Zootaxa 4019 (1): 378–413
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4019.1.15
http://zoobank.org/urn:lsid:zoobank.org:pub:54E60C63-EC98-424A-B66E-A72CA79B65E8

Spionidae (Annelida: 'Polychaeta': Canalipalpata) from Lizard Island, Great Barrier Reef, Australia: the genera *Malacoceros*, *Scolelepis*, *Spio*, *Microspio*, and *Spiophanes*

KARIN MEIßNER[1]* & MIRIAM GÖTTING[2]

[1]*Forschungsinstitut Senckenberg, Deutsches Zentrum für Marine Biodiversitätsforschung, Biozentrum Grindel, Martin–Luther–King–Platz 3, 20146 Hamburg, Germany.*
email: kmeissner@senckenberg.de
[2]*University of Turku, Department of Biology, Laboratory of Animal Physiology, 20014 Turku, Finland.*
email: miriam.gotting@utu.fi
[*]*Corresponding author*

Abstract

Seven species belonging to the spionid genera *Malacoceros*, *Scolelepis*, *Spio*, *Microspio*, and *Spiophanes* were found during the polychaete workshop on Lizard Island in August 2013. One species is new to science and named *Scolelepis inversa* n. sp., another *Scolelepis* species is probably also a new species but was represented in our samples by only a single specimen and not formally described. All other species have been reported previously from Australia. Species diagnoses of all species found during the workshop and of *Scolelepis balihaiensis* Hartmann-Schröder, 1979, *Microspio microcera* (Dorsey, 1977) and *M. minuta* (Hartmann-Schröder, 1962) have been critically reviewed and amended based on the study of type material. The potential synonymy of *Microspio minuta* (Hartmann-Schröder, 1962) and *M. microcera* (Dorsey, 1977) is discussed. The new combination *Spio jirkovi* (Sikorski, 1992) proposed by Sikorski (2013) is returned to *Malacoceros.* We added DNA barcodes for five species collected in the Lizard Island area to public databases which will be useful in future phylogenetic and phylogeographic studies. For *Microspio* we provide the first sequence data for this genus.

Key words : COI, *Malacoceros indicus*, *Microspio granulata*, morphology, *Scolelepis inversa* n. sp., *Scolelepis kudenovi*, *Spio blakei*, *Spiophanes viriosus*, taxonomy, 16S rDNA, 18S rDNA

Introduction

The spionid fauna of Australia has been studied by several authors. One of the most comprehensive studies was by Blake & Kudenov (1978) who studied the Spionidae from southeastern Australia and adjacent areas. The authors reported 68 species including four new genera and 43 new species. Hutchings & Turvey (1984) published a paper on the Spionidae of South Australia. Taxonomic revisions of certain genera were provided by Wilson (1990) (*Prionospio* and *Paraprionospio*), Meißner & Hutchings (2003) (*Spiophanes*), Sato-Okoshi *et al.* (2008) and Walker (2011) (polydorids), and by Greaves *et al.* (2011) (*Laonice*). Spionidae, as a widespread and common group, are of course also dealt with in faunistic papers studying Australian polychaetes in general. Good examples for such publications are those by Augener (1914) reporting about the results of the Hamburgian research expedition to SW Australia in 1905, by Hartmann-Schröder (1979, 1981, 1989, 1991a) who collected polychaetes along most of the Australian coasts, or the studies on the polychaete fauna of Careel Bay, New South Wales (Hutchings & Rainer 1979) and the Hawkesbury River and the southern estuaries of New South Wales (Hutchings & Murray 1984). There are also two occasional papers on Spionidae from Lizard Island. One is by Ben Eliahu *et al.* (1984) reporting about the occurrence of *Malacoceros indicus* (Fauvel, 1928) on the island, together with some taxonomic notes. A second paper by Dauer (1985) describes a new species, *Scolelepis hutchingsae*.

The present paper is an outcome of the polychaete workshop which took place on Lizard Island after the 11th International Polychaete Conference in Sydney in 2013. The aim of the workshop was to collect and study

 Accepted by P. Hutchings: 17 Jun. 2015; published: 18 Sept. 2015

polychaetes from different habitats in the Lizard Island area. Here the genera *Malacoceros*, *Scolelepis*, *Spio*, *Microspio*, and *Spiophanes* are covered. In addition to the description of new species, a review and update of some previously known species became necessary. Taxonomy has advanced over the last decade and additional characters are now incorporated into the species diagnoses and some generic diagnoses. For example, the type of nuchal organs, the appearance of metameric dorsal ciliated organs, or the presence of certain glandular structures should now be a standard among characters described for Spionidae. By the collection of fresh material during the workshop, it was also possible to provide information on molecular markers (DNA barcodes) for the Lizard Island spionid fauna. This allows an integrative approach to the taxonomy of the studied genera.

Material and methods

Study area

The study area is located on the northern Great Barrier Reef (270 km northeast of Cairns, Queensland, Australia). The Lizard Island group lies midway between the continental coast and the outer barrier reef. Lizard Island is the largest island in the area with about 10 km² in size. In the immediate vicinity are three smaller islands (Palfrey, South and Bird), and the nearby North Direction Island. The islands are surrounded by fringing-reefs. At the island shores smaller patches of mangroves and beaches with coralline sand, interspersed with sea grass and algae, are found.

Collection of material

Collection of the material took place during the polychaete workshop from 13–24 August 2013. Samples were collected by hand on SCUBA or snorkel. In the intertidal samples of sand or coral rubble were taken by means of shovels and corers. Algae were scraped from stones, corals or artificial hard-bottom. Samples were either sieved through 0.5 mm mesh or elutriated first or did not undergo any pre-treatment before they were presorted according to supraspecific taxa in the lab under the light microscope. The sampling depth was 0–25 m. Specimens were picked alive and originally fixed in 4% borax-buffered formaldehyde for morphological studies and in 96% ethanol for genetic studies. The formalin fixed specimens were later transferred to 70% ethanol. Selected specimens were fixed in Karnovsky´s fixative (Karnovsky 1965) for histological studies.

A selection of specimens was photographed alive in the lab by the workshop photographer Alexander Semenov with a Canon 5d Mark II equipped with Canon MP-E 1-5x Macro f2.8 lens + 2x Inon Z-240 strobes. For large individuals the lens was Canon 100mm f2.8L II USM Macro. For underwater shots the camera was combined with a Subal C5DM2 underwater housing. The majority of photos was taken with ISO100, 1/200sec shutter speed, aperture f13.

Morphology

Morphology was investigated using light and scanning electron microscopy (SEM). Methyl green staining is strongly recommended for observation of most characters by means of light microscopy. Specimens have to be transferred into water first and then dipped into an aqueous Methyl green solution. The staining fades completely when specimens are returned to ethanol. Ventral epidermal glands are best observed after transfer of specimens to ethanol (after methyl green staining in water).

Drawings were made using a camera lucida. Light micrographs were taken with an Olympus SC30 digital camera. For SEM studies, specimens were dehydrated in a graded ethanol series, critical-point dried, sputter coated with carbon and examined with a Leo 1525 scanning electron microscopes. Measurements of body width refer to the distance between the distal-most structures on the widest chaetiger seen on the anterior end in dorsal view (without chaetae). For details concerning the measurements of different species see information in the text. Descriptions of postchaetal lamellae refer to the dimensions of the lamellae along the y-axis (=dorsal-ventral axis) with the attributes “long” and “short”, and along the x-axis (proximal-distal axis) with the attributes “high” and “low”.

By the term “nuchal organ” we here refer to the ciliary bands on the dorsum posterior and posterolateral to the

prostomium. Metameric dorsal ciliated structures on anterior and some middle segments are referred to as dorsal ciliated organs.

The following abbreviations are used: tcb = transverse ciliary band, and in case specimens were incomplete: af = anterior fragment, mf = middle fragment.

In addition to the material collected during the expedition, specimens deposited in museum collections were examined. The following abbreviations are used for the various museums and institutions that provided loans of registered specimens and where newly collected material was deposited:

AM	Australian Museum, Sydney, Australia
LACM-AHF	Natural History Museum of Los Angeles County. Los Angeles, U.S.A.
NMV	Museum of Victoria, Melbourne, Australia
ZMH	Zoological Museum, Hamburg, Germany

Locality descriptions of material collected during the August 2013 Polychaetae Taxonomy Workshop (MI QLD 2329–MI QLD 2449) are listed as in Ribas & Hutchings (2015, *Zootaxa* 4019). Number of specimens under each registration number is one unless otherwise specified.

Histology

Some specimens of *Microspio granulata* and *Spio blakei*, originally fixed in formalin and later transferred into 70% ethanol, were transferred in a graded series of ethanol (70–30%) and subsequently washed in Na-Cacodylate buffer (0.05 M, ph 7.3). For better contrast the specimens were put in Osmiumtetroxide solution (1%) over night at 4°C. Then they were washed again in the buffer, dehydrated in a graded series of ethanol (30–100%) and infiltrated and embedded in Araldite epoxy resin or LR white resin (both Sigma-Aldrich Co. LLC). Sections with a thickness of 1 µm were cut using a Reichert-Jung rotatory microtome Ultracut E (Reichert, Inc.) and subsequently stained in 1% toluidine blue and pyronin G staining solution for 40 seconds. Micrographs were taken with an Olympus SC30 camera (Olympus Corporation).

Genetic analysis

Total genomic DNA was extracted from ethanol preserved animals using either an AutoGenprep 965 (AutoGen, MA, USA) according to the manufacturer's protocol or a commercially available kit. PCR amplifications of partial mitochondrial COI and 16S and nuclear 18S were performed in 10 µl reactions containing 0.25 µL BSA, 0.5 µL dNTP (2.5 mM each), 1 µL 10x NH_4 reaction buffer, 0.3 µL of each primer (10 µM), 0.5 µL $MgCl_2$ (50 mM), 0.1 µL DNA Polymerase (5 U/µL; Bioline, Taunton, MA, USA), and 2 µL of template DNA. The following primers were used: 18Sfw (Englisch & Koenemann 2001) and 18L (Halanych *et al.* 1995) for amplifying partially sequences of 18SrDNA, LCO1490 and HCO2198 (Folmer *et al.* 1994) for mitochondrial COI, and either 16Ssf and 16Ssr (Tsang *et al.* 2009, Tsang pers. comm.) or 16Sar and 16Sbr (Kessing *et al.* 1989) for amplifying mitochondrial 16S. The PCR temperature profile consisted of an initial denaturation at 94°C (5 min), followed by 37 cycles of denaturation at 94°C (30 s), annealing at 48–50°C (30 s) and extension at 72°C (45–60 s) followed by a final extension at 72°C (5 min). For sequencing, PCR products were purified using ExoSAP−IT (USB; Affymetrix, Cleveland, Ohio). Samples were incubated at 37°C for 30 min and the reaction was then deactivated at 80°C for 20 min. Sequencing reactions were performed in 10 µL volume containing 1 µL purified PCR product, 0.5 µL BigDye Terminator, 1.75 µL Big Dye Terminator reaction buffer, and 0.5 µL primer. Sequencing was performed using the PCR primers and the cycle profile consisted of 30 cycles of 95°C (30 s), 50°C (30 s) and 60°C (4 min). Products were cleaned up with the Sephadex G-50 (Sigma S−5897) method, dried, and stored at -20°C. Products were run on a 3730xl DNA Analyzer (Applied Biosystems).

TABLE 1. Haplotypes, collection data, and GenBank accession numbers of sequenced specimens.

Species	Haplotype	Collection locality	Reg.-No.	No. of haplotypes COI	Acc.-No. of COI	No. of haplotypes 16S	Acc.-No. of 16S	No. of haplotypes 18S	Acc.- No. of 18S
Spiophanes viriosus				1		0		1	
	LizSpio 85	MI QLD 2379	AM W44566.001		KP636518				KP636519
Scolelepis kudenovi				1		0		1	
	LizSpio 75	MI QLD 2429	AM W44836		KP636516				KP636517
Spio blakei				3		5		1	
	KJ271	MI QLD 2376	AM W44372		KP636499		KP636505		
	KJ272	MI QLD 2376	AM W44372				KP636504		
	KJ274	MI QLD 2376	AM W44372				KP636506		
	LizSpio 74	MI QLD 2376	AM W44372		KP636500				
	LizSpio 70	MI QLD 2376	AM W44372		KP636501		KP636502		KP636507
	LizSpio 71	MI QLD 2376	AM W44372				KP636503		
Malacoceros indicus				2		2		1	
	KJ270	MI QLD 2376	AM W44378		KP636509		KP636510		
	KJ269	MI QLD 2439	AM W44838.001		KP636508		KP636511		KP636512
Microspio granulata				1		1		1	
	KJ273	MI QLD 2379	AM W44480		KP636513		KP636514		KP636515

Some gene fragments were amplified following a slightly different protocol using either Phusion High-Fidelity DNA Polymerase (Biozym, Germany) with 3 µl DNA template or puReTaq™ Ready-To-Go™ polymerase chain reaction beads (GE Healthcare, UK) according to the manufacturers' protocols. The PCR primers were the same as above and the PCR reactions were performed with the following steps: initial denaturation at 94 to 98 °C (1 to 5 min); followed by 34 to 40 cycles at 94 to 98 °C (30 to 45 s), 45 to 52 °C (30 to 50 s) and 72 °C (60 s), and then a final extension at 72 °C (5 min). PCR products were then purified either from agarose gels (innuPREP Gel extraction kit, Analytik Jena, Germany) or from PCR reactions (QIAquick PCR purification kit, Qiagen, Germany or innuPREP DOUBLEpure kit, Analytik Jena, Germany) according to the manufacturers' protocols. Both strands were sequenced by a commercial service (GATC, Konstanz, Germany) with the same primers as used for PCR.

Sequences were aligned using the Clustal W option with default settings in BioEdit (Hall 1999) and proofread. Forward and reverse sequences of the same individual were merged. Genbank accession numbers of haplotypes are given in Table 1. Genetic distances were calculated using PAUP* version 4.0 b10 (Swofford 2000). Uncorrected p-distances were calculated for 18S and 16S sequences and kimura-2-parameter (K2P) distances for COI sequences. Additional sequence data for interspecies comparisons were retrieved from GenBank, included into the alignments and the ends of the sequences were trimmed.

Results

Taxonomic account

Spionidae Grube, 1850

Genus *Malacoceros* Quatrefages, 1843

Malacoceros Quatrefages, 1843; type-species: *Spio vulgaris* Johnston, 1827, designated by Pettibone, 1963.
Colobranchus Schmarda, 1861; type-species: *Colobranchus tetracerus* Schmarda, 1861, by monotypy.
Uncinia Quatrefages, 1865; type-species: *Colobranchus ciliatus* Keferstein, 1862 (= *C. tetracerus* Schmarda, 1861), by monotypy.
Scolecolepis Malmgren, 1867; type-species: *Spio vulgaris* Johnston, 1827, by original designation.
[Synonymy *fide* Blake & Kudenov, 1978]

Diagnosis. (after Delgado-Blas & Díaz-Díaz 2013, amended). Prostomium broad anteriorly, T-shaped, triangular-shaped, bell-shaped; broadly rounded along anterior margin; occipital antenna absent. Eyes present, irregularly arranged or arranged in pairs, or eyes absent. Caruncle entire, trilobed or buttonlike. Nuchal organs as two small ciliated grooves posteriolaterally to the caruncle. Palps ventrally grooved. Peristomium reduced to moderately developed. Eversible, sac-like proboscis. Cirriform branchiae from chaetiger 1 to end or nearly end of body; basally fused or free to notopodial lamellae; branchiae usually overlapping at dorsal midline in anterior segments, reduced in length and thickness in middle and posterior segments. Dorsal ciliated organs present or absent. Transverse ciliated bands across the dorsum present. Parapodia 1–3 may be shifted dorsally to subsequent segments. Chaetae include simple capillaries, scalpel chaetae, neuropodial uni-, bi-, tri- or quadridentate hooded hooks. Sabre chaetae present. Pygidium with 2, 4, 6, 6–8, or 15–30 anal cirri or with two anal cirri and a rounded or spatuliform dorsal lobe. Eggs with complex thick egg membranes ornamented resembling honeycombs with numerous cortical alveoli (Blake & Arnofsky 1999). Male gametes are ect-aquasperm type (Guérin & Kerambrun 1984).

Remarks. The generic diagnosis provided by Delgado-Blas & Díaz-Díaz (2013) includes a number of characters which formerly had not been considered. Hence it can be regarded an appropriate attempt for the refinement of diagnosis. Many generic diagnoses are evidently not sufficient and the assignment of species is not reliable. This applies also to *Malacoceros*. The latest example is the publication by Sikorski (2013) in which the author proposes the transfer of *Malacoceros jirkovi* Sikorski, 1992 to *Spio* Fabricius, 1785. In the same publication the author considers that the morphologically similar *M. indicus* might also belong to *Spio*. *Spio jirkovi* (Sikorski, 1992) comb. nov. is established based on 1) the fixed number of four anal cirri opposed to a size-variable number of anal cirri in *Malacoceros*, 2) the absence of anterolateral horns and 3) the arrangement of teeth in a tandem

pattern instead of a pair-wise arrangement. These arguments seem disputable. A fixed number of four anal cirri is not exclusive for *Spio* but quite widespread among Spionidae. None of the published generic diagnoses for *Malacoceros* state a size-variable number of anal cirri to be diagnostic. The term anterolateral horns might refer to morphologically similar but non-homologous structures within Spionidae (*Rhynchospio*, *Glandulospio*, *Scolecolepides*, *Glyphochaeta*, *Pygospiopsis*, *Lindaspio*, *Atherospio*, *Spiophanes*, *Microspio*, etc.) and a detailed review of this character is certainly required for all taxa (Meißner *et al.* 2014). However, the prostomial shape of *S. jirkovi* being subtriangular, seems rather unusual for *Spio*. The absence of paired teeth is not uncommon among *Malacoceros* species (e.g., *M. jennicus* Graff, Blake & Wishner, 2008, *M. fuliginosus* (Claparède, 1870), *M. tetracerus* (Schmarda, 1861), *M. cariacoensis* Delgado-Blas & Díaz-Díaz, 2010). On the other hand, *M. indicus*, the species Sikorski (2013) considers closely related to *S. jirkovi*, has paired apical teeth and hence contradicts Sikorski´s line of argument.

There are also good reasons why *S. jirkovi* is not in agreement with the generic diagnosis of *Spio*. For this species nuchal organs being small elongate grooves lateral to the posterior tip of the prostomium have been observed (Meißner *et al.* 2014). Metameric dorsal ciliated organs are not discernable (Meißner *et al.* 2014). The same applies to *M. indicus* (this paper and cited literature herein). For *Spio* nuchal organs with short median and long lateral ciliary bands, extending to chaetiger 2 or 3, are typical and metameric dorsal ciliated organs are usually present and easily detected under the light microscope after methyl green staining. Ventral epidermal glands are usually present in anterior and middle chaetigers of *Spio* species. Such glands could not be detected in *M. jirkovi* nor in *M. indicus*. Therefore we do not agree with the new combination proposed by Sikorski (2013) and regard *Malacoceros jirkovi* as the valid name for the species. Nethertheless we admit, that the generic diagnosis of *Malacoceros* (and of several other genera) might not be sufficient in its current version.

Malacoceros indicus **(Fauvel, 1928)**

(Fig. 1)

Scolelepis indica Fauvel, 1928: 93, figs 2g–m.—Fauvel 1930: 35, figs 7g–m; Fauvel 1953: 313–314, figs 165g–m; Monro 1931: 25; Berkeley & Berkeley 1941: 21; Reish 1961: 277.

Malacoceros indicus.— Pettibone 1963: 99; Day 1967: 477, figs 18.5.p–u; Blake & Kudenov 1978: 195; Blake 1983: 219; Blake 1996: 105–107, fig. 4.4; Ben-Eliahu *et al.* 1984: 96; Dauer & Ewing 1991: 395–400, fig. 1; Imajima 1991: 6–9, figs 2a–g, 3a–j.

Malacoceros (*Malacoceros*) *indicus*.— Foster 1971a: 50–53, figs 93–99; Foster 1971b: 1455–1457, figs 1–6.

Spio punctata.— Hartman 1961: 89–90, plate 11, figs1–3; Hartman, 1969: 175, figs 1–3; *fide* Blake, 1996.

[Synonymy *fide* Williams 2007]

Material examined. AM W.44376, MI QLD 2376 (2 af), formalin; AM W.44384, MI QLD 2376, af, formalin; AM W.44377, MI QLD 2376, af, formalin; AM W.44378, MI QLD 2376, af, mf, palps, 96% ethanol; AM W.44565, MI QLD 2422, af, formalin; AM W.44835, MI QLD 2422, af, formalin; AM W.44834, MI QLD 2422, af, formalin; AM W.44838, MI QLD 2422, af, formalin; AM W.44834.001, MI QLD 2422, mf, no longer extant; AM W.44858, MI QLD 2439, af, formalin; AM W.44858.001, MI QLD 2439, mf, ethanol; AM W.44859, MI QLD 2438, af, formalin.

