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The genus *Boccardia* (Polychaeta: Spionidae) associated with mollusc shells on the south coast of South Africa

C.A. SIMON[1,3], T.M. WORSFOLD[2], L. LANGE[1] AND J. STERLEY[1]

[1]Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa, [2]Unicomarine, 7 Diamond Centre, Works Road, Letchworth Garden City, Hertfordshire, SG6 1LW, UK, [3]Present address: Department of Botany and Zoology, Stellenbosch University, Stellenbosch 7602, South Africa

Three species of Boccardia *(*B. polybranchia, B. pseudonatrix *and* B. proboscidea*) were associated with mollusc shells on the south and south-east coasts of South Africa.* Boccardia polybranchia *was widely distributed along the coast and falls within the known distribution range of this species. Comparisons with material from other, international, locations showed that some specimens have been misidentified. No characters could be found to characterize distinct species for different regions within the range of* B. polybranchia*, as currently recognized.* Boccardia pseudonatrix *was found only at the most eastern site, increasing its known distribution range.* Boccardia proboscidea*, a non-indigenous species, was found only on abalone farms and was most abundant in the west.*

Keywords: *Boccardia*, South Africa, molluscs, reproduction, aquaculture

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INTRODUCTION

The genus *Boccardia* Carazzi, 1893 currently includes 22 species, 14 of which are found boring into, or associated with molluscs, coralline algae, rock or foliose algae (see Ruellet, 2004 for review). To date, two species have been recorded in the wild (i.e. dissociated from mariculture) in southern Africa (Day, 1955, 1961, 1967): *Boccardia polybranchia* (Haswell, 1885) and *Boccardia pseudonatrix* Day, 1961; a third, *Boccardia* cf. *ligerica* (Ferronnière, 1898) mentioned by Day (1967), was transferred to *Boccardiella sensu* Blake & Kudenov (1978). *Boccardia polybranchia* was recorded widely along the south coast of South Africa and in Namibia; no indication was given of its habitat in South Africa, while it was recorded from shallow dredgings in Namibia (Augener, 1918; Day, 1967). By contrast *B. pseudonatrix* was found only once boring into rock in Knysna on the south coast of South Africa (Day, 1961). More recently the non-indigenous *B. proboscidea* Hartman, 1940 was detected on cultured abalone (*Haliotis midae* Linnaeus, 1758) at several on-shore aquaculture facilities (Simon *et al.*, 2006; Simon & Booth, 2007; Simon *et al.*, in review), stimulating renewed interest in shell-infesting *Boccardia* species in South Africa.

This paper provides a revision of the *Boccardia* species associated with both wild and cultured molluscs along the south coast of South Africa. The opportunity is also taken to describe *B. polybranchia* from South African material, provide comparisons with populations from other regions and discuss some of the taxonomic and nomenclatural issues associated with the species.

Corresponding author:
C.A. Simon
Email: csimon@sun.ac.za

MATERIALS AND METHODS

Molluscs were collected from the intertidal or shallow subtidal from five sites along the south and south-east coasts of South Africa in February and March 2005 and April 2006 (Figure 1). Worms were removed by immersing shells in a vermifuge, 0.05% phenol in seawater, for three hours to overnight. Once the worms abandoned their burrows, they were transferred to fresh seawater, relaxed with clove oil, preserved in 4% saline formaldehyde solution and stored in 70% ethanol. Material from abalone farms in Saldanha Bay on the south-west coast, Hermanus and Gansbaai on the south coast, and Haga Haga on the south-east coast was removed by dissolving the shells in which the worms had been fixed (in 4% saline formaldehyde solution and stored in 70% ethanol) in 5% HNO_3 diluted in 70% ethanol (Simon *et al.*, 2006; Simon & Booth, 2007).

For scanning electron microscopy (SEM), the specimens were dehydrated in a series of increasing concentrations (80–100%) of ethanol, critical point dried and sputter coated. Specimens were viewed on Vega Tescan and Leo 1430 VP scanning electron microscopes. Descriptions for each of the species were prepared, based on South African material. Partial synonymies were produced to include significant taxonomic works. Specimens are lodged at the Iziko South African Museum, Cape Town, South Africa.

RESULTS AND DISCUSSION

SYSTEMATICS

Family SPIONIDAE Grube, 1850
Genus *Boccardia* Carazzi, 1893
Boccardia cf. *polybranchia* (Haswell, 1885),

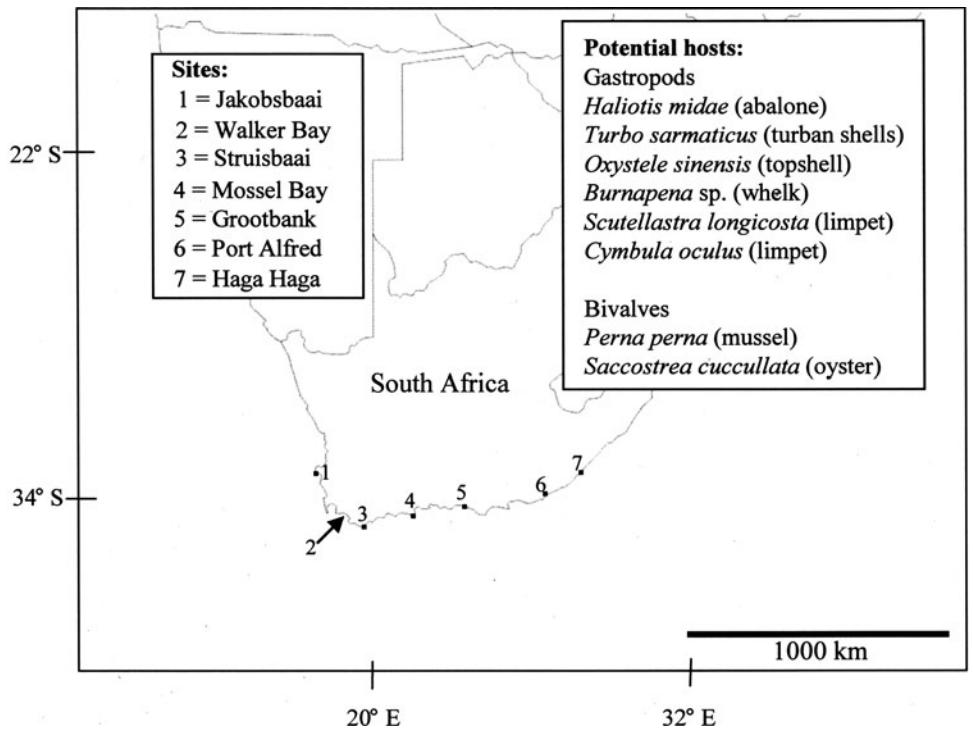

Fig. 1. Location of sampling sites and list of potential molluscan hosts collected.

sensu Blake & Kudenov, 1978
Figures 2 & 3

? Perialla claparedei Kinberg, 1866, p. 253; 1910, p. 63, figure 9
? Polydora (*Leucodore*) *polybranchia* Haswell, 1885
Polydora (*Boccardia*) *polybranchia* Carazzi, 1893, p. 16, pl. 2, figures 1–3
Polydora polybranchia Söderström, 1920, p. 256, figure 167
Polydora (*Boccardia*) *polybranchia* Fauvel, 1927, pp. 58–59; Okuda, 1937
Boccardia polybranchia Imajima & Hartman, 1964, p. 279; Day, 1967, pp. 463–464; Blake & Kudenov, 1978, pp. 236–238; Blake, 1983, pp. 248.

MATERIAL EXAMINED

South Africa: Western Cape Province: Mossel Bay, 34°10′56″S 22°07′20″E, March 2005, associated with the turban shell *Turbo sarmaticus* Linnaeus, 1758 (SAMC, A21475 [7], A21476 [2, including slides]), mussel *Perna perna* Linnaeus, 1758, abalone *Haliotis midae* and limpet *Scutellastra longicosta* (Lamarck, 1819); A21477 (SEM); Eastern Cape Province: Grootbank (Tsitsikamma), 33°59′14″S 23°32′36″E, March 2005, associated with *H. midae* and *T. sarmaticus* A21515 & A21524 (SEM).

