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Description of two new species of *Desmoscolex* Claparède, 1863 (Nematoda: Desmoscolecidae) from the Cassidaigne Canyon, Mediterranean Sea

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Abstract. Two new species of *Desmoscolex* (*Desmoscolex*) Claparède, 1863 from Cassidaigne Canyon (deep-sea Mediterranean), namely *Desmoscolex* (*Desmoscolex*) *nibelungus* sp. nov. and *Desmoscolex* (*Desmoscolex*) *valkyria* sp. nov. are described. *Desmoscolex* (*D.*) *nibelungus* has 17 main rings and the typical desmoscolecoid setal pattern. The most evident features to distinguish it from the rest of *D.* (*Desmoscolex*) with these characteristics are the protuding lip region not covered with concretion material, the cephalic region that apparently lacks setae and the beak-shaped posterior-most main ring. On the other hand, *D.* (*D.*) *valkyria* belongs to a group of nematodes with more than 18 main rings. This new species is mainly characterized by the number of rings (22–24), the vesicular amphideal fovea, a pair of subdorsal and a pair of subventral setae both on the penultimate main ring and a long spinneret of the terminal main ring. This is the first meiofauna species described from the Cassidaigne Canyon. With the description of these two new species of nematode, the number of described species of *Desmoscolex* (*Desmoscolex*) is now 106, with 47 species occurring in deep-sea environments and 10 species described from the Mediterranean Sea.

Keywords. Desmoscolecida, Nematoda, Cassidaigne Canyon, deep-sea.

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Introduction

The genus *Desmoscolex* Claparède, 1863 is one of the groups of nematodes best known by meiobenthologists because of their aberrant external appearance. The adult specimens belonging to this genus are characterized by a short and stout body shape, with a cuticle typically covered by foreign material that forms concretion rings called “desmen” (“*desmos*” in singular). These desmen are separated by interzones without concretion material. Some subgenera lack desmen or possess transverse rows of spines or pores (Decraemer & Rho 2014). Diagnostic characters that distinguish *Desmoscolex* from other desmoscolecid genera are the presence of paired subdorsal and subventral setae, a short pharynx and the common presence of ocelli or pigment spots in the anterior region of the body (Decraemer & Rho 2014).

Desmoscolex currently comprises 128 species (115 marine species, 3 marine/brackish species, 6 freshwater species, 3 terrestrial species and 1 freshwater/terrestrial species) classified in four subgenera: *Desmoscolex* (*Desmoscolex*) Claparède, 1863 comprises 106 species – included the two new species described in the present paper; *Desmoscolex* (*Desmolorenzenia*) Claparède, 1863 comprises 15 species; *Desmoscolex* (*Pareudesmoscolex*) Wiescher, 1962 comprises 4 species; and *Desmoscolex* (*Protricomoides*) Timm, 1970 comprises 3 species (Table 1).

The subgenus *Desmoscolex* (*Desmoscolex*) Claparède, 1863, which includes 94 marine species, is distinguished from other subgenera within *Desmoscolex* by the presence of main rings covered by concretion material along its entire body in the adult stage. These rings can be either rounded or quadricomoid in shape. In the latter case, the main rings on the front part of the body slope backward, extending into the following section, while the rings on the back part of the body slope forward, with no abrupt change in slope direction. In contrast, *Desmoscolex* (*Desmolorenzenia*) Claparède, 1863 features quadricomoid-shaped main rings that exhibit an abrupt change in slope direction at the level of a single, larger main ring (Freudenhammer 1975; Decraemer & Sturhan 1982). *Desmoscolex* (*Protricomoides*) Timm, 1970 is characterized by incomplete main rings located only in the anterior and/or posterior regions of the body. Finally, *Desmoscolex* (*Pareudesmoscolex*) Wiescher, 1962 lacks these rings entirely in the adult stage (Claparède 1863; Wiescher 1962; Timm 1970).

A high proportion (45 species) of the genus *Desmoscolex* was described or recorded from deep-sea ecosystems (World Register of Deep-Sea Species 2024). Within the high variety of deep-sea environments, canyons represent direct pathways from shallow to deep waters and are characterized by a great organic matter input and constant hydrological and biogeochemical variations (Shepard 1972; Amaro *et al.* 2016; Zeppilli *et al.* 2017). The metazoan meiofauna of the Cassidaigne Canyon (Calanques National Park, off the coast of Cassis, France) has not yet been investigated, although other groups, including benthic foraminifera (Fontanier *et al.* 2012, 2014, 2020), macrofauna (Stora *et al.* 2010) and megafauna (Fabri *et al.* 2014; Boury-Esnault *et al.* 2017; Chevaldonné *et al.* 2023) have been studied.

Here, we describe two new species of *Desmoscolex* (*Desmoscolex*) from the Cassidaigne Canyon.

Material and methods

A survey of benthic communities was carried out in the Cassidaigne Canyon, in the Gulf of Lions, NW Mediterranean Sea. The Cassidaigne Canyon is characterized by a narrow canyon axis (1 km in width) whose head (at 200 m depth) borders the Cassis Bay 7 km away from the coast (Fontanier *et al.* 2014). The animals used for the present description were found at depths between 605 and 1968 meters deep at different points within the canyon.

The sampling campaign was done on board of the *R/V JANUS II* from January to April 2022. Sediment samples were collected with an Ussler box corer (0.25 m²) and subsampled with a plexiglas tube (internal

Table 1 (continued on next four pages). List of valid species within the genus *Desmoscolex* Claparède, 1863 including their respective authors, their synonyms and the environments documented in their original descriptions. Species marked with * are synonymized within the corresponding subgenus for the first time in this study, based on the original description of both the subgenus and the species.

valid species	author	environment	synonymized names
<i>Desmoscolex (Desmoscolex) abyssorum*</i>	Decraemer, 1984	marine	<i>Desmoscolex abyssorum</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) adenotrichus*</i>	Lorenzen, 1969	marine	<i>Desmoscolex adenotrichus</i> Lorenzen, 1969
<i>Desmoscolex (Desmoscolex) adriaticus*</i>	Schepotieff, 1907	marine	<i>Desmoscolex adriaticus</i> Schepotieff, 1907
<i>Desmoscolex (Desmoscolex) algivorus</i>	Coomans, Vincx & Decraemer, 1985	fresh water	<i>Desmoscolex algivorus</i> Coomans, Vincx & Decraemer, 1985
<i>Desmoscolex (Desmoscolex) amaurus*</i>	Lorenzen, 1972	marine	<i>Desmoscolex amaurus</i> Lorenzen, 1972
<i>Desmoscolex (Desmoscolex) americanus*</i>	Chitwood, 1936	marine	<i>Desmoscolex americanus</i> Chitwood, 1936
<i>Desmoscolex (Desmoscolex) annulatus*</i>	Schepotieff, 1907	marine	<i>Desmoscolex annulatus</i> Schepotieff, 1907
<i>Desmoscolex (Desmoscolex) antarcticos</i>	(Timm, 1970)	marine	<i>Desmoscolex antarcticos</i> (Timm, 1970); <i>Protodesmoscolex</i> <i>antarcticos</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) aquaedulcis</i>	Stammer, 1935	fresh water	<i>Desmoscolex aquaedulcis</i> Stammer, 1935
<i>Desmoscolex (Desmoscolex) articulatus*</i>	Timm, 1978	marine	<i>Desmoscolex articulatus</i> Timm, 1978
<i>Desmoscolex (Desmoscolex) asetosus*</i>	Decraemer, 1975	marine	<i>Desmoscolex asetosus</i> Decraemer, 1975
<i>Desmoscolex (Desmoscolex) australicus*</i>	Decraemer, 1974	marine	<i>Desmoscolex australicus</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) balticus*</i>	Lorenzen, 1971	marine	<i>Desmoscolex balticus</i> Lorenzen, 1971
<i>Desmoscolex (Desmoscolex) bathyalis*</i>	Freudenhammer, 1975	marine	<i>Desmoscolex bathyalis</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) bathybius</i>	Timm, 1970	marine	<i>Desmoscolex bathybius</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) bengalensis*</i>	Timm, 1961	marine	<i>Desmoscolex bengalensis</i> Timm, 1961
<i>Desmoscolex (Desmoscolex) borealis*</i>	Kreis, 1963	marine	<i>Desmoscolex borealis</i> Kreis, 1963
<i>Desmoscolex (Desmoscolex) brachyrhynchus*</i>	Bussau, 1993	marine	<i>Desmoscolex brachyrhynchus</i> Bussau, 1993
<i>Desmoscolex (Desmoscolex) brevisetosus*</i>	Decraemer, 1974	marine	<i>Desmoscolex brevisetosus</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) californicus</i>	Timm, 1970	marine; brackish	<i>Desmoscolex californicus</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) campbelli*</i>	Allgén, 1946	marine	<i>Desmoscolex campbelli</i> Allgén, 1946
<i>Desmoscolex (Desmoscolex) chaetalatus*</i>	Freudenhammer, 1975	marine	<i>Desmoscolex chaetalatus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) chaetogaster*</i>	Greeff, 1869	marine	<i>Desmoscolex chaetogaster</i> Greeff, 1869; <i>Eudesmoscolex chaetogaster</i> (Greeff, 1869) Schuurmans stekhoven 1935
<i>Desmoscolex (Desmoscolex) complexus*</i>	Decraemer, 1984	marine	<i>Desmoscolex complexus</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) conurus*</i>	Steiner, 1916	marine	<i>Desmoscolex conurus</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) coronatus*</i>	Soetaert, 1989	marine	<i>Desmoscolex coronatus</i> Soetaert, 1989
<i>Desmoscolex (Desmoscolex) cosmopolites</i>	Timm, 1970	marine	<i>Desmoscolex cosmopolites</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) cristatus*</i>	(Allgén, 1932) Lorenzen, 1971	marine	<i>Desmoscolex cristatus</i> (Allgén, 1932) Lorenzen 1971; <i>Eudesmoscolex cristatus</i> (Allgén, 1932)

Table 1 (continued).

