutaraldehyde solution (24 h), rinsed in 0.1M Sodium Cacodylate buffer (three times for 10 min each), post-fixed in 1% Osmium tetroxide (2 h), rinsed in 0.1M sodium cacodylate buffer (three times for 10 min each), dehydrated through a graded ethanol series (35%, 50%, 60%, 70%, 80%, 90%, 95%, and 100%) (10 min each), dried using a critical point dryer (CPD) and mounted on stubs. The samples were coated with gold-palladium and viewed and photographed under a Jeol JSM-6400 Scanning Electron Microscope at the Institute of Bioscience,

Universiti Putra Malaysia (UPM) and Institute of Oceanography and Environment (INOS), Universiti Malaysia Terengganu, Malaysia.

The descriptions of the species were based upon the morphology of the holotype, unless otherwise stated. Variations in the remaining type and non-type materials are indicated in a separate section. Finally, all holotypes were deposited in the annelids collection of the South China Sea Repository and Reference Centre, Universiti Malaysia Terengganu (UMTAnn), while paratypes were deposited at the Lee Kong Chian Natural History Museum, National University of Singapore (NUS) (ZRC.Ann) and Natural History Museum of Los Angeles County (LACM-AHF). All non-type materials were deposited at the RRC (UMTAnn).

ABBREVIATIONS

Institutions

INOS	Institute of Oceanography and Environment;
LKCNHM	Lee Kong Chian Natural History Museum;
NHMLAC	Natural History Museum of Los Angeles County;
NUS	National University of Singapore;
RRC	Repository and Reference Center, Kuala Nerus, Terengganu;
UMT	Universiti Malaysia Terengganu;
UPM	Universiti Putra Malaysia.

General

CDS	Coastal defense structure;
CPD	critical point dryer;
GBIF	Global Biodiversity Information Facility;
ICZN	International Code of Zoological Nomenclature;
SCS	South China Sea;
SEM	scanning electron microscope;
St.	station.

Morphology

BL	Body length;
BW	body width;
C/UL	ratio, total length with respect to the length of the uniramous segment;
C/UW	ratio, total crown with respect to the maximum width of the uniramous segment;
RLUS	relative length of uniramous segment.

RESULTS

REMARK

A total of 619 individuals of Oweniidae belonging to two genera and two new species, *Owenia unipinnata* n. sp. (n = 100) and *Galathowenia minuta* n. sp. (n = 519), were collected from the study sites in samplings from only three different months (July, October and December 2021), with an absence of species observed in March 2021 and 2022. The highest occurrence was recorded in July for both species: *Galathowenia minuta* n. sp. (n = 466 individuals) and *O. unipinnata* n. sp. (n = 75 individuals), followed by October, *G. minuta* n. sp. (n = 50 individuals) and *O. unipinnata* n. sp. (n = 23 individuals), and December 2021 with three and two individuals, respectively, at breakwater areas of Kuala Nerus, Terengganu.

SYSTEMATICS

Family OWENIIDAE Rioja, 1917

Ammocharidae Malmgren, 1867: 185. — Kinberg 1867: 343; 1910: 70.

Oweniidae Rioja, 1917: 40. — Fauchald 1977: 114. — Nilsen & Holthe 1985: 18. — Capa *et al.* 2012: 240; 2019: 106.

DIAGNOSIS (adapted from Capa *et al.* 2012). — Cylindrical body. Prostomium and peristomium fused forming head. Nuchal organs absent. Mouth terminal or shifted ventrally. Anterior region with one to three uniramous segments, followed by biramous segments. Notopodial chaetae emerging from body wall, capillaries resembling small imbricate scales, smooth acicular chaetae. Tori with irregular rows of bidentate uncini. Parapodial branchiae or cirri absent. Thin-secreted layer tube encrusted with foreign objects. Distinct mitraria larvae. Presence of inter-epidermal nerve cord.

TYPE GENUS. — *Owenia* Delle Chiaje, 1844.

REMARKS

Delle Chiaje (1844) described the first oweniid genus and species, *Owenia fusiformis* Delle Chiaje, 1844. *Owenia* was proposed in honor of the illustrious British zoologist and paleontologist Richard Owen; whereas the specific epithet refers to the tapered (“fusiform”) shape of the worm tube. It seems that the name *Owenia* was popular during the 19th century because four other homonymous genera were later proposed in molluscs (*Owenia* Prosch, 1847), ctenophores (*Owenia* Kölliker, 1853), birds (*Owenia* Gray, 1855) and mammals (*Owenia* De Vis, 1888) (see Rioja 1917), although Delle Chiaje’s name prevails currently, according to the Principle of Priority (ICZN 1999, art. 23.4).

In 1846, Grube (1846) established the genus *Ammochares* Grube, 1846 comprising a single species, *A. ottonis* Grube, 1846. Subsequently, Malmgren (1867) created the new family Ammocharidae, designating *Ammochares* as the generic type name. *Myriochele* Malmgren, 1867 was later inducted into the family. Kinberg (1867) subsequently acknowledged Ammocharidae without referencing Malmgren. Claparède (1868) suggested *A. ottonis* and *O. fusiformis*, both described from the Mediterranean Sea, as the same species, hence rendering *Ammochares* synonymous with *Owenia*. Rioja (1917) proposed Oweniidae as a replacement name, but this was unnecessary as the family name is unaffected by the synonymy of its type genus (ICZN 1999, art. 40.1). Although Ammocharidae could have remained valid, Oweniidae is considered *nomen protectum* due to its prevailing use, consistent usage (ICZN 1999: Art. 40.2) and original authorship (ICZN 1999: Art. 40.2.1). Ammocharidae, which was likely last recognised as being valid approximately 90 years ago (Berkeley 1931), is thus categorised as *nomen oblitum* to ensure nomenclatural stability (ICZN 1999: Art. 40.2).

Updated accounts of the anatomy, biology, ecology, morphology, reproduction, phylogeny and taxonomy of this family have recently been reported (Capa *et al.* 2019; Villalobos-Guerrero 2021; Parapar *et al.* 2021).

Genus *Galathowenia* Kirkegaard, 1959

Galathowenia Kirkegaard, 1959: 67.

DIAGNOSIS (adapted from Capa *et al.* 2012). — Cylindrical head, anteriorly truncated, terminal mouth extending mid-ventrally as an elongated slit and presence of ventral pharyngeal organ. Breakage groove between first and second chaetiger. Y-shaped oesophageal commissure. First three segments uniramous, with capillaries on notopodia. Following segments biramous, notopodia with capillary chaetae only and neuropodial uncini with two obliquely arranged teeth.

TYPE SPECIES. — *Galathowenia africana* Kirkegaard, 1959, by original designation.

REMARKS

Galathowenia was established by Kirkegaard (1959) for *G. africana*, the holotype was collected during the “GALATHEA” expedition on the west coast of Africa. In addition to being differentiated based on the shape of the prostomium (anteriorly truncated) with a ventral cleft, *G. africana* species was characterised by having an “achaetous peristomium fused with the prostomium, the presence of two eye-spots and three thoracic segments without neuropodial hooks”. The validity of *Galathowenia* was later agreed upon by several taxonomists because of the shape of the prostomium (Fauchald 1977; Kirkegaard 1983, 1996; Blake 1984, 2000; Imaijima & Morita 1987; Parapar 2003b).

Currently, *Galathowenia* is featured by having a terminal mouth extending mid-ventrally as an elongated slit, the presence of a breakage groove between the first and the second segments, notopodia with only capillary chaetae on both uniramous and biramous segments, and uncini with a teeth of similar size and generally arranged obliquely (Capa *et al.* 2012). Among all genera, *Galathowenia* is more similar to *Myriochele* because of the lack of distal appendages. However, they can also be distinguished by: 1) the truncated and elongated head of *Galathowenia*; in contrast to the rounded head of *Myriochele*; 2) the absence of acicular notochaetae in *Galathowenia*, which are present in *Myriochele*; and 3) the presence of a breakage groove between segments 1 and 2 in *Galathowenia*, which is absent in *Myriochele*.

The species discrimination in *Galathowenia* is based on: 1) the presence/absence of eyes on head structures; 2) the number, relative length, and distribution of the anterior uniramous thoracic chaetigers; 3) the relative length of the first biramous abdominal segment; 4) the position of the longest chaetiger; 5) the shape and dentition of the uncini; and 6) through the posterior end which bears a different number and structure of lobes.

Galathowenia minuta n. sp.

(Fig. 2)

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TYPE MATERIAL. — **Holotype.** South China Sea, Malaysia, Terengganu • Kampung Kubang Badak, Kuala Nerus; 5°24'12.6"N, 103°06'15.5"E; 2–8 m depth; 24.7.2021; Ibrahim leg.; decantation; UMTAnn 2184.

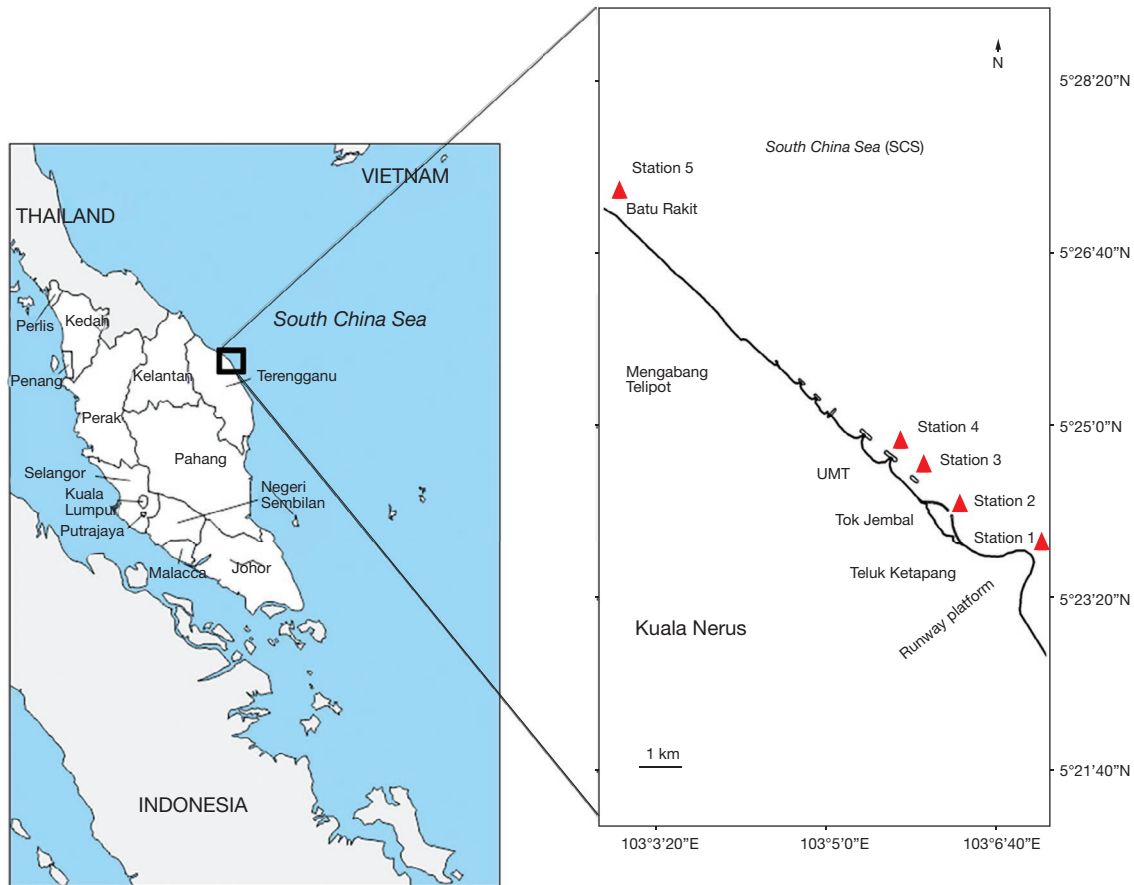


FIG. 1. — Sampling positions along the coastal defence structure areas of Kuala Nerus, Terengganu: **station 1**, groyne (1.1: 5°23'25.7"N, 103°06'59.9"E; 1.2: 5°23'47.5"N, 103°07'04.3"E; 1.3: 5°23'58.0"N, 103°06'26.6"E); **station 2**, semi-enclosed jetty type breakwater (Inside lagoon: 5°24'08.2"N, 103°06'06.6"E; Outside lagoon: 5°24'12.6"N, 103°06'15.5"E); **station 3**, parallel breakwater without tombolo (3.1: 5°24'21.6"N, 103°05'56.7"E; 3.2: 5°24'32.4"N, 103°05'54.2"E; 3.3: 5°24'32.0"N, 103°05'45.7"E); **station 4**, Parallel breakwater with tombolo (4.1: 5°24'38.2"N, 103°05'39.4"E; 4.2: 5°24'45.9"N, 103°05'40.3"E; 4.3: 5°24'42.9"N, 103°05'33.4"E); **station 5**, Batu Rakit (5°27'09.0"N, 103°02'58.4"E).

