

Revalidation of the stygobiotic species *Haber zavreli* (Hrabě, 1942) (Clitellata, Naididae, Tubificinae) with discussion on the closely related species *Haber speciosus* (Hrabě, 1931) and *Haber monfalconensis* (Hrabě, 1966)

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Abstract

During studies of aquatic fauna in wells situated near Kraków (South Poland), many specimens of clitellates were found. The detailed description of the setal formula and genital organs of the collected individuals made it possible to distinguish *Haber zavreli* (Hrabě, 1942) from the related species: *H. speciosus* (Hrabě, 1931) including synonymized *H. simsi* and its forms known from the USA (*H. speciosus simsi* and *H. speciosus fluminialis*) and *H. monfalconensis* (Hrabě, 1966). In addition, remarks concerning the morphologically similar *Haber vetus* (Semernoy, 1982) described from Lake Baikal and the stygobiotic species *H. turquinae* (Juget & Lafont, 1979) are included.

Keywords

Oligochaete worms, southern Poland, stygobiont, wells

Introduction

The genus *Haber* Holmquist, 1978 was established by Holmquist (1978), as a result of a revision of *Pelosclex* Leidy, 1850, a species-rich genus and heterogeneous. Its definition was completed later and slightly modified by Milligan (1986). According to these authors, the genus *Haber* can be defined as follows:

- body wall without papillae and usually without adherent particles.
- modified spermathecal and penial setae of similar shape present in X and XI segments; each single seta is inserted in a conspicuous glandular sac (named also setal sac).
 - smooth or hispid hairs and pectinate (or bifid) setae in dorsal bundles and bifid setae in ventral ones.
 - male funnel fairly small, vas deferens long, in the majority of species with its distal part (ental – sensu Holmquist (1978, 1979 and Milligan (1986)) narrow and proximal (ectal) part 2–4 times broader; vas deferens opens apically to the tubular atrium.
 - ectal region of the atrium modified into an ejaculatory duct.
 - compact prostatic gland attached medially to the atrium.
 - penial apparatus bulb-like, usually muscular; its internal canal lined with epithelium fitted with thick basal membrane resembling cuticular penial sheath, but true cuticular penial sheath absent.
 - spermatheca with elongated ampulla and fairly short ectal duct, spermatozeugmata narrow, “worm-like”.
 - spermathecal pores paired, situated in different position in particular species.

Three taxa representing this genus were described by Hrabě (1931, 1942, 1966). The description of *Haber speciosus* (Hrabě, 1931) (originally *Tubifex speciosus*) was based on 12 individuals (8 mature) found in Lake Ochrida (Ohrid) at depths between 40–250 m. *Haber zavreli* (Hrabě, 1942) was described (as *Peloscolex zavreli*) from wells in the village Rajec (Slovakia) where numerous, mainly mature specimens were found. The last species, *H. monfalconensis* (Hrabě, 1966) was described as a subspecies of *H. speciosus* (originally *Tubifex speciosus monfalconensis*). The unknown number of specimens representing this taxon was collected in cave waters and in a spring in north-east Italy (Timavo region) (Hrabě 1966). Brinkhurst (1966) described very shortly *Haber simsi* (Brinkhurst, 1966) (as *Peloscolex simsi*) based on a single specimen from the diversion of the Frome River in Dorset (Great Britain). These four taxa were later synonymized by Brinkhurst and Jamieson (1971). Holmquist (1978, 1979), who re-examined the original materials of all three taxa described by Hrabě (*H. speciosus*, *H. zavreli* and *H. monfalconensis*) wrote: “there are several quite distinctive characters justifying a separation into the three species” and she redescribed them shortly (Holmquist 1979). According to her suggestion *H. monfalconensis* exclusively was assigned to the species status (Martin et al. 2017; Fauna Europaea 2021). *H. zavreli* was mentioned as an “independent” species only by Brinkhurst (1981), who indicated that its subspecific or specific rank has yet to be determined. In zoological lists it is still treated as a synonym of *H. speciosus* (Martin et al. 2017; Fauna Europaea 2021; WoRMS 2021).