Brazil: Rio de Janeiro, *Perialla claparadei* (6 syntypes, SMNH 742). Australia: Coff's Harbour (2, AM, W13033), Jervis Bay (2, AM, W 24941). France: Biarritz (1, MNHNP UE 429).

MORPHOLOGY OF NEW MATERIAL

Medium-sized species, up to 20.3 mm long for 79 chaetigers. Prostomium bifid, caruncle extending to posterior margin of chaetiger 2, with lateral nuchal organs (Figures 2A & 3A); middle of caruncle swollen, no occipital antenna (Figures 2A & 3A). Up to two pairs of eyes. Preserved specimens tan with dark pigmentation along margin of prostomium, on dorsal surface of peristomium and chaetiger 1, on posterior chaetigers (Figure 3A, F & H), and sometimes on pygidium. Anterior end of body attenuated, widest at chaetiger 5 but from chaetiger 6 approximately the same width as chaetiger 4; posterior half of body narrows. Chaetiger 5 approximately three times as long as chaetigers 4 and 6.

Chaetiger 1 reduced, with small notopodia, lacking notochaetae (Figures 2A & 3A). Notochaetae on anterior chaetigers in three rows, first row with short winged chaetae, middle row chaetae slightly longer and spear-shaped; chaetae of last row longest, slender and lanceolate. No specialized notochaetae in posterior chaetigers. Hooded hooks from chaetiger 7, with 6–7 per ramus initially, then up to 11 hooks per ramus on later chaetigers (Figure 2D, E). No constriction on shaft; main fang 90° to shaft; secondary tooth about 45° to main tooth (Figure 3B). In all specimens examined, hooded hooks on chaetigers 7–9 accompanied by fascicles of up to three ventral inferior capillary chaetae (Figures 2D & 3D); a single ventral inferior capillary chaeta may be present with hooded hooks on more posterior chaetigers.

Chaetiger 5 has dorsal row of two or three falcate spines, ventral row of three or four bristle-topped spines (Figure 3C) and fascicle of ventral inferior capillary chaetae. Older falcate spines not strongly curved. Branchiae on chaetigers 2–4 and posteriorly from chaetiger 6 for 70–80% of body length. From chaetigers 6–16, branchiae short and broad, connected to notopodial lobe (Figures 2A, B, D & 3A & D). Succeeding branchiae filiform, longer than anterior branchiae, not connected to notopodia; branchiae never overlapping along midline of body (Figures 2E & 3A). Dorsal ciliary organs between and along inner surface of anterior branchiae (Figure 2A, B).

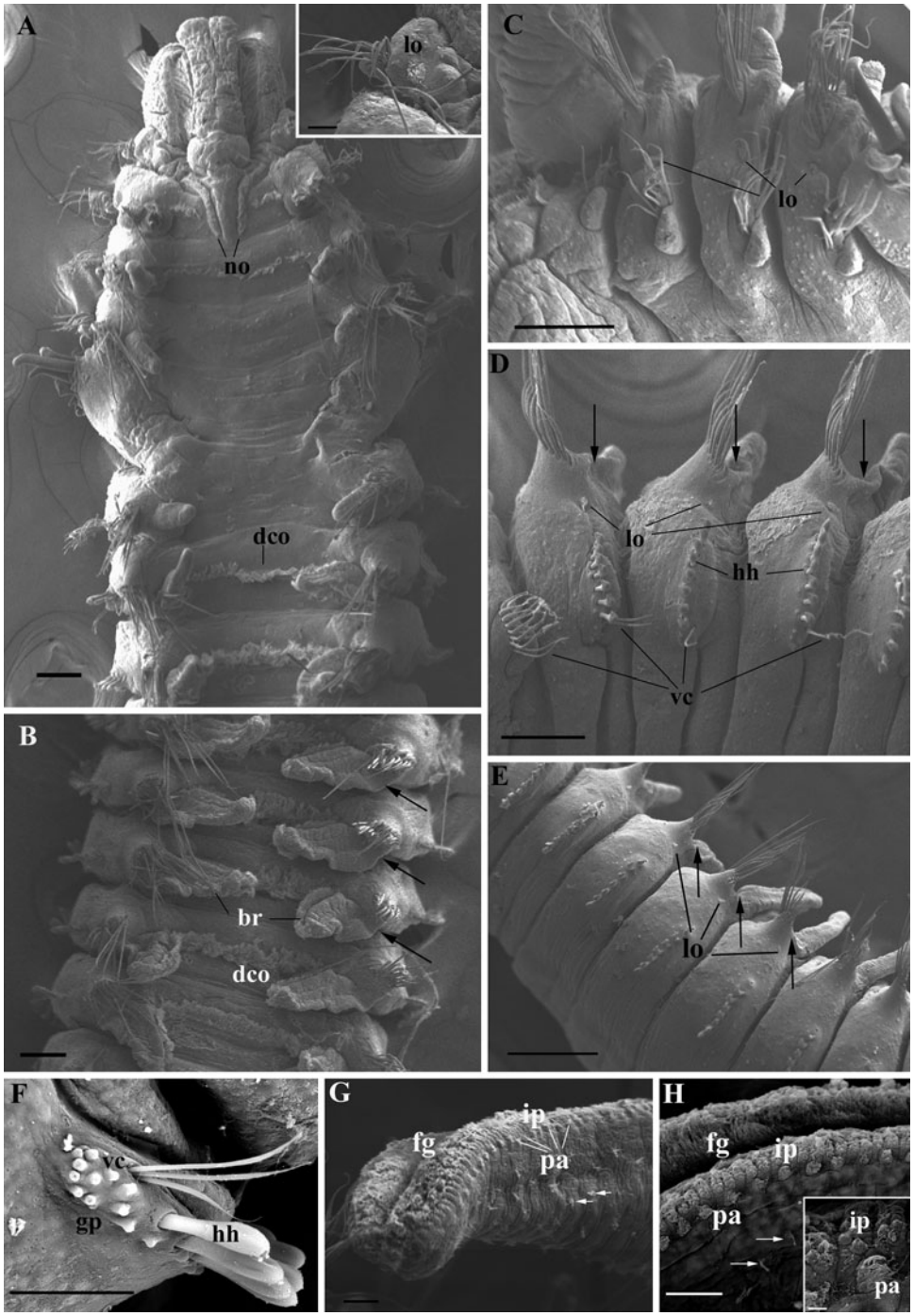

Fig. 2. *Boccardia polybranchia sensu* Blake & Kudenov, 1978, adult morphology. (A) Dorsal anterior showing ciliary bands of nuchal organs (no) and dorsal ciliary organs (dco). Inset shows lateral organ (lo) on first chaetiger; (B) dorsal mid-body showing branchiae (br) on chaetigers 10–14. Note attachment of the branchiae to the notopodial lobes (arrows); (C) lateral anterior showing lateral organs (lo) on chaetigers 2–4; (D) lateral view of chaetigers 6–10, showing lateral organs (lo) and connection of branchiae with notopodial lobes (arrows), hooded hooks (hh) with one or two ventral inferior capillary chaetae (vc); (E) ventro-lateral view of chaetigers posterior to chaetiger 16, showing lateral organs (lo) and change in the structure of the branchiae which are not here connected to notopodial lobes (arrows); (F) hooded hooks (hh) with external openings of glandular pouches (gp) and ventral inferior capillary chaetae (vc); (G & H) latero-frontal surface of palps showing the feeding groove (fg) large papillae with long cirri (pa) and inner row of papillae (ip), with tufts of cirri or cilia scattered on lateral and abfrontal surface of the palps (arrows). Scale bars: A–D, 100 μm; E, 200 μm; F, 25 μm; G, 20 μm; H, 10 μm. Insert to A, 30 μm; insert to H, 2.5 μm.

Paired glands composed of a few large sacs observed in chaetigers 7–9 (Figure 3G). External openings visible at base of hooded hooks on these chaetigers (Figure 2F).