valid species	author	environment	synonymized names
<i>Desmoscolex (Desmoscolex) curvespiculatum</i> *	Decraemer, 1984	marine	<i>Desmoscolex curvespiculatum</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) deconincki</i> *	Decraemer, 1974	marine	<i>Desmoscolex deconincki</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) decraemerae</i> *	Soetaert, 1989	marine	<i>Desmoscolex decraemerae</i> Soetaert, 1989
<i>Desmoscolex (Desmoscolex) demerarae</i> *	Decraemer, 1983	marine	<i>Desmoscolex demerarae</i> Decraemer, 1983
<i>Desmoscolex (Desmoscolex) dimorphus</i> *	Decraemer, 1974	marine	<i>Desmoscolex dimorphus</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) draconemoides</i>	Timm, 1970	marine	<i>Desmoscolex draconemoides</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) dussarti</i>	Juget, 1969	fresh water	<i>Desmoscolex dussarti</i> Juget, 1969
<i>Desmoscolex (Desmoscolex) eftus</i> *	Freudenhammer, 1975	marine	<i>Desmoscolex eftus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) falcatus</i> *	Lorenzen, 1972	marine	<i>Desmoscolex falcatus</i> Lorenzen, 1972
<i>Desmoscolex (Desmoscolex) fennicus</i> *	Lorenzen, 1969	marine	<i>Desmoscolex fennicus</i> Lorenzen, 1969
<i>Desmoscolex (Desmoscolex) frigidus</i> *	Timm, 1978	marine	<i>Desmoscolex frigidus</i> Timm, 1978
<i>Desmoscolex (Desmoscolex) galeatus</i> *	Freudenhammer, 1975	marine	<i>Desmoscolex galeatus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) geraerti</i> *	Decraemer, 1974	marine	<i>Desmoscolex geraerti</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) gerlachi</i>	Timm, 1970	marine	<i>Desmoscolex gerlachi</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) gladisetosus</i>	Timm, 1970	marine	<i>Desmoscolex gladisetosus</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) grandiamphis</i> *	Inglis, 1967	marine	<i>Desmoscolex grandiamphis</i> Inglis, 1967
<i>Desmoscolex (Desmoscolex) granulatus</i> *	Decraemer, 1975	marine	<i>Desmoscolex granulatus</i> Decraemer, 1975
<i>Desmoscolex (Desmoscolex) italicus</i>	Timm, 1970	marine	<i>Desmoscolex italicus</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) keiensis</i> *	Kreis, 1934	marine	<i>Desmoscolex keiensis</i> Kreis, 1934
<i>Desmoscolex (Desmoscolex) koloensis</i>	Decraemer, 1984	fresh water; terrestrial	<i>Desmoscolex koloensis</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) labiosus</i> *	Lorenzen, 1969	marine	<i>Desmoscolex labiosus</i> Lorenzen, 1969
<i>Desmoscolex (Desmoscolex) laevis</i> *	Kreis, 1928	marine	<i>Desmoscolex laevis</i> Kreis, 1928
<i>Desmoscolex (Desmoscolex) lanceosetatus</i>	Jung, Kihm & Rho, 2024	marine	<i>Desmoscolex lanceosetatus</i> Jung, Kihm & Rho, 2024
<i>Desmoscolex (Desmoscolex) lanuginosus</i> *	Panceri, 1876	marine	<i>Desmoscolex lanuginosus</i> Panceri, 1876
<i>Desmoscolex (Desmoscolex) lapilliferus</i> *	Freudenhammer, 1975	marine	<i>Desmoscolex lapilliferus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) lemani</i>	Juget, 1969	fresh water	<i>Desmoscolex lemani</i> Juget, 1969
<i>Desmoscolex (Desmoscolex) leptus</i> *	Steiner, 1916	marine	<i>Desmoscolex leptus</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) lissus</i> *	Steiner, 1916	marine	<i>Desmoscolex lissus</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) longiamphis</i>	Timm, 1970	marine	<i>Desmoscolex longiamphis</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) longirostris</i> *	Bussau, 1993	marine	<i>Desmoscolex longirostris</i> Bussau, 1993
<i>Desmoscolex (Desmoscolex) longisetosus</i>	Timm, 1970	marine	<i>Desmoscolex longisetosus</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) lorenzeni</i> *	Freudenhammer, 1975	marine	<i>Desmoscolex lorenzeni</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) macramphis</i> *	Decraemer, 1984	marine	<i>Desmoscolex macramphis</i> Decraemer, 1984

Table 1 (continued).

valid species	author	environment	synonymized names
<i>Desmoscolex (Desmoscolex) macrophasmatus*</i>	Decraemer, 1984	marine	<i>Desmoscolex macrophasmatus</i> Decraemer, 1984; <i>Desmoscolex macrophasmata</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) max</i>	Timm, 1970	marine	<i>Desmoscolex max</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) membranifer*</i>	Soetaert, 1989	marine	<i>Desmoscolex membranifer</i> Soetaert, 1989
<i>Desmoscolex (Desmoscolex) membranosus*</i>	Decraemer, 1974	marine	<i>Desmoscolex membranosus</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) michaelsoni*</i>	Steiner, 1916	marine	<i>Desmoscolex michaelsoni</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) minor*</i>	Schepotieff, 1907	marine	<i>Desmoscolex minor</i> Schepotieff, 1907
<i>Desmoscolex (Desmoscolex) minutus*</i>	Claparède, 1863	marine	<i>Desmoscolex minutus</i> Claparède, 1863
<i>Desmoscolex (Desmoscolex) multiannulatus*</i>	Decraemer, 1983	marine	<i>Desmoscolex multiannulatus</i> Decraemer, 1983
<i>Desmoscolex (Desmoscolex) nanus*</i>	Steiner, 1916	marine	<i>Desmoscolex nanus</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) nibelungus</i>	sp. nov.	marine	
<i>Desmoscolex (Desmoscolex) nudus*</i>	Chitwood, 1951	marine	<i>Desmoscolex nudus</i> Chitwood, 1951
<i>Desmoscolex (Desmoscolex) nymphianus*</i>	Decraemer, 1974	marine	<i>Desmoscolex nymphianus</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) obscurus*</i>	Bussau, 1993	marine	<i>Desmoscolex obscurus</i> Bussau, 1993
<i>Desmoscolex (Desmoscolex) opacus*</i>	Bussau, 1993	marine	<i>Desmoscolex opacus</i> Bussau, 1993
<i>Desmoscolex (Desmoscolex) parabyssorum*</i>	Soetaert, 1989	marine	<i>Desmoscolex parabyssorum</i> Soetaert, 1989
<i>Desmoscolex (Desmoscolex) parafalklandiae*</i>	Allgén, 1955	marine	<i>Desmoscolex parafalklandiae</i> Allgén, 1955
<i>Desmoscolex (Desmoscolex) parakoloensis</i>	Decraemer, 1984	fresh water	<i>Desmoscolex parakoloensis</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) paraleptus*</i>	Decraemer, 1975	marine	<i>Desmoscolex paraleptus</i> Decraemer, 1975
<i>Desmoscolex (Desmoscolex) paralongisetosus*</i>	Decraemer, 1983	marine	<i>Desmoscolex paralongisetosus</i> Decraemer, 1983
<i>Desmoscolex (Desmoscolex) parvospiculatus*</i>	Decraemer, 1996	marine	<i>Desmoscolex parvospiculatus</i> Decraemer, 1996
<i>Desmoscolex (Desmoscolex) pelophilus*</i>	Steiner, 1916	marine	<i>Desmoscolex pelophilus</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) perspicuus*</i>	Freudenhammer, 1975	marine	<i>Desmoscolex perspicuus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) petalodes*</i>	Lorenzen, 1972	marine	<i>Desmoscolex petalodes</i> Lorenzen, 1972
<i>Desmoscolex (Desmoscolex) prampramensis*</i>	Steiner, 1916	marine	<i>Desmoscolex prampramensis</i> Steiner, 1916
<i>Desmoscolex (Desmoscolex) proboscis*</i>	Lorenzen, 1972	marine	<i>Desmoscolex proboscis</i> Lorenzen, 1972
<i>Desmoscolex (Desmoscolex) pusillus*</i>	Lorenzen, 1969	marine	<i>Desmoscolex pusillus</i> Lorenzen, 1969
<i>Desmoscolex (Desmoscolex) pustulatus*</i>	Freudenhammer, 1975	marine	<i>Desmoscolex pustulatus</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) quadricomoides</i>	Timm, 1970	marine	<i>Desmoscolex quadricomoides</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) remifer</i>	Timm, 1970	marine	<i>Desmoscolex remifer</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) roscoffiensis*</i>	Decraemer, 1979	marine	<i>Desmoscolex roscoffiensis</i> Decraemer, 1979
<i>Desmoscolex (Desmoscolex) rostratus</i>	Timm, 1970	marine	<i>Desmoscolex rostratus</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) rotundicephalus</i>	Jung, Kihm & Rho, 2024	marine	<i>Desmoscolex rotundicephalus</i> Jung, Kihm & Rho, 2024
<i>Desmoscolex (Desmoscolex) rudolphi*</i>	Steiner, 1916	marine	<i>Desmoscolex rudolphi</i> Steiner, 1916

Table 1 (continued).

