Morphology and biology of *Laetmonice producta producta* Grube (Polychaeta: Aphroditidae) in the Bellingshausen Sea and Antarctic Peninsula (Southern Ocean, Antarctica)

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Abstract

The present paper reports on some morphological and biological features of the scale-worm *Laetmonice producta producta* Grube, 1877 (Polychaeta: Aphroditidae) in the northwestern sector of Antarctica. A total of 114 specimens were collected during the 2003 and 2006 cruises of the BENTART project on the shelf and upper slope of the Antarctic Peninsula and the Bellingshausen Sea. Specimens were collected using an Agassiz trawl at 22 stations covering a depth ranging from 115 to 1431 m. Bathymetric distribution, abundance and sizes, diet, presence of endosymbionts and epibionts, and some observations related to parapodial structure and chaetal types are discussed in relation to taxonomy and environmental characteristics and compared to previous data.

Keywords:

Introduction

The scale-worm *Laetmonice producta* (Polychaeta: Aphroditidae) was described by Grube (1877) from the Kerguelen Islands. Later, McIntosh (1885, 1900) described four varieties on the basis of the general proportions of the prostomium and ocular peduncles, eye pigment, length and ornamentation of chaetae, and the number of ventral papillae. Hutchings and McRae (1993) characterised the Australian material of this species in comparison to other co-generic species on the basis of the absence of hooked notochaetae, the presence of a basal spur and a fringe of distal hairs in the neurochaetae, and 18 or more pairs of elytra on the body dorsum; they also compiled all differences among varieties and suggested that these probably represent different species (Hutchings & McRae 1993). Stiller (1996) reported three subspecies of *L. producta* in Antarctica: *L. p. producta* Grube, 1877, *L. p. wyvillei* McIntosh, 1885 and *L. p. benthaliana* McIntosh, 1885, maintaining the first two as subspecies and establishing the differences among them in terms of prostomial and parapodial issues, but considering the latter as a subspecies of *Laetmonice filicornis* Kinberg, 1856.

Laetmonice producta producta is a large-sized (up to 180 mm), slow-growing, long-living predatory epibenthic species (Micaletto et al. 2003), and is among the most common polychaetes on the shelf of the Antarctic continental margin (e.g. HartmannSchröder & Rosenfeldt 1992; San Martín & Parapar 1997; Pabis & Sicinski 2010). Limited and sometimes anecdotal information, however, is available about its biology (Stiller 1996; Sabatella 2000; Piraino & Montiel 2001; Micaletto et al. 2002, 2003).

Present study draws upon the polychaete material collected in two surveys conducted off the northwest coast of the Antarctic continent, namely the Spanish BENTART (Bentos Antártico) 2003 and 2006 cruises. Both cruises were carried out onboard the R/V Hespérides during the austral summers of 2002–2003 and 2005–2006 respectively. Some results on polychaetes have been published by Parapar and Moreira (2008), López (2008, 2010, 2011), Parapar et al. (2011), and Moreira and Parapar (2011).

In this study we report results on the examination of specimens of *L. p. producta* in the Bellingshausen Sea and Antarctic Peninsula, in order to provide: (1) additional morphological and taxonomic information after scanning electron microscope (SEM) examination, (2) complementary data about some biological features, such as diet, size-class structure, and reproduction, (3) new data on endobionts and epibionts, and (4) data on life state after capture, survival in aquaria and behaviour in response to experimental manipulations in aquaria. These results will be compared with published data about the same polychaete species in Antarctica (e. g. Stiller 1996; Sabatella 2000; Piraino & Montiel 2001; Micaletto et al. 2002, 2003).

Materials and methods

Study area and sample collection

We analysed 114 individuals of *Laetmonice product producta* sampled during the BENTART 2003 (24 Jan–3 Mar) and 2006 (2 Jan–17 Feb) cruises onboard the R/V Hespérides. Specimens were collected using an Agassiz trawl at several stations distributed along the NW sector of the Antarctic Ocean, from the Antarctic Peninsula (AP) to Thurston Island in the Bellingshausen Sea (BS) and in proximity to Peter I Island (PI) (Figure 1). Most specimens were fixed in situ in a buffered 4% formaldehyde seawater solution and preserved in 70% ethanol; some individuals were maintained alive in aquaria aboard ship. More details on sampling device, sediment features, structure of the infaunal assemblages and polychaete diversity can be found in Sáiz et al. (2008) and Parapar et al. (2011).
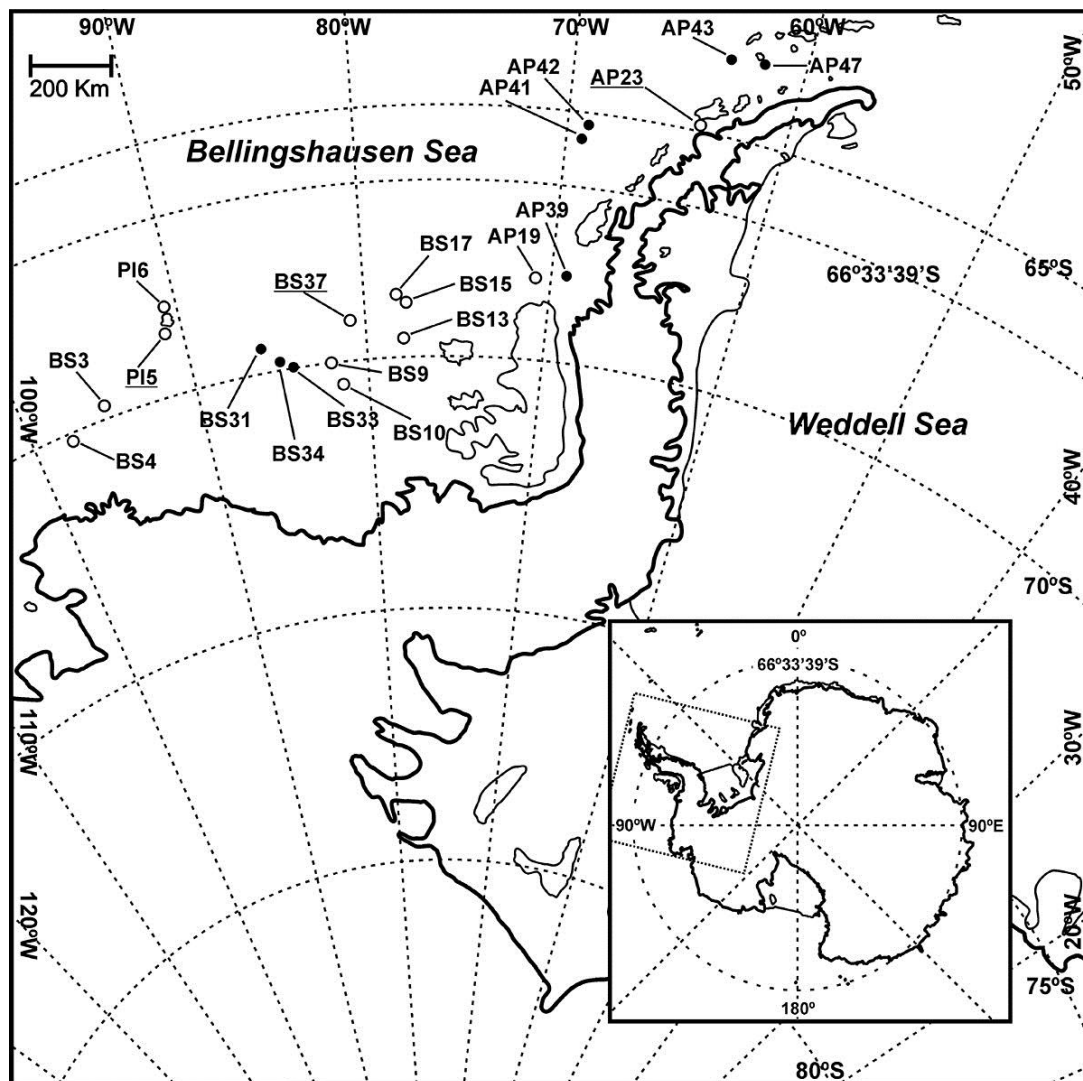

Figure 1. Stations where *Laetmonice producta producta* was sampled with the Agassiz trawl. BENTART (Bentos Antártico) 2003 (open circles) and 2006 (black circles). Station codes: AP, Antarctic Peninsula; BS, Bellingshausen Sea; PI, Peter I Island. The three stations accounting for almost 65% of total abundance of *L. productcta* are underlined.

Because it was not possible to estimate accurately the sampled area with the Agassiz trawl, and because extraction of *L. p. producta* specimens has not been exhaustive, reliable quantitative comparisons among stations (i.e. according to depth, geographical area) and with other studies were not possible.

Most specimens of *L. producta producta* (MNCN 16.01/14341–14449) and all specimens of *Veneriserva pygoclava meridionalis* (MNCN 16.01/14450–14453) were deposited in the collections of the Museo Nacional de Ciencias Naturales of Madrid, Spain (MNCN). Those body parts used for examination with SEM were prepared by critical point drying, covered with gold in a BAL-TEC SCD 004 evaporator, and examined and photographed under a JEOL JSM-6400 SEM at the SAI (Servizos de Apoio á Investigación, UDC, Spain). Several specimens of *L. p. producta*, SEM stubs and vials with gut contents, epibionts and faecal material are deposited in the personal collection of the authors (JP and MCG).

Life state and survival

Once collected from the Agassiz trawl, animals were inspected and the four most active specimens transferred to a 30-l tank kept in a cold chamber in order to maintain water temperature between –0.5◦C and −1◦C (see also García-Castrillo Riesgo 1997). The evaluation of the initial life state – sensu GarcíaCastrillo Riesgo (1997) – of the specimens right after collection was assessed using the formula proposed by this author (Table I in García-Castrillo Riesgo 1997) through an algorithm based on the visual recognition of external traits (alterations, breaks, losses, etc) and vitality (responses to stimuli). The assessment of survival was carried out according to a 120-h time programme and quantified through an algorithm based on direct observations and relative criteria (Table II in García-Castrillo Riesgo 1997). The animals were kept in the aquarium for 5 d and examined for survival and life state at 2, 6, 12, 20 and 32 h, and then every 12 h, for a total of 120 h.

