



# Occurrence of *Chromadorita regabi* sp. nov. (Nematoda: Adenophorea), a nematode egg predator of *Alvinocaris muricola* (Crustacea: Decapoda: Caridea: Alvinocarididae) from a deep cold seep area of the Gulf of Guinea

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## Abstract

Several individuals belonging to a new species of the genus *Chromadorita* (Nematoda: Adenophorea) were collected in a cold-seep area in the Gulf of Guinea during two French cruises: BIOZAÏRE 2 (2001) and BIOZAÏRE 3 (2003–2004) on board the R/V *L'Atalante*. In this area, rich chemosynthetic benthic communities have been discovered at 3150 m depth in the large pockmark field named Regab. *Chromadorita regabi* sp. nov. was found among the eggs in ovigerous specimens of the shrimp *Alvinocaris muricola*. The combination of long size (1500–2200 µm), nine strong preanal papillae and relatively small dorsal tooth with weak musculature distinguishes this species from all known congeneric ones. An identification key to all known species of *Chromadorita* is provided.

**Keywords:** *Chromadorita regabi*, cold seep, Gulf of Guinea, *Alvinocaris muricola*

## Introduction

Nematodes are the most numerous multicellular animals on Earth (Heip et al. 1985) and they are also among the most abundant marine and deep-sea taxa (Lambshhead et al. 2003). They usually comprise 70–90% of the meiobenthos from bottom sediments (Mokievsky et al. 2007). According to Appeltans et al. (2012) there are 11,900 known free-living nematode species (12% of the total 61,400 species estimated); at present, the nematodes represent 6900 of the 11,900.

Deep-sea bottoms comprise about 91% of the seabed, but the known nematode species have been described from within a bottom area of less than 100 m<sup>2</sup>. Accordingly, deep-sea nematode diversity, ecology and distribution are greatly understudied (Miljutin et al. 2010), especially for nematodes associated with chemosynthetic environments (i.e. seeps and vents) (Vanreusel et al. 2010; Tchesunov 2015).

Chemosynthetic environments, such as hydrothermal vents and cold seeps, differ from adjacent deep-sea areas

in terms of physical (e.g. high temperature), chemical (e.g. high sulphide concentration, low oxygen levels) and biological conditions (Van Gaever et al. 2009; Bezerra et al. 2013). Their primary metabolic energy derives from chemical processes instead of depending on settling phytodetrital matter from the euphotic zone (Van Dover et al. 2002). Since they were discovered in 1977 (Dinet et al. 1988), many studies have been conducted on their microbioma (Boetius & Suess 2004; Orcutt et al. 2008) and macro- and megafauna (Segonzac 1992; Tyler et al. 2003; Desbruyères et al. 2006; Sarrazin et al. 2015), but much less work has been done on the smaller (< 1 mm) benthic component, the meiofauna (Vanreusel et al. 2010; Sandulli et al. 2015; Tchesunov 2015).

Chemosynthetic habitats are inhabited by typical meiofauna characterised by a low density and diversity (Van Gaever et al. 2006; Vanreusel et al. 2009; Gollner et al. 2010). In chemosynthetic habitats nematodes are usually the dominant taxon, followed

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by copepods in vents and foraminiferans in cold seeps (Zeppilli et al. 2017). In the Atlantic, vent meiofauna represents up to 50% of the total faunal diversity and it is characterised by generalist nematodes and endemic copepods (Sarrazin et al. 2015). Studies carried out along the East Pacific Rise (e.g. Zekely et al. 2006; Copley et al. 2007; Gollner et al. 2010) reported low diversity values for nematodes inhabiting vent areas, and a dominance of single species or a few species belonging to the well-known genera *Thalassomonhystera*, *Geomonhystera*, *Anticoma* and *Chromadorita*. At deep-sea seeps worldwide, meiofauna biodiversity, and particularly that of nematodes, is reduced (Levin 2005; Van Gaever et al. 2009; Lampadariou et al. 2013). A single nematode species of *Halomonhystera* dominated sediments around a mud volcano area in the Arctic Ocean (Van Gaever et al. 2006), whereas seep sediments in the Gulf of Guinea were dominated by only two species of nematodes: *Sabatiera mortensenii* and *Desmodora* sp. (Van Gaever et al. 2009). Conversely, in the Mediterranean Sea seep areas, a high nematode diversity without dominance of any genera was reported (Zeppilli et al. 2011, 2012).

