

Groundwater oligochaetes (Annelida, Clitellata) from the Mercantour National Park (France), with the descriptions of one new genus and two new stygobiont species

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ABSTRACT

Although recognized as an outstanding hotspot of biodiversity for both flora and fauna, the Mercantour massif remains almost totally unexplored in terms of its groundwater fauna. This work presents the first overview of groundwater oligochaete assemblages of the Mercantour National Park after a standardized exploration of both consolidated (fractured massif) and unconsolidated (porous) aquifers. About 40 species of oligochaetes were found at 49 stations representative of the main hydrogeological basins of the Mercantour National Park, from both spring and hyporheic zone habitats. Five stygobiont species are identified, probably all new to science, of which two are formally described: *Aberantidrilus stephaniae* Martin n. gen., n. sp. (Naididae Ehrenberg, 1828, Phallo-drilinae Brinkhurst, 1971) and *Marionina sambugarae* Schmelz n. sp., a species belonging to the widespread *Marionina argentea* (Michaelsen, 1889) species complex (Enchytraeidae Vejdovský, 1879). The freshwater subterranean species formerly attributed to *Abyssidrilus* Erséus, 1992 are transferred to *Aberantidrilus* Martin n. gen., which means that *Abyssidrilus* is now restricted to its marine, abyssal species. A dozen of the Mercantour species can be considered as stygophiles. Most stygobiont species are recorded from hyporheic habitats, and stygophiles have a more balanced distribution between both kinds of

KEY WORDS
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Mercantour,
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new species,
new genus.

habitats. The near absence of stygoxene species from the hyporheic zone suggests that this habitat is less affected by the epigeal environment than springs. The dominance of enchytraeids among the groundwater oligochaete fauna is here confirmed, and the lumbriculid genus *Trichodrilus* Claparède, 1862 is also a characteristic faunistic element of the underground freshwater oligochaete communities. The possibility that *Aberrantidrilus cuspis* n. comb. *sensu* Sambugar *et al.* (1999) is a complex of cryptic species is discussed in the framework of recent progress in the knowledge of groundwater biodiversity.

RÉSUMÉ

Les oligochètes (Annelida, Clitellata) des eaux souterraines du Parc national du Mercantour (France), avec la description d'un nouveau genre et de deux nouvelles espèces stygobiontes.

Bien qu'il soit reconnu comme un remarquable point chaud de biodiversité pour sa flore et sa faune, le massif du Mercantour reste presque totalement inexploré quant à sa faune souterraine. Ce travail rapporte le premier aperçu des assemblages d'oligochètes des eaux souterraines du Parc national du Mercantour, suivant une exploration standardisée des aquifères consolidés (massif fracturé) et non consolidés (poreux). Environ 40 espèces d'oligochètes ont été trouvées dans 49 stations représentatives des principaux bassins hydrogéographiques du Parc national du Mercantour, ainsi que des sources et de la zone hyporhéique. Cinq espèces stygobiontes ont été identifiées, probablement toutes nouvelles pour la science, parmi lesquelles deux sont ici formellement décrites, *Aberrantidrilus stephaniae* Martin n. gen., n. sp. (Naididae Ehrenberg, 1828, Phallo-drilinae Brinkhurst, 1971) et *Marionina sambugarae* Schmelz n. sp., une espèce appartenant au complexe d'espèces *Marionina argentea* (Michaelson, 1889) (Enchytraeidae Vejdovský, 1879) à large répartition. Les espèces d'eaux douces souterraines autrefois attribuées *Abyssidrilus* Erséus, 1992 sont transférées dans le genre *Aberrantidrilus* Martin n. gen., restreignant ainsi *Abyssidrilus* à ses espèces marines abyssales. Douze des espèces du Mercantour peuvent être considérées comme stygophiles. La plupart des espèces stygobiontes proviennent des habitats hyporhéiques tandis que les stygophiles se répartissent de façon plus équilibrée entre les deux types d'habitats. La quasi-absence d'espèces stygoxènes dans la zone hyporhéique suggère que cet habitat est moins affecté par l'environnement épigé que les sources. La dominance des enchytraéides au sein de la faune des oligochètes des eaux souterraines est ici confirmée, ainsi que le genre *Trichodrilus* Claparède, 1862 en tant qu'élément faunistique le plus caractéristique des communautés d'oligochètes des eaux douces souterraines. Enfin, la possibilité qu'*Aberrantidrilus cuspis* n. comb. *sensu* Sambugar *et al.* (1999) soit un complexe d'espèces cryptiques est discutée dans le cadre des progrès récents dans la connaissance de la biodiversité des eaux souterraines.

MOTS CLÉS
Clitellata aquatiques,
Oligochètes,
eaux souterraines,
Mercantour,
combinaisons nouvelles,
espèces nouvelles,
genre nouveau.

INTRODUCTION

Present knowledge on groundwater invertebrates stresses the high proportion of oligochaetes in invertebrate communities living in porous and in consolidated aquifers (Giani *et al.* 2001; Creuzé des Châtelliers *et al.* 2009). Because of complex hydrological connections between surface and ground waters, oligochaete assemblages generally include species originating from both habitats, often resulting in high frequencies of occurrence, abundance and diversity (Dole 1983; Strayer 2001; Lafont & Malard 2001). Nevertheless, in contrast to crustaceans, ecological studies on the groundwater fauna have rarely considered oligochaetes at the species level (Creuzé des Châtelliers *et al.* 2009). As a result, our knowledge of the geographical distribution of groundwater oligochaetes is highly incomplete and strongly biased by the uneven allocation of sampling effort and/or the lack of identifications at the species level (Artheau & Giani 2006). As in other European countries, distributional data in France are still rare; the most recent review stressed the existence of large geographic areas that are totally unexplored (Ferreira *et al.* 2003, 2007). The Mercantour massif is one of these poorly investigated regions, with only three stygobiont species reported in ground waters so far (one mollusc and

two crustaceans; Boeters 1970; Henry 1980). Yet the Mercantour region is recognized as an outstanding hotspot of biodiversity for both flora and fauna (e.g., Ozenda & Borel 2006; Giudicelli & Derrien 2009; Deharveng *et al.* 2015; Villemant *et al.* 2015, this issue). Nevertheless, inventories have often focused on key groups (usually vertebrates) to the detriment of other taxa (entomofauna, mosses, lichens, etc.) or of specific ecosystems (such as ground waters). Based on this observation, the Mercantour-ATBI program (All Taxa Biodiversity Inventory) was conceived with the aim to fill such gaps in our knowledge (Leccia *et al.* 2009). A global inventory of species was supported in this exceptional environment and the exploration of groundwater biodiversity was actively encouraged. This has allowed study of this fauna by qualified specialists.

The Mercantour region is located at the confluence of several climatic and biogeographic influences (Continental, Mediterranean, Alpine and Ligurian) and as such, displays a large diversity of ecological conditions, reflected by high altitudinal and thermal ranges, extremely variable geological substrates, insolation, and soil types (Olivier *et al.* 2015) (this issue). For groundwater invertebrates, this exceptional situation may favour the development of a mosaic of environmental conditions underground, related to heterogeneity

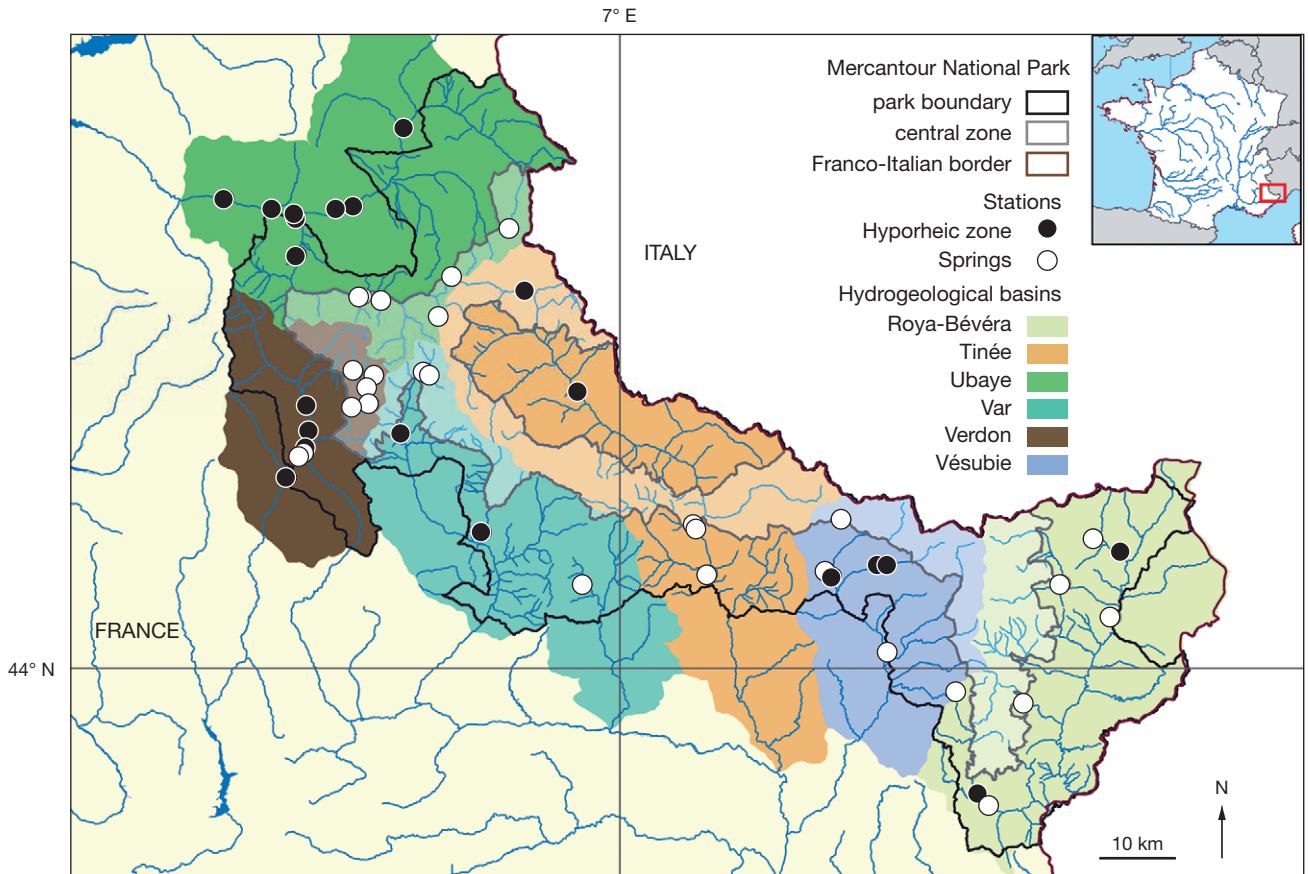


Fig. 1. — Location of the stations where oligochaetes were found in the Mercantour National Park.

in the structure of hydrogeological networks, distribution of resources, thermal conditions, and discontinuity between aquifers (Comité de Bassin RMC 1995a-c).

This work reports on the groundwater oligochaete assemblages of the Mercantour region after a standardized exploration of both consolidated (fractured massif) and unconsolidated (porous) aquifers. The discovery of species new to science leads to the erection of a new phallodriline genus, *Aberrantidrilus* n. gen., to accommodate freshwater subterranean species formerly attributed to *Abyssidrilus* Erséus, 1992. Morphological descriptions of *Aberrantidrilus stephaniae* Martin, n. gen., n. sp. and *Marionina sambugarae* Schmelz, n. sp. are provided.

