J. Mar. Biol. Ass. U.K. (2000), **80**, 299–309
Printed in the United Kingdom

Revision of the nudibranch genus *Cadlina* (Gastropoda: Opisthobranchia) from the Southern Ocean

Michael Schrödl

Zoologische Staatssammlung München, Münchhausenstraße 21, 81247 München, Germany.
E-mail: schroedl@zi.biologie.uni-muenchen.de

The taxonomy of Magellanic and Antarctic cadlinids has been for many years in extreme disorder, and the species were not reliably identifiable. Recent collections in Chile and Argentina, mainly by SCUBA, and re-examination of type material provided data for a comprehensive revision. The present study gives new morphological information on all southern species, both by scanning electron microscope examinations of cuticular structures and detailed microanatomical investigation of the genitalia. The high Antarctic *Cadlina affinis* does not possess an aberrant androdiaulic genital system but, as all other doridoidean nudibranchs, a triaulic system with a separate vagina and nidamental duct. The vaginal duct is short and leaves the vagina distally, distinguishing this species from other known cadlinids. The genitalia of the holotype of *C. kerguelensis* from Kerguelen Island have been re-examined. In contrast to previous assumptions, it is not conspecific with cadlinids from South Georgia and the Magellanic region because of clear differences in the genital system. The south-western Atlantic *C. magellanica* is redescribed and considered to be conspecific with the holotype of *C. falklandica* from the Falklands. A specimen previously assigned to *C. falklandica* from South Georgia, however, differs from other southern cadlinids due to genital features and is redescribed as *C. georgiensis* sp. nov. The Argentinian species *C. laevigata* and *C. berghi*, cannot be clearly distinguished from *C. sparsa*, of which a lectotype has been designated and, therefore, are regarded as junior synonyms. Five *Cadlina* species from the Southern Ocean are regarded to be valid, and their biogeography is briefly discussed.

INTRODUCTION

Compared to other Chromodorididae, members of the nudibranch genus *Cadlina* Bergh, 1878 have generally more similar body shapes and coloration and, thus, are more difficult to distinguish from each other. While there are a few tropical cadlinids, most *Cadlina* species occur in northern and southern temperate waters, indicating a bipolar distribution for the genus (see Rudman, 1985). From the Southern Hemisphere 19 *Cadlina* species have been reported (see Marcus, 1955; Miller, 1980; Gosliner, 1987; Rudman, 1984, 1985, 1990). Of them, *C. evelinae* Marcus, 1958 from Brazil was transferred to the genus *Tyrinna* Bergh, 1898 by Rudman (1984), and *C. juvenca* Bergh, 1898 from the Juan Fernández Islands and northern Chile was recently shown to be a junior synonym of *Tyrinna nobilis* Bergh, 1898 by Schrödl & Millen (in press).

No less than eight nominal *Cadlina* species have been reported from the Magellanic Province and Antarctica, the Southern Ocean (Bergh, 1894; Thiele, 1912; Odhner, 1926, 1934; Schrödl, 1996). All are very similar externally and their anatomy is poorly known, since they were incompletely described on the basis of single or few preserved and often immature specimens. This has led to curiosities like the highly aberrant androdiaulic genital system of *Cadlina affinis* Odhner, 1934 mentioned by Odhner (1934), and to some contradicting synonymy proposals (see Odhner, 1926, 1934; Marcus, 1955; Miller, 1980; Schrödl, 1996), and altogether made southern cadlinids unidentifiable. The present study provides a comprehensive taxonomic revision which is based on detailed re-examination of museum material of poorly known southern species. Recent collections off South America supply data on living specimens (Schrödl, 1996; this study) and material for a comprehensive anatomical study.

MATERIALS AND METHODS

Extensive nudibranch collecting on the Chilean and Argentinian coasts using SCUBA yielded 13 cadlinid specimens. The nudibranchs were observed in their habitat, described and photographed in living condition, then relaxed using a 10% $MgCl_2$ solution and fixed in 70% ethanol. Larger specimens were dissected and described anatomically. Cuticular structures were examined using scanning electron microscope (SEM). In addition, all available museum material of southern *Cadlina* species has been re-examined.

SYSTEMATICS

Family CHROMODORIDIDAE Bergh, 1891
Genus *Cadlina* Bergh, 1878
Cadlina affinis Odhner, 1934
(Figure 1)

Synonymy

Cadlina affinis Odhner, 1934: 251–254, figures 17–19, pl. 1, Figures 7, 8; Marcus 1955: 123;
Miller 1980: 171.

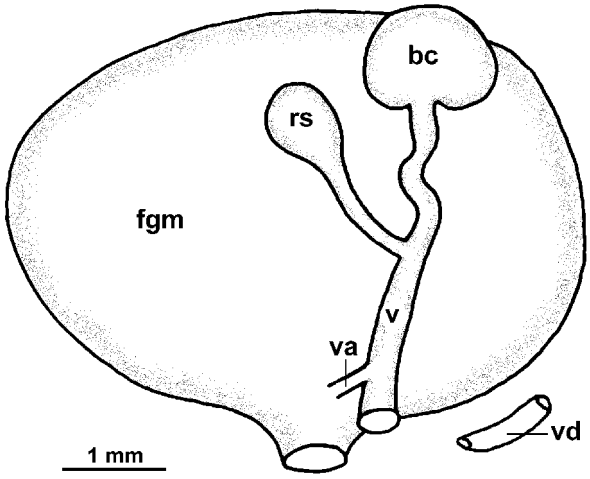

Figure 1. *Cadlina affinis*, semischematic outline of the reproductive system (paratype no. 1934.10.5.41). bc, bursa copulatrix; fgm, female gland mass; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens portion. Scale bar: 1 mm.

Material studied

Cadlina affinis: holotype (by original designation), dissected, 15 mm preserved body length, British Museum of Natural History (BMNH) no. 1934.10.5.39, 'Terra Nova' Expedition, Station 356, McMurdo Sound, off Granite Harbour, at 92 m depth. Three paratypes, dissected; 13 mm, BMNH no. 1934.10.5.40, Station 340 (76°56′ S 164°12′ E), at 293 m depth; 20 mm, BMNH no. 1934.10.5.41, Station 355 (77°46′ S 166°8′ E), at 547 m depth; 14 mm, BMNH no. 1934.10.5.42, Station 340 (76°56′ S 164°12′ E), at 293 m depth.

Description

All four type specimens were dissected originally by Odhner (1934) and most inner organs were damaged. Body lengths of their preserved remains range between 13 and 20 mm (Table 3). External characters largely agree with Odhner's (1934) description. However, the holotype has large, knob-like notal tubercles up to 0.7 mm in diameter. Tubercles and notal tissue contain layers of needle-like spicules. Numerous subepithelial glands open onto the notal surface. The holotype has broad triangular oral tentacles 'with a small pit in the middle of the frontal surface' as illustrated by Odhner (1934, figure 17), the paratypes have more usual triangular tentacles with a lateral furrow. All specimens have two separate genital openings, a common atrial opening which may be everted with the separate male and female ducts visible and, closely posterior, the nidamental opening. Jaws and radulae were missing.