Diagnosis. Prostomium with distinct anterolateral horns or with anterolateral projections; prostomium posteriorly extended into short caruncle which terminates at the end of chaetiger 1. Branchiae present from chaetiger 1 for most of body length; cirriform with elongate, slender tip, separate from notopodial lamellae; first pair of branchiae usually about same length or longer than notopodial lamellae; branchiae often overlapping at midline in anterior mid-body region. Neuropodial postchaetal lamellae rounded, with small medial nipple-like projection in chaetigers of middle body region. Neuropodial bi-, tri-, or quadridentate hooded hooks present from chaetigers 28–115, 3–11 hooks per fascicle.

Description. (based on specimens examined in the course of the present study). All specimens incomplete; longest specimen 154 chaetigers, 2.2 mm wide and 41 mm long; other specimens 0.8–3.8 mm wide and 11.2–27 mm long. Prostomium bell-shaped to sub-triangular, larger specimens with distinct anterolateral horns (Fig. 1A, B), smaller specimens with anterolateral projections; prostomium posteriorly extended into short protuberant caruncle which terminates at the end of chaetiger 1 (Fig. 1B). Prostomium usually with two groups of black eyes positioned on posterior half at maximal width of prostomium is reached, up to six eyes in one group, arranged in irregular

patches or vertical rows (Fig. 1B). Occipital antenna absent. Peristomium not well developed. Palps detached, but scars of palp insertion discernable laterally to beginning of caruncle anterior to first chaetiger. Nuchal organs not unambiguously discernable, probably as small elongate grooves laterally to the posterior tip of the prostomium. Metameric dorsal ciliated organs not discernable. Dorsal crests absent but transverse ciliary bands across dorsum in well-preserved specimens present until posterior chaetigers.

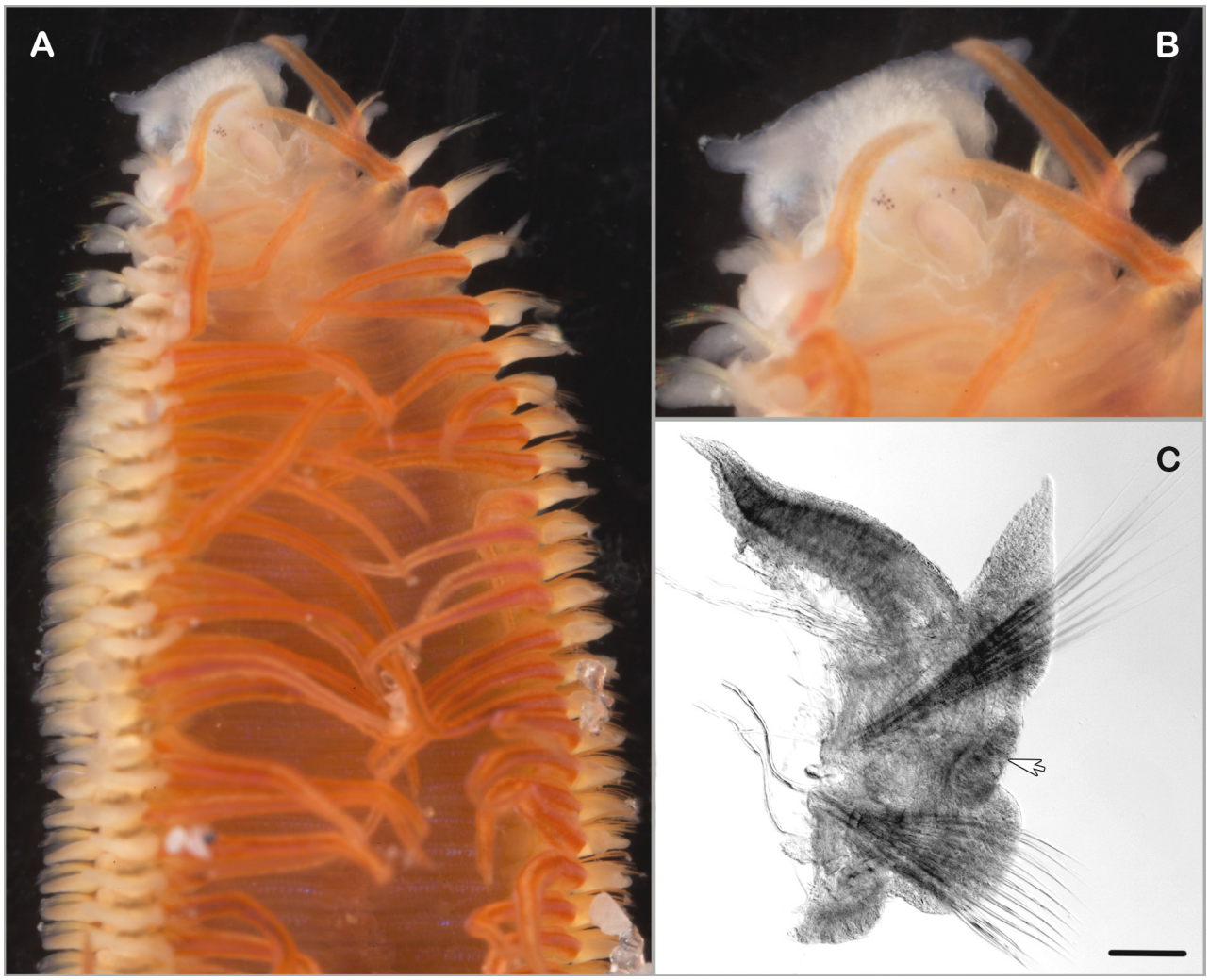

FIGURE 1. *Malacoceros indicus* (Fauvel, 1928), MI QLD 2429 (A, B); AM W.44838, MI QLD 2422 (C). A. Anterior end of live specimen, palps removed; B. Enlargement of detail from A, prostomium and anteriormost chaetigers, note protuberant caruncle and anterolateral horns; C. Left parapodium from 23rd chaetiger; note rounded shape of neuropodial postchaetal lamella with small (very indistinct) pointed tip and interramal bulge indicated by arrow. Scale bars: A, B no scale available, specimens are at least 3 mm wide, C = 100 µm. Photo: A, B—A. Semenov.

Dorsal branchiae present from chaetiger 1 until the end of fragment; cirriform with elongate, slender tip, separate from notopodial lamellae throughout (Fig. 1A–C); first branchiae either slightly shorter, about same length or even longer than notopodial lamellae, from about third chaetiger reaching full length and often reaching dorsal midline or branchiae from both sides overlapping at midline (Fig. 1A); after first third of fragment (from about chaetiger 50) branchiae becoming thinner and shorter, but still distinctly longer than notopodial lamellae. Interparapodial lateral pouches absent.

Parapodia on chaetiger 1 positioned slightly more dorsally than on following chaetigers, there in lateral position. Notopodial postchaetal lamellae lanceolate, slender, becoming shorter posteriorly; neuropodial postchaetal lamellae of first and also second chaetiger elongate and tapered, then becoming rounded (Fig. 1C), often with small pointed tip on outer margin, but nipple-like projection rarely accentuated; more posteriorly neuropodial lamellae lower. Both parapodial rami without prominent prechaetal lamellae prechaetal thickened

swelling (Fig. 1C) developing from chaetiger 3, present in near interramal position until about chaetigers 30–40, thereafter inconspicuous.

Chaetae in anterior and middle chaetigers capillaries; in neuropodia with very fine granulations near tip and with narrow sheaths, arranged in two rows, chaetae in anterior row shorter than in posterior row; in notopodia chaetae alimbate and rather smooth, arranged in two rows, chaetae in anterior row shorter than in posterior row; few very long smooth capillaries present in uppermost position in notopodia. From middle body region capillaries and hooks present; in specimens up to 1.4 mm wide neuropodial hooks in neuropodia present from chaetiger 31–39, in two very large specimens (anterior fragment 2.2 mm wide with 154 chaetigers or 3.8 mm wide with 83 chaetigers) hooks either present from chaetiger 121 or absent; hooks hooded with three apical teeth above main fang, consisting of one pair of teeth and additional minute apical tooth (difficult to observe due to size); 3–6 hooks present per fascicle; hooks accompanied by 1–3 thin smooth capillaries in superior position; notopodia with smooth capillaries without sheaths, first arranged in two irregular rows, more posteriorly bundle of capillaries of different length; very long capillaries present in notopodia in superiormost position. Capillaries in inferiormost position in neuropodia from chaetiger 2, numbering up to five (in very large specimen up to 15), chaetae arranged in a bundle; these capillaries slightly stronger and shorter than other capillaries in neuropodium; hook-bearing chaetigers with few (up to five) slightly granulated sabre chaetae with narrow sheath in inferiormost position; in more posterior chaetigers only 1–3 sabre chaetae present.

Pygidium not observed (all specimens incomplete).

Pigmentation. Pigment neither discernable in live or formalin preserved specimen.

Methyl green staining pattern. Inconspicuous. Prostomium, branchiae and postchaetal lamellae most intensely stained.

Remarks. *Malacoceros indicus* is, based on current knowledge, a very widespread species. Intraspecific variability is acknowledged to be large. For example, the number of secondary teeth in neuropodial hooks are observed to range from two (Blake (1996) for specimens from California), three (Williams (2007) for specimens from the Philippines, also this paper for Lizard Island specimens), to four (Imajima (1991) for specimens from Japan). Foster (1971b) found tri- and quadridentate hooks in the same parapodium in specimens from the Carribean. Also the number of hooks per fascicle varies: our specimens have 3–6 hooks per fascicle, Williams (2007) reports up to 7 hooks, Foster (1971b) 7–8 hooks, Blake (1996) 7–10, Imajima (1991) up to 11. The first presence of neuropodial hooks was observed in chaetigers 31–121 (Lizard Island, present paper), chaetigers 28–62 (Williams 2007), 30–57 (Imajima 1991), 30–35 (Blake 1996), and at the 37th chaetiger (Foster 1971b). This character seems to be size-dependent in the specimens collected at Lizard Island since only the largest two individuals exhibit a very late start of neuropodial hooks (see description above). Hooks might be continously lost in middle chaetigers during ontogenesis.

The prostomial shape varies with the development of anterolateral horns. Among specimens from Lizard Island only the two large individuals (2.2 and 3.8 mm wide) have anterolateral horns whereas all other specimens (0.8–1.4 mm wide) have anterolateral projections. In the literature the species is usually illustrated having anterolateral projections and rarely short anterolateral horns (compare Foster 1971b, Imajima 1991, Blake 1996, Williams 2007). We noticed that specimens from Lizard Island have a protuberant caruncle. This is obviously also the case in specimens from the Philippines (compare illustrations provided by Williams (2007)). All other above mentioned authors have provided illustrations displaying a differently shaped caruncle and did not mention such a development in their descriptions.

Information on three different molecular markers is provided for *M. indicus* from Lizard Island in the course of the present study. Since data from other localities are not available from sources like GenBank or BOLD a comparative analysis could not be undertaken. The inclusion of both molecular and morphological data should be aspired too for future studies to verify the species status of *M. indicus*.

Habitat / Ecology. In the Lizard Island area the species was found in shallow water on sandy beaches, between seagrass and mangroves. The species was also found from sandy beaches, in the shallow subtidal (<5 m) in Boracay of the Aklan province in the Philippines (Williams 2007). Records from Japan are from shallow water to 159 m water depth (Imajima 1991). Foster (1971a) reported the species from the Bahamas and Puerto Rico from shallow water from sandy bottom and *Thalassia* beds. Records from Costa Rica (Golfo de Nicoya) account for subtidal habitats (11–18 m water depth) with muddy sand or sand (Dean 2004). Dauer & Ewing (1991) classified the species as an indiscriminate surface deposit-feeder.

Distribution. Australia (Queensland, NSW), New Caledonia, Philippines, Japan, India, SW Africa, Caribbean, Chile, USA (southern California, Massachusetts to Georgia), Costa Rica (Golfo de Nicoya).

Genus *Scolelepis* Blainville, 1828

Scolelepis Blainville, 1828; type-species: *Lumbricus squamata* Müller, 1806, by monotypy.
Aonis sensu Audouin & Milne-Edwards, 1833 [Not Savigny, 1822] (misapplication of Savigny´s genus for *Nereis caeca* (Nephtyidae))
Asetocalamyzas Tzetlin, 1985 (dwarf male of a spionid, not a parasitic syllid as originally described)
Nerine Johnston, 1838 (subjective synonym)
Nerinides Mesnil, 1896 (subjective synonym)
Pseudomalacoceros Czerniavsky, 1881 (subjective synonym)
Scolecolepis Malmgren, 1867 (unjustified emendation)
[Synonymy *fide* Read, 2015]

Diagnosis. Prostomium pointed on anterior margin, sometimes truncate, posteriorly extended into pointed caruncle, rarely flattened or depressed or blunt, caruncle attached or detached; occipital tentacle present or absent. Peristomium well-developed, with or without lateral wings encompassing prostomium partially. Nuchal organs and metameric dorsal ciliated organs not discernable (by means of light microscopy). Palps without median ciliated groove, but usually with two distinctly or indistinctly separated bands of transverse rows of cilia present. Branchiae present from chaetiger 2, continuing to near end of body, in anterior chaetigers completely fused to notopodial lamellae or distally free; accessory branchiae present or absent. Anterior chaetae limbate capillaries, usually arranged in two rows; posteriorly hooks and capillaries present, hooks with 0–3 apical teeth with a falcate or straight shaft (subgenus *Scolelepis*) or multidentate with large main fang, several apical teeth and curved shaft (subgenus *Parascolelepis*). In *Parascolelepis* palpal sheaths are well-developed, in *Scolelepis* palpal sheaths are short and fused to the palp. Pygidium with oval disc or multilobed.

Remarks. According to Eibye-Jacobsen (1997) *Scolelepis* (*Parascolelepis*) appears to be defined on the basis of good autapomorphies, whereas *Scolelepis* (*Scolelepis*) may well be paraphyletic. Some authors have used *Scolelepis* and *Parascolelepis* as full genera (e.g., Blake & Arnofsky 1999, Williams 2007) though a formal statement regarding this matter was not given.

Scolelepis (*Scolelepis*) *inversa* n. sp.

(Figs 2, 3)

Type material. Holotype: AM W.44474, MI QLD 2396, formalin.

Diagnosis. Prostomium narrow, anteriorly pointed, and with slight constriction at the level of chaetiger one, posteriorly extended into pointed, erect caruncle which is not attached to dorsum. Low transversal ciliated bands (tcb) present throughout body and as dorsal crests in posteriormost chaetigers. Chaetiger 1 well developed, with small slender notopodial lamellae, in prechaetal instead of postchaetal position; notochaetae and neurochaetae present. Branchiae present throughout body; anterior branchiae long, cirriform and longer than notopodial postchaetal lamellae, with tips almost touching one another above dorsal midline, branchiae from middle chaetigers even longer. Notopodial postchaetal lamellae foliate and folded, with rounded tip, completely fused to branchiae until chaetiger 16; from chaetiger 17 foliate and folded with pointed tip becoming free from branchiae distally. Anterior body region with stout capillaries in both rami; in notopodia in two rows, in neuropodia of about chaetigers 6–16 in three rows. Hooded hooks bidentate with upright apical tooth in neuropodia from chaetiger 23 numbering up to nine hooks per fascicle; in notopodia hooks of the same appearance from about chaetiger 35, 1–5 hooks per fascicle. Pygidium with ventral, entire cushion.

Description. Holotype complete but fragmented specimen: one anterior fragment with 25 chaetigers, one middle fragment with seven chaetigers, one posterior fragment with 28 chaetigers (altogether 60 chaetigers); body width 2.2 mm (measured at anterior middle body region, chaetae and postchaetal lobes omitted), total length of all fragments 21.9 mm. Prostomium anteriorly pointed, projecting over peristomium, narrow with slight constriction at level of chaetiger one, posteriorly extended into pointed, erect caruncle not attached to dorsum (Fig. 2A); two pairs of black eyes arranged in trapezoid, anterior pair crescent-shaped, wider apart than posterior pair, eyes of posterior pair round, pairs very close to each other, almost forming one row and positioned at the prostomial

constriction. Peristomium moderately developed, forming low lateral wings partially encompassing prostomium posteriorly. Palps rather thin, short, reaching back to about chaetiger 12–15; with thickened base (sheath, Fig. 3D) with irregular groups of cilia; palps with two weakly separated rows of mucus secreting cells and accompanying cilia (Fig. 3E, F), long rows approximately 46 µm long, short rows approximately 18 µm long. Low but distinct tcb´s present in anterior and middle body region, well developed dorsal crests present in about last 20 chaetigers (Fig. 2G).

Chaetiger 1 well developed, with subulate postchaetal lamellae in both rami, notopodial lamellae small and slender, in prechaetal instead of postchaetal position, neuropodial lamellae larger and in postchaetal position; notochaetae and neurochaetae present (Fig. 2A). Branchiae from chaetiger 2, present throughout body; anterior branchiae long cirriform, longer than notopodial postchaetal lamellae (Fig. 2A), with tips almost touching one another above dorsum; from middle chaetigers branchiae even longer and distinctly longer than notopodial lamellae (Fig. 2B–D); in posterior chaetigers again almost touching above dorsum, only slightly longer than notopodial lamellae or of about same length (Fig. 2E–G). Notopodial postchaetal lamellae foliate, folded, completely fused to branchiae until chaetiger 16 (Fig. 2A, B); from chaetiger 17 foliate and folded with pointed tip becoming free from branchiae distally (Fig. 2C–E); posterior chaetigers with foliate but less folded notopodial postchaetal lamellae, pointed tips free from branchiae, lower portion of notopodial lamellae broadly rounded (Fig. 2F). Neuropodial postchaetal lamellae broadly rounded, from chaetiger 18 slightly notched, from chaetiger 21 divided into large rounded neuropodial lamellae and inferior conical lobe with rounded tip; in posterior chaetigers neuropodial postchaetal lamellae foliate with well developed superior part and in almost interramal position, inferior lobe conical to subtriangular with rounded tip (Fig. 2B–F). Prechaetal lobes absent.

Capillary chaetae and bidentate hooded hooks in neuropodia and notopodia; first chaetiger with bundle of thin capillaries in notopodia, neuropodia with two rows of stouter capillaries with sheaths, capillaries of both rows of about same length; neuropodia of chaetigers 2–5 with slightly granulated capillaries in two rows, in chaetigers 6–16 in three rows (Fig. 3A), capillaries of anterior row with broad sheaths (Fig. 2I) and in second and third row with narrower sheaths (Fig. 2H); after chaetiger 16 until about chaetigers 20/21 stout capillaries, in succedent chaetigers thinner, arranged in two rows; in notopodia of chaetigers 2–21 stout, broadly sheathed capillaries with granulations near the tips, arranged in two rows of about same length; in following chaetigers notochaetae thinner and longer with very narrow sheaths and without granulations; superior fascicle of thin long capillaries with narrow sheaths present in notopodia up to about chaetiger 30, with slight granulations in anterior third of the body; inferior fascicle of thin, long capillaries with narrow sheaths in position of sabre setae in neuropodia present throughout body (Fig. 2J), with slight granulations until anterior middle body region, sabre chaetae absent. Neuropodial hooks from chaetiger 23, numbering 4 per fascicle first, then increasing to 9 hooks per fascicle more posteriorly, notopodial hooks from about chaetiger 35, 1–5 hooks per fascicle but usually 4, all hooks hooded, bidentate with upright apical tooth (Figs 2K, 3B); hooks accompanied by few thin, long, smooth capillaries with very narrow sheaths or more posteriorly without sheaths in neuropodia, capillaries in superior position in the neuropodial ramus; in notopodia hooks accompanying smooth capillaries of normal thickness with narrow sheaths arranged in irregular rows.

Pygidium with ventral, entire cushion and dorsal anus (Fig. 2G).

Pigmentation. Formalin fixed specimen of whitish colour, with tiny spot of brownish pigment at the constriction of the prostomium next to the eyes.

Methyl green staining pattern. Inconspicuous; prostomium, peristomium, pygidium, branchiae and parapodial lobes most intensely stained.

Remarks. *Scolelepis inversa* n. sp. is most similar to *S. precirriseta* Blake & Kudenov, 1978. The two species are the only known species of *Scolelepis* in which the dorsal lamella of chaetiger 1 is in prechaetal instead of postchaetal position (Fig. 2A). In both species the shape of the prostomium is also very similar. However, there are also several differences: *S. inversa* n. sp. has bidentate hooded hooks with an upright apical tooth from chaetiger 23 in neuropodia and from about chaetiger 35 in notopodia whereas in *S. precirriseta* hooks with three pairs of small apical teeth are present in neuropodia from chaetigers 15–20, and notopodial hooks are unknown. In *S. inversa* n. sp. the postchaetal notopodial lamellae are completely fused to the branchiae in chaetigers 2–16 whereas branchiae and notopodial lamellae are fused only at the base in anterior chaetigers of *S. precirriseta*. In addition, *S. inversa* n. sp. has stout capillaries with broad sheaths arranged in up to three rows present in parapodia of the anterior body region (Fig. 3A).