Lateral organs observed on all chaetigers except the fifth, although not always visible on all specimens examined (Figure 2A, insert, C&E); largest on chaetigers 1 and 2 (Figure 2A, insert).

Row of large (5.5 μm diameter) papillae, 4.5 μm apart on outer latero-frontal edge of palps (Figure 2G, H). Each papilla bears a cirrus. Between the outer row of papillae and the feeding groove are rows of papillae (1.5 μm diameter), arranged in groups of three, and perpendicular to feeding groove, 1.75 μm apart, with shorter cilia or cirri (Figure 2H). Tufts of cilia or cirri scattered over lateral and abfrontal surface (Figure 2G).

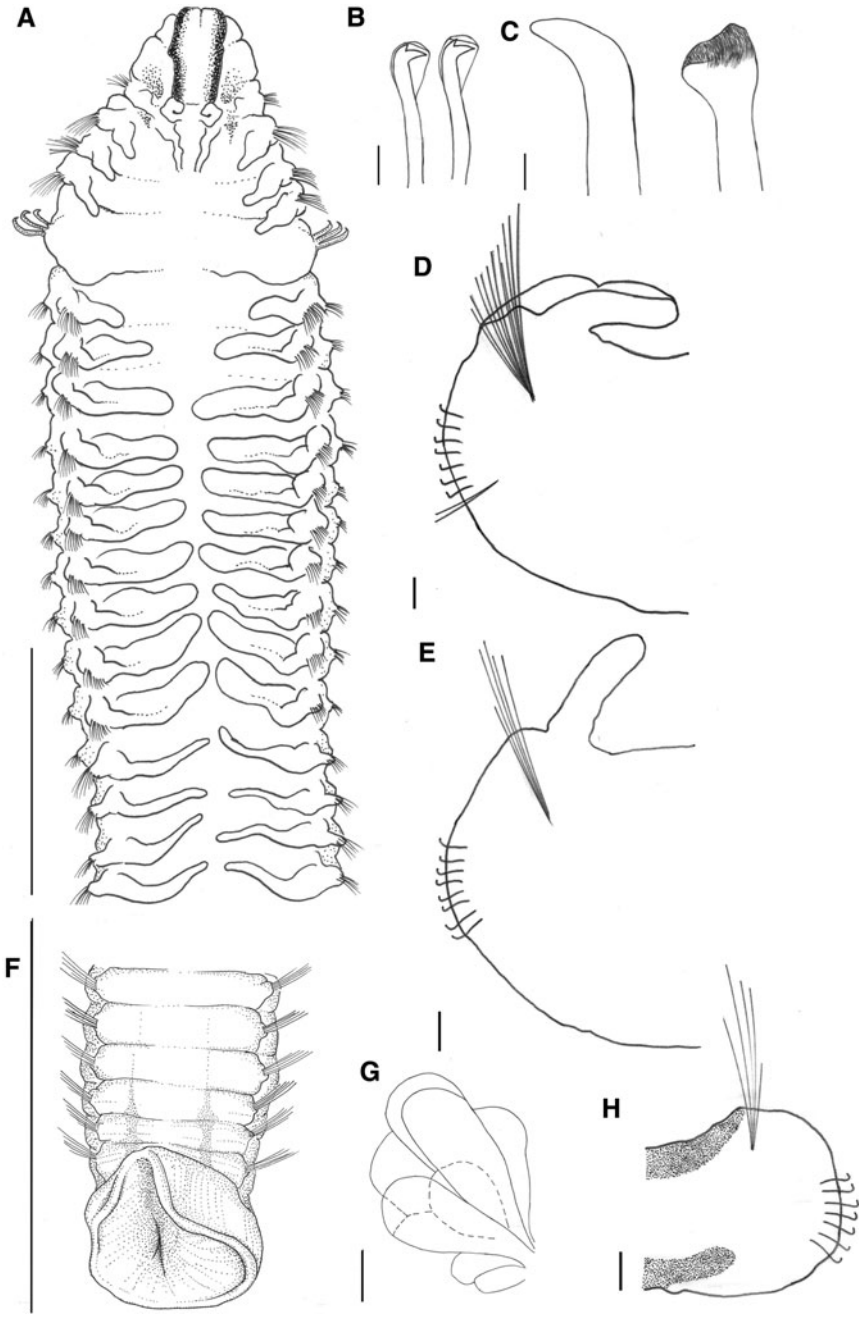

Fig. 3. *Boccardia polybranchia sensu* Blake & Kudenov, 1978. (A) Dorsal anterior showing the change in structure of branchiae after chaetiger 15; (B) hooded hooks; (C) falcate and brush-topped spines from chaetiger 5; (D) anterior view of left parapodium of chaetiger 9 showing the fold of skin connecting the branchia and notopodial lobe; (E) anterior view of left parapodium of a chaetiger posterior to chaetiger 17, without the fold of skin between the branchia and notopodial lobe; (F) dorsal view of pygidium, showing some pigmentation; (G) gross structure of the glandular pouches; note the relatively few, large pouches; (H) anterior view of right parapodium of posterior chaetiger showing the pigmentation on the dorsal and ventral surfaces. Scale bars: A, F, 1 mm; B, C, 20 μm; D, E, G, H, 50 μm.

Pygidium thick and fleshy, as wide as penultimate chaetiger, with dorsal notch (Figure 3F), sometimes also with ventral notch.

REMARKS

The specimens here assigned to *Boccardia polybranchia sensu* Blake & Kudenov (1978) were similar to each other (see more below & Table 1). Common to the *B. polybranchia* taxon as currently recognized are the bifid shape of the prostomium, length of the caruncle, absence of notochaetae on chaetiger 1, general pigmentation pattern (with some exceptions), distribution and number of hooded hooks (but see specimens from Jervis Bay, Table 1), shape and number of the modified spines on chaetiger 5 and distribution and general structure of the branchiae. The paired glands in chaetigers 7–9 of the specimens from South Africa and Jervis Bay, New South Wales, are composed of a few large sacs. The gross structure of these glands is not widely reported and it is not known how sensitive it is as a taxonomic character (but see Fauvel, 1927; Hartman, 1940).

Table 1. Morphological characteristics of the *Boccardia polybranchia* (Haswell, 1885) complex, *sensu* Blake & Kudenov, 1978 from South Africa, South America, Australasia and Europe.

Locality	**Rio de Janeiro**	**Australia (Coff's Harbour)**	**Australia (Jervis Bay)**	**South Africa**	**Biarritz**	**Naples**	**Japan**
Specimen examined	**SNHM 742, types of *Perialla claperedei***	**NSW, W13033**	**W 24941**	**This study**	**MNHNP UE 429**		
Reference	**Kinberg, 1866, 1910; personal observation**	**Blake & Kudenov, 1978; personal observation**	**Personal observation**	**Personal observation**	**Fauvel, 1927; personal observation**	**Carazzi, 1893**	**Okuda, 1937; Imajima & Hartman, 1967**
Length (mm)	Incomplete specimens	15	1 complete specimen: 6.25	15–20	17	20	20–25
Number of chaetigers	Incomplete specimens	75	51	70–80	76	60	80
Shape of prostomium	Bifid, shallow median groove along prostomium	Bifid, weakly indented, shallow median groove along prostomiun	Bifid, weakly indented, shallow median groove along prostomiun	Bifid, weakly to moderately indented, shallow median groove along prostomium	Bifid	Bifid	Bifid
Notochaetae on chaetiger 1	No	No	No	No	No	No	No
Pigmentation	When present, very faint along prostomium	Margin of prostomium; faint on dorsal surface of anterior chaetigers	Margin of prostomium; faint on dorsal surface of anterior chaetigers, 1 specimen with pigmented posterior chaetigers	Margin of prostomium; sometimes along median groove, peristomium, dorsal of chaetiger 1, posterior chaetigers	Margin of prostomium; nothing on posterior chaetigers	Margin of prostomium; on anterior part of body	?
Number of eyes (pairs)	2	2	2	2	2?	2	Variable number
Posterior extent of caruncle	To posterior end of chaetiger 2	To posterior end of chaetiger 2 or 3	End of chaetiger 2, or beginning of chaetiger 3	Most to end of chaetiger 2, some to mid chaetiger 3	End of chaetiger 2	End of chaetiger 2 to anterior of chaetiger 3	End of chaetiger 3 to anterior of chaetiger 4
Shape of spines on chaetiger 5, with number of each type	Falcate spines: 2(1)*; club-shaped, bristle-topped: 3(1)	Falcate spines: 3; club-shaped, bristle-topped: 4	Falcate spines: 1–2; club-shaped, bristle-topped: 2–3	Falcate spines: 2(3); club-shaped, bristle-topped: 3(4)	Falcate spines: 2; club-shaped, bristle-topped: 3	Falcate spines; club-shaped, bristle-topped	Falcate spines and club-shaped, bristle-topped
Number of hooded hooks on chaetiger 7	5–7	7 or 8	4 or 5	6	7	?	?
Maximum number of hooks	7–9	11–13	6–8	11 or 12	8	7–9	?
Ventral inferior chaetae with hooded hooks	3 or 4 on chaetigers 7–9, later 1 chaeta on some more posterior chaetigers	On chaetigers 7–9, later 1 chaeta on some more posterior chaetigers	On chaetigers 7–9	3 or 4 on chaetigers 7–9 on all individuals, some may have 1 intermittently on posterior chaetigers	On chaetigers 7–9	?	?