Remains of genitalia are still present in the largest paratype (BMNH 1934.10.5.41). A short distal, muscular portion of the vas deferens is still *in situ*, cuticular armature was not detected. The distal female genitalia are outlined in Figure 1. The vagina is a relatively wide tube inserting into the spherical bursa copulatrix. The stalk of the smaller, ovate receptaculum seminis branches off the vagina at about half of its length. The short vaginal duct (regarded as part of the vagina by Odhner, 1934) splits off the vagina in an unusual, very distal position. The presence of a separate nidamental opening was overlooked by Odhner (1934).

Remarks

Odhner (1934: figure 18) described *C. affinis* as having an androdiaulic genital system with a common nidamental and vaginal opening. This condition would be unique within doridoidean nudibranchs and resembles that of dexiarchian and bathydoridoidean nudibranchs (see Schrödl et al., unpublished data). However, re-examination of the (damaged) types shows the presence of a distinct nidamental duct with a separate opening, and of male and female genital ducts opening into a common atrium. Remains of the genitalia of the largest paratype confirm the presence of a normal triaulic genital system in *C. affinis* with vaginally arranged allosperm receptacles and an extremely short vaginal duct in a very distal position. This latter condition clearly distinguishes *Cadlina affinis*, the only known high Antarctic *Cadlina* species, from congeners from lower latitudes (see Table 3). In contrast, the general body shape of preserved *C. affinis* is very similar to that of preserved South American cadlinids and cannot be used as a distinguishing character as claimed by Odhner (1934).

Cadlina kerguelensis Thiele, 1912
(Figure 2)

Synonymy

Cadlina kerguelensis Thiele, 1912: 250–251; pl. 19, figures 23–24; Odhner 1926: 57; 1934: 253–254; Marcus 1955: 122; Miller 1980: 171.

Material studied

Cadlina kerguelensis: holotype (by monotypy), dissected specimen and one microscopic slide with the radula, Zoological Museum Berlin (ZMB) no. 63281, Deutsche Südpolar Expedition, Observatory Bay, Kerguelen, 17 June 1902, at low depth.

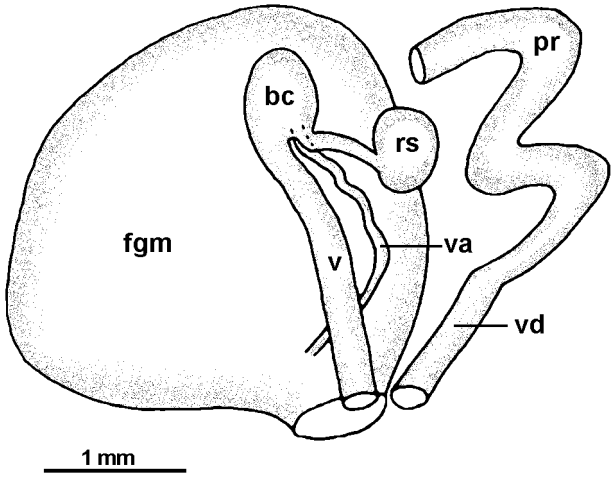

Figure 2. *Cadlina kerguelensis*, reproductive system of the holotype. bc, bursa copulatrix; fgm, female gland mass; pr, prostatic vas deferens; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens. Scale bar: 1 mm.

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

Description

According to Thiele (1912), the preserved holotype originally measured 13.5 mm; the notum was covered with low knobs. The remains of the holotype measure 10 mm in length and 3 mm in width. The blackish coloration appears to be due to fixation with osmium. Only parts of the foot and distal genitalia are in reasonable preserved condition, while the notum, lateral body portions, and the anterior digestive system are lost or damaged. The right rhinophore is perfoliate with about ten lamellae. The foot is bilabiate with a, possibly natural, notch in the upper lip and an artificial notch in the lower lip. Oral tentacles are triangular lobes. The genital openings are situated on the right side in the anterior third of the body, immediately behind the rhinophore.

The jaw rodlets bear bifid cusps. The (damaged) radula has about 60 teeth rows with up to 25 lateral teeth per half row. As illustrated by Thiele (1912: pl. 19, figures 23, 23A) the rhachidian teeth are claw-like. Rhachidians are smaller than the first laterals, but not unusually small as suspected by Marcus (1955). The first laterals possess some inner and outer denticles beside the main cusp. Further laterals have an increasing number of outer denticles and become more erect and saw-like in shape.

Despite the small body size, the anterior genitalia are well-developed and fill out the entire anterior body cavity. The structure of the genital system has been examined (Figure 2). The ampulla seems lost. Remains of the vas deferens show a proximal, convoluted, prostatic portion, passing into a short, straight, distal portion. No cuticle has been detected. The vagina is a long, wide tube, terminating in an ovate to spherical swelling which appears to be the bursa copulatrix. From the base of the bursa two further ducts arise: one is the moderately narrow stalk of the receptaculum seminis. The second, vaginal duct is long, narrow and highly convoluted. It inserts into the female gland mass distally near to the nidamental duct.

Remarks

The brief original description of the single known specimen of *C. kerguelensis* by Thiele (1912) was supplemented by Odhner (1926) who noted the presence of notal tubercles and glands opening onto the notum as in *C. falklandica*. Due to incomplete knowledge of *C. kerguelensis*, a synonymy with *C. falklandica* and *C. affinis* appeared possible (Odhner, 1926, 1934; Miller, 1980). The detailed data on the genital system of *C. kerguelensis* presented herein, however, clearly contradicts conspecifity. The origin of both the stalk of the receptaculum seminis and the vaginal duct from the base of the bursa copulatrix distinguishes *C. kerguelensis* from *C. affinis* and from all other southern cadlinids (Table 3).

Cadlina magellanica Odhner, 1926
(Figures 3 & 4A,B)

Synonymy

Cadlina magellanica Odhner, 1926: 58–60, figures 37–41, pl. 2, figures 24, 25; Carcelles & Williamson 1951: 314; Marcus 1955: 123; Miller 1980: 171.

Cadlina magallanica Marcus, 1959: 87 (misspelling).

Cadlina falklandica Odhner, 1926: 60–62, figures 42–43, pl. 2, figures 26, 27.

(non *C. falklandica* from South Georgia, figures 44, 45).

Cladlina falklandica Carcelles & Williamson, 1951: 314 (misspelling).

Material studied

Cadlina magellanica: holotype (by original designation), dissected specimen, 7 mm, Swedish Museum of Natural History (SMNH) type number 1014, Punta Arenas, Chile, Swedish Feuerland Expedition, 14 December 1895, at 27 m depth. One specimen, dissected, 7 mm, SMNH no. 14732, Cape Valentin, Swedish Feuerland Expedition, 12 March 1896, at 270 m depth, on dead shells. One specimen, dissected, 9 mm preserved length, Bahía Mansa, south of Punta Arenas, collected by S. Millen, S. Gigglinger & M. Schrödl, 5 January 1995, at 2–3 m depth, on rocks.

Cadlina falklandica: holotype (by original designation), dissected, 7 mm preserved length, SMNH type number 1024, Falkland Islands, Berkeley Sund (51°33′ S 58°00′ W), Swedish Antarctic Expedition, 19 July 1902, at 16 m depth, gravel and shells with algae.