MATERIAL AND METHODS

The surface hydrological network of the French side of the Mercantour massif is divided into six major hydrogeological basins drained by the Ubaye, Verdon, Tinée, Var, Vésubie and Roya-Bévéra streams (Fig. 1). The inventory of groundwater biodiversity of the Mercantour National Park was carried out according to a protocol designed to give an overview of the different hydrogeological basins, as well as of the main groundwater habitats (Dole-Olivier *et al.* 2015, this issue), i.e. springs (as outlets of consolidated aquifers) and the hypor-

heic zone of streams (as contact zone with alluvial aquifers) (Appendix 1). Other aquatic habitats, such as the unsaturated zone of the massifs (caves) were rare, and wells (deep alluvia) were almost non-existent in this region. Sampling was carried out in spring-summer 2009 for the Tinée, Vésubie, Var and Roya-Bévéra catchments, and in summer 2010 for the Ubaye and Verdon catchments. Six sites were sampled in the Tinée, Vésubie and Var catchments, nine in the Roya-Bévéra catchment (two hyporheic sites, seven springs) and 13 in the Ubaye and Verdon catchments (see Olivier *et al.* 2015).

To capture most of the species living in springs, samples were taken using drift and Surber nets and, when possible, a Bou-Rouch pump (Bou 1974; Malard *et al.* 2002), to explore the different microhabitats. The Bou-Rouch pump was also used to investigate the hyporheic zone of streams. In this case, local heterogeneity was evaluated by taking at least three replicate-samples of 10 L at a 50 cm depth in alluvia. The sampled material was preserved in the field with 95% ethanol and sorted in the laboratory. Oligochaetes were mounted and identified as described below.

MORPHOLOGICAL STUDY

Specimens were stained in alcoholic carmine, dehydrated, cleared in xylene, whole mounted in Canada balsam, and examined under a Leica compound microscope with differential interference contrast (DIC). Drawings were made by

TABLE 1. — List of oligochaetes (Annelida, Clitellata) from ground waters in the Mercantour National Park. Presence of a species is indicated by a shaded cell. Stygobiont species are highlighted in bold; stygophile species are preceded by an asterisk. Figures refer to the stations in which the species was present (see Appendix).

Family, Subfamily	Species	Hyporheic zone	Spring
Naididae			
Ehrenberg, 1828			
Naidinae Ehrenberg, 1828	Naidinae sp.	18, 34	7, 25, 48
	<i>Nais bretscheri</i> Michaelsen, 1899		4
	<i>Nais communis</i> Piguët, 1906		7, 25, 28, 30, 38, 49
	<i>Nais pseudobtusa</i> Piguët, 1906	50	
	<i>Nais</i> sp.		4, 7, 25, 43
	<i>Nais stolci</i> Hrabě, 1981		4, 12
	<i>Nais variabilis</i> Piguët, 1906	14	12
Pristininae	* <i>Pristina rosea</i> (Piguët, 1906)		13
Lastočkin, 1921	* <i>Pristina longiseta</i> Ehrenberg, 1828	20	
	* <i>Pristina osborni</i> (Walton, 1906)	35	
	* <i>Pristina</i> sp.		13, 47
Phalodrilinae	<i>Aberrantidrilus stephaniae</i> Martin, n. gen., n. sp.	2	
Brinkhurst, 1971			
Rhyacodrilinae	* Rhyacodrilinae sp.	2	
Hrabe, 1963			
Tubificinae	<i>Aulodrilus</i> sp.?	2	
Vejdovský, 1884			
	Tubificinae sp.		7, 13, 47
Lumbriculidae			
Vejdovský, 1884	Lumbriculidae sp.		12
	* <i>Stygodrilus heringianus</i> Claparède, 1862	1	37, 41
	<i>Stygodrilus</i> sp. 1	2	
	* <i>Stygodrilus</i> sp. 2	2	41
	<i>Trichodrilus</i> sp. 1	14	
	<i>Trichodrilus</i> cf. <i>tenuis</i> Hrabě, 1960	1, 2, 15	
	<i>Trichodrilus</i> sp.	1, 2, 14, 16, 17, 18, 20, 36	38
Lumbricidae			
Claus, 1876	* <i>Eiseniella</i> cf. <i>tetraedra</i> (Savigny, 1826)		6
	* <i>Eiseniella tetraedra</i> (Savigny, 1826)		13
	Lumbricidae sp.		41, 47, 48
Enchytraeidae			
Vejdovský, 1879	<i>Achaeta</i> sp.	44	5
	<i>Buchholzia appendiculata</i> (Buchholz, 1863)		47
	<i>Buchholzia</i> sp.		47, 48
	<i>Cernosvitoviella</i> cf. <i>minor</i> Dózsa-Farkas, 1990		23, 37
	<i>Cernosvitoviella</i> cf. <i>parviseta</i> Gadzińska, 1974	15, 33, 36	22
	<i>Cernosvitoviella</i> cf. <i>tridentina</i> Dumnicka, 2004	1	
	<i>Cernosvitoviella minor</i> Dózsa-Farkas, 1990		37
	<i>Cernosvitoviella</i> sp.	1, 9, 32, 34, 36, 44	21, 22, 25, 28, 37, 38, 39, 40, 48
	<i>Cernosvitoviella tatrensis</i> (Kowalewski, 1916)		22
	<i>Cognettia cognettii</i> (Issel, 1905)		48
	<i>Cognettia glandulosa</i> (Michaelsen, 1888)		12, 23, 37
	<i>Cognettia</i> sp.		12, 21, 48
	<i>Cognettia sphagnetorum</i> (Vejdovský, 1878)		12, 22, 24, 28, 37, 48
	Enchytraeidae sp.	1, 11, 15, 20, 33, 44, 46	5, 9, 12, 22, 23, 28, 47, 48, 49
	<i>Enchytraeus buchholzi</i> group Vejdovský, 1879	14	9, 37, 48
	<i>Enchytraeus</i> sp.	32, 46	12, 29, 30, 39, 40
	<i>Fridericia</i> cf. <i>auritoides</i> Schmelz, 2003		48
	<i>Fridericia</i> cf. <i>bulboides</i> Nielsen & Christensen, 1959		22
	* <i>Fridericia perrieri</i> (Vejdovský, 1878)		49
	<i>Fridericia</i> sp.	45	5, 13, 21, 37, 41
	<i>Henlea perpusilla</i> Friend, 1911		5, 21, 29, 41
	<i>Henlea</i> sp. Michaelsen, 1889		13
	* <i>Marionina argentea sensu lato</i> (Michaelsen, 1889)	1	22, 23, 28, 38, 47
	* <i>Marionina mendax</i> Rota, 2013	1	
	<i>Marionina sambugarae</i> Schmelz, n. sp.	1, 11, 33	22, 25, 37, 41
	<i>Mesenchytraeus armatus</i> (Levinsen, 1884)		3, 12, 38, 40, 48
Haplotaxidae	* <i>Haplotaxis</i> cf. <i>gordioides</i> (Hartmann, 1821)	44	24, 38, 41, 48

means of a camera lucida. The type material is deposited at the Royal Belgian Institute of Natural Sciences (IRScNB), Brussels (Belgium) and the Muséum national d'Histoire naturelle (MNHN), Paris (France). Segment numbers are designated by Roman numerals and septa are denoted by Arabic numbers of the adjacent segments (e.g., septum 10/11 lies between

segments X and XI). The comparison table of morphological characters between *Aberrantidrilus* Martin, n. gen. species was produced using the computer-aided identification software Xper2 v.2.3.1 (Ung et al. 2010). By convention, specimens are designated alphabetically when there are many on the same slide, following a horizontal scanning starting from top left.

The anatomical terms of location “proximal” and “distal” are usually defined in reference to: 1) the point of attachment or origin of a feature; or 2) the midpoint of the body (e.g., Maggenti (Basinger) & Maggenti 2005). Although both references coincide in human anatomy, they may lead to confusion, and have indeed done so in the past, when applied to the internal organs of oligochaetes, making a clarification necessary. In our species descriptions, the terms “proximal” and “distal” always refer to the point of origin of a structure, which should be understood in a spatial or even embryologic framework. Because atria and spermathecae develop from an epidermal (ectodermal) invagination (see e.g., Gustavsson & Erséus 1997), “proximal” and “distal” designate parts of these structures close to, or far from, the atrial and spermathecal pores, respectively. This interpretation is in line with the leading literature on the Oligochaeta. Our interpretation corresponds perfectly with that of Brinkhurst & Jamieson (1971), when they describe “spermathecae... with... discrete ducts... with a proximal swelling” in *Kincaidiana freidris* Cook, 1966, as illustrated in their fig. 5.4K (Brinkhurst & Jamieson 1971). This issue was more thoroughly addressed by Martin & Ait Boughrou (2012: 20, 21).

LINGUISTIC CONVENTION

The classification adopted here follows the definition of an enlarged taxon Naididae Ehrenberg, 1828 (see Erséus *et al.* 2008, 2010), including the former family Tubificidae Vejdovský, 1884 and the recently erected subfamily Rhyacodriloidinae (Martin, Martínez-Ansemil & Sambugar, 2010). However, the former Tubificidae constitutes a homogeneous group, not only morphologically but also from an ecological point of view. For convenience, we will use the vernacular name “tubificid” hereinafter to designate this paraphyletic assemblage when necessary.

ABBREVIATIONS

Abbreviations used in the figures

a	atrium;
ab	amorphous body;
apr	anterior prostate gland;
ds	dorsal seta;
m	muscle;
mp	male pore;
ov	ovary;
pp	porophore;
ppr	posterior prostate gland;
ps	penial seta;
sf	sperm funnel;
sp	spermatozoa;
spa	spermathecal ampulla;
spd	spermathecal duct;
spp	spermathecal papilla;
vd	vas deferens;
vs	ventral seta.

Institutions

MNHN	Muséum national d’Histoire naturelle, Paris;
IRScNB	Institut royal des Sciences naturelles de Belgique, Bruxelles.

RESULTS

About 40 species of oligochaetes were found at 49 stations, from a total of 53 sampled stations representative of the main hydrogeological basins of the Mercantour National Park, as well as of the spring and hyporheic zone habitats (Fig. 1; Appendix). They are summarized, by family, in Table 1. In this species list, five species were collected only from springs and the hyporheic zone, and are considered stygobionts: *Aberrantidrilus stephaniae* Martin, n. gen., n. sp., a thalassoid taxon (a stygobiont derived from marine ancestors, which colonized continental ground waters from the marine environment) belonging to the primarily marine subfamily Phallodrilinae Brinkhurst, 1971 (Naididae Ehrenberg, 1828); three limnicoid stygobionts (*sensu* Boutin & Coineau 2005), viz. *Stylodrilus* sp. 1, *Trichodrilus* sp. 1, and *Trichodrilus* cf. *tenuis* (all Lumbriculidae Vejdovský, 1884); and *Marionina sambugarae* Schmelz, n. sp. (Enchytraeidae Vejdovský, 1879), a species belonging to the widespread *Marionina argentea* (Michaelsen, 1889) species complex (Schmelz & Collado 2010), which has recently been differentiated into four species (Rota 2013). All of these species are probably new to science; two are here formally described as new, while the other three are suggested to be new, pending the examination of additional material (see below). In addition, about ten species can be considered as stygophiles, according to Artheau & Giani (2006): all *Pristina* Ehrenberg, 1828 species, *Stylodrilus heringianus* Claparède, 1862, *Eiseniella tetraedra* (Savigny, 1826), *Fridericia perrieri* Vejdovský, 1878, *Marionina mendax* Rota, 2012, *Haplotaxis* cf. *gordioides*, and possibly a specimen mentioned as Rhyacodrilinae sp.