Paratypes. South China Sea, Malaysia, Terengganu • 5 specimens; Kampung Kubang Badak, Kuala Nerus; 5°23'25.7"N, 103°06'59.9"E; 24.VII.2021; Ibrahim leg.; decantation; UMTAnn 2185, LACM-AHF 13506-13507, ZRC.ANN 1616-1617.

ADDITIONAL NON-TYPE MATERIALS. — **South China Sea, Malaysia, Terengganu** • 44 specimens; Kuala Nerus; St. 1; 5°23'25.7"N, 103°06'59.9"E; 24.VII.2021; RRC • 5 specimens; Kuala Nerus; St. 2; 5°24'12.6"N, 103°06'15.5"E; 24.VII.2021; RRC • 20 specimens; Kuala Nerus; St. 3; 5°24'21.6"N, 103°05'56.7"E; 24.VII.2021; RRC • 20 specimens; Kuala Nerus; St. 4; 5°24'42.9"N, 103°05'33.4"E; 24.VII.2021; RRC • 11 specimens; Kuala Nerus; St. 5; 5°27'09.0"N, 103°02'58.4"E; 24.VII.2021; UMTAnn 2328-2427.

ETYMOLOGY. — The specific epithet was selected after the Latin adjective *minuta* (-us, -um) meaning tiny, in reference to the body size of the species. The name is proposed in the feminine, to match the gender of the genus (ICZN 1999: Art. 31.2).

TYPE LOCALITY. — Kuala Nerus, Terengganu, Malaysia.

DISTRIBUTION. — Known only from the type locality.

DESCRIPTION (based on holotype)

Short, slender, thread-like body, cylindrical in cross-section, BL: 10 mm, BW: 0.02 mm, 18 segments. Brownish colour in alcohol, slightly transparent, with some brownish pig-

mented spots encircling segment 4 immediately after tori (Fig. 2A). Elongated head, truncated prostomium, terminal mouth extending mid-ventrally as an elongated slit (Fig. 2A). Two ventrolateral brownish eyespots. First three anterior segments uniramous, each with notochaeta only. First and second segments twice as long as third segment (RLUS 2:2:1). White oesophageal commissures, ventral longitudinal band, Y-shaped in anterior segment, extending to segment 5. Anterior biramous segments starting from 4th segment throughout, three times longer than wide, segment 7th being longest; following ones becoming posteriorly slightly tapered and shorter, far posterior ones much compressed (Fig. 2B). Capillary notochaetae on both uniramous and biramous segments decreasing in size ventrally, basally slightly striated, median and distal regions with spinules; typically, more abundant in uniramous segments (3-9 capillary chaetae) than in biramous ones (3-4 capillary chaetae), the latter with far longer capillary chaetae posteriorly (Fig. 2E) but single in last three segments. Ventrolateral neurochaetae from segment 4, transverse rows of hooked uncini in long, broad tori (Fig. 2F, G). Tori along anterior to middle segments longer than wide, with dense oblique rows of uncini (Fig. 2G); in posterior segments (segment 14 and above)

much shorter and smaller, with fewer uncini (less than 20), lying in rows forming oval fields. Bidentate, long-shafted, numerous uncini (around 100) in mid-body (6th to 7th) segments, fewer toward posterior end. Long teeth of uncini, nearly equal in size, arranged obliquely because one offset higher (Fig. 2F, G). Pygidium with terminal anus and two blunt lobes (Fig. 2B, D). Tube slightly longer than animal, slender, cylindrical in cross-section, composed of thin secreted layer, ornamented with sand grains and fragments of shells (Fig. 2C, D).

VARIATION

Number of total segments: 17-18. Total body length: 5-15 mm. Maximum body width: 0.02 ± 0.002 mm. Most specimens incomplete, laborious to extract from their tubes, especially at the middle and posterior parts, those variations could be greater than reported above. Most specimens lack pigmentation pattern, some have patchy brownish spots on mid-dorsal surface of head and pigmented band entirely encircling distal end of segment 4 (immediately after tori). No prominent constriction or division exists between head and first segment in most of the specimens. The first and second segments have transverse grooves or constrictions. Longest segment, 7, infrequently segments 6-9.

ECOLOGICAL NOTES

Galathowenia minuta n. sp. lives in shallow coastal areas with a depth of 2-8 m, inhabiting very fine sands of up to 86.70%, with a percentage of total organic matter of 1.6-6.3%.

REMARKS

Galathowenia minuta n. sp. can be distinguished from *G. annae* Capa, Parapar & Hutchings, 2012 based on several features. In *G. minuta* n. sp. the RLUS is 2: 2: 1, whereas in *G. annae* it is 1: 2: 1. In *G. minuta* n. sp. the brown pigmented band presents encircled segment 4, whereas in *G. annae*, the brownish red pigmented areas is present at the head with some pigmented bands in the four anterior segments. The longest segment in *G. minuta* is the 7th segment, whereas, in *G. annae*, it is the 6th. *Galathowenia minuta* n. sp. has two blunt pygidial lobes, whereas *G. annae* has three prominent digitiform lobes (the dorsal one is slightly smaller than the two lateral ones) (Capa *et al.* 2012). *Galathowenia minuta* n. sp. is smaller (5-15 mm BL; 0.018-0.022 mm BW) than *G. annae* (5-11 mm BL; 0.05-0.1 mm BW).

In terms of similarity, *G. minuta* n. sp. has a similar RLUS to that of *G. australis* (Grube, 1866) and *G. oculata* (Zachs, 1923), 2:2:1. However, they differ by the absence of eyespots and the presence of long and short capillary chaetae in *G. australis* and a higher number of segments (>23) as well as a pigmented dorsal head in *G. oculata* (Parapar, 2003). In addition, segments 5-9 are the longest in *G. minuta* n. sp., with the segment 7 being the longest most frequently, whereas, in *G. australis* and *G. oculata*, the segments 4-6 and the segment 5 are the longest, respectively. More detailed information regarding the similarities and differences among *Galathowenia* species worldwide is presented in Appendix 1.

The nearest record to Malaysia of *Galathowenia* species stems from Indonesia with *Owenia lobopygidiata* Uschakov, 1950 (currently accepted as *G. lobopygidiata* (Uschakov, 1950) and *G. eurystoma* (Caullery, 1944), with the latter then being assigned as *Myriochele eurystoma* (Caullery, 1944) (Kirkegaard 1956; Parapar *et al.* 2021; GBIF 2022). *Galathowenia lobopygidiata* was recorded in the Banda trench, Indonesia and seems doubtful as incomplete specimens (without the anterior part, and only the posterior part being present) were described (Parapar & Moreira 2015). The transfer of the genus *Owenia* into *Galathowenia* for *lobopygidiata* species occurred as Koh *et al.* (2003) reported an identical anterior end structure for *Galathowenia* (without a branchial crown) compared with *O. lobopygidiata* samples from the Zoological Institute, Russian Academy of Science. Regarding the Malaysian specimens, they do not represent *G. lobopygidiata* as the one recorded in Indonesia, as this species from the Okhotsk Sea locality has nine short, finger-shaped papillae in one row around the anus (Uschakov 1950).

In terms of habitat location, *G. minuta* n. sp. shares the same coastal habitat with *G. oculata* (12-2500 m in depth), *G. quelis* Capa, Parapar & Hutchings, 2012 (1-60 m in depth), and *G. annae* (13-18 m in depth) (Parapar 2003a; Capa *et al.* 2012). However, the species has been classified as new based on several distinct morphological characters, especially the RLUS, pigmentation, and anal lobes. *Galathowenia minuta* n. sp. has RLUS of 2:2:1, whereas *G. annae*, *G. oculata* and *G. quelis* have RLUS of 1:2:1, 1:1:1 and 1:2:1, respectively. In addition, *G. minuta* n. sp. has pigments encircling segment 4, whereas *G. annae* bears pigments at the anterior four segments. *Galathowenia oculata* in general has pigments on the dorsal head, whereas *G. quelis* does not have any pigmentation. *Galathowenia minuta* n. sp. is completed with two blunt anal lobes, similar to *G. quelis*. However, *G. annae* and *G. oculata* have three prominent digitiform lobes, with one located dorsally and another two located laterally (Capa *et al.* 2012) (Appendix 1).

Genus *Owenia* Delle Chiaje, 1844

Owenia Delle Chiaje, 1844: 48. — Nilsen & Holthe 1985: 18. — Blake 2000: 117.

DIAGNOSIS (adapted from Capa *et al.* 2012). — Head with prostomial tentacular crown. Mouth elongated anteriorly. First three segments uniramous with capillaries only. Following segments biramous with capillaries on notopodia and more than 20 irregular rows of bidentate uncini. Teeth arranged side by side on neuropodial tori. Pygidium formed by terminal rim or with a pair of weakly developed lobes. Tube tapered toward both ends, covered by foreign objects imbricated like roof tiles.

TYPE SPECIES. — *Owenia fusiformis* Delle Chiaje, 1844, by original designation.



FIG. 2. — *Galathowenia minuta* n. sp. holotype, UMTAnn 2184: **A**, anterior end, dorsal view; **B**, posterior end, lateral view; **C**, grain sand cemented tube; midbody part; **D**, grain sand cemented tube; posterior end; **E**, posterior chaetigers with long capillary chaeta; lateral view; **F**, transverse rows of hooked uncini; mid body; **G**, hooked uncini in oblique position mid body. Abbreviation: **S**, segment. Scale bars: A, B, 200 μ m; C, D, E, 100 μ m; F, G, 10 μ m.

Owenia unipinnata n. sp.
(Fig. 3A–J)

[urn:lsid:zoobank.org:act:5117124A-E8A6-48DB-9164-82382A27F42D](https://doi.org/10.21203/rs.3.rs-21244-E8A6-48DB-9164-82382A27F42D)

TYPE MATERIAL. — **Holotype.** South China Sea, Malaysia, Terengganu • Female; Kampung Kubang Badak, Kuala Nerus; 5°24'21.6"N, 103°05'56.7"E; 2–8 m depth, 24.VII.2021; Ibrahim leg.; decantation; UMTAnn 2186.

Paratypes. South China Sea, Malaysia, Terengganu • 5 specimens, Kampung Kubang Badak, Kuala Nerus; 5°23'25.7"N, 103°06'59.9"E; 24.VII.2021; Ibrahim leg.; decantation; UMTAnn 2187, LACM-AHF 13508–13509; ZRC.ANN 1618–1619.

ADDITIONAL NON-TYPE MATERIALS. — South China Sea, Malaysia, Terengganu • 5 specimens, Kuala Nerus, St. 1: 5°23'25.7"N, 103°06'59.9"E, 24.VII.2021; RRC • 3 specimens; Kuala Nerus; St. 3; 5°24'21.6"N, 103°05'56.7"E; 24.VII.2021; UMTAnn 2428–2435.

TYPE LOCALITY. — Kuala Nerus, Terengganu, Malaysia.

DISTRIBUTION. — Known only from the type locality.

ETYMOLOGY. — The specific epithet is formed by the Latin words *uni-*, a prefix meaning single or one, and *pinnata* (-us, -um), which denotes the presence of branches or tentacles. The name of the species refers to the single and isolated tentacle present basally in the ventral-most area of the tentacular crown. The name is proposed in the feminine, to match the genus gender (ICZN 1999, Art. 31.2).