valid species	author	environment	synonymized names
<i>Desmoscolex (Desmoscolex) segonzaci</i> *	Decraemer, 1983	marine	<i>Desmoscolex segonzaci</i> Decraemer, 1983
<i>Desmoscolex (Desmoscolex) sieverti</i> *	Freudenhammer, 1975	marine	<i>Desmoscolex sieverti</i> Freudenhammer, 1975
<i>Desmoscolex (Desmoscolex) spinostris</i> *	Decraemer, 1984	marine	<i>Desmoscolex spinostris</i> Decraemer, 1984
<i>Desmoscolex (Desmoscolex) spinosus</i> *	Decraemer, 1976	marine	<i>Desmoscolex spinosus</i> Decraemer, 1976
<i>Desmoscolex (Desmoscolex) tenuiseta</i> *	Filipjev, 1922	marine	<i>Desmoscolex tenuiseta</i> Filipjev, 1922
<i>Desmoscolex (Desmoscolex) timmi</i> *	Decraemer, 1974	marine	<i>Desmoscolex timmi</i> Decraemer, 1974
<i>Desmoscolex (Desmoscolex) valkyria</i>	sp. nov.	marine	
<i>Desmoscolex (Desmoscolex) vanoyei</i> *	De Coninck, 1943	marine	<i>Desmoscolex vanoyei</i> De Coninck, 1943
<i>Desmoscolex (Desmoscolex) variabilis</i> *	Soetaert, 1989	marine	<i>Desmoscolex variabilis</i> Soetaert, 1989
<i>Desmoscolex (Desmoscolex) velifer</i>	Timm, 1970	marine	<i>Desmoscolex velifer</i> Timm, 1970
<i>Desmoscolex (Desmoscolex) vinealis</i> *	Weischer, 1962	terrestrial	<i>Desmoscolex vinealis</i> Weischer, 1962
<i>Desmoscolex (Desmoscolex) yongei</i> *	Decraemer, 1974	marine	<i>Desmoscolex yongei</i> Decraemer, 1974
<i>Desmoscolex (Desmolorenzenia) camerunensis</i>	Decraemer & Sturhan, 1997	terrestrial	–
<i>Desmoscolex (Desmolorenzenia) cooleni</i>	(Decraemer, 1978)	marine	<i>Desmoscolex cooleni</i> (Decraemer, 1978); <i>Desmolorenzenia cooleni</i> Decraemer, 1978
<i>Desmoscolex (Desmolorenzenia) coreensis</i>	Rho, Kim & Chang, 2007	marine	<i>Desmoscolex coreensis</i> Rho, Kim & Chang, 2007
<i>Desmoscolex (Desmolorenzenia) crassicaudus</i>	(Timm, 1970)	marine	<i>Desmoscolex crassicauda</i> (Timm, 1970); <i>Desmolorenzenia crassicauda</i> (Timm, 1970)
<i>Desmoscolex (Desmolorenzenia) curvicaudus</i>	(Timm, 1978)	marine	<i>Quadricoma curvicauda</i> Timm, 1978; <i>Tricoma (Quadricoma)</i> <i>curvicauda</i> (Timm, 1978)
<i>Desmoscolex (Desmolorenzenia) desmoscoleoides</i>	(Timm, 1970)	marine	<i>Desmolorenzenia desmoscoleoides</i> (Timm, 1970); <i>Desmoscolex</i> <i>desmoscoleoides</i> (Timm, 1970); <i>Quadricoma desmoscoleoides</i> Timm, 1970; <i>Tricoma (Quadricoma)</i> <i>desmoscoleoides</i> Timm, 1970
<i>Desmoscolex (Desmolorenzenia) eurycriscus</i>	Filipjev, 1922	marine	<i>Desmolorenzenia eurycriscus</i> (Filipjev, 1922); <i>Desmolorenzenia</i> <i>longicauda</i> (Timm, 1970); <i>Desmoscolex (Desmolorenzenia)</i> <i>longicauda</i> Timm, 1970; <i>Desmoscolex eurycriscus</i> Filipjev, 1922; <i>Desmoscolex longicauda</i> (Timm, 1970); <i>Quadricoma</i> <i>eurycriscus</i> (Filipjev, 1922); <i>Quadricoma longicauda</i> Timm, 1970; <i>Tricoma (Quadricoma)</i> <i>eurycriscus</i> Filipjev, 1922; <i>Tricoma</i> <i>(Quadricoma) longicauda</i> (Timm, 1970)
<i>Desmoscolex (Desmolorenzenia) frontalis</i>	Gerlach, 1952	marine	<i>Desmoscolex frontalis</i> Gerlach, 1952
<i>Desmoscolex (Desmolorenzenia) goubaultae</i>	Decraemer, 1986	marine	<i>Desmoscolex goubaultae</i> Decraemer, 1986

Table 1 (continued).

valid species	author	environment	synonymized names
<i>Desmoscolex (Desmolorenzenia) hupferi</i>	(Steiner, 1916)	marine	<i>Desmoscolex hupferi</i> Steiner, 1916; <i>Desmolorenzenia hupferi</i> (Steiner, 1916); <i>Quadricoma hupferi</i> (Steiner, 1916) Timm, 1970; <i>Tricoma (Quadricoma) hupferi</i> (Steiner, 1916)
<i>Desmoscolex (Desmolorenzenia) montanus</i>	(Decraemer & Sturhan, 1982)	terrestrial	<i>Desmolorenzenia montana</i> Decraemer & Sturhan, 1982; <i>Desmolorenzenia montanus</i> Decraemer & Sturhan, 1982; <i>Desmoscolex (Desmolorenzenia) montana</i> (Decraemer & Sturhan, 1982); <i>Desmoscolex montana</i> (Decraemer & Sturhan, 1982) Decraemer 1984
<i>Desmoscolex (Desmolorenzenia) parvus</i>	(Timm, 1970)	marine	<i>Desmolorenzenia parva</i> (Timm, 1970); <i>Desmoscolex parvus</i> (Timm, 1970); <i>Quadricoma parva</i> Timm, 1970; <i>Tricoma (Quadricoma) parva</i> Timm, 1970
<i>Desmoscolex (Desmolorenzenia) pedunculus</i>	Rho, Kim & Chang, 2007	marine	<i>Desmoscolex pedunculus</i> Rho, Kim & Chang, 2007
<i>Desmoscolex (Desmolorenzenia) platycricus</i>	Steiner, 1916	marine	<i>Desmoscolex platycricus</i> Steiner, 1916; <i>Desmolorenzenia platycricus</i> Steiner, 1916
<i>Desmoscolex (Desmolorenzenia) vittatus</i>	Lorenzen, 1969	marine	<i>Desmolorenzenia vittata</i> (Lorenzen, 1969); <i>Desmoscolex vittatus</i> Lorenzen, 1969; <i>Quadricoma vittata</i> (Lorenzen, 1969); <i>Tricoma (Quadricoma) vittata</i> (Lorenzen, 1969)
<i>Desmoscolex (Pareudesmoscolex) lacinosus</i>	Lorenzen, 1969	marine; brackish	<i>Pareudesmoscolex lacinosus</i> Lorenzen, 1969
<i>Desmoscolex (Pareudesmoscolex) lacustris</i>	Juget, 1969	fresh water	<i>Pareudesmoscolex lacustris</i> Juget, 1969
<i>Desmoscolex (Pareudesmoscolex) papillosus</i>	(Schulz, 1935)	marine; brackish	<i>Eudesmoscolex papillosus</i> Schulz, 1935; <i>Pareudesmoscolex papillosus</i> (Schulz, 1935)
<i>Desmoscolex (Pareudesmoscolex) pratensis</i>	Lorenzen, 1969	marine	<i>Pareudesmoscolex pratensis</i> Lorenzen, 1969
<i>Desmoscolex (Protricomoides) pravus</i>	Decraemer, 1985	marine	–
<i>Desmoscolex (Protricomoides) squamosus</i>	Timm, 1970	marine	<i>Desmoscolex squamosus</i> (Timm, 1970)
<i>Desmoscolex (Protricomoides) noctuabundus*</i>	Bussau, 1993	marine	<i>Desmoscolex noctuabundus</i> Bussau, 1993

diameter 10.5 cm) 2 cm into the sediment for meiofaunal analysis. Samples were fixed in 6% formalin and stained with Rose Bengal.

Meiofauna was separated from the sediment using Ludox[®] HS-40 flotation method (Sommerfield & Warwick 1996) followed by a centrifugation at 3000 rpm for 10 mins. No prior sieving was performed before the extraction. After Ludox extraction, the suspended solution was washed in a 63 µm mesh size sieve. The protocol was repeated three times to guarantee better efficiency of the extraction. Finally, the resulting samples were preserved in ethylene glycol 20% (Williamson & Russel 1965).

Meiofauna was sorted at high taxonomic level under a stereo microscope. Desmoscolecoid nematodes were prepared for light microscopy using the De Grisse (1969) protocol and single mounted in glycerine surrounded by a ring of paraffin. For species identification, an Olympus® BX51-P microscope with differential interference contrast optics was used, also equipped with an Olympus® DP-23 camera. Measurements were made using the OLYMPUS cellSens Standard ver. 3.2 software. Image plates and line art illustration were made with Adobe® Photoshop, Illustrator CC 202X and Inkscape ver. 1.3.2. Type material was deposited at the Museum für Naturkunde Berlin, collection "Vermes", catalogue of Free-Living Worms, ZMB 12957-12964.

Results

Taxonomy

Class Chromadorea Inglis, 1983
Order Desmoscolecida Filipjev, 1929
Family Desmoscolecidae Shipley, 1896

Genus *Desmoscolex* Claparède, 1863

Diagnosis (emended from Decraemer & Rho 2014)

Body cuticle with large main rings, separated by narrower or similarly wide interzones (one to five annules). Interzones smooth or with transverse row of fine spines or pores. Paired subdorsal and subventral somatic setae show various patterns. Often, red-brown pigment spots near the anterior intestine. Pharynx short, cylindrical, with junction opposite the posterior end of main ring two or the anterior end of main ring three in species with 17–18 rings. Intestine usually overlaps postrectally. Females didelphic-amphidelphic with outstretched ovaries, a spermatheca, and a vulva at posterior end of main ring 10 in 17-ring species. Juveniles with fine annules, each with spines or warts, no desmen.

Subgenus *Desmoscolex* Claparède, 1863

Diagnosis (emended from Decraemer 1983)

Presence of desmen along entire body in the adult stage. The majority of the species (74) have seventeen main rings surrounding the annulated cuticle, nine species have eighteen main rings, 3 have less than seventeen main rings and 13 species have more than eighteen main rings. Rings rounded or quadricomoid. In the quadricomoid form, anterior rings slope backward, posterior rings slope forward, with no abrupt change in slope direction.

Remarks

The present work raises the count of species of *Desmoscolex* (*Desmoscolex*) to 106 (see Table 1). Additionally, *Desmoscolex noctuabundus* Bussau, 1993 is proposed to be synonymized as *Desmoscolex (Protricomoides) noctuabundus*. According to Bussau (1993), the species exhibit incomplete main rings immediately after the cephalic region, followed by a bare cuticle, and ending with incomplete main rings extending from the anal region to the posterior end of the body. This pattern aligns with the description of the subgenus *Desmoscolex (Protricomoides)* Timm, 1970. It is worth noting that the use of the subgenus is optional, and both forms, with or without the subgenus, are valid as synonyms according to the ICZN code (1999). Table 1 provides an updated list of valid species of the genus *Desmoscolex*, along with their corresponding synonyms based on the original description of both the subgenus and the species. Species marked with * in the table are synonymized within the corresponding subgenus for the first time in this study.

Desmoscolex (Desmoscolex) nibelungus sp. nov.

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Figs 1–4, Tables 1–3, 6

Diagnosis

Desmoscolex (Desmoscolex) nibelungus sp. nov. is mainly defined by: (1) presence of 17 main rings with typical desmoscolecid setae arrangement: nine pairs of subdorsal setae and eight pairs of subventral setae; (2) thick somatic setae, except for wiry terminal pair (3) slightly elongated subdorsal setae on the 16th ring and more elongated subdorsal setae on the 17th ring; (4) apparent absence of cephalic setae; (5) rounded cephalic region, with lip region not covered by concretion material; (6) strongly ventrally curved, beak-shape last main ring.

Etymology

The specific name ‘*nibelungus*’ refers to the cycle of four epic music dramas composed by Richard Wagner called The Ring of the Nibelung (‘Der Ring des Nibelungen’ in German). Name chosen due to the presence of rings on the nematode’s body.

Type material

Holotype

MEDITERRANEAN SEA • ♂, adult (mounted in glycerine); Cassidaigne Canyon, Station U07; 43°0′5.940″ N, 5°19′12.510″ E; depth 1056 m; 11 Jan. 2022; CREOCEAN enterprise leg.; ZMB 12957; ZMB.