Apparently, nematodes of deep-sea vents and seeps have not developed any obvious adaptations, but they must tolerate sulphidic or anoxic conditions (Vanreusel et al. 2010; Bezerra et al. 2013). For instance, the species *Oncholaimus campyloceroides*, inhabiting vents, can produce sulphur droplets, whereas other species of the genus *Oncholaimus* show epibiotic association with microorganisms, and members of the genus were found in high concentrations around the most active sites at the deep-sea Lucky Strike hydrothermal vent (Mid-Atlantic Ridge, MAR) (Tchesunov 2015; Zeppilli et al. 2017). Nematodes of the genus *Halomonhystera* are found to be ovoviviparous, and this method of reproduction has been considered an adaptation to thrive in these extreme environments (Van Gaever et al. 2006; Zeppilli et al. 2015). Nematodes living in seep habitats seem to have developed special physical characteristics, including a longer and thinner body shape, which are favourable for life in thiobiotic conditions (Bezerra et al. 2013; Lampadariou et al. 2013). Increased body length is considered an adaptation to sulphidic conditions in that nematodes can easily cover the distance between anoxic, sulphidic and oxic, sulphide-free sediments (Soetaert et al. 2002; Schratzberger et al. 2004), whilst the expansion of the body surface facilitates the access to oxygen for respiration (Jensen 1987). Bezerra et al. (2013) recently described a new genus with two new species, from low-activity seep areas, belonging to the family Ethmolaimidae (superfamily Chromadoroidea).

Members of this family are regularly found in association with chemosynthetic ecosystems and in the thio-bios; they can inhabit deep sediment layers with low oxygen and high sulphide concentrations (Shirayama & Ohta 1990; Zeppilli & Danovaro 2009).

Contrary to many macro-invertebrates from deep seeps (Dubilier et al. 2008), hitherto no known nematode species show evidence of symbionts. Nematodes with endo- and ectosymbiotic chemosynthetic bacteria do exist, but are mainly restricted to shallow waters (Dubilier et al. 2008; Vanreusel et al. 2010), while most seep and vent nematodes are classified as deposit feeders, based on their small buccal cavity and absence of teeth, except for chromadorids and desmodorids with teeth in their buccal cavity (Dinet et al. 1988; Vanreusel et al. 2010). Actually, predators have so far never been found to be abundant in deep-sea seeps or vents, although they are a common part of the nematode community in many other ecosystems, including shallow-water vents, such as the *Oncholaimus* species in Mediterranean shallow vents (Vanreusel et al. 2010). Despite the fact that there is no clear evidence of endosymbionts in seep nematodes, it is possible that they could benefit from free-living chemoautotrophic bacteria as a food source (Van Gaever et al. 2009).

Non-parasitic associations between nematodes and aquatic multicellular animals have been known since 1834, when the marine non-parasitic nematode *Odontobius ceti* (De Vauzème, 1834) was found on baleen plates (De Vauzème 1834), while associations with unicellular organisms (e.g. suctorian ciliates) have been seldom reported (Fernandez-Leborans et al. 2017).

At the beginning of the 20<sup>th</sup> century, descriptions of associations of different kinds (e.g. epibiosis, parasitism, commensalism) between meiobenthic organisms (i.e. nematodes and copepods) and larger invertebrates became evident from the literature (Petter 1987).

Dinet and co-authors (1988) investigated the meiofauna inhabiting the hydrothermal vents of the East Pacific Rise and Explore Ridge and reported the presence of meiobenthic copepods associated with macro- and megabenthic organisms (e.g. Vestimentifera; Humes & Dojiri 1980). The nature of this association could be parasitic or commensal.

Some nematode species, known to be free-living species, were reported as parasites of shrimps and fishes (Overstreet 1973; Justin et al. 2002). The genus *Leptolaimus*, for instance, has been recognised as a facultatively commensal nematode in the gills of both brown and white penaeid shrimp from ponds. It is not clear how shrimps acquire the nematodes or how long the roundworms remain in their hosts.

Monhysterid nematodes have been identified as typically commensalistic and most often occur within

the mouthparts and gills of marine and freshwater Crustacea, and in the American oyster *Crassostrea virginica* (Meyers et al. 1985; Holovachov et al. 2011). Lorenzen (1986a) reported the presence of the free-living nematode *Odonobius ceti* (Monhysteridae) from the baleen plates of whales.

Within the family Chromadoridae, *Chromadorida majae* was found in the gill-chamber and amongst the eggs of the decapod *Maja squinado* inhabiting the Mediterranean Sea (Wieser 1968). Lorenzen (1986b) reported the presence of *Chromadorida ceratoserolis* amongst eggs in the marsupium of the marine benthic isopod *Ceratoserolis trilobitoides* from Antarctic waters at depths ranging from 233 to 728 m. In total, 15 species of adenophorean nematodes are known to live epibiotically on marine, freshwater and terrestrial crustaceans all belonging to the Peracarida or Decapoda (Lorenzen 1986b). In a recent work, Holovachov and co-authors (2011) described a new species of non-parasitic Chromadoridae living epibiotically associated with the deep-sea gastropod *Skenea profunda* (North East Atlantic, 2830 m depth). Similarly, *Chromadorina bioculata* and *C. leuckarti* were found associated with zebra mussel (attached to the mantle; Karatayev et al. 2003; Mastitsky et al. 2008).