Continued

Table 1. Continued

Locality	**Rio de Janeiro**	**Australia (Coff's Harbour)**	**Australia (Jervis Bay)**	**South Africa**	**Biarritz**	**Naples**	**Japan**
Specimen examined	**SNHM 742, types of *Perialla claperedei***	**NSW, W13033**	**W 24941**	**This study**	**MNHNP UE 429**		
Reference	**Kinberg, 1866, 1910; personal observation**	**Blake & Kudenov, 1978; personal observation**	**Personal observation**	**Personal observation**	**Fauvel, 1927; personal observation**	**Carazzi, 1893**	**Okuda, 1937; Imajima & Hartman, 1967**
Shape of pygidium	?	Large disc, wider than posterior chaetigers, split into two lateral halves	Small disc, as narrow as posterior chaetigers, divided into four lobes	Small, thickened disc, sometimes dorsally notched	Small, divided into four lobes.	'Smooth'	Small thickened disc, sometimes dorsally notched
Per cent of branchiate chaetigers	?	75%	80%	70–85%	80%	60%	To near anal end
Branchiae connected to notopodial lobes	From chaetigers 6–16/17	From chaetigers 6–16/17	From chaetigers 6–14	From chaetigers 6–16	From chaetigers 6–16	?	Yes
Shape of branchiae on anterior chaetigers	Chaetigers 6–16/17: broad and flat	Chaetigers 6–16/17: broad	Chaetigers 6–14: short, broad	Chaetigers 6–16: broad and flat, short on chaetiger 6, never touch mid-dorsum	Chaetigers 6–16: broad and flat		
Shape of branchiae on mid an posterior chaetigers	Filiform	Filiform, not touching or overlapping along midline	Thin, difficult to see	Filiform, longer and thinner	Filiform, longer and thinner	Filiform?	Long and straight
Habitat	Benthic	Amongst *Galeolaria* tubes and coralline algae on rocks and in rock pools	Amongst *Galeolaria* tubes and coralline algae on rocks and in rock pools	*Haliotis midae*, *Turbo sarmaticus*, oyster and limpet shells	Muddy tubes on rocks and *Lithothamnion*?	Sand	?
Other information	Two occipital tentacles	The broad branchiae narrower than SA specimens	Branchiae seem longer than in other Australian specimens, and overlap along the midline. This may be an artefact of the orientation of the specimens				

*, number in parentheses denotes the number of spines that had not yet extended beyond the surface of the chaetiger.

The South African specimens do, however, differ from other populations of *B. polybranchia* with respect to some of the characters. For example, the anterior branchiae of the specimens from South Africa and France are wider than those from Coff's Harbour and Jervis Bay. The only other description that mentions the attachment of the branchiae to the notopodial lobes is that of Imajima & Hartman (1964) for specimens from Japan, but no observations are made concerning a different structure to the branchiae after chaetigers 16 or 17. There is also considerable variation in the structure of the pygidium. In the specimens from South Africa, Biarritz and Jervis Bay, the pygidium is a small disc; it may be as wide as, or slightly wider than, the posterior chaetigers, notched dorsally, and sometimes divided into four lobes. The pygidia of the specimens from Coff's Harbour are much wider than the posterior chaetigers and split into two lateral halves. While the caruncles of most specimens (including those from South Africa) extend to the end of chaetiger 2, or the middle of chaetiger 3, those from Japan are longer, although this may be related to body length (Imajima & Hartman, 1964; Sato-Okoshi & Takatsuka, 2001). The specimens compared also differ with respect to habitat; those from South Africa are associated with mollusc shells while the others are found in sandy or muddy tubes, associated with *Lithothamnion* and other coralline algae or *Galeolaria* (Serpulidae) tubes. The structure of the feeding palps of *B. polybranchia* in the current study differed considerably from that of specimens recorded as the same species, from Vancouver Island, Canada (Qian & Chia, 1997). The larger, widely spaced, papillae on the latero-frontal edge of the palps, the regular arrangement of the smaller papillae and the tufts of cirri or cilia (these cannot be distinguished in preserved specimens) on the lateral and abfrontal surfaces described in the current study were not observed in the Canadian specimens. The specimens in the current study lack the large density of mucus glands described by Qian & Chia (1997).

No morphological characteristics were found that could distinguish between the specimens examined and assign them to separate species. Observed differences may be due to the size of the specimens (e.g. number of hooded hooks per ramus, number of branchiae attached to notopodial lobes, shape of pygidium) or preservation (pigmentation patterns and intensity). Although some species (e.g. *Dipolydora armata* (Langerhans, 1880)) do appear to be cosmopolitan (Radashevsky & Nogueria, 2003), the presence of the same species from such varied habitats and locations is usually indicative of either morphologically similar/identical sibling species (e.g. *Marenzallaria* spp: Bastrop & Blank, 2006) or of translocations mediated by human activity (e.g. *Boccardia proboscidea*: Simon *et al.*, in review). Further work, including molecular studies and examination of material from more, different, localities will be necessary to elucidate this problem.

In addition to the specimens examined above, specimens lodged as *Boccardia polybranchia* from Macquarie Island and Kilcunda (AM W4742–W4743 and NMV G3011, respectively) were examined. These matched the description of *B. wellingtonensis* Read, 1975 (see Table 2).

NOMENCLATURAL CONSIDERATIONS

The original description of *Boccardia polybranchia* (Haswell, 1885), collected on oyster farms along the Hunter River, New South Wales, Australia, was limited, without figures and there are no type specimens (see also Blake & Kudenov, 1978). More comprehensive descriptions, assigned to the same species, were subsequently produced by, amongst others, Carazzi (1893) and Fauvel (1927) for specimens collected in Naples and France, respectively. In 1978, Blake & Kudenov tried to provide a better description of *B. polybranchia* from the type locality. The only *Boccardia* species that they found at Hunter River was identified as *B. chilensis* Blake & Woodwick, 1971; they recorded specimens fitting the Carazzi (1893) description of *B. polybranchia* from Coff's Harbour, 325 km north of the Hunter River, and at Kilcunda, Victoria. These specimens, along with others from Macquarie Island, were used for their description but no neotypes were designated (presumably because the specimens came from localities too far from the type locality). Close examination of the above specimens during the current study showed that those from Kilcunda and Macquarie Island are in fact closer to *Boccardia wellingtonensis* (Table 2), while those from Coff's Harbour (and others from Jervis Bay, New South Wales) match the descriptions by Carazzi (1893) and Fauvel (1927) more closely than they do that of Haswell (1885) (Tables 1 & 3).