DESCRIPTION (BASED ON HOLOTYPE)

Complete specimen, elongated body, cylindrical in cross-section, BL: 10 mm long, BW: 0.065 mm, 15 segments. Creamy-white colour in alcohol, with no pigmentation. Body divided into three sections: tentacular crown, thorax and abdomen. Short, anteriorly cylindrical, posteriorly tapering and dorsoventrally flattened with two lobes (Fig. 3A, D). Fragile mid and posterior body, tightly attached to tube by hooks. Short tentacular crown (C/UL ratio *c.* 0.5), narrow (C/UW ratio *c.* 0.75), with three pairs of tentacles, slightly longer dorsal-most pair; each tentacle with short, subdistal ramification that slightly lengthens toward dorsal tentacles (Fig. 3B, C), except mid-ventral paired tentacle proximally with isolated and digitiform ramification (Fig. 3B); second dichotomy located very close to distal end, with two or three smooth lobe-like tips, with oral grooves present at the third pair of tentacles (dorsal side). Dorsally and ventrally split tentacular crown. Distinct separation between left and right paired tentacles, marked V-shaped slit at mid-ventral side (Fig. 3B, C). Two brown long elliptical eyespots present lateroventrally at base of crown (Fig. 3B, C). Junction between thorax and tentacle crown marked by short, barely membranous, straight collar, closely aligned with body wall, without covering eyespots. First and third segments half as long as third segment (RLUS): 1–2–1. Uniramous segments with three pairs of poorly developed notopodia with capillary chaetae. First and second segments present in a larger number of chaetae and shorter, at ventrolateral position; third and subsequent segments with fewer and longer chaetae located at dorsolateral side, closer to the first biramous notopodia (tori and capillary chaeta). Notochaetae with shafts composed of densely packed scales (Fig. 3E). Uniramous

neuropodia absent. Presence of constriction on 5th segment. Width of biramous segment decreasing posteriorly, posterior segments short, compact, flattened and tapering off. Poorly developed notopodia in biramous parapodia with capillary chaeta similar to uniramous notochaetae, displaced more dorsally. Gold-coloured notochaetae bundle present from 8th segment toward posterior end (Fig. 3D). Neuropodial tori from the 4th segment, continue toward posterior end; tori wide, with several rows of neurochaetal hooks. Long, narrow and nearly rectangular tori, almost encircling the body, separated only by the notochaetal bundles on dorsal surface (Fig. 3G). First two biramous segments longer than total uniramous segment length. Longest segment 6th. Similar neurochaetal uncini throughout, consisting of hooks with shaft ending in two teeth, with left teeth bending toward the right teeth, concave side of teeth bearing approximately 45° angles with three bends per tip (Fig. 3F). Longitudinal lines present at mid ventral (two lines) position, from uniramous region to posterior part. Pygidium flattened with two lobes. Methylene blue stain concentrated at lateral side of collar and less concentrated at lateral side of uniramous region and longitudinal line (Fig. 3C). Absence of staining at mid-dorsal and ventral collar and thorax (Fig. 3C). Tube short, and tapered posteriorly; made of overlapping exogenous materials of quartz grains and shell fragments (outer layer), cemented together and arranged like roof tiles (Fig. 3H). Inner sheath consisting of a translucent successive layers, attached tightly to the neurochaetal hooks.

VARIATION

Number of total segments: 5–13. Total body length: 3–10 mm. Maximum body width: 0.03–0.065 mm. Some paratypes without simple solitary ramification at mid-ventral paired tentacles. Tips of tentacles completed with two to three small, smooth lobes. Some paratypes with three simple ramifications at the most dorsal paired tentacles. Crown length to thorax ratio either 0.3 or 0.5. Most paratypes without pigments. One of them with less concentrated brown pigmentation at tentacles (with the exception of the base and tip of the crown) and collar (just a band around the dorsal collar). One paratype heavily pigmented at the base of tentacles (with the exception of the tips of the crown), less concentrated at the collar and half-uniramous region. Varying relative length of uniramous segment (RLUS), mostly 1–2–1. Longest segment either 5th or 6th. Posterior segments of a few complete paratypes simply rounded and slightly pointed.

ECOLOGICAL NOTES

Owenia unipinnata n. sp. lives in shallow coastal areas of 2–8 m in depth, inhabiting moderately (up to 60.47%) to very fine sandy (up to 86.70%) bottoms with a percentage of total organic matter in the range of 1.6–6.3%.

BIOLOGICAL NOTES

Ovigerous females of *Owenia unipinnata* n. sp. (BW: 0.05–0.065 mm; oocyte diameter: 100–120 µm) were found in July 2021, during the southwest monsoon season.

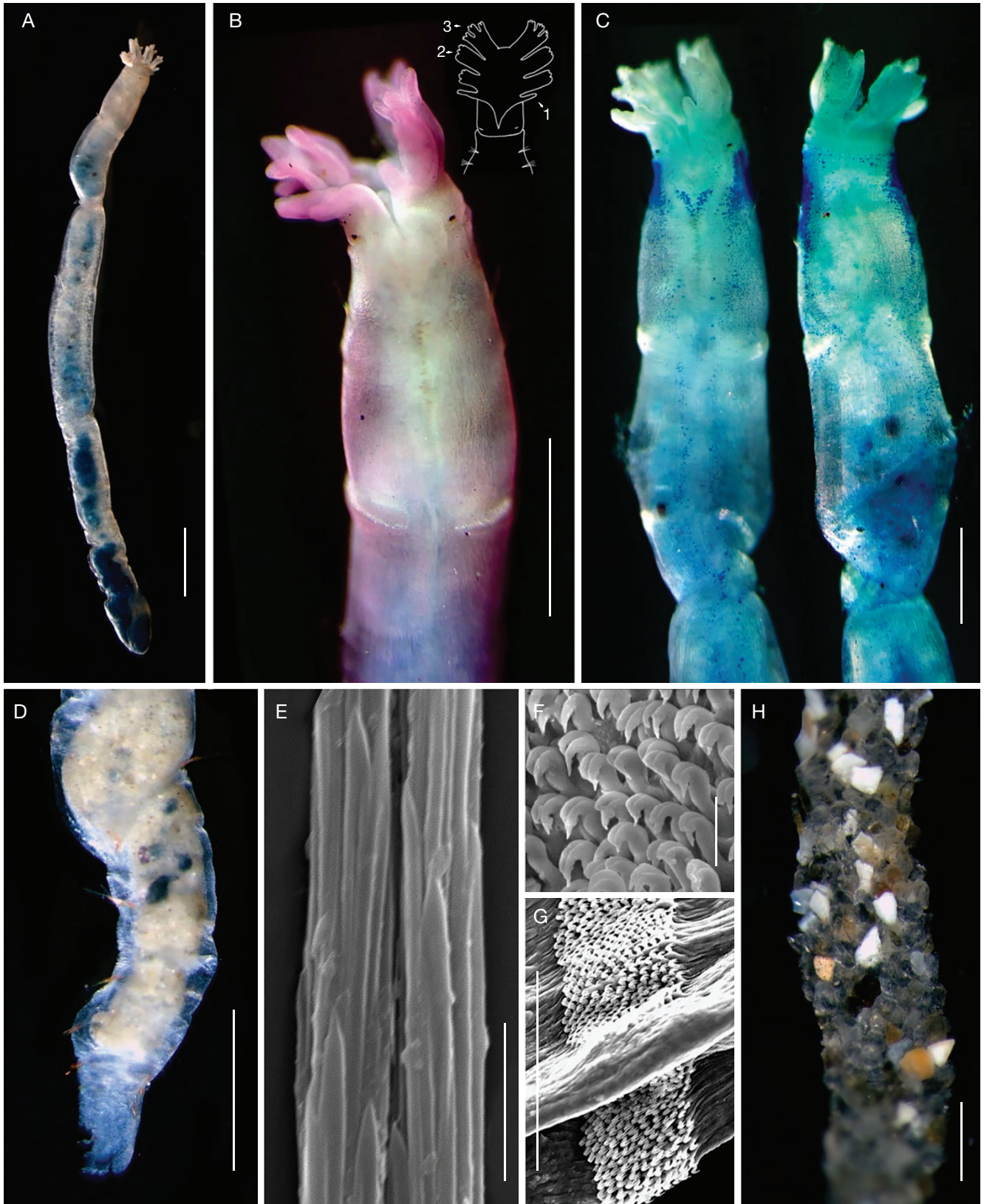


FIG. 3. — *Owenia unipinnata* n. sp. holotype, UMTAnn 2186: **A**, complete full body of individual, with posterior part slightly bend towards the body; **B**, anterior end, ventral view, stained using rose bengal (microscopic image) with schematic diagram (completed with **numbered arrows**) of tentacular crown showing simple solitary ramification; **C**, anterior end, ventral (left) and dorsal (right) views, stained using methylene blue; **D**, flattened posterior end with broken lobes and gold coloured notochaeta; **E**, capillary chaeta with densely packed scales; **F**, hooked uncini with left teeth bend towards the right teeth; **G**, tori almost encircles the body; **H**, overlapping quartz grains and shell fragments of tube. Number **1**, **2**, **3**, indicate the number of ramifications. Scale bars: A, 1 mm; B, C, D, G, H, 100 μ m; E, F, 5 μ m.

KEY TO THE GENERA AND SPECIES OF OWENIIDAE RIOJA, 1917
FROM THE SOUTH CHINA SEA (SCS)

1. Head with a crown of tentacles..... *Owenia* Delle Chiaje, 1844..... 3
- Head without of a crown of tentacles 2
2. Truncated head; groove present between first and second segments; mouth with mid-ventral slit forming large lateral lips *Galathowenia* Kirkegaard, 1959 5
- Rounded head; groove absent between first and second segments; button-hole-shaped mouth with low lips around *Myriochele* Malmgren, 1867 6
3. Tentacular crown with four pairs of long dichotomies and multi-branched tentacles; crown three-quarters as long, or as long as uniramous segment 4
- Tentacular crown with three pairs of short dichotomies and poorly-branched tentacles; crown half as long as uniramous segment *O. unipinnata* n. sp.
4. Cephalic region with prominent membranous collar; pygidium with 10 or more lobes surrounding anus; no lateroventral eyespots *O. collaris* (Hartman, 1955)
- Cephalic region with barely conspicuous collar; pygidium with two lobes; presence of lateroventral eyespots ...
..... *O. fusiformis* (Delle Chiaje, 1844)
5. No lateroventral eyespots; pygidium with eight or more finger-like lobes surrounding anus; dwelling in deep waters *G. lobopygidiata* (Uschakov, 1950)
- Presence of lateroventral eyespots; pygidium with only two blunt lobes; dwelling in shallow water
..... *G. minuta* n. sp.
6. Tubes with accumulations of sponge spicules, foraminiferans or shell fragments exclusively; long size (15-20 mm, 25 segments); calibrated and aligned spicules, dwelling in deep water *M. minor* Caullery, 1944
- Tubes with accumulations of sand grains exclusively; short size (3-4 mm, 16 segments); dwelling in estuarine waters *M. picta* Southern, 1921

REMARKS

Owenia unipinnata n. sp. is the smallest and thinnest species recorded to date (TL: 3-10 mm; BW= 0.030-0.065 mm). Among all valid *Owenia* species, the most similar to *O. unipinnata* n. sp. are *O. bassensis* Ford & Hutchings, 2005 (from Australia) and *O. vieitezi* Díaz-Díaz, Parapar & Moreira, 2020 (from north-western coast of the Gulf of Venezuela) based on the presence of three pairs of tentacles. However, *O. unipinnata* n. sp. differs from *O. bassensis* mainly because of the presence of one major ramification, the absence of a peristomial collar, the presence of methyl green speckles concentrated on the thorax, and larger body size (length and width) in the Australian species (Parapar & Moreira 2015).

Owenia unipinnata n. sp. closely resembles the Venezuelan *O. vieitezi* species in having three pairs of tentacles and three major ramifications. Nevertheless, each tentacle with the three ramifications is located firstly very close to the crown base, secondly at mid-length, and thirdly very close to the distal end (Díaz-Díaz *et al.* 2018), which is totally different from that observed for *O. unipinnata* n. sp. The *O. unipinnata* n. sp. straightforwardly has three minor and simple ramifications, with the first solitary one situated at the mid-ventral paired tentacle, and another two ramifications located at the dorsal most paired tentacles. In addition, the brown colouration is present in the dorsal and lateral tentacles of the branchial crown of *O. vieitezi*, and is absent in the *O. unipinnata* n. sp. Appendix 2 provides more information on the similarities and differences among *Owenia* species worldwide.

