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A report of the unusual presence of *Haplotaxis* cf. *gordioides* in a terrestrial subsoil and first isotopic analysis of its trophic position

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Abstract

Haplotaxis is a genus of aquatic oligochaetes for which only limited information is available on its taxonomy, distribution, habitat and diet. During a soil survey in southern Poland, specimens of *Haplotaxis* cf. *gordioides* were unexpectedly found in terrestrial mineral subsoils, isolated from any apparent water source. This discovery provides an opportunity to investigate two aspects of *Haplotaxis*: habitat and diet. For the first time, the predatory nature of *Haplotaxis* has been assessed using stable isotope analysis of carbon and nitrogen and compared with detritivorous worms. In addition, the natural habitat of this genus was reconsidered through a literature review. This new terrestrial record raises questions about the habitat preference of *Haplotaxis*, suggesting that their rare soil presence may be due to challenges of extraction rather than actual absence. The finding highlights our limited understanding and exploration of subsoil fauna, including macrofauna. It also provides the first independent evidence for the predatory behaviour of *Haplotaxis*.

Key words: Clitellata, Luvisol

Introduction

Haplotaxis (Hoffmeister 1843) (Haplotaxidae, Clitellata) is a genus of aquatic oligochaetes that is poorly known in several respects relating to its taxonomy, distribution, habitat and diet.

The genus has been documented throughout the world, with the exception of Antarctica. To date, almost 90% of all localities where the genus is recorded in Biodiversity database PlutoF are related to the type species *Haplotaxis gordioides* (Hartmann in Oken, 1819) or "*Haplotaxis* cf. *gordioides*" (Abarenkov *et al.*, 2010). This species is the only one with a broad distribution across the Palaearctic region, while the other three species in this biogeographical zone are restricted to a single locality (*Haplotaxis gastrochaetus* Yamaguchi, 1937, a well in Japan) or a single lake (*Haplotaxis dubius* (Hrabě, 1931), Lake Ohrid; *Haplotaxis ascaridoides* Michaelsen, 1905, Lake Baikal (Hrabě, 1931; Michaelsen, 1905; Timm & Martin, 2019; Yamaguchi, 1937). Recently, the species has been shown to be a complex of species, undescribed or to be considered as *species inquirendae*, in the absence of a discriminating morphological characterisation (Martin *et al.*, 2023) . As a result, the real biogeographic range of *Haplotaxis* species (endemic vs. cosmopolitan) remains to be investigated.

Haplotaxis species are usually reported as aquatic, present in numerous bodies of surface water and in groundwater (e.g., Artheau & Giani, 2006; Martin *et al.*, 2008; Timm & Martin, 2019; Timm & Martin, 2015). There are, however, a few references to a terrestrial or semi-terrestrial habitat (e.g., Dumnicka *et al.* 2020; Erséus, 2005; Giard, 1894; Hesse, 1923; Kasprzak 1979; Schlotthauber, 1860; Thienemann, 1912), so there is still uncertainty as to the exact nature of their habitat.

Finally, all *Haplotaxis* species have a large, muscular pharynx, which is associated with a presumed predatory lifestyle (Martin *et al.* 2024). This is an unusual behaviour in aquatic oligochaetes, a fundamentally detritivorous

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group that feeds mainly on bacteria contained in ingested sediment, or micro-algae when phytophilous species live in the water column (Timm & Martin, 2015). Apart from isolated observations suggesting predation on other oligochaetes (inferred from residual chaetae in the intestines) (Brinkhurst & Marchese, 1987; Michaelsen, 1932) or salmon eggs (Gates, 1971), there are no observations of how *Haplotaxis* species feed in their natural environment, so their actual trophic position in the food chain remains unclear.

During a soil survey in a region of southern Poland, we recently observed the unexpected presence of a few specimens of *Haplotaxis* cf. *gordioides* in terrestrial, mineral subsoil, apparently far from any source of surface or underground water. This discovery has enabled us to address two aspects of the genus that are still poorly known, namely its habitat and diet. For the first time, the presumed predatory trophic position of this worm was assessed by comparing its C and N stable isotope composition with that of coexisting detritivorous worms, and the natural habitat of this supposedly aquatic worm was clarified by comparing this observation with a review of the relevant literature.

Materials and methods

Study site. The site was located in the Pieniny Spiskie region, the Pieniny Mountains, in southern Poland (N49°26'18" E20°13'58") at an altitude of 560 m a.s.l. .800 meters from the research site, there is a monitoring point of the Polish Geological Institute (epsh.pgi.gov.pl), which indicates that the groundwater level is at 5.1 meters. The mean annual precipitation and temperature are 613 mm and 12°C, respectively. The soil under investigation is situated in an area that has been unused for approximately 3 to 5 years, as determined by observations of shrubs and plants in the meadow. Previously, it was used as agricultural grassland (Fig. 1).

FIGURE 1. Landscape context of the sampling area; left: June 2022, right: September 2022 (Photos by A. Józefowska).

Methods. Sampling was conducted in June and September 2022, respectively. First, two specimens of *Haplotaxis* were found during routine soil excavation (to 1 m depth) in preparation of a soil profile description. Second, one more *Haplotaxis* sp. was found at the same location when an open pit (60x80 cm and 100 cm depth) was excavated and all earthworms, *Haplotaxis* and large nematodes found were collected. In addition, soil material from 0–15, 15–30, 30–45, and 45–60 cm layers was taken for the extraction of enchytraeids (wet funnels technique with heating (O'Connor, 1962). Soil was sampled from 0–15, 15–30, 30–45, and 45–60 cm layers, dried and sieved (2-mm mesh) for analysis.

Texture were measured using a Fritsch GmbH Laser Particle Sizer ANALYSETTE 22. The soil organic carbon (SOC) and total N content (TN) were measured using a LECO TruMac® CNS analyzer. The soil pH was determined potentiometrically in water (pH-H_2O) and 1M KCl at a 1:2.5 w/v ratio. The exchangeable acidity (HA) was measured in 1 M calcium acetate ($Ca[OAc]_2$), and the basic exchangeable cations were measured in 1 M ammonium acetate (NH_4Ac) using spectroscopy (ICP-OES; iCAP 6000 Series). The cation exchange capacity (CEC) was calculated as the sum of the exchangeable cations and HA. The base saturation (BS) was calculated as sum od cations divided by CEC.