The present paper describes a new species of the genus *Chromadorita* (Nematoda, Adenophorea) occurring among the eggs of the alvinocaridid ovigerous shrimp *Alvinocaris muricola* (Williams 1988), collected in a cold-seep area in the Gulf of Guinea. In this area, rich chemosynthetic communities have been discovered at a depth of 3150 m in a large pockmark field (Olu et al. 2009). This active area, named Regab, is characterised by high methane concentrations supporting a massive bacterial production (Andersen et al. 2004). The Regab site, where *A. muricola* has been observed forming high-density populations (Ramirez-Llodra & Segonzac 2006), is characterised by a community dominated by bivalves including large mytilids such as *Bathymodiolus* aff. *boomerang*, vesicomid clams *Laubiericoncha chumi* and *Christineconcha regab*, and vestimentiferans, such as *Escarpia southwardae* (Olu-Le Roy et al. 2007; Marcon et al. 2014 and references therein). The shrimps live as epibionts over the mussel or the clam beds, or among the vestimentiferans, or even over the sediment (Komai & Segonzac 2005). *Alvinocaris muricola* (Carida, Alvinocarididae) is one of the eight shrimp species described to date from chemosynthetic communities associated with hydrothermal vents, brine or cold seeps (Komai & Segonzac 2005), and it is a scavenger on the mussel bed fauna (Ramirez-Llodra & Segonzac 2006).

The meiofaunal abundance within the Regab seep varied between 20 ind. 10 cm<sup>-2</sup> and 873 ind. 10 cm<sup>-2</sup>

(Van Gaever et al. 2009). The meiobenthos was characterised by small-scale (i.e. metres) patchiness, low species richness and the dominance of *Desmodora* sp. and *Sabatieria mortenseni*, a cosmopolitan nematode indicator of anoxic to suboxic sediments. The large size, high individual body weight and dominance of these species at the cold-seep site resulted in a significantly higher nematode biomass compared to the surrounding sites (Sibuet & Vangriesheim 2009; Van Gaever et al. 2009). The increased nematode biomass and subsurface distribution maxima suggest that meiobenthic community at Regab is based on chemosynthesis.

## Materials and methods

Nematode samples studied here – from nine non-gravid females, three gravid females and six males, for a total of 18 nematodes – were extracted from the eggs of several ovigerous female *Alvinocaris muricola* shrimps found in a cold-seep area (Regab), Gulf of Guinea, west equatorial African margin, off Angola, at 3150 m depth, 8 km north of the Congo channel (Figure 1). Sampling activities were conducted during two French cruises: BIOZAÏRE 2 (November–December 2001; Sibuet 2001) and BIOZAÏRE 3 (December 2003–January 2004; Khrpounoff 2003) on board the French R/V *L'Atalante*, by means of a slurp gun (suction apparatus) mounted on the ROV *Victor 6000*, and through beam trawling.

In this cold-seep area of 800 m in diameter, a 15–20 m deep pockmark is formed by the association of several individual pockmarks, resulting in a large area characterised by seepages of methane, gas hydrates and carbonate crusts, and covered with a dense chemosynthetic community (Van Gaever et al. 2009). Faunal assemblages are patchily distributed, dominated either by the bivalves *Bathymodiolus* aff. *boomerang* and *Calyptogena* sp., or by siboglinid tube-worms *Escarpia southwardae* (Andersen et al. 2004; Marcon et al. 2014).

Specimens of the decapod *Alvinocaris muricola*, collected by a slurp gun (BIOZAÏRE 2, PL 146–09, slurp gun 1, Regab site, 05°47.80'S, 09°42.60'E, –3151 m) and by a beam trawl (BIOZAÏRE 3, beam trawl CP 20, 4 km south-west of Regab site, 05°46.89'S, 09°44.66'W, –3113 m) were fixed on board in formalin and preserved in ethanol. From the broods of three ovigerous *A. muricola* females (BIOZAÏRE 2) a total of 15 nematodes were extracted, while three more nematodes, one of which was found with the anterior part in an egg, were extracted from one ovigerous females (BIOZAÏRE 3).