Laboratory analysis

Once in the laboratory, fixed individuals were measured in length from prostomium to pygidium. For each specimen, the number of chaetigers was counted. Each individual was examined under a binocular microscope to check for the presence of epibionts. For studies on gut content, reproductive condition and presence of endosymbionts in the coelom, specimens of *L. p. producta* were dissected ventrally under the stereomicroscope. The coelomic cavity was inspected to assess egg development and presence of the polychaete *Veneriserva pygoclava meridionalis* Micaletto, Gambi & Cantone, 2002. Symbiont prevalence and intensity was considered following Micaletto et al. (2002) and was calculated for the total number of specimens collected. The stomach was also opened to study its contents, and volume of food was quantified using a relative fullness empirical scale: 0% (empty), <10%, 10% to 50% and >50%. The occurrence of food items was estimated and expressed as a percentage (%). For each of several female specimens, the maximal diameter of 60 eggs was measured with a microscope provided with a micrometer.

Results and Discussion

Distribution and abundance

Studied specimens were caught in the three areas sampled during the BENTART cruises: Antarctic Peninsula (AP; 7 stations, 39 specimens), Bellingshausen Sea (BS; 11 st., 32 spec.) and Peter I Island (PI; 2 st., 43 spec.) (Figure 1; Table I). Although the distribution of the specimens across the three areas is apparently homogeneous, three stations (one for each area) contributed almost 65% of specimens, namely st. PI5 (40 spec., 35.1% of total), AP23 (19, 16.7%) and BS37 (14, 12.9%). Furthermore, although the PI stations are within the Bellingshausen Sea, environmental conditions and benthic fauna (particularly assemblages of polychaetes and mollusks) are closer to those found in the Antarctic Peninsula (Troncoso et al. 2007; Sáiz et al. 2008; Troncoso & Aldea 2008; Parapar et al. 2011). The specimens were collected over a wide range of depths (Table I). Those found at shallower depths (< 200 m) were obtained south of the Shetland Islands (AP43, AP47), Peter I Island (PI5, PI6) and Marguerite Bay (AP39), while those collected at greater depths (> 1000 m) were found at stations in the central area of the Bellingshausen Sea (BS3, BS15, BS17, BS31) and off the Antarctic Peninsula (AP42). The bathymetric range is wider than that reported by Micaletto et al. (2003) for the Weddell Sea and King George Island (200–850 m).

Taxonomy and parapodial features

Specimens were identified following the classic studies done in the area, such as those of McIntosh (1885), Horst (1917) and Hartman (1965) and more recent descriptions (e.g. Hutchings & McRae 1993; Stiller 1996; Barnich & Fiege 2003; Imajima 2003). Hartman (1965) gathered all information about the geographical distribution of the nominal species, extending its known distribution range from the Kerguelen Islands to the South Georgia Islands and Antarctic Peninsula, also restricting its presence to waters south of 67∘03 and between 35–640 m depth. Hartman (1965) re-evaluated the presence in Antarctica of the subspecies *L. producta benthaliana* McIntosh, 1885 and *L. producta wyvillei* McIntosh, 1885 and restricted their distribution to the Australian Sector (abyssal to 4540 m depth) and to the Australian littoral and eastern sectors (50–5707 m depth), respectively. Hutchings & McRae (1993, Table 9) presented a detailed description of the Indo-Pacific material and gathered previously reported differences among the varieties of *L. p. producta*. Stiller (1996) presented a study of the distribution and biology of aphroditids and polynoids in Weddell and Lazarev Seas (Antarctica) and reported the presence of both *L. p. producta* and *L. p. wyvillei* in the Antarctic Peninsula and South Shetland islands while considering *L. p. benthaliana* as a subspecies of *L. filicornis*. Our specimens seem to fit with the description of *L. p. producta* after Hutchings & McRae (1993) and Stiller (1996); thus the diagnostic characters of the nominal species are the number of segments (44–47) and elytra (20), the general prostomial appearance (nuchal flaps and presence of eyes) and the general shape of notochaetae and neurochaetae. However, a revision of this species in the Antarctic waters would be

desirable because, as recognized by Hutchings and McRae (1993, p. 335), "if these varieties are examined in detail, these would be found to belong to separate species". Although this is not the main purpose of this work, we also present additional observations on taxonomically relevant traits that could be helpful in a future revision of the taxon.

Aphroditidae exhibit one of the most diverse chaetal composition among polychaetes (e.g. Gathof 1984; Chambers 1985; Blake 1995a); for instance, members of the genus *Laetmonice* have up to nine chaetal types distributed in various tufts in the parapodia (see Hutchings & McRae 1993, p. 316, figs. 32, 45 – 46; Barnich & Fiege 2003, p. 18, figs. 4 – 5; Imajima 2003, p. 30, fig. 16). The first four chaetigers show peculiar structures and are endowed with chaetae which differ from those in the remaining parapodia, namely: type 1: short, fine and stiff golden-yellow bristles, in chaetiger 1 ("tentacular segment") and type 2: pinnate neurochaetae, in chaetigers 2 to 4. From chaetiger 5 onwards, the chaetal types of notopodia depend on whether they are cirrigerous or elytrigerous. Elytrigerous notopodia (Figure 2a) have the following: type 3: dorsal tuft of golden-yellow acicular notochaetae; type 4: lateral

Table I. Coordinates and depths of stations where *Laetmonice producta producta* was sampled with the Agassiz trawl in the BENTART (Bentos Antártico) 2003 and 2006 cruises. AP, Antarctic Peninsula; BS, Bellingshausen Sea; PI, Peter I Island.

Station	Latitude S	Longitude W	Date	Individuals	End.	Epib.	Depth (m)
BS3	70°17.58′	95°11.86′	01/02/2003	1			1431
BS4	70°52.86′	98°26.12′	02/02/2003	1			425
PI5	68°56.70′	90°35.70′	04/02/2003	40		2	126
PI6	68°49.61′	90°48.78′	05/02/2003	3		1	210
BS9	70°14.40′	81°47.03′	11/02/2003	4			532
BS10	70°44.31′	81°27.85′	11/02/2003	1			497
BS13	69°49.56′	77°43.68′	15/02/2003	3		1	605
BS15	68°57.15′	78°14.01′	17/02/2003	7		1	1408
BS17	68°54.88′	78°14.16′	18/02/2003	2			2044
AP19	68°04.13′	70°52.38′	20/02/2003	1	1		513
AP23	64°55.95′	63°38.40′	25/02/2003	19	2	3	655
BS31	69°56.98′	86°19.27′	28/01/2006	5			1426
BS33	70°15.90′	84°11.45′	30/01/2006	2		1	438
BS34	70°08.20′	84°51.68′	31/01/2006	7	2	2	603
BS37	69°26.38′	80°51.62′	03/02/2006	14	1		495
AP39	68°07.62′	69°36.20′	07/02/2006	3		1	157
AP41	65°28.29′	69°01.71′	10/02/2006	1			350
AP42	65°09.99′	68°56.18′	10/02/2006	4			1272
AP43	63°21.71′	64°17.68′	11/02/2006	3		2	254
AP47	63°28.01′	62°12.91′	13/02/2006	19		3	115

tuft of golden-brown harpoon notochaeta; type 5: small tuft of pale yellow unidentate notochaetae; type 6: latero-ventral tuft of short, mud-covered fine capillary notochaetae. Cirrigerous parapodia have less chaetal diversity; chaetae are arranged in two tufts of fine pale yellow unidentate and goldenyellow smooth acicular notochaetae (type 7), and also chaetae similar to type 6. All neuropodia from chaetiger 3 backwards bear a dorsal tuft of 3–5 golden-yellow chaetae provided with a basal spur and a distal fringe (type 8; Figure 3a, b) and, limited to chaetigers 2–4, a ventral tuft of pinnate chaetae (type 9; Figure 3c, d) (more details in Hutchings & McRae 1993).

The aforementioned chaetae are distributed in four general bundles that are conspicuous to the naked eye and may play different biological roles (see Figure 14):

1. Dorsal acicular notochaetae (type 3). These chaetae form a dorsal incomplete coverage over the elytra. These chaetae do not form a genuine felt as occurs with the capillary chaetae in the genus Aphrodita Linnaeus, 1758 but provide additional active protection to the elytra.
2. Latero-dorsal harpoon notochaetae (type 4). These long and pointed chaetae lay over the dorsum of the body but are raised if physically stimulated, playing an active role in defense against predators.
3. Lateral unidentate notochaetae (type 7). Originating from cirrigerous parapodia, they form a dense lateral body-covering felt which seems not be used for locomotion (the latter mainly conducted by neurochaetae), but probably plays a passive defense role against predators.
4. Ventral neurochaetae (types 8 and 9). These are the most rigid and resistant to breakage of the chaetae and rarely appear broken. They clearly serve for locomotion, by rowing on the sediment surface.

Types 1 and 2 are limited to the anterior parapodia; types 5 (unidentate) and 6 (capillary) are shorter and finer chaetae, obscured by the above-mentioned types, and probably with a regressive biological role (see below).

The observation by light microscope and SEM of selected parapodia and chaetae allowed us to make observations on issues that were poorly addressed previously.