This work aims to reassess the species status of *Haber zavreli* based on: 1) new material collected in a well near the Kraków city; 2) original descriptions and other literature data concerning related species: *H. speciosus* (including *H. simsi* and two forms from the USA: *H. speciosus simsi* and *H. speciosus fluminialis* (Milligan 1986) and

H. monfalconensis). In addition, taxonomical remarks on the morphologically similar epigeal species *Haber vetus* (Semernoy, 1982) and the poorly described stygobiont *H. turquinae* (Juguet & Lafont, 1979) will be made.

Material and methods

In 2016, studies on aquatic fauna were done in some wells dug in the cretaceous marls near Kraków (Southern Poland). Samples from the bottom of the wells were collected using an Ekman sampler, washed on 200 µm net mesh and fixed in 75% ethanol. The invertebrates were sorted under a stereoscopic microscope (magnification 10×). Whole specimens of clitellates were mounted in Canada balsam.

Biological material: 55 mature and 106 juvenile specimens were collected in one of the studied wells. 10 May 2016: 136 individuals (37 mature, 99 juv.), 2 August 2016: 25 individuals (18 mature, 7 juv.). Collected specimens were deposited in the Natural History Museum, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków and in private Dumnicka's collection in the Institute of Nature Conservation, Polish Academy of Sciences in Kraków.

Locality: dug well in Prandocin Wysiółek village (50°15.100'N, 20°05.677'E in DDM system), 240 m asl, depth of the well – 8.1 m, bottom covered with muddy sediments. Physico-chemical parameters of water in particular dates: water temperature 10.3, 12.2 °C; pH 6.9, 7.0; conductivity 836, 826 µS; oxygen concentration 7.04, 6.72 mg O₂ L⁻¹; calcium 148.2, 167.7 mg L⁻¹; sulphates 136.3, 133.3 mg L⁻¹; nitrates 40.7, 38.6 mg L⁻¹; phosphates 0.017, 0.023 mg L⁻¹.

Results

Haber zavreli (Hrabě, 1942)

Peloscolex zavreli Hrabě 1942: 23–26 (description of species, type locality: Rajec u Žiliny, in wells);

Peloscolex speciosus (partim) (Brinkhurst and Jamieson 1971): 514–515;

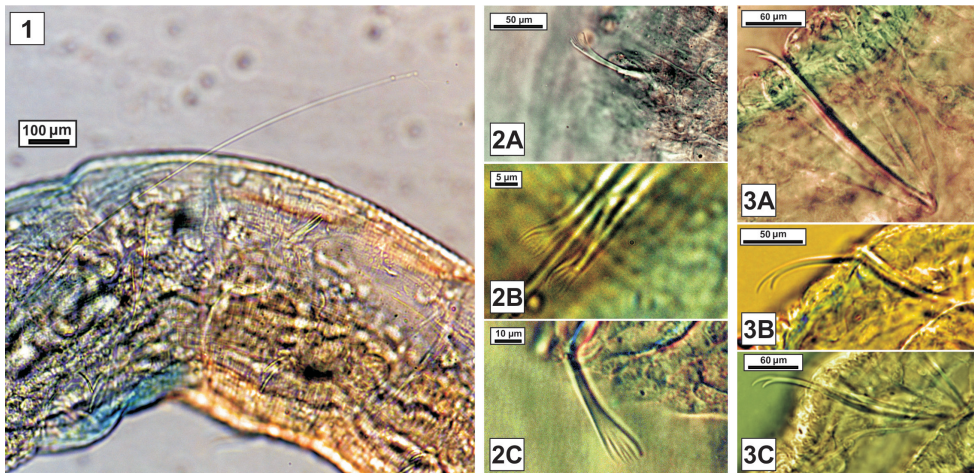
Peloscolex zavreli (Kasprzak 1973): 421–422 (short description of two specimens found in the wells in the Beskidy Mts, Poland)

Haber zavreli (Holmquist 1979): 52–53 (redescription);

Peloscolex speciosus zavreli (Hrabě 1981): 87–88 (distribution, short taxonomic discussion);

Haber zavreli (Brinkhurst 1981): 1062 (citation)

Redescription. Almost all mature specimens without the posterior part of the body. Length of complete mature individuals: 10–11 mm, number of segments: 64–68. Body wall without papillae and without mucous cover, usually smooth, but in some specimens with tiny wrinkles (Fig. 1).