Nematodes were mounted on glass slides and identified with a Leica DLMS compound

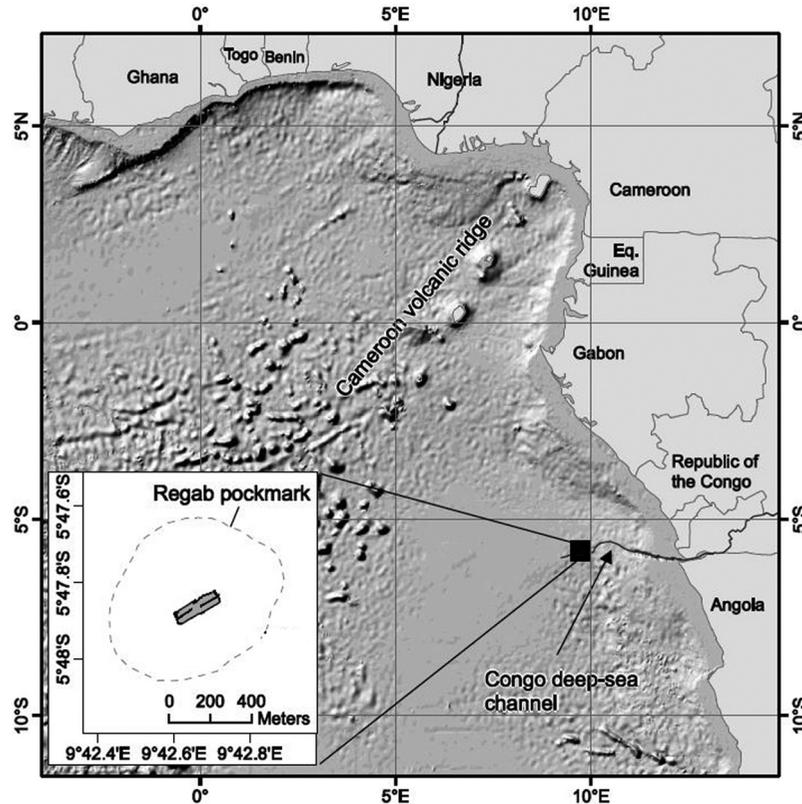


Figure 1. Location of the Regab pockmark along the Congo–Angola margin and the approximate outline of the pockmark (insert map left corner; grey rectangle represents the area explored by ROV *Victor 6000*). Modified from Marcon et al. (2014).

microscope (1000× magnification), using a pictorial key to nematode genera (Warwick et al. 1998) and the NeMys database (<http://www.marinespecies.org>). Species description was made from glycerol slides using interferential contrast microscopy, and drawings were made with a camera lucida. Images of the specimens were taken with an Axio Apotome-digital camera and processed with ZEN imaging software. All measurements are in  $\mu\text{m}$  and all curved structures were measured along the arc. Slides with the type specimens of the new species are deposited in the collection of the Muséum national d'Histoire naturelle, Paris (MNHN).

Abbreviations used:

a, b, c	ratios of de Man (1880);
a	body length divided by maximum body diameter;
b	body length divided by pharyngeal length;
c	body length divided by tail length;
V%	ratio [distance from anterior end to vulva]/body length, in %;
cbd	corresponding body diameter;
mbd	maximum body diameter;

L	length;
W	width;
H	height;
Supplements	preanal papillae.

## Systematics

Phylum Nematoda

Class Adenophorea

Subclass Chromadoria Pearse, 1942

Order Chromadorida Chitwood, 1933

Suborder Chromadorina Filipjev, 1929

Superfamily Chromadoroidea Filipjev, 1917

Family Chromadoridae Filipjev, 1917

Subfamily Hypodontolaimina de Coninck, 1965

Genus *Chromadorita* Filipjev, 1922

*Chromadorita regabi* sp. nov.

(Figures 2–5)

*Type species.* *Chromadorita demaniana* Filipjev, 1922. The genus *Chromadorita* presents a homogeneous cuticle ornamentation. A slightly more pronounced punctuation may be present at the level of the