Concerning habitat and distribution observations, it is worth noting that, except for *M. sambugarae* Schmelz, n. sp., the stygobiont species are almost entirely recorded from hyporheic habitats. Stygophiles have a more balanced distribution between the two kinds of habitats, although *Haplotaxis* cf. *gordioides* is clearly more frequent in springs. Lastly, although stygoxene species may be present in the hyporheic zone, the bulk of them were found in springs.

SYSTEMATICS

Family NAIDIDAE Ehrenberg, 1828
Subfamily NAIDINAE Ehrenberg, 1828
Genus *Nais* Müller, 1773

Nais communis Piguet, 1906/
Nais variabilis Piguet, 1906

Nais communis Piguet, 1906: 247.

Nais variabilis Piguet, 1906: 253.

MATERIAL EXAMINED. — Station 7: slide 10.357.04(c); station 12: slide 10.349.01(b); station 14: slide 11.251.03(a); station 25: slides 11.264.07, 11.264.08; station 28: 11.265.03; station 30: slide 10.349.06(a); station 37: slides 11.259.04, 11.259.05; station 38: slide 11.258.03(a,b); station 49: slide 10.351.02; IRScNB, I.G. 32392.

REMARKS

Recent molecular data have shown that these two species are actually an assemblage of at least five distinct evolutionary lineages, representing a morphological continuum covering the variation of the *Nais communis/variabilis* complex (Envall *et al.* 2012). No morphological revision of this complex has been carried out so far, which prevents an identification of these cryptic species otherwise than with molecular data. Although morphologically very similar, *N. communis* and *N. variabilis* are said to be different in their ability to swim (*N. variabilis*) or not (*N. communis*), and in an abrupt or gradual dilatation of oesophagus from VII (*N. variabilis* and *N. communis*, respectively) (Piguet 1906). On preserved material, only this last character can be assessed. In spite of uncertainties about the exact nature of both species, we tentatively distinguish our taxa (Table 1) on the basis of this character, pending an assessment of its discriminatory value in the future.

Subfamily PHALLODRILINAE Brinkhurst
in Brinkhurst & Jamieson, 1971

Aberrantidrilus Martin, n. gen.
(Fig. 2)

TYPE SPECIES. — *Aberrantidrilus stephaniae* Martin, n. sp. (Fig. 2)

OTHER INCLUDED SPECIES. — *Aberrantidrilus cuspis* (Erséus & Dumnicka, 1988) n. comb. and *A. subterraneus* (Rodríguez & Gi-ani, 1989) n. comb.

DIAGNOSIS. — Freshwater subterranean phallodrilines. Somatic setae all bifid, similar in all bundles, or with upper tooth much reduced or absent in posterior bundles. Penial setae present, bifid or single-pointed, one per bundle, orientated in anterior direction. Atria covered by a thick muscular layer, opening to exterior on conical male protuberances (porophores). Posterior prostate gland small, attached by a short stalk to proximal end of atrium, at base of pseudopenis. Spermathecal pores in segment XII, on the ventral portion of the body; spermathecae with short ducts and thin-walled ampullae.

ETYMOLOGY. — The name *Aberrantidrilus* (from *drilos*, “worm” in Greek and *aberrans*, *-tis*, present active participle of the Latin *aberrare*, “wander, stray, deviating from”) refers to the aberrant location of the spermathecal pores of the species, in segment XII. Spermathecae are in X (or at least anterior to the atrial segment) in all tubificids except one other phallodriline, *Mexidrilus postspermathecus* (Erséus 1980).

REMARKS

The decision to erect a new genus to accommodate all the freshwater subterranean species formerly attributed to *Abyssidrilus* Erséus, 1992 is supported by a unique combination of characters, rather than formally proposed apomorphies, namely the location of spermathecal pores in XII, the unisetal condition of penial setae and their teeth directed anteriorly. The fact that the three species included in *Aberrantidrilus* Martin, n. gen. are found in subterranean freshwater, as opposed to the marine *Abyssidrilus*, is considered as additional evidence to support this decision.

The genus *Abyssidrilus* is commonly defined as a monophyletic group of species sharing slender, often sharply single-pointed,

somatic setae, a synapomorphy unique for the subfamily (Erséus 1992). Although more or less seen in the subterranean freshwater forms *A. cuspis* n. comb. and *A. subterraneus* n. comb., this character is not present in *A. stephaniae* Martin, n. gen., n. sp. in spite of its great similarity and assumed phylogenetic closeness to those species. *Aberrantidrilus stephaniae* Martin, n. gen., n. sp. has all somatic setae bifid, with teeth of similar length (see description below), which would render questionable the synapomorphy proposed for *Abyssidrilus* if the species were kept in the latter genus.

The location of spermathecal pores in XII is an exceptional condition in tubificids, so far only seen in *Aberrantidrilus* Martin, n. gen. species and *Mexidrilus postspermathecus* Erséus, 1980. If only for the rarity of this condition, it is tantalizing to consider the latter species as the closest relative to this assemblage of thalassoid stygobionts. *Mexidrilus postspermathecus* is a subtidal oligochaete, known from the West coast of Norway (Erséus 1980), with a depth distribution in accordance with the hypothesis usually put forward to explain the origin of thalassoid lineages, namely an evolution from marine ancestors by stranding following the regression of marine embayments (Notenboom 1991; Holsinger 1993; Boutin & Coineau 2005). Assuming a derivation from the *Abyssidrilus* clade, the closest relative to the thalassoid species would be a deep-sea species, *Abyssidrilus stilus*, so far only found at about 4900 m depth in the Indian Ocean. This implies an invasion of the subterranean domain via an unknown common ancestor that lived at moderate depths (Erséus 1992). Although sharing a unisetal penial “bundles” condition with *Aberrantidrilus* Martin, n. gen., *Abyssidrilus stilus* differs from the latter in having spermathecae in X, with spermathecal pores dorsal to the lateral line, and penial setae directed posteriorly.

Aberrantidrilus stephaniae
Martin, n. sp.
(Fig. 2)

TYPE MATERIAL. — **Holotype.** MNHN HEL 524, slide 11.019.01, sexually mature, mated specimen. Legit M.-J. Dole-Olivier. Type locality: Bévéra River, Sospel, Mercantour National Park, France (station H2BEV, replicate sample No 1, sample code SED66, Sospel 1), 43°52'41.01"N, 7°26'56.94"E, 372 m a.m.s.l., hyporheic zone in alluvial aquifer, 5.VIII.2009.

Paratypes. Type locality (station H2BEV, replicate sample No 1, sample code SED66, Sospel 1), 5.VIII.2009; IRScNB, I.G. 32392, slide 11.017.01: 1 immature specimen (a) and 2 sexually mature, mated specimens (b, c); MNHN HEL 524, slide 11.007.04: 1 mature, mated specimen; IRScNB, I.G. 32392, vial AB31536628: 10 specimens in absolute alcohol (8 immature, 2 mature and mated, 2 fragments). Type locality (station H2BEV, replicate sample No 2, sample code SED58, Sospel 3), 5.VIII.2009; IRScNB, I.G. 32392, slide 11.019.06: 1 mature, mated specimen, slide 11.033.01: 1 immature specimen (b on slide).

OTHER MATERIAL. — Many specimens in absolute alcohol, from unsorted material, mostly immature and/or fragments. Type locality (station H2BEV, replicate sample No 2, sample code SED58, Sospel 3), 5.VIII.2009; IRScNB, I.G. 32392, vial AB31515995. Type locality (station H2BEV, replicate sample No 3, sample code SED 62, Sospel 2), 5.VIII.2009; IRScNB, I.G. 32392, vial AB31515997.

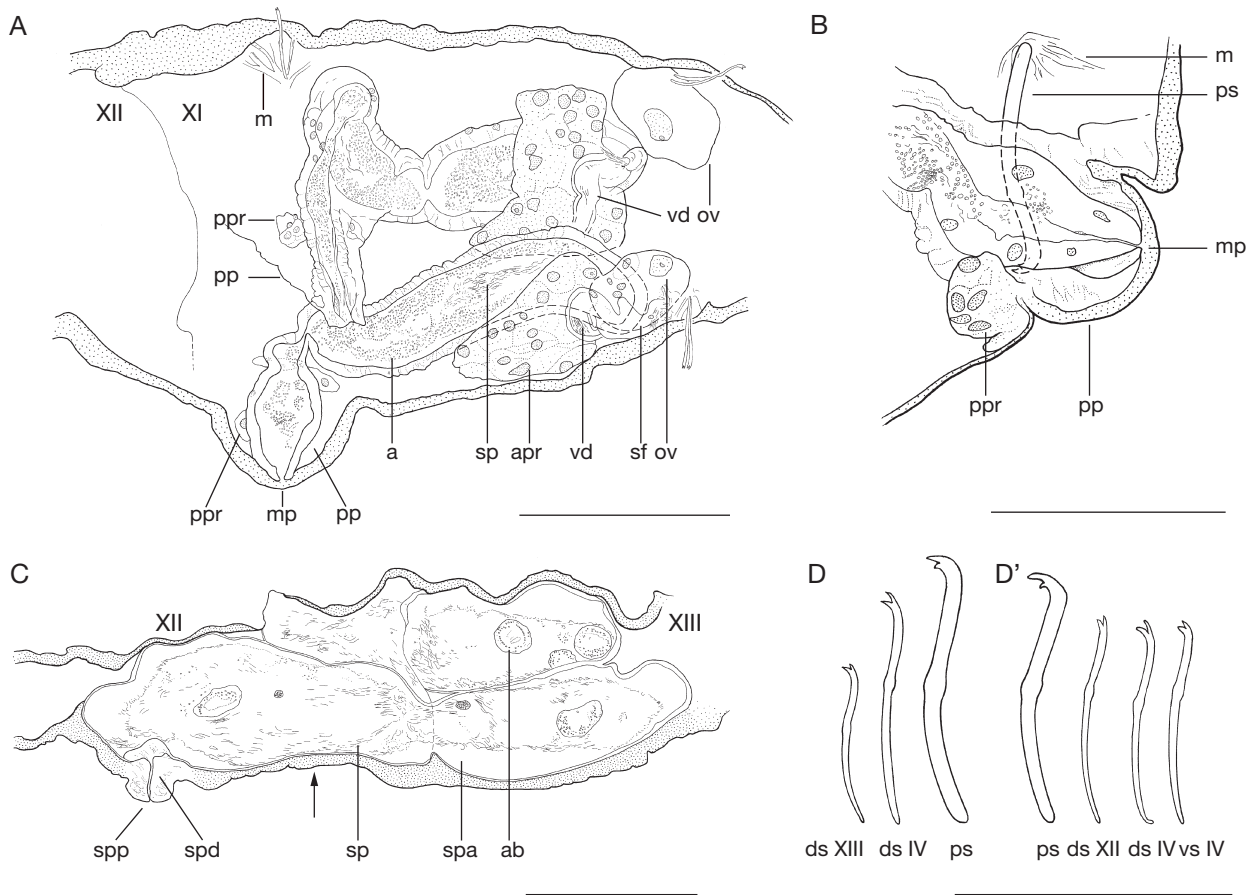


FIG. 2. — *Aberrantidrilus stephaniae* Martin, n. gen., n. sp.: **A**, male genitalia (paratype MNHN HEL 524 slide 11.007.04); **B**, detailed sketch of the pseudopenis area, showing posterior prostate (ppr) and penial seta (ps) (paratype IRScNB I.G. 32392 slide 11.019.06); **C**, spermathecae in segment XII (paratype IRScNB I.G. 32392 slide 11.017.01c); **D**, **D'**, unmodified and penial setae (ps) (D. IRScNB paratype I.G. 32392 slide 11.017.01b; D'. IRScNB holotype I.G. 32392 slide 11.019.01). Abbreviations: see Material and methods. Scale bars: A, C, 100 μ m; B, D, D', 50 μ m.