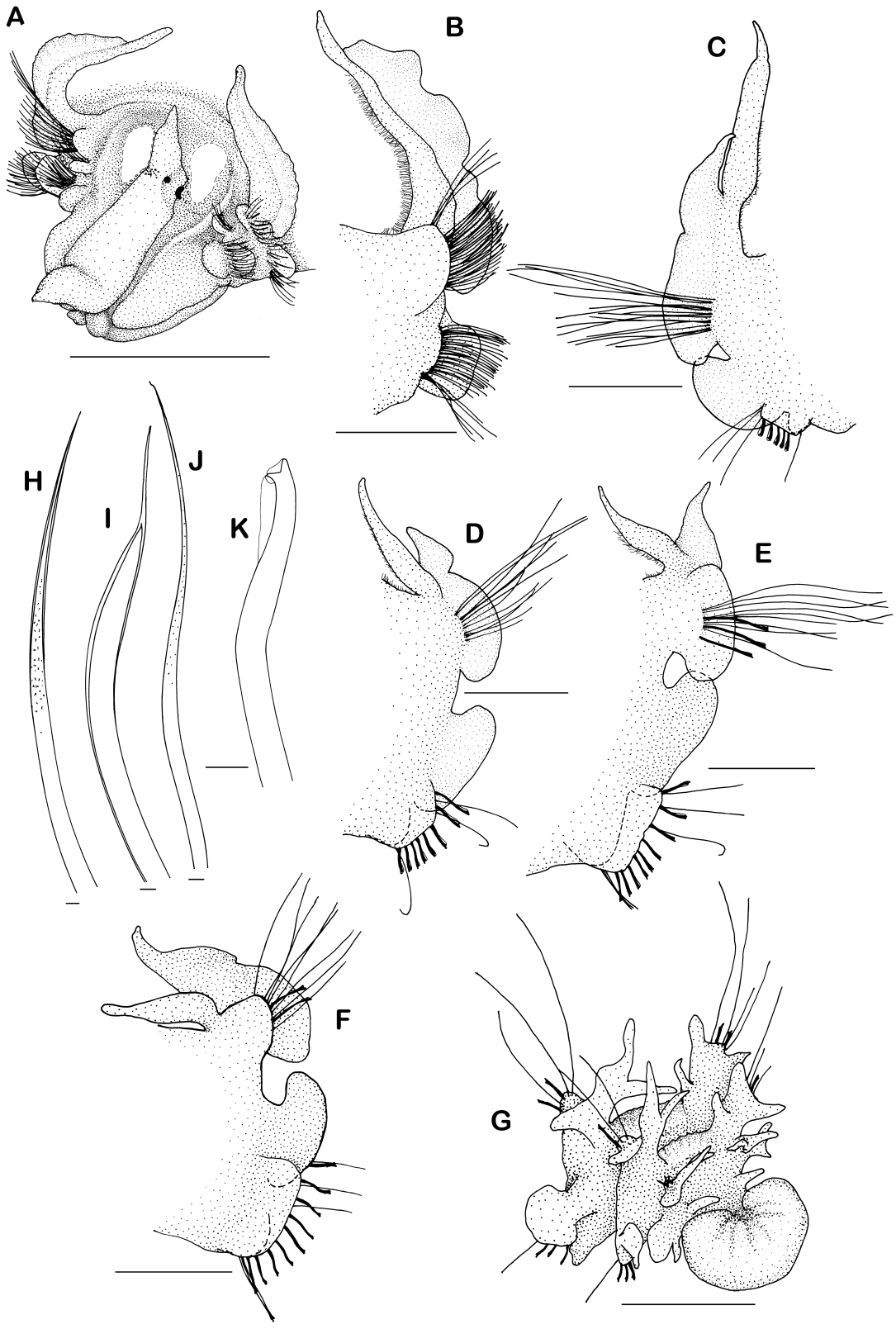

FIGURE 2. *Scolelepis inversa* n. sp., holotype, AM W.44474, MI QLD 2396. A. Anterior end, dorsal-oblique view, palps removed; B. Parapodium from chaetiger 10, anterior view; C. Same from chaetiger 25; D. Same from chaetiger 33; E. Same from 13th last chaetiger; F. Same from 9th last chaetiger; G. Posterior end with pygidium with ventral, entire cushion, dorsal-oblique view; H. Capillary from 10th neuropodium; I. Stout, broadly sheathed capillary from 10th neuropodium; J. Inferior capillary from 10th neuropodium; K. Bidentate hooded hook with upright apical tooth from 33rd neuropodium. Scale bars: A = 1 mm, B–G = 0.5 mm, H–J = 5 µm, K = 10 µm.

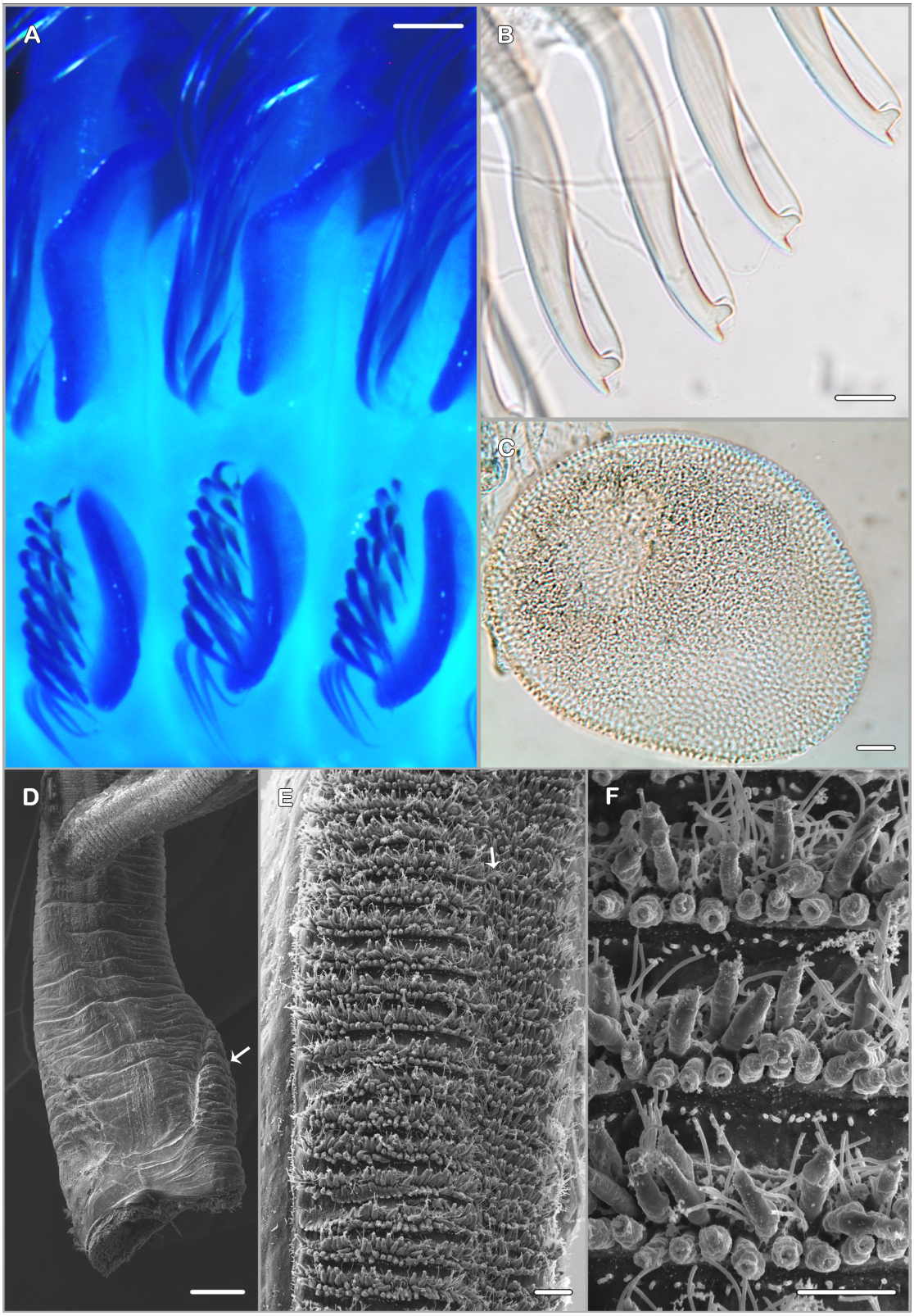

FIGURE 3. *Scolelepis inversa* n. sp., holotype, AM W.44474, MI QLD 2396. A. Chaetigers 11–13, lateral view (note stout capillaries arranged in three rows in neuropodia); B. Neuropodial bidentate hooded hooks from chaetiger 33 (note upright apical tooth), accompanying capillaries not shown; C. Egg with ornamented egg envelope resembling honeycombs; D. Palp, thickened base (sheath) indicated by arrow, note irregular groups of cilia on the left side of the palp base; E. Palp ciliation and mucus secreting cells at the distal part (near tip), arrow indicates indistinct division between long and short transverse rows of cilia and mucus secreting cells; F. Detail of palp ciliation and arrangement of mucus secreting cells at the distal part. Scale bars: A, D = 100 µm, B, C = 20 µm, E 10 µm, F = 5 µm.

The general arrangement of mucus secreting cells and cilia on palps of *S. inversa* n. sp. is in good agreement with the palp ciliary pattern of *Scolelepis alisonae* Williams, 2007 and *Scolelepis magnicornuta* Williams, 2007. All three species exhibit long and short rows of cilia (and mucus secreting cells in *S. inversa* n. sp.) that are indistinctly separated, with the long rows 41–46 µm in length and the short rows 18–26 µm in length. In *S. inversa* n. sp. the number of mucus secreting cells is very high (compared to the number of cilia).

Etymology. "inversa" - Latin for reversed (turned backward) in order. The name refers to the prechaetal postion of the notopodial lamellae in the first chaetiger.

Habitat / Ecology. The species was found in sand underneath stones at extreme low tide not far from the beach. Eggs are present in segments of the middle and posterior body region; eggs with an ornamented egg envelope resembling honeycombs (Fig. 3C), dimensions 203 x 164 µm.

Distribution. So far only known from the type locality at Lizard Island, Australia, Queensland.

Scolelepis (*Scolelepis*) *kudenovi* Hartmann-Schröder, 1981

(Fig. 4)

Scolelepis (*Scolelepis*) *kudenovi* Hartmann-Schröder, 1981: 52, figs 124–129.—Maciolek 1987: table 1; Imajima 1992: 17–18, figs 11, 12.

Type material. Holotype: ZMH P16497, S. Pacific Ocean, Western Australia, Canarvon, Pelican point, inner beach, fine sand with detritus and *Posidonia* seedlings, 19.5 °C, 13 Oct 1975, af.

Other material examined. AM W.44836, MI QLD 2429, af, formalin; AM W.44836.001, mf, 96 % ethanol, no longer extant.

Diagnosis. Prostomium anteriorly trifid, median lobe sharply pointed, anterolateral lobes tapered; prostomium with transverse furrow in front of caruncle; caruncle subulate, slightly inflated, attached to dorsum. Low transversal ciliated bands present throughout the body. Chaetiger 1 well developed with chaetae in both rami. Branchial tips always free from notopodial postchaetal lamellae. Hooded hooks bidentate with very upright apical tooth in neuropodia from about chaetigers 38–44 (Australian specimens) or bidentate hooks from chaetigers 26–33 (Japanese specimens, Imajima 1992); in notopodia hooks from about chaetiger 98 (Australian holotype) or 55–62 (Japanese specimens). In Japanese specimens pygidium with ventral, entire cushion, unknown for Australian specimens.

Description. Based on re-examination of holotype and original description by Hartmann-Schröder (1981). Holotype fragmented specimen: one anterior fragment with nine chaetigers, three middle fragments of different length (66, 54, and 3 chaetigers); body width about 1 mm (measured at 8th chaetiger), total length of all fragments 42 mm. Prostomium anteriorly trifid, median lobe sharply pointed and considerably projecting over anterolateral lobes and peristomium, anterolateral lobes tapered but not pointed, only slightly projecting over peristomium; prostomium with transverse furrow at level of palpal insertion and beginning of chaetiger 1, beyond this furrow extended into subulate, slightly inflated caruncle reaching end of chaetiger 1, caruncle attached to dorsum (Fig. 4A). Palps rather thin and short, reaching back to about chaetiger 5, palpal base thickened. According to original description two pairs of eyes arranged in trapezoid, anterior pair smaller and further apart than posterior pair, both pairs close to each other almost forming one row (at the time of re-examination of the holotype no longer discernable). Peristomium moderately developed without forming wings. Low but distinct transversal ciliated bands (tcb´s) present throughout body.

Chaetiger 1 well developed, with subulate postchaetal lamellae in both rami, notopodial lamellae slightly longer and more slender than neuropodial lamellae; notochaetae present. Branchiae from chaetiger 2, present throughout length of fragment; anterior branchiae cirriform with rounded tip, not much longer than notopodial postchaetal lamellae of same chaetiger and fused to it at base; from chaetiger 8 branchiae elongate and pointed, distinctly longer than notopodial lamellae and fused to it except at its tip; from about chaetiger 40 branchiae continously decreasing in length until posterior body region, notopodial lamellae attached to basal part of branchiae. Notopodial lamellae in anterior chaetigers tapered, lower portion rounded, fused to branchiae but distally free, slightly folded; from middle body region lower portion becoming detached from branchiae and tapered; in far posterior chaetigers lamella somewhat triangular, fused to branchiae over a narrow portion. Prechaetal notopodial lamellae triangular, indistinct, present until about chaetiger 40. Neuropodial postchaetal lamellae rounded from chaetiger 2, from chaetiger 38 slightly notched and becoming divided into large rounded

neuropodial lamellae and small conical ventral (or subpodial) lobe from about chaetiger 48; neuropodial lamellae foliate and in approximate interramal position from chaetiger 50.

Anterior chaetae all capillaries with narrow sheaths; arranged in two rows in both rami, capillaries in anterior row slightly shorter and granulated, capillaries in posterior row smooth or slightly granulated; 2–3 superiormost very long chaetae present in notopodia. Parapodia of the middle body region with capillaries having narrow sheaths arranged in two rows; neurochaetae granulated and about the same length in both rows; notochaetae in anterior row shorter, granulated, in posterior row longer, only slightly granulated; two very long superiormost capillaries present in notopodia. From chaetiger 44 neuropodial hooded hooks present, hooks bidentate with very upright apical tooth surmounting main fang (Fig. 4B), hooks numbering up to 14 per fascicle accompanied by 1–2 superior and 1–2 inferior smooth alimbate capillaries; notochaetae smooth capillaries with very narrow sheaths or alimbate, first arranged in irregular rows, more posteriorly arranged in a bundle; notopodial hooks from chaetiger 98, same appearance as in notopodia, maximally three per fascicle, together with several capillaries. Inferior capillaries or sabre chaetae not observed.

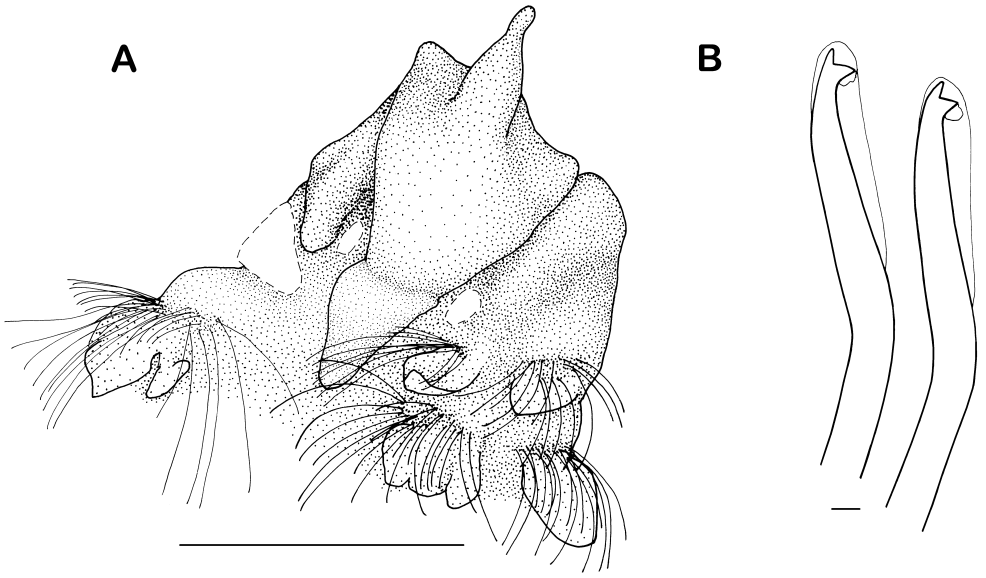

FIGURE 4. *Scolelepis* (*Scolelepis*) *kudenovi* Hartmann-Schröder, 1981, holotype, ZMH P16497. A. Anterior end, dorsal view, first left parapodium removed, palps lost; B. Neuropodial bidentate hooded hooks from posterior chaetiger, note upright large apical tooth. Scale bars: A = 0.5 mm, B = 10 µm.

Nature of the pygidium unknown based on examination of the incomplete holotype. Imajima (1992) identified specimens from Japan as *S. kudenovi* (see remarks below) and observed an entire ventral cushion as well as a dorsal anus.

Notes on the single specimen examined in the course of the present study: Specimen in poor condition, broken just behind the caruncle and distorted so that prostomial and peristomial features difficult to observe, observation of anteriormost chaetigers also unreliable. Anterior fragment with about 51 chaetigers, total length 9.8 mm, width ~1 mm (measured at chaetiger 10, chaetae and postchaetal lobes omitted). Prostomium anteriorly trifid with long pointed median lobe, posteriorly less tapered, separated from anterior part of the prostomium by shallow transverse furrow, caruncle slightly inflated, attached to dorsum. Palps lost. Low but distinct tcb´s present throughout the fragment present. Chaetiger 1 with postchaetal lamellae and capillary chaetae in both rami. Branchiae from chaetiger 2, separated from notopodial lamellae at tip, in further posterior chaetigers branchiae and notopodial lamellae basally fused; neuropodial postchaetal lamellae rounded, from chaetiger 33 neuropodial postchaetal lamellae slightly notched, becoming divided into foliate subulate neuropodial lamellae and small conical ventral (or subpodial) lobe by chaetiger 37. Neuropodial hooded hooks present from about chaetiger 38, numbering 1–5 per fascicle; notopodial hooks absent in examined anterior fragment.

A middle fragment of the specimen from the Lizard Island area was used for molecular studies and is no longer extant (sequences are uploaded to GenBank, Acc. No. KP636516, Table 1).

Pigmentation. Colour of formalin fixed specimen white without any pigmentation.

Methyl green staining pattern. Inconspicuous. Prostomium, peristomium, branchiae and postchaetal lamellae most intensely stained.

Remarks. Though our specimen from Lizard Island is in poor condition it could be identified as *S. kudenovi* Hartmann-Schröder, 1981. The most striking features of this species are the prostomial shape (anteriorly trifid with slightly inflated caruncle attached to the dorsum and separated from the anterior part of the prostomium by a shallow transverse furrow) and the bidentate hooks with a strikingly upright apical tooth. There is also good agreement in details concerning parapodial postchaetal lamellae, chaetae, branchiae, the development of the first chaetigers and the presence of transversal ciliated bands throughout the body. Slight differences concerning the presence of hooks in neuropodia might be attributed to different growth stages of examined specimens: In the Lizard Island specimen neuropodial hooded hooks start from about chaetiger 38, numbering 1–5 per fascicle, whereas Hartmann-Schröder (1981) states the neuropodial hooks to start on chaetiger 44 in the holotype, numbering up to 14 per fascicle. Imajima (1992) found *Scolelepis* specimens in Japan which he identified as *S. kudenovi*. Based on his description and illustrations, differences to the Australian specimens concern the prostomial shape in that the prostomium is anteriorly long and pointed in the Japanese specimens instead of being anteriorly trifid as in the Australian specimens. Also, Imajima (1992) describes up to 17 hooks per fascicle being first present in neuropodia of chaetigers 26–33 and in notopodia from about chaetigers 55–62. In Australian specimens neuropodial hooks start later and are fewer in numbers (see above); notopodial hooks in contrast start much later than in the Japanese specimens and were first observed by Hartmann-Schröder (1981) from chaetiger 98. At all localities specimens had 2–3 notopodial hooks per fascicle in respective chaetigers. Both authors reported hooks to be of the same shape in both rami and described them as bidentate and hooded. However, Hartmann-Schröder (1981) provides an illustration of hooks which clearly shows a large upright apical tooth surmounting the main fang whereas in Imajima's (1992) illustrations the apical tooth is less distinct, smaller in comparison and not strictly upright. Re-examination of the holotype of *S. kudenovi* reveals that Hartmann-Schröder's illustrations are correct and very well reflect the nature of the hooks in this species. The specimen from Lizard Island has the same type of hooks and thus agrees well with the original species description (Fig. 4B). Unfortunately taxonomic information on *S. kudenovi* is restricted to the above mentioned publications and intraspecific variability is largely unknown. In any case, records of *S. kudenovi* from Japan should be critically reviewed, including the information on the pygidium added to the description of *S. kudenovi* based on examination of complete specimens from Japan.