Collected and extracted worms were identified to species (Lumbricidae), family (Enchytraeidae), or phylum level (Nematoda), freeze-dried and packaged into miniature tin cups for dual C and N stable isotope ratio analysis by Elemental Analyser—Isotope Ratio Mass Spectrometer, as reported by (Schmidt *et al.*, 2004). Animals were packed and measured individually. Only one *Haplotaxis* worm, collected in June 2022 and not chemically preserved, was measured. While replication was low, analytical precision of these measurements was high compared to measured differences between taxa. The precision (standard deviations, n=4) for standards (soy protein) measured along with the samples was 0.02‰ and 0.03‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Results

Soil properties. The soil is acid, has a silt and silt loam texture and belongs to Albic Luvisols (Siltic, Cutanic, Epidystric) (Fig. 2). The soil is characterised by a low soil organic carbon and nitrogen content, base saturation and pH. However base saturation increases with depth of soil profile what is typical in this type of soil (Table 1). The research site was located on a slope, there are no traces of groundwater in the soil profile and no evidence of groundwater stagnation (Fig. 2).

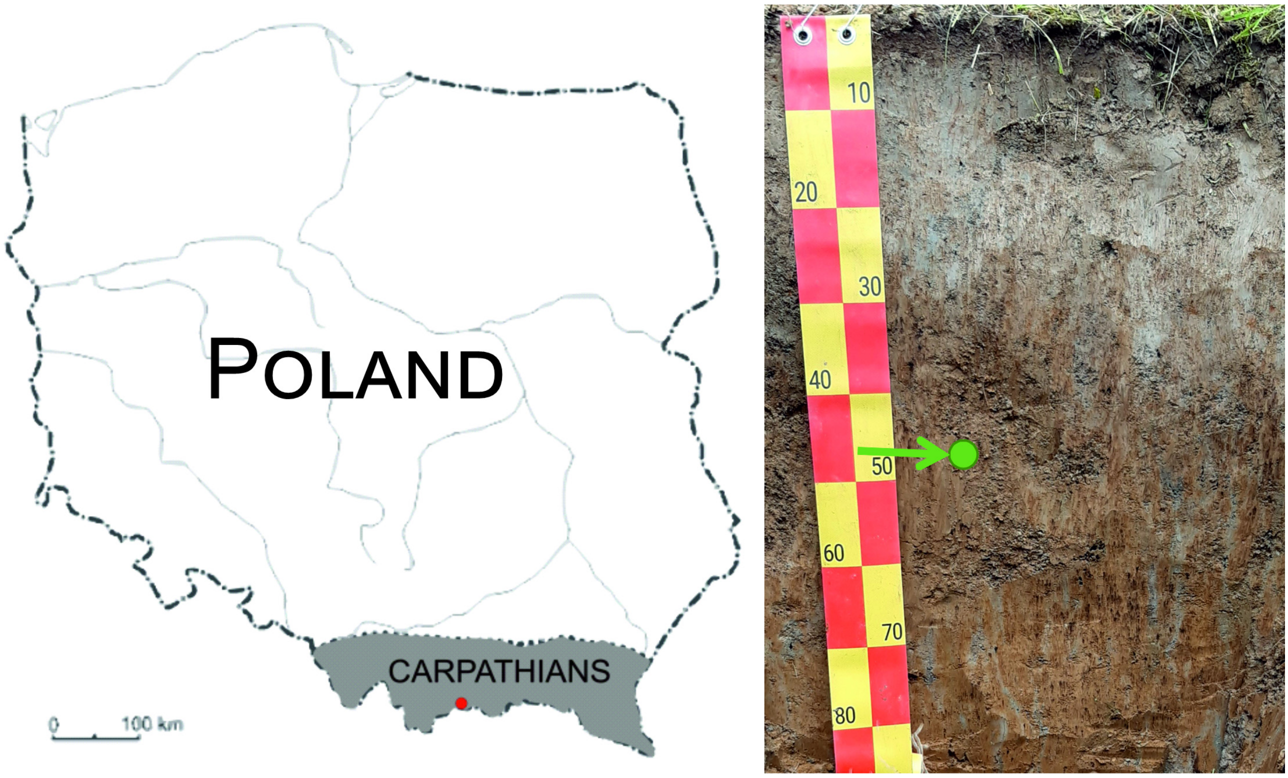

FIGURE 2. Left: Overview map showing the location of the study site. Right: soil profile of Albic Luvisol (Siltic, Cutanic, Epidystric), green dot indicates approximate depth of the specimens found in June 2022 (Photo by A. Józefowska).

Soil fauna. The density of earthworms was low with 39.1 individuals per m^2 (ind. m^{-2}). However, it is worth noting here that the sampling time (September) was not optimal for this animal group. Adults of two species were found during the study: *Aporrectodea rosea* (Savigny in Cuvier, 1826) and *Lumbricus terrestris* (Linnaeus, 1758), which were used in the isotopic analysis. The density of enchytraeids averaged 56325 ind. $m^{-2.}$ Most enchytraeids were in the topsoil (0–15 cm, 54518±22590 ind. m^{-2}) and their density successively decreased deeper into the soil profile (15–30 cm, 1205±1205 ind. m^{-2} and 30–45 cm, 602±602 ind. m^{-2}) to reach zero at a depth of 45–60 cm. *Haplotaxis* sp. was found at a depth of 45–60 cm (Fig.3). Two large nematode individuals were found in the 30–45 cm layer and were used in isotopic comparison.

TABLE 1. Soil pH, soil organic carbon and nitrogen content, texture and sorption properties of four soil layers (TN—total nitrogen, SOC—soil organic matter, HA—hydrolytic acidity, CEC—cation exchange capacity, BS—base saturation, cations, CEC and HA expressed in units of cmol(+)/kg soil).

Properties	**0–15 cm**	**15–30 cm**	**30–45 cm**	**45–60 cm**
pH in H_2O	4.6	4.9	5	5.1
pH in KCl	4.2	4.3	4.3	4.2
TN (%)	0.2	0.08	0.04	0.04
SOC (%)	2.26	0.76	0.34	0.22
SOC:TN ratio	11.5	9.8	7.8	6
Sand (%)	18	2	2	1
Silt (%)	75	87	85	83
Clay (%)	7	10	13	15
Ca^{2+}	4.13	3.84	6.55	9.23
K^{+}	0.32	0.13	0.18	0.27
Mg^{2+}	0.88	0.54	1.44	2.61
Na^{+}	0.02	0.02	0.04	0.05
HA	14.16	9.42	8.69	10.18
CEC	19.42	13.95	18.89	22.35
BS (%)	27.58	32.45	48.55	54.44

FIGURE 3. *Haplotaxis* sp. in its soil environment immediately after excavation; left: June 2022, right: September 2022 (Photos by A. Józefowska).