REMARKS

All oweniid species recorded from the South China Sea are included, with the exception of *Galathowenia eurystoma* (Caullery, 1944) which remains taxonomically unresolved. The species originally described in the shallow to deep waters of Indonesia (32-1570 m) was proposed to be *Myriochele* (Caullery 1944). However, Capa *et al.* (2012) stated that it belongs to *Galathowenia* based on the diagnostic features that characterise this genus. The species was too briefly described using incomplete specimens, hampering its comparison with other species. In addition, considering the broad depth of the distribution range, with specimens presenting pigmentation differences (Caullery 1944), it is likely that more than one species is involved here.

Owenia fusiformis (Delle Chiaje, 1844) was scarcely described in samples from the Mediterranean Sea but the type material was never deposited. The species has been recorded at all sea depths and latitudes explored to date (Ford & Hutchings 2005). Nevertheless, detailed morphological analyses of worldwide populations have demonstrated differences that confined its distribution to the original region and the recognition of new species (Koh *et al.* 2003). Hence, it is likely that *O. fusiformis* recorded in the SCS represents undescribed species.

Owenia collaris (Hartman, 1955) from Southern California, USA, was redescribed by Blake (2000) using type material and its distribution was delimited to that area. Other worldwide records of the species particularly those from the SCS need to be reassessed.

Galathowenia lobopygidiata (Uschakov, 1950) was initially described as *Owenia* based on specimens collected from the deep waters of the Okhotsk Sea, Russia. However, it was later reclassified under the genus *Galathowenia* because of the remarkable similarity in the head structure within the genus (Koh *et al.* 2003). *Galathowenia lobopygidiata* was also reported from Banda Trench, Indonesia. The presence of *G. lobopygidiata* in the Banda Trench region is possible because the maximum depth of the trench (7440 m) is in the hadopelagic zone, while the Okhotsk Sea of 3372 m is in the abyssopelagic zone. Both regions have similar extreme conditions of high pressure, low temperature and complete darkness. The range of salinity which contributes greatly to the growth and survival rate of polychaetes, may also explain the presence of this species, as the salinity range of the Banda trench and Okhotsk Sea does not differ much (Banda Trench: 34.60 to 34.65‰, Okhotsk Sea: 32.5‰ and lower) (Radchenko *et al.* 2010; Suyadi *et al.* 2018).

DISCUSSION

In the last half-century, the systematic study of Oweniidae has covered several regions across the world, including Antarctica, Arctic and North Atlantic waters, Western Mediterranean, California, Gulf of Mexico, Caribbean Sea, Yellow Sea, Japan, and Australia (Parapar *et al.* 2021).

In particular, *Galathowenia* has been documented mostly in the temperate waters of both hemispheres, such as in West Africa, Antarctica, Russia, and the Okhotsk and Norwegian Seas. However, this genus has also been recorded in tropical regions, as *G. kirkegaardii* de León-González & Sanchez-Hernández, 2012, which was originally described from the Southern Gulf of Mexico. *Owenia*, which is the most studied owenid genus, has been documented in various countries and regions such as Norway, Greenland, Iceland, Denmark, Sweden, Brazil, Japan, Korea, the Persian Gulf, Madagascar, New Zealand, and Venezuela. Both genera have been well studied and recorded in the Pacific Ocean of the United States and Australia.

The most frequently recorded *Galathowenia* species are *G. fragilis* (Nilsen & Holthe 1985) and *G. oculata* (Zachs 1923), particularly in North America and Europe (Parapar 2003b; Villalobos-Guerrero 2021). In contrast, the most often described *Owenia* species is *O. fusiformis*, which acts as the pioneer of the genus, including in Australia, Southern Asia, and the Indo-Malay Archipelago, during the 19th and 20th centuries (Parapar & Moreira 2015). *Owenia assimilis* has also been widely reported especially from the Nordic countries of Norway, Iceland, Finland, Denmark, and Sweden (Koh & Bhaud 2001; Koh *et al.* 2003; Ford & Hutchings 2005).

In the South China Sea (SCS), only three genera (i.e., *Galathowenia* Kirkegaard, 1959; *Myriochele* Malmgren, 1867; and *Owenia* Delle Chiaje, 1844,) and 10 species of oweniids have been documented: *Galathowenia lobopygidiata* (Uschakov, 1950) and *O. collaris* Hartman, 1955 from Indonesia; *M. eurystoma* Caullery, 1944 and *M. minor* Caullery, 1944

from Indonesia and the Philippines; *M. picta* Southern, 1921 from Indonesia and Vietnam; *O. fusiformis* Delle Chiaje, 1844 from Indonesia, the Philippines, Singapore, Thailand and Vietnam; *G. minuta* n. sp. and *O. unipinnata* n. sp. from Malaysia; as well as species originally described in the SCS: *Owenia assimilator* Caullery, 1944, *M. minor* Caullery, 1944, and *M. picta* Southern, 1921 from Indonesia; and *O. orientalis* (Grube, 1878) from the Philippines (Pamungkas & Glasby 2019; Salazar-Vallejo *et al.* 2014). *Myrioglobula* which is recognised as a junior synonym of *Myriochele*, has never been reported in the water region. The oweniid species from Indonesia were retrieved during the Siboga Expedition in 1899-1900, the most successful marine expedition in Indonesia (Pamungkas & Glasby 2019).

However, after evaluating these records and the additions from Malaysian waters, some taxa are newly incorporated or excluded. The descriptions of *Galathowenia minuta* n. sp. and *O. unipinnata* n. sp. represent new species in the SCS, with *Galathowenia* being recorded for the first time in this ecoregion. Conversely, two *Owenia* species, i.e., *O. assimilator* and *O. orientalis*, are excluded from the list as *O. assimilator* has been misidentified. In the case of *O. orientalis*, the changes were made according to Ford & Hutchings (2005), who stated that the type material is not available and the brief and poorly illustrated description renders this species impossible to compare with any other currently accepted species or in brief, becoming a *nomen nudum*. In summary, the *Owenia* records in the SCS are mostly a contribution from Indonesia (six valid species), followed by the Philippines (three valid species), and Vietnam (two species) (Gallardo 1968; Ford & Hutchings 2005; Pamungkas & Glasby 2019). Thailand and Singapore recorded a single species of *O. fusiformis*, which has also been found in Indonesia and the Philippines (Glasby *et al.* 2016).

According to the global comparative synoptic table of the characters of *Galathowenia* and *Owenia* species description, the information retrieved from the literature is considered neither uniform nor standardised. Some crucial or inconsequential features of the species description are missing, as they are not even mentioned or discussed in detail. This could lead to misinterpretation by taxonomists who may require specific information from the sources for their research. It is suggested that the style of the species description in future studies be standardised and contain complete information pertaining to characters. This will assist in gathering information and thus, in making appropriate comparisons for subsequent morphological research.

Among all of the *Galathowenia* and *Owenia* species recorded worldwide, *G. minuta* n. sp. and *O. unipinnata* n. sp. from Terengganu, Malaysia are currently considered as the smallest and thinnest oweniids species worldwide with a maximum BW of 0.02 ± 0.002 mm and 0.030-0.065 mm, respectively. Moreover, removing specimens from their tubes is a challenging process. In the case of *G. minuta* n. sp., dissection often causes damage particularly to the delicate middle and posterior parts, tightly in contact with the tube. Extracting individuals from elongated tubes is more challenging with only a few specimens successfully removed without dam-

age. In the case of *O. unipinnata* n. sp., removing the grains from the tube is straightforward, but the risky part involves extracting the second layer of the thin, transparent tube at the posterior region, tightly attached to the body segments. Successful extraction requires treating the specimens with ethanol, placing them on a glass slide and covering them with a cover slip. Rapid examination of external morphology under a compound microscope is crucial to prevent specimen breakage after re-submersion in ethanol. Using glycerin for temporary fixation necessitates proper sealing of the cover slip with lacquer to avoid drying issues.

Within the one-year sampling duration, Oweniidae that dominated during July 2021 (southwest monsoon) showed a decreasing pattern of occurrence toward December 2021 (northeast monsoon season) and were totally absent during another two sampling occasions (March 2021 and March 2022). The highest occurrence of the oweniids during the southwest monsoon season might be attributed to the high organic matter content and warming of coastal waters, enhancing the potential breeding of the species, and suppressing the others (Deart & Britayev 2014). This six-month occurrence pattern (from July to December 2021) of these minute-sized organisms indicates a short life cycle with seasonal reproduction, affected by environmental controllers of nutrient availability, photoperiod, salinity and temperature (Smart 2008). The abrupt decline in the number of oweniids toward the monsoonal season might be attributed to the disturbance in the community structure, caused by either pollution or hydrodynamic activity at the breakwater area. In addition, it is attributed to the coastal water cooling and the low organic matter content in sediments throughout the seasons, as supported by Deart & Britayev (2014).

In addition to the presence of organic matter content, the presence of members of Oweniidae is hypothesised to be highly correlated with the silt and clay fractions (Luckenbach 1986; Callaway 2018). The species successfully increased the stability and heterogeneity of the sediments. In general, stable sediment which can be represented by the presence of a dense aggregation of oweniid tubes, highly supports a high local benthic diversity by favoring larval settlement and providing shelter for other invertebrates (Callaway *et al.* 2010; Parapar *et al.* 2021). For instance, the presence of oweniid tubes at a density of 500-1000/m² and small anemone at a shallow subtidal site in Southern California are suggested to help stabilise the sediment against erosion, with contributions from the secreted mucous and binding of diatoms, bacteria, the oweniids themselves, and/or undetected organisms (Fager 1964).

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APPENDICES

APPENDIX 1. — Differences and similarities of *Galathowenia* Kirkegaard, 1959 species worldwide. Abbreviation and symbols: +, presence; –, absence; **NS**, not stated; **RLUS**, relative length of uniramous segment; *, incomplete type specimens for Indonesia, loss of anterior part; **, smaller specimens probably juveniles. Measurements in mm.

Species	Type locality	Length	Width	Eyes	Ventral pharyngeal organ	Thoracic chaetigers	RLUS	Constriction
<i>Galathowenia africana</i> Kirkegaard, 1959	Cabinda coast, Angola	50-70	0.5	+	+	+	1:1:1/ 1: 2: 2	–
<i>Galathowenia annae</i> Capa, Parapar & Hutchings, 2012	Botany Bay, Sydney, Australia	5-11	0.05-0.1	+	+	+	1:2:1	–
<i>Galathowenia arafurensis</i> Capa, Parapar & Hutchings, 2012	Arafura sea, Australia	28	0.6-0.8	+	+	+	1:1.5:1	–
<i>Galathowenia australis</i> (Grube, 1866)	St Paul Island (Sub Antarctic Indian Ocean)	10-15	0.5-1.0	–	+	+	2: 2: 1	–
<i>Galathowenia fragilis</i> (Nielsen & Holthe, 1985)	Norwegian Sea/ Boreo Arctic	30	0.8	–	+	+	1:2:1	+
<i>Galathowenia kirkegaardii</i> De León-González & Sanchez-Hernández, 2012	Veracruz, Gulf of Mexico	12	0.2 mm	+	+	+	1:1:1	+
<i>Galathowenia lobopygidiata</i> (Uschakov, 1950)	Okhotsk Sea	NS*	2-4	NS	+	+	NS	–
<i>Galathowenia oculata</i> (Zachs, 1923)	White Sea/ Boreo Arctic	4-35**	0.25-1.25	+	+	+	1:1:1 / 1:1:0.5	–
<i>Galathowenia piltzi</i> Blake, 2000	Santa Maria Basin, California	27	0.5	–	+	+	1:1:1	–
<i>Galathowenia pygidialis</i> (Harman, 1960)	Off San Francisco coast, California,	57-90	0.6-1	–	+	+	1.5:1:1	+
<i>Galathowenia quelis</i> Capa, Parapar & Hutchings, 2012	North of Sydney, Australia	13	0.15	+	+	+	1: 2: 1	–
<i>Galathowenia scotiae</i> (Hartman, 1978)	Weddel Sea, Antarctica	32-64	1-1.5	–	+	+	1:2:1	+
<i>Galathowenia minuta</i> n. sp.	Kuala Nerus, Terengganu, Malaysia	5-15	0.02	+	+	+	2:2:1	–

Appendix 1. — Continuation.