ETYMOLOGY. — The species is named after Stéphanie Marchais, playwright, in memory of the “Binôme #2” experience (“Universcience, Les sens des mots”), a dramatized “Art et science” meeting between a scientist and a dramatist, which led to “Baikal Amour Magistral”, a play that draws inspiration from the scientific activity of one of us (PM) on oligochaetes from Lake Baikal, and on evolutionary relationships between Oligochaeta and Hirudinea. The name is a genitive.

DISTRIBUTION. — Currently only known from the Mercantour National Park, France, hyporheic habitats (Fig. 3).

DESCRIPTION

Length of (fixed) holotype 4.5 mm, 23 segments (complete specimen). Maximum width 99–179 μ m (in the genital region). Prostomium rounded or slightly pointed, about as long as wide. Segments II–VI with a slight secondary annulation, mostly visible on contracted specimens. Clitellum hardly noticeable, extending over XI– $\frac{1}{2}$ XII. Somatic setae 38–43 μ m long, 1.5 μ m thick, 2–5 per bundle anteriorly, 1–3 per bundle in postclitellar segments. Somatic setae all bifid, with upper tooth of similar length to lower or slightly shorter (Fig. 2D [ds, vs]), similar in all bundles. Ventral setae of XI modified into penial setae (Fig. 2B, D [ps]), one at each male pore, sigmoid, distinctly bifid, with upper tooth longer than lower,

with teeth directed towards anterior end of worm. Penial setae 50–64 μ m long, 3.3–3.5 μ m thick, with distinct nodulus slightly proximal to middle. Ventral (penial) setae absent on XI in mature paratype MNHN Hel 11.007.04 (Fig. 2A). Male pores (Fig. 2A, B [mp]) on prominent, external, protruded porophores (Fig. 2A, B [pp]), posterior to middle of XI; penial setae between porophores and mid-ventral line. Spermathecal pores on distinct papillae (Fig. 2C [spp]) near, or anterior to, middle of XII, between lateral lines and lines of ventral setae.

Pharyngeal glands in (IV)V–VI. Anterior and posterior sperm sacs projecting to IX and XI, respectively; egg sac extending to XIII. Male genitalia (Fig. 2A) paired. Vas deferens poorly visible, shorter than atrium (Fig. 2A [vd]), entering apical end of atrium. Atrium (Fig. 2A [a]) slender, spindle-shaped and curved near ectal part, terminating in a retractable pseudopenis, 207–287 μ m long, 39–47 μ m wide, with 3–6 μ m thick outer muscular layer, giving atrium an crumpled external appearance; atrium with granular epithelium and lumen containing scattered bundles of sperm (Fig. 2A [sp]); ciliation of inner epithelium not seen. Two prostates attached to atrium. Anterior prostate gland very large, attached by a short stalk to apical end of atrium, near

TABLE 2. — Comparison between *Aberrantidrilus* n. gen. species (type specimens and other material from Sambugar *et al.* 1999).

Character	<i>Aberrantidrilus</i>		<i>A. cuspis</i> (Erséus & Dumnicka, 1988) n. comb.				<i>A. cf. cuspis</i>	
	<i>A. stephaniae</i> , n. gen., n. sp.	<i>A. subterraneus</i> (Rodriguez & Giani, 1989) n. comb.		“La Spezia” n. comb.	“Udine” n. comb.	“Aven de la Cuisinière” n. comb.	“Romana” n. comb.	“Skocjanske” n. comb.
body width at largest (µm)	139-164	127.5	190-280	–	128	–	–	–
penial setae	present	present	present	present	present	present	–	present
number of penial setae	1 per bundle	1 per bundle	1 per bundle	1 per bundle	1 per bundle	1 per bundle	–	1 (2) per bundle
length of penial setae (µm)	50-64	?	100-120	75-77	50	57-60	–	–
width of penial setae (µm)	3.3-3.5	1.5	5-7	3.5-4.0	–	3.5	–	–
length of somatic setae (µm)	38-43	31.5-35.7	40-55	42	–	47	–	–
width of somatic setae (µm)	1.5	?	2.5-5.0	–	–	1.5	–	–
ectal tip of penial seta	bifid	simple pointed	simple pointed	bifid	bifid	bifid	–	bifid
length of upper tooth of setae in anterior segments	subequal or similar to lower	reduced	subequal or similar to lower	subequal or similar to lower	subequal or similar to lower	subequal or similar to lower	subequal or similar to lower	subequal or similar to lower
length of upper tooth of setae in posterior segments	subequal or similar than lower	reduced	reduced; absent	reduced; absent	reduced; absent	absent	absent	absent
length ratio penial/somatic setae	Mean:1.39	?	Mean:2.32	Mean:1.81	–	Mean:1.24	–	–
number of setae in anterior segments	2-5	2-5	2-5	–	3-6	–	–	–
number of setae in posterior segments	1-3	3	2-4	–	–	–	–	–
atrial length (µm)	207-287	100	275-350	–	–	–	–	–
atrial width (µm)	39-47	30	28-40	–	–	–	–	–
location of spermathecal ampulla	in XII-XIII	in XII	in XII-XIII	–	–	–	–	–
longitudinal location of spermathecal pore	near middle of XII	near 11/12	near middle of XII	–	–	–	near 11/12	–

junction with vas deferens. Posterior prostate gland small, attached by a short stalk to ectal end of atrium, at base of pseudopenis (Fig. 2A, B [ppr]; gland often barely visible). One pair of spermathecae (Fig. 2C) in XII, with large, elongated, thin-walled ampulla (Fig. 2C [spa]), extending into XIII, and short, muscular ducts (Fig. 2C [spd]). Sperm as a random mass in ampullae, with amorphous round bodies (Fig. 2C [ab]), possibly of secretory origin.

REMARKS

Aberrantidrilus stephaniae Martin, n. gen., n. sp. is the third species of the thalassoid, subterranean freshwater genus *Aberrantidrilus* Martin, n. gen. It is similar to *Aberrantidrilus cuspis* n. comb. in nearly all respects, except that the penial setae are

distinctly bifid instead of lance-shaped with “sharply pointed tips”, and the bifid somatic setae have teeth of similar length on all segments, instead of having the upper tooth much reduced or absent on the posterior segments. In addition, compared with *A. cuspis* n. comb., the penial setae are smaller in length and diameter by roughly a factor of two in *A. stephaniae* Martin, n. gen., n. sp. Despite their similar body length (4.8 vs 4.5 mm, respectively), their penial to somatic setal length ratios are quite different (2.32 vs 1.39) (Table 2). *Aberrantidrilus subterraneus* n. comb. is distinguished from its congeners by the shape of the spermathecae and the location of spermathecal ampullae in XII only, somatic setae with upper tooth shorter and much thinner than lower on all segments, and the penial setae simple-pointed, slender and much thinner (Table 2).

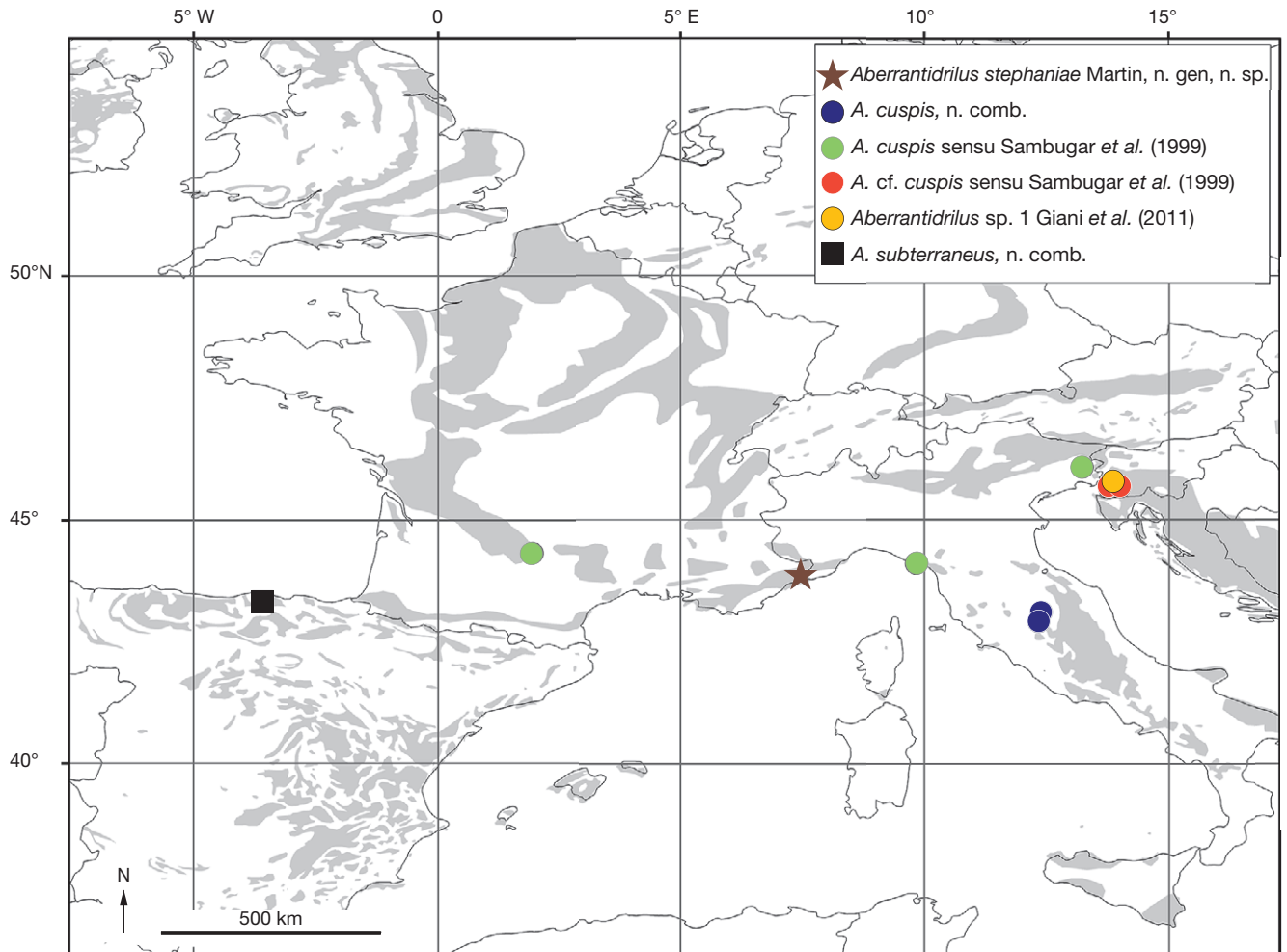


FIG. 3. — Geographical distribution of groundwater *Aberrantidrilus* Martin, 2015 species in Southern Europe. The shaded patterns indicate the areas of carbonate rock outcrops (exposed karst terrains; Williams & Fong 2010).