Figures 1–3. *Haber zavreli* (Hrabč, 1942) **1** fragment of the body with hair seta and tiny wrinkles seen on dorsal side **2** shape of dorsal pectinate setae: **2A** in V segment **2B** in VII segment **2C** in XV segment **3** shape of ventral setae: **3A** in IV segment **3B** in VIII segment **3C** in XV segment.

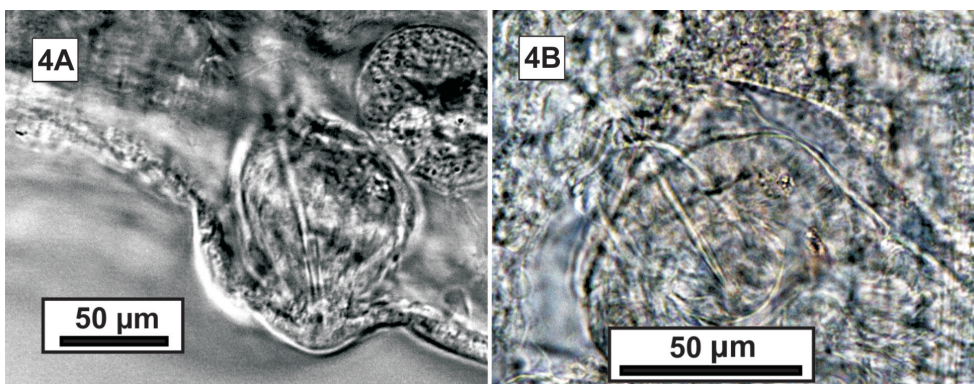
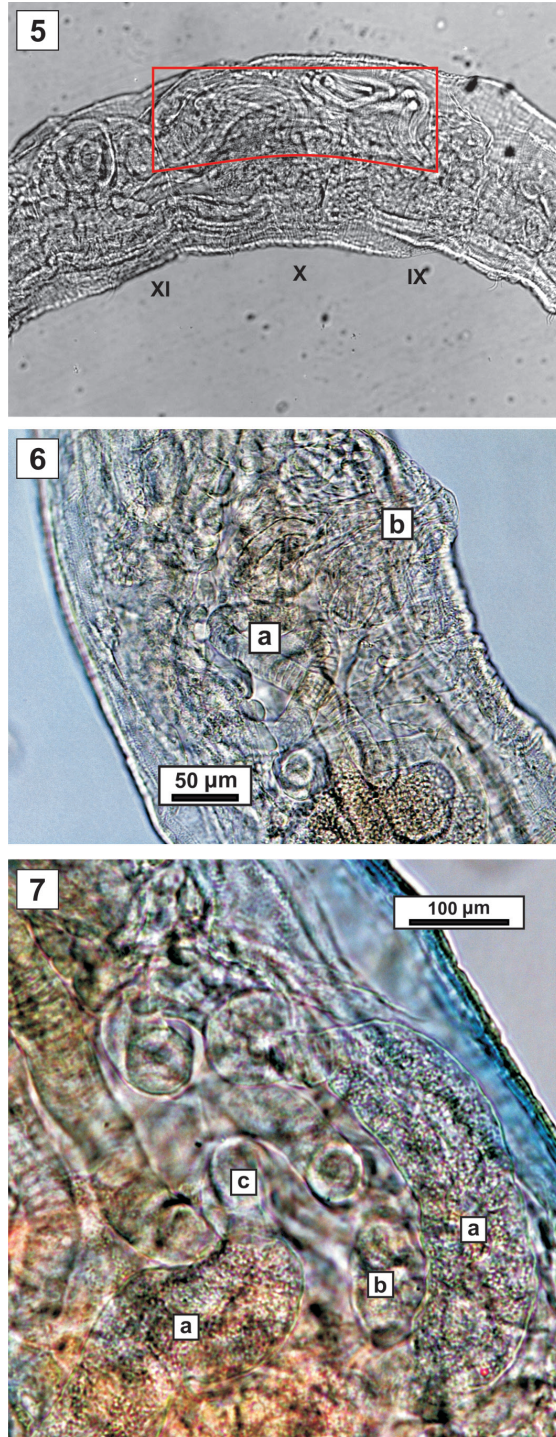


Figure 4. *Haber zavreli* (Hrabč, 1942) **A** spermathecal seta in glandular sac **B** penial seta in glandular sac.

