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ORIGINAL ARTICLE

First time in Italy. Is the elusive aquatic megadrile *Sparganophilus* Benham, 1892 (Annelida, Clitellata) accelerating its dispersal in Europe?

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ABSTRACT

During field studies in River Mincio, northern Italy, populations of the aquatic megadrile Sparganophilus tamesis *Benham, 1892 were discovered, the worms being particularly abundant among the roots of* Vallisneria spiralis *L. This finding represents the first record of Sparganophilidae in Italy. A morphological account, with photographs of worms and cocoons, as well as field and laboratory remarks on density, behaviour and habitat, are provided. The view of* S. tamesis *being senior synonym to* S. eiseni *Smith, 1895 is favoured, as is the hypothesis of the arrival and spreading of* Sparganophilus *in Europe amongst the roots of water plants.*

Key words: Sparganophilidae, taxonomy, Nearctic freshwater oligochaetes, Italian inland waters, mode of introduction, association with Vallisneria*.*

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INTRODUCTION

The aquatic megadrile family Sparganophilidae (Clitellata: Oligochaeta) are very slender worms, ranging as adults from 70 to 200 mm in length and 2 to 3.5 mm in maximal width, spending their life in the mud or amongst the roots of aquatic plants at the edges or bottom of water bodies. The family comprises one genus and about a dozen species, nearly all restricted to the south eastern USA. The type species, *Sparganophilus tamesis* Benham, 1892, originally discovered in River Thames, England, is today largely accepted as native to eastern North America and widespread there from southeastern Canada to the Gulf States, plus isolate collections in Mexico and Guatemala (Reynolds, 2008). Another two species appear endemic to California and Oregon, and immature sparganophilids have been reported from a swampy forest in Guyana (Stacey and Coates, 1996).

The occurrence of the family outside of America is limited to few records of *S. tamesis* in northern and central European countries: England (both in the wild and in aquatic gardens: River Thames, Windermere Lake, Cheshire Meres, Kew Gardens, Pencarrow, Greenford; Benham, 1892; Friend, 1911, 1921 as *Helodrilus elongatus*, then *Sparganophilus elongatus*; Cernosvitov, 1945; Jamieson, 1971; Sherlock and Carpenter, 2009); France (River Moselle near Nancy; Tétry, 1934 as *Pelodrilus cuenoti*); Switzerland (Lake Lèman in Geneva; Zicsi and Vaucher, 1987; Bouché and Qiu, 1998 as *Sparganophilus langi*); and Germany (River Alster in Hamburg; Graefe and Beylich, 2011) (Fig. 1). Jamieson (1971) revisited the types of *S. tamesis* at the British Museum and found two errors in Benham's (1892) otherwise excellent account, that partly justified the proliferation of synonyms: the upper chaetal couples, mistakenly illustrated as lateroventral rather than laterodorsal, and the prostate-like glands, overlooked but present (small because the type specimens were submature). Jamieson (1971: pp. 813-814, figs 15.14 U, X) rectified these errors and concluded that: i) all European records known until then were referable to one and the same species, *S. tamesis*; ii) *S. tamesis* had a junior synonym also in the widespread North American species, *S. eiseni* Smith, 1895.

Because of its resemblance to certain American Rhinodrilidae (= Glossoscolecidae), Benham (1892) speculated that *S. tamesis* had arrived in the Thames, which *is visited by all sorts of traffic*, *via* cocoons associated with imported water plants from North America. The proximity of the type locality to Oxford Botanic Gardens, and the species occurrence also in artificial tanks gave further support to Benham's belief. Still today, according to Sims and Gerard (1985, 1999), *the British records can all be associated with gardens containing imported aquatic plants*. Aquatic plants have thus from the beginning been implicated as having a role in transporting *Sparganophilus* worms over long distances, but the nature and the importance of the association with plants for the survival and maintainance of the worms' populations have never been addressed.

During field studies in River Mincio, northern Italy, abundant oligochaetes were noticed thriving among the roots of the tape-grass *Vallisneria spiralis* L. (Fig. 2A), and most of them turned out to belong to the Sparganophilidae. We herein report on this first record of a Nearctic megadrile family in Italy, and discuss the identification of the worms as *S. tamesis*, as well as the potential role of plants such as *Vallisneria* in the arrival, establishment and spread of the species.