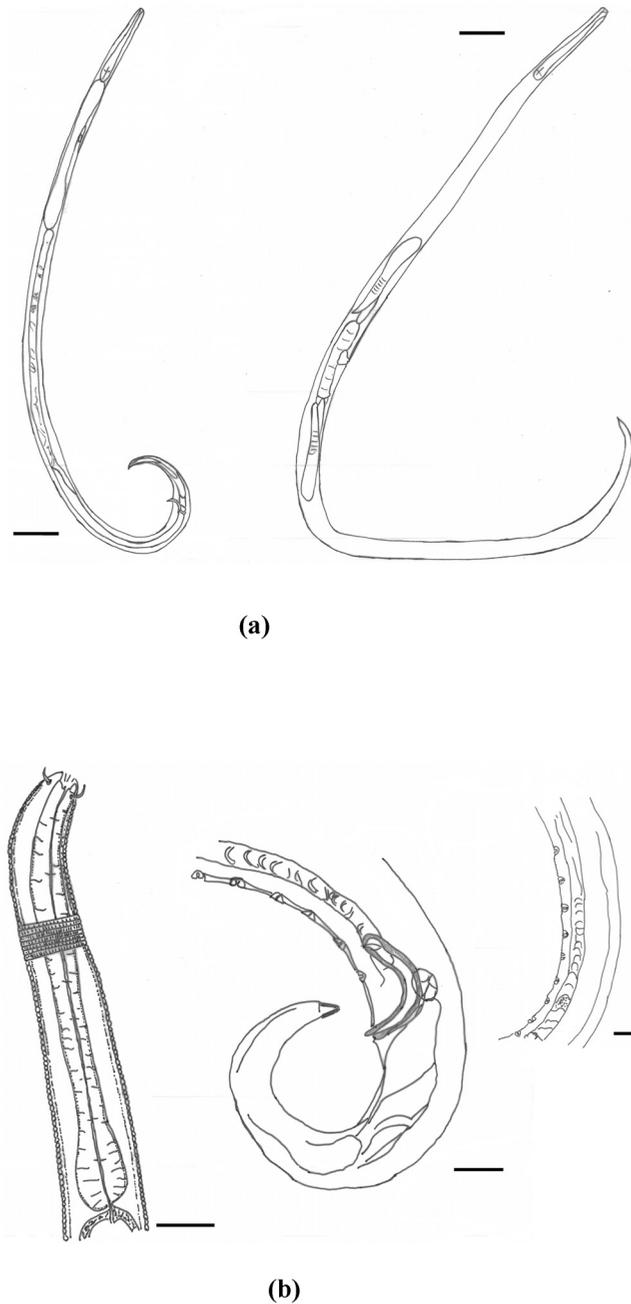


Figure 2. (a) *Chromadorita regabi* sp. nov. Drawings of the male (left) habitus and female (right) habitus. (b) *Chromadorita regabi* sp. nov. Drawings of the male anterior part (left), the copulatory apparatus (centre) and the nine preanal supplements (right). Scale bars: A = 100  $\mu$ m; B = 100  $\mu$ m, 20  $\mu$ m and 10  $\mu$ m (from left to right).

lateral field. One dorsal hollow tooth and one or two ventrosublateral teeth present; rarely one indistinct dorsal tooth only. Tiny denticles may be also present. Pharynx may be swollen anteriorly; single posterior bulb. Precloacal supplements may be present or absent.

*Type material.* Collection number MNHN-BN507 (PL 146-09): three males – one as holotype, formalin fixed, mounted on slide in glycerin and collected from the eggs of ovigerous female shrimps *Alvinocaris muricola* collected at Regab cold seep (Gulf of Guinea, west equatorial African margin).

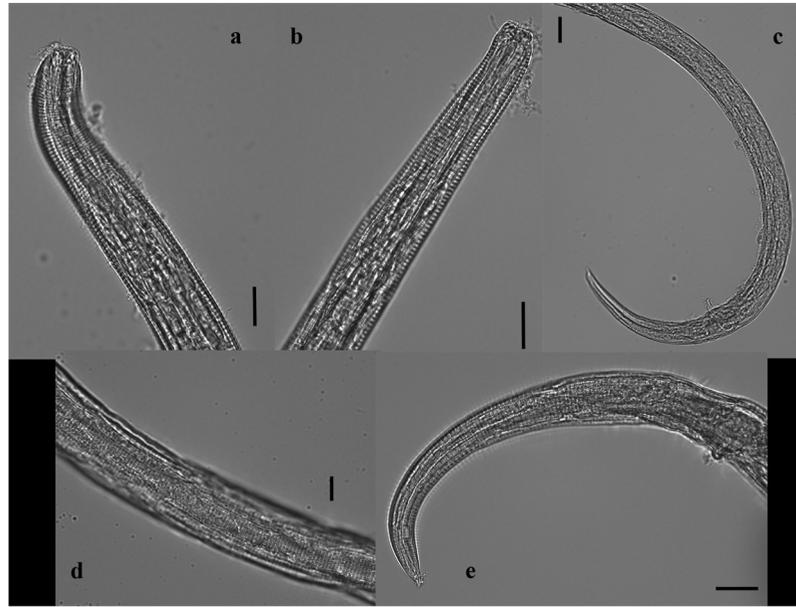


Figure 3. *Chromadorita regabi* sp. nov. Light micrographs of (a) male head; (b) female head; (c) posterior region of male; (d) cuticular ornamentation in the middle of the body region of the male; and (e) posterior region of female. Scale bars: 100 µm.

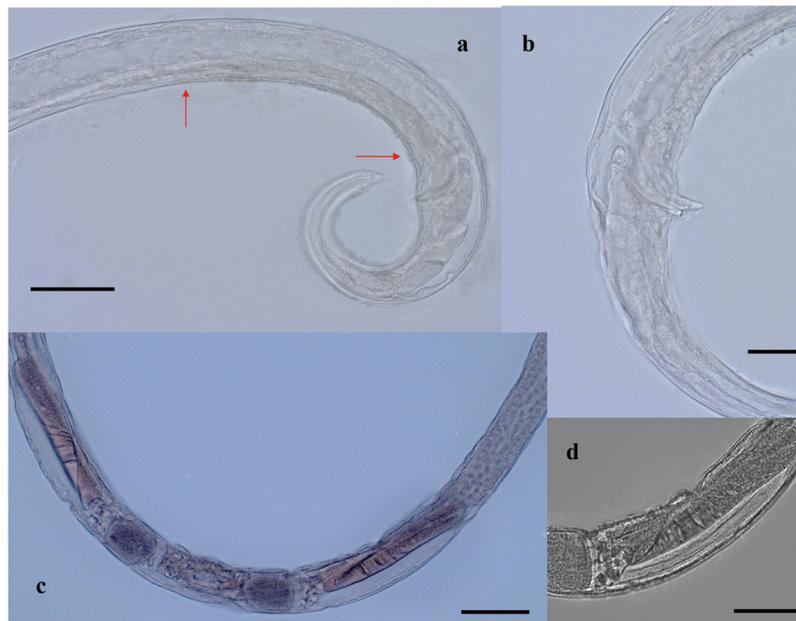


Figure 4. *Chromadorita regabi* sp. nov. Light micrographs of (a) the nine cup-shaped preanal papillae from the male (red arrows indicating the 1<sup>st</sup> and the 9<sup>th</sup> papillae); (b) spicule and apophysis; (c) reflexed ovaries, vulva and eggs from the female; and (d) detail of the ovary. Scale bars: A, C, D = 100 µm; B = 50 µm.