Trophic position of soil fauna. C and N isotope ratios for investigated soil fauna are presented in Figure 1. The range in isotope ratios for investigated soil fauna was large, from -30‰ to -25‰ for $\delta^{13}C$ and from 5‰ to 13‰ for $\delta^{15}N$. *A. rosea,* an endogeic earthworm, was isotopically close ($\delta^{13}C$ and $\delta^{15}N$ values of -25.25±0.24‰ and 9.07±0.48‰, respectively) to examined enchytraeids ($\delta^{13}C$ and $\delta^{15}N$ -25.91±0.15‰ and 9.37±0.56‰). Both groups were clearly separated from anecic, litter-feeding *Lumbricus terrestris* ($\delta^{13}C$ and $\delta^{15}N$ -26.63‰ and 4.51‰). Nematodes had much more negative $\delta^{13}C$ values (-28.70±0.86‰) but their $\delta^{15}N$ values (7.71±0.60‰) were roughly intermediate between endogeic and anecic earthworms. Most interestingly, *Haplotaxis* sp. had the highest $\delta^{15}N$ value (12.70‰) and also the least negative $\delta^{13}C$ value (-25.08‰), clearly indicating a higher trophic position than the other investigated animals.

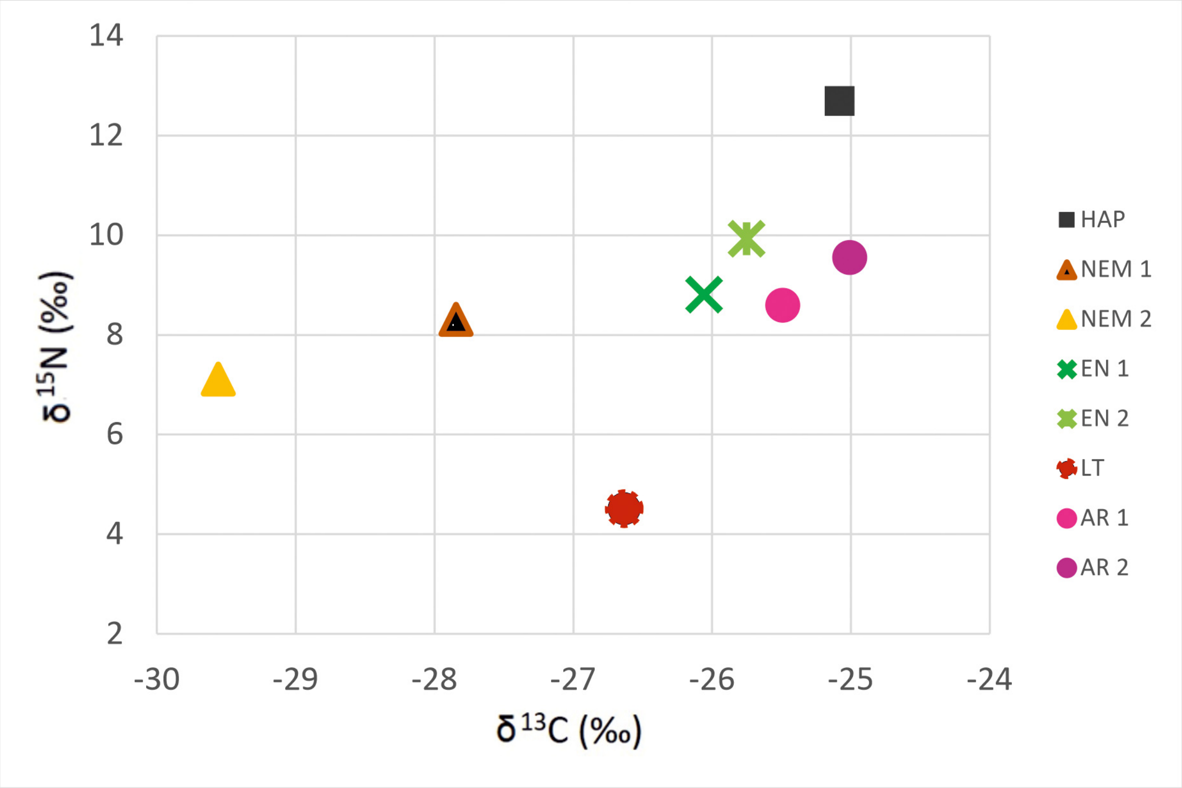

FIGURE 4. Biplot of C and N stable isotope ratios of investigated soil fauna. HAP—*Haplotaxis* sp., NEM—Unidentified *nematod*es, EN—Unidentified enchytraeids, LT—*Lumbricus terrestris,* AR—*Aporrectodea rosea.* Each point is a single individual.

Discussion

Habitat—Aquatic or terrestrial? Historically, the question of whether *Haplotaxis* is an aquatic or terrestrial genus arose very early on. The type species, *Haplotaxis gordioides*, was discovered by Georg Leonhard Hartmann in the well of his property in St. Gallen (Switzerland) (Hartmann, 1821). Published in a local journal, *Neue Alpina*, this discovery remained unknown for a long time. In 1837, Dugès reported a new species, *Tubifex uncinarius* (= *H. gordioides*), specifying that it lived in the same environment as *Tubifex filiforme* (Dugès, 1828) (= *Tubifex tubifex* (Müller, 1774)), i.e. "in water at a shallow depth, on the banks of streams and sometimes under stones, or in soil that is often well watered... ("…dans le terreau souvent bien arrosé")" (Dugès, 1837: 32). The word "terreau" is ambiguous because, in French, it refers to soil rich in organic matter of plant or animal origin; in this case, it is assumed that Dugès was referring to the soil enriched with organic matter that is naturally deposited on the banks of streams where the flow of water is low. Hoffmeister (1843) described *Haplotaxis menkeana* on the basis of specimens found by a certain Hofrath Menke in the "muddy bottom of open wells". Hoffmeister (1845) considered that the genus name *Haplotaxis* had already been taken by a plant genus and (incorrectly from present nomenclature) decided that the genus should be renamed *Phreoryctes*, whose etymology clearly alludes to the phreatic nature of its habitat (*phrear* = well; *oryctes* = burrower). Subsequently, the genus was reported on several occasions in the 19th century, e.g., in wells (Giard, 1889; Leuckart, 1861; Leydig, 1865), fountains (Leydig, 1865) and even between filamentous green algae floating in more or less large masses in the Rhône river (i.e., "conferves") (Claparède, 1860) but also under the deepest stones on the banks of the Rhine river (Noll, 1874) or under a stone, in a damp bottom (Giard, 1894).