Paratypes

MEDITERRANEAN SEA • 2 ♂♂, adult (mounted in glycerine); same data as for holotype.; ZMB 12958 to 12959; ZMB • 1 ♀, adult (mounted in glycerine); same data as for preceding; ZMB 12961; ZMB • 1 ♀, adult (mounted in glycerine); Cassidaigne Canyon, Station U06; 43°2′20.352″ N, 5°21′0.096″ E; depth 605 m; 11 Jan. 2022; CREOCEAN enterprise leg.; ZMB 12960; ZMB.

Description

See Table 2 for a summary of the most relevant measurements of the type material.

Body short (249–310 µm), dorsally curved in holotype and one female paratype (M1 and F1), S-shaped in one male paratype (M2), straight in one male paratype (M3) and ventrally curved in one female paratype (F2). Body slightly tapered towards anterior end (at level of cephalic region) and tail. Width almost uniform over rest of body. Body with 17 well-separated main rings covered by concretion material on annulated body cuticle. Main rings relatively rounded and separated by 3–4 cuticle annules (Figs 1A, 2A, 3A, 4A).

Somatic setae inserted in peduncle and following typical desmoscolecid setal pattern of nine subdorsal and eight subventral pairs (see below). Both subdorsal and subventral setae thick, with cylindrical base and tapering towards distal end. Terminal setae of different shape, with thin and wiry appearance (Fig. 3D). Subdorsal and subventral setae with similar shape and length (Table 2), except for slightly elongated subdorsal setae on 16th main ring (16 µm) and more elongated subdorsal setae on 17th ring (17–31 µm).

Nine pairs of subdorsal somatic setae present on 1st, 3rd, 5th, 7th, 9th, 11th, 13th, 16th–17th main rings. One male specimen (M2) has one subdorsal setae located on second ring instead of on third one. Eight pairs of subventral somatic setae located on 2nd, 4th, 6th, 8th, 10th, 12th, 14th–15th main rings (Table 2).

Cephalic region globular, moderately wider than long, slightly truncated anteriorly, with distinct lip region. Head cuticle completely covered with concretion material except beneath amphideal fovea. Amphideal fovea covering nearly completely lateral sides of cephalic region. Labial sensilla not detected. Cephalic setae apparently absent, not discernible in optical microscopy (Figs 1C, 3C, 4B). Short cheilostome at level of protruding lip region, leading to short (extending over 2 rings), nearly cylindrical pharynx without posterior pharyngeal bulb (Figs 1B, 2B, 3B). In females, intestine with postrectal sac (Fig. 4A) and anal tube protruding from 15th main ring.

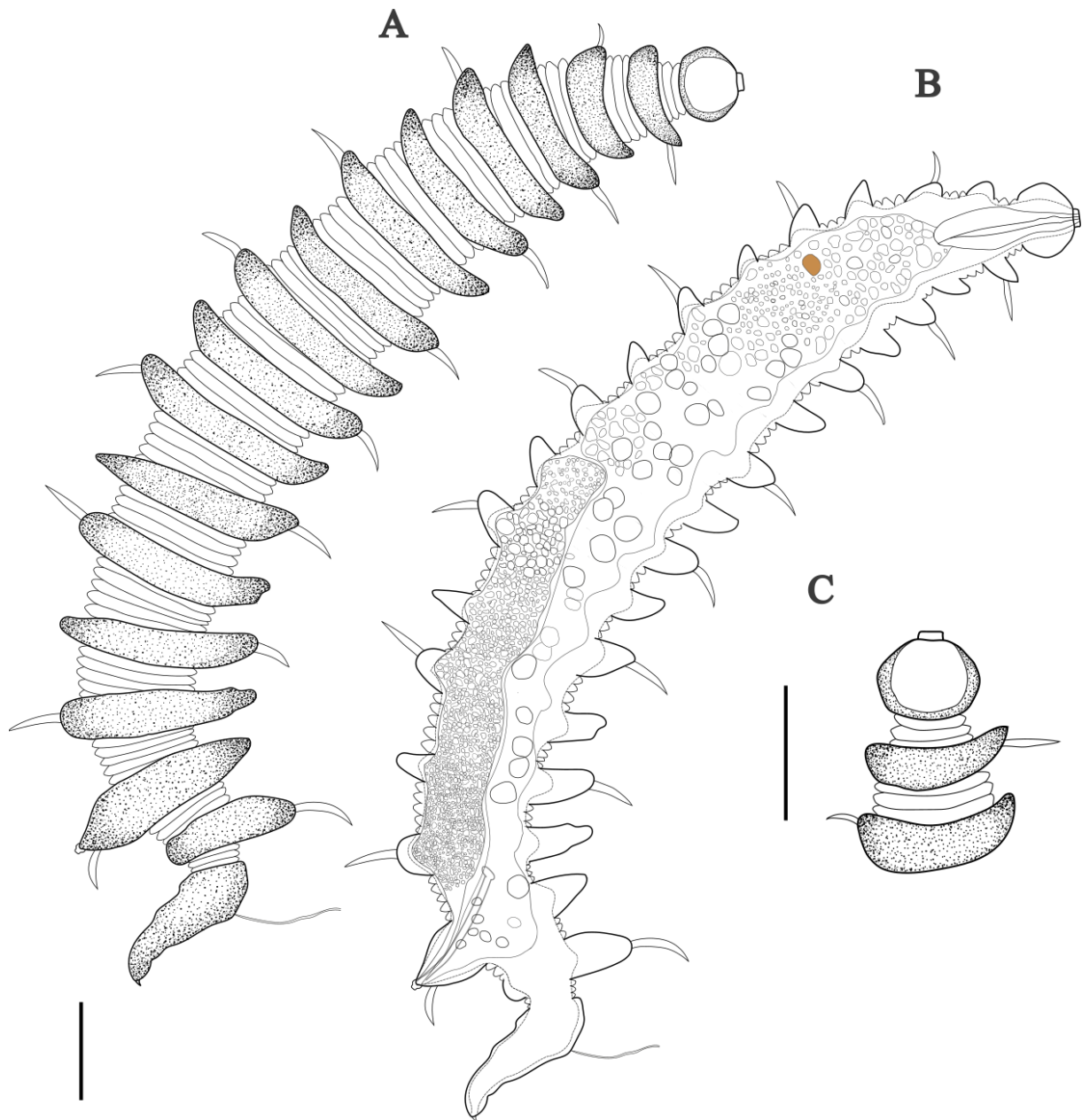


Fig. 1. Line art illustrations of *Desmoscolex (Desmoscolex) nibelungus* sp. nov., ♂, adult, holotype (ZMB 12957; ZMB). **A.** Habitus in lateral position. **B.** Habitus in optical section. **C.** Cephalic region in lateral position. Scale bars = 10 μ m.

One pair of pigment spots as orange, oval areas with well-defined border, present at level of 4th–5th main rings (Figs 1B, 2B, 3D, 4A).

Males monorchic with single testis outstretched and extending anteriorly up to level of 9th desmos. Spicules (36–39 μm) slightly curved and cephalated. Gubernaculum absent. Cloacal tube broad, opening to exterior on 15th main ring (Figs 1B, 3A). Both female paratypes with reproductive system inconspicuous. Even though hard to distinguish, reproductive system of female paratype (F1) didelphic-amphidelphic, with anterior branch extending from base of 7th main ring and posterior one to 15th main

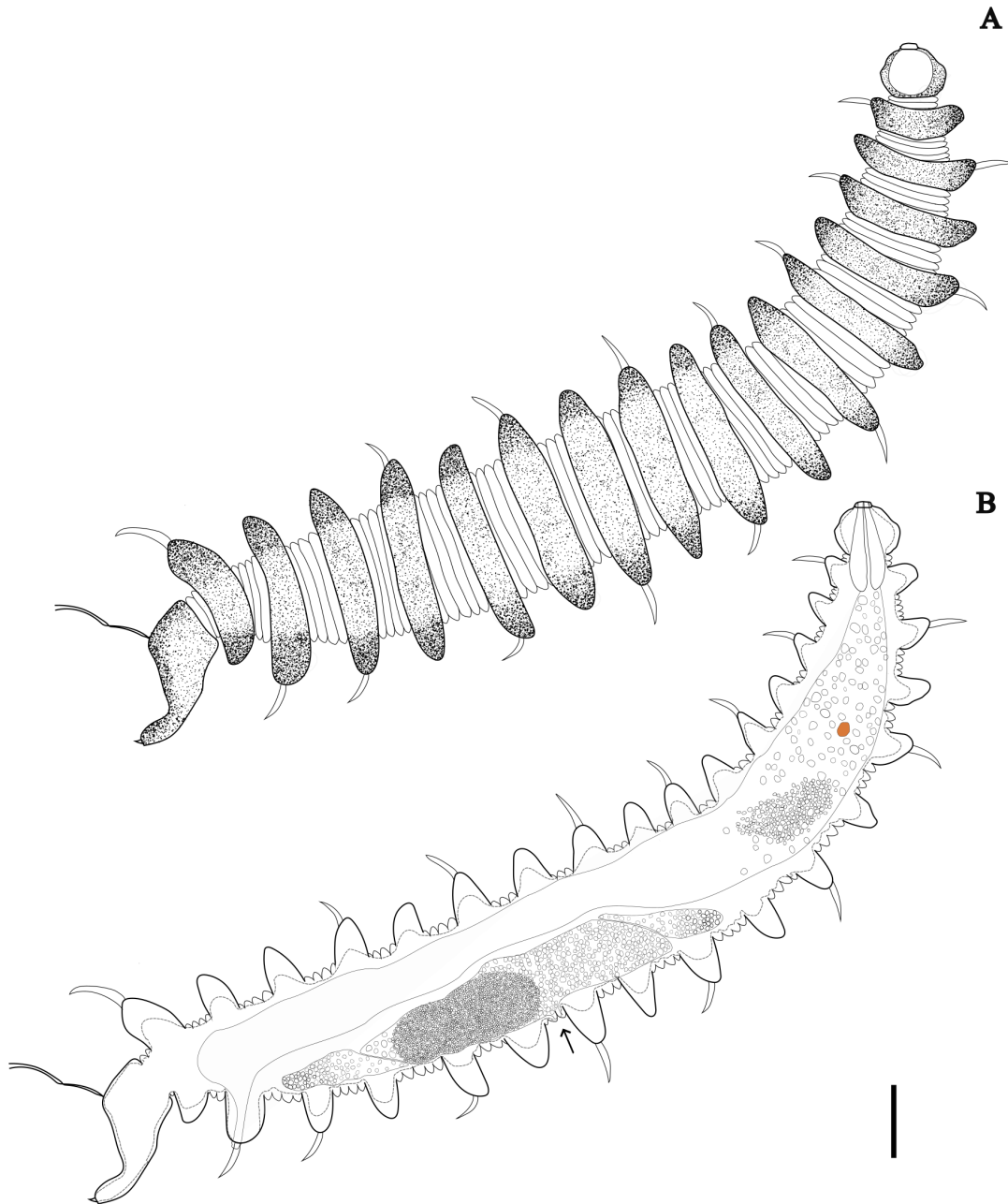


Fig. 2. Line art illustrations of *Desmoscolex (Desmoscolex) nibelungus* sp. nov., ♀, adult, paratype (ZMB 12960; ZMB). **A.** Habitus in lateral position. **B.** Habitus in optical section. The arrow highlights the position of the vulva. Scale bar = 10 μm .

ring. Vulva appearing at posterior end of 10th main ring. Oocytes are observed between main rings 11 and 13 (Fig. 2)

Tail with 2 main rings. Last main ring completely covered with concretion material, about 2,5–3 × as long as wide, and composed of wider and cylindrical anterior part with insertion of terminal pair of setae at its base (Figs 3E, 4D). Posterior part of last main ring strongly curved ventrally. Spinneret minute, not covered with concretion material.