Two males – paratypes; two gravid females – paratypes; five non-gravid females – paratypes. Collection number MNHN-BN508 (PL 147–10): one gravid female – paratype; collection number MNHN-BN509 (Bioz 2): two males – paratypes; one gravid female – paratype; two non-gravid females – paratypes. Collection number MNHN-

BN510 (Bioz 3): one non-gravid female – paratype; one male – paratype. The paratypes are from the same site as the holotype, from different eggs of ovigerous female shrimps *Alvinocaris muricola*.

*Etymology.* The species name refers to the locality of collection, Regab cold seep.

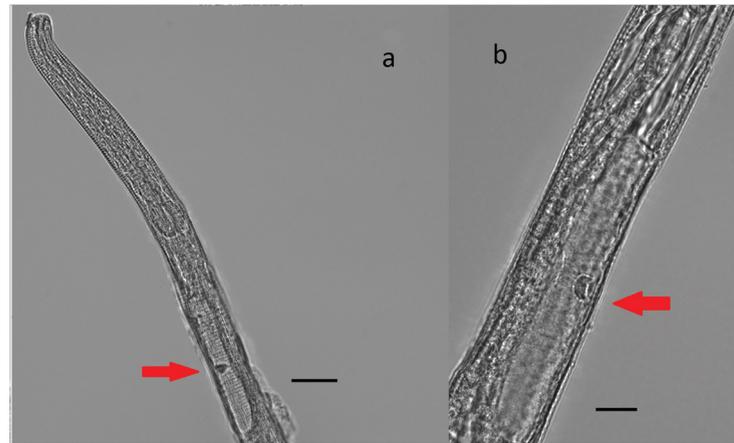


Figure 5. *Chromadorita regabi* sp. nov. Light micrographs of the female. (a) Anterior region showing pharynx with posterior bulbus and ventral gland (red arrow). (b) Detail of the ventral gland (red arrow) behind the pharynx, on the ventral side of the gut. Scale bars: A = 20 µm; B = 50 µm.

Table I. Morphometrics of *Chromadorita regabi* sp. nov. Data presented as minimum–maximum values. All measurements in µm. HT: holotype; -: non-gravid females; +: gravid females.

Character	HT ♂	5 ♂♂	9 ♀♀ (-)	3 ♀♀ (+)
Total body length	1822	1510–2170	1140–2300	2120–2370
A	49.2	41.9–54.3	30.4–44.4	42.4–49.9
B	9.8	10.2–14.0	6.9–12.3	10.6–11.8
C	9.3	11.3–15.2	6.7–10.2	8.5–10.3
Head diameter	14	10–25	13–20	15–20
Length of cephalic setae	8	8	8–10	5–10
Buccal cavity (L)	7	7–9	7–8	6–7
Buccal cavity (W)	5	3–7	3–6	3–4
Oesophagus (L)	185	138–193	138–235	200–210
Bulb (L)		35–44	20–40	38–45
Oesophagus corresponding body diameter	36	34–43	21–52	46
Maximum body diameter	37	35–45	25–55	48–50
Vulva distance from anterior	–	–	489–1100	900–1000
V%	–	–	43–52	38–47
Gonad (L)	375	250–575	150–350	210–220
Spicule (L)	62	39–53	–	–
Supplements (W)	5	3–6	–	–
Supplements (H)	3	2–3	–	–
Supplements – distance from anus	24	25–38	–	–
Supplements – distance between them	12	13–17	–	–
Tail (L)	195	118–180	170–280	225–250

*Measurements.* See Table I.

#### *Taxonomic accounts.*

*Male.* Long nematode, 1822 µm in length, and 37 µm in width. Cuticle homogeneous over total body length, with transverse rows of rod-like punctuations. No lateral differentiations. No somatic setae. Head tapering towards anterior end. Four 8 µm long cephalic setae. No amphid visible. Small buccal cavity with one dorsal hollow tooth and two smaller subventral teeth. Pharynx with posterior bulbus. No strong musculature around

dorsal tooth. Ventral gland reaching behind the pharynx, on the ventral side of the gut. One testis present, at the right side of the gut. Two spicules, 62 µm long, strongly curved and cuticularised. Simple needle-like apophysis. Nine strong cup-shaped preanal papillae present, first one at 24 µm from anus, others separated from each other by 9 to 12 µm. Each papilla measures 5 µm at its base and is 3 µm high.

*Female.* Body length can exceed that of the male (maximum body length 2370 µm). Two reflexed

ovaries; the anterior one right and the posterior one left of the gut. Vulva about 8 µm long and weakly cuticularised.