Singular long and smooth hair seta (Fig. 1) in all dorsal bundles (exceptionally two setae in anterior segments). Pectinate setae with long teeth in all segments (Fig. 2A–C). The length of external and intermediate teeth is almost the same, but external ones are stouter. In anterior segments 5–7 intermediate teeth (Fig. 2A, B) and distal end of the setae shovel-shaped, in posterior segments it is goblet-shaped with 3–4 intermediate teeth (Fig. 2C). In the anterior dorsal bundles 1–2 setae, in the posterior segments – 1 seta. All ventral setae with the upper teeth longer than the lower (Fig. 3A–C): in anterior segments about two times longer (Fig. 3A), from segment VIII this difference is smaller (Fig. 3B, C). The singular modified spermathecal and penial seta is present respectively in segments X and XI. They are thin and sharp-ended with hollowed distal part (Fig. 4A, B) and they are inserted inside glandular sacs. The length of setae of mature individuals: hair setae up to 1000 µm long; dorsal anterior: 103–132 µm;



Figures 5–7. *Haber zavreli* (Hrabč, 1942) **5** Fragment of the body with spermathecal ampulla (marked by red frame) filled with long spermatozeugmata **6a** fragment of vas deferens **6b** penial apparatus **7** ectal part of male genital apparatus: **a** atria **b** prostate gland **c** ejaculatory duct.

posterior: 87–103 μm ; ventral anterior: 230–243 μm ; ventral posterior: 148–160 μm ; spermathecal setae: 55–70 μm and penial setae 55–63 μm .

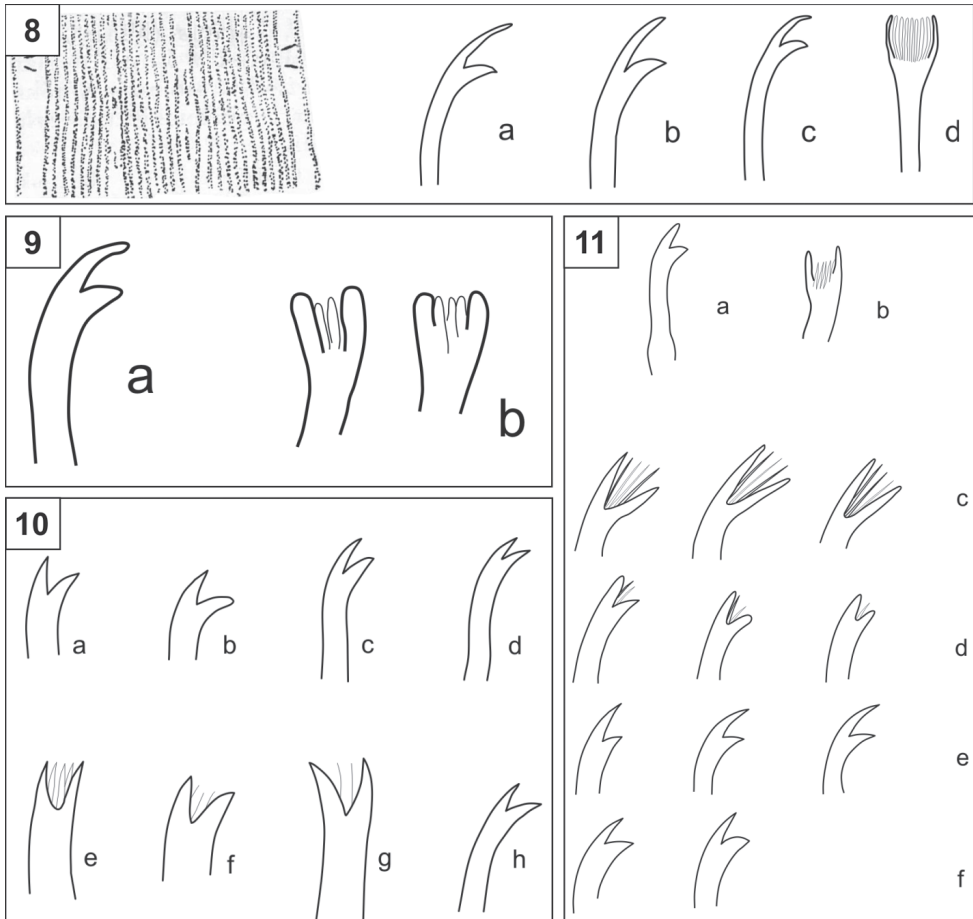
Long, irregular sac-like ampullae of spermathecae (Fig. 5) sometimes reach IX segment, short spermathecal duct set off suddenly from ampulla and its ectal opening occurs slightly dorsally from the line of spermathecal setae. The long, “worm-like” spermatozeugmata either fill whole ampulla or are concentrated in its ental part. Male funnel small, vas deferens very long, coiled (Fig. 6a) with distal part slightly thinner and shorter than proximal one. Proximal part of vas deferens narrower than tubular atrium (Fig. 7a) and enters to it apically. Prostate gland small and compact enters to atrium almost medially (Fig. 7b). Thin ejaculatory duct markedly sets off from the atrium (Fig. 7c). Penial apparatus elongated with two, well visible bulges – one with basal membrane (the so-called “penis sheath”), and the second one with penial seta (Fig. 6b).