Differential diagnosis

Based on similarities in the number of main rings, the somatic setal pattern, the globular cephalic region and circular amphids, *D. (D.) nibelungus* sp. nov. is grouped with other 14 species: *D. (D.) australicus* Decraemer, 1974; *D. (D.) bathyalis* Freudenhammer, 1975; *D. (D.) borealis* Kreis, 1963; *D. (D.) coronatus* Soetaert, 1989; *D. (D.) galeatus* Freudenhammer, 1975; *D. (D.) gerlachi* Timm, 1970; males of *D. (D.) gladisetosus* Timm, 1970; *D. (D.) lapilliferus* Freudenhammer, 1975; *D. (D.)*

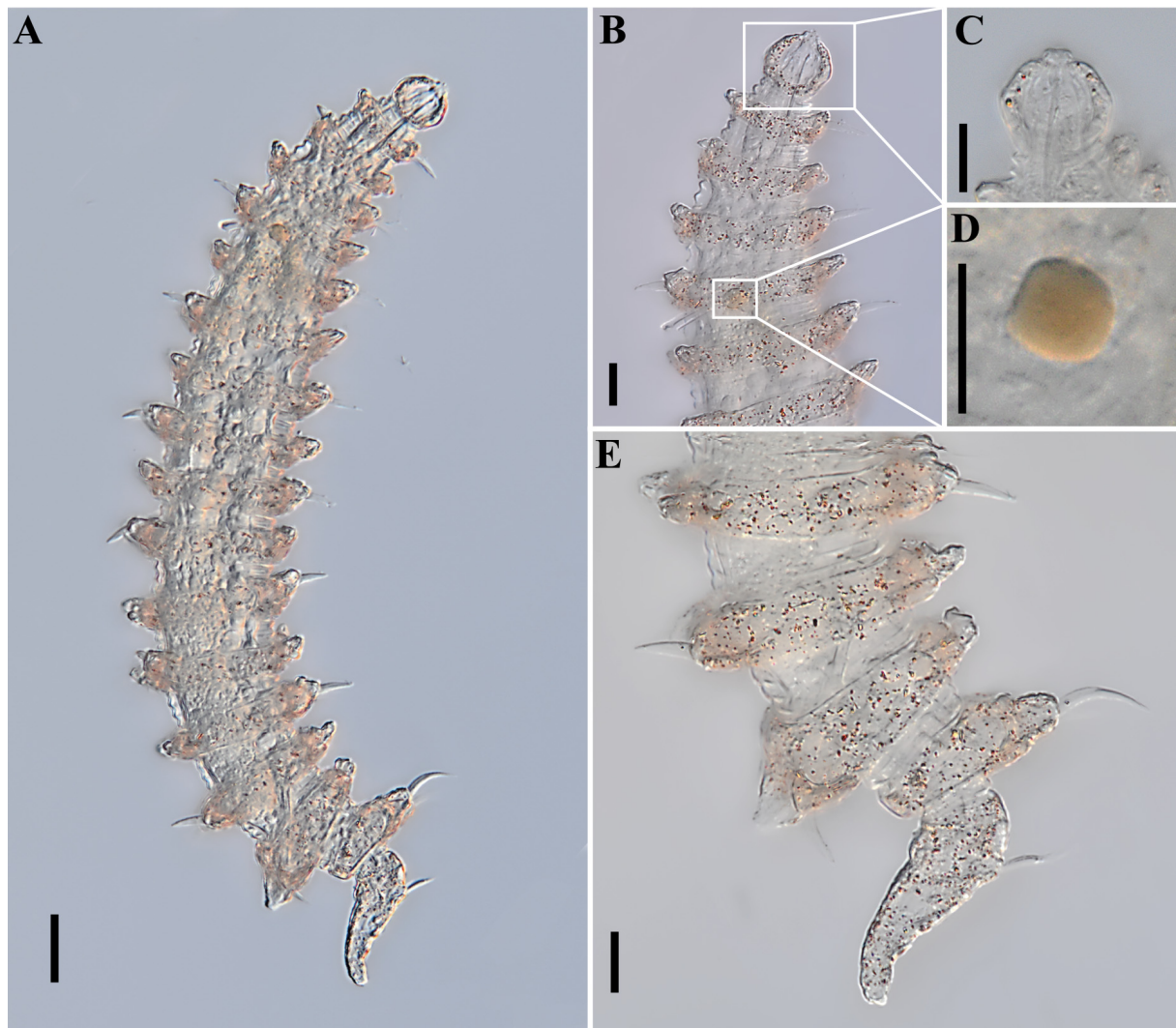


Fig. 3. *Desmoscolex (Desmoscolex) nibelungus* sp. nov. **A–B, E.** Holotype, ♂ (ZMB 12957; ZMB). **C–D.** Paratype, ♂ (ZMB 12959; ZMB). **A.** Overview. **B.** Anterior region. **C.** Detail of the cephalic region. **D.** Pigment spot. **E.** Lateral view of the posterior region. Scale bars: A = 20 µm; B–E = 10 µm.

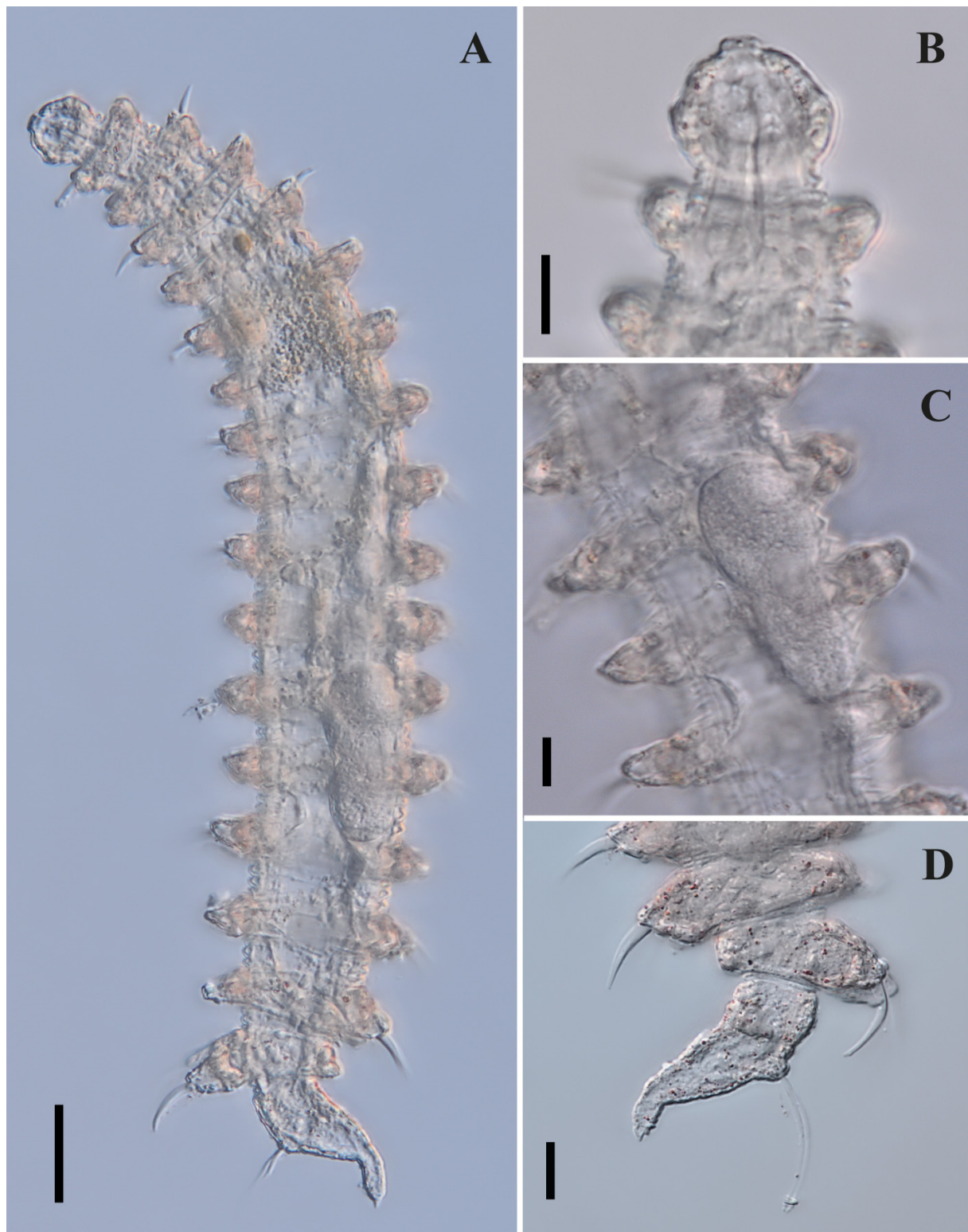


Fig. 4. *Desmoscolex (Desmoscolex) nibelungus* sp. nov. **A–C.** Paratype, ♀ (ZMB 12960; ZMB). **D.** Paratype, ♀ (ZMB 12961; ZMB). **A.** Overview. **B.** Detail of the cephalic region. **C.** Detail of the ovary between 11th and 13th main ring. **D.** Detail of the tail. Scale bars: A = 20 µm; B–D = 10 µm.