1. Both cirrigerous and elytrigerous parapodia are endowed with an ear-like structure located at the anterior side of the notopodial ventral lobe, at the base of the golden-brown harpoon and short, fine capillary chaetal bundle (Figures 2a and 4b). Its cuticle is profusely perforated (Figure 4d), which suggests a secretory function, and from the edge of this area, rows of silk-like fibers could be seen (Figure 4a, c). This structure probably represents the opening of the "parapodial glandular organs" (PGO) present in other polychaetes such as Spionidae for building their tubes (Meißner et al. 2012); these are also found in the scale-worm family Acoetidae Kinberg, 1865 showing the same function ("spinning glands", "web glands";
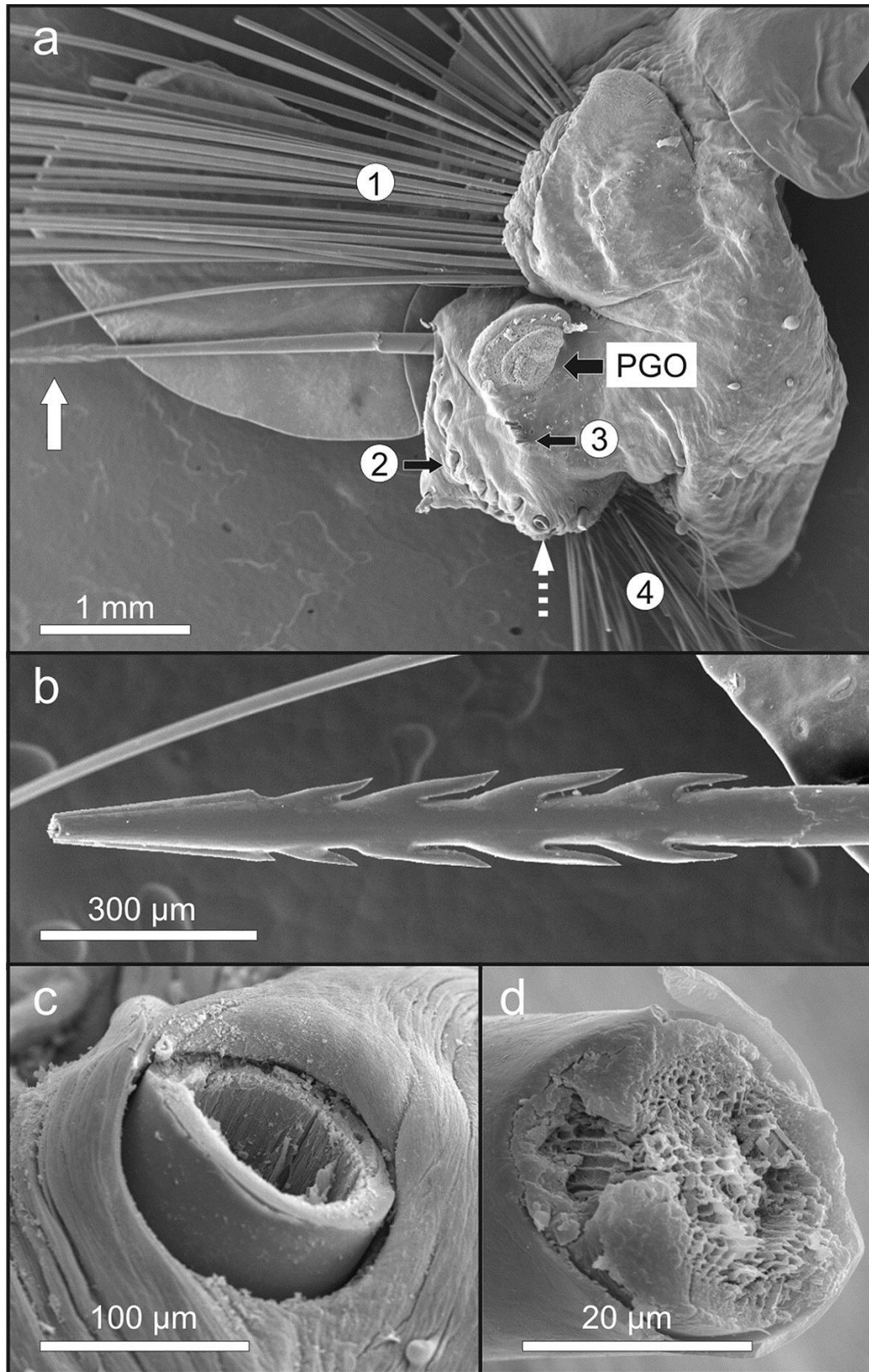
Figure 2. Scanning electron microscope (SEM) micrographs of some morphological features of elytrigerous notopodia and notochaetae of *Laetmonice producta producta*: (a) anterior view of notopodia showing different types of notochaetae, (b) tip of harpoon notochaeta (solid white arrow in a), (c, d) proximal part of broken harpoon [dotted white arrow in (a)] and capillary chaetae. Chaetal types: 1, acicular; 2, harpoon; 3, unidentate; 4, capillary.

Pettibone 1989). These glands are said to be also present in some Aphroditidae (e.g. genus Aphrodita) but in this case used for the elaboration of their characteristic protective dorsal felt (Blake 1995b; Fauchald & Rouse 1997). This structure is considered by Rouse and Fauchald (1997) to be synapomorphic for both scale-worm families. Some species of *Laetmonice* (not *L. p. producta*) are said to have a dorsal feltage, but poorly developed (Hutchings & McRae 1993). Hutchings and McRae (1993) state that this protective felt is made up by the capillary
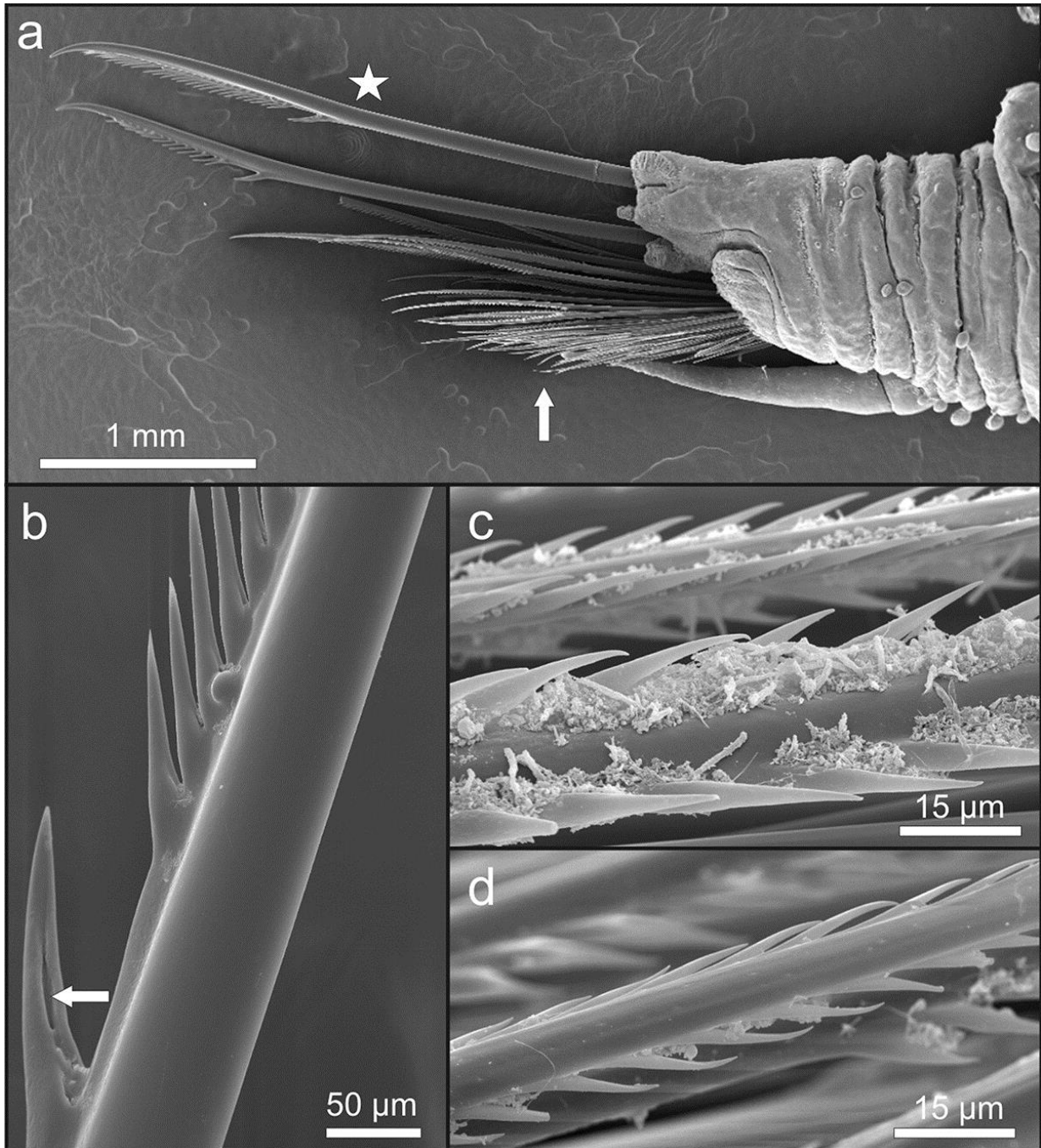
Figure 3. Scanning electron microscope (SEM) micrographs of chaetiger 3 neuropodium of *Laetmonice producta producta*: (a) anterior view of neuropodium, (b) detail of "basal spur" and first proximal teeth of "fringe of hairs" in long upper neurochaeta (star in a), (c, d) anterior and posterior view of pinnate neurochaetae (arrow in a).

chaetae (type 6) tuft; in *L. p. producta* these chaetae form a lateralventral tuft of short chaetae (#4 in Figure 2a) and therefore presumably without this function. This may suggest that the spinning glands (used in the elaboration of the tubes in Acoetidae) and capillary chaetae (used in the elaboration of the dorsal felt in Aphroditidae) are non-homologous structures as suggested by Almeida et al. (2003) and both persist in the parapodia of *Laetmonice* but without their original function, i.e. the passive protection of the body. The latter might be performed by the presence and erection of the stout dorsal acicular and harpoon chaetae (types 3 and 4) and the ejection of chemical substances though the anus (see below under *Behaviour in aquarium*).

This possibility would be suggested by the presence, very close to PGO, of the unidentate chaetae (type 5), the low number, short and fine size, and different internal structure (see below) of which suggest that these may be similar to the brush chaetae associated with the production of fibers by the spinning glands of the Acoetidae, but here the structures could be regressed because of disuse.