A species very close to *S. kudenovi* specimens from Japan is *Scolelepis* (*Scolelepis*) *sagittaria* Imajima, 1992, so far only known from Japan. The species has an anteriorly trifid prostomium. Parapodial postchaetal lamellae, chaetae, branchiae, and the development of the first chaetigers is very similar to *S. kudenovi*. In contrast to *S. kudenovi*, a species only bearing bidentate hooks, a single superior tridentate hooded hook occurs next to bidentate hooded hooks in the neuropodia and all notopodial hooks are tridentate.

Habitat / Ecology. In Australia the species was found intertidally in fine sand with detritus and *Posidonia* seedlings (Western Australia), around Lizard Island in sand. The record from Japan is from 45 m water depth (Imajima 1992).

Distribution. Japan: off Shimoda, Australia: WA, QLD.

Scolelepis (*Scolelepis*) sp.

Material examined. AM W.45019, MI QLD 2441, af, formalin.

Comparative material examined. Holotype of *Scolelepis* (*Scolelepis*) *balihaiensis* Hartmann-Schröder, 1979, ZMH P15527, S Pacific Ocean, Western Australia, Broome, near Bali Hai, from encrustation of rock crevices in rock pools, 23 Sep 1975. Holotype of *Scolelepis* (*Scolelepis*) *brevibranchia* Hartmann-Schröder, 1991b, ZMH P20219, S Pacific Ocean, S Chile, Bahia Quillaipe, eulittoral, mud, af. Holotype of *Scolelepis carunculata* Blake & Kudenov, 1978, NMV G2992, S Pacific Ocean, Victoria, Storeham, Westernport Bay, Station V47, 20 Dec 1965, almost complete.

Description. Notes on a single specimen: Anterior fragment of 33 chaetigers, 1.1 mm wide, 10.4 mm long. Prostomium anteriorly slightly truncated, posteriorly pointed with unattached caruncle; two pairs of minute black eyes in trapezoid arrangement located where prostomium is extended into a caruncle, anterior pair further apart; palps missing. Peristomium well developed forming low lateral wings partially encompassing prostomium posteriorly.

Chaetiger 1 reduced, with small elongate notopodial lamellae and larger rounded neuropodial lamellae; notochaetae absent. Branchiae from chaetiger 2, present throughout length of fragment. Notopodial lamellae folded, lower portion rounded; from chaetiger 2 distally free from branchiae; first branchiae and notopodial lamellae about the same length but from chaetiger 13–18 branchiae increasingly longer than notopodial lamellae and separation becoming more conspicous; from about chaetiger 24 branchiae and notopodial lamellae again shorter, separated distally, notopodial lamellae foliate and folded. Prechaetal notopodial lamellae small, rounded, most conspicuous from chaetigers 13–18. Neuropodial postchaetal lamellae rounded anteriorly, from chaetiger 18 slightly notched, becoming divided into large rounded neuropodial lamellae and small conical ventral (or subpodial) lobe, neuropodial lamellae foliate and in almost interramal position from chaetiger 20.

Anterior chaetae all capillaries without or with very narrow sheath; arranged in two rows in both rami, capillaries in anterior row slightly shorter, with very fine inconspicuous granulations near tip, capillaries in posterior row smooth. From chaetiger 20 neuropodial hooded hooks present, hooks bidentate with rudimentary apical tooth surmounting main fang, hooks numbering up to ten per fascicle, accompanied by few thin smooth alimbate capillaries anteriorly to the hooks; notochaetae smooth capillaries with very narrow sheaths, arranged in two rows with anterior chaetae distinctly shorter than posterior ones; notopodial hooks absent in examined specimen (af). Inferior capillaries in position of sabre chaetae in anterior and middle chaetigers, in hook-bearing chaetigers 1–2 granulated sabre chaetae with narrow sheaths present.

Pygidium not present in fragmented specimen from Lizard Island.

Pigmentation. Colour of formalin fixed specimen white without any pigmentation.

Methyl green staining pattern. Inconspicuous. Posterior unattached tip of the caruncle, branchiae and postchaetal lamellae most intensely stained.

Remarks. The incomplete specimen from Lizard Island could not be assigned to any known species of *Scolelepis*. The fragment is rather short and thus important characters could not be examined. For this reason a species name has not been assigned.

The specimen is similar to *S. phyllobranchia* Blake & Kudenov, 1978 in that the notochaetae are lacking in the first chaetiger, the prostomium is anteriorly slightly truncated, and in the presence of bidentate hooded hooks from about chaetiger 20 or 23, respectively. There are also several differences: the posterior part of the prostomium of *S. phyllobranchia* is described as elevated mound with small apical papilla whereas the specimen from Lizard Island is posteriorly pointed with an unattached caruncle. The branchiae and notopodial prechaetal lamellae of anterior chaetigers were observed to be totally fused in *S. phyllobranchia* whereas the branchial tips are separated from the postchaetal lamellae in the Lizard Island specimen. The typical stalks on posterior chaetigers from which separate notopodial lamellae and branchiae branch in *S. phyllobranchia* could not unambiguously identified in our specimen though the development of leaf-like lamellae and branchiae in posterior chaetigers of the incomplete specimen (chaetiger 33 being the last chaetiger) could be observed.

The lack of notochaetae in the first chaetiger together with a posteriorly pointed prostomium is also shared with following species of the genus *Scolelepis* (*Scolelepis*) from the Pacific and Indian Oceans: *S. carrascoi* (Maciolek, 1987), *S. bullibranchia* Rossi, 1982, *S. dicha* Hutchings, Frouin & Hily, 1998, *S. laciniata* Eibye-Jacobson, 1997, *S. oligobranchia* (Khlebovitch, 1959), *S. planata* Imajima, 1992, *S. towra* Blake & Kudenov, 1978, *S. vexillatus* (Hutchings & Rainer, 1979), and *S. williami* (de Silva, 1961). However, all species have characters which separate them from our specimen. *S. bullibranchia* has tridentate hooks and branchiae with darkened glandular inclusions. In *S. dicha, S. williami* and *S. laciniata* notopodial lamellae and branchiae are only basally fused and the branchiae are much longer than the notopodial lamellae whereas in our specimens only the tips of branchiae are free and the length of branchiae and folded notopodial lamellae is not very different. In contrast, *S. oligobranchia, S. towra* and *S. vexillatus* have branchiae which are completely fused to notopodial prechaetal lamellae in anterior chaetigers. *S. planata* can be distinguished because its caruncle is flattened with distal point rather than being pointed and unattached. Also, neuropodial hooks are multidentate in *S. planata*, *S. towra,* and *S. carrascoi* instead of being bidentate.

Another species described lacking notochaetae on the first chaetiger and having a posteriorly pointed prostomium is *Scolelepis balihaiensis* Hartmann-Schröder, 1979 from Western Australia. Examination of the holotype revealed that notochaetae are present instead of absent in the first chaetiger (although partially hidden by the palps). Also, the information is added to the original description that the caruncle is not attached in the holotype. *S. balihaiensis* is morphologically very similar to *S. carunculata* Blake & Kudenov, 1978 but *S.*

carunculata has only unidentate or bidentate hooks in posterior notopodia whereas *S. balihaiensis* has tridentate hooks in the notopodia.

Habitat / Ecology. The species was found in sandy mud with filamentous algae in 15 m water depth.

Distribution. The single specimen, an anterior fragment, was found NW of Watson's Bay in the Lizard Island area, Queensland.

Genus *Spio* Fabricius, 1785

Spio Fabricius, 1785; type-species: *Nereis filicornis* Müller, 1776.
Paraspio Czerniavsky, 1881; type-species: *Spio decoratus* Bobretzky, 1870, by monotypy.
Euspio McIntosh, 1915; type-species: *Euspio mesnili* McIntosh, 1915.

Diagnosis. (Bick & Meißner 2011, amended) Prostomium anteriorly rounded, truncate or slightly incised, lacking frontal or lateral horns; eyes present or absent; digitiform occipital antenna absent, but posterior portion of prostomium may be raised or inflated. Nuchal organ with short median and long lateral ciliary bands, extending to chaetiger 2 or 3. Metameric dorsal ciliated organs present. Branchiae present from chaetiger 1, continuing almost throughout the body, completely separate from or basally fused with notopodial lamella, often reduced in size on chaetiger 1. Ventral epidermal glands usually present in anterior and middle chaetigers. Notochaetae and anterior neurochaetae all capillaries; capillaries, hooded hooks and inferior sabre chaetae on middle and posterior chaetigers. Pygidium with four anal cirri.

Spio blakei Maciolek, 1990
(Figs 5–7)

Spio blakei Maciolek, 1990: 1110, Tables 1–2. [Rename of homonym: identification of *Spio pacifica* Blake & Kudenov, 1978 as homonym of *Spio martinensis pacifica* Berkeley, 1927]
Spio pacifica Blake & Kudenov, 1978: 228–230, figs 28a–k.

Material examined. AM W.43926, MI QLD 2340 (2 af), formalin; AM W.43927, MI QLD 2340 (2 af), formalin; AM W.44119, MI QLD 2366 (2 mf), formalin; AM W.44371, MI QLD 2376 (>50), formalin; AM W.44478, MI QLD 2376, complete but fragmented, formalin; AM W.44381, MI QLD 2376 (6 af), formalin; AM W.44372, MI QLD 2376 (18 afs), 96% ethanol; AM W.44374, MI QLD 2378 (17 af), formalin; AM W.44565, MI QLD 2422 (3 af), formalin; AM W.44841, MI QLD 2429, af, formalin, with eggs; AM W.44860, MI QLD 2439, complete but fragmented, formalin; AM W.44863, MI QLD 2438, complete but fragmented, formalin; AM W.44476, MI QLD 2394, af, mf, formalin.

Diagnosis. Prostomium broadly rounded, posterior end short, extending to chaetiger 1, barely tapered. Nuchal organs with short median and long lateral ciliary bands, median bands extending to tcb of chaetiger 2 and recurved lateral bands up to chaetiger 3; metameric dorsal ciliated organs double-paired, usually present from chaetiger 3. Branchiae from chaetiger 1, continuous to almost end of body, length of first pair of branchiae about two thirds length of second pair; branchiae mostly free from notopodial lamellae. Ventral epidermal glands present from about chaetiger 3 to posterior middle body chaetigers; two pairs of glands per chaetiger. Postchaetal lamellae rounded, notopodial prechaetal lamellae present in anterior and middle chaetigers. From chaetiger 11 row of 4–5 tridentate hooded hooks replacing posterior row of capillaries in neuropodia, uppermost tooth very inconspicuous. Pygidium with two pairs of anal cirri, dorsal pair thinner and shorter.

Description. (based on specimens examined in the course of the present study) Longest specimen 61 chaetigers, 0.75 mm wide and about 11 mm long. Prostomium broadly rounded, slightly expanded at anterolateral margin, with inconspicuous median furrow (Figs 5A, B, 6A), anterior margin slightly projecting over peristomium; posterior end short, extending to chaetiger 1, barely tapered (Fig. 6A); usually with two pairs of black eyes arranged in trapezoid, anterior pair larger, almost crescent-shaped, further apart than posterior pair; prostomium separated from peristomium by a considerable furrow (Fig. 6A).

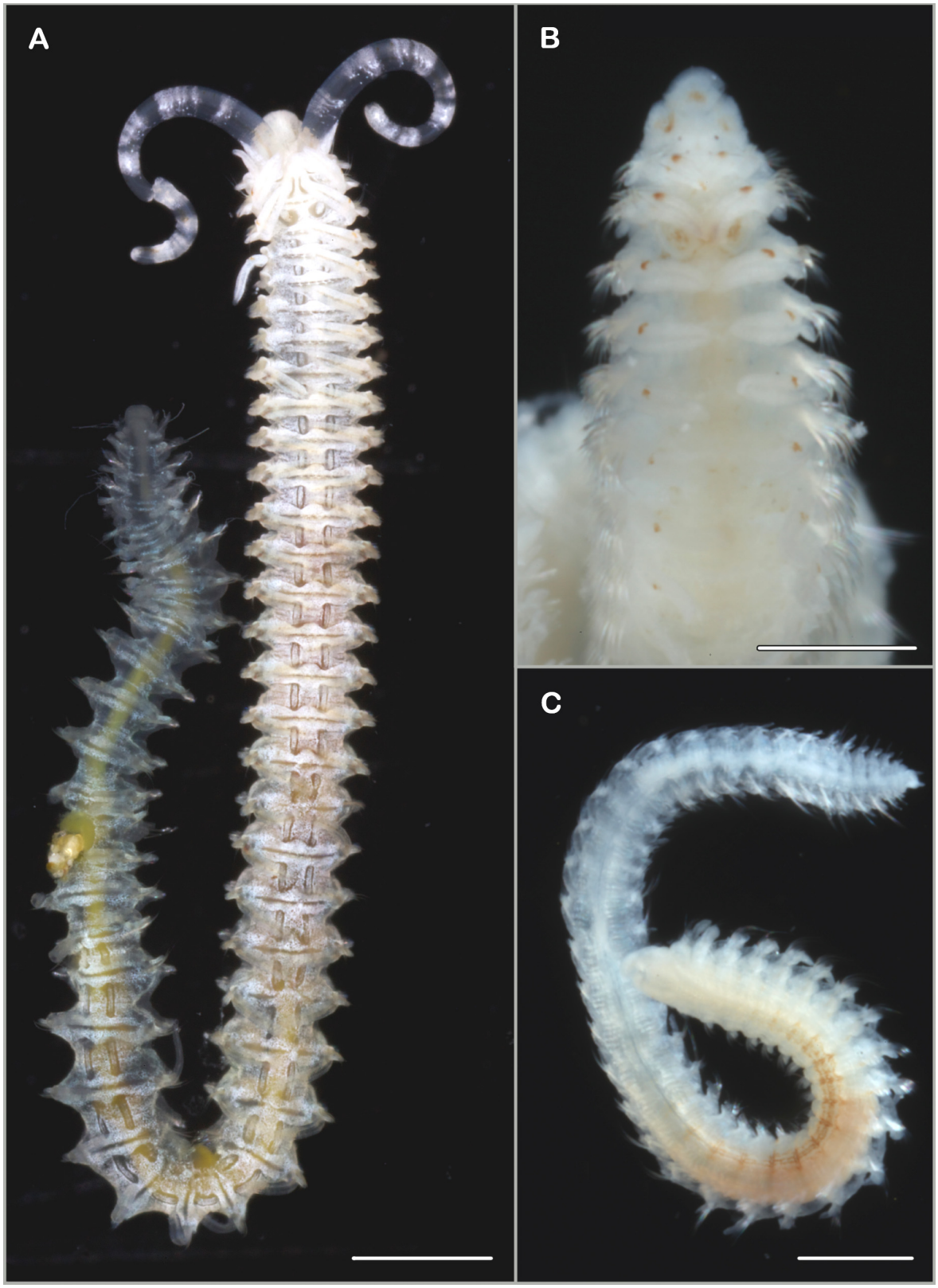

FIGURE 5. *Spio blakei* (Blake & Kudenov, 1978): Examples for pigmentation patterns. A. Live complete specimen, dorsal view, MI QLD 2408; B. Specimen fixed in formalin, anterior end, dorsal view, AM W.44860, MI QLD 2439; C. Complete specimen fixed in formalin, ventral view, AM W.43371, MI QLD 2376. Scale bars: A, C = 1 mm, B = 0.5 mm. Photo: A—A. Semenov.

Nuchal organs and metameric dorsal ciliated organs distinct in well-preserved and living specimens; nuchal organs with short median and long lateral ciliary bands, median bands extended to tcb of chaetiger 2 and recurved lateral bands up to chaetiger 3 (Figs 5A, B, 6A); metameric dorsal ciliated organs double-paired, usually present from chaetiger 3 (Figs 5A, 6A), posteriorly extending to the end of the middle body region, slightly longer in further posterior segments (Fig. 6B); tcb´s discernable throughout the body (Fig. 6A–C).

Ventral epidermal glands present from about chaetiger 3 to posterior middle body region; two pairs of glands per chaetiger: median pair slightly posteriorly to centerline on ventral side of the respective glandophorous chaetiger, second pair in lateral position directly at the centerline of the chaetiger (Fig. 7A–D) (best observed with SEM or after methyl green staining, also observable in live specimens).

Branchiae from chaetiger 1, continuous to near end of body, with only about last three chaetigers abranchiate; length of first pair of branchiae about two thirds the length of second pair (Fig. 6A–C); longest branchiae on chaetigers 2–10, almost reaching dorsal midline (Fig. 6A), after about chaetiger 10 branchiae decreasing in length (Fig. 6B); branchiae mostly free from postchaetal notopodial lamellae. First notopodium not distinctly shifted dorsally. Notopodial postchaetal lamellae rounded, slightly tapered superiorly and longer than chaetal row. Neuropodial postchaetal lamellae also rounded, only slightly longer than chaetal row in anterior and middle chaetigers. Notopodial prechaetal lamellae present in anterior and middle chaetigers.

Notopodial chaetae all capillaries; in anterior chaetigers arranged in two rows, anterior capillaries slightly shorter than capillaries of posterior row (Fig. 6A), stout, heavily granulated, with distinct sheaths, capillaries of posterior row less stout, slightly granulated, with narrow sheath; additional superior fascicle of 2–3 long, thin capillaries without granulations present from chaetiger 1; capillaries of middle and posterior chaetigers not clearly arranged in rows, thin, non-granulated, of different length within a fascicle. Capillaries of anterior neuropodia arranged in two rows, capillaries of both rows of about same length, anterior capillaries stout, heavily granulated with distinct sheaths, capillaries of posterior row less stout, slightly granulated near tip, with sheaths; from chaetiger 11 posterior row of capillaries replaced by single row of 4–5 tridentate hooded hooks, uppermost tooth inconspicous, anterior row of thin, smooth and alimbate capillaries present in hook-bearing chaetigers, capillaries slightly longer than hooks (Fig. 6E); inferior fascicle of 3–4 long capillaries in position of sabre chaetae usually present from anteriormost chaetigers, hook-bearing chaetigers with 1–2 stout granulated sabre chaetae in inferiormost position, with narrow sheath or alimbate, appearance of sheath variable near the tip (Fig. 6D, also see Remarks).

Pygidium with two pairs of anal cirri: dorsal pair thinner and shorter, ventral pair in comparison very stout, almost cone-shaped and longer than dorsal pair (Fig. 6C).

Pigmentation. Live specimens of whitish colour and with orange-brown pigment on the anterior part of the prostomium, on the dorsal side of the peristomium next to the prostomium, on the dorsum in vicinity of the nuchal organs, and with pigment spots of the same colour anteriorly mid-way along the branchiae of about first eight chaetigers (Fig. 5A); palps with white circular bands (Fig. 5A). In formalin and ethanol fixed specimens orange-brownish pigment usually still observable following the same pattern as in live specimens (Fig. 5B), but in some specimens pigmentation completely lost; several specimens with brownish pigment on the ventrum from about the chaetigers 7–20 with pigmentation being most intense on segmental margins (Fig. 5C).

Methyl green staining pattern. Inconspicuous; prostomium, peristomium, branchiae and neuropodial prechaetal lobes most intensely stained; two longitudinal stripes become apparent on the ventrum in some specimens after methyl green staining. Position of ventral epidermal glands indicated by white dots in the centre of larger blue spots on the ventral surface of glandophorous chaetigers (most anterior and middle body chaetigers).

Remarks. In general, the specimens collected in the Lizard Island area are in good agreement with the description by Blake & Kudenov (1978). Minor deviations concern the prostomial shape. In the original description it is stated that a caruncle divided into two lobes surrounded laterally by paired, curved ciliated nuchal organs extending to middle of chaetiger 3 is present (Blake & Kudenov 1978). This observation is not corroborated by our results: SEM studies revealed that the posterior end of the prostomium is rather blunt and short whereas the nuchal organs follow the pattern typical for this genus (with short median ciliated bands extending to first tcb on chaetiger 2 and long recurved lateral ciliary bands not extending tcb on chaetiger 3). Blake & Kudenov (1978) described distally falcate sabre chaetae with partial hoods formed by extension of sheath. By means of SEM an unusual though variable development of the chaetal sheaths of sabre chaetae near the tip was discovered in specimens from Lizard Island (Fig. 6D) which might refer to the observations by Blake & Kudenov (1978).