Table 2. Measurements (μm) of type material of *Desmoscolex (Desmoscolex) nibelungus* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; Sd = subdorsal setae; Sv = subventral setae; Tmr = length of the terminal ring; Tmrw = maximum width of the terminal ring; V = vulva distance from anterior end of body; %V = $V/\text{total body length} \times 100$. Numbers enclosed in brackets provide information about the quantity of setae present on each ring. The measurements of the setae correspond to one of the pair, unless explicitly specified as unique.

	male			female	
	holotype	paratypes		paratypes	
specimen	ZMB 12957	ZMB 12959	ZMB 12958	ZMB 12960	ZMB 12961
total length	310	267	272	309	249
a	9	7	7	8	7
b	9	10	9	12	8
c	4	4	4	5	4
c'	1	2	1	1	1
maximum body width	35	36	39	37	36
maximum desmen width	51	46	52	55	50
length / width	9	7	7	8	7
head length	16	15	15	14	14
head width	16	17	17	17	18
Sd 1	11 (2)	12 (2)	11 (2)	12 (2)	10 (2)
Sd 2	–	12 (1)	–	–	–
Sd 3	10 (2)	12 (1)	11 (2)	11 (2)	11 (2)
Sd 5	11 (2)	14 (2)	10 (2)	12 (2)	8 (2)
Sd 7	12 (2)	12 (2)	12 (2)	11 (2)	10 (2)
Sd 9	10 (2)	12 (2)	11 (2)	10 (2)	9 (2)
Sd 11	10 (2)	11 (2)	11 (2)	13 (2)	10 (2)
Sd 13	10 (2)	12 (2)	11 (2)	12 (2)	12 (2)
Sd 16	16 (2)	16 (2)	16 (2)	16 (2)	16 (2)
Sd 17	21 (2)	17 (2) (broken)	31 (2)	24 (2)	24 (2)
Sv 2	8 (2)	9 (2)	8 (2)	9 (2)	8 (2)
Sv 4	10 (2)	10 (2)	10 (2)	9 (2)	9 (2)
Sv 6	10 (2)	11 (2)	10 (2)	9 (2)	10 (2)
Sv 8	13 (2)	12 (2)	10 (2)	13 (2)	10 (2)
Sv 10	11 (2)	12 (2)	10 (2)	11 (2)	11 (2)
Sv 12	10 (2)	14 (2)	11 (2)	10 (2)	12 (2)
Sv 14	11 (2)	15 (2)	13 (2)	11 (2)	13 (2)
Sv 15	11 (2)	13 (2)	11 (2)	11 (2)	14 (2)
tail length	72	68	71	72	59
Tmr	41	38	43	41	38
Tmrw	16	14	15	16	15
spicule length	39	38	36	–	–

Table 3 (continued on next page). Main differences between the species of *Desmoscolex* (*Desmoscolex*) Claparède, 1863 that share the following characteristics: 17 main rings; 9 pairs of subdorsal somatic setae on 1st, 3rd, 5th, 7th, 9th, 11th, 13th and 16th–17th main rings; eight pairs of subventral setae located on the 2nd, 4th, 6th, 8th, 10th, 12th and 14th–15th main rings; similar head and amphid shape. If only male or female of the species are included in the table, this means that the lacking gender doesn't present one of the aforementioned characteristics and, therefore, doesn't belong to this group. Abbreviations: N.A. = not applicable (this is because the species was described only after female specimens); N.S. = not specified; Sd = subdorsal setae; Sv = subventral setae.

species	cephalic setae	somatic setae	terminal ring	protuding lip region	spicule	gubernaculum
<i>D. (D.) nibelungus</i> sp. nov.	indiscernible	thick and with similar length, except for the slightly longer setae on 16 th ring and the long and wiry setae of the terminal ring	beak-shaped, strongly curved ventrally; minute spinneret	present	39 µm	absent
<i>D. (D.) australicus</i> Decraemer, 1974	present; slender with broader basal part (16 µm)	subdorsal setae with lance-shaped tips, thicker and longer than subventral ones (Sd: 11–23 µm; Sv: 7.5–9 µm)	conical, slightly curved ventrally; short spinneret	absent	29 µm	present (13 µm)
<i>D. (D.) bathyalis</i> Freudenhammer, 1975	present; with blunt tips	thin, of similar length except for the pair on the 1 st and last main rings (25 µm and 45 µm, respectively)	conico-cylindrical; short spinneret	absent	45 µm	absent
<i>D. (D.) borealis</i> Kreis, 1963	present	spine-like subventral setae on 15 th main ring	short and conical	absent	31 µm	absent
<i>D. (D.) coronatus</i> Soetaert, 1989	present; short and pedunculated	subdorsal setae longer than subventral, slightly elongated on 16 th and 17 th rings (15–16 µm and 19–20 µm, respectively)	conico-cylindrical, ventrally arcuate	present	21 µm	present (6–9 µm)
<i>D. (D.) galeatus</i> Freudenhammer, 1975	present; longitudinal notch on its dorsal half	subdorsal setae with lance-shaped tips, elongated in the 13 th , 16 th and 17 th rings (23 µm, 24 µm and 33 µm, respectively)	conical; short spinneret	absent	N.A.	N.A.
<i>D. (D.) gerlachi</i> Timm, 1970	present; thick with pointed tip (20 µm)	subdorsal setae with lance-shaped tip; subventral setae shaped like a swordblade	conico-cylindrical; long spinneret	absent	60 µm	absent
<i>D. (D.) gladisetosus</i> Timm, 1970 (male)	present; wiry appearance (15 µm)	sword-shaped, with open tip, except for pair 17 that has open blunt tip	conico-cylindrical; long spinneret	absent	42 µm	N.S.
<i>D. (D.) lapilliferus</i> Freudenhammer, 1975	present; with long dark curved tips	with long dark curved tips	conico-cylindrical; short spinneret	absent	30 µm	absent
<i>D. (D.) opacus</i> Bussau, 1993	present; cauliflower-shaped	all of similar shape and length except for subdorsal setae on 1 st , 16 th and 17 th main rings (24 µm, 22 µm and 38 µm)	conico-cylindrical; short spinneret	absent	30 µm	present (15 µm)

Table 3 (continued).

species	cephalic setae	somatic setae	terminal ring	protuding lip region	spicule	gubernaculum
<i>D. (D.) paraleptus</i> Decraemer, 1975	present; slender located at the extreme anterior (11 µm)	similar length; subdorsal with spatulate tip; subventral with acute tip	conical; long spinneret	absent	N.A.	N.A.
<i>D. (D.) perspicuus</i> Freudenhammer, 1975	present	short setae, increasing in length towards the tail (6–25 µm)	wider on the base; very long spinneret	absent	N.A.	N.A.
<i>D. (D.) petalodes</i> Lorenzen, 1972	present; with flag like tip	broader at the base, with thin tip	conical; long spinneret	absent	29 µm	present
<i>D. (D.) rotundicephalus</i> Jung, Kihm & Rho, 2024	absent	subdorsal setae longer than subventral with open tip	conical; short spinneret	present	30 µm	present (7 µm)
<i>D. (D.) yongei</i> Decraemer, 1974	present; hollow tubular with a filiform distal part (21 µm)	subdorsal setae with lance-shaped tip, longer than subventral (27–33 µm)	conical; minute spinneret	absent	44 µm	present (10 µm)

opacus Bussau, 1993; *D. (D.) paraleptus* Decraemer, 1975; *D. (D.) perspicuus* Freudenhammer, 1975; *D. (D.) petalodes* Lorenzen, 1972; *D. (D.) rotundicephalus* Jung, Kihm & Rho, 2024; and *D. (D.) yongei* Decraemer, 1974 (see Table 3). These species share as characteristics having 17 main rings along the body and same somatic setal pattern consisting of 9 pairs of subdorsal setae and 8 pairs of subventral ones. On the other hand, what distinguished *D. (D.) nibelungus* from the majority of the aforementioned group of species is the apparent lack of cephalic setae and its strongly ventrally curved, beak-shaped tail. The lack of cephalic setae is highly unusual; however, after careful examination of the type material under optical microscopy, no cephalic setae were observed. *Desmoscolex (D.) rotundicephalus* shares this peculiar characteristic with the species described here, as well as the uncovered lip region, the number of main rings and the somatic setae arrangement. Nevertheless, the somatic setae of *D. (D.) rotundicephalus* differ in length between subdorsal and subventral, though they share a similar shape. In contrast, the somatic setae of *D. (D.) nibelungus* are all of similar length, with the last pair exhibiting a wiry appearance. Additionally, the beak-shaped last main ring of *D. (D.) nibelungus* contrasts with the conical appearance of the last main ring in *D. (D.) rotundicephalus*.

Apart from differing in the apparent lack of cephalic setae and the particular tail shape, *D. (D.) australicus*, *D. (D.) gerlachi*, *D. (D.) paraleptus* and *D. (D.) yongei* have subdorsal somatic setae with spatulated or lance-shaped tip, unlike *D. (D.) nibelungus* sp. nov. (Timm 1970; Decraemer 1974, 1975). The presence of a long and thin terminal main ring as well as the short cephalic setae with blunt tips (Freudenhammer 1975) are useful to differentiate *D. (D.) bathyalis* from the new species described herein. Regarding *D. (D.) borealis*, it differs from *D. (D.) nibelungus* sp. nov. in its fusiform body shape and the spine-like setae observed on the 15th main ring (Kreis 1963). Both *D. (D.) coronatus* and *D. (D.) nibelungus* have a protuding lip region, not covered by concretion material. However, the subdorsal setae of *D. (D.) coronatus* are slightly longer than the subventral ones, it possesses short cephalic setae and a much shorter spicules in males (Soetaert 1989) (see Table 3).

Desmoscolex (D.) galeatus has cephalic setae and an elongated pair of subdorsal setae on the 13th and 16th–17th rings (Freudenhammer 1975), unlike *D. (D.) nibelungus* sp. nov., whose pair of subdorsal setae on the 13th main ring has average length (see Tables 2 and 3). Males of *D. (D.) gladisetosus* have wiry cephalic setae and a thin and long terminal main ring (Timm 1970), which differs from the

above-mentioned features that characterize the new species. Similarly, *D. (D.) lapilliferus* is notable for its somatic and cephalic setae with a long dark curved tip as well as a long and thin terminal main ring (Freudenhammer 1975), differing from *D. (D.) nibelungus*. The cauliflower-shaped cephalic setae of *D. (D.) opacus* distinguishes it from *D. (D.) nibelungus* (Bussau 1993). Unlike the species described in this study, *D. (D.) perspicuus* has short somatic setae, increasing in length towards the tail, as well as a long spinneret at its end (Freudenhammer 1975). Moreover, *D. (D.) nibelungus* apparently lacks cephalic setae, whereas *D. (D.) petalodes* possesses cephalic setae with flag-like tip (Lorenzen 1972).

***Desmoscolex (Desmoscolex) valkyria* sp. nov.**

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Figs 5–6, Tables 1, 4–5

Diagnosis

The main diagnostic characteristics of *Desmoscolex (Desmoscolex) valkyria* sp. nov. include: (1) high number of main rings (22–24); (2) rounded cephalic region with prominent vesicular amphid; (3) thick cephalic setae; (4) reddish pigment globules along the interior of body; (5) penultimate main ring with both pairs of subdorsal and subventral setae; (6) wide, short and conical end ring with very long spinneret.