Discussion

The body wall of the examined specimens is generally smooth. The fine, longitudinally arranged wrinkles (Fig. 8, left) originally described by Hrabě (1942) have not been observed. Holmquist (1979) reported the presence of fine ringlets in the post-clitellar part of the body and similar structures were present in some collected specimens, but thin cover of secretion was absent. Probably the presence or absence of fine wrinkles could be the result of different methods of material fixation.

According to original descriptions by Hrabě (1931, 1942, 1966), the shape of somatic setae is a good feature allowing to differentiate *H. zavreli* from *H. speciosus* and *H. monfalconensis* (Table 1). Of these three species, *H. zavreli* is the only one to have upper teeth of posterior ventral setae distinctly longer than lower ones and pectinate dorsal setae in all segments. The shape of ventral setae in collected specimens was almost identical to these on original Hrabě’s illustrations (Fig. 8a–c) whereas anterior dorsal pectinates differed a little from that drawn by Hrabě (1942) (Fig. 8d): in our specimens, the number of intermediate teeth was a little smaller than on Hrabě’s picture, but the shape of the setal ectal tip was identical (shovel-shaped). For *H. speciosus* only the shape of anterior setae was shown by Hrabě (1931) (Fig. 9a, b), whereas in the original description of *H. monfalconensis*, there are no drawings of setae (Hrabě 1966). For this reason, a descriptive comparison of setal shapes is only possible for the three species mentioned above (Table 1).

Ventral setae of the *H. speciosus* forms described by Milligan (1986) from the USA (*H. speciosus simsi* and *H. speciosus fluminialis*) (Fig. 10a–d) are similar to these observed in the nominative European form, but dorsal setae (Fig. 10e–h), especially of *H. speciosus simsi* (Fig. 10e, f) differ a little: instead of bifid setae present in posterior segments of the nominative form, pectinate setae with a few thin intermediate teeth were reported (Milligan 1986). Nevertheless, the anatomy of genital organs confirms that the American forms belong to *H. speciosus*. Ventral anterior seta (Fig. 11a) of the specimen described as *H. simsi* by Brinkhurst (1966) and synonymized later with *H. speciosus* (Brinkhurst and Jamieson 1971) is typical for last-mentioned species,



Figures 8–11. **8** *Haber zavreli* (Hrabě, 1942); Left: wrinkles on body surface; right: shape of the somatic setae **a** ectal part of ventral setae in segment III **b** in segment VIII **c** in posterior segments **d** anterior dorsal seta (after Hrabě 1942) **9** *Haber speciosus* (Hrabě, 1931); anterior somatic setae **a** ventral seta in segment II **b** dorsal setae (after Hrabě 1931) **10** somatic setae of *Haber speciosus* forms described by Milligan (1986) **a–d** ventral setae: *H. speciosus simsi* **a** anterior seta **b** posterior seta; *H. speciosus fluminialis* **c** anterior seta **d** posterior seta **e–h** dorsal setae: *H. speciosus simsi* **e** anterior seta **f** posterior seta; *H. speciosus fluminialis* **g** anterior seta **h** posterior seta (after Milligan 1986, modified) **11** *Haber simsi* (Brinkhurst, 1966) **a** anterior ventral seta **b** anterior dorsal seta (after Brinkhurst 1966) **c** anterior dorsal setae **d** posterior dorsal setae **e** anterior ventral setae **f** posterior ventral setae (after Bird and Ladle 1981).