Description

The preserved holotype of *C. magellanica* measures 7 mm in length, 4.5 mm in width and about 2 mm in height. The foot is narrow (1.5 mm). Other than mentioned by Odhner (1926), the mantle rim is not narrow; the notum is covered by knobby tubercles reaching about 0.2 mm in height and in diameter, spicules and subepithelial glands are clearly present in the notal tissue. The rhinophoral sheaths are tuberculate. The recently collected, living specimen was whitish. There are numerous mantle glands opening onto the notum but no mantle dermal formations (MDFs; see Garcia-Gomez et al., 1991) were detected.

Jaw and radular features of *C. magellanica* (radula formulae: 58×21–27.1.21–27) were described extensively by Odhner (1926), jaws and radulae were lost. The recently collected specimen also has small, bifid jaw rodlets (Figure 3A). The radula formula is 58×15.1.15 (S. Millen, personal communication). Like in the holotype, the rhachidian teeth are well-developed with a claw-like appearance (Figure 3B). The first laterals have some inner and outer denticles beside the large median cusp (Figure 3C). The laterals following possess an increasing number of outer denticles, the teeth successively become more erect and saw-like in shape (Figure 3D). Outermost laterals are reduced in size.

The re-examined genitalia of the holotype agree with the original description by Odhner (1926). Remains of the vas deferens are restricted to a wide, prostatic portion passing into a slightly narrower, muscular portion (Figure 4A). Odhner (1926) described the distal muscular vas deferens to be lined by hook-bearing cuticle which is also present in the recently collected specimen. The vagina of the holotype is long with a spherical bursa copulatrix. The vaginal duct branches off the vagina at about half its length. The ovate receptaculum seminis is relatively short stalked, rising from the vaginal duct close to the vagina (Figure 4A). Thus, allosperm receptacles are semi-serially arranged in the holotye. In the recently collected specimen the receptaculum seminis has a slightly longer stalk joining the vaginal duct directly at

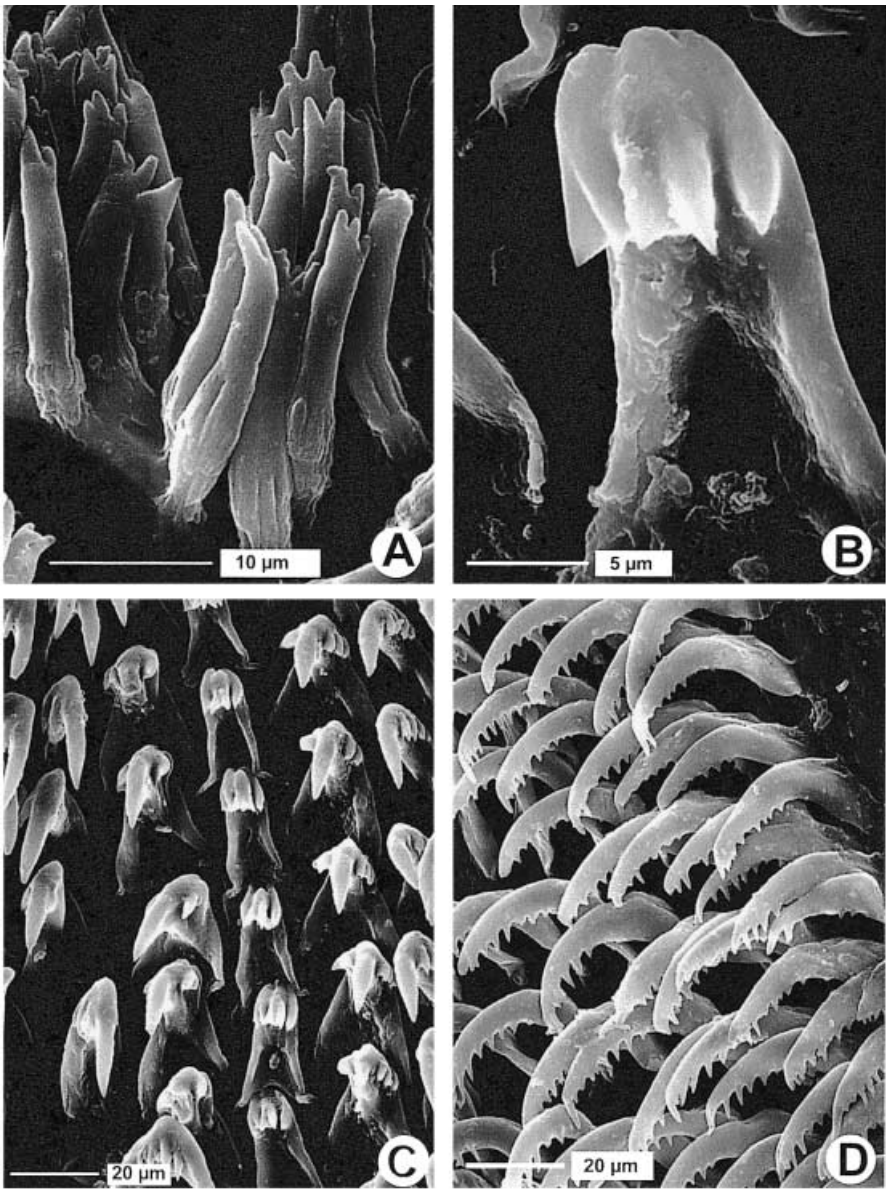

Figure 3. *Cadlina magellanica*, SEM micrographs of cuticular structures (specimen from Bahía Mansa: (A) lip rodlets; (B) rhachidian tooth; (C) central radula portion; (D) outer lateral teeth. Scale bars: B, 5 µm; A, 10 µm; C & D, 20 µm.

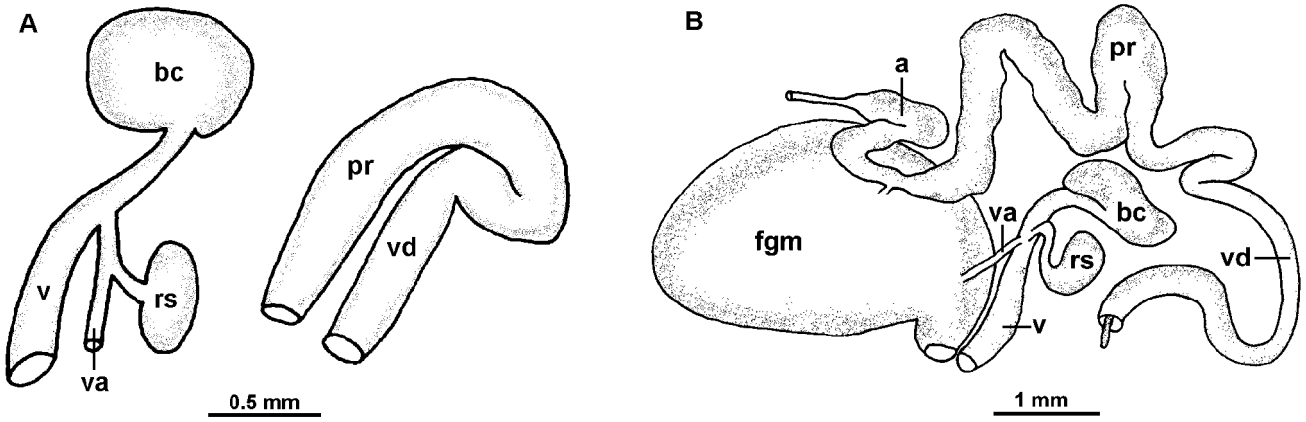

Figure 4. *Cadlina magellanica*, reproductive system: (A) remains of the holotype; (B) recently collected specimen. a, ampulla; bc, bursa copulatrix; fgm, female gland mass; pr, prostatic vas deferens; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens. Scale bars: A, 0.5 mm; B, 1 mm.