Species	No. of chaetigers	Cylindrical body	Pigments	Elongated head, truncated anteriorly	Terminal mouth extending mid-ventrally
<i>Galathowenia africana</i>	38 (3:35)	+	Segment 1: dark pigmented band at the dorsum close to cephalic membrane. Larger pigmented field covering the dorsum of chaetigers 1-3, lighter towards posterior	+	+ midventral oral cleft/ slit concealed by overlapping ventral membrane
<i>Galathowenia annae</i>	14-17 (3:11-14)	+ slender, thread-like thinnest species in <i>Galathowenia</i>	+ anterior 4 segments	+	+ ciliated
<i>Galathowenia arafurensis</i>	31 (3:28)	+	+ anterior body region (brown-red)	+	+
<i>Galathowenia australis</i>	16/18 (3:13-15)	+ short	+ pale brown	+	+ anterior end rounded with mouth located in a more ventral position (mouth closed)
<i>Galathowenia fragilis</i>	25 (3:22)	+ slender	–	+	+
<i>Galathowenia kirkegaardi</i>	25 (3: 22)	+ short, slender, transparent	+ 2 slim discreet lines	+ ciliated	+ lips slightly crenulate
<i>Galathowenia lobopygidiata</i>	NS	NS	NS	NS	NS
<i>Galathowenia oculata</i>	>23 (3:21-31)	+	+ dorsal head	+	+ ciliated, covered by overlapping membrane
<i>Galathowenia piltzi</i>	32 (3:29)	+	NS	+ slightly expanded	+ ciliated, covered by overlapping membrane
<i>Galathowenia pygidialis</i>	42/43 (3:39-40)	+	–	+	+ ciliated, surrounded by thickened lips, with distinct midventral cleft.
<i>Galathowenia quelis</i>	20 (3:17)	+	–	+	+
<i>Galathowenia scotiae</i>	25/28 (3:22-25)	+	+	+ ciliated around terminal mouth	+ ciliated, with 2 lips marking longitudinal midventral slit on peristomium when closed.
<i>Galathowenia minuta</i> n. sp.	17-18 (3:14-15)	+	+ encircling chaetiger 4	+	+

Appendix 1. — Continuation.

Species	Breakage/ transverse groove/ slit (between segment)	Thoracic chaetigers (uniramous, Notochaeta: capillary chaeta)	Well- developed ventral slit	Oesophageal commissures	Biramous abdominal chaetiger
<i>Galathowenia africana</i>	+ (chaetigers 1 and 2)	+	+	NS	+
<i>Galathowenia annae</i>	+ (chaetigers 1 and 2) on ventral and lateral sides	+	+	White ventral longitudinal band + Y shape in anterior segment	Anterior segment: 5 to >10× longer than wide. Posterior segment: shorter and compacted
<i>Galathowenia arafurensis</i>	+ (chaetigers 1 and 2)	+	+	White ventral longitudinal band + Y shape in anterior segment	Anterior segments: 5 to 6× longer than wide. Chaetiger 5: about 1.5× longer than chaetiger 4
<i>Galathowenia australis</i>	–	+ chaetiger 1 and 2 = 7 to 10 long capillary chaeta; chaetiger 3 = short and fewer capillary chaeta	–	Mid-ventral glandular Y shaped line beginning just posterior to peristomium as 2 lines, converge and merge in thoracic region	Chaetigers 4-6 slightly elongate
<i>Galathowenia fragilis</i>	+ (chaetigers 1 and 2)	+	+	NS	+
<i>Galathowenia kirkegaardi</i>	+	+	+	NS	+
<i>Galathowenia lobopygidiata</i>	NS	NS	+	NS	+
<i>Galathowenia oculata</i>	No thoracic transverse slit	+ short	+	NS	Anterior segments: 3-4× longer than wide
<i>Galathowenia piltzi</i>	NS	NS	+	NS	Chaetiger 4: short, same length as thoracics Chaetiger 5: as long as 1st 4 anterior chaetigers combined
<i>Galathowenia pygidialis</i>	+ (chaetigers 1 and 2)	+	+	NS	Chaetiger 4: short, same length as thoracics Chaetiger 5: about 2× length of anterior chaetigers 1-4 combined
<i>Galathowenia quelis</i>	+ (chaetigers 1 and 2), encircling the body	+ short	+	Y shaped in anterior segments	Anterior segment: 6 to 10× longer than wide. Posterior segment: shorter and compact
<i>Galathowenia scotiae</i>	+ (chaetigers 1 and 2)	+	+	Mid-ventral Y line beginning just posterior to peristomium as 2 lines, converge and merge in chaetiger 2	NS
<i>Galathowenia minuta</i> n. sp.	+ (chaetigers 1 and 2)	+	+	Y shaped in anterior segments	Anterior segments: 3-4× longer than wide. Posterior segment: shorter and compact

Appendix 1. – Continuation.

Species	Longest chaetiger	Capillary notochaeta	Posterior chaetiger	Thoracic neurochaeta (uncini)
<i>Galathowenia africana</i>	NS	Spinous	Shorter	Numerous neuropodial long shafted, bidentate hooks uncini, on transverse rows
<i>Galathowenia annae</i>	6	+ Decrease in size ventrally, proximal part smooth or slightly striated, mid and distal end covered with scales	Longer and fewer	Arranged in 4 irregular transverse rows, arranged in oblique row
<i>Galathowenia arafurensis</i>	8	Decreasing in length ventrally, proximal third smooth and distal end ornamented with scales	NS	Arranged on long and broad ventral tori, 12-16 transverse rows in oblique position
<i>Galathowenia australis</i>	4-6	Chaetigers 1 and 2: 7-10 long. Chaetiger 3: short capillary. Abdominal notopodia: dorsal bundle of long and a ventral bundle of short and smooth. Mid-body: 16-18 long and 7-10 short. Long capillary coated in the distal end by closely packed slender spinules	Not tapering	Chaetiger 4: numerous uncini irregularly arranged in dense fields, arranged obliquely
<i>Galathowenia fragilis</i>	5-6	Distally spinous, short scales. Anterior: abundant and shorter. Posterior: few and longer	NS	In oblique position
<i>Galathowenia kirkegaardii</i>	5	Smooth basally, from middle region with densely regular pointed scales arranged in spiralling bands	Slightly tapering	Numerous long-shafted, bidentate uncini in ventrolateral position, 45° anteroventral orientation
<i>Galathowenia lobopygidiata</i>	NS	Present	NS	+ numerous, long-shafted uncini
<i>Galathowenia oculata</i>	5	Long and narrow scales (slender) + minute spinules. Anterior: Abundant and shorter. Posterior: Few and longer	Tapered and shorter	+ small and numerous uncini, arranged in transverse rows. Long and narrow shaft, long neck. Arranged obliquely to a more side by side position
<i>Galathowenia piltzi</i>	4-6	Few, indistinct barbs, 5-12 chaetae per fascicle	Short, crowded	In oblique position
<i>Galathowenia pygidialis</i>	5-7	Few, indistinct barbs, 15-25 chaetae per fascicle	Short, crowded	+ small, numerous uncini arranged in dense fields, side by side at same level
<i>Galathowenia quelis</i>	5-6	Decreasing in length ventrally within each fascicle. Proximal part smooth or slightly striated; mid and distal end with sculpture resembling scales	Longer but fewer than anterior segments	+ Anterior: arranged in 6-8 transverse rows. Posterior: Decrease in size and number, arranged obliquely
<i>Galathowenia scotiae</i>	4-8	Minute spinules	Tapered, compressed segments, splaying out large notopodial chaetae	Uncini in ventrolateral position, arranged in several transverse rows of hooked setae, in oblique position
<i>Galathowenia minuta</i> n. sp.	5-9. Mostly 7	+ Decreasing in length ventrally, proximal part slightly striated and mid and distal end ornamented with spinules. Anterior: Abundant and shorter. Posterior: few and longer	Tapered, shorter and compact	+ mid body: numerous bidentate, hook and long shafted uncini. Posterior: few in number, arranged obliquely

Appendix 1. – Continuation.

Species	Tori	Teeth of uncini	Anus/ pygidium	Length of tube	Colour in alcohol
<i>Galathowenia africana</i>	+	NS	- or +	NS	NS
<i>Galathowenia annae</i>	Chaetiger 4: long and broad ventral tori. Posterior segments: much shorter tori	Convex	3 prominent digitiform lobes, dorsal slightly smaller than 2 lateral one	3 to 4 × longer than animal	Brownish or pale yellow
<i>Galathowenia arafurensis</i>	Long and broad ventral tori	Curved, nearly equal in size	7 short digitiform lobes, surrounding 2 papillae	NS	Brownish or pale yellow
<i>Galathowenia australis</i>	Chaetiger 4: nearly rectangular in shape	Long and slender	2 blunt anal lobes	NS	NS
<i>Galathowenia fragilis</i>	Shorter than <i>G. oculata</i> and fewer uncini	Located one above the other	5 to 6 lobes. 1-2 dorsal, 2 lateral and 2 ventral	Very long, thin and flexible. Slightly tapering towards hind end, frontal end conical	Brownish or pale yellow
<i>Galathowenia kirkegaardii</i>	Anterior and middle: longer than wide, numerous uncini (85-90) arranged in dense field formed of oblique rows of uncini. Posterior: (60-65) with rows forming oval field	Anterior: one tooth slightly above second. Posterior: Almost superimposed teeth	Tapered, with 2 conical pygidial lobes	NS	NS
<i>Galathowenia lobopygidiata</i>	Present	Two small teeth	9 short, finger-shaped papillae in one row around the anus	NS	NS
<i>Galathowenia oculata</i>	Anterior: long and broad, Posterior: short and broad.	Equal size, one offset slightly higher than second	2 or 3 blunt lobes. 2 lateral + 1 dorsal lobe	Very long, thin, cylindrical, and flexible	Pale yellow or pale vermillion in ethanol Light tan
<i>Galathowenia piltzi</i>	+	NS	4 lobes (2 large dorsal anal lobes and 2 low lateral ones)	NS	Light tan
<i>Galathowenia pygidialis</i>	+	+ nearly equal curved	7 to 9 encircling short lobes; anal cirri	NS	Light tan
<i>Galathowenia quelis</i>	+ Long and broad. Posterior: much shorter	+ bifid, 2 nearly equally convex teeth, one offset slightly higher than the other	Low ciliated rim; 2 low blunted lobes	2 to 3 × longer than animals	Pale yellow
<i>Galathowenia scotiae</i>	+	+ curved teeth nearly equal in length. Anterior: located one above the other or slightly offset from one another. Mid body: progressively located more side by side. Posterior: oblique position	5 to 11 irregular lobes; cirri, slightly petaloid, arranged around anus	Tube long, cylindrical and rigid	NS
<i>Galathowenia minuta</i> n. sp.	Anterior and mid segments: long and broad. Posterior segments: much shorter and a bit oval	+ nearly equally convex teeth, one offset slightly higher than the other	2 blunt anal lobes	Longer than the individuals, some even folded in the tube, super fragile	Brownish. Some are green

Appendix 1. – Continuation.