This species is assigned to the genus *Chromadorita* because of the homogeneous cuticle, without lateral differentiation, and the larger hollow dorsal tooth. All other species belonging to this genus and described so far are smaller in size or have a different number of preanal papillae. Only *C. ceratoserolis* described from the marsupium of the Antarctic isopod *Ceratoserolis trilobitoides* is larger in total body length than the newly described species. All other *Chromadorita* species are much smaller. *Chromadorita leuckartii*, *C. mucrodonta* and *C. tenuis* exceed 1000 µm in body length (to a maximum 1460 µm for *C. tenuis*) but they all have a different number of preanal papillae. The combination of its long size, the presence of nine strong preanal papillae, and the relatively small dorsal tooth with weak musculature helps distinguish this species from all the others.

*C. hyalocephala* presents between eight and 10 preanal papillae; *C. brachypharynx* and *schuurmanstekhoveni* are characterised by the presence of nine preanal papillae. Nevertheless, all these genera are < 1100 µm in body length and the preanal papillae are small.

### Conclusive remarks

Several “external” nematodes (so-called epibionts) have been reported on crustaceans. These nematodes can be considered free-living epibionts with limited impact on host survival (Longshaw 2011). Lorenzen (1986b) gives an overview of nematode species found in association with crustaceans. These epibionts are mainly associated with gill chambers of Decapoda. He refers to 10 different species of different taxonomic origin, belonging to the families Chromadoridae, Monhysteridae and Leptolaimidae. Some species (four) are associated with Amphipoda, Isopoda and even Mysidacea, but the association is only specified in one case.

The species *Chromadorita ceratoserolis* was found between eggs, specifically in the marsupium of the isopod *Ceratoserolis trilobitoides* (Lorenzen 1986b). This species not only exhibits the same kind of association with a crustacean as *C. regabi* sp. nov., but also represents the most closely related species, belonging to the same genus. Two other Chromadoridae species, *Chromadorina astacicola* and *Chromadorina maja* respectively, were found in the gill chambers of decapods, although *C. maja* has also been recorded from the marsupium (Lorenzen 1986b). The free-living nematode *Chromadorina bioculata* was reported in high

abundances as an endosymbiont of zebra mussel from fresh waters (Karatayev et al. 2003; Mastitsky et al. 2008). Nevertheless, this association appeared to be non-obligate for the nematode and it was suggested that *C. bioculata* uses the bivalve as shelter and for food (Karatayev et al. 2003). Holovachov et al. (2011) reported a similar association between the free-living nematode *Endeolophos skeneae* (Chromadoridae) and the deep-sea gastropod *Skenea profunda*. As for *C. bioculata*, the authors suggested that *E. skeneae* finds food and shelter from the gastropod, but this association remains a non-obligate one for the nematode.

Apart from studies mentioned above, the most common and documented associations of commensalism between free-living nematodes and aquatic and semi-aquatic multicellular animals involved the marine Monhysterida. Amongst studies conducted in chemosynthetic environments all over the world (e.g. Van Gaever et al. 2009; Hauquier et al. 2011; Pape et al. 2011; Setoguchi et al. 2014; Tchesunov 2015), the presence of chromadorids has been rarely or not reported. Instead, monhysterids are found to be deep-sea generalists known to dominate extreme environments such as hydrothermal vents and seeps, and *Halomonhystera* is a cosmopolitan genus that has been recovered from various marine sediments, including sulphidic sediments (Hauquier et al. 2011).

In a very few studies, one conducted along vents in the East Pacific Rise (Copley et al. 2007), one in a deep-sea cold seep in Japan (Shirayama & Ohta 1990) and one in a North Sea pockmark area (Dando et al. 1991), specimens of the genus *Chromadorita* were reported to be quite abundant (as the second or third most abundant group) in the sediments. Zekely et al. (2006) reported the presence of two different, but not identified, species of *Chromadorita* from MAR and East Pacific Rise vent areas.

Considering other epibiotic worms on crustaceans, nemertean worms were reported as obligate symbionts on decapod crustaceans, needing a host during almost their whole life cycle (Kuris & Wickham 1987). Similarly, Shields and Segonzac (2007) reported symbiotic nemertean worms infesting several species of crabs from deep-sea hydrothermal vents in the Pacific Ocean. Juveniles and regressed adults of nemerteans were exclusively reported, leading to the hypothesis that these worms can develop only by eating eggs of their hosts (Shields & Segonzac 2007). A new species of Polychaeta from shallow waters of Indo-West Pacific, *Polydora robi*, was found by Williams (2000) to be an active predator of host hermit crab embryos and newly fertilised eggs, and to cause negative effects on the hosts (Williams 2001, 2002).

The fact that no juveniles of *C. regabi* were reported from our samples leads us to suppose that the relationship between *C. regabi* and its host is not obligate for the developing of the nematode.

Lorenzen (1986b) maintained that no information was available on the food source of *C. ceratoserolis*. During sample collection, one specimen of *C. regabi* was found with the anterior part of its body inside an embryo of a female *A. muricola*, suggesting a predatory action (see also Komai & Segonzac 2005; Ramirez-Llodra & Segonzac 2006). The authors hypothesise that the presence of dark embryos, showing disrupted development compared to normal embryos, was due to the presence of the nematodes. The ability of *C. regabi* to pierce and suck the egg content is in agreement with the feeding behaviour of chromadorids in which they pierce and suck out the contents of hard-shelled cells (Vanreusel et al. 2010).