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

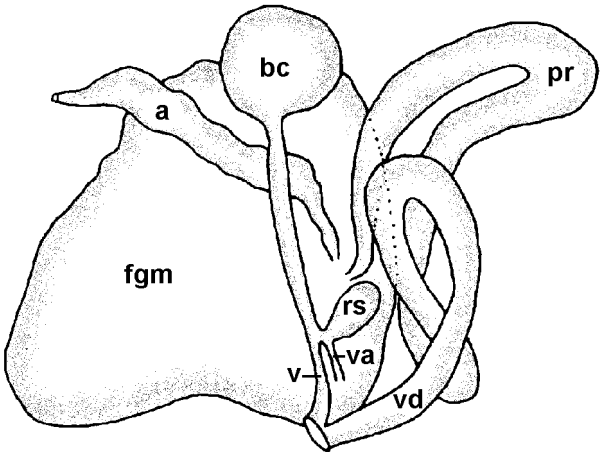

Figure 5. *Cadlina georgiensis* sp. nov., reproductive system of the holotype (redrawn from Odhner, 1926: figure 45; modified). a, ampulla; bc, bursa copulatrix; fgm, female gland mass; pr, prostatic vas deferens; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens. No scale.

the vagina (Figure 4B), i.e. the allosperm receptacles have a vaginal arrangement.

As mentioned for the holotype by Odhner (1926: figure 39), the cerebropleural ganglia of *C. magellanica* are separated by a deep furrow. A pair of distinct rhinophoral ganglia is attached to the cerebral ganglia; optical nerves are short.

Remarks

Cadlina magellanica is well characterized by its dense notal tuberculation coupled with the hook-bearing vas deferens cuticle. Slight differences between the holotype and the recently collected specimen regarding the position of the receptaculum seminis seem to be due to variation. The holotype of *C. falklandica* from the Falklands agrees regarding external, radular and genital features; the apparent absence of a vas deferens cuticle can be easily explained by its juvenile condition (see Odhner, 1926). In absence of any detectable differences, *C. falklandica* Odhner, 1926 is considered synonymous to *C. magellanica* Odhner, 1926; the latter is herein established as the valid name due to better anatomical knowledge.

An obviously fully mature specimen from South Georgia assigned to *C. falklandica*, according to Odhner (1926) differs from adult *C. magellanica* by lacking a hook-bearing cuticle of the vas deferens. It is described as *C. georgiensis* sp. nov. below. Further differences are the insertion of the vaginal duct into the distal third of the vagina in *C. georgiensis* sp. nov. (Figure 5) while inserting into the proximal half in *C. magellanica* (Figure 4A,B), and the very short vs moderately long stalk of the receptaculum seminis (Table 3).

Cadlina georgiensis sp. nov. (Figure 5)

Synonymy

Cadlina falklandica Odhner, 1926: 60–62 (partim), figures 44, 45.

Material studied

Cadlina georgiensis: holotype, dissected specimen, 13 mm preserved body length, SMNH no. 14734 (as *C. falklandica*), Moränenfjord, South Georgia (54°23′ S 36°25′ W), Swedish Antarctic Expedition, 26 May 1902, at 16 m depth, on stones with algae.

Description

The single known specimen was dissected and described by Odhner (1926: 61–62, figures 44 & 45). The remains of the preserved holotype measure 13 mm in length and 8 mm in width. The type is in a well-preserved condition externally. The notum is densely covered with different sized knob-like tubercles (up to 0.8 mm in diameter). Spicules and glands opening onto the notum are visible in the notal tissue. The rhinophores are perfoliate with about ten lamellae. The foot is damaged anteriorly. Oral tentacles are triangular with a lateral groove.

The lip cuticle is still *in situ*. The radula formula is 53×17.1.17 according to Odhner (1926), the radula is not included in the museum lot. There is a pair of white, well-developed, ribbon-like salivary glands. The stomach is largely embedded within the digestive gland. The large, bulbous caecum is freely visible; it is surrounded by the intestinal loop. The anterior genitalia (Figure 5) were described by Odhner (1926: figure 45). Remainders of the genitalia are in several pieces and strongly damaged. The cerebropleural ganglia are separated by a deep furrow. A pair of distinct rhinophoral ganglia is attached to the cerebral ganglia. The eyes have short optical nerves.

Remarks

Cadlina georgiensis sp. nov. is externally similar to *C. magellanica* due to its tuberculate notum. The larger tubercles of *C. georgiensis* may be explained by larger body size. In contrast to mature *C. magellanica* and all other South American cadlinids (Table 3), the ejaculatory part of the vas deferens (i.e. penis) of the fully mature specimen of *C. georgiensis* sp. nov. is not armed by a hook-bearing cuticle (Odhner, 1926). The absence (vs presence) of such a penial armature in mature specimens is regarded as being a significant distinguishing feature because of its obvious functional influence on copulation. *Cadlina kerguelensis* and *C. affinis* also lack any cuticular structures in the male reproductive system. *Cadlina georgiensis* sp. nov. differs from the two latter species mainly due a semi-serial arrangement of the allosperm receptacles and a very short stalked receptaculum seminis (see Table 3).

Cadlina sparsa (Odhner, 1921) (Figures 6 & 7)

Synonymy

Juanella sparsa Odhner, 1921: 255–256, pl. 8, figures 13 & 14.

Cadlina sparsa (Odhner): Odhner, 1926: 56–57; Marcus 1955: 122; 1959: 27–29, figures 39–44; 1961: 15, pl. 3, figures 43–45; McDonald & Nybakken 1980: 48–49; Jaeckle 1983: 93; Behrens 1991: 58; Schrödl 1996: 21, pl. 3, figure 16; 1997: 39–41.

Cadlina laevigata Odhner, 1926: 62–64, figure 46, pl. 2, figures 28 & 29; Carcelles & Williamson 1951: 314; Schrödl 1996: 21.

Cadlina berghi Odhner, 1926: 57; Marcus 1959: 30; Schrödl 1996: 21.