Etymology

The specific name ‘*valkyria*’ as noun in apposition refers to the female figures in Norse mythology who guide the souls of the dead to the Valhalla Hall of the god Odin and who star in the second opera of ‘The Ring of the Nibelung’.

Material examined

Holotype

MEDITERRANEAN SEA • ♂, adult (mounted in glycerine); Cassidaigne Canyon, Station U13; 43°0′47.050″ N, 5°45′32.220″ E; depth 952 m; 27 Apr. 2022; CREOCEAN enterprise leg.; ZMB 12962; ZMB.

Paratypes

MEDITERRANEAN SEA • 1 ♂, adult (mounted in glycerine); Cassidaigne Canyon, Station U08; 42°57′25.770″ N, 5°14′2.430″ E; depth 1530 m; 12 Jan. 2022; CREOCEAN enterprise leg.; ZMB 12963; ZMB • 1 ♂, adult (mounted in glycerine); Cassidaigne Canyon, Station U09; 42°51′32.040″ N, 5°14′34.620″ E; depth 1968 m; 13 Jan. 2022; CREOCEAN enterprise leg.; ZMB 12964; ZMB.

Description

See Table 4 for a summary of the most relevant measurements of the type material.

Body short (278–385µm), ventrally coiled in holotype, M1, and paratype, M2, but straight in paratype, M3. Body becomes tapered at level of cephalic region and at level of tail. Body wider at middle region. Body with 22–24 main rings.

Nine pairs of subdorsal somatic setae and nine subventral somatic setae. Male holotype (23 main rings) with subdorsal setae on the 1st, 3rd, 5th, 8th, 11th, 14th, 18th and 22nd–23rd rings. On the other hand, subventral ones appear on the 2nd, 4th, 7th, 10th, 13th, 16th, 19th and 21st–22nd main rings. Arrangement of setae exhibits variability between specimens, starting from 11th main ring for the subdorsal setae and from 13th main ring for subventral setae (Table 4). Penultimate ring always with both dorsal and ventral pairs of setae (Fig. 5A).

Cephalic region globular, slightly wider than long. Cephalic region cuticle completely covered with concretion material. Vesicular amphid extending to first main ring. Labial sensilla not identified. Thick cephalic setae, shorter than cephalic region width, located laterally (Figs 5C, 6B, 6C). Small mouth opening, leading to short (hardly extending over 2 rings), nearly cylindrical pharynx without posterior pharyngeal bulb (Figs 5B, 6A).

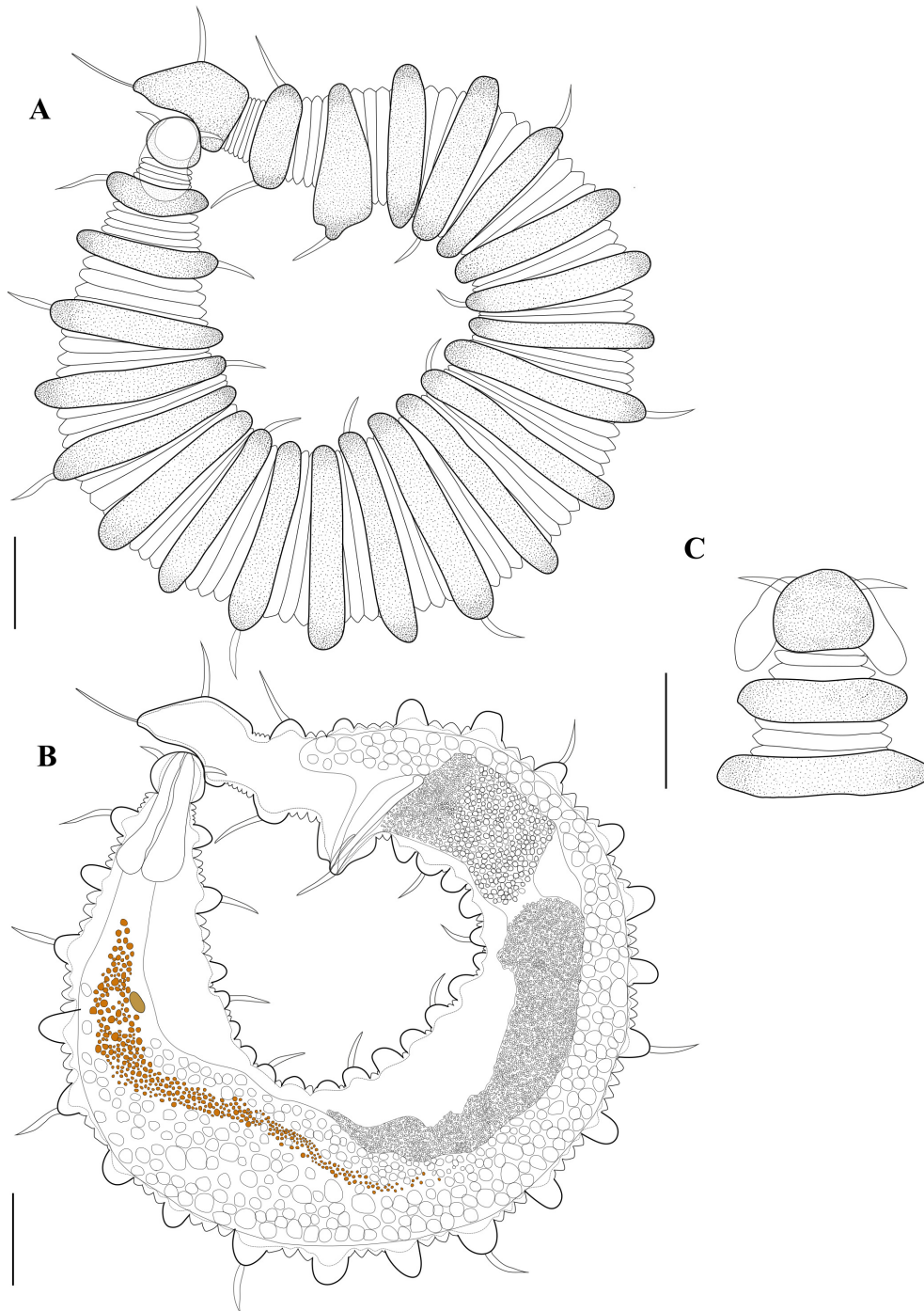


Fig. 5. Line art illustrations of *Desmoscolex (Desmoscolex) valkyria* sp. nov., ♂, adult. **A–B.** Holotype (ZMB 12962; ZMB). **C.** Paratype (ZMB 12963; ZMB). **A.** Habitus in lateral view. **B.** Habitus in optical section. **C.** Cephalic region region in ventral view. Scale bars = 20 μ m.

Pigment spot located between 3th and 5th rings. Reddish pigment globules appear along internal structures, from end of pharynx until middle region of body (Figs 5B, 6A), apparently associated with intestine.

Males monorchic with single testis outstretched and extending anteriorly up to level of 12th main ring. Spicule almost straight and cephalated (Figs 5B, 6A). Gubernaculum parallel to spicule. Cloacal tube broad, opening outside always on antepenultimate main ring, occurring on 21st main ring in holotype and paratype M3, and on 22nd ring in paratype M2. No females found.

Tail with two main rings. Last ring wide, short and conical with long and thin spinneret (12–13 µm) (Figs 5A, 6A, 6D).

Differential diagnosis

Among the 12 described species of *D. (Desmoscolex)* that have more than 18 rings, 10 of them have more than 27 main rings. The most important features of *Desmoscolex (D.) valkyria* sp. nov. that characterize the species include: number of main rings (22–24), two pairs of somatic setae from the penultimate ring and elongated spinneret (Table 5). Female specimens of *D. (D.) aquaedulcis* Stammer, 1935 have 22 rings, but differ in the number of subdorsal somatic setae: two pairs in *D. (D.) aquaedulcis* and nine pairs in *D. (D.) valkyria*. Females of *D. (D.) aquaedulcis* also have a long end-ring with a short and pointy spinneret, unlike the short and conical tail of *D. (D.) valkyria* with a long spinneret. Males of *D. (D.) californicus* Timm, 1970 have between 22 and 23 main rings, a vesicular amphid, a short and conical end-ring and red pigment globules. Nevertheless, *D. (D.) californicus* lacks two pairs of setae on the penultimate ring, and a long spinneret but has a triangular cephalic region instead of the globular cephalic region of *D. (D.) valkyria*.

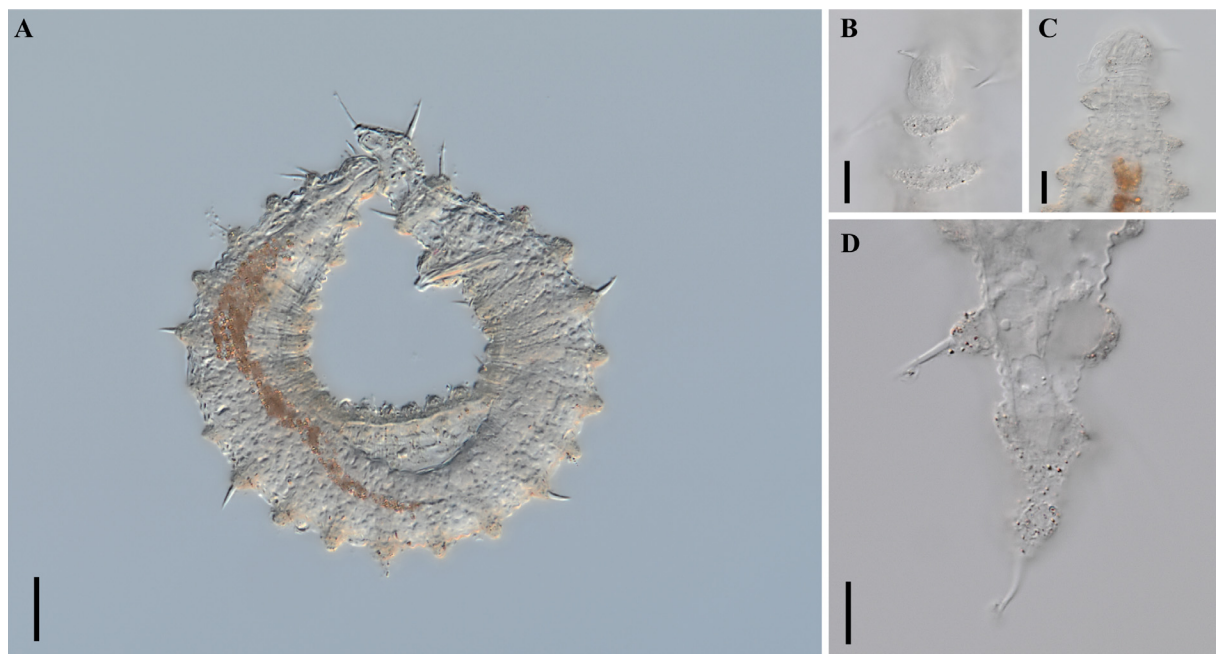


Fig. 6. *Desmoscolex (Desmoscolex) valkyria* sp. nov. **A–B.** Holotype, ♂ (ZMB 12961; ZMB). **C–D.** Paratype, ♂ (ZMB 12964; ZMB). **A.** Overview in lateral position. **B.** Detail of the cephalic region in lateral view. **C.** Detail of the cephalic region in ventral view. **D.** Detail of the tail in lateral position. Scale bars: A = 20 µm; B–D = 10 µm.