METHODS

Study area

The Mincio River is a 75 km long watercourse originating from Lake Garda and flowing into the Po River. Its watershed comprises a total surface of 775 km^2. During history, the river course has been profoundly altered by human interventions such as reclamation, irrigation, water protection and accommodation for navigation. In the upper part of the watershed, the river flows through a hilly and high-plains land of mainly moraine origin, where gravels and sand-gravels confer soils a high permeability. This upper section of the river has richly vegetated natural banks, an average depth of less than 1 m, pebbly substrate, and hosts large meadows of submerged rooted macrophytes, including *V. spiralis*, *Elodea* spp., *Myriophyllum* spp., *Ceratophyllum* spp. Along this stretch, which has clear waters with low concentrations of materials in suspension, water velocity is about 1 m s^{-1} and the flow rate about 10-15 m^3 s^{-1}.

Collecting sites and methods

Sparganophilus specimens were obtained from two sites (45°16’42.40”N, 10°42’31.66”E and 45°15’42.80”N, 10°41’46.64”E), along the upper section of the Mincio River between Goito and Pozzolo (province of Mantua), from October 2012 to September 2013. The sampling sites, distant 2.7 km along the river course, are marginal areas characterized by large patches of *V. spiralis*. Plant meadows slow water velocity, resulting in the accumulation of 20-30 cm thick fine sediments over the pristine gravel bottom. The organic matter content, measured as loss on ignition, varied between 9 to 12%. At these sites, the characterization of benthic biogeochemistry, including sediment-water in-

Fig. 1. Map of the records of *Sparganophilus* in Europe. Courtesy Google Earth.

teractions and their regulation by macrophytes and macrofauna, had started in 2008 (Pinardi *et al.*, 2009; Racchetti *et al.*, 2010; Soana and Bartoli, 2013), and the occurrence of unidentified oligochaetes and cocoons in close association with *V. spiralis* roots was noticed all along. During the present one-year survey both qualitative and quantitative observations were performed, as detailed below.

At monthly frequency, oligochaetes were recovered and transported alive to the laboratory to analyze morphological features (*e.g.,* body length, after narcotization with 10% ethanol) and the presence of clitellum. All captured specimens were identified as *Sparganophilus* (except for a single individual of *Criodrilus lacuum* Hoffmeister, 1845). They were maintained in sieved-*in situ* sediment packed into plexiglass microcosms, or in aquaria containing sediment and *Vallisneria*. Oxygen signal at surface opening of burrows was measured by a Unisense microsensor. In October 2012 and September 2013, 8 *Sparganophilus* specimens were fixed and preserved in 90% ethanol for closer taxonomic scrutiny. In September 2013, squared frames (31×31 cm, n=3) were used to estimate the density of *Vallisneria* shoots and to evaluate the abundance of *Sparganophilus* associated with roots. Plants within the frames (n=50 to 70) were gently extracted from the mud by hand and *Sparganophilus* worms were separated from the roots and counted. Cylindrical plexiglass cores (i.d.=8 cm, height=40 cm, n=10) were used to evaluate the worm densities in sediments devoid of plants. To this purpose, sediments within the cores (nearly 1 L per core) were sieved *in situ* with a 500 μm mesh.

In the morphological account presented herein, observations *in vivo* are based on n=60 adult specimens, all entire; those on fixed material concern a total of 8 specimens (5 entire): 7 fully mature and 1 submature. Segments are indicated by Roman numerals; intersegment and septa locations are designated by Arabic numerals.

RESULTS

Field and laboratory observations

Sparganophilus specimens were recovered from both bare and rooted substrates. In September, the worm densities in vegetated and bare sediment averaged 960±312 (n=6) and 293±88 ind m^{-2} (n=20), pooled data from the two sampling sites, respectively.

Vallisneria shoots density averaged 578±83 ind m^{-2}, meaning that each root hosted on average 1.7 worms. From June through early September nearly all *Sparganophilus* individuals were clitellate. Available data suggest that there was no dramatic seasonal variation in field population density, while we had a clear indication of the reproductive period (July-August), from the recovery of cocoons wrapped around the plant roots. Up to 8 cocoons were recovered from the roots of a single plant (Fig. 2B), corresponding to a maximum of nearly 4800 cocoons m^{-2}. We registered no mortality in the *Sparganophilus* samples maintained in sieved-*in situ* sediments in the laboratory, either as plexiglass microcosms or aquaria. Rather, the specimens captured in the spring became sexually mature in summer, and produced cocoons which thereafter hatched. Similarly to what observed in the field, it was apparent in laboratory cultures that both adults and juveniles preferred the rhizosphere as elective site.