Kuris and Wickham (1987) conducted a study on the nemertean predation effect on crustacean eggs. The authors showed that nemerteans punctured the egg's membrane, sucking the contents out and causing high egg mortality at different stages of development for several commercial crustacean species. Nematodes, together with flatworms, protozoans and some small polychaetes, were found in old polychaete egg masses (up to 10 days after deposition; Martin et al. 2000) feeding on the fertilised eggs. We hypothesise that *C. regabi* may predate on the shrimp eggs during its life cycle as free-living nematode. The eggs of *A. muricola* may represent one of the food sources "easily" accessible for the nematodes due to the high density of the shrimp at Regab site (Ramirez-Llodra & Segonzac 2006). We should also consider that the large caloric content of eggs and embryos indicates that the benefit of this predation is considerable for the nematode. However, a possible negative effect exerted by the nematode on the fecundity of the shrimp may be hypothesised, as previously documented for other epibiotic worms on crustacean eggs (Kuris & Wickham 1987; Williams 2001, 2002), but further studies are needed to address this issue.

#### Identification key to all known species of *Chromadorita*

The present identification key is based on 30 valid species found in the literature including the present new species *C. regabi*. The two species *C. arctica* and *C. inornata*, although reported as valid species (<http://www.marinespecies.org>), are not included in this key since their original description is not documented.

1 Body length 350–1500 µm .....	4
2 Body length 1500–2200 µm .....	5
3 Body length > 2200 µm .....	<i>C. ceratoserolis</i>
4.1 Dorsal tooth absent (only ventral teeth) .....	6
4.2 Small dorsal tooth (weak musculature) .....	7
4.3 Large hollow dorsal tooth .....	8
4.4 Large S-shaped dorsal tooth .....	9
5.1 Small dorsal tooth .....	<b><i>C. regabi</i> sp. nov.</b>
5.2 Large S-shaped dorsal tooth .....	<i>C. deseadensis</i>
6.1 Cuticle homogeneous with transverse rows of punctuations... ..	<i>C. mucrodonta</i>
6.2 Annulations with dots .....	10
7.1 Cuticle with dots that become jointed rods ..	11
7.2 Annulations with dots .....	12
8.1 Cuticle homogeneous with transverse rows of punctuations .....	13
8.2 Annulations with dots .....	14
8.3 Cuticle with dots that become jointed rods ..	15
8.4 Lateral dots finer than dots in the middle of the body .....	16
9.1 Cuticle homogeneous with transverse rows of punctuations .....	17
9.2 Annulations with dots .....	<i>C. tentabundum</i>
10.1 Preanal papillae N = 10 .....	<i>C. hyalocephala</i>
10.2* Preanal papillae absent .....	<i>C. heterophya</i> *
11.1 Preanal papillae absent .....	18
12.1 Preanal papillae N = 8 .....	<i>C. leuckarti</i>
12.2 Preanal papillae absent .....	<i>C. demaniana</i>
12.2* Preanal papillae absent .....	<i>C. leptopharynx</i> *
13.1 Preanal papillae N = 7–8 .....	<i>C. pachydema</i>
13.2 Preanal papillae absent .....	19
13.3 Preanal papillae N = 2 .....	<i>C. dimeris</i>
13.4 Preanal papillae N = 5 .....	<i>C. pentameris</i>
14.1 Preanal papillae absent .....	20
14.1* Preanal papillae absent .....	<i>C. paetzoldi</i> *
14.2 Preanal papillae N = 9 .....	<i>C. brachypharynx</i>
14.3 Preanal papillae N = 7 .....	<i>C. fennica</i>
15.1 Preanal papillae N = 1–5 .....	<i>C. abnormis</i>
15.2 Preanal papillae N = 9 ..	<i>C. schuurmanstekhoveni</i>
16.1 Preanal papillae N = 8 .....	<i>C. guidoschneideri</i>
16.2 Preanal papillae N = 10–13 .....	<i>C. tenuis</i>
17.1 Preanal papillae absent .....	21
18.1 Amphid absent .....	<i>C. brevisetosa</i>
18.2 Amphid large, kidney shaped. <i>C. nephramphidia</i>	
19.1 Amphid slit-like and making a spiral <i>C. abissalys</i>	
19.2 Amphid large (60% of the head diameter) and oval .....	<i>C. mucrocaudata</i>

- 19.3 Amphid small and oval ..... *C. nana*  
 19.4 Amphid reduced ..... *C. macrodonta*  
 20.1 Amphid absent ..... *C. minima*  
 20.2 Amphid kidney shaped ..... *C. pallida*  
 21.1 Amphid loop shaped ..... 22  
 21.2 Amphid slit-like ..... *C. obliqua*  
 22.1 Three large glands at the tail level ..... *C. minor*  
 22.2 Presence of ventromedial papillae, arrowhead shaped ..... *C. pharetra*

\* Original descriptions based only on females.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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