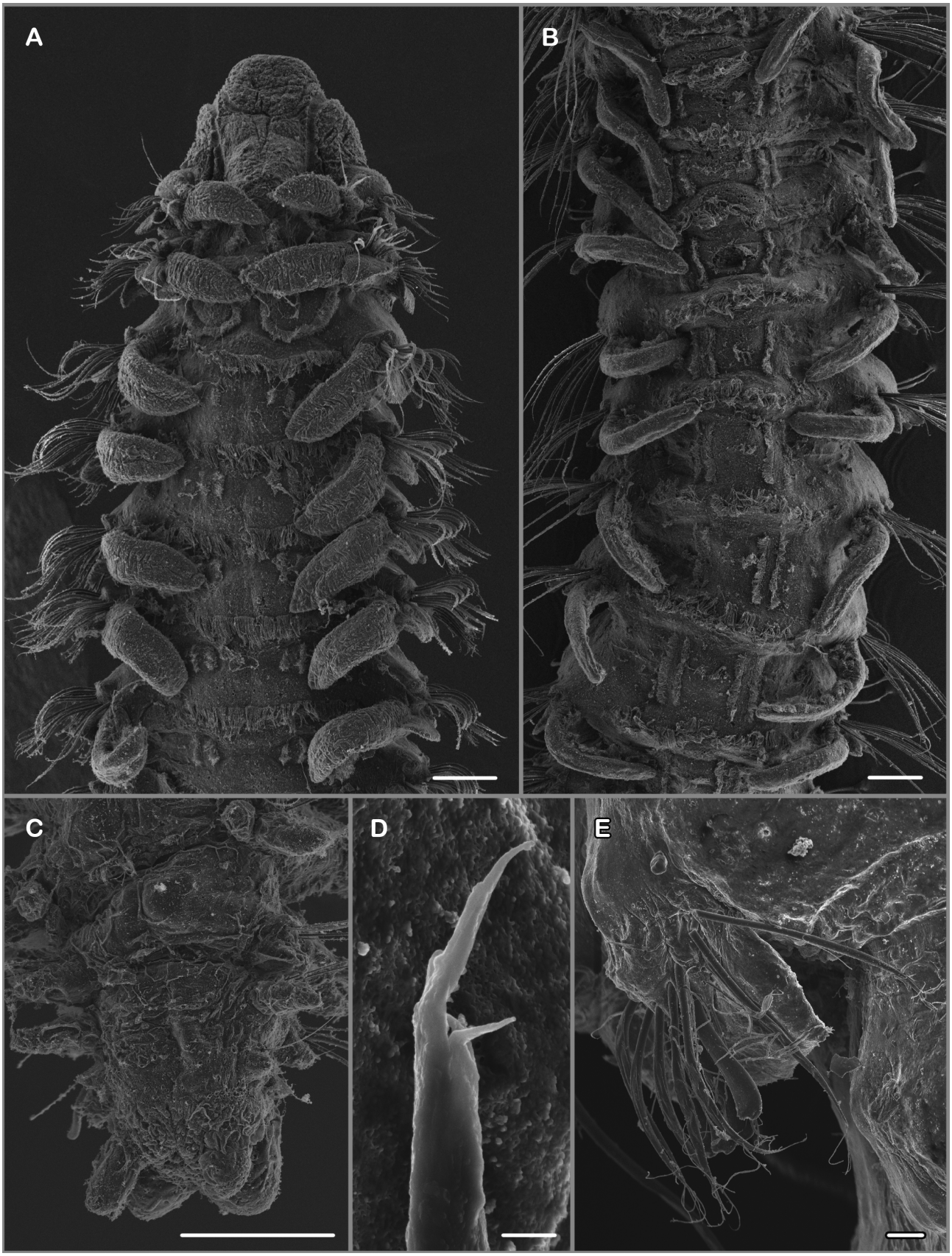

FIGURE 6. *Spio blakei* (Blake & Kudenov, 1978), AM W.44381, MI QLD 2376. A. Anterior end, dorsal view, palps removed; B. Middle body region, dorsal view; C. Posterior end, dorsal view; D. Sabre chaetae from 12th chaetiger; E. Neuropodium from 11th chaetiger, anterior view. Scale bars: A–C = 100 µm, D = 1 µm, E = 10 µm.

S. blakei can be distinguished from other *Spio* spp. with tridentate neuropodial hooks commencing on chaetiger 11 by the following combination of characters (compare Maciolek 1990, Table 2): small species, prostomium entire and rounded anteriorly, first branchiae about two-thirds the length of second pair of branchiae, 4–5 neuropodial hooks per fascicle in hook-bearing chaetigers, pygidium with four cirri with dorsal pair being shorter and more slender than ventral pair. Also the observation of nuchal organs, dorsal ciliated organs and the distribution of ventral epidermal glands can be used for species delimitation but unfortunately these characters are not sufficiently described for all currently known *Spio* species.

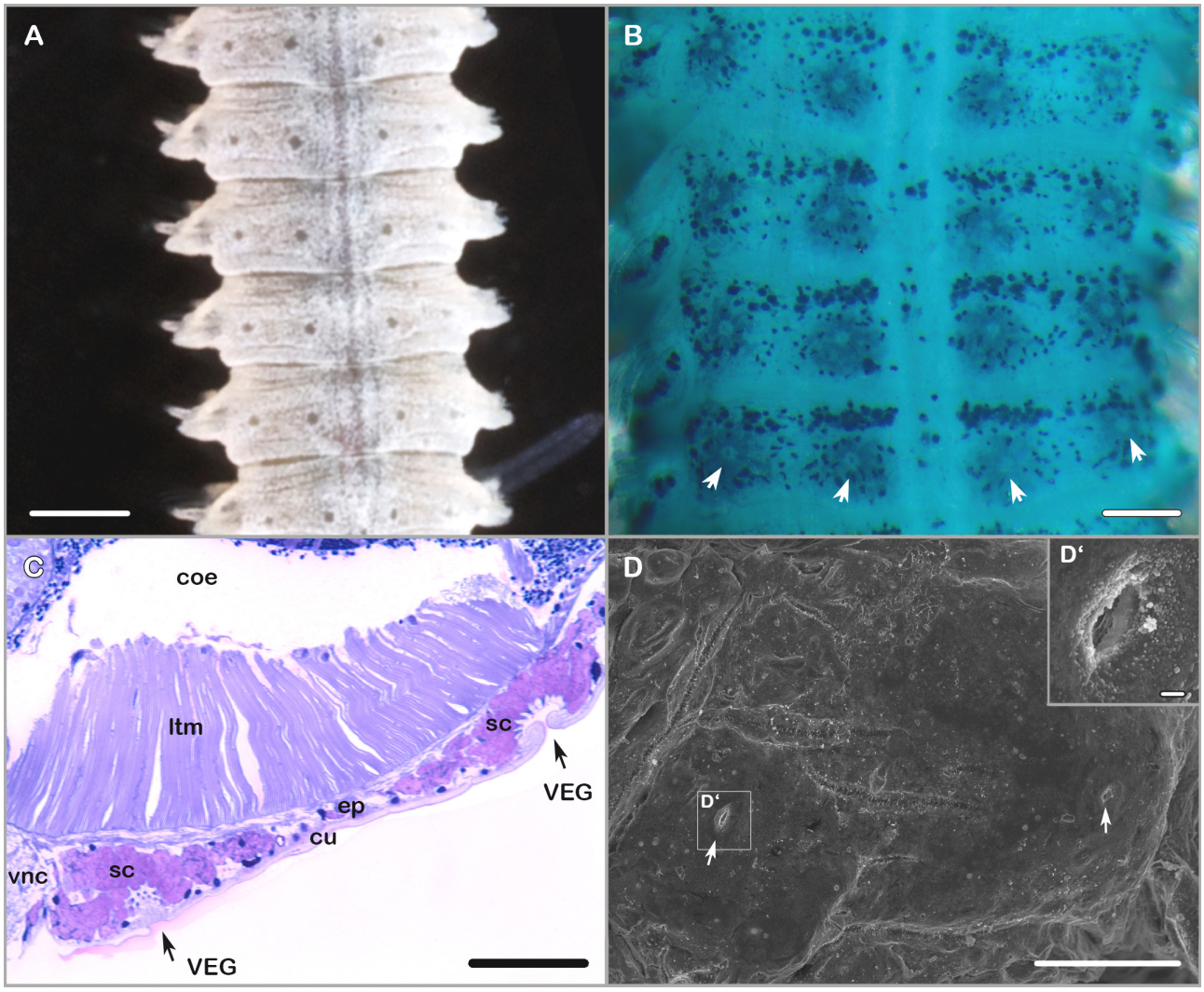

FIGURE 7. *Spio blakei* (Blake & Kudenov, 1978): Studies on the ventral epidermal glands (VEGs). A. Ventral surface of middle chaetigers in a live specimen, pores of VEGs numbering four per chaetiger apparent, AM W.45396, MI QLD 2433; B. Methyl green staining pattern of ventral surface of middle chaetigers (arrows point at white dots being the location of the opening pores of VEGs), AM W.44860, MI QLD 2439; C. Cross section of glandophorous chaetiger (arrows point at two VEGs), AM W.44371, MI QLD 2376; D. SEM image, left half of middle chaetiger, ventral surface (arrows point at gland openings), AM W.44381, MI QLD 2376. Abbreviations: coe = coelomic cavity, cu = cuticle, ep = epidermis, ltm = longitudinal musculature, sc = secretion cell, vnc = ventral nerve cord. Scale bars: A = 200 µm, B = 100 µm, C, D = 50 µm. Photo: A—A. Semenov.

Habitat / Ecology. In the Lizard Island area occurring intertidally in sand and fine sand. Other records in Australia from along the Eastern coasts in Queensland, New South Wales and Victoria (Blake & Kudenov 1978); also found in estuaries of New South Wales, in sandy mud at depths of 4–10 m in salinities of 29.8–35 ‰ (Hutchings & Murray 1984). Outside Australia the species has been reported from the Golfo de Nicoya (Costa Rica) from subtidal depths (20 m) and muddy sand (Dean 2004), and at Baja California Sur (Mexico) it was collected from 74 m water depth (de León-González 1998).

Distribution. Australia: Queensland, New South Wales, Victoria American Pacific coasts: Mexico: Baja California, Baja California Sur, Bahia San Quintin, Sinaloa peninsula (van der Heiden & Hendrickx 1982, de León-González 1998, Díaz-Castañeda *et al.* 2005); Costa Rica: Golfo de Nicoya (Dean 2004).

Genus *Microspio* Mesnil, 1896

Microspio Mesnil, 1896; type-species: *Spio mecznikowianus* Claparède, 1869.
Mesospio Gravier, 1911; type-species: *Mesospio moorei* Gravier, 1911, by monotypy.

Diagnosis. Prostomium anteriorly rounded to deeply incised, frontal or lateral horns always absent; eyes present or absent; occipital antenna present or absent. Nuchal organ with short median and long lateral ciliary bands, extending to chaetiger 2 or 3; metameric dorsal ciliated organs present. Branchiae present from chaetiger 2, restricted to anterior region or continuing to posterior end of body; partly fused at base with notopodial postchaetal lamellae. Notochaetae and anterior neurochaetae all capillaries; capillaries, hooded hooks and inferior sabre chaetae on middle and posterior chaetigers; hooks bi-, tri-, or multidentate. Pygidium with 2–4 anal cirri.

Microspio granulata Blake & Kudenov, 1978
(Figs 8–11)

Microspio granulata Blake & Kudenov, 1978: 232, fig. 30.—Hutchings & Turvey 1984: 13–14; Maciolek 1990: table 3.

Type material. Holotype: NMV F42947, S Pacific Ocean, New South Wales, Botany Bay, Towra Point, NSWSF station 329, associated with *Halophila*, Apr 1973, coll. Rand, af. Paratype: NMV F42950, S Pacific Ocean, New South Wales, Botany Bay, Towra Point, station 211, coll. NSW fish., af.

Other material examined. AM W.44379, MI QLD 2380, af, formalin; AM W.44016, MI QLD 2340, broken, formalin; AM W.47430, MI QLD 2340, af, formalin; AM W.44018, MI QLD 2340, broken, formalin; AM W.44381, MI QLD 2376 (2), formalin; AM W.45022, MI QLD 2437 (2 af), formalin; AM W.44472, MI QLD 2395, broken, formalin; AM W.44480, MI QLD 2397, af, 96% ethanol; AM W.44484, MI QLD 2399, af, formalin; AM W.43956, MI QLD 2342, broken, formalin.

Comparative material examined. Holotype of *Microspio minuta* (Hartmann-Schröder, 1962), ZMH P-14930, S Pacific Ocean, Chile, 4 km north of Taltal, eulitoral, from rhizoids of *Macrocystis* washed up on the beach, coll. G. Hartmann-Schröder, af. Holotype of *Microspio microcera* (Dorsey, 1977), LACM-AHF POLY 1137, North Pacific Ocean, USA, California, Channel Islands, San Clemente Island, Wilson Cove, 2 m, coralline algal mat (mostly *Lithothrix aspergillum*) with sand and shell debris, coll. J. Dorsey, Jun 1973. Paratype of *Microspio microcera* (Dorsey, 1977), LACM-AHF POLY 1138 (4 af), same locality and information as holotype. Non-type material of *Microspio microcera* (Dorsey, 1977), LACM-AHF POLY 6592, same locality and information as holotype, additional information: 32°00’18”N 118°33’26”W.

Diagnosis. Prostomium anteriorly deeply incised, posterior part slightly elevated, extended into a caruncle terminating at chaetiger 2. Notopodial ramus of chaetiger 1 reduced, without notochaetae, small rounded lamella dorsally to the neuropodium present and in addition dorsal lobe present in vicinity to the lateral band of the nuchal organ. Branchiae from chaetiger 2, branchiae on chaetiger 2 as long as those on chaetiger 3 in adult specimens, only few posteriormost chaetigers without branchiae. Pronounced ciliation on all tcb´s and at the inner side of the branchiae. From chaetiger 9 two to five bi- or tridentate neuropodial hooded hooks, apical tooth hardly discernible; sabre chaetae present in middle and posterior chaetigers. Pygidium with 4 anal cirri.

Description. (based on specimens examined in the course of the present study) Specimens from Lizard Island considerably smaller than type material collected in New South Wales. Largest complete specimen with 42 chaetigers, 1 mm wide, about 10 mm long. Prostomium deeply incised, projecting over peristomium, without prominent occipital papilla (which is present in the type material) (Figs 8A–C, 9A–C, 10A–C); posterior end extending to tcb on chaetiger 2, slightly elevated from about posterior pair of eyes (Figs 9A, B, 10C); two pairs of black eyes, arranged in trapezoid, anterior pair larger, crescent-shaped, widely spaced, posterior pair smaller, rounded, closely spaced (Figs 8A–C, 9A, B); only anterior part of prostomium distinctly separated from peristomium (Fig. 10B).

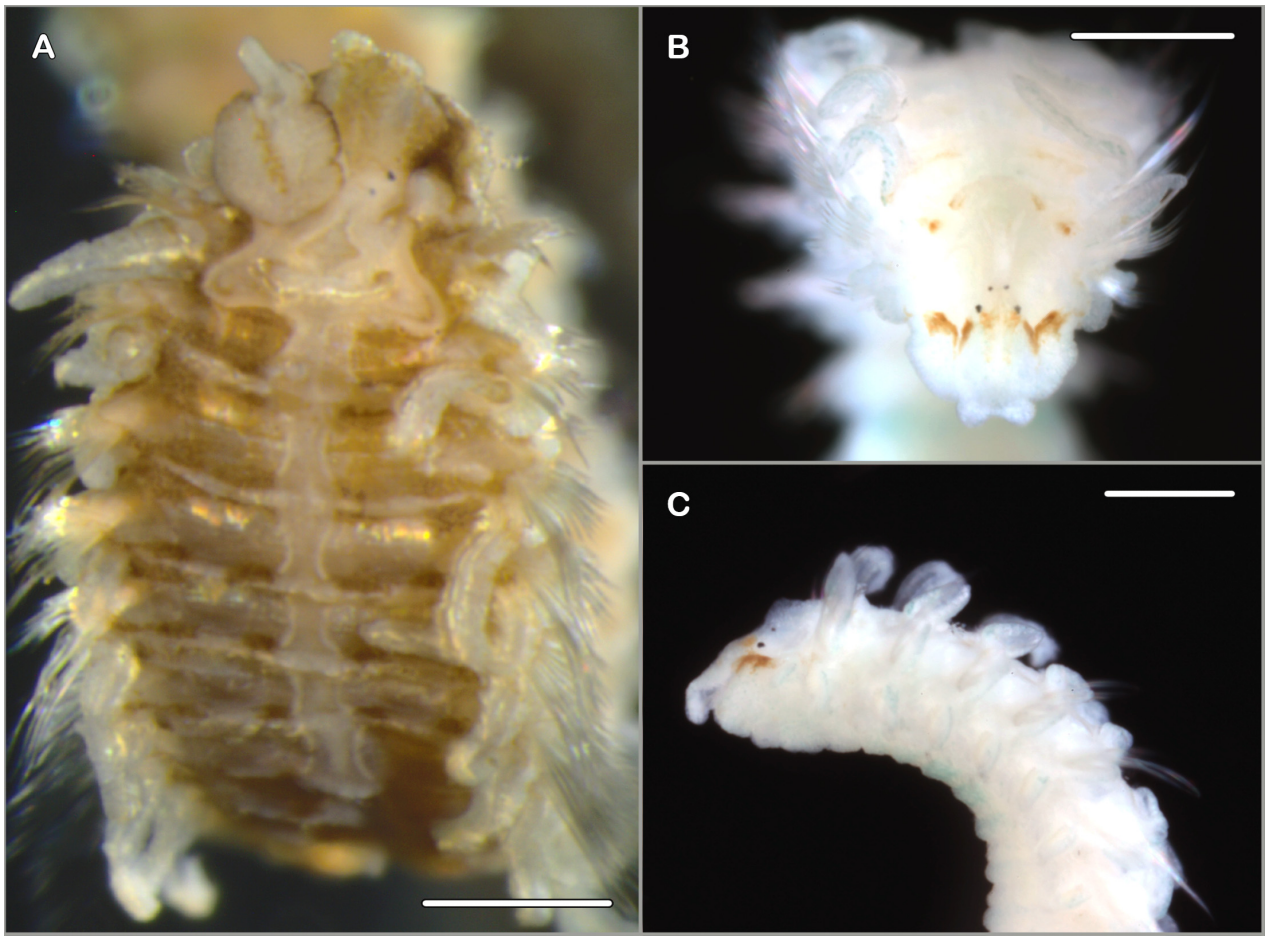

FIGURE 8. *Microspio granulata* Blake & Kudenov, 1978: Example for pigmentation pattern. A. Holotype fixed in formalin, dorsal view of anterior part, NMV F42947, type locality in NSW, Australia; B. Specimen fixed in formalin, anterior end, dorsal view, AM W.44381, MI QLD 2376, Lizard Island area; C. Same in lateral view. Scale bars: A–C = 0.4 mm.

Nuchal organ with short median and long lateral ciliary bands; median ciliary band laterally from the posterior part of prostomium, turning medial at its posterior tip, extending to end of chaetiger 2 (Figs 8A, 9A, B 10A, B); lateral ciliary band starting near palps, from there first turning outwards then inwards again, by that surrounding tcb on chaetiger 2, extending to end of chaetiger 3 (Figs 8A, 9A, B, 10A); long lateral ciliary band rather distinct, short median ciliary band only visible in well preserved specimens (SEM or methyl green staining required, but easily observed in large specimen from type material). Metameric dorsal ciliated organs present from chaetiger 3 to chaetiger 20 at maximum (usually to chaetigers 13–15), in between tcb´s of subsequent chaetigers (Figs 8A, 9A, 10A); one pair of single comma-shaped ciliary bands per chaetiger, first ciliary bands short then getting longer and more straight (Fig. 10E), eventually covering entire distance between tcb´s of subsequent chaetigers. Pronounced ciliation on all tcb´s and at the inner margin of branchiae (Fig. 10A, C, E).

Ventral epidermal glands present from about chaetiger 3 to posterior middle body region; two pairs of glands per chaetiger: median pair slightly posteriorly to centerline on ventral side of respective chaetiger, second pair laterally to median pair directly at centerline of the chaetiger (Fig. 11A–C) (best observed with SEM or after methyl green staining).

Branchiae from chaetiger 2, present throughout body except 5–9 posteriormost chaetigers (Figs 8A, 9A, C, 10A, C, D, E); first pair of branchiae as long as those on following chaetiger (Figs 8C, 9A, C, 10A), only in small specimens about half length of second pair of branchiae; branchiae on chaetigers 2(3)–5(6, 7) longest and most robust, nearly reaching midline dorsally; from about chaetigers 6–9 branchiae also long but more slender; in mid-body region about half as long as longest anterior branchiae, continuously decreasing in length towards end of body, in last three to four branchiate chaetigers considerately decreasing in length (Fig. 10D); branchiae free, cirriform and distally rounded (Fig. 9F–J), with long cilia on inner margin.