Schlotthauber (1860) was the first to cast doubt on the aquatic nature of *Haplotaxis* on the grounds that every time it was found in wells, it was only a few specimens, whereas he collected them in quantities in the Göttingen fauna (p. 122). Being so convinced that what was then called *Phreoryctes* lived in the terrestrial environment, he decided to change the name of the genus to *Georyctes*, i.e. the earth burrower (*ge* = earth; *oryctes* = burrower). Unfortunately, Schlotthauber was very vague about the exact environment in which he found his *Haplotaxis* specimens, merely stating that they were part of the Göttingen fauna and that it was not water but soil.

An important detail becomes apparent when reading Michaelsen (1899), because one learns that his reflection on *Haplotaxis gordioides* and its synonymy is based on the examination of specimens by M. Schlotthauber sampled in 1846 in Göttingen and deposited in the collections of the Museum of Natural History in Hamburg. Michaelsen described these specimens as forming a ball of about 6 cm thickness of more than a hundred closely intermingled worms. It can therefore be deduced that the numerous specimens observed by Schlotthauber corresponded to this ball.

Unless considering this ball to be an artefact resulting from grouping due to thigmotaxis of the worms during field collection (Timm & Martin, 2015), it is known that the ball formation occurs in other species of oligochaetes when the environmental conditions deteriorate (Stephenson, 1930). Such a behaviour was also noted in *Haplotaxis* by Hesse (1923). The latter found *Haplotaxis* specimens in quantities in the trenches (in the Alsace region), when he was a soldier during the First World War. Interestingly, he points out that when the soil is in a muddy state, the worms live in isolation, whereas they form compact balls when the soil dries out, like *Tubifex* sp. when the water that bathes the mud in which they live evaporates. However, he honestly admits that he could not decide whether to consider it as a purely terrestrial animal, accidentally dragged into the water table by rainfall, or as an animal that can live in both environments.

Thanks to the colossal work of Timm (2023), the PlutoF biodiversity database contains the location of all currently known occurrences of all freshwater oligochaetes, as well as a brief description of their habitat. Therein, 99% of the 638 records attributed to *Haplotaxis* as currently accepted (Brinkhurst, 1988) refer to an aquatic habitat (groundwater and surface water). Most of the time, the environment in which these animals live is described summarily, making it difficult, if not impossible, to assess the extent to which their presence in surface water is accidental or not. Since this compiled information is available, however, it appears that the environment in which *Haplotaxis* specimens are reported is always linked in one way or another to aquifers, caves, springs, wells, fountains or hyporheic zones, i.e. environments typical of groundwater (e.g., Cernosvitov, 1939; Dole-Olivier *et al.*, 2022; Dumnicka *et al.* 2020; Leruth, 1939; Martin *et al.*, 2023; Tétry, 1938).

In PlutoF, four occurrences explicitly mention the term "soil" in their description: Liu and Erséus (2017), Pleşa *et al.* (1964), Stegman (1960) and Thienemann (1928). However, a careful reading of the descriptions of these locations shows that all of them, with the exception of Thienemann (1928), refer to an aquatic habitat in relation to groundwater (hyporheic environment, area irrigated by a groundwater source (Pleşa *et al.*, 1964); "stream bank" (Stegman, 1960; cf. tab. 1), "saturated soil with seeping groundwater" (Erséus, 2005; Liu & Erséus, 2017). Although Thienemann (1928), referring to Thienemann (1912), mentions finding *Haplotaxis* in soil layers, he specified that these were located "just above the water table", in "soil kept moist by the water table". Observing cocoons next to a worm in a block of soggy clay dug out of a work pit near the spring catchments, he also deduced that these animals reproduce in this environment, which constitutes their primary habitat. He concluded by stating that *H. gordioides* is one of the subterranean forms living in or near the water table, and only appears at the surface when groundwater reaches the surface. This observation can be compared with the report by Erséus (2005) in Sweden.

The difficulty with aquatic oligochaetes is that they are pre-adapted to life in the subterranean environment and that, unlike other subterranean aquatic invertebrates, they do not display troglomorphic characters, so that their stygobiotic nature (Gibert *et al.*, 1994) can only be inferred from their exclusive presence in the subterranean environment (Creuzé des Châtelliers *et al.*, 2009). There are, however, several records of *Haplotaxis* sp. in locations where they live in association with genuine stygobionts, reinforcing the hypothesis that *Haplotaxis* sp. is indeed a stygobiont oligochaete: amphipods *Niphargus puteanus* (saline spring; Thienemann, 1913), *Niphargus virei* (trickles of water bubbling up among the gravels and pebbles of a small stream; Vandel, 1922), copepods *Paracyclops fimbriatus*, *Megacyclops viridis* and copepods Harpacticoides (hyporheic zone of the Criș Repede; Pleşa *et al.*, 1964), isopod *Phreatoasellus akyioshiensis* (well; Yamaguchi, 1937), amphipod *Crangonyx mucronatus* and isopod *Asellus stygius* (farm drain; Forbes, 1890), numerous stygobiont species (upwelling zone of the hyporheic zone of the River Ain; Dole-Olivier *et al.*, 2022).

Taking this information into account, the real nature of the *Haplotaxis* habitat can then be interpreted. At a local level, it is currently considered that the underground aquatic environment is made up of a multitude of habitats linked to the types of aquifer, and which differ in terms of the size and density of the openings in the matrix and their degree of connectivity (Robertson *et al.*, 2023). Eberhard *et al.* (2005) showed that in Australia (Pilbara), stygofauna are present wherever groundwater environments provide sufficient living space, whether in unconsolidated sediment, karstic or fractured rock aquifers. This observation also seems to apply to *Haplotaxis.* This oligochaete appears to be an animal capable of exploiting the smallest cracks in a fissured environment and of moving, not only in the phreatic zone but also in all the possible living spaces in aquifers for groundwater fauna (epikarst, vadose and epiphreatic zone). This could explain the unexpected presence of *Haplotaxis* specimens in our soil samples, in the position where they were found. Consequently, its presence in a purely terrestrial environment, or even an aquatic surface environment, is more indicative of an accidental presence in these environments, which are not very conducive to the life of these animals, particularly the terrestrial environment.