1. The internal structure of chaetae differs among types; most of them are hollow (e.g. acicular notopodial chaetae; #1 in Figure 2a; harpoon chaetae, #2 in Figure 2a, b, c; unidentate notochaetae of cirrigerous parapodia, and neurochaetae) while others possess a solid core crossed by hollow channels (short capillary notochaetae; #3 in Figure 2a, d). Most polychaete chaetae have additional hollow channels, which represent the lumina of the microvilli of the original chaetoblast (e.g. Figure 1 in Hausen 2005). This structure is visible in capillary chaetae; however, remaining chaetae in *L. p. producta* exhibit a different ultrastructure, in which the core of the chaetae consists of a wide channel surrounded by a thick cortex. This unusual structure may be related to the acquisition of greater flexibility and reduced weight to counteract the larger number of chaetae of the species.

2. The long and stout upper neuropodial chaetae are commonly described as provided with a prominent subdistal (also called "basal"/lower") spine ("tooth"/spur") and a distal fringe ("row of filamentous hairs"); much of this diverse terminology seems to suggest the different nature of both structures; our observations by SEM reveal a similar general structure in both (Figure 3b), which suggests a similar formation process.

3. Pinnae of pinnate neurochaetae of chaetigers 2 to 4 (Figure 3a, c, d) form a near 90◦ angle, as illustrated by Hernández-Moreno (2009), and not a 180◦ angle as is usually reported; this might be due to the image obtained from the microscope. In the literature, these chaetae are often incorrectly referred as "bipinnate" (Chambers 1985; Hutchings & McRae 1993; Barnich & Fiege 2003), which really mean "twice-pinnate".

Size-frequency distribution and egg development

The total length of specimens ranged from 5–141 mm and about 50% were 40–80 mm long (Figure 5); maximal sizes were smaller than those recorded from the Weddell Sea (Micaletto et al. 2003). Furthermore, Micaletto et al. (2003) reported greater lengths at shallow depths (200–400 m). Since the number of specimens analyzed here is much lower than in Micaletto et al. (2003), and the collection of specimens has not been exhaustive, it is not possible to establish any correlation with depth. The total length and the number of chaetigers are significantly related (F: 117.6; P < 0.0001; Figure 6). Egg sizes (i.e. maximal diameter) were measured in 18 female specimens between 73 and 141 mm long; sizes ranged from 115 to 320 μm (Figure 7). Our data are consistent with those obtained by Micaletto et al. (2003) from females of comparable size, but these authors also reported data from smaller mature females with smaller eggs (25–75 μm).
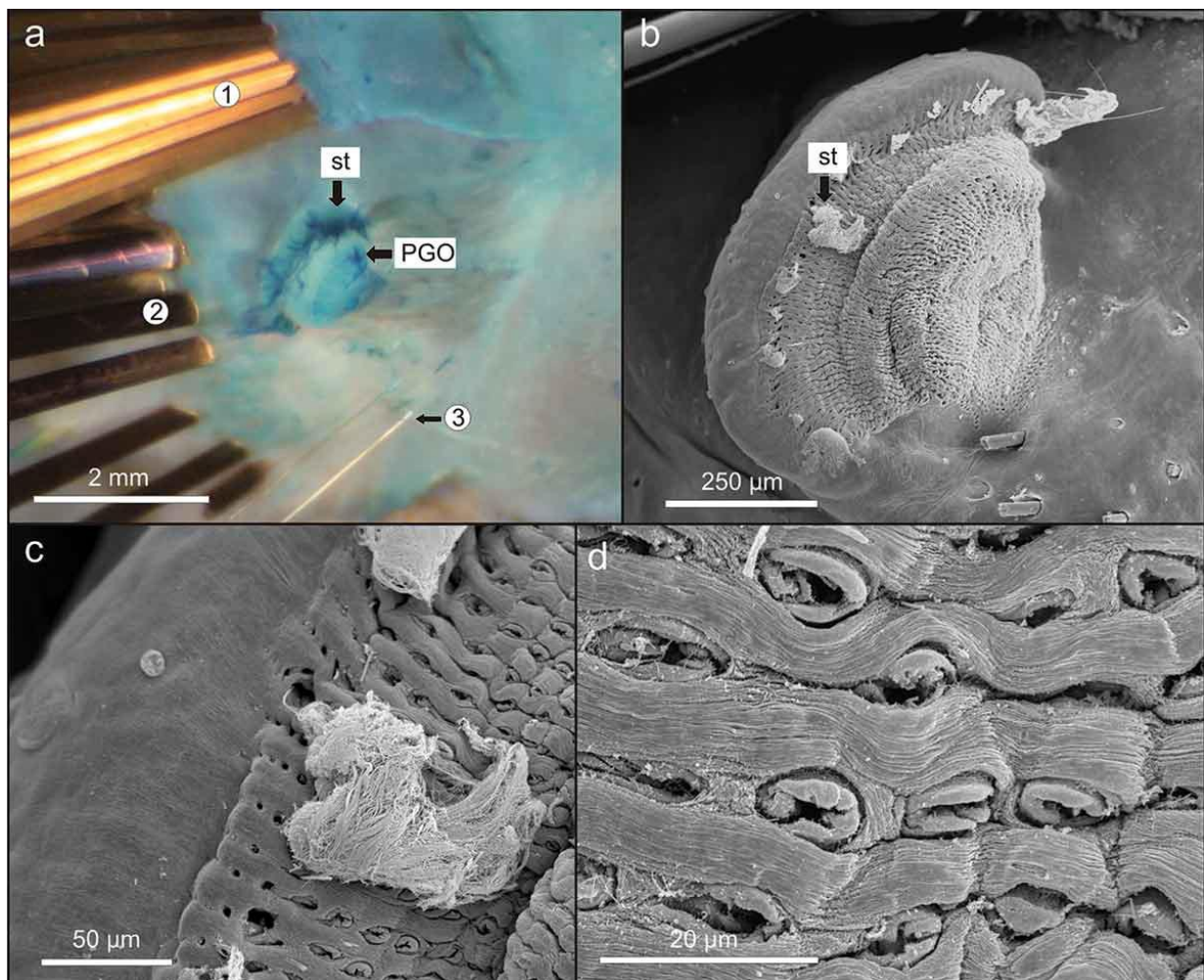
Figure 4. Light and scanning electron micrographs illustrating the external morphology of a parapodial glandular organ (PGO) in *Laetmonice producta producta*: (a) anterior side of parapodia showing position of PGO and fibrous threads (st), (b) detail of PGO, (c) silklike threads of fibrous material projecting from the edge of the cuticle perforated area, (d) cuticular openings. Chaetal types: 1, acicular; 2, harpoon; 3, unidentate.

Diet

The food content of 77 guts was analysed, of which 35 were empty (44.4%). Examination of stomachs with food showed that most of them (26.0%) were almost empty (< 10%; Figure 8a), and only in a few specimens (13.6%) was this value higher than 50%. In almost half of the specimens, sediment was a major component (44.4%; Figure 8b), either alone or combined with mucus (28.9%) or different types of organic material. As for the latter, ingested preys were recognizable in 24.4% of the cases while in 13.3% gut content was not recognizable (maybe pieces of flesh from a carcass). The presence of Foraminifera was probably due to the unselective ingestion of sediment, and that of trophozoites or cysts of gregarines was due to accidental ingestion of sporozoites with sediment or prey (Figure 8b). Preys which had been recently ingested could be identified (Figure 9) and these included the priapulid Priapulus tuberculatospinosus Baird, 1868 (Figure 9c, d), the amphipod Lepechinella cetrata Barnard, 1932 (Figure 9a), and the pycnogonid Nymphon australe (Figure 9b). Fragments of prey items were sometimes found at an advanced stage of digestion, as for an unidentified amphipod (Figure 9e) and nematode (Figure 10b, c), and the chaetae of Sabellidae and Spionidae polychaetes (Figure 10d–g). These results agree with those of Stiller (1996) who also reported sediment as the major food item, followed by amphipods and polychaetes. Our data also are consistent with the information about diet reported in the unpublished thesis by Sabatella (2000, available from MCG), and in the report of Piraino and Montiel (2001), both concerning specimens from the Eastern Weddell Sea. Remains of the cuticle of various arthropods, such as pycnogonids, isopods and amphipods, and of polychaetes (mainly Flabelligeridae), but also ophiuroids and sponge remains, as well as various amorphous materials and items, are listed in such papers. Piraino and Montiel (2001), in particular, found a relatively high predatory impact since 27 specimens of the 50 examined had a full gut.

Blegvad (1914) and Hunt (1925) reported the presence of remains of terebellid and sabellid polychaetes in the gut of Aphrodita aculeata Linnaeus, 1758. These observations suggested to Fauchald and Jumars (1979) the idea that aphroditids may feed on slow-moving animals; thus they were thought to be slow-moving carnivores. However, Mettam (1980) observed that A. aculeata kept in a laboratory could feed on a wide range of live preys including molluscs, crustaceans and polychaetes (Neanthes Kinberg, 1865 and Nephtys Cuvier, 1817); this suggested, in turn, more active predation behavior for these scale-worms (Mettam 1980). Our observations on *L. p. producta* diet reinforce this hypothesisbecause preys included sedentary as well as active epibenthic taxa (pycnogonids, amphipods) and active burrowing species (some polychaetes and priapulids).