Species	Tube	Habitat	Depth range (m)
<i>Galathowenia africana</i>	Tube walls – not overlapping fine sand grains	NS	32-42
<i>Galathowenia annae</i>	Sand grains	Estuaries, muddy and sandy sediments	13-18
<i>Galathowenia arafurensis</i>	Shell fragments and sponge spicules, overlapping like roof tiles	Soft bottoms composed of foraminiferans, dead molluscs and detritus	92-233
<i>Galathowenia australis</i>	Sand grains	NS	NS
<i>Galathowenia fragilis</i>	Large, encrusting, and diverse particles (sand, foraminiferans, sponge spicules); haphazard particles arrangement	NS	800-2600
<i>Galathowenia kirkegaardii</i>	Slender, cylindrical, stiff –3 layers–; inner a membranous lining, middle: sponge spicules, external (different sand sizes, mostly white and yellow)	Coastal lagoon, muddy bottom with high percentage of clay particles	NS
<i>Galathowenia lobopygidiata</i>	Thick sandy walls, dark brown	NS	NS
<i>Galathowenia oculata</i>	Up to 90 mm long and 1 mm wide. Made of small, oblong and clear sands	Found in all types of sediment, but mainly in coarse and sandy bottoms	63-1020/12-2500
<i>Galathowenia piltzi</i>	Small, clear sand grains and sponge spicules and organic debris	NS	92
<i>Galathowenia pygidialis</i>	Fine, clear quartz particles, darker minerals, fine sandy particles	NS	> 2000
<i>Galathowenia quelis</i>	Sand grains	Estuaries and sheltered bays in muddy and sandy sediments	1-60
<i>Galathowenia scotiae</i>	Membranous inner lining, externally coated with black volcanic sand, occasional sponge spicules and foraminiferan	NS	48-1592
<i>Galathowenia minuta</i> n. sp.	Tube walls with very small, not overlapping fine sand. Tube length = 1.5 cm	Coastal waters	4-8

APPENDIX 2. — Differences and similarities of *Owenia* Delle Chiaje, 1844 species worldwide. Abbreviations and symbols: +, presence; –, absence; NS, not stated; **RLUS**, relative length of uniramous segment.

Species	Type locality	Long (mm)	Wide (mm)	No. of chaetiger	Body (3 sections – tentacular crown, thorax and abdomen)	Eyes/ocular spots
<i>Owenia artifex</i> (Verrill, 1885)	Cape Cod, Massachusetts	24-36	1	NS	+	NS
<i>Owenia assimilis</i> (Sars, 1851)	Tromso, Bergen area, Norway	NS	NS	22-24	+	NS
<i>Owenia australis</i> Ford & Hutchings, 2005	New South Wales, Australia	NS	1	18-22	+	+ pale eyespot
<i>Owenia bassensis</i> Ford & Hutchings, 2005	Victoria, East Bass Strait, Australia	NS	0.72	18-22	+	+ elongated eyespot
<i>Owenia borealis</i> Koh, Bhaud & Jirkov, 2003	Iceland	8-31	1.25	22 (3+19)	+	NS
<i>Owenia caissara</i> Silva & Lana, 2017	Brazil	15-32	1.16-1.24 at collar height	16-21 (13:2-18: 3)	+	+ present ventrolaterally, partially covered by the collar
<i>Owenia caudisetosa</i> Hartmann-Schröder, 1959	Estero Jaltepeque, Salvador, Pacific	10	NS	15 (non-adult)	Whole surface is densely covered with large papillae, except segment 1-7	Not recognisable
<i>Owenia collaris</i> Hartman, 1955	Santa Catalina, USA	14-54	1-3.1	>20 (22)	With speckles (small spot or patch of colour) all over, especially in thorax. white spots throughout especially in thorax	–
<i>Owenia dichotoma</i> Parapar & Moreira, 2015	Australia	16	1	9 (incomplete)	+	+
<i>Owenia fusiformis</i> Delle Chiaje, 1844	Naples, Mediterranean Sea	150-360	1.8-5	<20/30	Thick and rigid. Short, anteriorly cylindrical, posteriorly tapering and dorsoventrally flattened	+ present lateroventrally
<i>Owenia gomsoni</i> Koh & Bhaud, 2001	Gomso estuary, South Korea	43.26 ± 2.95	2	NS	+ presence of specific colour patterns on body sides in living animals	+ disappear after fixation
<i>Owenia johnsoni</i> Blake, 2000	Tomales Bay, California	25	0.8/ 0.9	> 20 (22/23)	+	+ reddish ventrolateral eyes
<i>Owenia mirrawa</i> Ford & Hutchings, 2005	Darwin harbour, Australia	NS	0.56	14 (3+11)	+	+
<i>Owenia persica</i> Martin, Koh, Bhaud, Dutrieux & Gil, 2006	Persian Gulf	5.46	0.27-1.17	8-23 (11-26)	+	+
<i>Owenia petersenae</i> Koh & Bhaud, 2003	Wellington, New Zealand	NS	0.6-1.6	incomplete	+	NS
<i>Owenia picta</i> Parapar & Moreira, 2015	Australia	26	0.5	22	+	+ pale eyespots
<i>Owenia polaris</i> Koh, Bhaud & Jirkov, 2003	Norwegian sea	11-34	0.5-1.1	18-22	+	NS
<i>Owenia vieitezi</i> Díaz-Díaz, Parapar & Moreira, 2020	Gulf of Venezuela	13-21	0.8-1.5	20 (3+17)	+	+
<i>Owenia unipinnata</i> n. sp.	Kuala Nerus	10	0.065	15	Short, anterior cylindrical – tapering and flattened posteriorly. Mid and posterior body are fragile and tightly attached to the tube by the hooks	+ elongated eyespot (ventrolateral position)

Appendix 2. — Continuation.

Species	Crown	Tentacles to crown ratio (in %)
<i>Owenia artifex</i>	Very short, truncated tentacular crown with 5 pairs of tentacles, few dichotomies. Head appendages partly forked and partly bifurcate. 2 dorsal longest, about 6 divisions; upper lateral pair shorter, 4 small, blunt branches; below these are 2 shorter, smaller, lateral oars, only 1 forked.	NS
<i>Owenia assimilis</i>	4 pairs of tentacles. Short stumpy tips. 2-6 dichotomous branched from base to the tip. Length of branchiae is unequal, shorter on ventral face. Tentacle crown diameter is slightly smaller than the diameter of the thorax.	80
<i>Owenia australis</i>	4 pairs of tentacles, lacking any major ramification. Tips of tentacles with multiple small lobes; distinct separation between left and right hands pairs of tentacles by a V shaped lobe located on dorsal surface crown. Long and thin tentacles.	80
<i>Owenia bassensis</i>	3 pairs of tentacles with one major ramification. Each tentacle divided about 1/2 along its length into a pair with small terminal lobes. Distinct separation between left and right hands pairs of tentacles marked as a V shaped structure, no distinct lobe present between pairs.	75
<i>Owenia borealis</i>	4 pairs of tentacles, numerous short terminal lobes, Tentacle apparatus consists of 8-14 branched arms. May consists of 4, 5 or 7 arms. Each arm branches on 2 tentacles, which then bifurcate and form 2 short bulbs with small Y shaped tips on each. Number of dichotomies varies from 1 to at least 4.	90
<i>Owenia caissara</i>	5 pairs of tentacles. Tentacular crown and thorax separated by a thin membrane forming a collar. Dorsal branches longer than ventral branches.	80
<i>Owenia caudisetosa</i>	4 pairs of long and thin tentacles, dichotomously branches, dorsally and ventrally split, bilaterally symmetrical. The tips are divided into 2-4 small bifid lobes.	NS
<i>Owenia collaris</i>	4 pairs of tentacles, long and thin dichotomous branches, terminate in fine slender tips.	50
<i>Owenia dichotoma</i>	4 pairs of tentacles, very short crown, fewer, dichotomous branches and ramifications. Tentacles provided with the major division close to the base of the crown, thus appearing as if 8 pairs of short tentacles.	68
<i>Owenia fusiformis</i>	4 pairs of long and thin tentacles, dichotomously branches, dorsally and ventrally split, bilaterally symmetrical. The tips are divided into 2-4 small bifid lobes.	70
<i>Owenia gomsoni</i>	5 or more pairs of tentacles. Presence of specific colour patterns on the branchial stems. Branchial plume mounted on a base with 5 pairs of lobes. Branchiae are equal or subequal.	80
<i>Owenia johnsoni</i>	4 pairs of long and thin tentacles. Dichotomous branches (4+). Numerous dichotomies, terminate in fine slender tips.	80
<i>Owenia mirrawa</i>	4 pairs of tentacles with several ramifications. Distinct separation between left and right pairs of tentacles by a V shaped lobe located on dorsal surface of crown. Major divisions close to base.	85
<i>Owenia persica</i>	4 pairs of tentacles. Dorsal and ventral tentacles branch in equal size.	50
<i>Owenia petersenae</i>	4 pairs of tentacles, with few subterminal branches. Dichotomies or major divisions of tentacles are only observed at the distal end.	62
<i>Owenia picta</i>	4 pairs of long tentacles, with no major division, fewer tentacular crown ramifications. Bilobed structure between the tentacles of the left and right sides in ventral view. Tips of tentacles with multiple small lobes with a distal sulcus.	55
<i>Owenia polaris</i>	4 pairs of short tentacles with few dichotomies; tips with few branches. Dichotomies springing up at the base of the branchial trunk.	75
<i>Owenia vieitezi</i>	3 pairs of tentacles of similar length, sometimes the dorsal most is slightly longer. Each tentacle with 3 ramifications; first close to crown base; second located at mid-length and third close to distal end.	85
<i>Owenia unipinnata</i> n. sp.	3 pairs of tentacular crown of almost similar length, the dorsal most is slightly longer. No ramification. Each tentacle commonly bears 2 to 3 lobes at the tips of the crown. No. of lobes increases progressively from medioventral to mediodorsal (up to 5) with oral groove present prominently at third pairs of tentacles (dorsal side).	60

Appendix 2. — Continuation.

Species	Collar	Crown length to thorax ratio (C/T)	Pigment
<i>Owenia artifex</i>	NS	NS	NS
<i>Owenia assimilis</i>	Thin, slightly rounded or curved, oblique with one direction	0.25/ 0.5	NS
<i>Owenia australis</i>	Distinct, straight, closely aligned with body wall, slightly overlapping base of crown	0.2-0.5	Pale brown
<i>Owenia bassensis</i>	Straight, closely aligned with body wall, slightly overlapping base of crown	0.66	NS
<i>Owenia borealis</i>	Slightly V shaped (angular), smooth, thin with a sharp edge lying close to the base of tentacle crown, angle ranges from 140 to 170°, oblique with angle at the level of the lateral notch	0.25/ 1.2	–
<i>Owenia caissara</i>	Rectilinear with a lateral slit (77 and 67°)	0.48	Dark brown at the base and near the apex of tentacles
<i>Owenia caudisetosa</i>	Slightly V shaped, Dorsal side slightly stained, narrow belt, mid ventral side has 2 circular dark spots, median V well-defined, wider than long	0.9	More or less broad, brown pigment stripe at base of tentacle flaps and secondary lobes, especially on the dorsal side
<i>Owenia collaris</i>	Pigment, almost straight	0.4	Present at tentacular crown (distinctly) + collar (broad diffuse brown band) + peristomial collar. Transverse pigment band on tentacular trunk (darker more concentrated pigment outlining bases)
<i>Owenia dichotoma</i>	Distinct, straight, closely aligned with body wall, slightly overlapping base of crown	0.33	–
<i>Owenia fusiformis</i>	Slightly V shaped. Dorsal side slightly stained, narrow belt. Mid ventral side has 2 circular dark spots, median V well-defined, whole figure wider than long	0.9	Outlining bases of tentacular trunk, pigment band anterior to collar, on collar.
<i>Owenia gomsoni</i>	Curved, marked, laterally incised, collar-like fold at the boundary between branchial plume and thorax. Thickened, slightly V shaped	0.5	2 lateral white pigmented bands
<i>Owenia johnsoni</i>	V shaped	0.9	–
<i>Owenia mirrawa</i>	Distinct, straight, closely aligned with body wall, slightly overlapping base of crown. Small lobe presents just below the lateral notch	0.6	–
<i>Owenia persica</i>	Angular. Dark dorsal side, narrow bracket. Mid-ventral side has circular spots and median V diffuse. Whole figure longer than wide. Lateroventral sides have 2 dark bands, longer than wide, wider at tip	0.7	Irregular patches of light brown pigment located ventrally in freshly collected specimens
<i>Owenia petersenae</i>	Anteriorly convex with long medio-lateral slit/ curve	0.6	–
<i>Owenia picta</i>	Straight, closely aligned with body wall, slightly overlapping base of crown. Sometimes expanded in a large dorsal lobe	similar width	Brown pigmentation or speckles on most ventral part of peristomium and anterior part of first thoracic chaetiger
<i>Owenia polaris</i>	V shaped (angular). Lateral notch of the collar is at open angle. The edge of the collar is folded. Oblique collar, with an angle at the level of the lateral notch	0.4/ 1.2	NS
<i>Owenia vieitezi</i>	Very distinct, straight. Closely aligned with body wall, slightly overlapping base of crown	0.8	Brown horizontal lines in ventral and lateral anterior parts of peristomium and basal and median part of the 2 dorsal most pairs of tentacles
<i>Owenia unipinnata</i> n. sp.	Barely membranous, straight, closely aligned with body wall, without covering eyespot	0.5	–

Appendix 2. — Continuation.