In their review of groundwater oligochaetes from Southern Europe, Sambugar *et al.* (1999) reported additional material from France, Italy and Slovenia (Fig. 3), ascribed to *A. cuspis* n. comb. in spite of significant differences in penial setae (distinctly bifid and shorter than those of the type material). In this respect, those specimens are most similar to *A. stephaniae* Martin, n. gen., n. sp., which suggests their attribution to *A. stephaniae* Martin, n. gen., n. sp. but a proper comparison is hardly possible due to insufficient descriptions (see Table 2). Giani *et al.* (2011) recently mentioned “*Abyssidrilus* sp. 1” from ground waters of Slovenia, which might be conspecific with specimens from Italy (Romana Cave, Trieste) and Slovenia (Škocjanske Cave), previously attributed to *Abyssidrilus* cf. *cuspis* by Sambugar *et al.* (1999), suggesting a complex of near-cryptic species (see also discussion below). However, without re-examining this material, it seems wiser, on the basis of current knowledge, to follow the taxonomic decision of Sambugar *et al.* (1999) and consider these specimens as conspecific with the form described by Erséus & Dumnicka (1988).

Subfamily RHYACODRILINAE Hrabě, 1963

Rhyacodrilinae sp.

MATERIAL EXAMINED. — Station 2: 2 immature specimens, slide 11.019.05, IRScNB, I.G. 32392.

REMARKS

Dorsal bundles with two pectinate and two smooth hair setae, ventral bundles with 2(3) bifid setae with teeth of similar length. Cœlomocytes present. These specimens are tentatively identified as Rhyacodrilinae, based on the presence of (badly preserved) cœlomocytes.

Subfamily TUBIFICINAE Vejdovský, 1876

Genus *Aulodrilus* Bretscher, 1899

Aulodrilus sp.

MATERIAL EXAMINED. — Station 2: slide 11.019.03a, 1 fragment (10 segments) of an immature specimen; IRScNB, I.G. 32392.

REMARKS

Dorsal bundles with 4–5 bifid setae per bundle, with upper tooth slightly shorter than lower, and 3–4 smooth and short hair setae. Up to seven setae in ventral bundles, with upper tooth slightly shorter than lower. No coelomocytes.

This specimen is tentatively attributed to the genus *Aulodrilus* Bretscher, 1899 on the basis of its setal features. It is also conceivable that it might belong to *Branchiura sowerbyi* Beddard, 1892, although in the latter species upper teeth in crochets are either absent or much shorter than those observed on the present specimen.

Family ENCHYTRAEIDAE Vejdovský, 1879

Genus *Marionina* Pfeffer, 1890

Marionina mendax Rota, 2013

Marionina mendax Rota, 2013: 125.

MATERIAL EXAMINED. — Station 1, slide 11.006.01(a): one fully adult specimen.

REMARKS

A recent revision of the common and widespread *Marionina argentea* (Michaelsen, 1889) (Rota 2013) resulted in the description of three new species, *Marionina deminuta* Rota, 2013, *M. mimula* Rota, 2013, and *M. mendax* Rota, 2013, and a more precise morphological diagnosis of *M. argentea sensu stricto*. Our specimen would previously have been identified as *M. argentea*. Twelve additional specimens in the present collection, belonging to the *Marionina argentea* group, belong to a new species, *M. sambugarae* Schmelz, n. sp., described below. Additional specimens in the collection belong to the *Marionina argentea* group, but due to poor fixation they could not be assigned to any of the nominal species within the group (i.e. they may or may not belong to either *M. mendax* or *M. sambugarae* n. sp.). *Marionina argentea sensu stricto* as defined by Rota (2013) was not found.

The specimen was identified as *M. mendax* based on the following observations: body length 2.4 mm, width at clitellum 0.12 mm; 22 segments; length of setae 40 µm on XI, 38 µm on XIII, pharyngeal glands in VI without dorsal lobes; preclitellar nephridia at 7/8, 9/10, efferent duct demarcated; coelomocytes oval, 10–16 µm long, with some coarse, refractile vesicles; clitellum closed dorsally, open ventrally, cells in dense transverse rows with hyalocytes distinctly larger than granulocytes, the latter mostly longer than wide, ventrolateral border of clitellum lined by granulocytes only; male pores in XII, male glandular bulb 22 µm long and 18 µm high; spermathecae each with two rounded ectal glands, diameter 12 and 8 µm, respectively.

Here we list only those characters that distinguish *M. mendax* from at least one of the other species of the *M. argentea* group (see Rota 2013: table 1), including *M. sambugarae* Schmelz, n. sp. (see below). The observable characters are in complete agreement with the original description of *M. mendax*, with the sole exception of a possible disagreement in the

number of transverse clitellar gland cell rows: 22 in our specimen, as opposed to 16 countable in fig. 1D of Rota (2013). However, this character is not dealt with in the text of the original description, and the figure may not show the full extension of the clitellum. The presence of only granulocytes at the ventrolateral border is not described in Rota (2013), but it is visible in her figure 1D (Rota 2013: fig. 1D [ggc]) and may distinguish the species from *M. deminuta*, which has a conspicuous longitudinal ventrolateral row of hyalocytes just above the male glands (cf. Rota 2013: fig. 3B); it is not clear, however, whether these are the bordering cells. Some characters could not be observed in our specimen, such as the posterior border of the brain.

Marionina sambugarae Schmelz, n. sp.

(Fig. 4)

Marionina cf. *argentea* [non *Marionina argentea* (Michaelsen, 1889)] – Giani *et al.* 2011: 93.

TYPE MATERIAL. — **Holotype**. MNHN HEL 526, slide 11.262.01, adult specimen (c), stained whole mount. Legit M.-J. Dole-Olivier. Type locality: Braissette, Uvernet-Fours, Mercantour National Park, France (station BRABA, sample code BRA, Braissette), 44°17'53.67"N, 6°47'13.84"E, 2440 m a.s.l., spring, 11.VIII.2010. **Paratypes**. Twelve adult specimens, stained whole mounts. Type locality (station BRABA, sample code BRA, Braissette), 11.VIII.2010; MNHN HEL 526, slide 11.262.01(a,d): 2 specimens, IRScNB, I.G. 32392, slide 11.264.02(c,e): 2 specimens. Tende, Roya River (station H1RO, replicate sample No 1, sample code PT1, Pont Tende), 5.VIII.2009; MNHN HEL 527, slide 11.006.01(c): 1 specimen, MNHN HEL 528 slide 11.006.02(a): 1 specimen. Colmars, Verdon River (station H3VER, sample code H3V, Haut Verdon 3 aval pont la Chaumie), 6.IX.2010; IRScNB, I.G. 32392, slide 11.255.04(a): 1 specimen. Allos (station RAVVER, sample code RAV, Source du ravin du Lac d'Allos), 2.VIII.2010; MNHN HEL 529, slide 10.343.01: 1 specimen. Allos (station MEOVER, sample code MEO, Méouilles), 3.VIII.2010; IRScNB, I.G. 32392, slide 11.258.06(b): 1 specimen. Colmars (station INFVER, sample code INF, Infiltrés), 5.VIII.2010; IRScNB, I.G. 32392, slide 11.259.07(b,c): 2 specimens. Uvernet-Fours (station CHARBA, sampling code CHAR, Charbonnière Fours St. Laurent), 1.IX.2010; IRScNB, I.G. 32392, slide 11.264.07(a): 1 specimen.

OTHER MATERIAL. — Six specimens from Slovenian caves, for further details see "*Marionina* cf. *argentea*" in Giani *et al.* (2011).

ETYMOLOGY. — Named in memory of the late Beatrice Sambugar, eminent researcher on subterranean oligochaetes, and a dear colleague.

DISTRIBUTION. — France, Mercantour National Park (Fig. 4); Slovenia, caves in Grosuplje and Logatec (Giani *et al.* 2011).

DESCRIPTION

Length *c.* 1.5 mm, diameter *c.* 0.1 mm, 21–24 segments. Two setae per bundle, absent on XII and laterally on II. Lateral setae not shifted dorsally. Setae straight and pointed ectally, curved entally. Maximum length 28–38 µm, small in II (21–24 µm), increasing in size from II to V to *c.* 30 µm; measured lengths ventrally on XI 28–35 µm, on XIII 28–38 µm. Setae of caudal segments not larger than those of XI or XIII. Epidermal gland cells not seen.

Head pore at 0/I, prostomium short, with two bulges in lateral view, separated into dorsal forefront and a ventral snout (cf. Rota 2013: fig. 1A), the latter with mid-frontal recess in epithelium. Brain posteriorly truncate or slightly incised, *c.* 70 µm long, about twice as long as wide, widest posteriorly. Pharyngeal pad about as long as wide or high. Postpharyngeal ganglia present. Pharyngeal glands in IV one unpaired dorsal lobe, no ventral lobes, in V one unpaired dorsal lobe and a pair of primary ventral lobes projecting anteriorly, in VI a pair of large and elongate ventral lobes, each with a small dorsal projection posteriorly; lobes in VI separate. Chloragocytes inconspicuous, diameter *c.* 12 µm. Dorsal blood vessel from XII, bifurcating anteriorly in III, behind pharyngeal pad, lateral commissural vessels in IV-V not observed. Midgut pars tumida in XV-XVI, covering one segment length. Preclitellar nephridia 2 pairs, at 7/8 and 9/10, anteseptale with coils of canal, separated from postseptale by slight constriction; postseptale about 1.5-2.0 × as long and high as anteseptale; efferent duct arising terminally, about as long as postseptale; no terminal vesicle. Coelomocytes *c.* 16 µm long, broadly oval, spindle-shaped in oblique view, filled with irregularly shaped vesicles; strongly refractile crystals present in some cells of some specimens.

Clitellum from XII-1/2 XIII, ending 1-2 cell rows before setae of XIII, not developed (= open) mid-ventrally and mid-dorsally (Fig. 4C). Dorsal and ventral borders of clitellum lined by flat granulocytes. Ventral clitellum-free area about as wide as distance between male pores, dorsal border of clitellum undulating. Gland cells laterally about 9 µm high and 9-16 µm wide, flatter dorso- and ventro-laterally. Cells in *c.* 21-24 dense to indefinite transverse rows (as defined by Schmelz & Collado 2010: 17).

Testes and sperm funnels in XI, ovaries and male pores in XII. Seminal vesicle absent, cysts of developing sperm in XI. Sperm funnels *c.* 50 µm long, diameter between 12 and 24 µm, depending on angle of observation. Collar *c.* 8 µm high and wide, merging into glandular body. Vasa deferentia ventrally in XII, diameter 4-5 µm, length not measurable, penetrating the male gland ("penial bulb") through its centre. Male glands roughly spherical, often slightly longer than wide and slightly wider than high, measured lengths 20-32 µm, measured widths 17-24 µm. Subneural glands absent.

Spermathecae consisting of ectal duct and ampulla; ampullae attached to oesophagus separately and latero-dorsally. Spermathecal ectal pores laterally at 4/5. Ectal glands not distinguished, ectal duct *c.* 22 µm long and 11 µm wide, with straight canal and undulating outer surface caused by bulges of cell nuclei. Ampulla spherical or oval, depending on level of contraction of animal, diameter *c.* 18 µm, walls 2-3 µm thick, inner and outer surface distinct, lumen filled with spermatozoa roughly arranged along long-axis; ental duct not seen, apparently short, if present at all.