Particularly when maintained in bare sediments, *Sparganophilus* worms developed in the laboratory a large network of burrows. Light brown halos were present along the burrow walls, suggesting ventilation and oxygen rich-water circulation induced by the worms within anoxic sediments. At the same time, recording of oxygen content at surface opening of burrows (generally more than 2 per individual) indicated strict anoxia (O$_2$ below 5 μM) for relatively long periods (2-3 hours).

Description of the material

Sparganophilidae Michaelsen, 1918
Sparganophilus Benham, 1892
Sparganophilus tamesis Benham, 1892

Body wall unpigmented, *in vivo* translucent, somewhat iridescent, the abundant blood vessels showing through, except at the opaque, pink-orange clitellum (Fig. 2A); in fixed specimens, body colour pink-yellowish with darker clitellum (Fig. 3A). Mean body length of live worms 105±23 mm, with a maximum of 154 mm. In fixed material, body size up to 130 mm in length and 3.5 mm in width (at clitellum). Segment number 187-262 (mean 225±27, n=5). Prostomium zygolobous. Dorsal pores absent. Chaetae 8 per segment, closely paired, average distances between lines at XXX, *aa: ab: bc: cd: dd* = 5.3: 1: 5.8: 1.3: 8.85, *dd*:*u* = 0.29.

Clitellum saddle-shaped on (½)XV–XXVI (n=3), XV–XXV (n=1), or XV–XXIII (n=3). Tubercula pubertatis as continuous bands on XVII–XXII (n=3) or XVII–XXIII (n=4), narrowing at both ends into dorsal ledge-like projections (Fig. 3B). Papillae *ab* in XXIII–XXVI, not always evident. Female pores in XIV anterior to chaetae *a*. Male pores inconspicuous, intraclitellar, on the upper margin of tubercula pubertatis in XIX (n=5) or XX (n=2), either at level with chaetae or closer to the anterior septum (18/19 or 19/20, respectively) (Fig. 3B). Spermathecal pores paired in 6/7–8/9, usually all aligned with chaetal line *c* (occasionally one pair displaced just above or below that level).

Hearts moniliform in VII–XI, the two last pairs largest. No gizzard, calciferous glands or typhlosole. Intestine beginning in IX. Nephridia from 12/13. Testes two pairs, in X and XI. Seminal vesicles in XI–XII, the posterior ones larger (Fig. 3D). Ovaries string-like in XIII. Small receptacula (ovisacs) on the posterior side of 13/14 housing a few maturing oocytes. Prostate-like (=tubular) glands associated with chaetae *ab* in XXIII–XXVI. Spermathecae club-shaped, three pairs in VII–IX (Fig. 3D). Cocoons appearing as minute, irregular, small *bean pods* (length = 7-8 mm), each containing up to three eggs (Fig. 2C).

Taxonomic remarks

The Mincio material fits well the diagnosis of *S. tamesis* provided by Jamieson (1971). All dissected specimens are consistent in their internal anatomy (Fig. 3D), but the observed variation in some external body features is remarkable, affecting, unprecedentedly, the segmental position of the male pores and the opening level of spermathecal pores. This confirms the view that *S. tamesis* is a variable species and raises further questions as to the whether all described species in the genus are distinct, valid taxa.

DISCUSSION

How many *Sparganophilus* species in Europe?

The synonymy between *S. tamesis* and *S. eiseni* established by Jamieson (1971) has not been accepted by Reynolds (1980, 2008) nor by Bouché and Qiu (1998). The latter authors even described worms from Switzerland as a separate species, *S. langi*, distinguished from both *S. tamesis* and *S. eiseni* by a slightly different position of the female pores and transition oesophagus-intestine (worms from the same Swiss lake had been earlier described in these regards as typical for *S. tamesis* by Zicsi and Vaucher, 1987). According to Graefe and Beylich (2011), the recognition of *S. langi* as a new species was due to a misleading characterization of *S. tamesis* in the key given by Reynolds (1980). Indeed, Reynolds (1980) described i) the dorsolateral chaetae (CD) as if more distant from one another than the lateral interval BC; ii) the male pores at level with chaetae AB; and iii) the female pores located between the chaetae B and C. Features ii) and iii) are probably mere miswriting, as Reynolds (1980) indicated the same aberrant location of genital pores for five other species of *Sparganophilus* described by himself, but never commented upon it when discussing intrageneric variation.