The presence of flesh fragments possibly from fish carcasses may suggest that *L. producta* can also behave as a scavenger. Similarly, the presence in its gut of large numbers of Foraminifera (*Cibicides* sp. and *Bulimina* sp.) together with sediment may suggest a sediment-feeding behaviour, but also some accidental ingestion. Hutchings (2000) reported the observation of *L. producta* specimens with

Foraminifera in gut diverticula; this might indicate some sort of sediment selection as previously suggested by Day (1967).
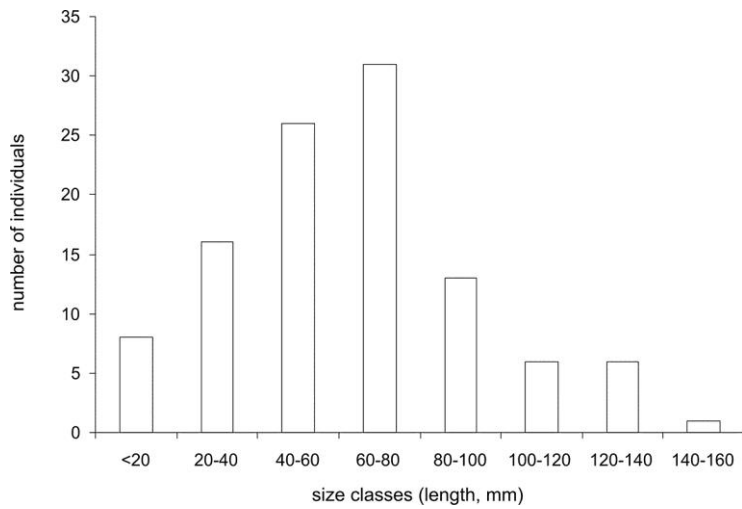

Figure 5. Size-frequency distribution of *Laetmonice producta producta* collected in the BENTART 2003 and 2006 cruises (all specimens pooled together).
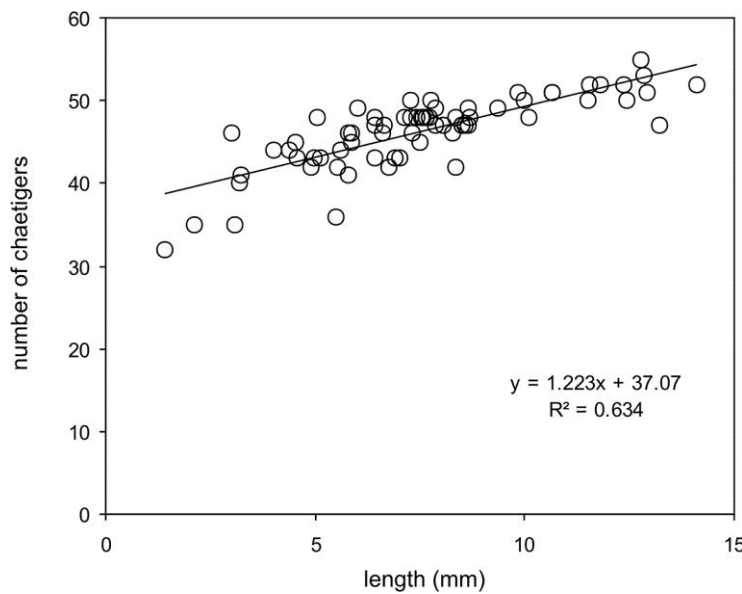

Figure 6. Relationship between total length (mm) and number of chaetigers in *Laetmonice producta producta* (all specimens pooled together).
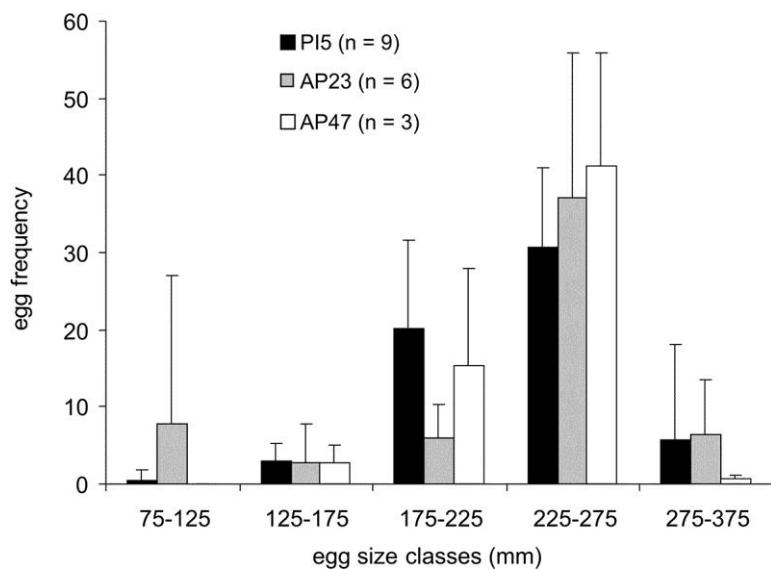
$y = 1.223x + 37.07$
$R^2 = 0.634$

Figure 7. Mean size-frequency distribution of eggs in females of *Laetmonice producta producta* in selected stations (2003: PI5, AP23; 2006: AP47). n, number of females where eggs were measured.

Faeces were collected from two individuals kept in aquaria, and revealed the presence of capillary and lyrate polychaete chaetae (Figure 11a), probably belonging to a nephtyid polychaete, and of cysts of gregarines (Figure 11b). Mettam (1980) also reported undigested remains in the ejected faecal pellets of *A. aculeata*, including a set of polychaete jaws, aciculae and chaetal bundles.

Endobionts

Two types of endobionts were found in *L. p. producta*: (1) in the digestive tract, a protozoan gregarine (Phylum Apicomplexa: Class Sporozoea), and (2) in the coelomic cavity, the dorvilleid polychaete *Veneriserva pygoclava meridionalis* Micaletto, Gambi & Cantone, 2002.

Mature trophozoites of gregarines (Figure 10a) were found in the gut of a specimen from AP5; there were oocysts, i.e. a stage formed after the coupling of the gamonts, in five individuals (st. PI5, 1 spec.; AP23, 4; Figure 11b). Gregarines are intestinal parasites of many terrestrial and marine invertebrates, particularly of nereidid and pisionid (Ganapati 1946) as well as capitellid polychaetes (Wagenbach et al. 1983) where they pass two of the three steps of their life cycle: (1) the growing phase from sporozoite (ingested with food) to trophozoite (initially adherent to the intestinal epithelium and then free when mature), and (2) the preliminary phase of the gamogonia stage that occurs within a cyst and leads to the
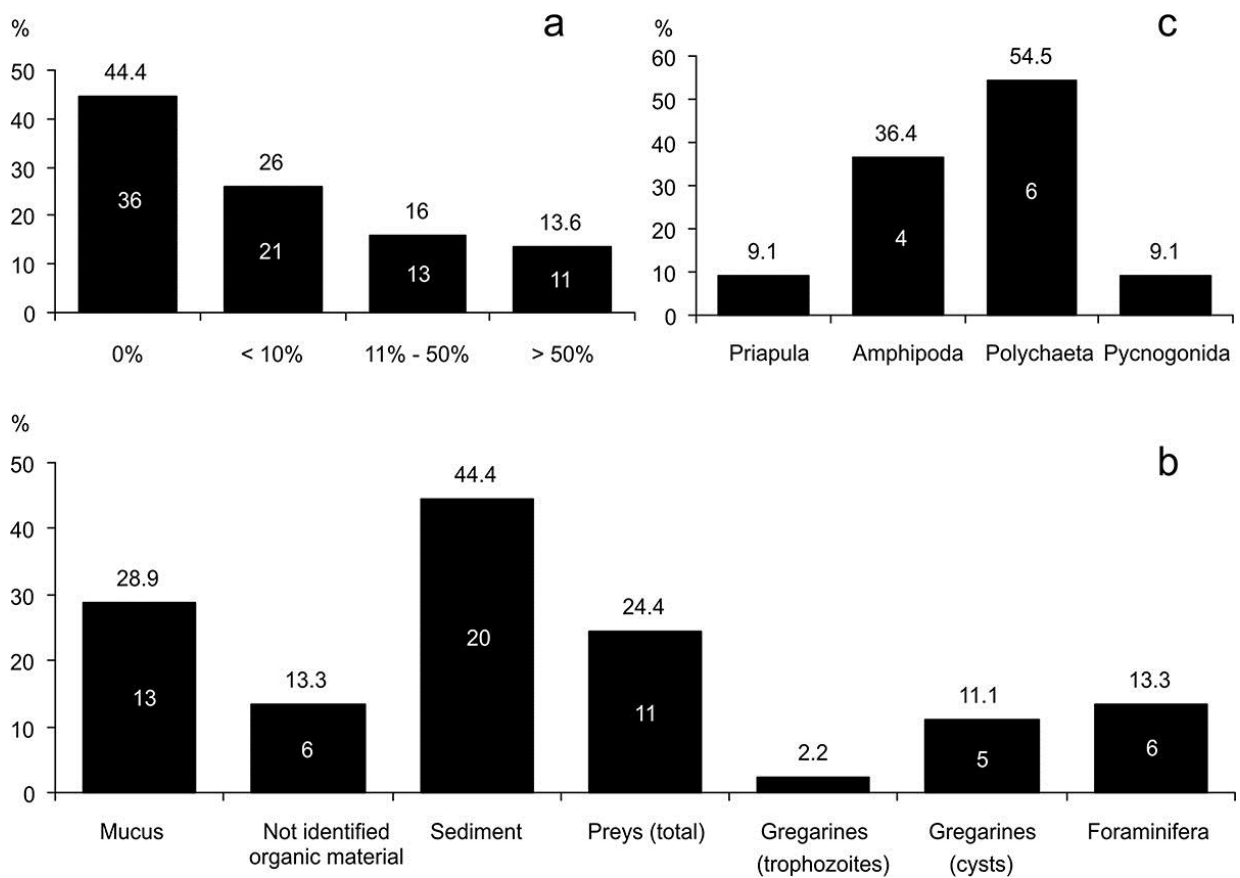

Figure 8. Diet features of *Laetmonice producta producta*: (a) histograms of frequency distribution of the repletion degree in all individuals analysed, (b) type of items found in the stomach contents, (c) types of prey. Number inside box: total of individuals (no value = 1 specimen); percentage at the top.

formation of gametes. The oocysts are evacuated via the faeces at an early stage of gamete development (Takahashi et al. 2008). The observed sporozoites in the AP5 specimen may belong to *Cygnicollum lankesteri* Desportes & Theodorides, 1986; the latter was described in specimens of *L. producta* from Crozet Islands (Indian Ocean) (Desportes & Theodorides 1986). In our case, this parasite was observed only in specimens collected in near-shore waters (PI5, 126 m; AP23, 655 m). One specimen from PI5 kept in the aquarium showed cysts in the faeces (Figure 11b).