REMARKS

Marionina sambugarae Schmelz, n. sp. belongs to a complex of species that were previously identified as *Marionina argentea* (Michaelsen 1889), until it was split into four different species,

three of them new to science (Rota 2013): *M. mendax* Rota, 2013, *M. deminuta* Rota 2013, *M. mimula* Rota, 2013 and *M. argentea* (Michaelsen, 1889) *sensu stricto*. *Marionina sambugarae* Schmelz, n. sp. is therefore the fifth member of this species group, and the only one in the group with a dorsally interrupted clitellum. The taxonomic value of this character may be questioned because it is not dealt with in Rota (2013), nor is it mentioned in the descriptions of *M. argentea* by Michaelsen (1889), Nielsen & Christensen (1959) and Chalupský (1992). However, Schmelz & Collado (2010) state that the clitellum of *M. argentea* is dorsally developed, based on observations of numerous specimens from soil and surface freshwater habitats across Europe. Furthermore, Rota (2013) gives otherwise very detailed descriptions of the clitella in the four species – their ventral interruption included – hence a dorsally interrupted clitellum, if present, would have been mentioned and described.

Besides, further characters distinguish *M. sambugarae* Schmelz, n. sp. from each of the four other species (characters of *M. sambugarae* Schmelz, n. sp. in brackets). *Marionina argentea sensu stricto* (as conceived in Rota 2013) has: coelomocytes finely granulated, spindle-shaped, up to 25 µm long (vs coarsely granulated, oval, *c.* 16 µm long); nephridial postseptale merging gradually into efferent duct (vs abrupt rise of efferent duct); and one or two distinct spermathecal ectal glands (vs indistinct or absent). *Marionina mimula* has: brain deeply incised posteriorly (vs truncate or slightly indented); dorsal blood vessel bifurcating in I (vs bifurcation in III); coelomocytes finely granulated (vs coarsely granulated); male gland diameter 32-48 µm (vs 20-32 µm); and a rosette of 7-8 spermathecal ectal glands (vs indistinct or absent). *Marionina deminuta* has: 16-21 segments (vs 21-24); setae at XI and XIII 19-24 µm long (vs 28-38 µm); coelomocytes finely granulated, spindle-shaped (vs coarsely granulated, oval); ventral border of clitellum consisting of hyalocytes (vs granulocytes); and two conspicuous spermathecal ectal glands (vs glands inconspicuous or absent). *Marionina mendax* has: pharyngeal glands in VI without dorsal projections or lobes (vs with dorsal projections). This subtle character, newly introduced by Rota (2013) to distinguish among species of the *M. argentea* complex, seems indeed to be constant: the only specimen in the collection without dorsal lobes in VI has a dorsally complete clitellum, and was hence identified as *M. mendax*.

M. sambugarae Schmelz, n. sp. is evidently most similar to *M. mendax*, these perhaps being sister species. Similarities extend to the coelomocytes, the shape of the prostomium, and the distribution pattern of lateral clitellar gland cells (cf. Rota 2013 Fig. 1A, D). Among the five species in the group, only *M. mendax* and *M. sambugarae* Schmelz, n. sp. have oval and coarsely granulated coelomocytes. In the other three species, coelomocytes are spindle-shaped and very finely granulated.

Granules in the coelomocytes of the types of *M. sambugarae* Schmelz, n. sp. are smaller than the granules in living specimens of *M. mendax*, and they are not present in all cells and specimens. Coarse refractile granules of enchytraeid coelomocytes

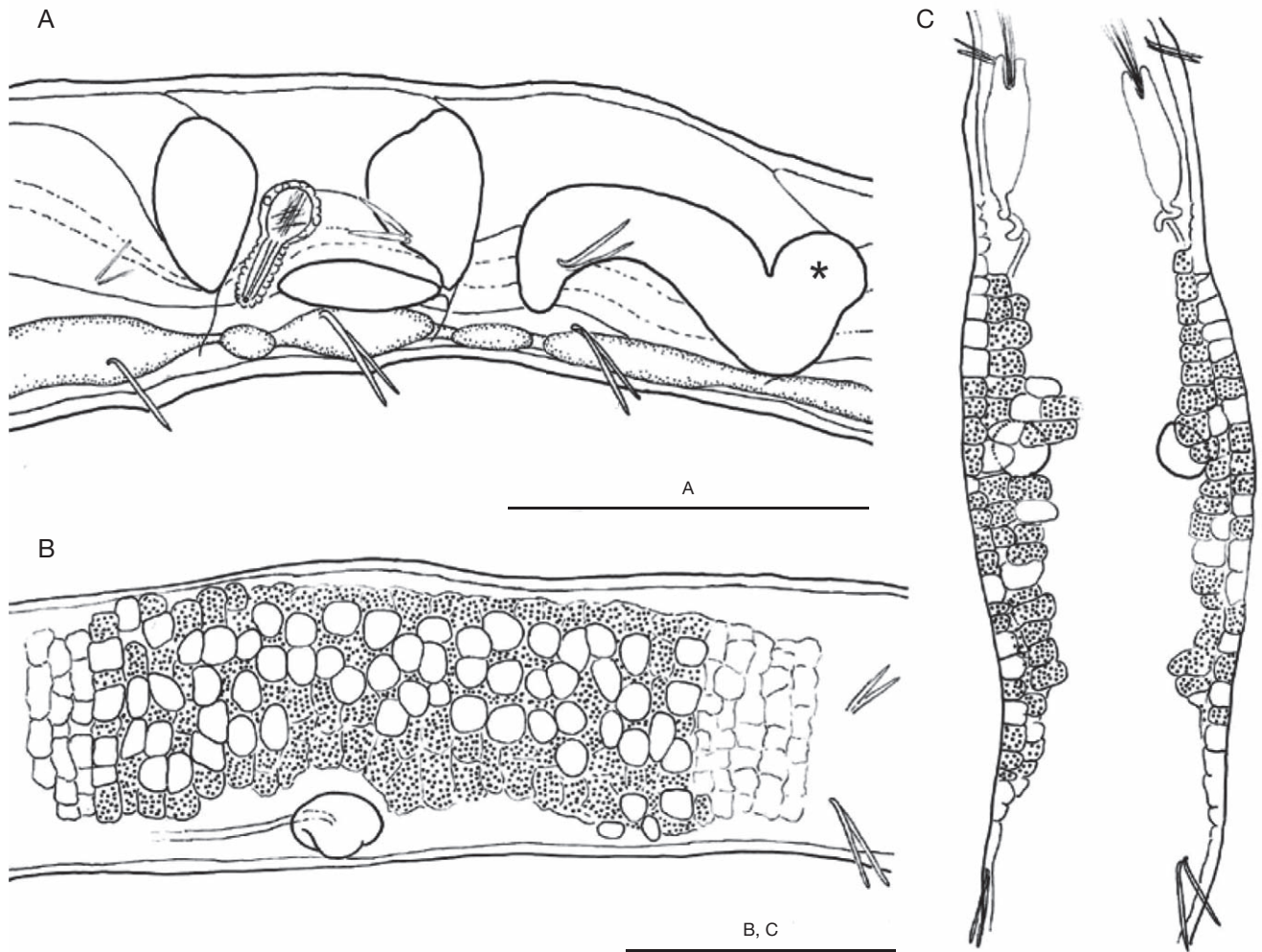


FIG. 4. — *Marionina sambugarae* Schmelz, n. sp.: **A**, segments IV-VI, lateral view (facing left) (paratype MNHN HEL 11.262.01d); **B**, clitellar region, lateral view (holotype MNHN HEL 11.262.01c); **C**, clitellar region, dorsal view, showing dorsally interrupted clitellum (paratype IRScNB I.G. 32392 slide 11.264.02e). Symbols: *, dorsal lobe of pharyngeal gland in VI. Scale bars: 100 µm.

are best seen in living specimens and they usually disappear completely during clearing and dehydration. In exceptional cases they may be preserved, as in some specimens of the types series, the holotype included. Nevertheless, the true aspect of the granules in *M. sambugarae* Schmelz, n. sp. can only be inferred, because living specimens were not available. Since granules in cells of the single specimen identified as *M. mendax* are as small as those in the types of *M. sambugarae* Schmelz, n. sp., we assume that the live aspect of the coelomocytes is similar in the latter to that in *M. mendax*: cells completely filled with irregularly shaped refractile crystals, leading to a bright white colour of specimens under reflected light. The alternative character state of fine granulation, realized in the other species of the *M. argentea* group, can be excluded, because fine granulation leads to a fine and regular pattern of coelomocyte vesicles after fixation, different from the irregular patterns seen in *M. sambugarae* and also illustrated for *M. mendax* (Rota 2013: fig. 1A).

A further possible distinguishing character of *Marionina sambugarae* Schmelz, n. sp. is the absence of spermathe-

cal ectal glands. Rota (2013) illustrates conspicuous ectal glands for all four species described, and ectal glands are also described for *Marionina argentea* in Nielsen & Christensen (1959), although they are not seen in the corresponding figure (Nielsen & Christensen 1959: fig. 140). It cannot be excluded that inconspicuous ectal glands are present in *M. sambugarae* Schmelz, n. sp. and have become invisible due to the fixation method.

A dorsally interrupted clitellum was also recorded in six specimens identified as “*Marionina cf. argentea*” in a previous study on groundwater oligochaetes in Slovenia (Giani *et al.* 2011), and it was already supposed there that these specimens might represent a new species because the clitellum is closed dorsally in *Marionina argentea* (Schmelz & Collado 2010). The Slovenian material conforms to the description of *M. sambugarae* Schmelz, n. sp., but it is not included in the type series. The fact that this species has been found in subterranean habitats of France and Slovenia and not in surface habitats across Europe, suggests that *Marionina sambugarae* Schmelz, n. sp. is a true stygobiont species.

Genus *Cernosvitoviella* Nielsen & Christensen, 1959

Cernosvitoviella cf. *tridentina* Dumnicka, 2004

Cernosvitoviella tridentina Dumnicka, 2004: 133.

MATERIAL EXAMINED. — Station 1, slide 11.006.02. IRScNB, I.G. 32392.

REMARKS

The single adult specimen is posteriorly severed. It conforms to most of the details in the original description of *C. tridentina* from the Italian Alps, the male efferent system included. The spermathecae also agree, except that the ectal duct is shorter than originally described, measuring *c.* 30 µm by 9 µm, being only 1.5 × as long as the spherical ampulla (its diameter 20 µm). In the original description, the ectal duct is 4–5 × as long as the ampulla; dimensions are not given. It is impossible to say at the moment whether this difference is intra- or interspecific. Different ectal duct lengths are known in *C. atrata* (Bretscher, 1903), but that taxon may be a species complex. The clitellum is dorsally closed in our material and the prostomium has numerous internal papillae; these details are not originally described for *C. tridentina*. There are up to nine setae per bundle. Coelomocyte are broadly oval or rounded in *C. tridentina*; they were not seen in our material. The present record, if identified correctly, would be the first after the original description.

Cernosvitoviella cf. *parviseta*
Gadzinska, 1974

Cernosvitoviella parviseta Gadzinska, 1974: 403.

MATERIAL EXAMINED. — Station 15, slide 11.252.02(b,d): 2 immature specimens, 11.252.02(c): 1 adult specimen; station 22, slide 11.262.01(b): 1 mature specimen; station 33, slide 11.255.04(b): 1 adult specimen; station 36, slide 11.257.02: 1 mature specimen. IRScNB, I.G. 32392.