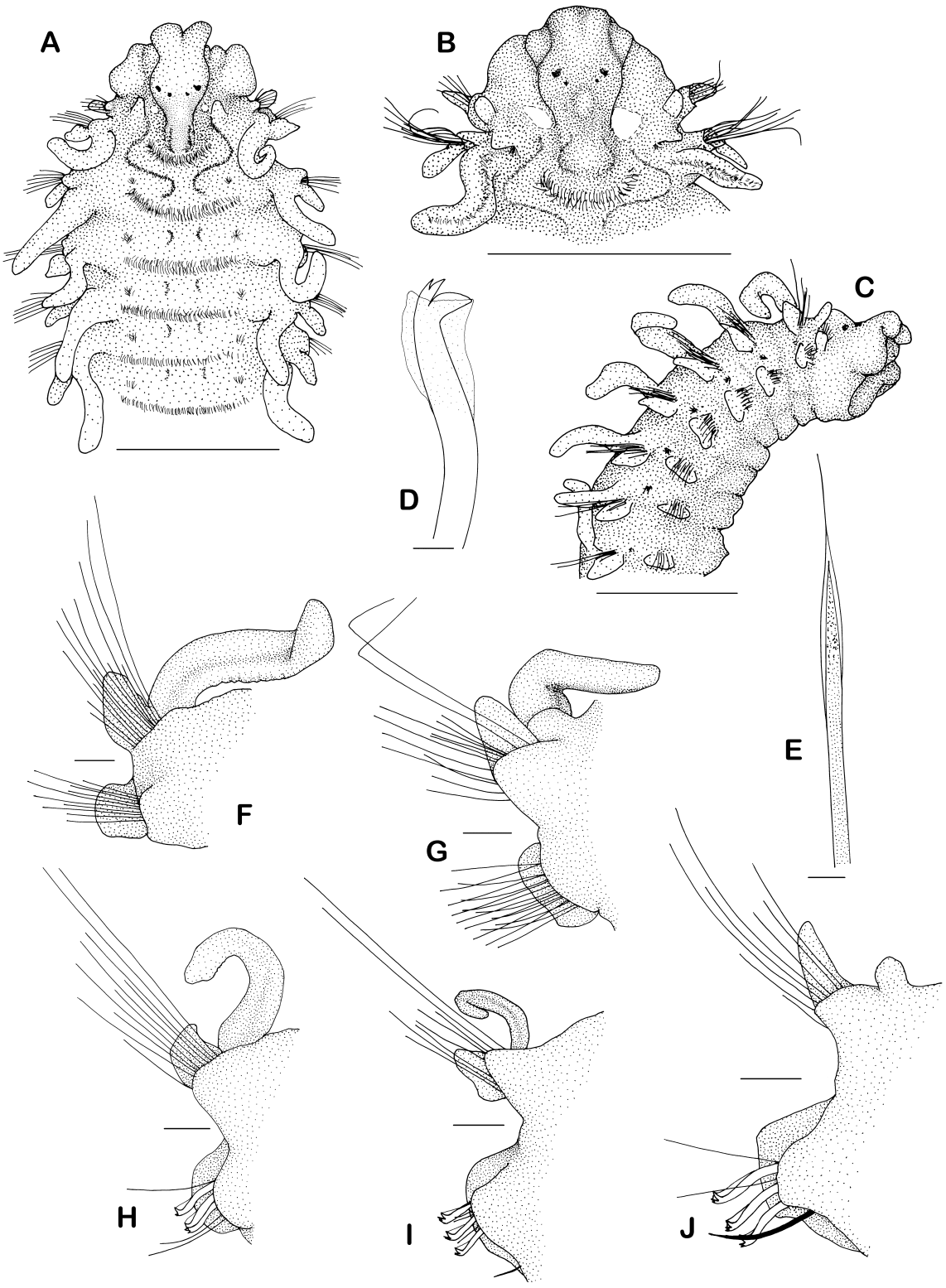

FIGURE 9. *Microspio granulata* Blake & Kudenov, 1978, AM W.44018, MI QLD 2340 (A, C); AM W.44016, MI QLD 2340 (B); AM W.43927, MI QLD 2340 (D–J). A. Anterior end, dorsal view, palps removed; B. Close-up of anterior end, dorsal-oblique view with focus on nuchal organ and first chaetiger, chosen view improves observation of small rounded prechaetal lobe in neuropodium; C. Anterior end, lateral view, palps removed; D. Tridentate neuropodial hook from 9th chaetiger; E. Anterior notochaetae from 2nd chaetiger; F. Parapodium from 2nd chaetiger, anterior view; G. Same from 5th chaetiger; H. Same from 9th chaetiger; I. Same from 17th chaetiger; J. Same from 9th last chaetiger being last branchiate chaetiger. Scale bars: A–C = 500 µm, D, E = 10 µm, F–J = 50 µm.

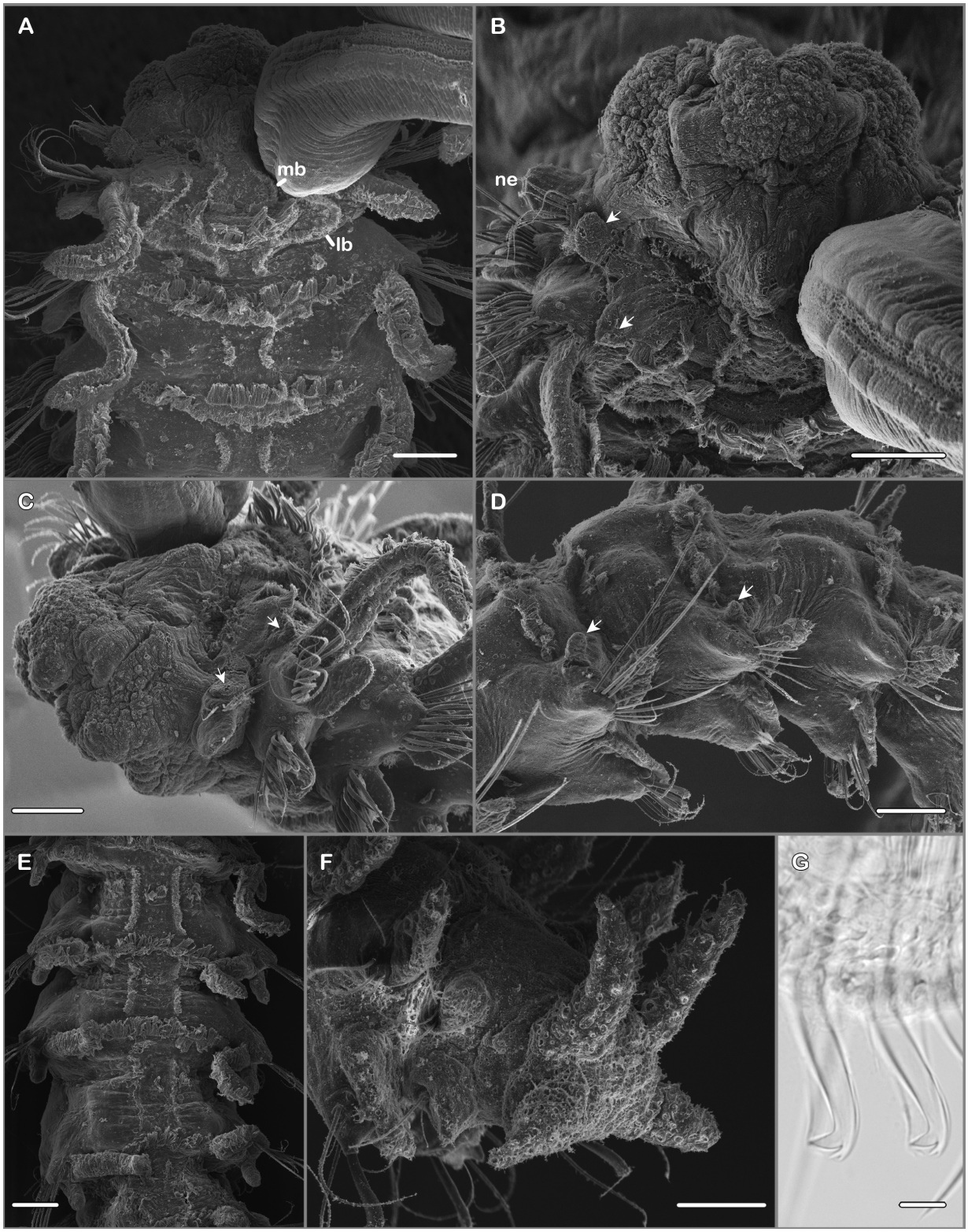

FIGURE 10. *Microspio granulata* Blake & Kudenov, 1978, AM W.44016, MI QLD 2340 (A–F); AM W.43927, MI QLD 2340 (G). A. Anterior end, dorsal view (labels refer to ciliary bands of the nuchal organ); B. Anterior end, antero-dorsal view with focus on indented anterior margin of the prostomium and on the first parapodium (label refers to the neuropodium, arrows point at lobes dorsally to neuropodial chaetae); C. Chaetigers 1–3, left side, lateral view (arrows point at lobes dorsally to neuropodial chaetae); D. Posterior chaetigers with second last and last branchiate parapodia (branchiae indicated by arrows), left side, lateral oblique view; E. Chaetigers 12–16, dorsal view; F. Pygidium, lateral oblique view; G. Tridentate hooded hooks from 9th last chaetiger. Abbreviations: lb = lateral band (nuchal organ), mb = median band (nuchal organ), ne = neuropodial postchaetal lamella. Scale bars: A–F = 100 µm, G = 10 µm.

First parapodium slightly shifted dorsally; neuropodium well developed; notopodium reduced without notochaetae (Figs 9A–C, 10 B, C); small rounded lamella present dorsally to neuropodium and additional dorsal lobe present in vicinity to lateral band of nuchal organ (Figs 9A, B, 10B, C) (see remarks). Notopodial postchaetal lamellae on anterior chaetigers subtriangular, slightly rounded at base (Fig. 9F, G); slightly decreasing in size along body (Figs 9H, I); in posterior chaetigers long triangular to almost cirriform (Fig. 9J). Neuropodial postchaetal lamellae low and rounded; in anteriormost chaetigers as long as chaetal row, in mid-body region longer than chaetal row; in posteriormost chaetigers shorter again (Figs 9F–J, 10C). Prechaetal lamellae absent.

Notopodial chaetae all capillaries; arranged in two distinct rows in anterior and middle chaetigers (Fig. 10C), in posterior chaetigers no longer arranged in distinct rows; anterior row of chaetae shorter and stouter than chaetae in posterior row (Fig. 10C), chaetae granulated with narrow sheath (Fig. 9E); otherwise chaetae smooth with very narrow sheaths; additional superior fascicle of long capillaries present. Neuropodia with rows of capillaries and hooded hooks as well as sabre chaetae in inferior position; capillaries of anterior neuropodia arranged in two rows, short, stout and distinctly granulated capillaries in anterior row, long, smooth, alimbate capillaries in posterior row; in middle chaetigers neuropodial capillaries of about same length; 3–5 tridentate hooded hooks replacing posterior row of capillaries from chaetiger 9; main fang with apical tooth and additional small uppermost tooth, uppermost tooth best seen in posterior parapodia (Figs 9D, 10G); hooks accompanied by anterior row of thin alimbate capillaries (Fig. 10D); few smooth, long capillaries in inferiormost position usually present before hooks start, hook-bearing chaetigers with one or two stout, distally granulated sabre chaetae with narrow sheath (Fig. 9I, J).

Pygidium with four cirriform anal cirri, in adult specimens of about equal size, in younger specimens dorsal pair sometimes slender or slightly longer; dorsolaterally attached pair pointing to dorsal direction; ventrolaterally attached pair pointing laterally; anus terminal (Fig. 10F).

Pigmentation. Formalin and ethanol fixed specimens with orange-brownish stripe across peristomium and prostomium (Fig. 8A–C); in addition some pigment of the same colour anteriorly to tcb´s of chaetigers 3 and 4 (Fig. 8B); in heavily pigmented specimens pigment present anteriorly and posteriorly to tcb´s of some anterior chaetigers (Fig. 8A).

Methyl green staining pattern. Inconspicuous. Branchiae, anterior half of prostomium and peristomium, and postchaetal lamellae most intensely stained. Ventral epidermal glands visible as four white dots on a bluish background on the ventral side of anterior and middle body chaetigers (Fig. 11A).

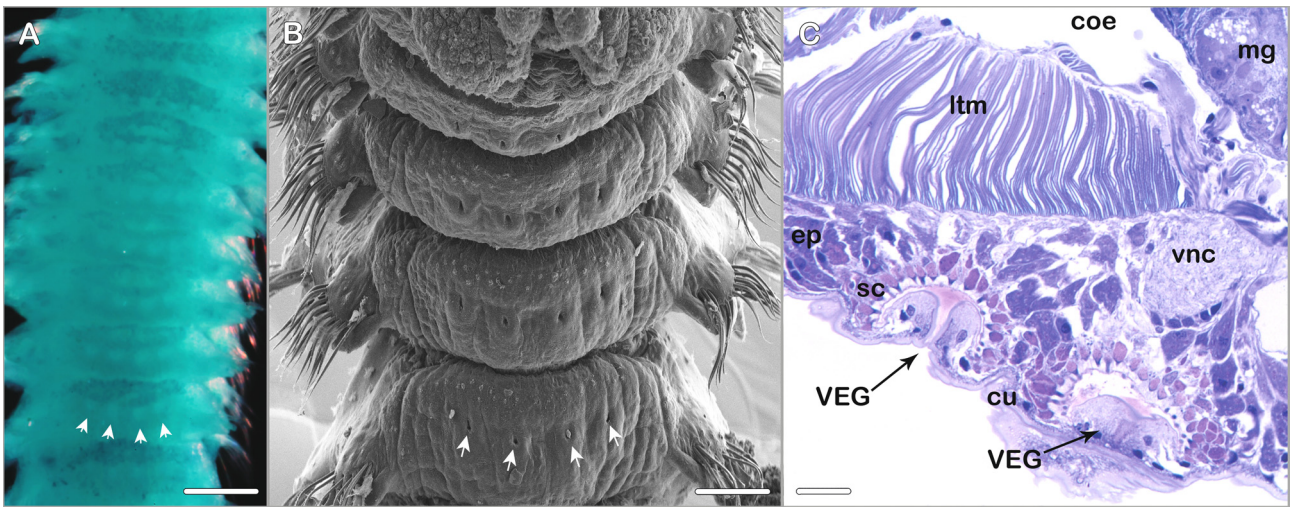

FIGURE 11.*Microspio granulata* Blake & Kudenov, 1978: Studies on the ventral epidermal glands (VEGs). A. Methyl green staining pattern, anterior end, ventral surface of anterior chaetigers (arrows point at white dots being the location of the VEGs), AM W.44381, MI QLD 2376; B. SEM image, anterior end, ventral surface of anterior chaetigers (arrows point at gland openings), AM W.44016, MI QLD 2340; C. Cross section of glandophorous chaetiger (arrows point at two VEGs), AM W.44018, MI QLD 2340. Abbreviations: coe = coelomic cavity, cu = cuticle, ep = epidermis, ltm = longitudinal musculature, mg = mid gut, sc = secretion cell, vnc = ventral nerve cord. Scale bars: A, B = 100 µm, C = 20 µm.

Remarks. *Microspio granulata* was described by Blake & Kudenov (1978) based on material from the New South Wales coast near Sydney. Examination of specimens collected in the Lizard Island area revealed minor differences to the original description. After examination of the type material it could be concluded that some observed deviations are partially explained by the different sizes of specimens (the Lizard Island specimens are considerably smaller than the type specimens). Other discrepancies might be attributed to imprecise observations. Information about additional characters is now provided in the amended species description.

Fully grown specimens exhibit a distinct occipital papilla which is not present in smaller specimens, a merely slight elevation can be observed instead in the smaller specimens from Lizard Island. The type specimens are more heavily pigmented than the specimens collected around Lizard Island (Fig. 8). The ciliation of branchiae and tcb´s is less pronounced in the type material compared to the Lizard Island material. Blake & Kudenov (1978) observed "... a transverse hood reminiscent of dorsal collars seen in genus *Streblospio* present posterior to prostomium, surrounded laterally and posteriorly by curved nuchal grooves". It is likely that this observation of a hood by Blake & Kudenov (1978: fig. 30) was actually the tcb with long cilia on the second chaetiger and the ciliated bands of the nuchal organ in immediate vicinity. The nuchal organ of *M. granulata* is in good agreement with the general pattern typical for many *Spio* or *Microspio* species in consisting of a short median ciliated band and a longer curved or re-curved lateral ciliated band. The metameric dorsal ciliated organs of *M. granulata* are described for the first time in the present study. The presence of ventral epidermal glands (VEGs) was not mentioned in the original species description but two pairs of VEGs per chaetiger are present in anterior and middle chaetigers (Fig. 11). Blake & Kudenov (1978) observed the presence of genital pouches from chaetiger 12, decreasing in size to chaetiger 29. Though this character was illustrated in the original species description it could not unambiguously be identified while examining material from Lizard Island or in the type material. Instead the type specimens exhibited lateral openings in form of vertical slits in the body wall from chaetiger 12. Gametes could be detected in both, the type specimens and in the recently collected Lizard Island specimens, in the latter lateral openings were absent. Genital pouches in terms of ventrolateral intersegmental pouches present in other spionid genera could not be observed in *M. granulata*. Blake & Kudenov (1978) state 8–9 neuropodial hooks to occur per fascicle from chaetiger 9 whereas 3–5 hooks were present in the Lizard Island specimens and 5–6 hooks were observed by us in the larger type specimens. Since complete specimens were among specimens recently collected on Lizard Island information on the pygidium could be added to the species description.

The probably most important discovery, as it is also important for e.g., species delimitation, concerns the first chaetiger. Blake & Kudenov (1978) described the first chaetiger as "reduced, with small digitiform notopodial lamellae shifted dorsally, lacking notosetae...". We partially agree with this view: the first chaetiger is reduced, the neuropodial ramus is fully developed whereas the notochaetae are absent. However, the problem is that not only one lobe or lamella which could be attributed to the notopodial ramus is present dorsally to the neuropodium but two (Figs 10B, C). The lamella directly dorsally to the neuropodium is not easy to detect with light microscopy since it nestles in immediate vicinity of the neuropodial chaetae (Fig. 10C). The more dorsally positioned lobe is in comparison more distinct after methyl green staining. An associated ciliated tuft could be detected by means of SEM (Fig. 10B). The interpretation of this arrangement is not straightforward. The lamella directly above the neuropodium might be the notopodial lamella whereas the dorsalmost lobe could be interpreted as a branchial remnant (this view perhaps corroborated by the presence of the tuft of cilia being either part of the branchial ciliation or the transverse ciliated band usually starting next to the branchiae). This hypothesis would question the currently accepted generic diagnosis of *Microspio* that states that branchiae start on chaetiger 2. Detailed anatomic studies might shed light on this problem which currently is unresolved. However, the presence of the two lobes or lamellae helps differentiating between *M. granulata* and the morphologically very similar *Microspio microcera* (Dorsey, 1977) from the Eastern Pacific Ocean. In *M. microcera* a single lobe dorsally to the neuropodium is easily detected after methyl green staining. The presence of this lobe is not mentioned in the original description (Dorsey 1977) but has been illustrated by Maciolek (1990). After examination of the type material the following information on *M. microcera* can be added: the nuchal organ is as described for *M. granulata*; metameric dorsal ciliated organs as one pair of single comma-shaped ciliary bands per chaetiger present from chaetiger 3 to about chaetiger 15; first branchiae on chaetiger 2, about half or two thirds the length of the second pair of branchiae on chaetiger 3, branchiae on chaetigers 3–5 most stout, in subsequent chaetigers thinner but slightly longer, branchial distribution otherwise very similar to *M. granulata*; two pairs of ventral epidermal glands depictable as large white dots after methyl green staining until about chaetiger 11; sabre chaetae present in all hook-bearing chaetigers,

inferior bundle of capillaries in anterior and middle chaetigers most probably present; longest paratype with 28 chaetigers 4.7 mm long and 0.6 mm wide, with eggs. In conclusion, *M. microcera* is morphologically very similar to *M. granulata* but can be distinguished by the presence of only one lobe dorsally to the neuropodium in the first chaetiger instead of two lobes; also, in *M. microcera* the first branchiae are always considerably shorter than the second pair of branchiae whereas they are of about the same length in *M. granulata*; mature specimens of *M. granulata* exhibit an occipital papilla which is not distinct in smaller specimens of this species and is absent in *M. microcera*.

Another morphologically similar species is *M. minuta* (Hartmann-Schröder, 1962). Unfortunately, the type material is not in good condition and important characters like the shape of nuchal organs, the metameric dorsal ciliated organs, ventral epidermal glands or the first chaetiger cannot be observed. The general habitus of the species, however, is in very good agreement with *M. microcera*. Also details from the original species description (in German language) imply great morphological similarity between the two species: small size (holotype with 26 chaetigers 2.5 mm long), prostomium distinctly bifid, caruncle not conspicuous; branchiae from chaetiger 2 throughout the body, ciliated, cirriform, free from notopodial lamellae except at the base, first five pairs of branchiae distinctly longer than posterior branchiae, decreasing in length continously within a short distance; notopodial postchaetal lamellae ovate to tongue-shaped, neuropodial postchaetal lamellae broadly rounded; all parapodia with granulated capillaries with broad sheaths, notochaetae longer than neurochaetae, capillaries in posterior chaetigers shorter, more slender and less numerous; neuropodial bidentate hooded hooks from chaetiger 9, usually 2–3, maximally 4 per fascicle, accompanied by simple capillaries; pygidium with four cirri of equal length. Blake (1983) presents an emended description of *M. minuta* providing information on the presence of sabre chaetae in hook-bearing chaetigers, on the tridentate nature of neuropodial hooks, on the nuchal organs and the metameric dorsal ciliated organs, the two latter fitting at least partially the description of these features in *M. microcera*. The only reliable distinguishing character between *M. minuta* and *M. microcera* seems to be the complete reduction of the first notopodium in *M. minuta*, in contrast the notopodial lobe of the first chaetiger is still present in *M. microcera*. Considering the fact, that this notopodial lobe is not easy to detect in these small species and has been overlooked in the past it cannot be ruled out that *M. microcera* is a junior synonym of *M. minuta*. Both species occur in the Eastern Pacific Ocean, intertidally to 18 m water depth, either associated with coralline algal mats (Dorsey 1977) or between rhizoids of *Macrocystis* washed up on the beach (Hartmann-Schröder 1962). If new material becomes available for examination the validity of the two species has to be verified.