The original description by Haswell (1885) is very generic, and it is very difficult to be certain of what animal was really described. Blake & Kudenov (1978) suggested that '. . . *B. chilensis* may actually be what Haswell originally described, but because of inadequate descriptions, the lack of type material and alteration of the type locality, that can probably never be ascertained.' There are certain similarities between Haswell's (1885) description and Australian material assigned to *B. chilensis* by Blake & Kudenov (1978). For example, chaetiger 5 is described as bearing a row of five falcate spines and another row of five that 'end in a broad head having the form of an inverted cone with an oblique base; on the base of the cone are one or two small conical elevations' (Haswell, 1885); the modified spines on chaetiger 5 are present in equal numbers. Also, while Haswell (1885) does not specifically mention notochaetae on the first chaetiger, he does state that some anterior chaetigers bear long chaetae (Haswell, 1885; Blake & Woodwick, 1971; Table 3), a feature that is very clear in *B. chilensis*. Haswell's (1885) description is, however, also inadequate as a description of the species currently described as *B. chilensis*, in that it omits, for example, mention of the occipital antenna typical of that species.

Perialla claparedei Kinberg, 1866 described from Rio de Janeiro, was synonymized with *B. polybranchia* by Soderström (1921) and this was confirmed by Blake (1983). *Perialla claparedei* is very similar to the specimens of *B. polybranchia* from Biarritz, South Africa and New South Wales that were examined (see Table 1). However, none of the *P. claparedei* specimens from the type series are complete, and none are heavily pigmented. It is therefore difficult to confirm if it is the same as the *B. polybranchia* examined in this study. Furthermore, there is some doubt that all/many of the *B. polybranchia* in South America had been correctly identified. For example, Blake (1983) had synonymized *B. wellingtonensis* with *B. polybranchia* after examining many South American specimens. Sato-Okoshi & Takatsuka (2001) reversed this synonymy with respect to some specimens collected in Chile. Preliminary observations of some specimens from Argentina suggest that these resemble *B. wellingtonensis* more closely than they do *B. polybranchia* (personal observation, see Table 2), and we were unable to

Table 2. Morphological characteristics of *Boccardia wellingtonensis* Read, 1975 and *Boccardia polybranchia* (Haswell, 1885) from Victoria and Maquarie Island, Australia and Argentina that have been re-identified as *B. wellingtonensis*.

Locality	**New Zealand**	**Chile**	**Argentina**	**Australia Maquarie Island; Victoria**
Specimen Reference	**Read, 1975; Type description**	**Sato-Okoshi & Takatsuka, 2001**	**Personal observation, R. Elias (originally described as *B. polybranchia*)**	**W4742, W4743, F43011 Personal observation, Blake & Kudenov, 1978 (originally described as *B. polybranchia*)**
Length (mm)	20	18	18	15
Number of chaetigers	80	85	75	80
Shape of prostomium	Incised/strongly bifid, deep median groove	Strongly bifid, deep median groove	Strongly bifid, deep median groove	Strongly bifid, deep median groove
Notochaetae on chaetiger 1	No	No	No	No
Pigmentation	Sides of dorsal prostomium and in caruncle groove	Margins of prostomium, line down centre of caruncle, dorsal anterior to chaetigers 6–12; palps	Margins of prostomium, line down centre of caruncle, anterior part of body behind palps	Margin of prostomium and palps, along centre of caruncle along groove, on dorsal surface of chaetigers 1–3, faint pigmentation on posterior chaetigers
Number of eyes (pairs)	Up to 3	Up to 3	2	2
Posterior extent of caruncle	To anterior chaetiger 2; poorly defined posteriorly	To posterior end of chaetiger 1 to mid chaetiger 2	To posterior end of chaetiger 1 to mid chaetiger 2; clear, projecting	To posterior end of chaetiger 1
Shape of spines on chaetiger 5	Falcate spines: 4; brush-topped, club-shaped: 5	Falcate spines: 4; brush-topped, club-shaped: 5	Falcate spines: 2; brush-topped, club-shaped: 3–4	Falcate spines: 2–3; club-shaped, bristle-topped: 3–4
Number of hooded hooks on chaetiger 7	?	?	7	5 or 6
Maximum number of hooks	8	9	9	6–8
Ventral inferior chaetae with hooded hooks	On chaetigers 7–10	On chaetigers 7–9, sometimes up to chaetiger 11	From 7–9	On chaetigers 7–9
Shape of pygidium	Flat collar; four lobes, ventral pair larger	Four lobes, ventral pair larger	Four lobes; ventral pair larger	Small, divided into four lobes
Per cent of branchiate chaetigers	65%	75%	75%	75%
Branchiae connected to notopodial lobes	No	?	No	No
Shape of branchiae	Slim, do not overlap in mid-dorsum	Long, thin, overlap in mid-dorsum	Long, thin, overlap in mid-dorsum	Very short on chaetiger 6, slightly longer on chaetiger 7, then increasing to maximum on ~chaetiger 8/9; shorten posteriorly; filiform
Habitat	Organically enriched sand, intertidal rock crevices	Mud, sand, sandstone	Mussel beds	Shells, coralline algae, soft sediment

secure '*B. polybranchia*' from Brazil. It is, however, likely that there are several species currently included within *B. polybranchia* in South America; this situation is currently being reviewed (R. Elías, personal communication).

Given the confusion concerning the nomenclature and identity of *B. polybranchia* outlined above, its apparent cosmopolitan distribution, its importance as a potential pest on commercially important bivalves and as a pollution indicator species (Borja *et al.*, 2000; Vallarino *et al.*, 2002; Ruellet, 2004), it is important to clarify this problem. This would, however, require an extensive revision of the species, ideally including molecular comparisons from different localities, which is beyond the scope of the current study.

DISTRIBUTION

This species was previously recorded in Namibia, Saldanha Bay on the west coast of South Africa and from east of Cape Agulhas to north of East London (Augener, 1918; Day, 1967). Thus, the distribution of the species in the current study falls within its known range in South Africa. *Boccardia polybranchia* is considered cosmopolitan, and has, *sensu* Blake & Kudenov, 1978, been recorded from Australia (New South Wales), South America (Brazil, Argentina, Straits of Magellan, Tierra del Fuego, Peru) and the Kerguelen Islands (Blake, 1983; Elías *et al.*, 2006). In the northern hemisphere it has been recorded in the Mediterranean (Naples) (Carazzi, 1893), English Channel,

Table 3. Morphological characteristics of *Boccardia polybranchia* (Haswell, 1885) based on the type description, and *Boccardia chilensis* Blake & Woodwick, 1971.

	Boccardia polybranchia	***Boccardia chilensis***			
Locality	**Hunter River, New South Wales**	**Chile**	**Australia**	**Chile**	**New Zealand**
Reference	**Haswell, 1885, Type description**	**Blake & Woodwick, 1971; Type description**	**Blake & Kudenov, 1978**	**Sato-Okoshi & Takatsuka, 2001**	**Read, 1975**
Length (mm)	?	28		20	10
Number of chaetigers		125		105	80
Shape of prostomium	Bifid, separated by a wide notch	Bifid	Bifid	Deeply incised	Deeply incised
Notochaetae on chaetiger 1	Possibly: 'some of the setae of the anterior parapodia are very long and filiform'	Yes	Yes, long	Yes, long	?
Pigmentation	?	None	?	Live animals: light tan; greenish black on prostomium & peristomium and chaetigers 1–4; black and white	White on anterior chaetigers and posterior third of body
Number of eyes (pairs)	2	0	?	2	2
Posterior extent of caruncle	? (~Narrow groove from the mouth to the third segment?)	End chaetiger 2, occipital tentacle, dorsal ridge from chaetigers 3–8	End chaetiger 2; occipital tentacle; mid dorsal swelling chaetigers 5–8	End chaetiger 2; occipital tentacle; mid-dorsal swelling on chaetigers 5–6	Occipital tentacle; mid dorsal swelling chaetigers 5–8
Shape of spines on chaetiger 5	Gently curved hook with blunt apex: 5; broad-headed in the form of an inverted cone with an oblique base, one or two small conical elevations at base of cone: 5	Falcate spines and distal concavity with central cone	Falcate spines: 4; distal concavity with central cone: 4	Falcate spines: 5; spines, expanded tips no bristles: 6	Falcate spines: 4; distal concavity with central cone: 4
Number of hooded hooks on chaetiger 7	?	?	?	?	?
Maximum number of hooks	6–10	16	?	16	12
Ventral inferior chaetae with hooded hooks	?	?	?	?	From chaetiger 7 to end
Shape of pygidium	?	Simple collar with ventral incision or notch and further divided into weakly developed lobes	Fleshy pad, weakly divided	Fleshy pad, weakly divided	Fleshy pad, weakly incised
Per cent of branchiate chaetigers	?	Nearly 100%	?	Nearly 100%	~50%
Branchiae connected to notopodial lobes	?	No	No	No	?
Shape of branchiae	?	Fingerlike, branchiae on chaetigers 2–4 longer than succeeding branchiae	?	Branchiae on chaetiger 2 longer than on chaetigers 3, 4 and 6	Branchiae on chaetiger 2 twice as long as on chaetiger 3
Habitat	Oysters	Sub- and intertidal, rocky habitats	Oyster beds; rock pools; coralline algae	Intertidal mud, sand, coralline algae	Coralline algae; mollusc shell