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

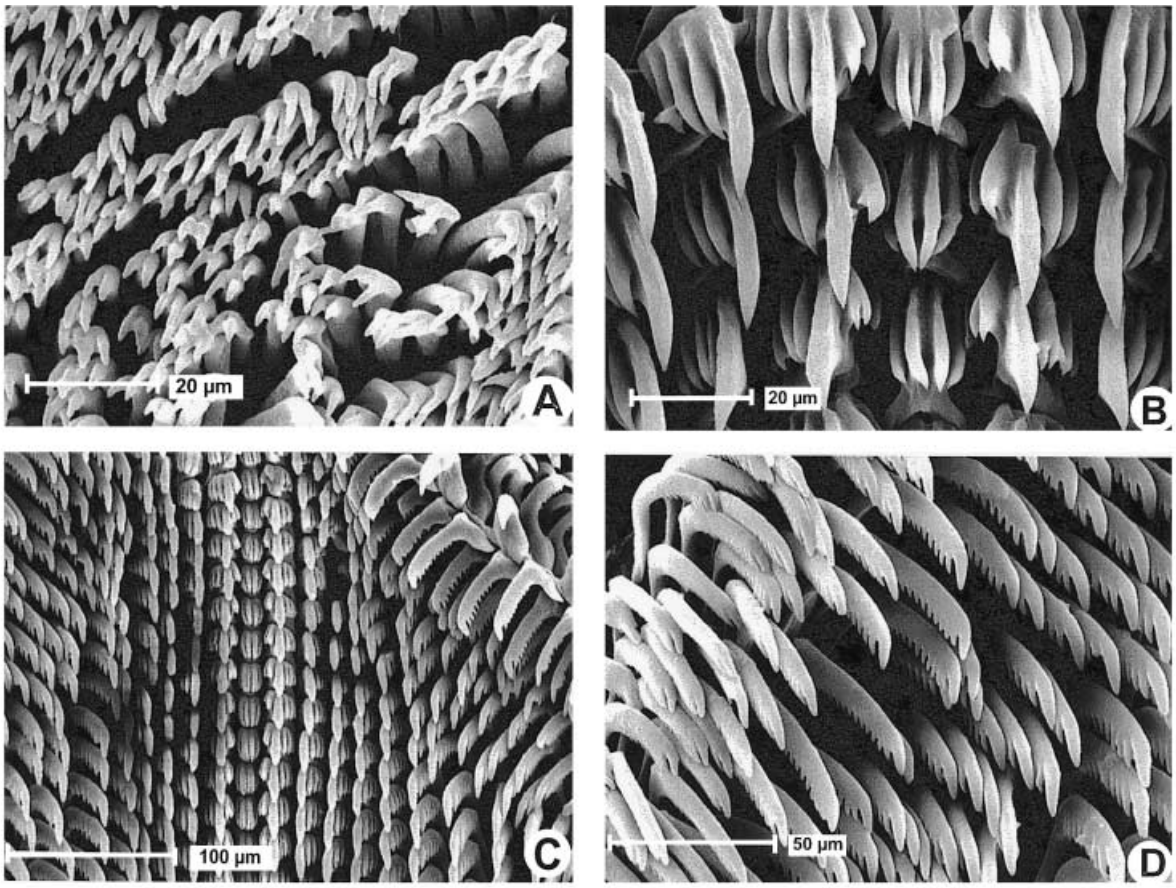

Figure 6. *Cadlina sparsa*, SEM micrographs of cuticular structures: (A) jaw rodlets (21 mm specimen from Bahía Coliumo); (B) central radula, detail (21 mm specimen from Bahía Coliumo); (C) central and lateral radular teeth (14 mm specimen from Bahía Camarones); (D) outermost radular teeth (14 mm specimen from Bahía Camarones). Scale bars: A & B, 20 µm; D, 50 µm; C, 100 µm.

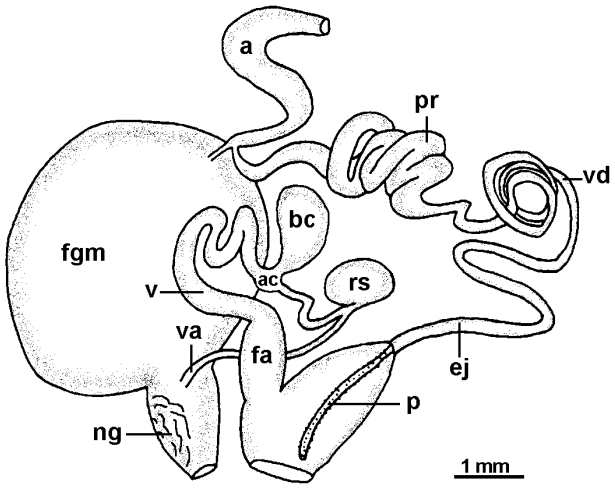

Figure 7. *Cadlina sparsa*, reproductive system of the largest (16 mm) specimen from Camarones. a, ampulla; ac, accessory gland; bc, bursa copulatrix; ej, ejaculatory vas deferens portion; fa, female atrium; fgm, female gland mass; ng, nidamental gland; p, everted penis; pr, prostatic vas deferens; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens. Scale bar: 1 mm.

Material studied

Cadlina sparsa (as *Juanella*): lectotype, dissected, 14 mm body length, SMNH type no. 1019, Masatierra, Chile, 1 April 1917, coll. Bäckström, at 30–40 m depth, sand with encrusting red algae. Two paralectotypes, 7 and 10 mm length, dissected, collected together with the lectotype. One specimen, dissected, 20 mm, Bahía de Coliumo (36°32′ S 72°57′ W), collected by M. Schrödl, 26 April 1992, at 12 m depth, on rocks. One specimen, B. de Coliumo, coll. M. Schrödl, 28 January 1994, at 15 m depth, feeding on sponges. Four specimens, the largest dissected, 7–21 mm, ZSM no. 19960709 (one specimen), B. de Coliumo, coll. M. Schrödl, 27 February 1995, at depths of 5–6 m, on cave walls with sponges. Six specimens, two dissected, 10–17 mm, Bahía Camarones (44°53′ S 65°39′ W), collected by S. Gigglinger & M. Schrödl, 9 January 1994, at 2–8 m depth, crawling on rocks and on exposed algae.

Cadlina laevigata: holotype (by monotypy), 7 mm body length, SMNH type no. 2301, Feuerland Expedition, 9 November 1895, Puerto Madryn, Argentina, at 3–9 m depth, sand and mud.

Description

Living specimens from Chile reach 28 mm in length, preserved body dimensions are given in Table 1. The ground coloration of Argentinian and smaller Chilean specimens is whitish, larger Chilean ones are salmon. There are innumerable, small subepithelial glands opening onto the notum which may be translucent or, i.e. in large Chilean specimens, brownish coloured. Aggregations of

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

the latter are visible as darker areas. All specimens have a variable number of more or less spherical MDFs arranged in an irregular submarginal row. MDFs reach about 0.2 mm in diameter and are visible through the notal tissue as white or yellowish spherules. In larger Chilean specimens most MDFs are marked by dark spots, forming the 'ocular spots' mentioned by Odhner (1921). Most Argentinian specimens from Bahía Camarones have variable numbers of ocular spots which are absent in a few specimens. During fixation, MDFs were observed to expulse their yellow contents onto the notum. The notum is covered by scattered, different-sized, knob-like to conical tubercles. Notal tissue and tubercles are spiculate. There are 10 to 16 uni- or bipinnate gills. The rhinophores are perfoliate with 10–15 lamellae. Oral tentacles are triangular lobes with a lateral groove. The foot is narrow, bilabiate anteriorly, without notches in living specimens.

Lip rodlets have bifid cusps (Figure 6A). The numbers of radular rows vary between 59 and 68, there are 24–28 laterals on each side of the rhachidian teeth (see Table 1). The rhachidians are claw-like (Figure 6B). The first lateral teeth possess some inner and outer denticles beside the large median cusp. Further laterals have an increasing number of outer denticles with the teeth successively getting more erect and saw-like in shape (Figure 6C). Outermost laterals are reduced in size (Figure 6D). There is pair of well-developed, ribbon-like salivary glands. The stomach is embedded within the digestive gland. A large bulbous caecum is freely visible; it is surrounded by the intestinal loop.