Finally, other similar records of *Haplotaxis* in terrestrial environments could be explained in this way. In his catalogue of Belgian oligochaetes, Tétry (1940: 4) mentions a *Haplotaxis* found in a garden, at a depth of one metre, in Grand-Sart (Wavre, Belgium), a region particularly well endowed with small streams and other bodies of stagnant water, suggesting proximity to the water table. The catalogue of the RBINS collections even mentions a specimen found in a "leek" taken from a garden (3/3/1948, Hoves-Enghien, I.G. 15919, unpublished data). Finally, a specimen of *Haplotaxis* sp. (identification: A. Tétry, 1939) is reported under a stone in a damp meadow at Melreux (16/4/1936; I.G. 10820, unpublished data), a locality underlain by karst aquifers.

This interpretation would partly explain the presence of *Haplotaxis* cf. *gordioides* in our soil samples: by spreading in the damp earth above the water table, some individuals may “get lost” in areas far from the water table, where proximity to the surface can lead to the environment drying out. However, it is worth noting that the location of the research site on a slope (approx. 1080 m above sea level) with mineral soil not fed by groundwater up to at least 150 cm deep, and the distance from the nearest water reservoir (located approximately 770 m above sea level) by approximately 750 m does not fully confirm this interpretation. From a hydrological point of view (Aquilina *et al.* 2023), these waters can be connected; however, soil morphology indicated that the groundwater level is below the occurrence of *Haplotaxis* sp. It should also be emphasized that research on soil organisms is very rarely carried out at a depth greater than 30 cm, which may also be the reason for poor knowledge of the soil fauna occurring in subsoil.

In our samples, some excavated *Haplotaxis* specimens also appear to be folded in on themselves (Fig. 3). This behaviour has already been observed in “true” earthworms, which burrow deep into the soil during the dry summer months in search of a moist environment (Holmstrup *et al.*, 2016; Stephenson, 1930). The explanation of the unexpected presence of *Haplotaxis* specimens in our soil samples, in the position in which they were found, maybe that these animals move in the soil when it is fully saturated, e.g., when snow is melted or after a rain period, and become trapped by an unexpected drying out of the damp soil in which they could move. It would then put itself in this survival position, probably to limit body evaporation. Martin *et al.* (2023) recently demonstrated that in Switzerland, *Haplotaxis cf. gordioides* is a species complex with a narrow distribution. An ongoing genetic study (Martin *et al.*, unpubl. data) suggests that this observation can be extended to the European level and that the Polish specimens may belong to a species of their own. Consequently, it cannot be ruled out that they exhibit a particular adaptation that makes them more tolerant to the dryness of the terrestrial environment than their congeners.

Feeding mode—A predator among detritivores? The highly muscular pharynx in *Haplotaxis* is usually considered an adaptation for prey ingestion (Brinkhurst & McKey-Fender, 1991; Martin *et al.* 2024). *H. ichthyophagous* Gates, 1971, found in Californian salmon and trout redds, likely feeds on broken egg yolk (Gates, 1971). Remains of oligochaete chaetae were found in the intestines of *H.* cf. *gordioides* (Brinkhurst & Marchese, 1987) and *H. vermivorus* Michaelsen, 1932 (Michaelsen, 1932). In France, ventral chaetae of *Psammoryctides* were observed in the intestine of a *Haplotaxis* specimen from the collection of N. Giani (currently held at the MNHN, Paris) (Fig. 5). Notably, *Psammoryctides* Hrabě, 1964 is common in aquatic subterranean environments (springs, hyporheic zones, caves) (Artheau & Giani, 2006; Dole, 1983; Lafont *et al.*, 1992).

The present isotope ratio analysis and comparison with other, detritivore oligochaetes is the first confirmation of *Haplotaxis* as a predator, a conclusion arrived at independently of morphological or observational data. The positioning of *Haplotaxis* above other investigated oligochaetes (i.e. 3.6 and 3.4‰ higher in δ^{15}N than endogeic earthworms and enchytraeids, respectively) unambiguously assigns this worm to a trophic position that is exactly one level higher (Hyodo, 2015) than their detritivore relatives that are known to feed on the finest soil organic matter fractions (Schmidt *et al.*, 2004). Both the δ^{15}N and δ^{13}C spacings compared to co-occurring nematodes were much too large (i.e. 5.0‰ and 3.6‰), ruling out any suggestion that these large-bodied nematodes could be the main prey for *Haplotaxis*.