whereas dorsal setae “seem to be intermediate to those of *P. speciosus* (...) and *P. zavreli*” (Brinkhurst 1966, p. 736) (Fig. 11b). The setae of specimens determined by Bird and Ladle (1981) as *H. simsi* (Fig. 11c–f) resemble those of *H. zavreli*, but due to the lack of full description of genital organs of these specimens, it is not possible to determine their taxonomic status. A distinctive feature of the genus *Haber* is the shape of genital setae – it is similar in all discussed species.

The main features of the genital organs which allow distinguishing between species attributed to the *Haber speciosus* group were described (Table 1) and illustrated

Table 1. Comparison of the setal formula and genital organs structure of three closely related species: *Haber speciosus* (Hrabě, 1931), *H. zavreli* (Hrabě, 1942) and *H. monfalconensis* (Hrabě, 1966) (after Hrabě 1931, 1942, 1966; Holmquist 1979, modified and complemented).

Species feature	<i>H. speciosus</i> (Hrabě, 1931)	<i>H. zavreli</i> (Hrabě, 1942)	<i>H. monfalconensis</i> (Hrabě, 1966)
No of hair setae: in anterior segments in posterior segments	2–3 1 (0)	1 (2) 1	1–2 1
Dorsal setae in anterior segments	1–3; lateral teeth obtuse, almost parallel, short, 2–3 intermediate teeth	1 (2); lateral teeth long acute, inter-mediate teeth slightly shorter, up to 8	1–2 (3); lateral teeth long, acute, upper tooth slightly longer, intermediate teeth fine
Dorsal setae in posterior segments	1; bifid	1 (2); pectinate, 3–4 intermediate teeth	1; bifid, teeth short, equal, upper thinner
Ventral setae in anterior segments	3–4; upper teeth slightly longer	2–3; upper teeth two times longer	3–4; upper teeth longer, from VIII teeth equal
Ventral setae in posterior segments	1–2; teeth equal (?)	2; upper teeth longer	3–2; teeth short, equal or upper slightly shorter
Localization of spermathecal pores	between the line of ventral and dorsal setae	near the line of ventral setae	in line of ventral setae
Spermathecal duct	comparatively long, set off gradually from ampulla	short, set off abruptly from ampulla	short, set off gradually from ampulla
Spermathecal ampulla	comparatively small, sac-like	well developed, long and irregular sac	comparatively small, sac-like
Male funnel	small	small	small
Vas deferens	long	long	long
Distal part of vas deferens	distinctly thinner and slightly shorter than proximal part	moderately thinner; length of both parts similar or proximal part a little longer	moderately thinner and markedly shorter than proximal part
Proximal part of vas deferens	broad, even wider than atrium	narrower than atrium	broad, about the same width as atrium
Ejaculatory duct	gradually set off from atrium	abruptly set off from atrium	gradually set off from atrium

(Fig. 12A–C) by Holmquist (1978, 1979). The most characteristic features for *H. zavreli* are: (1) shape and dimension of spermathecal ampulla which is distinctly bigger than in two other species; (2) localisation of spermathecal pores near the line of ventral setae, but not in this line; (3) the ectal part of vas deferens narrower than atrium whereas in remaining species it is broader or has the same width as atrium and (4) non-gradual transition between atrium and ejaculatory duct.

According to Holmquist (1978) the construction of the penial apparatus is very specific in the *Haber* genus. The basal membrane lying in the internal canal of the penial bulb resembles cuticular penial sheath and this name was used in species descriptions by Hrabě (1931; 1942; 1966), Brinkhurst (1966), Juget and Lafont (1979) and the others.