The reproductive system (Figure 7) is similar in the Chilean and Argentinian specimens dissected. The vas deferens is extremely long. The proximal, prostatic portion is convoluted while the muscular, narrower distal portion forms an irregular spiral. The ejaculatory vas deferens portion is lined internally by a hook-bearing cuticle and covered by an additional muscular (penial) sheath. There is no distinct penial papilla. The everted penis is the long and flagelliform hooked portion of the vas deferens. There is a distinct female atrium opening into the male atrium distally. The muscular vagina is long, narrow and convoluted. The allosperm receptacles are semi-serially arranged. The bursa copulatrix is spherical. The vaginal duct leaves the vagina proximally. At this junction, the vagina is more or less swollen possibly having an accessory gland as found in *Cadlina willani* by Miller (1980). The ovate, muscular receptaculum seminis has a short stalk. The vaginal duct is long and inserts into the female gland mass distally. A bulbous, glandular swelling of the nidamental duct is interpreted as an accessory nidamental gland.

Remarks

Bergh (1894) was the first to describe a cadlinid specimen with few notal knobs from central Argentina. He assigned it to *C. repanda* (Alder & Hancock, 1842)

Table 1. *Comparative data on* Cadlina sparsa*: distribution, external and radular characters.*

Specimens	Collecting location	Body length (preserved)	Notal tubercles	Glands opening onto notum	Gills	Radula formula
Cadlina laevigata Odhner, 1926, holotype	Puerto Madryn, central Argentina	7 mm (juvenile)	central notum nearly smooth, marginally small knobs	present	11	55×18.1.18
Cadlina berghi Odhner, 1921, holotype	off Cabo Delgado, northern Argentina	23 mm	scattered, pointed knobs	?	12	96×31.1.31
Cadlina sparsa (Odhner, 1921), lectotype	Juan Fernández Islands	14 mm	scattered, conical, with spicules	present	?	56×21.1.21
Cadlina sparsa, paralectotypes	Juan Fernández Islands	7, 10 mm	scattered, knob-like	present	?	
Cadlina sparsa det. Schrödl, 1996	Bahía Camarones, central Argentina	8–16 mm	some with nearly smooth notum, others with scattered rounded or conical knobs, with spicules	present	10–12	60×30.1.30; 63×25.1.25
Cadlina sparsa det. Schrödl, 1996	Bahía Coliumo, central Chile	7–21 mm	smaller specimens with nearly smooth notum, others with scattered rounded or conical knobs up to 0.8 mm in diameter and in height, with spicules	present	10–16	59×24.1.24; 68×28.1.28
Cadlina sparsa det. Marcus, 1959	Chiloé Island, southern Chile	21–25 mm	different shaped papillae containing spicules	present	12	69×30.1.30
Cadlina sparsa, det. Marcus, 1961	San Diego, California	18 mm	shape variable	?	12	84×29.1.29
Cadlina sparsa, cf. Behrens, 1991	California	to 36 mm (living)	scattered (figure)	?	?	37–69×24–28.1.24–28

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

Table 2. *Comparative data on* Cadlina sparsa*: reproductive characters.*

Specimens	Vas deferens	Vas deferens cuticle	Arrangement of seminal receptacles	Insertion of vaginal duct	Length of vaginal duct	Stalk of seminal receptacle
Cadlina laevigata Odhner, 1926, holotype	juvenile	in development	juvenile	juvenile	juvenile	juvenile
Cadlina berghi Odhner, 1921, holotype	very long, enrolled prostatic portion, short muscular portion	present	vaginal (see pl. 7, figure 9), or semi-serial (see text)	?	long (as uterine duct)	not short
Cadlina sparsa (Odhner, 1921), lectotype	?	present, with hooks (Odhner, 1926)	?	?	?	?
Cadlina sparsa, paralectotypes	very long	?	?	?	?	?
Cadlina sparsa det. Schrödl, 1996 (Bahía Camarones)	very long, convoluted prostatic portion, enrolled muscular portion, straight ejaculatory portion with muscular sheath	present, with hooks	semi-serial	proximal third	moderately long	short
Cadlina sparsa det. Schrödl, 1996 (Bahía Coliumo)	very long, convoluted prostatic portion, enrolled muscular portion, straight ejaculatory portion with muscular sheath	present, with hooks	semi-serial	proximal third	moderately long	relatively short
Cadlina sparsa det. Marcus, 1959	long prostatic and long muscular portion	present, with hooks	semi-serial	proximal third	long	relatively short
Cadlina sparsa, det. Marcus, 1961	proximal vas deferens glandular	with hooks	?	?	?	?
Cadlina sparsa, cf. Behrens, 1991	?	?	?	?	?	?

(=*C. laevis* (L., 1767)) which is known from the northern hemisphere. Odhner (1926) doubted this bipolarity and regarded Bergh's specimen as a new species which he called *C. berghi* Odhner, 1926. His main reasons were the very long radula of *C. berghi* with 96 rows and the apparent vaginal arrangement of the seminal receptacles, whereas most other South American cadlinids have a semi-serial arrangement. However, Bergh's specimen externally agrees with the juvenile holotype of *C. laevigata* from central Argentina which also lacks extensive notal tuberculation. Different numbers of radular rows (96 vs 55) may be explained by different body sizes (21 vs 7 mm), and there is no further reason to doubt conspecifity.

Schrödl (1996) identified additional cadlinids from southern Argentina with sparse notal tuberculation and ocular spots as *C. sparsa*, a species which is well-known from the south- and north-eastern Pacific (see Behrens, 1991). The present study shows no clear morphological differences between Californian, Chilean and Argentinian populations of *C. sparsa* on one hand, and the Argentinian *C. laevigata* and *C. berghi* on the other (Tables 1 & 2). The vaginal arrangement of the seminal receptacles of *C. berghi* sketched by Bergh (1894: pl. 7, figure 9) was stressed as a distinguishing feature from other South American cadlinids having a semi-serial arrangement by Odhner (1926). However, in his description Bergh (1894) mentioned the 'spermatocyst' as being 'attached to the uterine (=vaginal) duct', thus indicating a semi-serial rather than a vaginal arrangement. Recently collected Argentinian *C. sparsa* appear to have fewer MDFs and are brighter coloured than Chilean specimens, but there is considerable variation within each population, and overlap between them. While Chilean specimens were always found inactive in crevices near sponges or hidden on rockwalls or in small caves, Argentinian specimens crawled around freely on a variety of substrates including fronds of macroalgae. This may be due to different modes of life or just due to certain phases of strong activity, e.g. part of mating behaviour. In conclusion, as long as no significant morphological differences are known, both *C. laevigata* and *C. berghi* are considered to be junior synonyms of *C. sparsa*.