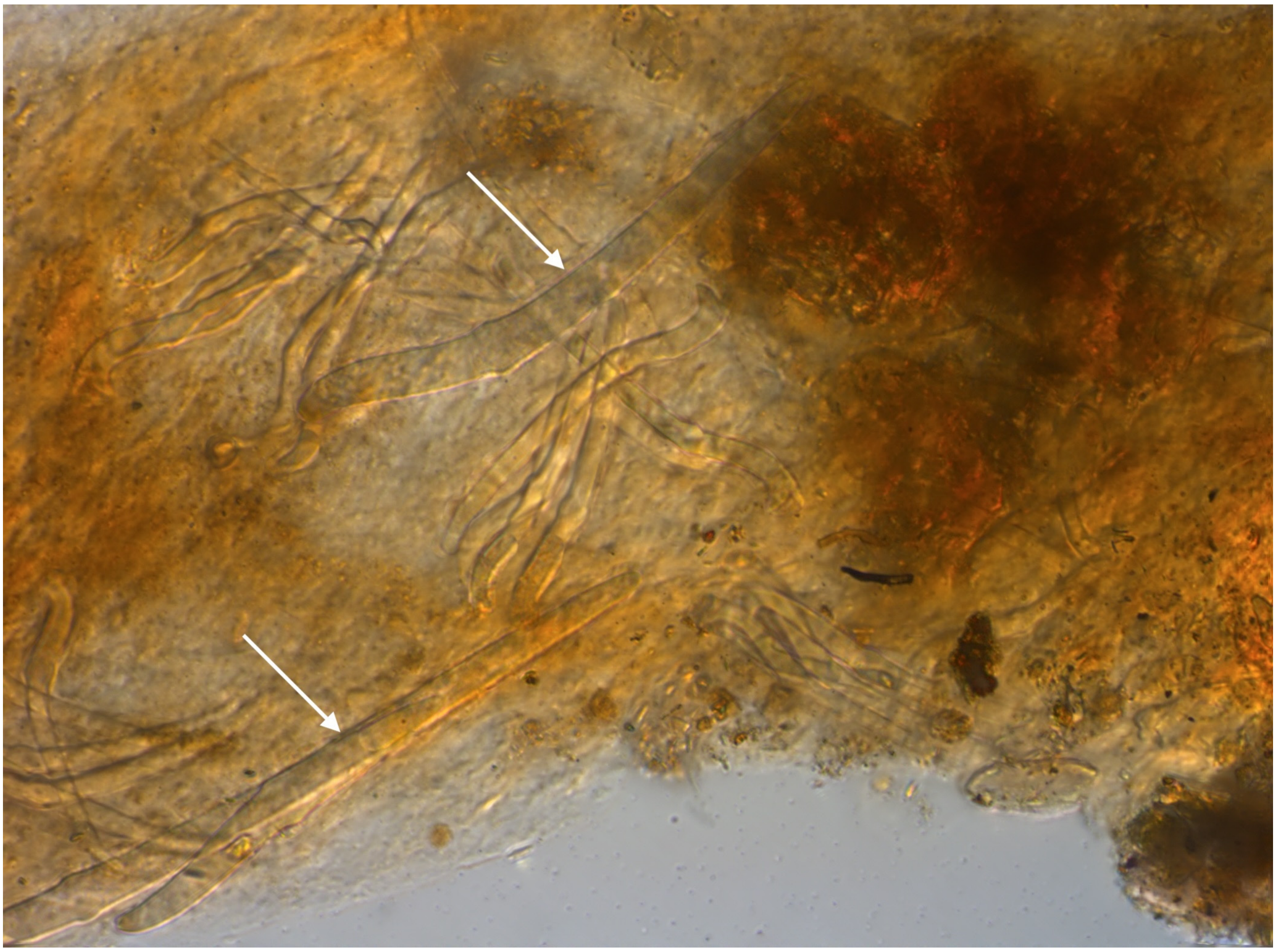

FIGURE 5. Oligochaete chaetae in the intestinal contents of a *Haplotaxis* sp. collected in France (post-clitellar region of the worm). Arrows indicate outside ventral chaetae of the predator *Haplotaxis*. The other chaetae are thought to belong to *Psammoryctides* sp. (Photo by P. Martin).

However, the feeding method in *Haplotaxis* remains largely unknown. By analogy with the mode of predation observed on the predatory lumbriculid *Phagodrilus* McKey-Fender, 1988 on other oligochaetes, Brinkhurst and McKey-Fender (1991) speculated that *Haplotaxis* might have a similar mode of predation, projecting its body in a spiral around large worms and probably using the large, hooked ventral chaetae to facilitate capture. As a result, some have compared *Haplotaxis* to a snake, assuming that it grips its prey oligochaetes with its extended prostomium and peristomium and then constrict the prey boa-like with its very long body and ventral chaetae (Timm & Martin, 2015).

However, other oligochaetes are known to have particularly well-developed chaetae in the anterior segments (e.g., *Limnodrilus tendens* (Semernoy, 1982), *Lycodrilides schizochaetus* (Michaelsen, 1901), and these are interpreted in the context of their mode of locomotion (Semernoy, 2004). Similarly, it can be hypothesised that the number (1 chaeta per dorsal and ventral bundle) and particular shape of the ventral (broad and sickle-shaped) and dorsal (reduced to absent) chaetae in *Haplotaxis* are the result of specific constraints linked to locomotion in the fissures of the subterranean aquatic environment, which probably are very different from those of surface sediments or terrestrial environment.

Lastly, *Haplotaxis* should probably be seen as an opportunistic scavenging predator, rather than a strict predator. Trophic position inferred from isotopic compositions cannot distinguish between predation (live prey) and scavenging (dead prey) (Birkhofer *et al.*, 2017). Due to the absence of photosynthesis, the underground aquatic environment relies on a random and scarce supply of food from the surface, which sinks into these habitats and is unevenly distributed. As a result, the biodiversity of subterranean ecosystems appears to be truncated both at the bottom of trophic networks (no primary producers) and at the top (very few strict predators) (Gibert & Deharveng, 2002). In Benin, one of us (PM) collected many *Haplotaxis* using traps baited with beef on which they feed. The attraction of this piece of meat is evidence of the sensory faculties developed in *Haplotaxis*, a likely adaptation to low food shared by many other subterranean invertebrates (Hüppop, 2012).

Conclusions

A new, documented record of *Haplotaxis* sp. in the subsoil layers of terrestrial mineral soil is being reported here. As discussed above, *Haplotaxis* sp. is commonly recorded and considered as an aquatic organism. Therefore, it becomes reasonable to ask whether the occasional recording of these organisms in the soil is due to their rare occurrence in terrestrial habitats or rather their easier extraction from aquatic habitats. This chance finding shows our limited knowledge and the infrequency with which we explore the subsoil fauna, including macro-fauna. Furthermore, this record provides the first independent confirmation that *Haplotaxis* is a predator. The collected *Haplotaxis* sp. material has been donated to taxonomic experts who are presently conducting a comprehensive revision of the entire genus.

References

Abarenkov, K., Tedersoo, L., Nilsson, R.H., Vellak, K., Saar, I., Veldre, V., Parmasto, E., Prous, M., Aan, A., Ots, M., Kurina, O., Ostonen, I., Jõgeva, J., Halapuu, S., Põldmaa, K., Toots, M., Truu, J., Larsson, K.-H. & Kõljalg, U. (2010) PlutoF—a Web Based Workbench for Ecological and Taxonomic Research, with an Online Implementation for Fungal ITS Sequences. *Evolutionary Bioinformatics*, 6, EBO.S6271.
https://doi.org/10.4137/EBO.S6271

Aquilina, L., Stumpp, C., Tonina, D. & Buffington, J.M. (2023) Hydrodynamics and geomorphology of groundwater environments. *In*: *Groundwater Ecology and Evolution.* Academic Press, San Diego, California, pp. 3–37.
https://doi.org/10.1016/B978-0-12-819119-4.00014-7

Artheau, M. & Giani, N. (2006) A checklist of the groundfreshwater Oligochaeta and Polychaeta in France : an overview. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, Biologie, 76, 229–255.

Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P.A., Klapwijk, M., Mestre, L., Roubinet, E., Schroeder, M., Stenberg, J.A., Porcel, M., Björkman, C. & Jonsson, M. (2017) Methods to identify the prey of invertebrate predators in terrestrial field studies. *Ecology and Evolution*, 7 (6), 1942–1953. [PMID: 28331601, PMCID: PMC5355183]
https://doi.org/10.1002/ece3.2791

Brinkhurst, R.O. & Marchese, M.R. (1987) A contribution to the taxonomy of the aquatic Oligochaeta (Haplotaxidae, Phreodrilidae, Tubificidae) of South America. *Canadian Journal of Zoology*, 65, 3154–3165.
https://doi.org/10.1139/z87-474

Brinkhurst, R.O. & McKey-Fender, D. (1991) The anatomy of the pharynx of two predatory aquatic oligochaetes. *Canadian Journal of Zoology*, 69, 669–675.
https://doi.org/10.1139/z91-098

Brinkhurst, R.O. (1988) A taxonomic analysis of the Haplotaxidae (Annelida, Oligochaeta). *Canadian Journal of Zoology*, 66, 2243–2252.
https://doi.org/10.1139/z88-332

Cernosvitov, L. (1939) Etudes biospeologiques. X (1). Catalogue des oligochètes hypogés. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, XV (22), 1–92.