In the light of the intrapopulation variation observed in our material, and because the type re-examination by Reynolds (1980) has been only partly confirmed in a recent publication (Reynolds, 2008), we follow here the claims made by Jamieson (1971) and agree with Sims and Gerard (1985, 1999) that taxonomic separation between European (*S. tamesis*) and North American specimens (*S. eiseni*) was owed to *a misinterpretation of variations due to growth and the diverse effects of different techniques of fixation and preservation, plus some minor (?phenotypic) setal differences*.

Importation of *Sparganophilus* to Europe

The American origin of Sparganophilidae is confirmed by molecular phylogenetics (Jamieson *et al.*, 2002; James and Davidson, 2012), which places the family as sister taxon to Komarekionidae, a monotypic earthworm family living in mesic forest soils on the Appalachian Mountains. Interestingly, the same studies suggest the two families to belong to a relict group sister to all other Crassiclitellata (James and Davidson, 2012). This *archaic* relationship contrasts with former hypotheses of *Sparganophilus* being closely related to Glossoscolecidae (Benham, 1892; Michaelsen, 1918; Cernosvitov, 1945; Jamieson, 1971) or to Lumbricidae (Sims, 1980, Reynolds and Cook, 1993), proposing instead the common ancestor of the Crassiclitellata clade as common ancestor with either of these families (James and Davidson, 2012).

Several allochthonous invasive organisms have become established in the upper Mincio, such as the bivalves *Corbicula fluminalis* (O.F. Müller, 1774) and *Dreissena polymorpha* (Pallas, 1771), the oligochaete tubificoid *Branchiura sowerbyi* Beddard, 1892, and the North American spiny-cheek crayfish *Orconectes limosus* Rafinesque, 1817 (Bedulli and Franchini, 1978; A. Laini, *personal observation*; www.parcodelmincio.it). It is remarkable that these alien invertebrates are all known to have stable populations in Lake Garda as well (see Ciutti *et al.*, 2011), lake from which River Mincio originates. It is also worth noting that not only the *Elodea* spp. plants but also *Orconectes* spp. crayfish are part of the native North American habitats of *Sparganophilus* (Baker, 1922; Patrick, 1996) and often accompany *Sparganophilus* in its allochthonous range (Jackson and Grey, 2013), being all tolerant of slow-flowing waterways, even with poor quality or polluted water. Muddy bottoms are preferred by these organisms, but also bottoms with gravel and pebbles with a considerable amount of organic substratum. We thus favour Benham's (1892) original hypothesis of the arrival of *Sparganophilus* in Europe *amongst the roots of some water plants, such as* Anacharis alsinastrum [=Elodea canadensis], *from North America, and like it have increased and multiplied in our rivers*.

Sparganophilus adaptations to aquatic life and association with submerged vegetation

The absence of a gizzard, the extended circulatory apparatus (longitudinal tegumentary vessels, rich plexus of blood vessels around the nephridia, an elaborate capillary plexus in the subepidermal body wall, a perienteric blood network consisting of a capillary plexus in the anterior segments and a blood sinus posteriorly), the absence of dorsal pores, the symmetrical position of the couples of chaetae at the four corners, are all features typical for truly aquatic oligochaetes, whether microdriles or megadriles, and whether primarily aquatic or secundarily reverted to aquatic life. And so are the shape and dorsal location of the pygidial slit (Fig. 3C), which permit the addition of segments by secondary growth and their gradual sealing, while the anus remains open for defecation (Omodeo, 1984); and, finally, the cocoons structured to remain anchored and sheltered among plant roots (Fig. 2B).

Sparganophilus owes its name to having been discovered among the roots and lower parts of the leaves of *Sparganium ramosum* growing *in black, evil-smelling mud on the banks of Thames* (Benham, 1892). Cernosvitov (1945) reported it to favour localities in Windermere with a considerable amount of organic substratum, and to occur under medium-sized stones, but more abundant in sand among the roots of *Littorella*, and even more in black, firm sulphide-smelling mud among the roots of *Phragmites*. Tétry (1934) found her worms in apparently bare, muddy, very moist sand, either submerged or thinly covered with water, on the banks of river Moselle. Zicsi