Species	Glandular ridges	RLUS	Chaetiger 3	Uniramous thorax
<i>Owenia artifex</i>	NS	NS	Presence of long, broad band of uncini and a group of slender setae above. Several segments long and round, not distinctly separated by a sulcus; several antennal segments short and indistinct, 3, 4, or more bearing setae	Short first 2 segments, with an upper fascicle of slender acute setae, but no lower ones
<i>Owenia assimilis</i>	NS	NS	NS	+
<i>Owenia australis</i>	–	1: 2: 0.5	NS	Similar width as crown
<i>Owenia bassensis</i>	–	1: 2: 0.5	NS	Similar in width as crown
<i>Owenia borealis</i>	NS	1: 2: 0.5	NS	Fusion of 2 most anterior uniramous chaetigers, form the jointed double segment without dissepiments. Third uniramous chaetiger with very small chaetigerous sacs, separated from anterior jointed double segment by a dissepiment
<i>Owenia caissara</i>	+	1: 2: 0.5	Capillary notochaetae in dorso-lateral position	Lateral bundles on first 2 segments, dorso-lateral on third segment
<i>Owenia caudisetosa</i>	+ at dorsal	NS	NS	Clearly separated segments
<i>Owenia collaris</i>	–	1: 1.5: 1	Short, constricted dorsally, notochaeta shifted dorsally, located close to notochaetae of abdominal segment 1	Short, not morphologically distinct segment
<i>Owenia dichotoma</i>	NS	1: 2: 1	NS	Similar in width as crown
<i>Owenia fusiformis</i>	+ at dorsal	1: 2: 0.5	Short, constricted dorsally	Robust, as long as its wide
<i>Owenia gomsoni</i>	+ at dorsal	1: 1.5: 1.5	NS	Present
<i>Owenia johnsoni</i>	+/-	NS	Short, reduced with notochaeta shifted dorsally, located close to notochaetae of abdominal segment 1	narrow, twice as long as wide
<i>Owenia mirrawa</i>	–	1: 2: 1	NS	Width is similar as crown
<i>Owenia persica</i>	NS	1: 2.5: 1	NS	Longer, 3 bundles
<i>Owenia petersenae</i>	–	1: 2: 1	NS	NS
<i>Owenia picta</i>	NS	1: 2.5: 0.5	NS	Present
<i>Owenia polaris</i>	NS	1: 2.5: 0.5	NS	NS
<i>Owenia vieitezi</i>	NS	1: 2: 1 or 1: 2.5: 0.2	Fewer chaeta but longer than those of first 2, located more dorsally	Present
<i>Owenia unipinnata</i> n. sp.	+	1: 2: 1	Notochaeta located dorsally, closer to tori and notochaetae of chaetiger 4	Present

Appendix 2. — Continuation.

Species	Abdominal	Longest chaetiger Notochaetae	
<i>Owenia artifex</i>	Several segments are long and round, not distinctly separated by a sulcus	6	Slender acute
<i>Owenia assimilis</i>	Very elongated	NS	Symmetric scales, ratio of the free part of the scale to its total length is close to 1: 2
<i>Owenia australis</i>	Width uniform in mid body, decreases posteriorly. 16 chaetigerous segments	5	Abdomen notochaeta similar to thoracic notochaeta, arranged dorsally, shaft composed of densely packed scales along entire length, arranged in spiralling bands along shaft with tips of the scales splayed
<i>Owenia bassensis</i>	Width is uniform	6	Shafts composed of densely packed scales along the entire length, scales arranged in spiralling bands along shaft with tips of scales splayed
<i>Owenia borealis</i>	NS	NS	Long, symmetry setae scales; ratio of the free part of the scale to its total length is close to 1: 3
<i>Owenia caissara</i>	Each segment with one pair of capillary notochaeta bundles and one neuropodial ring almost encircling the body. First abdominal segment with rows up to 23 hooks, in 0 to 90° angles in relation to antero-posterior body axis	NS	Long and thin scales with oval transition
<i>Owenia caudisetosa</i>	Carries eggs in the 4th segment. In the abdomen, boundaries are indicated only by position of bristles	NS	Spinous. Third chaetiger shorter than preceding chaetigers.
<i>Owenia collaris</i>	Presence of dorsal longitudinal curved lines	5th	Thin, bristled, serrated
<i>Owenia dichotoma</i>	Width decreases posteriorly. Notochaeta arranged dorsally. First abdominal segment slightly longer than total thoracic length	NS	Shaft composed of densely packed scales
<i>Owenia fusiformis</i>	Anterior ones long, posterior ones short. Presence of dorsal longitudinal curved lines	5, 6 or 7 or 8	Spinous. Third chaetiger shorter than preceding chaetigers
<i>Owenia gomsoni</i>	Notopodial capillary chaetae and minute neuropodial hooks with 2 curved teeth at the apex	NS	Covered in closely packed scales, not spinulous. The scaly cover is not total and leave's the seta's base quite smooth. Scales only begin to peel away from the shaft at the tip of the setae, giving an almost spiny appearance. Scales are very slender, with a length / width ratio always over 3
<i>Owenia johnsoni</i>	Capillary notochaeta and dense fascicle of minute hooked neuropodial uncini formed into tight bands nearly encircling body. Presence of dorsal longitudinal curved lines	5, 6 or both of equivalent length	Relatively thin, smooth, with minute bristles or fibril endings
<i>Owenia mirrawa</i>	Uniform width. Width decreases posteriorly. Abdominal notopodia poorly developed with capillary chaeta similar to thoracic notochaeta	6	Abdominal notochaeta arranged dorsally. Shafts composed of densely packed scales along entire length, scales arranged in spiralling bands along shaft with tips of scales splayed
<i>Owenia persica</i>	Notopodial capillary chaeta and minute neuropodial hooks	NS	Distance between the tips of 2 successive scales is longer. Scales are oval all along scaled region
<i>Owenia petersenae</i>	NS	NS	NS
<i>Owenia picta</i>	Width uniform in mid body, decreases posteriorly. Abdominal chaetiger 1 about as long as all thoracic segments	5	Shafts composed of densely packed scales. Abdominal notochaeta arranged dorsally
<i>Owenia polaris</i>	NS	NS	Symmetry setae scales, the ratio of the free part of the scale to its total length is close to 1: 2
<i>Owenia vieitezi</i>	Abdominal segment 1 about same length or slightly longer than total thoracic length (crown excluded). Abdominal segments decreasing in length and width from chaetiger 5 onwards, being posterior segments short and compact	5/6	Shafts composed of densely packed scales
<i>Owenia unipinnata</i> n. sp.	Abdominal segment's width decreases posteriorly. Capillary chaetae similar to thoracic notochaetae, arranged more dorsally	6	Similar between thoracic and abdominal

Appendix 2. — Continuation.

Species	Notopodia	Neuropodia
<i>Owenia artifex</i>	Upper fascicle of slender acute setae	Long, broad band of uncini
<i>Owenia assimilis</i>	NS	NS
<i>Owenia australis</i>	+	+
<i>Owenia bassensis</i>	Capillary chaetae, similar to thoracic notochaeta	+
<i>Owenia borealis</i>	NS	NS
<i>Owenia caissara</i>	Capillary chaeta only	Ring with rows of minuscule bidentate hooks
<i>Owenia caudisetosa</i>	First 2 located at lateral sides of the body. Third to tenth situated along mid-dorsal line	Tori appearing from chaetiger 4 and continuing to posterior end
<i>Owenia collaris</i>	Consist of notochaeta starting from first chaetiger to the posterior	Contain neurochaeta beginning on setiger 4 and continuing to posterior. Closely packed uncini at anterior end of segment
<i>Owenia dichotoma</i>	Capillary chaeta similar to thoracic notochaeta	+
<i>Owenia fusiformis</i>	First 2 located at lateral sides of body. Third to tenth situated along the mid-dorsal line	Tori appearing from chaetiger 4 and continuing to posterior end
<i>Owenia gomsoni</i>	Capillary chaeta (elongated scales)	Dorso-ventral tori covering 9 or 10 of the circumferences of the body
<i>Owenia johnsoni</i>	Capillary chaeta (elongated scales)	+
<i>Owenia mirrawa</i>	Capillary chaeta only	+
<i>Owenia persica</i>	NS	NS
<i>Owenia petersenae</i>	NS	NS
<i>Owenia picta</i>	Capillary chaeta similar to thoracic notochaetae	Thoracic neuropodia absent
<i>Owenia polaris</i>	NS	NS
<i>Owenia vieitezi</i>	Notopodia 3 with fewer chaetae but longer than those of notopodia 1 and 2, located more dorsally. Abdominal notopodia well developed	Present
<i>Owenia unipinnata</i> n. sp.	Consist of capillary chaeta only. Notopodia 1 and 2 with more chaeta, located at ventrolateral position, the third and the rest is with fewer and longer chaeta, located more dorsally. Capillary chaeta similar to thoracic notochaeta	Tori appears from chaetiger 4 and continue to the posterior end

Appendix 2. — Continuation.

Species	Neurochaeta (uncini)
<i>Owenia artifex</i>	Long, broad band of uncini
<i>Owenia assimilis</i>	On the first abdominal segment, hook orientation is approximately 90° or more in relative to body axis. Some hooks face posterior part of the body. Hooks have no shoulder. In front view, 2 teeth are of different length. In apical view, the slit between the teeth is very narrow, widening only at apical end. Teeth are very close together
<i>Owenia australis</i>	Similar throughout, consist of hooks which consist of a shaft ending in 2 teeth side by side with no distinct separation between shaft and teeth
<i>Owenia bassensis</i>	Similar throughout abdomen, consist of hooks with shaft ending in 2 lateral teeth with no distinct separation between shaft and teeth
<i>Owenia borealis</i>	Hooks on the first abdominal segment form an angle of 45° with the body's longitudinal axis. The protrusion of the teeth, estimated with a distance A, is 1.75 micron; squashing of the teeth on the head of the shaft is moderate. In the front view, the 2 teeth are of different lengths. In the apical view, the slit between the teeth originates dorsally and widens abruptly at the front
<i>Owenia caissara</i>	Up to 23 hooks on a single row in a first abdominal segment, moderate teeth curvature. Hooks with 0-90° in relation to anteroposterior body axis. Teeth on hooks with a space in between, in an inverted V-shape. Hooks with rectilinear shoulder
<i>Owenia caudisetosa</i>	Long shafted - bidentate uncini. Two teeth side by side nearly at same level. Hooks of first torus with dorsally aligned teeth. Arranged in regular rows on the tori. Each uncinus has a well-developed manubrium
<i>Owenia collaris</i>	Dense fascicles of minute hooked neuropodial uncini formed into tight bands that nearly encircle body. Uncini with long shafted bearing expanded subterminal manubrium and 2 long, curved teeth situated side by side, one slightly higher and offset from the other. Hooks are in a 30 to 45° on the first abdominal segment
<i>Owenia dichotoma</i>	Similar through, consists of hooks with shaft ending in 2 teeth side by side
<i>Owenia fusiformis</i>	Starts from chaetiger 4. Long shafted - bidentate uncini. Present in all abdominal segments. Two teeth side by side nearly at same level. Hooks of first torus with dorsally aligned teeth. Arranged in regular rows on the tori. Each uncinus has a well-developed manubrium
<i>Owenia gomsoni</i>	Teeth of bidentate hooks vertically offset. Each uncinus has a long manubrium or shaft, its head carries 2 teeth arranged side by side. In position on the body, the hooks point forwards
<i>Owenia johnsoni</i>	Long, shaft bearing expanded subterminal manubrium and 2 long curved teeth situated side by side, one slightly higher and offset from the other. Hooks of first torus with teeth clearly displaced dorsally. Hooks are in a 45° on the first abdominal segment
<i>Owenia mirrawa</i>	Similar along entire length of abdomen, made up of hooks which consist of a shaft ending in 2 teeth side by side with no distinct separation between the shaft and teeth
<i>Owenia persica</i>	Two curved teeth at the apices. Hooks lacks shoulders. Teeth are shorter. Hooks very numerous, arranged in dense patches. Forward direction of hooks corresponds to the anterior of ventral face
<i>Owenia petersenae</i>	Hooks on the first abdominal segment are aligned at a 90° angle to the antero-posterior direction of the body
<i>Owenia picta</i>	Similar through, consists of hooks with shaft ending in 2 teeth side by side
<i>Owenia polaris</i>	Hooks observed on the first abdominal segment form an angle of 0-20 degree with the longitudinal axis of the body. The tooth length, estimated with distance A is 2.35 - 2.40 micron, squashing of teeth on the head of the shaft is moderate: the value of distance B is close to 0.85 micron. The hooks have no shoulders, indicating that the bases of the teeth are narrower than the shaft. In the front view, the 2 teeth are of different lengths and tooth direction is often oblique relative to the shaft direction. In the apical view, the slit between the teeth originates dorsally and widens abruptly at the front
<i>Owenia vieitezi</i>	Similar throughout, consists of hooks with shaft ending in 2 teeth side by side
<i>Owenia unipinnata</i> n. sp.	Similar through, consists of hooks with shaft ending in 2 teeth, with left teeth bend towards the right teeth, concave side of teeth bears approximately 45° with 3 bands per tip