Other species of *Microspio* with neuropodial hooks from the 9th chaetiger differ from *M. granulata* in regard to the prostomial shape, the presence of notochaetae in chaetiger one or the branchial distribution along the body (see Maciolek 1990, Table 3, and description of *M. atlantica* Langerhans, 1880).

Habitat / Ecology. In the Lizard Island area the species occurred in the intertidal, in sand among seagrass and algae (*Halimeda*). At localities in South Australia and New South Wales the species also occurred in sand, *Zostera* sea grass beds, associated with *Halophila* (see collection data type material), or among mussels (Hutchings & Murray 1984, Hutchings & Turvey 1984).

Distribution. Australia: Queensland, New South Wales, South Australia.

Genus *Spiophanes* Grube, 1860

Spiophanes Grube, 1860; type-species: *Spiophanes kroyeri* Grube, 1860, by monotypy.
Morants Chamberlin, 1919; type-species: *Morants duplex* Chamberlin, 1919, by monotypy, junior synonym.

Diagnosis. Prostomium subtriangular, bell-shaped or rarely rounded, anterior margin never incised; frontal or lateral horns present or absent; eyes present or absent; occipital antenna present or absent. Nuchal organs as two ciliated bands along dorsum, differing in length but maximally extending to chaetiger 17, or as pair of dorsal loops not extending beyond chaetiger 6; metameric dorsal ciliated organs rarely present. Branchiae absent. Dorsal ciliated crests usually present. Body divided into three different regions: 1) Anterior region extending to chaetiger 4, with well developed parapodial lamellae; 2) Middle body region: from chaetiger 5 to last chaetiger bearing capillary chaetae rather than hooks in neuropodia (either chaetiger 13, 14 or 15 depending on species); chaetigers usually with parapodial glandular organs: organs on chaetigers 5–7(8) can exhibit a chaetal spreader of different types (see Meißner & Hutchings 2003), opening often absent on chaetiger 8, rarely absent on chaetigers 5–7; from chaetiger 9, gland opens as simple vertical slit; 3) Posterior region: indicated by presence of neuropodial hooks.

Ventrolateral intersegmental pouches present or absent between neuropodia. Chaetiger 1 with 1–2 conspicuous crook-like chaetae in neuropodium; otherwise neurochaetae in anterior and middle body region all capillaries, arranged in 1–2 rows; posterior region with quadridentate hooks, hood absent or present. Notochaetae all capillaries, in middle body region usually arranged in three rows; otherwise in two rows or in indistinct rows. Bacillary chaetae may be exposed from chaetigers 5–8. One to two ventral sabre chaetae usually from chaetiger 4, rarely from chaetigers 5 or 10, or sometimes not present until neuropodial hooks appear. Pygidium with two or more anal cirri.

Spiophanes viriosus Meißner & Hutchings, 2003

Spiophanes viriosus Meißner & Hutchings, 2003: 123, figs 1a, 2e, h, 4, 5.
Spiophanes cf. *kroeyeri*.—Blake & Kudenov 1978: 225, fig. 27, in part.
Spiophanes sp. 2.—Wilson & McDiarmid 2003.

Material examined. AM W.44566, MI QLD 2379, af, formalin.

Diagnosis. Prostomium with distinct anterolateral projections. Occipital antenna present. Nuchal organs as two long parallel ciliary bands along dorsum. Chaetal spreader of "2+3 type" (see Meißner & Hutchings 2003) with undulate opening in chaetigers 5–7. Ventrolateral intersegmental pouches present from between chaetigers 14–15. Neuropodial hooks starting on chaetiger 15, hooks quadridentate without hood. Sabre chaetae from chaetiger 4. Dark brownish pigment posteriorly along vertical slit of glandular organs of chaetigers 9–12, most conspicuous on chaetiger 9.

Description. For a detailed species description see Meißner & Hutchings (2003). Descriptive notes here on single specimen examined in the course of the present study: Anterior fragment with 20 chaetigers, total length 4.1 mm, width 0.65 mm (measured at chaetiger 4, chaetae and postchaetal lobes omitted). Two groups of red eyes on the prostomium, four small round eyes on each side. Nuchal organs as two long parallel ciliary bands along dorsum, slightly diverging at end and terminating on chaetiger 16. Dorsal ciliated crests apparent from chaetiger 16 until the end of the fragment. From chaetiger 15, one row of maximally four quadridentate hooks without hood present in neuropodia. Sabre chaetae start on chaetiger 4. Ventrolateral intersegmental pouches first fully developed between chaetigers 15 and 16. Yellow-brown pigment in neuropodia of chaetiger 9.

Remarks. The specimen is in good agreement with the original description by Meißner & Hutchings (2003). Minor deviations concern the greater number of eyes, the length of the nuchal organ which is slightly shorter in the specimen from Lizard Island, and the first presence of fully developed ventrolateral intersegmental pouches between chaetigers 15 and 16 instead of between chaetigers 14 and 15 as originally described for *S. viriosus*. Only four neuropodial hooks in one row are present in the Lizard Island specimen whereas initially 5–7 hooks are mentioned in the original description. The observed differences could be due to the small size of the examined specimen from the present collection.

Habitat / Ecology. In the Lizard Island area a single specimen in subtidal depths in coral sand at Yonge Reef.

Distribution. Australia: Queensland.

Molecular data

We successfully obtained sequences for five spionid species from Lizard Island: *Microspio granulata* (COI, 16S and 18S), *Malacoceros indicus* (COI, 16S and 18S), *Spio blakei* (COI, 16S and 18S), *Scolelepis kudenovi* (COI and 18S), and *Spiophanes viriosus* (COI and 18S). The sequence length ranged from 348 bp (16S) to 579 bp (COI), and all sequence data was deposited in GenBank (Table 1).

Only in *M. indicus* and *S. blakei* more than one haplotype was found. The mean genetic distances between *M. indicus* haplotypes were 0.26% in 16S and 0.17% in COI, corresponding to 1 substitution each. Between *M. fuliginosus* (Claparède, 1870) (retrieved from GenBank; EF446961-2, AY525632, EF432012-16, EF431961-2) and *M. indicus* mean distances of 9.4% in 18S, 27.4% in COI and 28.9% in 16S were found. In *S. blakei* the 5 haplotypes of 16S showed a maximal distance of 1.15% (4 substitutions), and the 3 haplotypes of COI a p-distance of 0.35% (2 substitutions). Mean distances of *S. blakei* to *S. filicornis* (Müller, 1776) sequences from Genbank were 4.8% in 18S (FR823430-1), 18.5% in 16S (FR823435-6), and 27.5% in COI (FR823425-6). The COI of *M. granulata* differed by 41.4% from *S. filicornis* and 44.0% from *S. blakei*.

Within all available *Scolelepis* COI sequences, *S. kudenovi* revealed closest relationship to *S. daphoinos* Zhou, Ji & Li , 2009 (19.6%, GU362687) and *S. foliosa* (Audouin & Milne Edwards, 1833) (20.8%, KF369182). The distances to *S. eltaninae* Blake, 1983 (KF713383) and *S. squamata* (O.F. Müller, 1806) (HM473679-80) were 22.4% and 30.6% respectively.

For interspecies relationship in the genus *Spiophanes*, we added the *S. viriosus* COI haplotype of this study to an alignment consisting of 290 bp of *Spiophanes* sequences from GenBank (GQ202696-GQ202715, Meißner & Blank 2009). The genetic distances (p-distance) to the other species were within the previously reported range of 15.0% (*S. kroyeri* Grube, 1860) to 19.7% (*S. pisinnus* Meißner & Hutchings, 2003).

Discussion

Seven species belonging to the genera *Malacoceros*, *Scolelepis*, *Spio*, *Microspio*, and *Spiophanes* were found during the polychaete workshop on Lizard Island in August 2013. One species is new to science and named *Scolelepis inversa* n. sp., another species is probably also a new species but was represented in our samples by a single specimen, a rather short anterior fragment, and therefore not formally described as a new species (*Scolelepis* sp.). All other species have been reported previously for Australia. Species diagnoses of all species found during the workshop and of few additional species (*Scolelepis balihaiensis* Hartmann-Schröder, 1979, *Microspio microcera* (Dorsey, 1977), *Microspio minuta* (Hartmann-Schröder, 1962)) of which the type material has been examined in the course of the present study have been critically reviewed and amended. The potential synonymy of *Microspio minuta* (Hartmann-Schröder, 1962) and *M. microcera* (Dorsey, 1977) is discussed. Also, the new combination *Spio jirkovi* (Sikorski, 1992) proposed by Sikorski (2013) is not accepted and the species again assigned to *Malacoceros.* The study revealed the urgent need for taxonomic research on the studied taxa.

The generic diagnosis of *Malacoceros* is under debate (see remarks under the species diagnosis in the present paper). *Malacoceros indicus* (Fauvel, 1928) has an almost cosmopolitan distribution and occurs in the Pacific, Indian and the Atlantic Oceans. Intraspecific variability has been documented to be large (Foster 1971b, Imajima 1991, Blake 1996, Williams 2007, Delgado-Blas & Salazar-Silva 2011 and present paper), but the species has not yet been resolved into a species complex. Also, it can currently not be ruled out that it is a very widely distributed species. It will not be easy to answer this question based on studies of morphological characters alone. The present paper for the first time provides information on genetic markers for *M. indicus*, however, there are currently no data from other localities for comparison from public sources. Also, for *Scolelepis* delimitation of species is difficult based on morphology. The reliability of many characters is hard to judge in this genus since intraspecific variability, either attributable to ontogenetic development, ecological adaptation or individual variation, has not been studied in detail. There is only one exception by Hutchings *et al.* (1998), who investigated the relationship between body length, maximum anterior width and the chaetiger on which neuropodial hooded hooks are first present for *Scolelepis dicha* Hutchings, Frouin & Hily, 1998. There was some evidence that with increasing size the hooks begin later, suggesting some chaetal replacement with increasing length and presumably age (Hutchings *et al.* 1998). Important morphological characters for the identification of *Scolelepis* species are however the prostomial shape and the appearance of postchaetal lamellae and branchiae. Unfortunately, there is no information of intraspecific variation of such characters in the literature. Dauer (1987), Eibye-Jacobsen (1997) and Williams (2007) found that palp ciliation patterns are of taxonomic importance. So far palp ciliation patterns of nine species of *Scolelepis* have been described (Dauer 1983, 1987, 1994, Eibye-Jacobsen 1997, Eibye-Jacobsen & Soares 2000, Williams 2007). In the present study information on this feature was added for *S. inversa* n. sp. and found to be in accordance with the general pattern described for the genus, though the number of mucus secreting cells was very high compared to the number of accompanying cilia. In summary, the observation of palp cilation patterns seems useful but information is only available for the minority of *Scolelepis* species. In many instances, palps are missing on preserved specimens and hence information is not easy to gather. The lack of data also applies to sequence information. Unfortunately, due to the low number of specimens, information on molecular markers could only be provided for *S. kudenovi*. COI sequences of four other *Scolelepis* species were available from GenBank (*S. daphoinos, S. foliosa*, *S. eltaninae*, *S. squamata*). Among the available species genetic distance was lowest to *S. daphoinos* Zhou, Ji & Li, 2009 but with 19.6% within the range (17.6%–30.6%) found between the other species of this genus. These values are comparable to interspecific distances previously reported within spionid genera (e.g.,

Blank & Bastrop 2009, Mahon *et al.* 2009, Meißner & Blank 2009, Carr *et al.* 2011). *S. daphoinos* has indeed been considered to be morphologically similar to *S. kudenovi* (Zhou *et al.* 2009). However, from a more general point of view the sample of available *Scolelepis* sequences is very small (more than 80 species are described) and hence does not allow statements about phylogenetic relationships and species status based on molecular data.

Microspio granulata and *Spio blakei* are two species well-known from different regions in Australia, the latter species potentially also occurs across the Pacific. The two species were among the most abundant Spionidae in the sampling area and specimens could be fixed for different purposes. Morphological studies included SEM studies and proved to be very useful for the descriptions of nuchal organs and metameric dorsal ciliated organs. For *S. blakei* details on the caruncle and the nuchal organ found in the original description (Blake & Kudenov 1978) were slightly corrected and information about the dorsal ciliated organs was added. It was found that nuchal organs follow the pattern typical for this genus (with short median ciliated bands extending to first tcb on chaetiger 2 and long recurved lateral ciliary bands not extending tcb on chaetiger 3) and that metameric dorsal ciliated organs are double-paired. *M. granulata* also has a nuchal organ composed of a short median ciliated band and a longer lateral ciliated band. The metameric dorsal ciliated organs are pairs of single comma-shaped ciliated bands arranged between tcb´s of subsequent chaetigers. The presence of a hood, reminiscent of dorsal collars seen in the genus *Streblospio* observed by Blake & Kudenov (1978), was not corroborated by our results.

Another structure that has recently attracted attention in connection with taxonomic studies on *Spio* are the ventral epidermal glands (Maciolek 1990, Meißner *et al.* 2011, Bick & Meißner 2011). Distinct distribution patterns of glands can be distinguished among different *Spio* species and they represent a consistent specific character (Meißner *et al.* 2011). The presence of these glands is documented in the present paper for *S. blakei* and also for *M. granulata*. Two pairs of glands per chaetiger were found in *S. blakei* and likewise in *M. granulata*. Also the general anatomy of the glands seems very similar in both species. At the same time it appears to be in good agreement with the structure of the acinar type of epidermal glands described by Rößger *et al.* (2015) found in *Spio* sp. from the beaches of the Balearic Island Ibiza, Spain. The glands are in intraepidermal position. A reservoir, numerous gland cells as well as canal cells forming the cuticularized pore region are easily recognized in cross-sections of glandophorous chaetigers (Figs 7C, 11C). The documentation of ventral epidermal glands is the first for a species of *Microspio*. This might give evidence for the close relationship of *Spio* and *Microspio.* An alternative explanation could be that *M. granulata* does not belong to *Microspio.* In this connection the interpretation of the superior lobe in the first chaetiger is of interest again (compare Remarks under *M. granulata*). An associated ciliated tuft could be detected by means of SEM and hence the dorsalmost lobe could be interpretated as a branchial remnant. Branchiae start on the first chaetiger in *Spio* but on the second in *Microspio* according to currently accepted diagnoses. On the other hand the number of ciliary bands constituting the metameric dorsal ciliated organs is supposedly two in *Microspio* (as also observed in *M. granulata*, present paper) and four in *Spio* (compare e.g., *S. blakei*, present paper) (Söderström 1920). The separation of *Spio* and *Microspio* is a long discussed and not yet resolved problem (see Bick & Meißner 2011). Unfortunately the sequence representation in the molecular databases for both genera is low. With *M. granulata* we provided the first sequence information for the genus *Microspio*. Additional data from both genera are needed to further evaluate the identity (and validity) of *Microspio* and *Spio*.

A single specimen of *Spiophanes viriosus* was found during the polychaete workshop. The species is probably more abundant in subtidal waters rather than in shallow water directly on the beach (compare location data in Meißner & Hutchings 2003), the region most intensively sampled during the workshop. The specimen was in good agreement with the original description and minor deviations were attributed to its small size. In the present study, we also provided sequence data for *S. viriosus* (COI and 18S). Sequencing of partial 16S failed as already before in another study on *Spiophanes* (Meißner & Blank 2009), most likely because the available universal 16S primers are not working in this genus. The analysis of the COI dataset including all available *Spiophanes* species revealed genetic distances that were within the previously reported range for this genus (15.0%–19.7%, Meißner & Blank 2009) and within other spionid genera (e.g., Blank & Bastrop 2009, Mahon *et al.* 2009, Meißner & Blank 2009, Carr *et al.* 2011).

In conclusion, in the present study we showed that characters which were more recently discovered to be of taxonomic importance are not well represented in available generic or species diagnoses. The problems to find reliable diagnostic characters has always been difficult in the family Spionidae (e.g., *Scolelepis*, this study, e.g., Bick *et al.* 2010, Greaves *et al.* 2011). In Spionidae the false species assignment due to the use of inappropriate

characters is a persistent problem which probably is further complicated by the existence of paraphyletic taxa. This indicates that the inclusion of additional morphological characters is needed to solve long-standing problems in spionid taxonomy. The integration of sequence data might help. But this is currently hampered by the fact that the present sequence coverage in public databases is low for most spionid genera. Additional sequence data are thus urgently needed and hence future species collection should include, whenever possible, material which is suitable for both taxonomic and molecular studies. We argue for an integrative taxonomic approach (Dayrat 2005), in which taxonomy and DNA barcoding (Ratnasingham *et al.* 2007) complement each other to delineate species and generic boundaries. DNA sequences and related species information (e.g., voucher data, geographic data, and pictures) will support morphological studies by species identification through DNA barcoding and will be valuable resources for phylogeographic studies or phylogenetic reconstructions.

Acknowledgements

We would like to thank all people involved in the organization and realization of the polychaete workshop, namely Pat Hutchings, Anna Murray, Anne Hoggett and Lyle Vail. Participation in the workshop was a great opportunity to do research in the Great Barrier Reef under excellent working conditions. We would also like to thank colleagues who provided material from their collections for this study: Helen Stoddart and Steven Keable (Australian Museum, Sydney, Australia), Leslie Harris (Natural History Museum of Los Angeles County, Los Angeles, U.S.A.), Chris Rowley (Museum Victoria, Melbourne, Australia), Petra Wagner and Katrin Philipps-Bussau (Zoological Museum, Hamburg, Germany). We are grateful to Sabine Gaude (Hamburg University), who did the lab work for histological studies, to Karen Jeskulke (DZMB Hamburg, Senckenberg) for doing the lab work for the genetic analyses and to Amy Driskell (Smithsonian's National Museum of Natural History) for support while work was conducted in the labs of the Smithsonian institution in Washington. Renate Walter (University of Hamburg) gave assistance for the SEM studies. Antje Fischer (DZMB Hamburg, Senckenberg) found literature in the libraries and made it accessible for us and to other colleagues working in the project. Dieter Fiege (Senckenberg Institute Frankfurt) also provided some references. Geoff Read is thanked for keeping an eye on the spionids in WoRMS. Andreas Bick and James A. Blake made very valuable comments on a former version of the manuscript. The study was funded by the Lizard Island Research Foundation under permit no G12/35718.1, issued by the Great Barrier Reef Marine Park Authority.

References

Audouin, J.V. & Milne-Edwards, H. (1833) Classification des annélides et description de celles qui habitent les côtes de la France. *Annales des Sciences Naturelles*, *Paris*, 30, 411–425.

Augener, H. (1914) Polychaeta II: Sedentaria. *In:* Michaelsen, W. & Hartmeyer, R. (Eds.), *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*. Gustav Fischer Verlag, Jena, pp. 1–170.

Ben-Eliahu, M.N., Hutchings, P.A. & Glasby, C.J. (1984) *Ceratonereis lizardensis* n. sp. (Polychaeta; Nereididae) and *Malacoceros indicus* (Spionidae) from a mangrove habitat at Lizard Island, North Queensland. *Proceedings of the first international polychaete conference, Sydney, Linnean Society of New South Wales*, 1984, 91–97.

Berkeley, E. & Berkeley, C. (1941) On a collection of Polychaeta from Southern California. *Bulletin of the Southern California Academy of Sciences*, 40, 16–60.

Berkeley, E. (1927) Polychaetous annelids from the Nanaimo district. Part 3. Leodicidae to Spionidae. *Contributions to Canadian Biology and Fisheries*, 3, 405–422.

Bick, A. & Meißner, K. (2011) Redescription of four species of *Spio* and *Microspio* (Polychaeta, Spionidae) from the Kuril Islands and Peter the Great Bay, northwest Pacific. *Zootaxa*, 2968, 39–56.

Bick, A., Otte, K. & Meißner, K. (2010) A contribution to the taxonomy of *Spio* (Spionidae, Polychaeta, Annelida) occuring in the North and Baltic Seas, with a key to species recorded in this area. *Marine Biodiversity*, 40, 161–180. http://dx.doi.org/10.1007/s12526-010-0040-5

Blainville, H. de. (1828) *Dictionnaire des Sciences Naturelles*. F.G. Levrault, Strasbourg, 47, 368–501.

Blake, J.A. (1983) Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. *Biology of the Antarctic Seas XIV*, 39, 205–288. http://dx.doi.org/10.1029/AR039p0205

Blake, J.A. (1996) Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision

of the genus *Polydora* Bosc, 1802. *In*: Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. The Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae.* Santa Barbara Museum of Natural History, Santa Barbara, pp. 81–223.