France (Fauvel, 1927; Ruellet, 2004) and Japan (Imajima & Hartman, 1964).

HABITAT

In the current study, the worms bored into the shells of a range of molluscs, including the abalone *Haliotis midae*, the turban shell *Turbo sarmaticus*, the limpets *Scutellastra longicosta* and *Cymbula oculus* and the bivalves *Perna perna* and *Saccostrea cucullata*. *Boccardia polybranchia sensu* Blake & Kudenov, 1978 has been recorded from amongst coralline algae, algae and *Galeolaria* tubes (Blake & Kudenov, 1978) and from sand and rocks and in the intertidal algal zone (Blake, 1983). In Italy and France they inhabit sandy and muddy tubes and are associated with oyster shells (Carazzi, 1893; Fauvel, 1927; Borja *et al.*, 2000; Ruellet, 2004).

Boccardia proboscidea Hartman, 1940
Figures 4 & 5

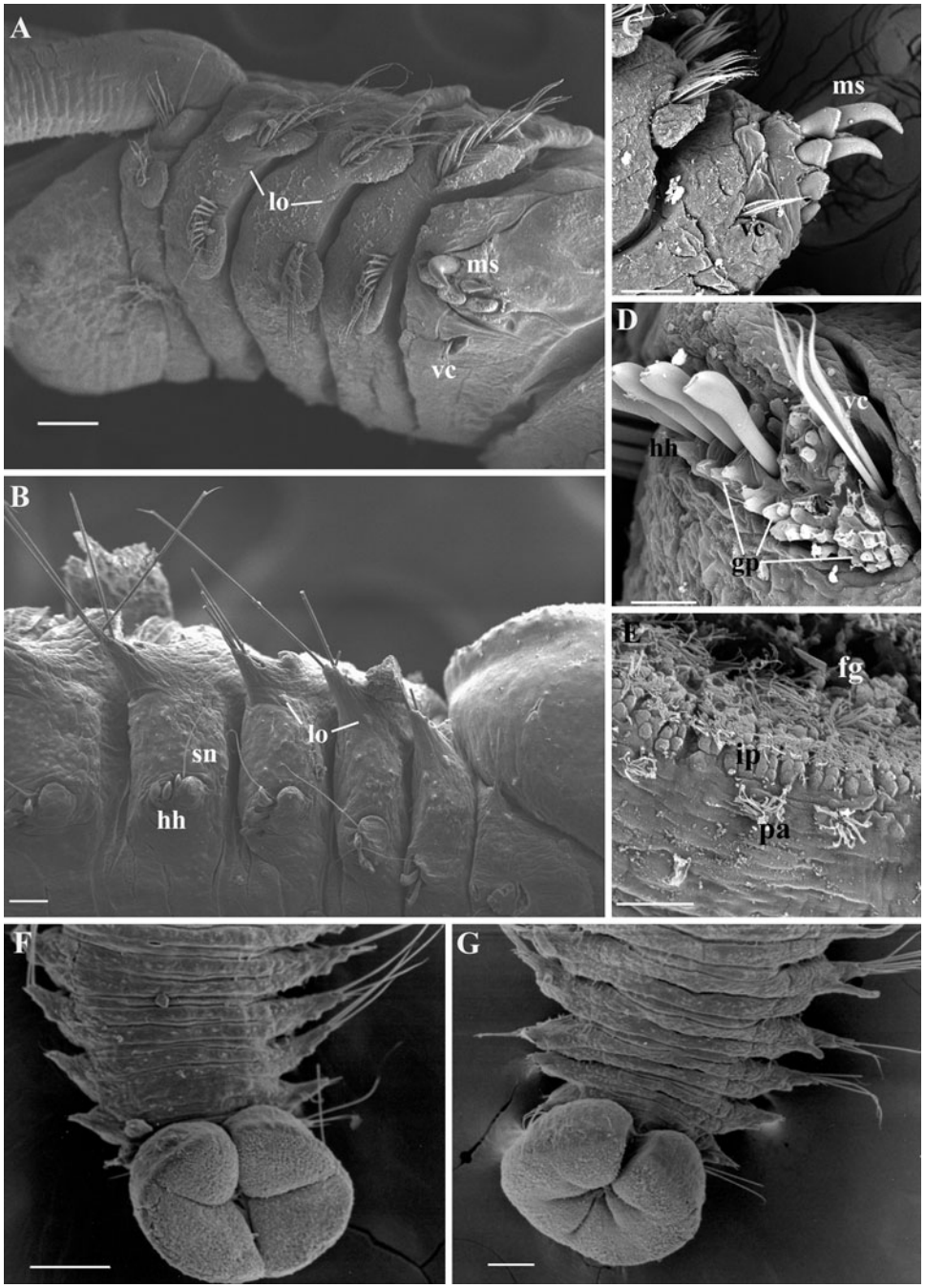

Fig. 4. *Boccardia proboscidea*. (A) Lateral anterior showing lateral organs (lo) on chaetigers 2 and 3, and modified spines (ms) and ventral inferior capillary chaetae (vc) on chaetiger 5; (B) ventral posterior, showing lateral organs (lo) and single superior neuropodial capillary chaeta (sn) dorsal to the hooded hooks (hh) on each chaetiger; (C) ventral view of modified spines (ms) and ventral capillary chaetae (vc) of chaetiger 5; (D) hooded hooks (hh) with external openings of glandular pouches (gp) and ventral inferior chaetae (vc); (E) latero-frontal surface of the palps showing the feeding groove (fg) large papillae with long cirri (pa) and inner row of papillae (ip); (F & G) dorsal views of pygidia of different worms. Scale bars: A, C, F & G, 100 μm; B, 30 μm; D, 25 μm; E, 10 μm.