Appendix 2. — Continuation.

Species	Tori (almost encircling the body)	Short posterior end	Pygidium
<i>Owenia artifex</i>	NS	Indistinct	Simple, with minute papillae
<i>Owenia assimilis</i>	NS	+	NS
<i>Owenia australis</i>	+ broken only by the notochaetal bundles on the dorsal surface	Compact	With small papillae around anus
<i>Owenia bassensis</i>	+ wide sessile tori, broken only by the notochaetal bundles	Width decreases posteriorly, compact	Pygidium with small papillae around anus
<i>Owenia borealis</i>	NS	NS	Has 3 lobes clearly visible, one dorsal and 2 laterals, the latter separated by a medioventral slit
<i>Owenia caissara</i>	Up to 23 rows in first abdominal segment	Without a dorsal groove	NS
<i>Owenia caudisetosa</i>	Appears from chaetiger 4, long, narrow, nearly rectangular	Presence of simple capillary chaeta	A pair of weakly developed lobes. Sometimes with short anal cirri. Anus opens at the terminal.
<i>Owenia collaris</i>	Neurochaeta girdles from 4th setiger	With dorsal groove	Anal opening positioned dorsally, surrounded by 10 or more simple flattened lobes. With small papillae around anus
<i>Owenia dichotoma</i>	Presence, except on dorsal surface between notochaetal bundles	Compact	NS
<i>Owenia fusiformis</i>	Long, narrow, nearly rectangular; third to 9th chaetigers extend nearly around the body	Without capillary chaeta. With dorsal groove. Gradually tapers off	A pair of weakly developed lobes. Sometimes with short anal cirri. Anus opens at the terminal.
<i>Owenia gomsoni</i>	+	NS	No recognisable ventral lobes
<i>Owenia johnsoni</i>	As tight bands	Without groove	Anal opening positioned dorsally, surrounded by 10 or more simple flattened lobes; 4 or more lobes
<i>Owenia mirrawa</i>	Broken only by the notochaetal bundles on the dorsal surface	Compact	NS
<i>Owenia persica</i>	Dorso-ventral	NS	NS
<i>Owenia petersenae</i>	NS	NS	NS
<i>Owenia picta</i>	+ except on dorsal surface between notochaetal bundles.	Compact	Multilobed
<i>Owenia polaris</i>	Bears hooks	NS	1 dorsal lobe bordered by 2 short slits and 2 lateroventral lobes; medioventral slit not very marked.
<i>Owenia vieitezi</i>	+ except on dorsal surface between notochaetal bundles	NS	Simple
<i>Owenia unipinnata</i> n. sp.	Appears from chaetiger 4, continue to the posterior end, separate only by the notochaetal bundles	Compact, gradually tapers off	Flattened 2 lobes

Appendix 2. — Continuation.

Species	Tube	Methyl green/ methylene blue staining
<i>Owenia artifex</i>	Long, slender, flexible, covered with small imbricated grains of sand, attached only by inner ends. Freely moveable one upon another	NS
<i>Owenia assimilis</i>	Calcareous flat particles, overlapping, roof tile like pattern, no observable mineral particles, built with randomly disposed grains and the external tube surface is not smooth	Highly similar to staining pattern of <i>O. borealis</i>
<i>Owenia australis</i>	Longer than the individual, composed of quartz grains and shell fragments	Speckles concentrated on thorax and pair of ventral longitudinal lines
<i>Owenia bassensis</i>	Longer than individuals, composed of quartz grains and shell fragments	Speckles concentrated on thorax and forming lateral wedges over notopodia
<i>Owenia borealis</i>	65 mm long, diameter close to 3 mm. Built from roughly flattened particles. Particles are not attached by small section; more often inserted along their larger surface. A minority of particles are long and attached by their small section, giving a ray-like pattern. Rays are directed forwards, to the end of the tube (location of head). Thick wall	NS
<i>Owenia caissara</i>	Made of medium and coarse particles (481 - 586 µm in size), coalesced by mucus in an imbricated pattern. In cross-section, smaller particles near lumen and larger on tube edge. Quartz particles dominates (99%), followed by magnetite (0.6%), biotite (0.37%) and shell and echinoderm fragments (0.03%). Tubes from 26 to 57 mm long	Tentacular branches unreceptive to staining, dorsal side of the collar and 2 longitudinal dorso-lateral lines strongly stained. On the ventral side, the 2 v shaped lines were unreceptive to methyl green but the border of these lines and the collar were strongly stained
<i>Owenia caudisetosa</i>	Consists of grains of sand	NS
<i>Owenia collaris</i>	Cylindrical or spindle-shaped tube, up to 90 mm long, of overlapping shell fragments and/ sand grains. Each grain is attached at its one end, giving tube a tiled appearance. Tube lining is close-fitting, chitinous and tough and composed of fine filaments secreted by seven pairs of thread glands. Tube grains, usually light-coloured, are cemented together by the buccal organ, concealed by the crown. Tubes tape at both ends	Entire body covered with speckles, concentrated mostly in thoracic region; peristomial collar not especially stained; pair of long ventral lines present, mid-ventrally not stained; lateral thoracic wedge well developed; v shaped area extending from mouth posteriorly to end chaetigers
<i>Owenia dichotoma</i>	Coated by quartz grains and shell fragments piled on top of one another like roof tiles	NS
<i>Owenia fusiformis</i>	Short, tapering towards both ends (fusiform), covered thickly with more or less translucent secreted layers of foreign objects + flat shells arranged like roof tiles	Branchiae uniformly light green when stained using methyl green
<i>Owenia gomsoni</i>	A marked preference for quartz grains and silicious elements during tube construction	Tentacular branches strongly receptive to staining. V shaped lines strongly receptive to methyl green
<i>Owenia johnsoni</i>	NS	Prostomial collar densely stained, pair of long ventral lines present; lateral thoracic wedge present near notopodia, V shaped area extending from mouth to chaetiger 3
<i>Owenia mirrawa</i>	Longer than individuals, made of quartz grains and shell fragments cemented together	Diffuse entire collar as well as formed paired ventral longitudinal lines and longitudinal curved line on anterior abdominal segments
<i>Owenia persica</i>	Made of sand grains of very homogenous. Overall arrangement resembles a tiled roof. Sand grains usually flat, all side of similar length	Branchiae is unreceptive to staining. Dorsal side of collar with a dark narrow bracket, mid ventral side of collar with circular spots and median diffuse, latero-ventral sides of collar with 2 dark bands, ventral side of abdominal region with 2 parallel longitudinal lines
<i>Owenia petersenae</i>	Spindle-shaped, formed with carbonated particles representing shell echinoderm, balanid fragments. These particles are flat and inserted into the mucus by their side. Particles are perpendicular to the tube wall, without giving aspect of roof tiles	Tentacular branches are receptive to staining
<i>Owenia picta</i>	Coated by quartz grains and shell fragments	NS
<i>Owenia polaris</i>	Up to 60 mm long; the diameter is between 1.70-2.6. Tube is built from approximately spherical particles. These particles have no major faces and seem to be inserted in no particular order. A second kind of particle (spicules of sponges) is long and attached by its smallest section, giving characteristic ray-like pattern. The wall is not so thick as in <i>O. borealis</i> . The material is predominantly silicious (mineral part with quartz and organic part with sponge spicules)	Tentacular branches are receptive to staining

Appendix 2. — Continuation.

Species	Tube	Methyl green/ methylene blue staining
<i>Owenia vieitezi</i>	Coating depends on locality; sometimes covered with overlapping shell fragments of different sizes but mostly covered by quartz grains	Limited to both sides of the ventral Y shaped line, particularly in abdomen
<i>Owenia unipinnata</i> n. sp.	Short, tapered posteriorly. Made of overlapping quartz grains and shell fragments (outer layer), cemented together and arranged like roof tiles. Inner layer consists of translucent layer, attached tightly to the neurochaetal hooks	Concentrated at lateral side of collar and less concentrated at lateral side of thoracic region and longitudinal line. Absent of staining at mid dorsal and ventral

Appendix 2. — Continuation.

Species	Body colour	Depth (m)
<i>Owenia artifex</i>	Anteriorly whitish, the head and buccal segment reddish, with a pale ring behind the tentacles; towards the posterior end the segments are pale flesh-colour, translucent, showing the red vessels and an orange, internal, convoluted organ	122
<i>Owenia assimilis</i>	Pale yellow-green	2-460
<i>Owenia australis</i>	Preserved specimens creamy white	NS
<i>Owenia bassensis</i>	Preserved specimens creamy white	45-49
<i>Owenia borealis</i>	Preserved specimens probably creamy white	41-1350
<i>Owenia caissara</i>	Living specimen with dark brown colouration at the base and terminal region of tentacular branches. Red tinged thorax and beginning of abdomen due to body transparency, which highlights vascularisation; remaining abdomen pinkish. Preserved specimens probably creamy white, except one pair of reddish ocelli at ventrolateral base of tentacular branches, partially covered by collar and brown spots basally on tentacular branches and on terminal regions	NS
<i>Owenia caudisetosa</i>	NS	NS
<i>Owenia collaris</i>	Preserved specimens light tan	NS
<i>Owenia dichotoma</i>	Preserved specimens creamy white with no pigmentation	2-11
<i>Owenia fusiformis</i>	Preserved specimens reddish or pale yellow. Living greenish or yellow, often brown pigments on anterior part and lighter transverse glandular bands	From littoral to at least 1700, possibly to 4554
<i>Owenia gomsoni</i>	White or light brown	NS
<i>Owenia johnsoni</i>	Preserved specimens light tan	NS
<i>Owenia mirrawa</i>	Preserved specimens creamy white	NS
<i>Owenia persica</i>	Preserved specimens probably white cream, although a pair of reddish ocular spots may be observed by light microscopy. Some irregular patches of light brown pigment can be observed ventrally in freshly collected specimens	NS
<i>Owenia petersenae</i>	Holotype has no specific area differentiated by colouration. However, the anterior part formed by the tentacles and thoracic segments is very pale; by the body after the first abdominal segment is light brown	20-30
<i>Owenia picta</i>	Preserved specimens creamy white	4.5-14.5
<i>Owenia polaris</i>	NS	12-930
<i>Owenia vieitezi</i>	Preserved specimens creamy white	NS
<i>Owenia unipinnata</i> n. sp.	Preserved specimens creamy white with no pigmentation	2-8