Blake, J.A. & Arnofsky, P.L. (1999) Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia*, 402, 57–106. http://dx.doi.org/10.1007/978-94-017-2887-4_4

Blake, J.A. & Kudenov, J.D. (1978) The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Memoirs of the National Museum of Victoria*, 39, 171–280.

Blank, M. & Bastrop, R. (2009) Phylogeny of the mud worm genus *Marenzelleria* (Polychaeta, Spionidae) inferred from mitochondrial DNA sequences. *Zoologica Scripta*, 38, 313–321. http://dx.doi.org/10.1111/j.1463-6409.2008.00370.x

Bobretzky, N. (1870) On the fauna of the Black Sea (Auszug *Spio decoratus*). *Zapiski Kievskogo Obshchestva Estestvoispytateley*, 1, 188–274.

Bone, D. & Viéitez, J. (2002) Spionidae (Annelida: Polychaeta) from the Parque National Morrocoy, Falcón, Venezuela. *Revista de Biología Tropical (San Jose)*, 50, 69–75.

Carr, C.M., Hardy, S.M., Brown, T.M., Macdonald, T.A. & Hebert, P.D.N. (2011) A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS ONE*, 6, 1–12. http://dx.doi.org/10.1371/journal.pone.0022232

Chamberlin, R.V. (1919) New polychaetous annelids from Laguna Beach, California. *Pomona College Journal of Entomology and Zoology*, 11, 1–23.

Claparède, E. (1869) Les Annélides Chétopodes du Golfe de Naples. Seconde partie. *Mémoirs de la Société de Physique et d'Histoire Naturelle de Genève*, 20 (1), 1–225.

Claparède, E. (1870) Les Annélides Chétopodes du Golfe de Naples. Troisième partie. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève,* 20 (2), 365–542.

Czerniavsky, V. (1881) Material ad zoographiam Ponticam. Fasc. III Vermes. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 55, 211–363.

Dauer, D.M. (1983) Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). *Marine Biology*, 77, 279–285. http://dx.doi.org/10.1007/bf00395817

Dauer, D.M. (1985) A new species of *Scolelepis* (Polychaeta: Spionidae) from Lizard Island, Australia. *Proceedings of the Biological Society of Washington*, 98, 678–681.

Dauer, D.M. (1987) Systematic significance of the morphology of spionid polychaete palps. *Bulletin of the Biological Society of Washington*, 7, 41–45.

Dauer, D.M. (1994) Functional ciliary groups of the feeding palps of spionid polychaetes. *Bulletin du Muséum National d'Histoire Naturelle. Paris,* 162, 81–84.

Dauer, D.M. & Ewing, R.M. (1991) Functional morphology and feeding behavior of *Malacoceros indicus* (Polychaeta: Spionidae). *Bulletin of Marine Science*, 48, 395–400.

Day, J.H. (1967) *A monograph on the polychaeta of southern Africa. Part 2. Sedentaria*. Trustees of the British Museum (Natural History), London, 383 pp. [pp. 459–841]

Dayrat, B. (2005) Towards integrative taxonomy. *Biological Journal of the Linnean Society*, 85, 407–415. http://dx.doi.org/10.1111/j.1095-8312.2005.00503.x

de León-Gonzáles, J.A. (1998) Spionidae and Opheliidae (Annelida: Polychaeta) from the western coast of Baja Californica, Mexico. *Bulletin of Marine Science*, 62, 7–16.

de Silva, P.H.D.H. (1961) Contributions to the knowledge of the polychaete fauna of Ceylon. Part 1—Five new species, two new varieties and several new records principally from the southern coast. *Spolia Zeylandica*, 29, 164–194.

Dean, D. (2004) Marine biodiversity of Costa Rica: Class Polychaeta (Annelida). *Revista de Biología Tropical*, 52, 1–69.

Delgado-Blas, V.H. & Díaz-Díaz, Ó. (2010) Description of two new species of *Malacoceros* and *Rhynchospio* spionids (Polychaeta: Spionidae) from the Grand Caribbean region. *Revista Chilena de Historia Natural*, 83, 249–257. http://dx.doi.org/10.4067/s0716-078x2010000200006

Delgado-Blas, V.H. & Díaz-Díaz, Ó. (2013) *Malacoceros longiseta*, a new species of Spionidae (Annelida: Polychaeta) from Venezuela. *Marine Biodiversity*, 43, 181–187. http://dx.doi.org/10.1007/s12526-013-0144-9

Delgado-Blas, V.H. & Salazar-Silva, P. (2011) Taxonomic catalogue of the Spionidae (Annelida: Polychaeta) of the Grand Caribbean. *Zootaxa*, 2782, 39–66.

Díaz-Castañeda, V., de Leon-Gonzalez, A. & Arellano, E.S. (2005) Structure and composition of the polychaete community from Bahia San Quintin, Pacific Coasta of Baja California, Mexico. *Bulletin of the Southern California Academy of Sciences*, 104, 75–99. http://dx.doi.org/10.3160/0038-3872(2005)104[75:sacotp]2.0.co;2

Dorsey, J.H. (1977) A new species of *Rhynchospio* (Polychaeta: Spionidae) from San Clemente Island, California. *Bulletin of the Southern California Academy of Sciences,* 76, 1–4.

Eibye-Jacobsen, D. (1997) A new species of *Scolelepis* (Polychaeta: Spionidae), highly abundant on the sand beaches of

western Phuket Island, Thailand. *Bulletin of Marine Science*, 60 (2), 240–251.
Eibye-Jacobsen, D. & Soares, A.G. (2000) New records of *Scolelepis* (Polychaeta: Spionidae) from the sandy beaches of Madagascar, with the description of a new species. *Bulletin of Marine Science*, 67, 571–586.
Englisch, U. & Koenemann, S. (2001) Preliminary phylogenetic analysis of selected subterranean amphipod crustaceans, using small subunit rDNA gene sequences. *Organisms Diversity and Evolution*, 1, 139–145.
http://dx.doi.org/10.1078/1439-6092-00011
Fabricius, O. (1785) Von dem *Spio*-Geschlecht einem neuen Wurmgeschlecht. *Nereis seticornis* und *Nereis filicornis*, mit Abbildungen. *Schriften der Berlinischen Gesellschaft naturforschender Freunde*, 6, 256–270.
Fauvel, P. (1928) Annélides Polychètes nouvelles de l'Inde. *Bulletin du Muséum National D'Histoire Naturelle*, 34, 90–96.
Fauvel, P. (1930) Annelida Polychaeta of the Madras Government Museum. *Bulletin of the Madras Government Museum, new series, Natural History Section*, 1 (2), 1–72.
Fauvel, P. (1953) *Annelida Polychaeta. The fauna of India including Pakistan, Ceylon, Burma and Malaya*. The Indian Press, Ltd, Allahabad, 507 pp.
Folmer, O., Black, M., Hoen, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
Foster, N.M. (1971a) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Studies on the fauna of Curaçao and other Caribbean Islands*, 36, 1–150.
Foster, N.M. (1971b) Redescription of the spionid polychaete *Malacoceros* (*Malacoceros*) *indicus* (Fauvel 1928). *Journal of the Fisheries Research Board of Canada*, 28, 1455–1457.
http://dx.doi.org/10.1139/f71-224
Graff, J.R., Blake, J.A. & Wishner, K.F. (2008) A new species of *Malacoceros* (Polychaeta: Spionidae) from Kick'em Jenny, a hydrothermally active submarine volcano in the Lesser Antilles Arc. *Journal of the Marine Biological Association of the United Kingdom*, 88, 925–930.
http://dx.doi.org/10.1017/s0025315408001884
Gravier, C. (1911) Sur les espèces nouvelles de Polychètes provenant de la seconde expédition antarctique francaise (1908–1910). *Bulletin du Museum d'Histoire Naturelle*, *Paris*, 17, 310–316.
Greaves, E., Meißner, K. & Wilson, R. (2011) New *Laonice* species (Polychaeta: Spionidae) from western and northern Australia. *Zootaxa*, 2903, 1–20.
Grube, E. (1850) Die Familien der Anneliden. Archiv für Naturgeschichte 16, 249–364.
Grube, A.-E. (1860) Beschreibung neuer oder wenig bekannter Anneliden. *Archiv für Naturgeschichte*, 26, 71–118.
Guérin, J.P. & Kerambrun, P. (1984) Role of reproductive characters in the taxonomy of spionids and elements of speciation in the *Malacoceros fuliginosus* complex. *Fortschritte der Zoologie*, 29, 317–333.
Halanych, K.M., Bacheller, J.D., Aguinaldo, A.M.A., Liva, S.M., Hillis, D.M. & Lake, J.A. (1995) Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science*, 267, 1641–1643.
http://dx.doi.org/10.1126/science.7886451
Hall, T.A. (1999) BIOEDIT: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
Hartman, O. (1961) Polychaetous annelids from California. *Allan Hancock Pacific Expeditions*, 25, 1–226.
Hartman, O. (1969) *Atlas of the sedentariate polychaetous annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.
Hartmann-Schröder, G. (1962) Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychchaeten und Ostracoden. Teil 2. Die Polychaeten des Eulitorals. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut*, 60 (Supplement Volume), 57–167.
Hartmann-Schröder, G. (1979) Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). *Mitteilungen aus dem Hamburger Zoologischen Museum und Institut*, 76, 77–219.
Hartmann-Schröder, G. (1981) Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 6: Die Polychaeten der tropisch-subtropischen Westküste Australiens (zwischen Exmouth im Norden und Cervantes im Süden). *Mitteilungen aus dem Hamburger Zoologischen Museum und Institut*, 78, 19–96.
Hartmann-Schröder, G. (1989) Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden Teil 14. Die Polychaeten der antiborealen und subtropischen Küste Südost-Australiens zwischen Lakes Entrance (Victoria) im Süden und Maclean (New South Wales) im Norden. *Mitteilungen aus dem Hamburger Zoologischen Museum und Institut*, 86, 11–63.
Hartmann-Schröder, G. (1991a) Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 16: Die Polychaeten der subtropisch-tropischen bis tropischen Ostküste Australiens zwischen Maclean (New South Wales) und Gladstone (Queensland) sowie von Heron Island (Großes Barriere-Riff). *Mitteilungen aus dem Hamburger Zoologischen Museum und Institut*, 88, 17–71.
Hartmann-Schröder, G. (1991b) Beitrag zur Polychaetenfauna der Bahia Quillaipe (Süd-Chile). *Helgoländer Meeresuntersuchungen*, 45, 39–58.
http://dx.doi.org/10.1007/bf02365635

Hutchings, P. & Murray, A. (1984) Taxonomy of polychaetes from the Hawkesbury River and the southern estuaries of New South Wales, Australia. *Records of the Australian Museum*, Supplement 3, 1–118. http://dx.doi.org/10.3853/j.0812-7387.3.1984.101

Hutchings, P. & Rainer, S. (1979) The polychate fauna of Careel Bay, Pittwater, New South Wales, Australia. *Journal of Natural History*, 13, 745–796. http://dx.doi.org/10.1080/00222937900770561

Hutchings, P. & Turvey, S.P. (1984) The Spionidae of South Australia (Annelida: Polychaeta). *Transactions of the Royal Society of South Australia*, 108, 1–20.

Hutchings, P., Frouin, P. & Hily, C. (1998) Two new species of Spionidae (Polychaeta) from Tahiti, French Polynesia. *Proceedings of the Biological Society of Washington*, 111, 799–806.

Imajima, M. (1991) Spionidae (Annelida, Polychaeta) from Japan. VI. The genera *Malacoceros* and *Rhynchospio*. *Bulletin of the National Science Museum, Tokyo,* Series A, 17, 5–17.

Imajima, M. (1992) Spionidae (Annelida, Polychaeta) from Japan. VIII. The genus *Scolelepis*. *Bulletin of the National Science Museum, Tokyo,* Series A, 18, 1–34.

Johnston, G. (1827) Contributions to the British Fauna. *Zoological Journal, London*, 3, 321–336.

Johnston, G. (1838) Miscellanea zoologica, Aricidae. *Magazine of Zoology and Botany*, 2, 63–73.

Karnovsky, M.J. (1965) A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *Journal of Cell Biology*, 27, 137–138.

Keferstein, W. (1862) Untersuchungen über niedere Seethiere. *Zeitschrift für wissenschaftliche Zoologie*, 12, 1–147.

Kessing, B., Croom, H., Martin, A., McIntosh, C. & Owen McMillan, W. (1989*) The Simple Fool's Guide to PCR*. University of Hawaii, Honolulu, 23 pp.

Khlebovich, V.V. (1959) Species of Polychaeta worms from the Kuril Islands, which are new or recorded for the first time in the USSR fauna. *Zoologichesky Zhurnal*, 38, 167–181.

Langerhans, P. (1880) Die Wurmfauna Madeiras. II. *Zeitschrift für wissenschaftliche Zoologie*, 33, 271–316.

Maciolek, N.J. (1987) New species and records of *Scolelepis* (Polychaeta: Spionidae) from the East coast of North America, with a review of the subgenera. *Bulletin of the Biological Society of Washington*, 7, 16–40.

Maciolek, N.J. (1990) A redescription of some species belonging to the genera *Spio* and *Microspio* (Polychaeta: Annelida) and descriptions of three new species from the northwestern Atlantic Ocean. *Journal of Natural History*, 24, 1109–1141. http://dx.doi.org/10.1080/00222939000770701

Mahon, A.R., Mahon, H.K., Dauer, D.M. & Halanych, K.M. (2009) Discrete genetic boundaries of three *Streblospio* (Spionidae, Annelida) species and the status of *S. shrubsolii*. *Marine Biology Research*, 5, 172–178. http://dx.doi.org/10.1080/17451000802317683

Malmgren, A.J. (1867) Annulata Polychaeta; Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae. Hactenus cognita, *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 24, 1–127. http://dx.doi.org/10.5962/bhl.title.13358

McIntosh, W.C. (1915) *Monograph of the British marine annelids. Vol. III. Part I. - Text. Polychaeta, Opheliidae to Ammocharidae*. Ray Society, London, 1–366.

Meißner, K. & Hutchings, P. (2003) *Spiophanes* species (Polychaeta: Spionidae) from Eastern Australia – with descriptions of new species, new records and an emended generic diagnosis. *Records of the Australian Museum*, 55, 117–140. http://dx.doi.org/10.3853/j.0067-1975.55.2003.1379

Meißner, K., Bick, A., Guggolz, T. & Götting, M. (2014) Spionidae (Polychaeta: Canalipalpata: Spionida) from seamounts in the Northeast Atlantic. *Zootaxa*, 3786 (3), 201–245. http://dx.doi.org/10.11646/zootaxa.3786.3.1

Meißner, K. & Blank, M. (2009) *Spiophanes norrisi* n. sp. (Polychaeta: Spionidae) - a new species from the NE Pacific coast, separated from the *Spiophanes bombyx* complex based on both morphological and genetic studies. *Zootaxa*, 2278, 1–25.

Mesnil, F. (1896) Etudes de morphologíe externe chez les Annelìdes: les Spionidiens des cotes de Manche. *Bulletin Scientifique de la France et de la Belgique*, 29, 110–287.

Monro, C.C.A. (1931) Polychaeta, Oligochaeta, Echiuroidea and Sipunculoidea. Great Barrier Reef (Queensland) Expedition, 1928–1929. *Scientific Reports of the British Museum* (*Natural History*), 4, 1–37.

Müller, O.F. (1776) Zoologiae Danicae prodromus: seu Animalium Daniae et Norvegiae indigenarum. Characteres, Nomina, et Synonyma imprimis popularium. *Havniae*, 32, 1–274. http://dx.doi.org/10.5962/bhl.title.13268

Müller, O.F. (1806) *Zoologica Danica seu Animalium Daniae et Norvegiae rariorum ac minus notoruum. Descriptiones et Historia.* Havniae, 160 pp.

Pettibone, M.H. (1963) Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of *Scolelepis*. *Proceedings of the Biological Society of Washington*, 76, 89–104.

Quatrefages, A. de (1843) Déscription de quelques espèces nouvelles d'Annélides errantes recueillies sur côtes de la Manche. *Magasin de Zoologie de Paris,* Série 2, 5, 1–16.

Quatrefages, A. de (1865) Histoire naturelle des Annéles marinaet d'eau douce. Annélides et Gephyriens. *Paris a la librairie encyclopédique de Roret*, 1, 1–588.

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular*

Ecology Notes, 7, 355–364.
http://dx.doi.org/10.1111/j.1471-8286.2007.01678.x

Read, G. (2015) *Scolelepis* Blainville, 1828. *In:* Read, G. & Fauchald, K. (Eds.), World Polychaeta database. Available from: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=129623 (accessed 12 February 2015)

Reish, D.J. (1961) A new species of *Micronereis* (Annelida, Polychaeta) from the Marshall Islands. *Pacific Science*, 15, 273–277.

Ribas, J. & Hutchings, P. (2015) Lizard Island Polychaete Workshop: sampling sites and a checklist of polychaetes. *Zootaxa*, 4019 (1), 7–34.
http://dx.doi.org/10.11646/zootaxa.4019.1.4

Rößger, A., Meißner, K., Bick, A. & Müller, C.H.G. (2015) Histological and ultrastructural reconstruction of ventral epidermal glands of *Spio* (Polychaeta, Spionidae, Annelida). *Zoomorphology.* [published online]
http://dx.doi.org/10.1007/s00435-015-0264-9

Rossi, M.M. (1982) A new species of *Scolelepis* (Polychaeta: Spionidae) from Californian sand beaches. *Bulletin of the Southern California Academy of Sciences*, 81, 97–100.

Sato-Okoshi, W., Okoshi, K. & Shaw, J. (2008) Polydorid species (Polychaeta: Spionidae) in south-western Australian waters with special reference to *Polydora uncinata* and *Boccardia knoxi*. *Journal of the Marine Biological Association of the United Kingdom*, 88, 491–501.
http://dx.doi.org/10.1017/s0025315408000842

Savigny, J.C. (1822) Système des annelides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les caractères tant distinctifs que naturels des ordres, familles et genres, avec la description des espèces. *Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en`Égypte pedant l'expédition de l'Armée Francaise. Troisième Partie. Systèmes de diverses classes d'animaux sans vertèbres*. de l'Imprimerie Impériale, Paris, pp. 3–128. [separate reprint from Description de l'Égypte, without plates]

Schmarda, L.K. (1861) *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Vol. 1. Turbellarien, Rotatorien und Anneliden.* Wilhelm Engelmann, Leipzig, xviii + 66, 15 fine hand-coloured plates.

Sikorski, A.V. (1992) A new species of *Malacoceros* (Polychaeta: Spionidae) from the Norwegian Sea. *Explorations of the Fauna of the Seas*, 43, 105–108.

Sikorski, A.V. (2013) New combination for *Malacoceros jirkovi* and a key for *Spio* (Polychaeta: Annelida) from Norwegian waters and adjacent Arctic areas. *Zoosystematica Rossica*, 22, 172–180.

Söderström, A. (1920) *Studien über die Polychätenfamilie "Spionidae", Inaugural-Dissertation.* Almqvist och Wiksells boktryck, Uppsala, 286 pp.

Swofford, D.L. (2000) *PAUP* Phylogenetic analysis using parsimony (*and other methods)*. *Version 4*. Sinauer Associates, Sunderland, Massachusetts.

Tsang, L.M., Chan, B.K.K., Shih, F.-L., Chu, K.H. & Chen, A. (2009) Host-associated speciation in the coral barnacle *Wanella milleporae* (Cirripedia: Pyrgomatidae) inhabiting the *Millepora* coral. *Molecular Ecology*, 18, 1463–1475.
http://dx.doi.org/10.1111/j.1365-294x.2009.04090.x

Tzetlin, A.B. (1985) *Asetocalamyzas laonicola* gen. et sp. n., a new ectoparasitic polychaete from the White Sea. *Zoologichesky Zhurnal,* 64, 269–298.

van der Heiden, A. & Hendrickx, M.E. (1982) *Inventario de la fauna marina y costera del sur de Sinaloa, Mexico*. Universidad Nacional Autonoma de Mexico, Instituto de Ciencias del Mar y Limnologia, Estacion Mazatlan, 135 pp.

Walker, L.M. (2011) A review of the current status of the *Polydora*-complex (Polychaeta: Spionidae) in Australia and a checklist of recorded species. *Zootaxa*, 2751, 40–62.

Williams, J.D. (2007) New records and description of four new species of spionids (Annelida: Polychaeta: Spionidae) from the Philippines: the genera *Dispio, Malacoceros, Polydora,* and *Scolelepis*, with notes on palp ciliation patterns of the genus *Scolelepis*. *Zootaxa*, 1459, 1–35.

Wilson, R.S. (1990) *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from Southern Australia. *Memoirs of the Museum Victoria*, 50, 243–274.

Wilson, R.S. & McDiarmid, H. (2003) *Spionidae (Polychaeta) — A DELTA database of genera, and Australian species.* CSIRO Publishing, Melbourne.

Zhou, J., Ji, W.W. & Li, X.Z. (2009) A new species of *Scolelepis* (Polychaeta: Spionidae) from sandy beaches in China, with a review of Chinese *Scolelepis* species. *Zootaxa*, 2236, 37–49.