Laetmonice p. producta hosts the endosymbiotic dorvilleid polychaete *Veneriserva pygoclava meridionalis*, which may be present in about 50% of the specimens in some populations, mostly from deeper bottoms (Micaletto et al. 2002). Six specimens of *L. p. producta* out of the 114 examined had this endosymbiont in the coelomic cavity (symbiont prevalence: 5.1%). Individuals with parasites were found in all sampled areas, i.e. the Antarctic Peninsula (st. AP19, 1 spec.; AP23, 1) and the Bellingshausen Sea (BS34, 3; BS37, 1), and were either small (51–63 mm long) or large (105–140 mm long). The number of *Veneriserva* specimens found per *L. p. producta* host (i.e. symbiont intensity) was always one; all symbionts were broken, without eggs. These results show a low rate of symbiont prevalence when compared to values of 19.4% obtained by Micaletto et al. (2002), who also found differences among geographic areas, i.e. higher percentage of parasitism in the Weddell Sea (27.7%) than in King George Island, Antarctic Peninsula (7.5%). Symbiont intensity was similar to the results of Micaletto et al. (2002), who found that 78% of the specimens were affected by one symbiont only and 19.6% by two symbionts, with a maximum of six symbionts per host.

Epibiosis

Epibiosis was present in specimens of all sizes and in all geographic areas sampled, although it was much more common in individuals of PI and AP than of BS. It is noteworthy the high density and diversity of organisms found in specimens collected off Low Island (AP47), the larger individual (135 mm long) being the one exhibiting the highest diversity and numbers of epibionts.

Globigerinid foraminiferans such as *Cibicides* sp. (Figure 12c) and several species of bryozoans – an unknown tubulliporid, and the cheilostomes *Antarctothoa bougainvillei* (D'Orbigny, 1842) and *Osthimosia bicornis* (Busk, 1881) (Figure 13) – were the most common epibionts found on the BENTART *L. p. producta*. Unidentified juvenile sponges (Figure 12d), bougainvillid hydroids (Figure 12a, b) and unidentified ascidians were also found. The epibionts appear to grow mainly over the dorsal and lateral chaetal felt viz. unidentate and acicular notochaetae of cirrigerous parapodia, but also in acicular and harpoon notochaetae of elytrigerous parapodia; epibiosis on neurochaetae was much less common. In the aforementioned specimen from AP47, some epibionts (foraminiferans and bryozoans) were also found on the elytra, dorsal cirri and even on some neurochaetae. The bryozoan A. bougainvillei is a common taxon (Rogick 1956; Hughes et al. 2008) widely reported in the Antarctic Peninsula littoral (López de la Cuadra & García Gómez 2000; Moyano 2005). It is a generalist

colonizing species with a low specificity for substrata, previously recorded over the giant isopod *Glyptonotus antarcticus* Eights, 1852 (Key & Barnes 1999) and *L. producta* (Moyano 1972). Hutchings (2000) reported the presence of epizoons such as spirorbid polychaetes and barnacles on the dorsal felt of aphroditids; slow-motion and epifaunal behavior make them good candidates for being colonised by other invertebrates.
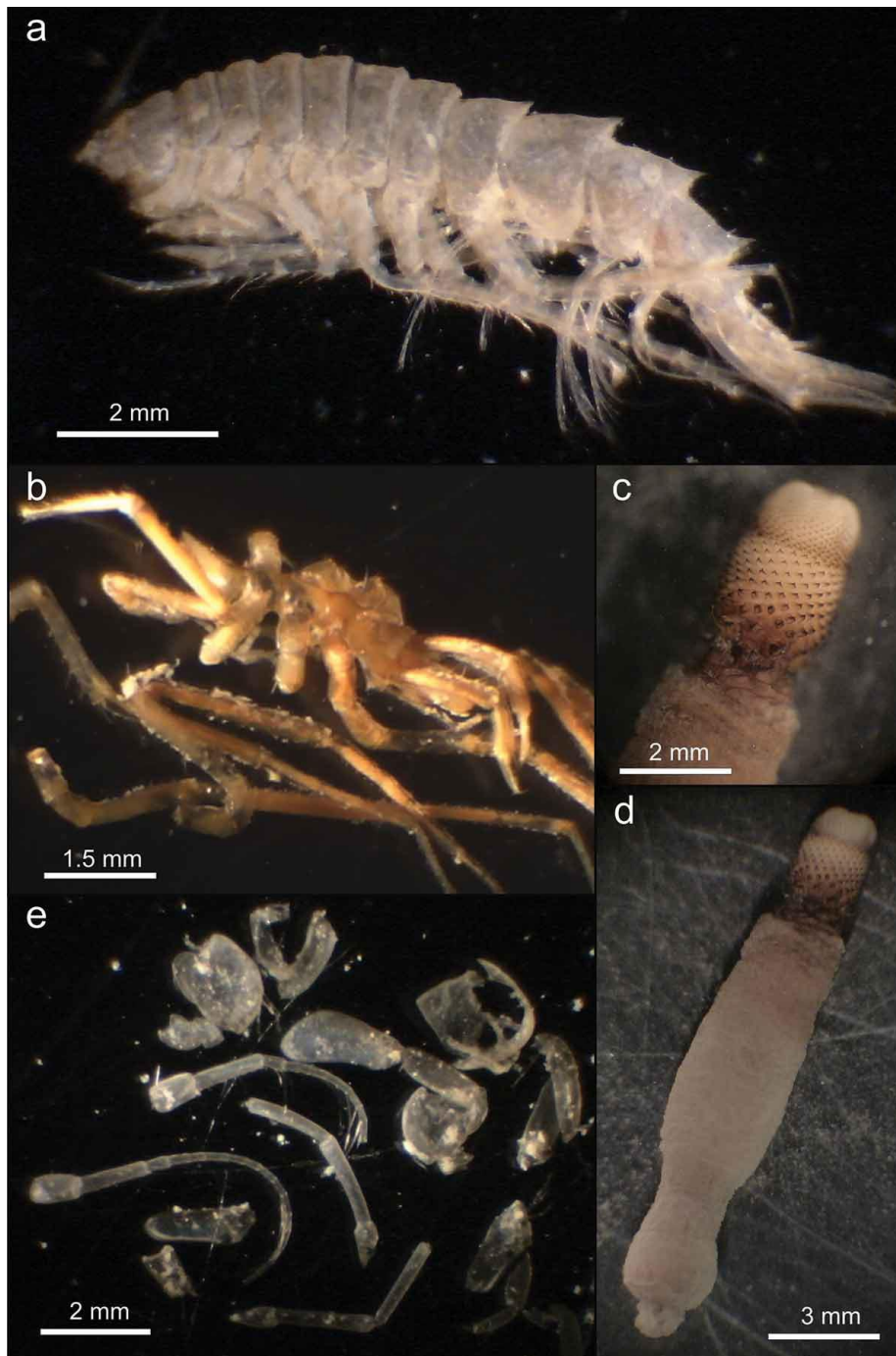

Figure 9. Identified preys in the stomach of *Laetmonice producta producta*: (a) the amphipod *Lepechinella cetrata* (st. AP23), (b) the pycnogonid *Nymphon australe* (st. AP23), (c, d) the priapulid *Priapulus* sp. (st. AP5), (e) pieces of appendages and exoskeleton of an undetermined amphipod (st. AP23).
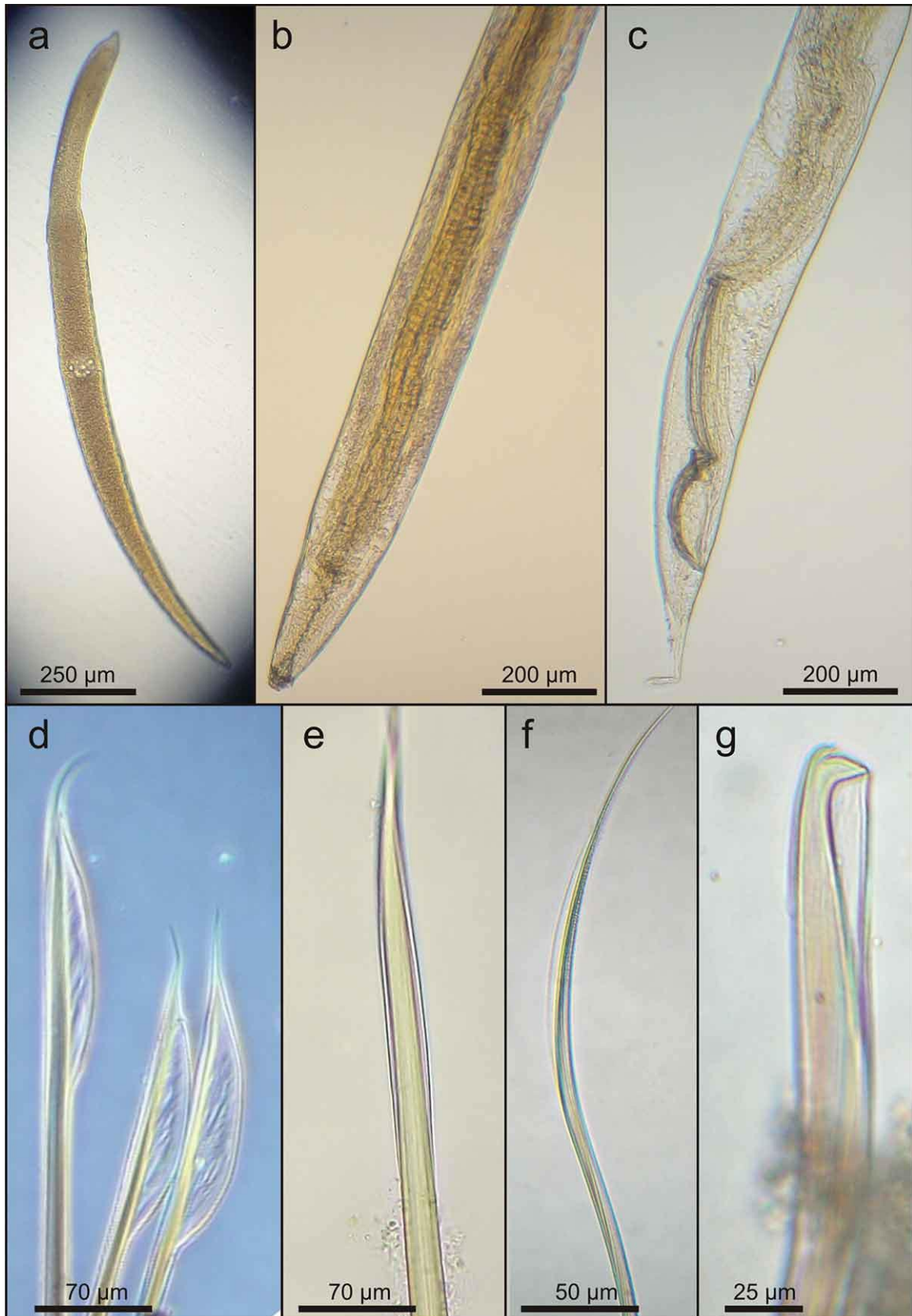
Figure 10. Food items in the stomach of *Laetmonice producta producta*: (a) mature trophozoite of a symbiotic gregarine (st. AP5), (b, c) anterior and posterior end of a nematode (st. AP23), (d, e) limbate and bilimbate chaetae of a sabellid polychaete (st. BS5), (f) limbate chaetae of a sabellid (st. BS9), (g) hooded hook of a spionid polychaete (st. AP23).