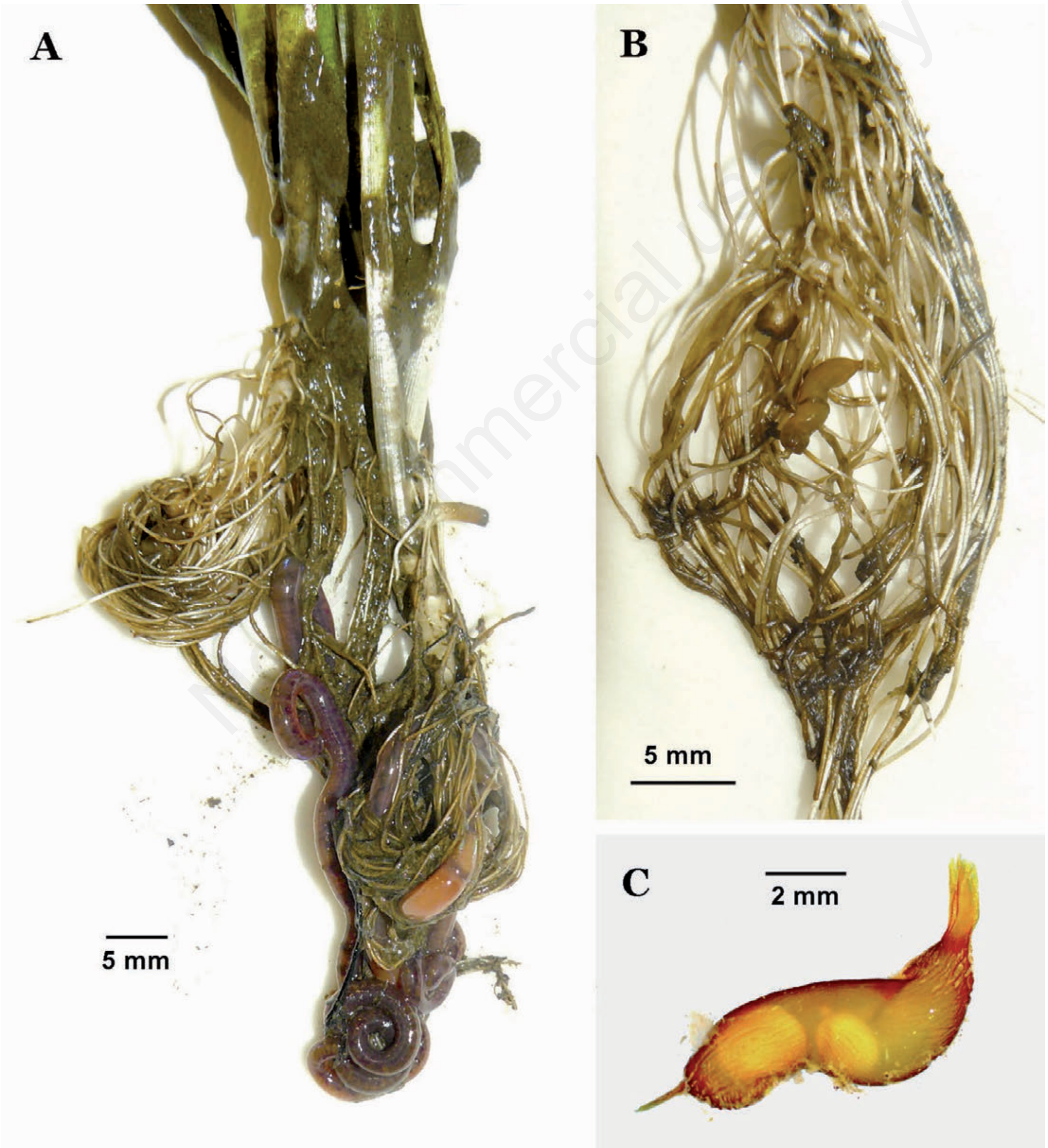

Fig. 2. In River Mincio *Sparganophilus tamesis* Benham, 1892 occurs mostly in close association with the rhizosphere of *Vallisneria spiralis*. A, Live clitellate specimen showing through the mud surrounding the roots of *Vallisneria*. B, Cocoons from the field, wrapped around the plant roots. C, Cocoon laid in the laboratory, containing two developing eggs.

and Vaucher (1987) collected *S. tamesis* in Geneva lake from mud, sometimes under stones at 2-3 m depth. Reynolds (1977) describes the North American populations (*S. eiseni*) as thriving in mud well under water or in saturated soils. The distribution in North America (Reynolds, 2001) indeed includes numerous collections from under significant depths of water.