Table 4 (continued on next page). Measurements (μm) of type material of *Desmoscolex* (*Desmoscolex*) *valkyria* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; Sd = subdorsal setae; Sv = subventral setae; Tmr = length of the terminal ring; Tmrw = maximum width of the terminal ring; N.A. = not available, denotes instances where characters were not discernible due to the specimen's position. Numbers enclosed in brackets provide information about the number of setae present on each ring. The measurements of the setae pertain to one of the pairs unless explicitly specified as unique.

specimen	male		
	holotype	paratypes	
	ZMB 12962	ZMB 12963	ZMB 12964
total length	313	278	385
a	7	8	9
b	13	10	12
c	6	6	7
c'	1	1	1
maximum body width	42	36	45
maximum desmen width	50	42	52
head length	13	13	13
head width	15	16	18
cephalic setae	5	6	7
pharynx length	24	28	31
Sd 1	12 (2)	9 (2)	8 (2)
Sd 3	9 (2)	7 (2)	NS
Sd 5	7 (2)	6 (2)	6 (2)
Sd 8	8 (2)	8 (2)	6 (2)
Sd 11	8 (2)	7 (2)	7 (2)
Sd 14	9 (2)	–	8 (2)
Sd 15	–	7 (2)	–
Sd 17	–	–	10 (2)
Sd 18	8 (2)	–	–
Sd 19	–	7 (2)	–
Sd 21	–	–	12 (2)
Sd 22	12 (2)	–	17 (2)
Sd 23	13 (2)	11 (2)	–
Sd 24	–	14 (2)	–
Sv 2	5 (2)	5 (2)	3 (2)
Sv 4	6 (2)	4 (2)	5 (2)
Sv 7	7 (2)	6 (2)	7 (2)
Sv 10	8 (2)	7 (2)	7 (2)
Sv 13	8 (2)	8 (2)	8 (2)
Sv 15	–	–	9 (2)
Sv 16	8 (2)	–	–
Sv 17	–	9 (2)	–
Sv 18	–	–	8 (2)
Sv 19	9 (2)	–	–
Sv 20	–	9 (2)	13 (2)

Table 4 (continued).

	male		
	holotype	paratypes	
Sv 21	9 (2)	–	11 (2)
Sv 22	10 (2)	9 (2)	–
Sv 23	–	9 (2)	–
tail length	49	49	58
Tmr	22	26	24
Tmrw	15	14	19
spicule length	30	27	20
gubernaculum	13	12	7
spinneret	13	N.A.	12

Table 5. Main differences between species of *Desmoscolex* (*Desmoscolex*) Claparède, 1863 with between 22 and 24 main rings. If only male or female of the species are included in the table, this means that the lacking gender does not present one of the aforementioned characteristics and, therefore, does not belong to this group.

species	amphideal fovea	somatic setae arrangement	terminal ring
<i>D. (D.) valkyria</i> sp. nov.	vesicular; extending over 1 st ring	9 pairs of subdorsal; 9 pairs of subventral	conical; very long spinneret
<i>D. (D.) aquaedulcis</i> Stammer, 1935 (♀)	oval	9 pairs of subdorsal; 1 pair of subventral	conico-cylindrical; short spinneret
<i>D. (D.) californicus</i> Timm, 1970 (♂)	vesicular/elliptical, extending over 1 st ring	8 pairs of subdorsal; 8 pairs of subventral	conical; short spinneret

Discussion

The number of concretion rings covering the cuticle is constant in species with seventeen rings or less, but a variable number of main rings is a common characteristic in nematodes, with more than eighteen rings as in the case of *D. (D.) valkyria* sp. nov. that has between 22 and 24 main rings. Of the species with more than 18 rings, five possess a variable number of main rings due to sexual dimorphism or intraspecific variability: males of *Desmoscolex (Desmoscolex) aquaedulcis* have 18 main rings whereas females have 22 rings (Stammer 1935); males of *Desmoscolex californicus* have between 22 and 23 main rings, whereas females possess 18 (Timm 1970); males of *Desmoscolex (Desmoscolex) velifer* Timm, 1970 have between 43 and 44, and females have between 31 and 38 main rings (Timm 1970); specimens of *Desmoscolex (Desmoscolex) labiosus* Lorenzen, 1969 and *Desmoscolex (Desmoscolex) multiannulatus* Decraemer, 1983 have between 33 and 36, and 27 and 34 main rings, respectively (Lorenzen 1969; Decraemer 1983).

To date, only three other species of *Desmoscolex (Desmoscolex)* have been described from the Mediterranean deep sea, specifically from a deep-sea transect off Calvi (Corsica): *Desmoscolex (Desmoscolex) membranifer* Soetaert, 1989 and *Desmoscolex (Desmoscolex) parabyssorum* Soetaert 1989, at 530 m depth; and *Desmoscolex (Desmoscolex) variabilis* Soetaert, 1989 at 820 m depth. The specimens described in the present work were found between depths of 605 and 1968 meters. However, these three species have 17 main rings, unlike *D. (D.) valkyria* sp. nov., that possesses between

Table 6 (continued on next page). Comparative characteristics of *Desmoscolex* (*Desmoscolex*) Claparède, 1863 species lacking cephalic setae, from Jung *et al.* 2024, with the inclusion of *Desmoscolex* (*Desmoscolex*) *nibelungus* sp. nov. Abbreviations: M = male; F = female; – = unknown; Sd = subdorsal setae; Sv = subventral setae.

taxa	body length (µm)	number of main ring	setae arrangement	head	characters				locality
					amphid	subdorsal setae	subventral setae	habitat	
<i>D. (D.) asetosus</i> Decraemer, 1975	M: 225–250 F: 275, 320	17	Sd: ♂, ♀ (1,3,5,7,9,11,13,16,17) Sv: ♂, ♀ (2,4,6,8,10,12,14,15)	asymmetrical, bipartite, bent to the dorsal side	extends wide base with a bent lance-shaped tip	wide base with a sharp, short tip	sandy bottom with layer of silt and abundant foraminifera, 21.5 m	Lizard Island, Great Barrier Reef, Australia	
<i>D. (D.) lanceosetatus</i> Jug, Kihm & Rho, 2024	M: 295–440 F: 250–310	17	Sd: ♂, ♀ (1,3,5,7,9,11,13,16,17) Sv: ♂ (2,4,6,8,10,12,14,15), (2,4,6,8,10,12,15)	asymmetrical, bent to the dorsal side	vesicular, extends to the posterior margin of the first main ring	wide base with lance-shaped tip	silty sand, 48 m, 103 m	Jeju Island, Korea	
<i>D. (D.) nibelungus</i> sp. nov.	M: 267–310 F: 249–309	17	Sd: ♂, ♀ (1,3,5,7,9,11,13,16,17) Sv: ♂, ♀ (2,4,6,8,10,12,14,15)	globular, with protruding and uncovered lip region	circular, nearly covers all the lateral head region	thick, with a cylindrical base and tapering towards the distal end. Last pair with wiry appearance	deep sea, 605 m, 1056 m	Cassidaigne Canyon, France	
<i>D. (D.) obscurus</i> Bussau, 1993	M: 365 F: 445	17	Sd: ♂, ♀ (1,3,5,7,9,11,13,16,17) Sv: ♂ (2,4,6,8,10,12,14,15), ♀ (2,4,6,8,10,12,15)	–	vesicular, slightly beyond first main ring	lance-shaped tip	deep sea, 4154 m, 4174 m	Peru Basin	

Table 6 (continued).

taxa	body length (µm)	number of main ring	setae arrangement	characters					
				head	amphid	subdorsal setae	subventral setae	habitat	locality
<i>D. (D.) rostratus</i> Timm, 1970	F: 330	31	Sd: ♀ (1,4,7,11,15,19,23,29,31) Sv: ♀ (2,5,9,13,17,21,27)	asymmetrical with a long snout to first main ring	ovate, extending to first main ring	inconspicuous lanceol tip, single terminal subdorsal setae	–	rock dredge, 73 m	Indian Ocean
<i>D. (D.) rotundicephalus</i> Jug, Kihm & Rho, 2024	M: 275 F: 255–320	17	Sd: ♂, ♀ (1,3,5,7,9,11,13,16,17) Sv: ♂ (2,4,6,8,10,12,14,15), ♀ (2,4,6,8,10,12,15)	globular head with a protruding most of the head	oval, covering most of the head	tapering to an open tip without lance-shaped tip	normal fine structure	silty sand, 103 m	Jeju Island, Korea

22 and 24 desmen. Regarding *D. (D.) nibelungus* sp. nov., which also has 17 rings, it mainly differs from *D. (D.) membranifer* by the number of subventral setae (Soetaert 1989) – eight setae in *D. (D.) nibelungus* and six setae in *D. (D.) membranifer*; the flag-like cephalic setae of the latter species, in contrast to *D. (D.) nibelungus* sp. nov. that lacks cephalic setae; and the thin last desmos of *D. (D.) membranifer* (Soetaert 1989), unlike *D. (D.) nibelungus* that has a beak-shaped last desmos. On the other hand, both *D. (D.) parabyssorum* and *D. (D.) variabilis* have seven subventral setae (Soetaert 1989), differing from *D. (D.) nibelungus* that, as mentioned above, possesses eight subventral setae. Moreover, *D. (D.) parabyssorum* has short cephalic setae and a thin last desmos (Soetaert 1989), unlike *D. (D.) nibelungus* that lacks cephalic setae and has a beak-shaped last desmos. These last features of *D. (D.) nibelungus* also distinguish it from *D. (D.) variabilis*, that has long cephalic setae and a thin tail, sometimes the distal part is uncovered by concretion material (Soetaert 1989). Additionally, the somatic seta of *D. (D.) variabilis* end on a small spatulate tip (Soetaert 1989), not present in the somatic setae of *D. (D.) nibelungus*.

Jung *et al.* (2024) recently assessed the peculiarity of the lack of cephalic setae in certain species of *Desmoscolex*. In their study, they provide a comparative table of species within the genus that lack cephalic setae. Given that one of the species described herein – *Desmoscolex (Desmoscolex) nibelungus* sp. nov. – apparently also exhibits this unusual characteristic, we would like to add it to their comparative table (Table 6), to keep it updated and reflecting the most recent descriptions within the genus.

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