Life state, survival, and behaviour in aquarium

Although some individuals showed severe abrasions and lacerations on the body, most *L. p. producta* specimens obtained during both cruises appeared healthy despite the stress derived from capture. In these specimens, variables of the formula proposed by García Castrillo Riesgo (1997) had high scores (> 6.9), comparable with values obtained for sea stars and fishes, and far from those obtained for other annelids (< 4). Mobility of *L. p. producta* was not apparently affected nor the body damaged apart from the breakage of some notopodial chaetae. Furthermore, they seemed to adapt fairly well to the conditions of the tanks when on board, showing no apparent harm and surviving throughout the period of study.

Once collected from the trawl, specimens were deposited in a tray, displaying a typical thigmotactic behaviour, which disappeared when moved to aquaria. Two specimens from PI5 and two from AP3 were studied to assess long-term survival. Following García-Castrillo Riesgo (1997) to evaluate the life state, the variables (external aspect, motility, response to stimuli, stress and morphological alterations) had high values throughout the experiment. Animal response to stimuli such as food (arcturid isopods, fragments of a dendrochirotan holothurian, flabelligerid polychaetes and gammaridean amphipods) and presence/absence of bottom sediment and type (sand or mud) was also tested. As for food, the response
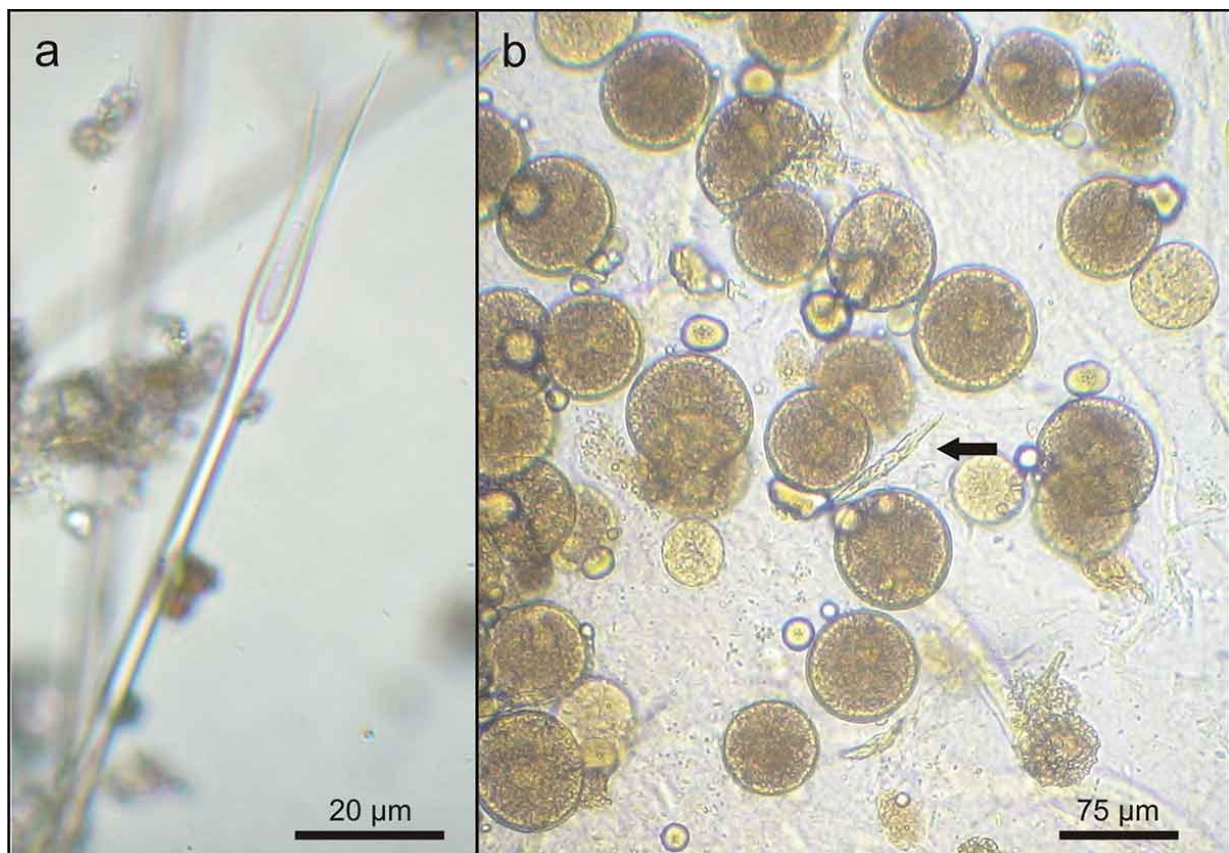

Figure 11. Faecal items of *Laetmonice producta producta* (st. PI5): (a) lyrate chaeta of a nephtyid polychaete, (b) oocystes of gregarines (arrow showing crystals of unidentified mineral).

was always negative, while significant differences of behaviour were found in the sediment factor; muddy sediments induced much higher activity than absence of sediment or presence of coarse sediment (i.e. fraction of sediment retained in the 5-mm sieve). The activity of the specimens was limited to slow crawling over the coarse sediment surface.
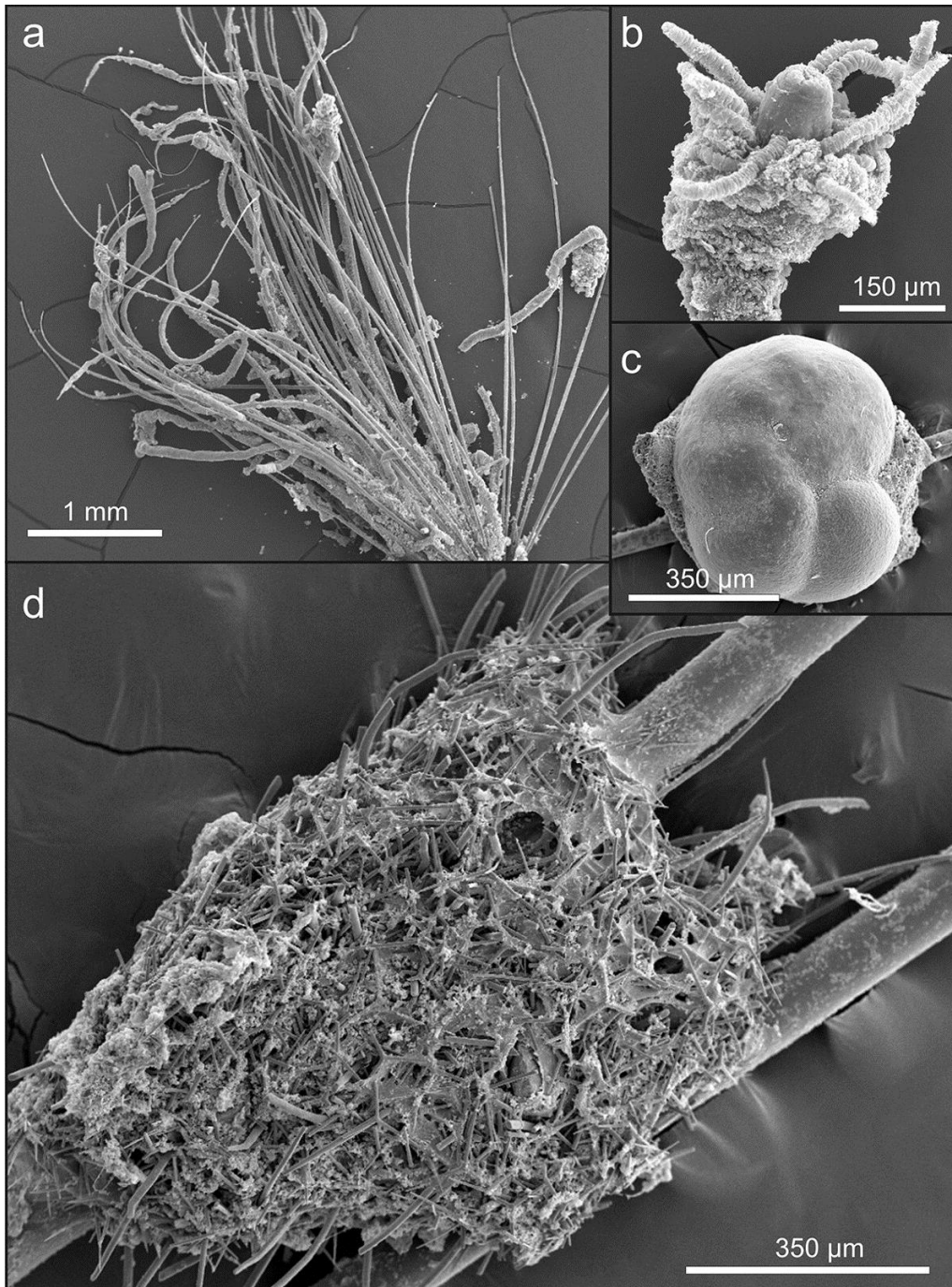

Figure 12. Epibionts on *Laetmonice producta producta*: (a) bouganvillid hydrozoan growing between a chaetal tuft (st. PI5), (b) detail of a polyp of the same species, (c) the globigerinid foraminiferan *Cibicides* sp. (st. AP47), (d) an unidentified young form of a sponge (st. AP47).