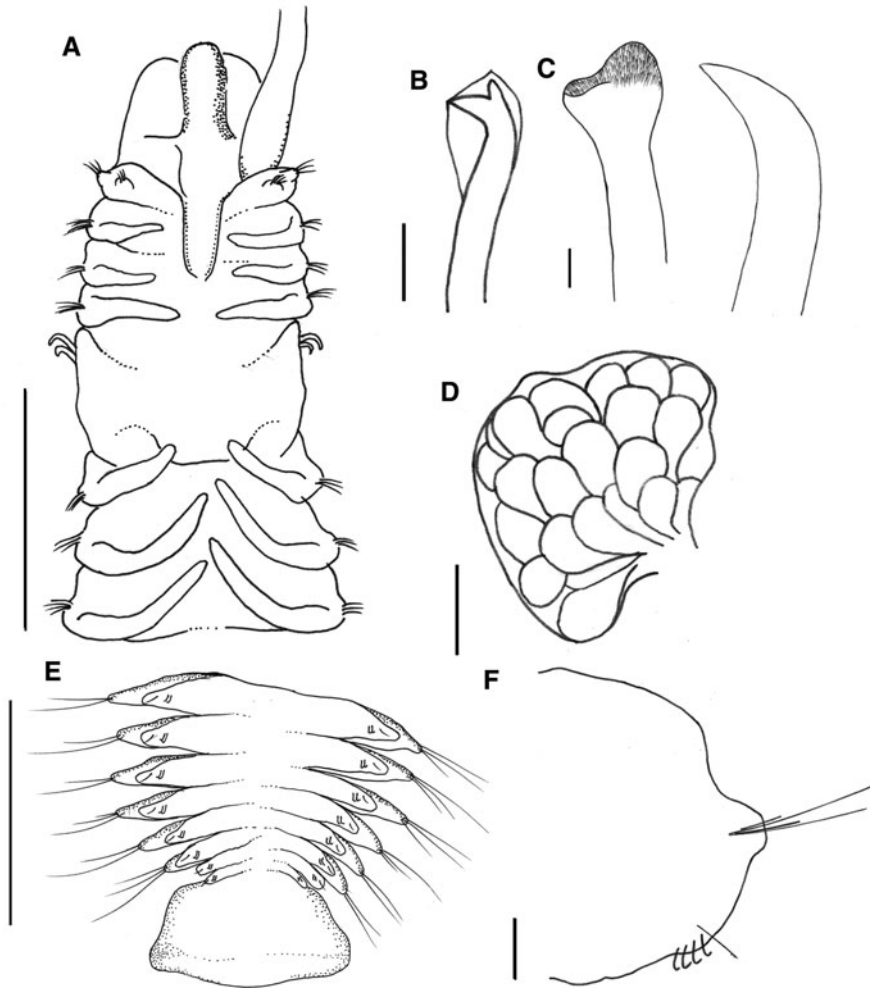

Fig. 5. *Boccardia proboscidea.* (A) Dorsal anterior; (B) hooded hook; (C) brush-topped and falcate spines of chaetiger 5; (D) gross structure of glandular pouches; note the relatively large number of small pouches; (E) ventral view of pygidium and posterior chaetigers; (F) anterior views of posterior right chaetiger, showing position of ventral superior chaeta relative to hooded hooks. Scale bars: A, 1 mm; B, C, 20 μm; D, F, 100 μm; E, 500 μm.

Boccardia proboscidea Hartman, 1940, pp. 382–387; Woodwick, 1963, p. 134, figure 2; Blake & Kudenov, 1978, pp. 238–239, figure 33; Gibson *et al.*, 1999, pp. 748–749, figures 3 & 4; Bailey-Brock, 2000, p. 28, figure 1.

MATERIAL EXAMINED

South Africa: Western Cape Province: Saldanha Bay, Jakobsbaai Sea Products (Pty) Ltd, January 2006, A21518 (17) & A21519 (22); Hermanus, Abagold (Pty) Ltd, August 2005, A21516 (14) and September 2005, A21517 (12), A21520 (SEM).

MORPHOLOGY OF NEW MATERIAL

Colour in life pale green, with bright red branchiae and black pigment along edge of prostomium; faint black markings on dorsal surface between chaetigers 1 and 2 and 2 and 3. Preserved specimens tan, dark line along the feeding groove of the palps and along margins of prostomium and caruncle.

Largest specimens examined 20 mm long for 99 chaetigers, but up to 33 mm long recorded in population dynamics study (Simon & Booth, 2007). Prostomium rounded (Figure 5A), sometimes weakly indented, with 2–3 pairs of eyes; caruncle extending to middle or posterior margin of chaetiger 3 (Figure 5A), with nuchal organs consisting of paired ciliary bands along caruncle.

Notopodial lobe of chaetiger 1 with short notochaetae (Figures 4A & 5A). Anterior chaetigers with approximately 17 broad notochaetae with short tapering ends and few long needle-like chaetae. Posterior notochaetae long, needle-like, with two or three short chaetae with slightly curved ends that face posteriorly. Neurochaetae broad and blade-like with tapering ends, on chaetigers 2–4 and 6 a few capillary chaetae also present.

Hooded hooks start on chaetiger 7; bidentate, without constriction on shaft, angle between main fang and shaft $>90^{\circ}$, angle between teeth 45° (Figure 5B). Seven or eight hooded hooks per ramus, decreasing to 2–4 on posterior chaetigers (Figure 4B). Chaetigers 7–9 with three long ventral inferior capillary chaetae (Figure 4D). Neuropodial lobe, associated with hooded hooks, up to chaetigers 10 or 11 (Figure 4D). Posterior chaetigers with single fine superior neuropodial chaeta (Figures 4B & 5E, F).

Chaetiger 5 with two heavy curved spines and three blunt, bristle-topped, spines on each side. Fascicle of short ventral inferior chaetae present (Figure 4C).

Branchiae filiform, separate from notopodial lobes, on chaetigers 2–4 and posteriorly from chaetiger 6 to near the

posterior end of the body (Figure 4A&G) but absent from last 2–10 chaetigers. Longest branchiae (which may be as long as animal is wide) on chaetigers 8 or 9, decreasing in length towards end of the body (Figures 4G & 5A).

Large paired glands with many small glandular pouches observed in chaetigers 7–9 (Figure 5D). More than 50 openings visible at base of hooded hooks on these chaetigers (Figure 4D).

Lateral organs observed on chaetigers 2, 3, 6 and posteriorly (Figure 4A, B).

Row of papillae (3 μm diameter) each bearing ~8 cirri, 10 μm apart on latero-frontal surface of palp (Figure 4F). Towards the feeding groove, rows of papillae (2 μm diameter) arranged in pairs, about 1 μm apart, running perpendicular to length of palps, lacking cirri (Figure 4E).

Pygidium a fleshy cuff with dorsal notch; may be divided into four lobes or by folds in the pygidium (Figure 4F, G); often wider than posterior-most chaetigers.

REPRODUCTION

The reproduction of this species was examined at two farms: Jakobsbaai Sea Products (Pty) Ltd and Abagold (Pty) Ltd, on the west and south coasts, respectively. Worms reproduce throughout the year, but with increased numbers from the end of winter to early summer (Simon & Booth, 2007). The worms are poecilogonous at both farms, with females producing capsules that contain: (a) adelphophagic and planktotrophic larvae; (b) planktotrophic larvae only; and (c) adelphophagic larvae only. At both farms, 50 to 80% of the brooding females brooded capsules containing both adelphophagic and planktotrophic larvae and brooding individuals were present throughout the year (Simon & Booth, 2007). Within each category, larvae were of comparable size at the two farms (maximum length of planktotrophic larvae: 375 and 400 μm; maximum length of adelphophagic larvae: 1100 and 1000 μm at Abagold and Jakobsbaai, respectively). There was a tendency for worms at Jakobsbaai Sea Products (Pty) Ltd to brood more adelphophagic larvae per capsule (number of planktotrophic larvae per capsule: mean = 3.98, maximum = 7, number of adelphophagic per capsule: mean = 4.6, maximum = 12), while the opposite was true at Abagold (Pty) Ltd (number of planktotrophic larvae per capsule: mean = 5.5, maximum = 25, number of adelphophagic per capsule: mean = 3.19, maximum = 17).

REMARKS

Petch (1995) conducted an extensive morphological comparison of *Boccardia proboscidea* from the United States of America (Alaska, Washington State and California), Canada (British Columbia), Japan, Panama and Australia. He found that all specimens matched the original description of the species, with the exception of those from Alaska and Panama, which he suggested would represent separate species. Specimens from South Africa correspond well with other descriptions with just a few differences. South African specimens are similar in size to those from California (Hartman, 1940; Woodwick, 1963), but larger than those described for Hawai'i (Bailey-Brock, 2000) and Japan (Sato-Okoshi, 2000) and smaller than those from Barkley Sound, western Canada (Sato-Okoshi & Okoshi, 1997). With respect to the shape of the pygidium, South African specimens differ from the type specimens (Hartman, 1940) but more closely resemble those described by Bailey-Brock (2000). The branchiae of South African specimens are longer than those described by Woodwick (1963, figure 2) and Petch (1995). The fine ventral superior chaetae dorsal to the hooded hooks were also described by Gibson *et al.* (1999) and Sato-Okoshi (2000).