Our observations on *Sparganophilus* cultured in the laboratory suggest that these worms can survive oxygen deficit, but we do not know whether they can be trans-

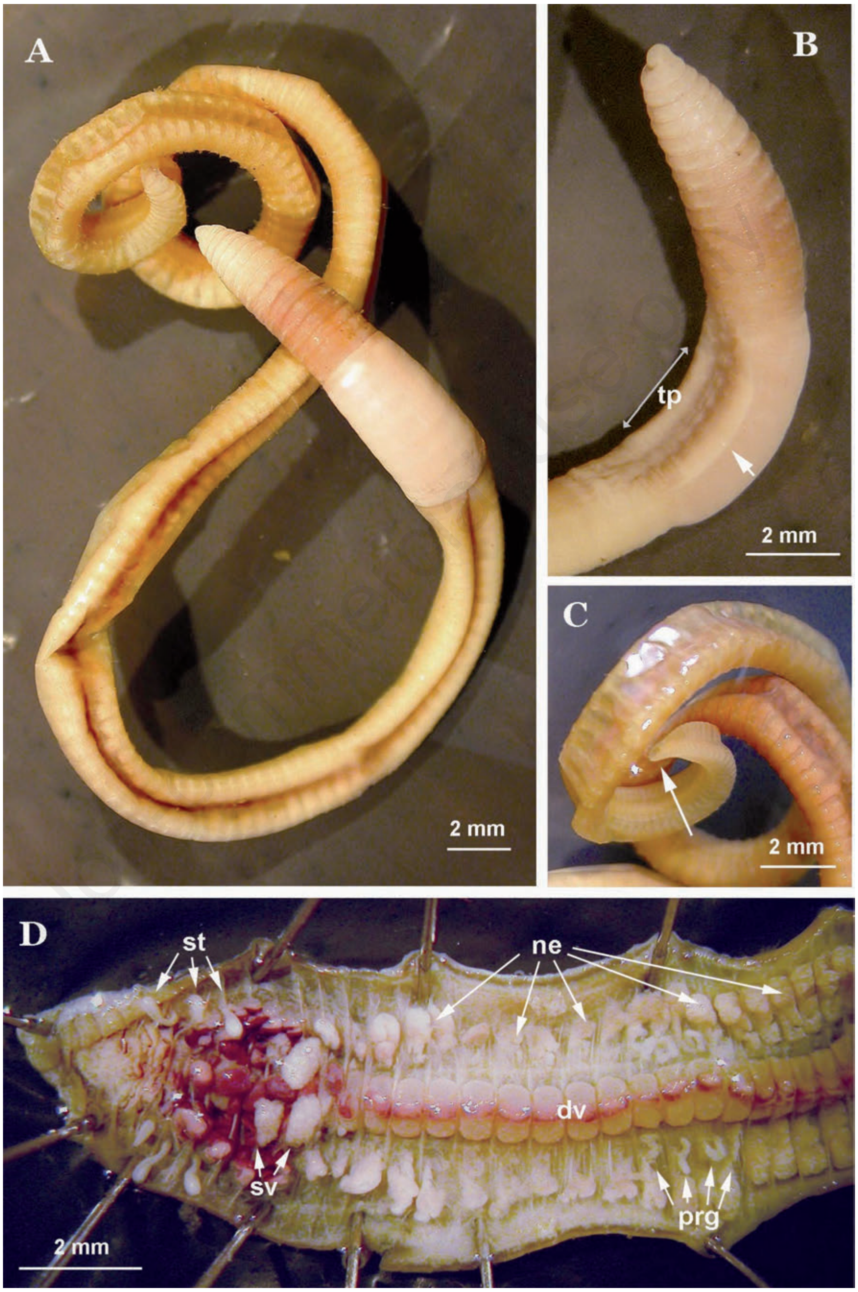

Fig. 3. Images of adult *Sparganophilus tamesis* worms after fixation. A) The body, cylindrical while alive, appears dorsally grooved throughout the postclitellar region in ethanol-preserved worms. B) Ventrolateral view of the anterior segments, showing the clitellum, tubercula pubertatis, the intraclitellar male pores (here in XX; arrowhead) and the ventral tumescence of the periclitellar region. C) Close-up of the tail coils to show the dorsal pygidial opening (anus; arrow). D) Dorsal view of the internal anatomy of another specimen with male pores in XX, perfectly consistent with that of specimens bearing the male pores in XIX. dv, dorsal blood vessel; ne, nephridia; prg, prostate-like glands; st, spermathecae; sv, seminal vesicles; tp, tubercula pubertatis.