REMARKS

Setae are longer (20–30 µm) than originally described (15 µm). Very similar to *Cernosvitoviella aggtelekiensis* Dózsa-Farkas, 1970, but the latter species is distinguishable by its larger setae (35–42 µm). A similar observation was made on subterranean specimens identified as *C. aggtelekiensis* in Giani *et al.* (2011), which have setal lengths intermediate between those of *C. parviseta* and *C. aggtelekiensis* as originally described, while other characters (see Schmelz & Collado 2010) fit both species. *Cernosvitoviella aggtelekiensis* and *C. parviseta* have never be redescribed, therefore the degree of intraspecific variability of setal lengths is unknown in both species. The two populations may belong to the same species, which could be *C. aggtelekiensis*, *C. parviseta*, or an undescribed species. A reinvestigation of the types of *C. aggtelekiensis* and *C. parviseta* is urgently needed.

Family HAPLOTAXIDAE Michaelsen, 1900

Genus *Haplotaxis* Hoffmeister, 1843

Haplotaxis cf. *gordiioides* (Hartmann, 1821)

Lumbricus gordiioides Hartmann, 1821: 45.

MATERIAL EXAMINED. — Five immature specimens and one fragment from different stations (Appendix; in ethanol 96%, station 48: vial AB31536763; station 44: vial AB31536652; station 38: vial AB31536690; station 41: vial AB31525643; station 24: vial AB31525625). IRScNB, I.G. 32392.

REMARKS

Haplotaxis gordiioides is considered to be a Holarctic species (although no fully mature specimen has ever been collected in North America; Wetzel 2006) in need of revision, which might prove to be a complex of cryptic species (Martin & Ait Boughrouss 2012: 88). For this reason, we prefer to refer these immature specimens to as *Haplotaxis* cf. *gordiioides*.

Family LUMBRICULIDAE Vejdovský, 1884

Genus *Stylodrilus* Claparède, 1862

Stylodrilus sp. 1

MATERIAL EXAMINED. — Station 2: 1 sexually mature, unmated specimen, slide 11.007.03 (first 14 segments) and vial AB31525649 (posterior part in 96% ethanol), IRScNB, I.G. 32392.

REMARKS

This is a *Stylodrilus* species with simple-pointed setae. Spermathecal and male pores are in IX and X, respectively. Only one spermathecal ampulla is visible, on left side of the specimen; ampulla, small, spherical, without sperm, probably partially-developed. Atria are small, pear-shaped, immediately ending with small penis. Vasa deferentia join atria sub-apically. Posterior blood vessels not visible. No current diagnosis of *Stylodrilus* species fits this description. This is most probably a new species, but it seems preferable to have additional material before formalizing a taxonomic decision. At best, *Stylodrilus sulci* (Hrabě, 1934) seems to be the closest relative, but that groundwater species has long, oval atrial ampullae, narrowing into a duct, without a penis. *Stylodrilus lemani* has atria immediately ending with a penis, but its atria are tubular, and posterior dorsolateral blind blood vessels are present, with numerous long, irregular appendages.

Stylodrilus heringianus Claparède, 1862

Stylodrilus heringianus Claparède, 1862: 263.

MATERIAL EXAMINED. — Station 2: slides 11.019.03(b,c), slide 11.019.04; station 41: slide 11.259.06(a): fragments of immature specimens. IRScNB, I.G. 32392.

REMARKS

These specimens are all similar, showing bifid setae with reduced upper tooth. As adults of *Stylodrilus heringianus* have been identified in the same site (station 41), they are tentatively attributed to *Stylodrilus heringianus* as well.

Genus *Trichodrilus* Claparède, 1862

Trichodrilus cf. *tenuis* Hrabě, 1960

Trichodrilus tenuis Hrabě, 1960: 271.

MATERIAL EXAMINED. — Many mature, mated specimens, IRScNB, I.G. 32392, station 1 (slides 11.006.04, 11.007.01, vial AB31536635), station 2 (slides 11.032.01, 11.032.02, vials AB31536765, AB31536719, AB31515927, AB31536665), station 15 (slide 11.252.01, vial AB31525637).

REMARKS

All these fragments probably belong to the same species, which can be ascribed to *Trichodrilus* sp. group II *sensu* Rodriguez & Giani (1994). This group of species is characterized by pear-shaped or spherical atria, not laterally compressed, all setae more or less alike, unmodified penial setae, two pairs of spermathecae in XI and XII, and posterior vasa deferentia penetrating into XI. According to Rodriguez & Giani (1994), the species within this group can barely be separated due to the variability of diagnostic characters within populations, or even to incorrect diagnoses in the original descriptions.

Our specimens have no lateral blood vessels in posterior segments, a character shared among this group by *T. claparedei* Hrabě, 1938, *T. hrabei* Cook, 1967, *T. medius* Hrabě, 1960, *T. moravicus* Hrabě, 1937, *T. seirei* Timm, 1979, and *T. tenuis* Hrabě, 1960. Our specimens can be characterized by spherical to ovoid atrial ampullae, 55–80 µm long, 54–68 µm wide, with thin muscle layer (2.5–4.0 µm thick), and distinct proximal ducts, which make them the closest to *T. tenuis*. However, atrial ampullae are entirely covered by high prostate cells, and ducts are half the size of diameter of ampullae, ending in small conical, external penes. In *T. tenuis*, atrial ampullae bear high prostate cells only in their distal part, ducts are very short, and end with minute porophores. Juget & des Châtelliers (2001) have described a peculiar structure of the spermathecae in material from the Lyon area (France) ascribed to *T. tenuis*, in which the proximal part of ampulla (wrongly indicated as the distal part) is differentiated into a so-called “pseudovestibule” at junction with spermathecal ducts. Such a structure is not seen on our material.

This is probably a new species but its description would ideally lie within a revision of *Trichodrilus* sp. group II *sensu* Rodriguez & Giani (1994), based on additional material and genetic characterization via DNA barcoding.

Trichodrilus sp. 1

MATERIAL EXAMINED. — One sexually mature, unmated specimen, IRScNB, I.G. 32392, slide 11.251.03b (first 14 segments); station 14 (Appendix).

REMARKS

This specimen can be characterized by tubular to quadrangular atria, 78 µm long, 57 µm wide (length/width = 1.4), with thin muscular layer (2.3–4.0 µm thick), short proximal ducts, 12 µm long, with small, conical, external penes, 8.8 µm long. Atria are covered by discrete groups of prostate cells. There are two pairs of spermathecae in XI and XII with large, ovoid ampullae and short (15 µm) ducts. Posterior blood vessels cannot be studied on this anterior fragment.

Among *Trichodrilus* species with tubular atria and two pairs of spermathecae, *T. leruthi* Hrabě, 1939, *T. intermedius* (Fauvel, 1903) and *T. tacensis* Hrabě, 1963 are probably the closest species to this specimen; however, atria of those species are slender (length/width = 2.4) and larger, and they do not have atrial ducts. *Trichodrilus* sp. 1 is probably a new species. Unfortunately, the scarcity of material and its suboptimal state of conservation prevent us from describing this taxon into more detail, or to formalize a taxonomic decision.

Trichodrilus sp.

MATERIAL EXAMINED. — Station 1, slide 10.357.03(a): one immature specimen, slide 11.007.01(a): one immature specimen, vial AB31536635: fragments; station 2, vial AB31536665: fragments; station 14, vial AB31536587: fragments; station 16, slide 11.252.03: 1 immature specimen, vial AB31536671: fragments; station 17, AB31515911: one immature specimen, fragments; station 18, vial AB31515632: fragments; station 20, vial AB31525675: 1 juvenile, fragments, vial AB31515636: fragments; station 36, vial AB31536747: fragments; station 38, vial AB31525674: fragments. RBINS, IG 32392.

REMARKS

This *Trichodrilus* material is only available as immature specimens or fragments, and cannot be identified at the species level. Most *Trichodrilus* species occupy ground water habitats and have localized distributions. Given the general trend in *Trichodrilus* for groundwater habitats, we consider these undetermined specimens as stygobionts.

DISCUSSION

DIVERSITY OF GROUNDWATER OLIGOCHAETES

The picture of oligochaete diversity obtained in ground waters of the Mercantour National Park agrees in many respects with previous studies in similar environments.

First, it follows the general observation of Artheau & Giani (2006) for groundwater annelids in France, namely that communities consist of a mixture of stygoxene, stygophile and stygobiont species. This is particularly true in the present study, given the types of groundwater habitats investigated: springs and the hyporheic zone of streams are surface related, ecotonal environments (Botosanaenu 1998; Datry *et al.* 2008; Williams & Wong 2010). Springs shelter the highest number of stygoxene, epigeal species, such as the generalist and cosmopolitan genus *Nais*, enchytraeids usually considered as living in soils or at the soil/freshwater

interface (such as *Achaeta* sp., *Buchholzia* spp., *Cognettia* spp., *Fridericia* spp., or *Henlea* spp.) (Schmelz & Collado 2010; Giani *et al.* 2011), or the terrestrial family Lumbricidae. This is likely related to the sampling protocol, which collects not only the drifting fauna, i.e. the fauna coming directly from the groundwater environment, but also the epigeal fauna living in contact with the sediments, outside of the massif. In contrast, hyporheic stations were selected in assumed upwelling sites; hence hyporheic samples are probably less affected by the epigeal environment than springs. In this respect, the near absence of stygobiont species in hyporheic samples, as well as the dominance of stygobiont species in this habitat is noteworthy. With at least three stygobiont species (from a total of five in this study), station 2 is also noticeable. This site is situated at a low altitude (372 m), in a hydrogeological zone of medium permeability and large pore size, and a rather high water specific conductance (> 500 µS/cm, Dole-Olivier *et al.* 2014), indicating strong connections with true ground water.

Second, the dominance of enchytraeids among the groundwater oligochaete fauna (Giani *et al.* 2001) is here confirmed, with no less than 18 enchytraeid taxa in ground waters of the Mercantour National Park (roughly 50% of all taxa). These figures need to be put into perspective, taking into account the fact that many enchytraeid taxa here recorded are accidental in ground water, but even so, the observed dominance remains. In accordance with Giani *et al.* (2001), the majority of stygobiont and stygophile taxa are lumbriculids and tubificids, although, in the latter case, the paucity of material does not enable us to draw a solid conclusion.

Third, in spite of a limited set of data, the genus *Trichodrilus* is confirmed as one of the more characteristic faunistic elements of the underground freshwater oligochaete communities (Giani *et al.* 2001; Creuzé des Châtelliers *et al.* 2009). In his contribution to the study of the genus *Trichodrilus*, Hrabě (1937: 3) already noted the remarkable species richness of the genus, its specificity to groundwater environments, and the restriction of most species to one locality [“Il résulte... 1° que le genre *Trichodrilus* dépasse par sa richesse en espèces les autres genres de la famille des *Lumbriculidae*,... ; 2° que la plupart des représentants du genre *Trichodrilus* appartiennent à la faune des eaux souterraines ; 3° que la plupart des espèces ne sont connues jusqu'à présent que d'un seul habitat.”]. Such a conclusion remains relevant nowadays, although made almost 80 years ago, and the observation that *Trichodrilus* specimens found in the Mercantour National Park are probably species new to science fits well into this global picture. Thirty-seven *Trichodrilus* species are presently known, nearly exclusively from the Western Palearctic region, with the exception of two poorly known species in the US, the Holarctic *T. allobrogum* Claparède, 1862, and the Nearctic *T. culveri* Cook, 1975. Most species occupy ground water habitats and have strongly localized distributions, many species being endemic. Only a few species are known from surface waters but, taking into account the general trend in *Trichodrilus* for groundwater habitats, they may also be seen as “accidental epigeal” species.