Creuzé des Châtelliers, M., Juget, J., Lafont, M. & Martin, P. (2009) Subterranean aquatic Oligochaeta. *Freshwater Biology*, 54, 678–690.
https://doi.org/10.1111/j.1365-2427.2009.02173.x

Dole, M. J. (1983) Le domaine aquatique souterrain de la plaine alluviale du Rhône à l'est de Lyon. I. Diversité hydrologique et biocénotique de trois stations représentatives de la dynamique fluviale. *Vie et Milieu*, 33 (3–4), 219–229.

Dole-Olivier, M.J., Creuzé des Châtelliers, M., Galassi, D.M.P., Lafont, M., Mermillod-Blondin, F., Paran, F., Graillot, D., Gaur, S. & Marmonier, P. (2022) Drivers of functional diversity in the hyporheic zone of a large river. *Science of the Total Environment*, 843, 156985.
https://doi.org/10.1016/j.scitotenv.2022.156985

Dugès, A. (1837) Nouvelles observations sur la zoologie et l'anatomie des Annelides abranches sétigères. *Annales des Sciences Naturelles*, Zoologie, 2 (8), 15–35.

Dumnicka, E. Galas, J. Krodkiewska, M. & Pociecha, A. (2020) The diversity of annelids in subterranean waters: A case study from Poland. *Knowledge and Management of Aquatic Ecosystems*, 421 (16), 1–11.

https://doi.org/10.1051/kmae/2020007

Eberhard, S.M., Halse, S.A. & Humphreys, W.F. (2005) Stygofauna in the Pilbara region, north-west Western Australia: a review. *Journal of the Royal Society of Western Australia*, 88, 167–176.

Erséus, C. (2005) Haplotaxis gordioides – oväntat fynd i Sverige av en sällsynt ringmask [Haplotaxis gordioides - unexpected discovery in Sweden of a rare ringworm]. *Fauna och Flora*, 100 (4), 42–43.

Forbes, S.A. (1890) On an American earthworm of the family Phreoryctidae. *Bulletin of the Illinois State Laboratory of Natural History*, 3, 107–116.
https://doi.org/10.21900/j.inhs.v3.189

Gates, G.E. (1971) On a new species of California earthworm, Haplotaxis ichthyophagous (Oligochaeta, Annelida). *Proceedings of the Biological Society of Washington*, 84 (25), 203–212.

Giard, A. (1889) Sur l'habitat de Phreoryctes Menkeanus Hoffm. *Bulletin scientifique de la France et de la Belgique*, 1889, 171.

Giard, A. (1894) Sur un nouveau ver de terre de la famille des Phreoryctidae (Phreoryctes endeca Gd.). *Comptes Rendus Académie des Sciences de Paris*, 118, 811–814.

Gibert, J. & Deharveng, L. (2002) Subterranean Ecosystems : A Truncated Functional Biodiversity. *BioScience*, 52 (6), 473–481.
https://doi.org/10.1641/0006-3568(2002)052[0473:SEATFB]2.0.CO;2

Gibert, J., Danielopol, D.L. & Stanford, J.A. (1994) *Groundwater ecology*. Academic Press, San Diego, California, 571 pp.

Hartmann, G.L. (1821) Beyträge zur Geschichte der Fadenwürmer, nebst Beschreibung einer bisher mit ihnen verwechselten Art von Regenwurm, Lumbricus Gordioides. Der Schweizerischen Gesellschaft für die gesammten Naturwissenschaften vorgelesen den 28 Junius 1819 von G. L. Hartmann. *Neue Alpina*, 1, 32–50.

Hesse, E. (1923) Sur l'habitat de Haplotaxis gordioides G. L. Hartmann. *Bulletin de la Société Zoologique de France*, 48 (1), 138–140.

Hoffmeister, W. (1843) Beitrag zur Kenntnis deutscher Landanneliden. *Archiv für Naturgeschichte*, 9 (1–2), 183–198.

Hoffmeister, W. (1845) *Bie bis jetzt bekannten Arten aus der Familie der Regenwürmer. Als Grundlage zu einer Monographie dieser Familie*. Friedriech Vieweg und Sohn, Braunschweig, 43 pp.

Holmstrup, M., Slotsbo, S., Henriksen, P.G. & Bayley, M. (2016) Earthworms accumulate alanine in response to drought. *Comparative Biochemistry and Physiology*, Part A: Molecular & Integrative Physiology, 199, 8–13.
https://doi.org/10.1016/J.CBPA.2016.04.015

Hrabě, S. (1931) Die Oligochaeten aus den Seen Ochrida und Prespa. *Zoologische Jahrbücher*, Abteilung für Systematik, Ökologie und Geographie der Tiere, 61 (1/2), 1-62.

Hüppop, K. (2012) Adaptation to low food. *In*: *Encyclopedia of caves*. Academic Press, Elsevier, Whaltham, pp. 1–9.
https://doi.org/10.1016/B978-0-12-383832-2.00001-3

Hyodo, F. (2015) Use of isotope in insect trophic ecology. *Entomological Science*, 18, 295–312.
https://doi.org/10.1111/ens.12128

Kasprzak, K. (1979) Skąposzczety (Oligochaeta) Pienin. 2 Naididae, Tubificidae, Haplotaxidae, Lumbriculidae, Branchiobdellidae, XXIV. *Fragmenta Faunistica*, 24, 1–24.
https://doi.org/10.3161/00159301FF1979.24.2.057

Lafont, M., Durbec, A. & Ille, C. (1992) Oligochaete worms as biological describers of the interactions between surface and groundwaters: a first synthesis. *Regulated Rivers: Research & Management*, 7, 65–73.
https://doi.org/10.1002/rrr.3450070109

Leruth, R. (1939) *La biologie du domaine souterrain et la faune cavernicole de la Belgique (Mémoires du Musée royal d'Histoire naturelle de Belgique ed. Vol. Mémoire No 87*. Musée royal d’Histoire naturelle de Belgique, Bruxelles, 506 pp.