When physically stimulated, such as by touching the dorsal surface of the body with a glass rod, the specimens showed a typical pattern consisting in raising of the notopodial chaetae, particularly the harpoon ones (Figure 14a). If stimulus intensity increased, specimens showed a conspicuous arching of the dorsal part of the body, raising the harpoon chaetae and also the neuropodial chaetae from the substrate (Figure 14b). Finally, if the stimulation continued, dark brown liquid was released from the anus. The same behaviour was previously documented in *Aphrodita aculeata* (Darboux 1899, 1900; Jordan 1904); this fluid consists of haem, derived from food in the gut, and non-haem brown pigment, excreted into the lumen by epithelial cells of the gut caeca (Dales & Pell 1971). The release of this fluid may have a defensive function (Dales & Pell 1971) similar to the widespread chemical defense strategy in Antarctic marine organisms, based on the production of repellent substances by different body parts (Avila et al. 2008).
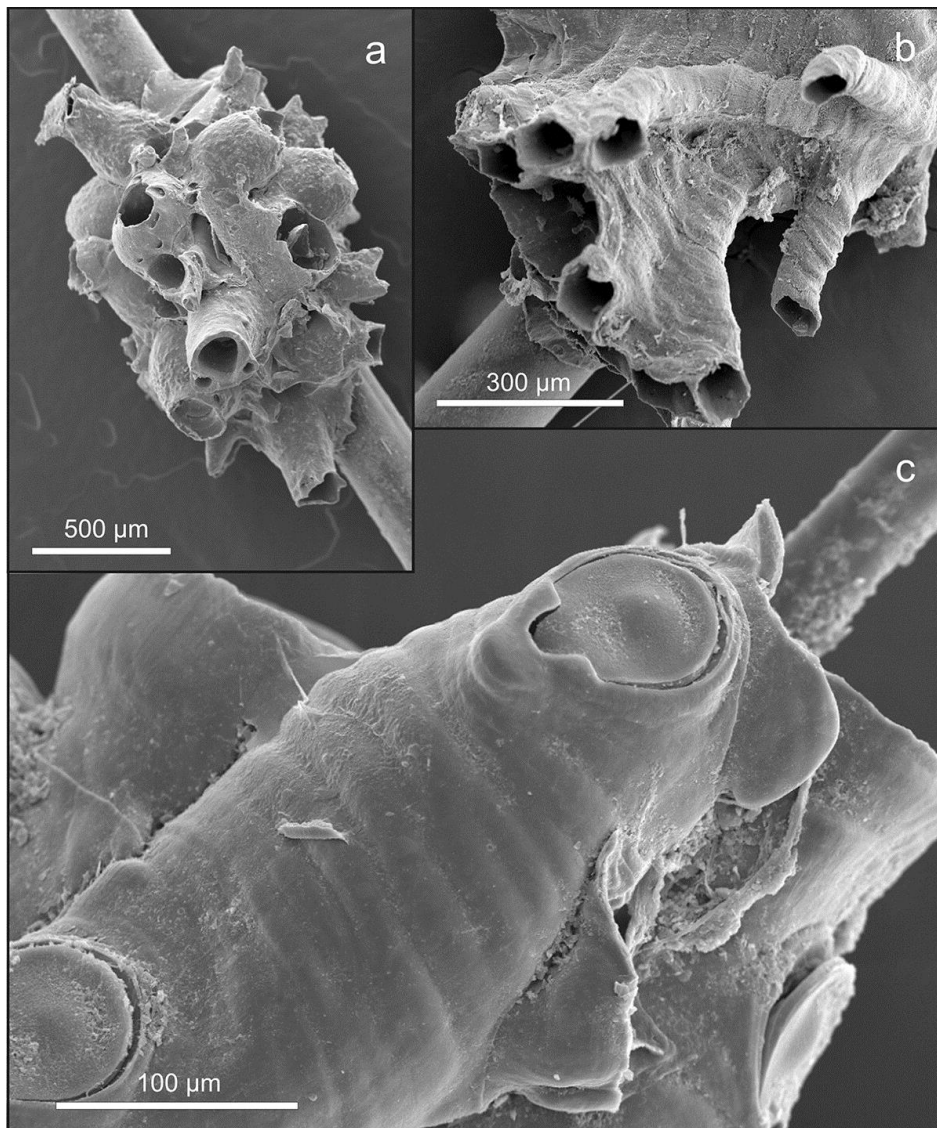

Figure 13. Epibiont bryozoans on *Laetmonice producta producta* (st. AP47): (a) colony of *Osthimosia bicornis*, (b) an unknown species of tubulliporid, (c) an autozoid of *Celleporella bougainvillei*.

Conclusions

Laetmonice producta is one the most ubiquitous and largest Antarctic polychaetes. Study of specimens of *L. p. producta* collected in the BENTART expeditions in the Bellingshausen Sea and Antarctic Peninsula showed, however, that its taxonomy is still far from being clarified and a global revision of the taxon is needed. This species has a wide variety of chaetae, with an internal structure different from that of many other polychaetes and that may serve as a substratum to many epibionts, foraminiferans and bryozoans in particular. The analysis of the gut contents suggests a diet consisting of a high variety of food items, possibly related to availability of preys, so that *L. p. producta* can switch from carnivore to scavenger. Experiments in aquaria revealed high resilience to stress derived from capture with the
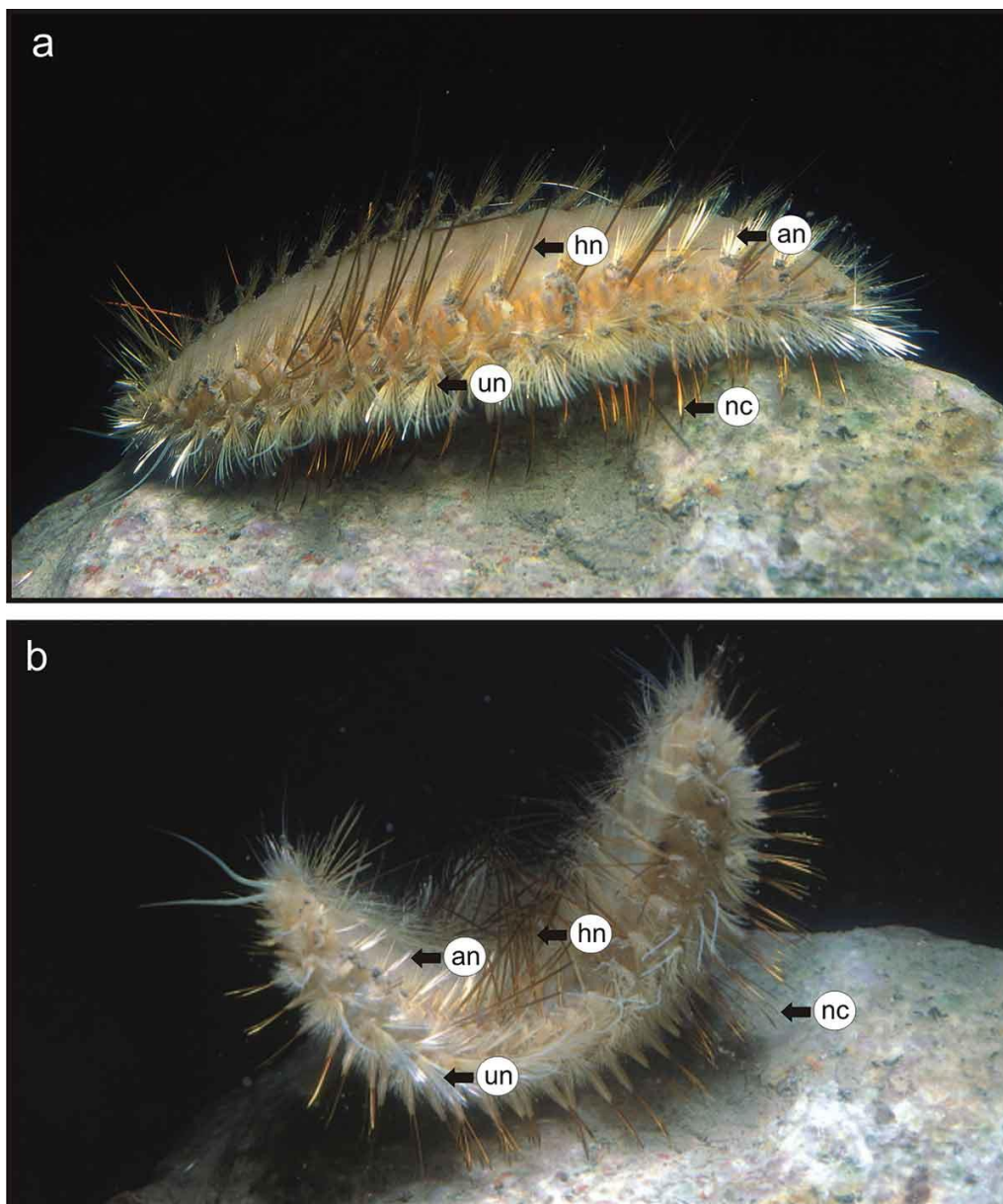

Figure 14. Behaviour displays of *Laetmonice producta producta* in aquarium: (a) rise of long brown notochaetae against a low-intensity stimulus, (b) dorsal arching of the body against a stimulus of higher intensity. an, acicular notochaetae;

usual benthic sampling gear and survival in aquaria. Defensive behaviour includes complex mechanisms related to active physical response by using different types of chaetae, also relying in chemical defence.

Acknowledgements

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