ABERRANTIDRILUS CUSPIS N. COMB. SENSU SAMBUGAR *ET AL.* (1999) : A COMPLEX OF CRYPTIC SPECIES?

Great progress has been made during the last decade in the knowledge of groundwater biodiversity (Gibert *et al.* 2009). Ground waters and hypogean habitats in general, have been shown to harbour remarkably high numbers of cryptic species, which might account for an important part of groundwater diversity (Trontelj *et al.* 2009). Extreme conditions of life in habitats with reduced environmental heterogeneity, such as ground waters, have likely promoted both convergent morphological evolution and morphological stasis (Wiens *et al.* 2003; Bickford *et al.* 2007; Lefébure *et al.* 2007; Eme *et al.* 2013). A high prevalence of cryptic species has been reported for several groundwater taxa, mostly crustaceans (Lefébure *et al.* 2006, 2007; Zakšek *et al.* 2009; Eme *et al.* 2013). The recent discovery of closely related species in subterranean oligochaetes, consistently differing in minute, although significant morphological details, suggests that this observation might be also applicable to oligochaetes, as illustrated by the following species pairs: *Troglo-drilus jugeti* Achurra, des Châtelliers & Rodriguez, 2012 and *Troglo-drilus galarzai* Giani & Rodriguez, 1988 (Achurra *et al.* 2012); *Rhyacodrilus falciformis* Bretscher, 1901 and *Rhyacodrilus pigueti* Achurra & Martinsson, 2013 (Martinsson *et al.* 2013); or *Rhyacodriloides latinus* Martin, Martínez-Ansemil & Sambugar, 2010 and *Rhyacodriloides aeternorum* Martin, Martínez-Ansemil & Sambugar, 2010 (Martin *et al.* 2010).

A. cuspis n. comb. sensu Sambugar *et al.* (1999) is likely to represent a complex of cryptic species, all the more so since the distribution of its variants is in accordance with the observation that groundwater species with ranges over 200 km are most likely an assemblage of cryptic species with much smaller geographic ranges (Trontelj *et al.* 2009). This view was recently challenged by Eme *et al.* (2013) who showed that some cryptic species in groundwater isopods may retain large geographic ranges, although such observations were rather the exception than the rule. Hence, in view of uncertainties regarding the variable *Aberrantidrilus* Martin, n. gen. material identified by Sambugar *et al.* (1999) as *A. cuspis* n. comb., new material for molecular studies is highly desirable, to clarify their taxonomical status and possibly to untangle their relationships.

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APPENDIX 1

List of the stations sampled in the Mercantour National Park, in which oligochaetes were present. Data reported for each sample are as follows: unique identifier (as referred to in Table 1); name of the station; station code; stream; municipality; date of sampling (d.m.y); Y coordinates; X coordinates; altitude (m); habitat (HPR = hyporheic zone; SPR = spring); hydrogeographic basin. Datum WGS84.

1. Pont Tende; H1RO; Roya; Tende; 05.VIII.2009; 44.09874; 7.58884; 844; HPR; Roya-Bévéra.
2. Sospel; H2BEV; Bévéra; Sospel; 05.VIII.2009; 43.8931; 7.42103; 372; HPR; Roya-Bévéra.
3. Galerie des Mesches; MESRO; n/a; Tende; 01.VII.2009; 44.07194; 7.52055; 1452; SPR; Roya-Bévéra.
4. Source Torraca; TORBEV; Bévéra; Sospel; 06.VII.2009; 43.88403; 7.43536; 363; SPR; Roya-Bévéra.
5. Source Vievola; VIERO; Roya; Tende; 06.VII.2009; 44.11115; 7.55752; 1027; SPR; Roya-Bévéra.
6. Source de la Fouige; FOURO; Roya; Tende; 07.VII.2009; 44.04393; 7.57981; 836; SPR; Roya-Bévéra.
7. Source de Mantegas; MANBEV; Bévéra; Moulinet; 07.VII.2009; 43.98073; 7.39589; 1609; SPR; Roya-Bévéra.
8. Source Maglia; MAGRO; Maglia; Breil-sur-Roya; 07.VII.2009; 43.97152; 7.47518; 817; SPR; Roya-Bévéra.
9. St Sauveur-sur-Tinée; H1TI; Tinée; Saint-Sauveur-sur-Tinée; 03.IV.2009; 44.08073; 7.1051; 475; HPR; Tinée.
10. Plan de l'Ovort; H3TI; Tinée; Saint-Etienne-de-Tinée; 23.VII.2009; 44.234127; 6.949775; 1083; HPR; Tinée.
11. Salso confluent; H2TI; Tinée; Saint-Dalmas-le-Selvage; 23.VII.2009; 44.319861; 6.887589; 1645; HPR; Tinée.
12. Pont de Paule; PAU3TI; Tinée; Roure; 16.IV.2009; 44.12142; 7.09027; 663; SPR; Tinée.
13. Pont de Paule; PAU1TI; Tinée; Roure; 16.IV.2009; 44.11874; 7.08986; 660; SPR; Tinée.
14. Bachelard 2 confluence Ubaye (Les Graves); H2BA; Bachelard; Barcelonnette; 14.IX.2010; 44.385021; 6.618713; 1120; HPR; Ubaye.
15. Ubaye 1 amont "Les thuiles"; H1UB; Ubaye; Saint-Pons; 14.IX.2010; 44.388588; 6.590952; 1100; HPR; Ubaye.
16. Ubaye 3 amont Faucon de Barcelonnette « La Fabrique »; H3UB; Ubaye; Faucon de Barcelonnette; 14.IX.2010; 44.39136; 6.688426; 1160; HPR; Ubaye.
17. Bachelard 1 aval station de pompage; H1BA; Bachelard; Uvernet-Fours; 15.IX.2010; 44.350429; 6.621042; 1205; HPR; Ubaye.
18. Ubate 5 amont pont "La Condamine Chatelard"; H5UB; Ubaye; La Condamine-Chatelard; 15.IX.2010; 44.457213; 6.747759; 1270; HPR; Ubaye.
19. Ubaye 2 amont Barcelonnette "La chaup"; H2UB; Ubaye; Enchastrayes; 15.IX.2010; 44.389389; 6.667952; 1145; HPR; Ubaye.
20. Ubaye 4bis en face Le Bourget (gravière); H4UBG; Ubaye; Meolans-Revel; 15.IX.2010; 44.398469; 6.536066; 1050; HPR; Ubaye.
21. Saume; SAUBA; n/a; Uvernet-Fours; 09.VIII.2010; 44.311441; 6.720417; 1825; SPR; Ubaye.
22. Braissette; BRABA; n/a; Uvernet-Fours; 10.VIII.2010; 44.298242; 6.787179; 2440; SPR; Ubaye.
23. Amont Lauzanier; LAUUB; n/a; Larche; 11.VIII.2010; 44.373323; 6.869389; 2350; SPR; Ubaye.
24. Restefond; RESUB; n/a; Jausiers; 13.VIII.2010; 44.331137; 6.802021; 2500; SPR; Ubaye.
25. Charbonnière Fours St. Laurent; CHARBA; n/a; Uvernet-Fours; 31.VIII.2010; 44.315692; 6.698083; 1825; SPR; Ubaye.
26. Barlatte; H2BAR; Barlatte; Guillaumes; 21.VII.2009; 44.115674; 6.839158; 870; HPR; Var .
27. Var; H1VAR; Var; Entraunes; 21.VII.2009; 44.199625; 6.743909; 1350; HPR; Var .
28. Résurgence Sanguinière; SAN2VAR; n/a; Entraunes; 09.VIII.2010; 44.2504333; 6.7746917; 2199; SPR; Var .
29. Source du Tailler; TAIVAR; Cians; Beuil; 21.VII.2009; 44.070944; 6.956141; 1510; SPR; Var .
30. Source Sanguinière; SAN1VAR; Ruisseau de Gorgias; Entraunes; 21.VII.2009; 44.252262; 6.771113; 2040; SPR; Var .
31. Haut Verdon 1 aval Allos (déchetterrie – amont du rejet); H1VER; Ubaye; Allos; 06.IX.2010; 44.224095; 6.631081; 1360; HPR; Verdon.
32. Haut Verdon 2 aval Allos (déchetterrie – aval du rejet); H2VER; Verdon; Allos; 06.IX.2010; 44.22339; 6.631754; 1355; HPR; Verdon.
33. Haut Verdon 3 aval pont la Chaumie; H3VER; Verdon; Colmars; 06.IX.2010; 44.202246; 6.635491; 1300; HPR; Verdon.
34. Haut Verdon 6 Villars Colmars (centre de vacances); H6VER; Verdon; Villars-Colmars; 07.IX.2010; 44.16208; 6.609921; 1200; HPR; Verdon.
35. Haut Verdon 4 Le Pont Haut, amont Colmars les Alpes; H4VER; Verdon; Colmars; 15.IX.2010; 44.186675; 6.631641; 1270; HPR; Verdon.
36. Haut Verdon 5 Colmars les Alpes (pont aval du village); H5VER; Verdon; Colmars; 15.IX.2010; 44.180404; 6.623732; 1235; HPR; Verdon.
37. Méouilles; MEOVER; n/a; Allos; 02.VIII.2010; 44.249484; 6.711916; 2273; SPR; Verdon.
38. Résurgence du Lac d'Allos; RLAVR; n/a; Allos; 02.VIII.2010; 44.239256; 6.702445; 2199; SPR; Verdon.
39. Source du ravin du Lac d'Allos; RAVVER; n/a; Allos; 02.VIII.2010; 44.224605; 6.706771; 2310; SPR; Verdon.
40. Pradelles; PRAVER; n/a; Allos; 03.VIII.2010; 44.252384; 6.688255; 1890; SPR; Verdon.
41. Infiltrés; INFVER; n/a; Colmars; 04.VIII.2010; 44.221312; 6.684114; 1943; SPR; Verdon.
42. Fontaines extérieur fortifications (à côté station H5V); S2FVER; n/a; Colmars; 15.IX.2010; 44.180059; 6.624019; 1240; SPR; Verdon.
43. Fontaines dans fortifications de Colmars les Alpes; S1FVER; n/a; Colmars; 18.VI.2010; 44.181413; 6.625998; 1240; SPR; Verdon.
44. Gendarmerie; H1VES; Boréon; Saint-Martin-Vésubie; 02.IV.2009; 44.07911; 7.25113; 1041; HPR; Vésubie.
45. Grange du Pisset; H2VES; Vésubie; Saint-Martin-Vésubie; 02.IV.2009; 44.08823; 7.31401; 1511; HPR; Vésubie.
46. Les Pontets; H3VES; n/a; Saint-Martin-Vésubie; 02.IV.2009; 44.088559; 7.307306; n/a; HPR; Vésubie.
47. Source Blanche, Le Preinas; BLAVES; Vésubie; Belvédère; 03.IV.2009; 44.01298; 7.31517; 644; SPR; Vésubie.
48. Source St Martin, Rte de Colmiane; MARVES; Boréon; Saint-Martin-Vésubie; 03.IV.2009; 44.08306; 7.24444; 1211; SPR; Vésubie.
49. Source de Salèse; SALVES; Boréon; Saint-Martin-Vésubie; 04.IV.2009; 44.12672; 7.261581; 1683; SPR; Vésubie.