Cadlina sparsa resembles *C. willani* from New Zealand regarding a, presumably, accessory vaginal gland in the

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

Table 3. *Comparative data on* Cadlina *species from the Southern Ocean.*

Species/ specimens	Collecting location	Body length (mm)	Notal tuberculation	Glands opening onto notum	Gills	Radula formula	Vas deferens, prostatic portion	Vas deferens, muscular portion	Vas deferens cuticle	Arrangement of seminal receptacles	Insertion of vaginal duct into vagina	Length of the vaginal duct	Stalk of receptaculum seminis
Cadlina affinis Odhner, 1934	McMurdo Sound, Antarctica	13–20	relatively dense, knob-like tubercles, with up to 0.7 mm in diameter	present	8–12	56×20.1.20 to 71×27.1.27	long	long	absent	vaginal	extremely distally	very short	long
Cadlina kerguelensis Thiele, 1912	Kerguelen Island	10	relatively dense, knob-like tubercles	present	?	∼60×25.1.25	long	short	absent	special vaginal	proximally, at base of bursa	long	long
Cadlina magellanica Odhner, 1926	Magellan Strait, Tierra del Fuego, Falklands	7	dense, knob-like tubercles, with a diameter and height of up to 0.2 mm	present	7 to 12	58×21.1.21 to 58×27.1.27	long	long	present, with hooks	vaginal to semi-serial	proximal half of the vagina	relatively short	moderately long
Cadlina georgiensis sp. nov.	South Georgia	13	dense, knob-like tubercles, up to 0.8 mm in diameter	present	?	53×17.1.17	long	long	absent	semi-serial	distal half (text); distal third (figure 45)	short	very short
Cadlina sparsa (Odhner, 1921)	North- and south-eastern Pacific, central and northern Argentina	7–25 (see Table 1)	scattered, low rounded or conical tubercles	present	10–16	37–96×18–31.1.18–31 (see Table 1)	very long	very long	present, with hooks	semi-serial	proximally	long	relatively short

Journal of the Marine Biological Association of the United Kingdom (2000)

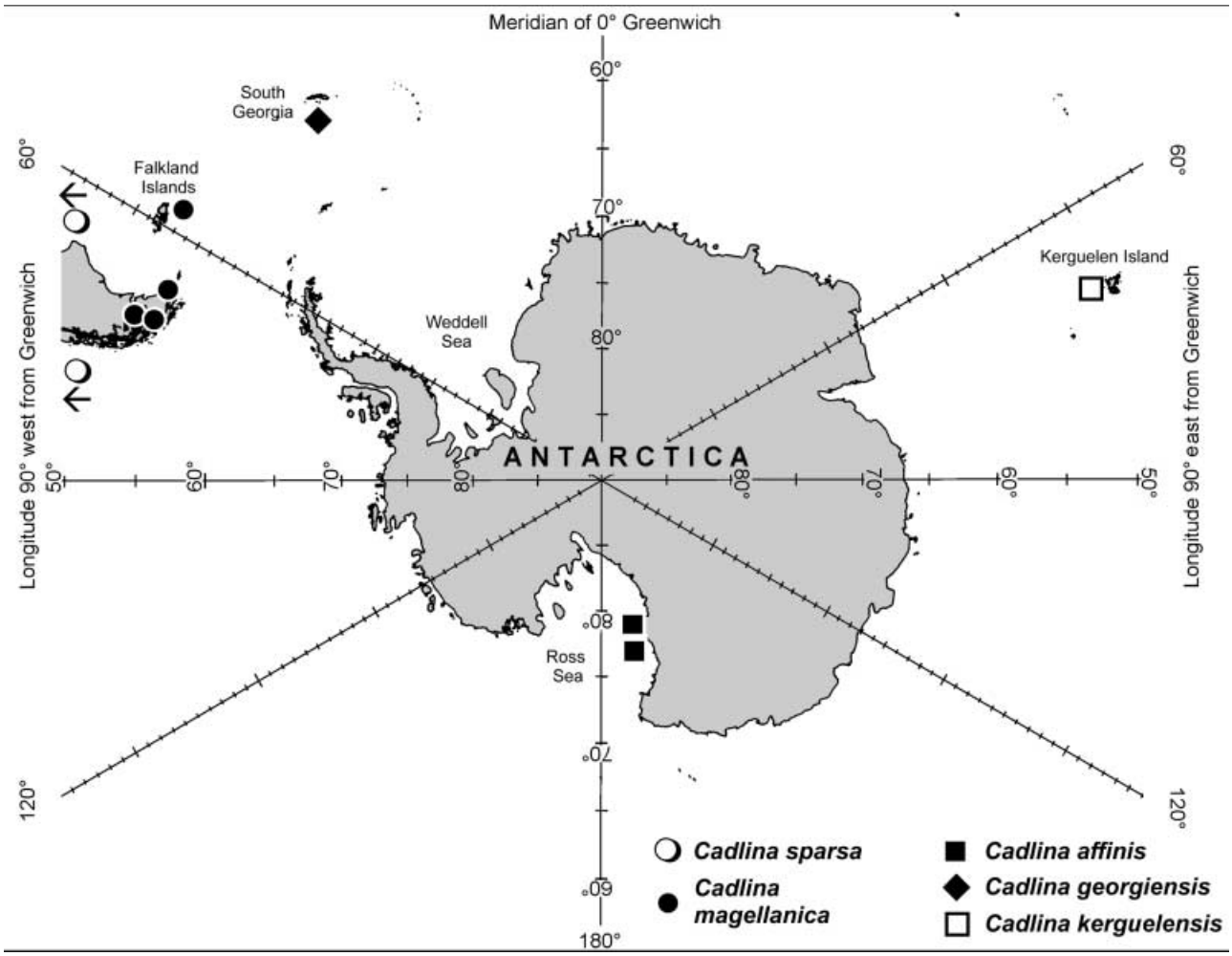

Figure 8. Geographic distribution of *Cadlina* species from the Southern Ocean.

same relative position at the junction of vagina and vaginal duct. While this gland is large in *C. willani* and, due to a short vagina, in a distal position (Miller, 1980), the 'accessory gland' of *C. sparsa* is small and situated proximally at the much longer vagina. Also the tropical, amphiatlantic *C. rumia* Marcus, 1955, was illustrated to possess a vaginal swelling at the insertion of the vaginal duct (Marcus, 1955: figure 87). Further studies are required on this character as well as on the putative accessory nidamental gland of *C. sparsa* which may be homologous to the 'vestibular' glands known from a variety of other Chromodorididae (see Rudman, 1984).

DISCUSSION

Southern cadlinids were traditionally separated mainly by external and radular characters (see Odhner, 1926, 1934; Marcus, 1955). However, specimens had not been described in living condition, and preserved material of all southern species is uniformly whitish with body proportions more or less distorted due to contraction. Also radular features are similar (see Table 3) and the low number of specimens examined has provided sparse information on variability. Therefore, southern cadlinid species were only tentatively identifiable to species level (see Odhner, 1934; Miller, 1980; Schrödl, 1996). Re-examination of the types of Antarctic, subantarctic and Magellanic species in the present study reveals several errors in the original descriptions. Most essentially, *C. affinis* is shown to have a triaulic genital system rather than an aberrant, androdiaulic one described by Odhner (1934). There is, however, a surprising variation in the structure and arrangement of anterior genitalia of southern cadlinids clearly characterizing the different species (Table 3). The high Antarctic *C. affinis* has a vaginal arrangement of allosperm receptacles as defined by Odhner (1926: 51), with the stalks of both the bursa copulatrix and the receptaculum seminis rising from the vagina (Figure 1). In contrast to other cadlinids, in *C. affinis* the vaginal duct joins the vagina in a very distal position. The subantarctic *C. kerguelensis*, endemic to Kerguelen Island, has both receptaculum seminis and vaginal duct directly joining the base of the bursa copulatrix (Figure 2). This condition may be interpreted as a special vaginal arrangement with an extremely reduced stalk of the bursa. *Cadlina georgiensis* sp. nov. has a semi-serial arrangement (see Odhner, 1926: 51) with the vaginal duct branching off the vagina, and the stalk of the receptaculum seminis inserting into the vaginal duct (Figure 5, Table 3). *Cadlina georgiensis* sp. nov. is only known from South Georgia and, according to Wägele (1991) and Schrödl (in press), the single nudibranch species endemic to this island. *Cadlina affinis*,

https://doi.org/10.1017/S0025315499001873 Published online by Cambridge University Press

C. kerguelensis, and *C. georgiensis* sp. nov. all lack cuticular armation in the vas deferens while a hook-bearing cuticle is present in all sexually mature cadlinid specimens from lower latitudes (Table 3). *Cadlina magellanica* is known from the southernmost tip of Patagonia, Tierra del Fuego, and, including its junior synonym *C. falklandica*, from the Falklands (Figure 8). Further collections from the poorly known Chilean fjord region will show if *C. magellanica* is restricted to south-western Atlantic waters and the eastern Magellan Strait as it appears with present knowledge.