ported alive in anoxic substrates over long distances. Earthworms are most often introduced to new territories by international trade of baits or ornamentals and horticultural products (Rota and Schmidt, 2006; Rota, 2013). *Sparganophilus* worms are strongly tygmotactic and form apparently inextricable tangles with roots, but in our experience, they are not prone to autotomy and rarely fragment *in vivo* with handling. Nevertheless, according to Evers *et al.* (2012), *S. eiseni* is not used commercially as bait and this may be due to its specialized habitat preferences. During this research, significant synergism has been detected between the bioturbation activities of *Sparganophilus* worms and the ecophysiology of *V. spiralis*. Both organisms seem to be capable to enhance the chemical oxidation of pore water and, as a consequence, the reoxidation of anaerobic end products and the coupling of oxidative and reductive processes. The roots of *V. spiralis* are characterized by elevated radial oxygen loss (Soana *et al.*, 2012) and this might enable *Sparganophilus* worms to explore and thrive in deeper, strictly anoxic sediments, where roots release oxygen and from which predators like fishes are excluded. Cocoons, which are generally located within dense primary roots, might also be protected and granted a higher probability to hatch by their tight interaction with *Vallisneria* rhizosphere.

CONCLUSIONS

Considering our field and laboratory observations on morphology, behaviour, reproduction and habitat, the allochthonous distribution of *Sparganophilus* might indeed have started from successful transportation of cocoons in mud around roots of aquatic plants similar to *Vallisneria*, even on such long distance as from one continent to another. *Vallisneria spiralis* is a stoloniferous species tolerant of eutrophication and capable of rapid clonal growth even in competitive vegetated environments (Xiao *et al.*, 2011; Soana *et al.*, 2012). Furthermore, the distribution of this and other invasive hydrophytes in Europe is changing due to climate change and consequent *relaxation* of the various barriers to their growth (Willby, 2007). This may well determine an increase of potential habitat also for associated organisms and accelerate their expansion to new locations on the continent.

REFERENCES

Baker FC, 1922. The molluscan fauna of the Big Vermilion River, Illinois. Illinois Biol. Monogr. 7:105-224.

Bedulli D, Franchini DA, 1978. [*Dreissena polymorpha* (Pall.): primi rinvenimenti nel fiume Po e predazione su di essa da parte di *Rattus norvegicus* (Berk.)].[Article in Italian]. Quad. Civ. Staz. Idrobiol. Milano 6:85-92.

Benham WB, 1892. A new English genus of aquatic Oligochaeta (*Sparganophilus*) belonging to the family Rhinodrilidae. Q. J. Microsc. Soc. 34:155-179.

Bouché MB, Qiu J-P, 1998. [Un nouveau *Sparganophilus* (Annelida: Oligochaeta) d'Europe, avec considérations paléogéographiques sur les Lumbricina].[Article in French]. Doc. Pédozool. Intégrol. 16:178-180.

Cernosvitov L, 1945. Oligochaeta from Windermere and the Lake District. P. Zool. Soc. Lond. 114:523-548.

Ciutti F, Beltrami ME, Confortini I, Cianfanelli S, Cappelletti C, 2011. Non-indigenous invertebrates, fish and macrophytes in Lake Garda (Italy). J. Limnol. 70:315-320.

Evers AK, Gordon AM, Gray PA, Dunlop WI, 2012. Implications of a potential range expansion of invasive earthworms in Ontario's forested ecosystems: a preliminary vulnerability analysis. Climate Change Research Report – Ontario Forest Research Institute 2012. Available from: http://www.mnr.gov.on.ca/stdprodconsume/groups/lr/@mnr/@climatechange/documents/document/stdprod_092861.pdf

Friend H, 1911. A new earthworm. Zoologist 15:192-193.

Friend H, 1921. Two new aquatic annelids. Ann. Mag. Nat. Hist. 7:137-141.

Gates GE, 1982. Farewell to North American megadriles. Megadrilogica 4:12-77.

Graefe U, Beylich A, 2011. First record of the aquatic earthworm *Sparganophilus tamesis* Benham, 1892 (Clitellata, Sparganophilidae) in Germany. Proceedings 5th Int. Oligochaete Taxonomy Meeting, Beatenberg, Switzerland, Abstract no. 25.

Jackson MC, Grey J, 2013. Accelerating rates of freshwater invasions in the catchment of the River Thames. Biol. Invasions 15:945-951.

James SW, Davidson SK, 2012. Molecular phylogeny of earthworms (Annelida: Crassiclitellata) based on 28S, 18S and 16S gene sequences. Invertebr. Syst. 26:213-229.

Jamieson BGM, 1971. Family Glossoscolecidae, p. 723-837. In: R.O. Brinkhurst and B.G.M. Jamieson (eds.), Aquatic Oligochaeta of the world. Univ. Toronto Press.