HABITAT

On cultured abalone in South Africa, *Boccardia proboscidea* is a secondary borer. It may form burrows on the surface of the shell (Figure 6A), in crevices on the shell surface as described for worms infesting the oysters *Ostrea edulis* and *Crassostrea gigas*, the barnacle *Balanus cariosus* and the abalone *Haliotis roei* (Sato-Okoshi & Okoshi, 1997; Bailey-Brock, 2000; Sato-Okoshi, 2000; Sato-Okoshi *et al.*, 2008) or it may occur in the burrows and blisters of *Polydora hoplura* and *Dipolydora capensis* (see also Woodwick, 1963). In extreme cases it forms 'mudpacks' which are covered with a thin layer of nacreous shell in the region of the respiratory pores. These packs usually contain several worms of different sizes and often cause the shell to break along the respiratory pores (Figure 6B). This pattern of infestation is similar to that of *Polydora uncinata* Sato-Okoshi, 1998 (Radashevsky & Olivares, 2005).

DISTRIBUTION

In South Africa, *Boccardia proboscidea* was found on cultured abalone at farms on the west, south and east coasts of South Africa. It is least abundant on the east coast. The presumed natural distribution range of *B. proboscidea* extends from Canada (British Columbia) to southern California, with unconfirmed reports from further south, and Japan (Hartman, 1940; Woodwick, 1963; Fauchald, 1977; Petch, 1995; Sato-Okoshi, 2000; Oyarzun *et al.*, in preparation). It has also been recorded from Australia (Blake & Kudenov, 1978), Hawai'i (Bailey-Brock, 2000), New Zealand (Read, 2004) and Spain (Martínez *et al.*, 2006) where it is considered non-native.

Boccardia pseudonatrix Day, 1961

Boccardia pseudonatrix Day, 1961, pp. 492–493, figure 5e–j

MATERIAL EXAMINED

Eastern Cape Province: Haga Haga, February 2005 A21521 (1) and April 2007, A21522 (7); A21523 (4, ethanol fixed).

MORPHOLOGY OF NEW MATERIAL

Specimens correspond well with the description by Day (1961); largest specimen, 20 mm long for 83 chaetigers, was larger than described previously. Prostomium bilobed; caruncle extending to chaetiger 2; middle of caruncle is dark; with one pair of eyes (in one specimen, a second pair observed in the pigment of the caruncle). A mid-dorsal ridge from chaetiger 5 to the middle of chaetiger 8. Notochaetae present on chaetiger 1. No modified posterior notochaetae. Notopodial lobes small, inconspicuous in posterior chaetigers. Hooded hooks from chaetiger 7; eight and two hooks per ramus in anterior and posterior chaetigers, respectively; no accompanying chaetae. Chaetiger 5 with anterior row of spines with swollen tips, a raised central cone and raised ridge, and posterior row of falcate spines. Branchiae on chaetiger 2 longer than those on chaetigers 3 and 4; others short, never overlapping mid-dorsum; posterior third of body abranchiate. Pygidium reduced, forming pair of flattened cushions.

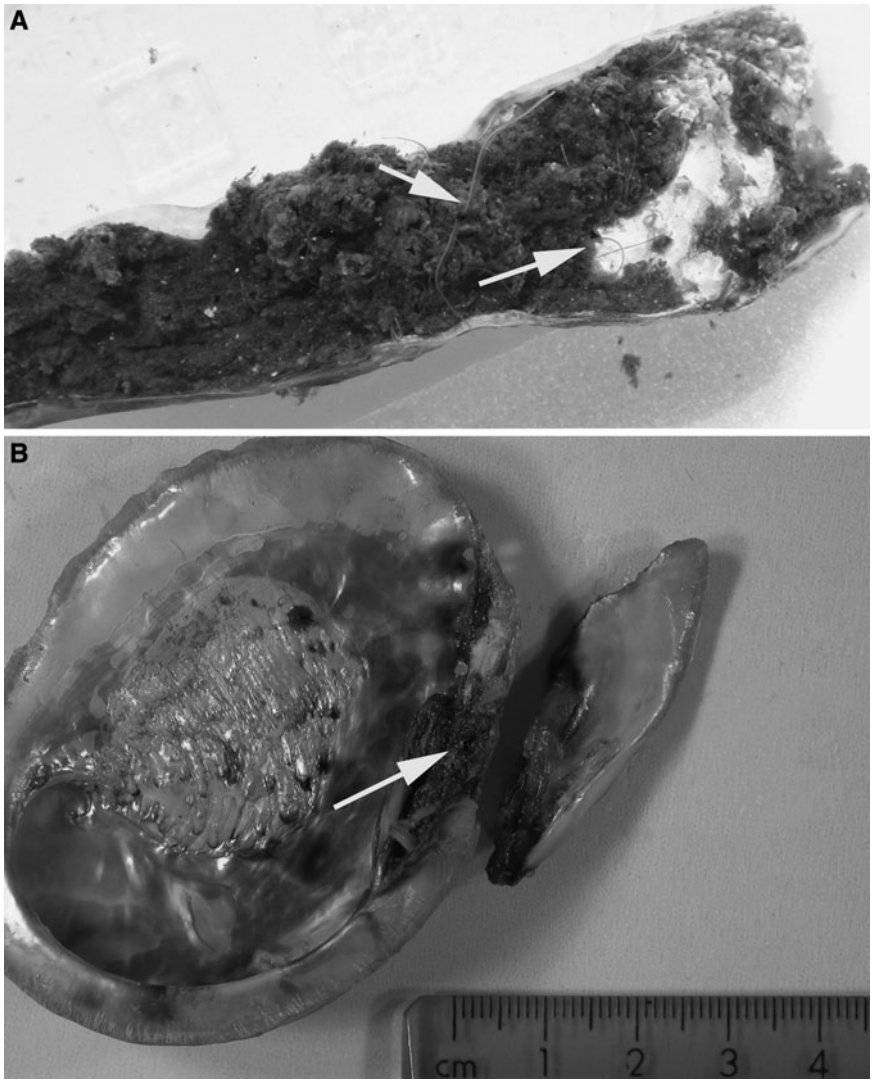

Fig. 6. Damage caused by *Boccardia proboscidea*. (A) Burrows formed on external surface of abalone shells, with *B. proboscidia* palps arrowed; (B) shell broken in the region of the respiratory pores, where it was weakened by infestation (arrow).

Female collected in April 2007 with ova in chaetigers 23–60.

HABITAT

Previously found in rock (Day, 1961) but associated with shells of cultured *Haliotis midae* and wild *Saccostrea cucullata* in current study.

DISTRIBUTION

Previously found only in Knysna (Day, 1961). In the current study found only at Haga Haga.

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Thanks are due to Andy Mackie (National Museum of Wales), Greg Rouse (Scripps Institution of Oceanography) and Frederik Pleijel (Göteberg University) for discussion of nomenclatural issues; the staff of South Africa National Parks and the Shell Museum and Aquarium, Mossel Bay, Anthony Bernard and Felicia Keulder for field assistance; abalone farmers who provided infested abalone; Pat Hutchings and Elin Sigvaldadóttir for finding references; Adrian Craig, Francesca Porri, Sophie Reinecke, Professor J.C. Zietsman and Mariaan Gaertner for translating manuscripts and Dylan McGarry for the drawings. Funding was provided by Marine and Coastal Management, the Abalone Farmers' Association of South Africa, a Rhodes University Joint Research Committee grant and a National Research Foundation post-doctoral grant.

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Correspondence should be addressed to:
C.A. Simon
Department of Botany and Zoology
Stellenbosch University
Stellenbosch 7602
South Africa
email: csimon@sun.ac.za