The most widespread and puzzling species is *Cadlina sparsa*. Originally reported from the Juan Fernández Islands off central Chile it was later described from the Chilean mainland (Marcus, 1959; Schrödl, 1996) as well as from the north-eastern Pacific (see Behrens, 1991). Like *Rostanga pulchra* MacFarland, 1905, which was also reported from the temperate south- and north-eastern Pacific (Schrödl, 1996), northern and southern populations of *C. sparsa* are not known, to date, to show clear morphological differences (Tables 1 & 2). Thus, bipolarity across the tropics is indicated (see Schrödl, 1997). The present study confirms previous records of *C. sparsa* from the central Argentinian coast (Schrödl, 1996). Also, in absence of significant differences, the present study suggests conspecifity of *C. sparsa* with the Argentinian *C. laevigata* and its synonym *C. berghi*. Since *C. sparsa* has not yet been reported from southern Patagonia, Chilean and Argentinian populations appear to be disjunct with limited gene flow at present. Slight differences in colouration may indicate beginning genetic divergence. In conclusion, there are five valid *Cadlina* species from the Southern Ocean which appear to be strictly allopatric (Figure 8).

Sandra Millen (Vancouver) and Sebastian Gigglinger (Munich) actively helped me in the field. The Department of Oceanography of the Universidad de Concepción, Chile, and my Professors Horst Bohn and Gerhard Haszprunar (Munich) are thanked for generously providing laboratory facilities. Heike Wägele (Bochum) is acknowledged for the use of her taxonomical database (funded by the DFG). David Reid (BMNH), Karin Sindemark and Anders Warén (SMNH), and Matthias Glaubrecht (ZMB) kindly allowed me to re-examine extensive museum material. Many thanks go to Sandra Millen who provided data on *Cadlina magellanica*. Jens Bohn (Munich) helped drawing the map, Teresa Saks (Munich) improved the language. Sandra Millen, Gerhard Haszprunar, and two anonymous referees provided useful comments on the manuscript. This study was supported by grants of the Deutsche Akademische Austauschdienst and of the Bayerische Ministerium für Unterricht und Kultus.

REFERENCES

Behrens, D.W., 1991. *Pacific coast nudibranchs*. Monterey: Sea Challengers.

Bergh, L.S.R., 1894. Die Opisthobranchien. *Bulletin of the Museum of Comparative Zoology*, **25**, 125–235.

Carcelles, A.R. & Williamson, S.I., 1951. Catálogo de los moluscos marinos de la Provincia Magallánica. *Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoológicas*, **2**, 225–383.

García-Gomez, J.C., Medina, A. & Covenas, R., 1991. Study of the anatomy and histology of the mantle dermal formations (MDFs) of *Chromodoris* and *Hypselodoris* (Opisthobranchia: Chromodorididae), *Malacologia*, **32**, 233–240.

Gosliner, T.M., 1987. *Nudibranchs of Southern Africa*. Monterey: Sea Challengers.

Jaeckle, W.B., 1983. Additions to the opisthobranch mollusk fauna of Marin county, California, with notes on the biology of certain species. *Veliger*, **26**, 93–95.

Marcus, E., 1955. Opisthobranchia from Brazil. *Boletim da Faculdade de Filosofia, Ciencias e Letras, Universidade de Sao Paulo, Zoology, 207*, **20**, 89–261.

Marcus, E., 1959. Lamellariacea und Opisthobranchia. Reports of the Lund University Chile Expedition 1948–49, no. 36. *Lunds Universitets Arsskrift N.F.(2)*, **55**, 1–133.

Marcus, E., 1961. Opisthobranch mollusks from California. *Veliger*, **3**, Supplement 185.

McDonald, G.R. & Nybakken, J.W., 1980. *Guide to the nudibranchs of California*. Milbourne, Florida: American Malacologists

Miller, M., 1980. *Cadlina willani*, a new dorid nudibranch (Gastropoda: Opisthobranchia) from New Zealand. *New Zealand Journal of Zoology*, **7**, 165–171.

Odhner, N.H., 1921. Mollusca from Juan Fernández and Easter Island. In *Natural history of Juan Fernández and Easter Island*, vol. 3 (ed. C. Skottsberg), pp. 219–254.

Odhner, N.H., 1926. Die Opisthobranchien. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*, **2**, 1–100.

Odhner, N.H., 1934. The Nudibranchiata. *British Antarctic Terra Nova Expedition, 1910–1913*, **7**, 229–310.

Rudman, W.B., 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society*, **81**, 115–273.

Rudman, W.B., 1985. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris aureomarginata*, *C. verrieri* and *C. fidelis* colour groups. *Zoological Journal of the Linnean Society*, **83**, 241–299.

Rudman, W.B., 1990. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: further species of *Glossodoris*, *Thorunna* and the *Chromodoris aureomarginata* colour group. *Zoological Journal of the Linnean Society*, **100**, 263–326.

Schrödl, M., 1996. Nudibranchia y Sacoglossa de Chile: Morfología exterior y distribución. *Gayana Zoología*, **60**, 17–62.

Schrödl, M., 1997. Range extensions of Magellanic nudibranchs (Opisthobranchia) into the Peruvian faunal province. *Veliger*, **40**, 38–42.

Schrödl, M., in press. Zoogeographic relationships of Magellan Nudibranchia (Mollusca: Opisthobranchia), with special reference to species of adjacent regions. In *Magellan-Antarctic. Ecosystems that drifted apart* (ed. W. E. Arntz and C. Ríos). *Scientia Marina*, **63**, Supplement 1.

Schrödl, M. & Millen, S.V., in press. Revision of the nudibranch gastropod genus *Tyrinna* Bergh, 1898 (Nudibranchia: Doridoidea). *Journal of Natural History*.

Schrödl, M., Wägele, H. & Willan, R.C., in review. Revision of (Mollusca: Opisthobranchia) with discussion of basal nudibranch phylogeny. *Zoologischer Anzeiger*.

Thiele, J., 1912. Die antarktischen Schnecken und Muscheln. In *Deutsche Südpolar-Expedition 1901–1903*, vol. 13 (ed. E. Drygalsky), pp. 183–285, Berlin.

Wägele, H., 1991. The distribution of some endemic Antarctic Nudibranchia. *Journal of Molluscan Studies*, **57**, 337–345.

Submitted 10 May 1999. Accepted 21 September 1999.