Jamieson BGM, Tillier S, Tillier A, Justine J-L, Ling E, James S, McDonald K, Hugall AF, 2002. Phylogeny of the Megascolecidae and Crassiclitellata (Annelida, Oligochaeta): combined versus partitioned analysis using nuclear (28S) and mitochondrial (12S, 16S) rDNA. Zoosystema 24:707-734.

Michaelsen W, 1918. [Die Lumbriciden, mit besonderer Berücksichtigung der bisher als Familie Glossoscolecidae zusammengefassten Unterfamilien].[Article in German]. Zool. Ib. Syst. 41:1-398.

Omodeo P, 1984. On aquatic Oligochaeta Lumbricomorpha in Europe. Hydrobiologia 115:187-190.

Patrick R, 1996. Rivers of the United States. 3. The eastern and southeastern States. J. Wiley & Sons: 829 pp.

Pinardi M, Bartoli M, Longhi D, Marzocchi U, Laini A, Ribaudo C, Viaroli P, 2009. Benthic metabolism and denitrification in a river reach: a comparison between vegetated and bare sediments. J. Limnol. 68:133-145.

Racchetti E, Bartoli M, Ribaudo C, Longhi D, Brito LEQ, Naldi M, Iacumin P, Viaroli P, 2010. Short term changes in pore water chemistry in river sediments during the early colonization by Vallisneria spiralis. Hydrobiologia 652:127-137.

Reynolds JW, 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. Life Sci. Misc. Publ. Royal Ontario Museum: 141 pp.

Reynolds JW, 1980. The earthworm family Sparganophilidae

(Annelida, Oligochaeta) in North America. Megadrilogica 3:189-204.

Reynolds JW, 2001. Sparganophilidae - are terrestrial oligochaetologists missing the habitat in North America? Megadrilogica 8:82-84.

Reynolds JW, 2008. Sparganophilidae (Annelida, Oligochaeta) distribution in North America and elsewhere, revisited. Megadrilogica 12:125-143.

Reynolds JW, Cook DG, 1993. Nomenclatura Oligochaetologica. Supplementum tertium. A catalogue of names, descriptions and type specimens of the Oligochaeta. New Brunsw. Mus. Monogr. Ser. (Nat. Sci.) 9:1-33.

Rota E, 2013. From Corsica to Britain: new outdoor records of Ocnerodrilidae (Annelida: Clitellata) in western Europe. Biodivers. Data J. 1:e985.

Rota E, Schmidt O, 2006. *Dichogaster bolaui* (Oligochaeta: Octochaetidae), an unusual invader in a swimming pool in Ireland. J. Nat. Hist. 40:161-167.

Sherlock E, Carpenter D, 2009. An updated earthworm list for the British Isles and two new 'exotic' species to Britain from Kew Gardens. Eur. J. Soil Biol. 45:431-435.

Sims RW, 1980. A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta). Bull. Brit. Mus. (Nat. Hist.) Zool. 39:103-124.

Sims RW, Gerard BM, 1985. Earthworms. Synops. Brit. Fauna (New Ser.) No. 31. Brill and Backhuys: 174 pp. (Revised in 1999).

Smith F, 1895. A preliminary account of two new Oligochaeta from Illinois. Bull. Ill. St. Lab. Nat. Hist. 4:138-148.

Soana E, Bartoli M, 2013. Seasonal variation of radial oxygen loss in *Vallisneria spiralis* L.: an adaptive response to sediment redox? Aquatic Bot. 104:228–232.

Soana E, Naldi M, Bartoli M, 2012. Effects of increasing organic matter loads on pore water features of vegetated (*Vallisneria spiralis* L.) and plant-free sediments. Ecol. Eng. 47:141-145.

Stacey DF, Coates KA, 1996. Oligochaetes (Naididae, Tubificidae, Opistocystidae, Enchytraeidae, Sparganophilidae and Alluroididae) of Guyana. Hydrobiologia 334:17-29.

Tétry A, 1934. Description d'une espèce française du genre *Pelodrilus*. C.R. Acad. Sci. Paris 199:322-324.

Willby NJ, 2007. Managing invasive aquatic plants: problems and prospects. Aquat. Conserv. 17:659-665.

Xiao K, Yu D, Wang L., Han Y, 2011. Physiological integration helps a clonal macrophyte spread into competitive environments and coexist with other species. Aquat. Bot. 95:249-253.

Zicsi A, Vaucher C, 1987. A propos de la présence de *Sparganophilus tamesis* Benham dans le lac Léman à Genève (Oligochaeta: Sparganophilidae). Rev. Suisse Zool. 94:861-864.