Leuckart, R. (1861) Bericht über die wissenschaftlichen Leistungen in der Naturgeschichte der niederen Thiere während des Jahres 1859. *Archiv für Naturgeschichte*, 26 (2), 103–264.

Leydig, F. (1865) Ueber Phreoryctes Menkeanus Hofm. nebst bemerkungen über den bau anderer Anneliden. *Archiv für mikroskopische Anatomie*, 1, 249–294.
https://doi.org/10.1007/BF02961416

Liu, Y. & Erséus, C. (2017) New specific primers for amplification of the Internal Transcribed Spacer region in Clitellata (Annelida). *Ecology and Evolution*, 7 (23), 10421–10439.
https://doi.org/10.1002/ece3.3212

Martin, P.J., Fend, S.V., Klinth, M.J., Martinsson, S., Torii, T. & Erséus, C. (2024) Towards an integrative revision of Haplotaxidae (Annelida: Clitellata). *Zoological Journal of the Linnean Society*, 202 (4), zlae141.
https://doi.org/10.1093/zoolinnean/zlae141

Martin, P., Knüsel, M., Alther, R., Altermatt, F., Ferrari, B. & Vivien, R. (2023) Haplotaxis gordioides (Hartmann in Oken, 1819) (Annelida, Clitellata) as a sub-cosmopolitan species: a commonly held view challenged by DNA barcoding. *Zoosymposia*, 23, 78–93.
https://doi.org/10.11646/zoosymposia.23.1.10

Martin, P., Martínez-Ansemil, E., Pinder, A., Timm, T. & Wetzel, M.J. (2008) Global diversity of oligochaetous clitellates ("Oligochaeta"; Clitellata) in freshwater. *Hydrobiologia*, 595, 117–127.
https://doi.org/10.1007/s10750-007-9009-1

Michaelsen, W. (1899) Beiträge zur Kenntnis der Oligochäten. *Zoologische Jahrbücher*, Abteilung für Systematik, Geographie und Biologie der Thiere, 12, 105–144. https://doi.org/10.5962/bhl.part.2028

Michaelsen, W. (1905) *Die Oligochaeten des Baikal-Sees. Wissenschaftliche Ergebnisse einer Zoologischen Expedition nach dem Baikal-See unter Leitnung des Professors Alexis Korotneff in den Jahren 1900–1902*. Commissions-Verlag von R. Friedländer & Sohn, Kiew und Berlin, 69 pp.

Michaelsen, W. (1932) Ein neuer Phreoryctes von der Tropeninsel Poeloe Berhala. *Miscellanea Zoologica Sumatrana*, 71, 1–7.

Noll, F.C. (1874) Ueber einen neuen Ringelwurm des Rheins. *Archiv für Naturgeschichte*, 40, 1, 260–270.

O'Connor, F.B. (1962) The extraction of Enchytraeidae from soil. *Progress in Soil Zoology*, 1962, 279–285.

Pleşa, C., Botea, F. & Racoviţă, G. (1964) Cercetări asupra faunei biotopurilor acvatice subterane din bazinul Crişului Repede [Research on the fauna of subterranean aquatic biotopes in the Criș Repede basin]. *Lucrările Institutului de Speologie "Emil Racoviță"*, 3, 367–396.

Robertson, A., Brancelj, A., Stein, H. & Hahn, H.J. (2023) Classifying groundwater ecosystems. *In*: Malard, F., Griebler, C. & Rétaux, S. (Eds.), *Groundwater Ecology and Evolution*. Academic Press, San Diego, California, pp. 39–60. https://doi.org/10.1016/B978-0-12-819119-4.00007-X

Schlotthauber, C. (1860) Beiträge zur Helminthologie. *Amtlicher Bericht über die Versammlung Deutscher Naturforscher und Aerzte, Göttingen*, 34, 121–133.

Schmidt, O., Curry, J.P., Dyckmans, J., Rota, E. & Scrimgeour, C.M. (2004) Dual stable isotope analysis (δ^{13}C and δ^{15}N) of soil invertebrates and their food sources. *Pedobiologia, Jena*, 48, 171–180. https://doi.org/10.1016/j.pedobi.2003.12.003

Semernoy, V.P. (2004) *Oligochaeta of Lake Baikal*. Nauka, Novosibirsk, 528 pp.

Stegman, L.C. (1960) A preliminary survey of earthworms of the Tully forest in central New York. *Ecology*, 41 (4), 779–782. https://doi.org/10.2307/1931812

Stephenson, J. (1930) *The Oligochaeta*. Oxford University Press, Oxford, 978 pp.

Tétry, A. (1938) *Contribution à l'étude de la faune de l'Est de la France*. Imprimerie Georges Thomas, Nancy, 453 pp.

Tétry, A. (1940) Les oligochètes de Belgique. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 16 (31), 1–24.

Thienemann, A. (1912) Der Bergbach des Sauerlandes. Faunistischbiologische Untersuchungen. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 1912, 1–12.

Thienemann, A. (1913) Die Salzwassertierwelt Westfalens. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 23, 56–68.

Thienemann, A. (1928) Haplotaxis gordioides, G. L. Hartmann als terrestrischer Wurm. *Archiv für Hydrobiologie*, 19, 377.

Timm, T. & Martin, P. (2019) Phylum Annelida. Class Clitellata: Subclass Oligochaeta. *In*: Rogers, D.C. & Thorp, J.H. (Eds.), *Thorp and Covich's Freshwater Invertebrates. 4th Edition*. Keys to Palaearctic Fauna. Academic Press, Boston, Massachusetts, pp. 364–482.

Timm, T. & Martin, P.J. (2015) Chapter 21. Clitellata: Oligochaeta. *In*: Thorp, J.H. & Rogers, D.C. (Eds.), *Thorp and Covich's Freshwater Invertebrates. 4th Edition*. Academic Press, Boston, Massachusetts, pp. 529–549. https://doi.org/10.1016/B978-0-12-385026-3.00021-8

Timm, T. (2023) A database of aquatic Oligochaeta (Annelida, Clitellata) with updated order names. *Zoosymposia*, 23, 35–40. https://doi.org/10.11646/zoosymposia.23.1.7

Vandel, A. (1922) Sur la faune d'eau douce des Pyrénées orientales. *Bulletin de la Société Zoologique de France*, 47 (5), 163–170.

Yamaguchi, H. (1937) Studies on the aquatic Oligochaeta of Japan. II. Occurrence of the subterranean oligochaete Haplotaxis gordioides (Hartmann) in Japan. *Annotationes Zoologicae Japonenses*, 16, 68–73.