According to original species descriptions (Hrabě 1931; 1942; 1966), cylindrical “penis sheath” is about 50 µm long in *H. speciosus*, about 67 µm in *H. zavreli* and it reaches up to 80 µm in *H. monfalconensis*. For *H. speciosus* the proportion between length and width of this structure differs in various papers (Fig. 13a–e): in the original description (Hrabě 1931) this proportion is about 2 : 1 (Fig. 13a) whereas in another paper by Hrabě (1966) it was reported to be about 4 : 1 (Fig. 13b). For *H. speciosus* described by Brinkhurst (1966) as *H. simsi* and American forms (*H. s. fluminialis* and *H. s. simsi*), these proportions fluctuate from 1.5 : 1 to 2 : 1 (Fig. 13c–e). Thickened basal membranes in *H. zavreli* (Hrabě 1942) and *H. monfalconensis* (Hrabě 1966) are elongated. The proportions between length and width reach 4 : 1 for *H. zavreli*

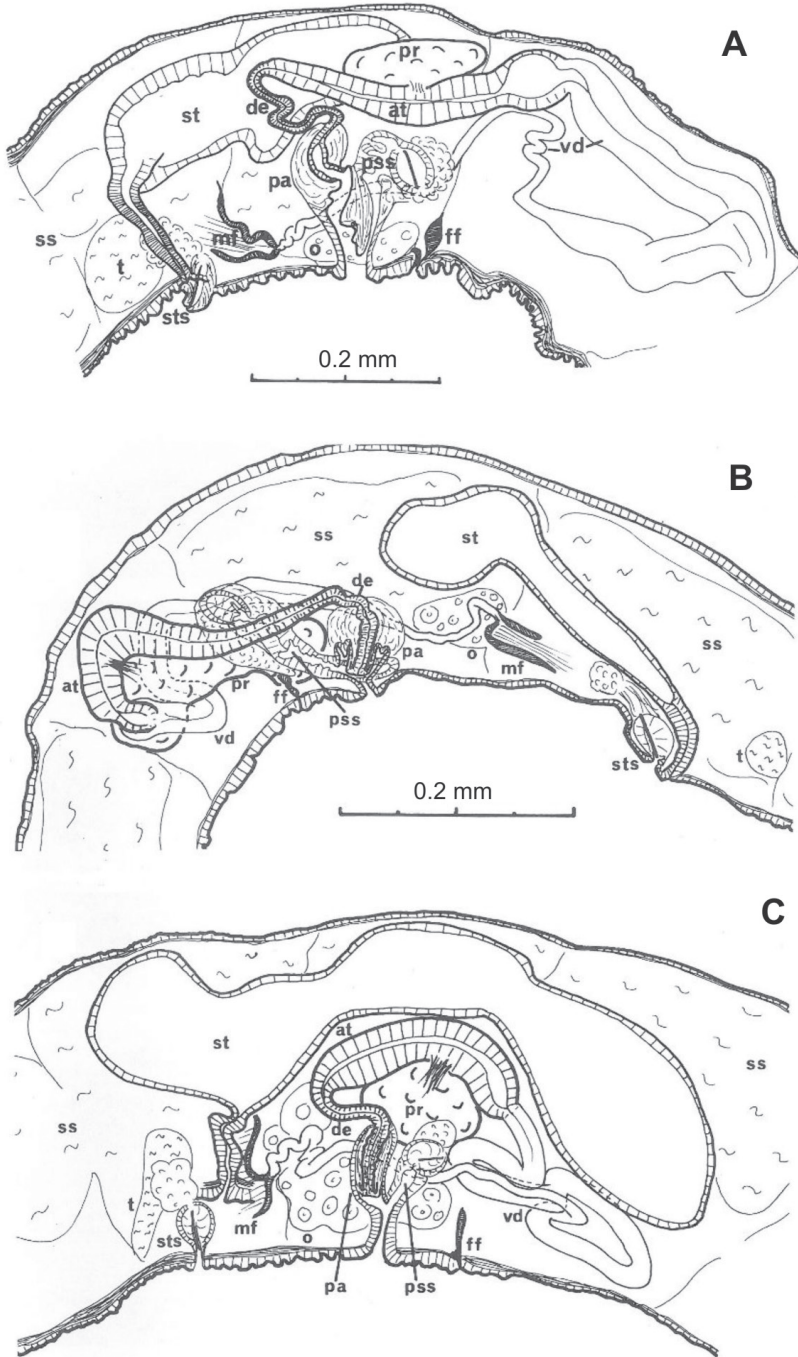
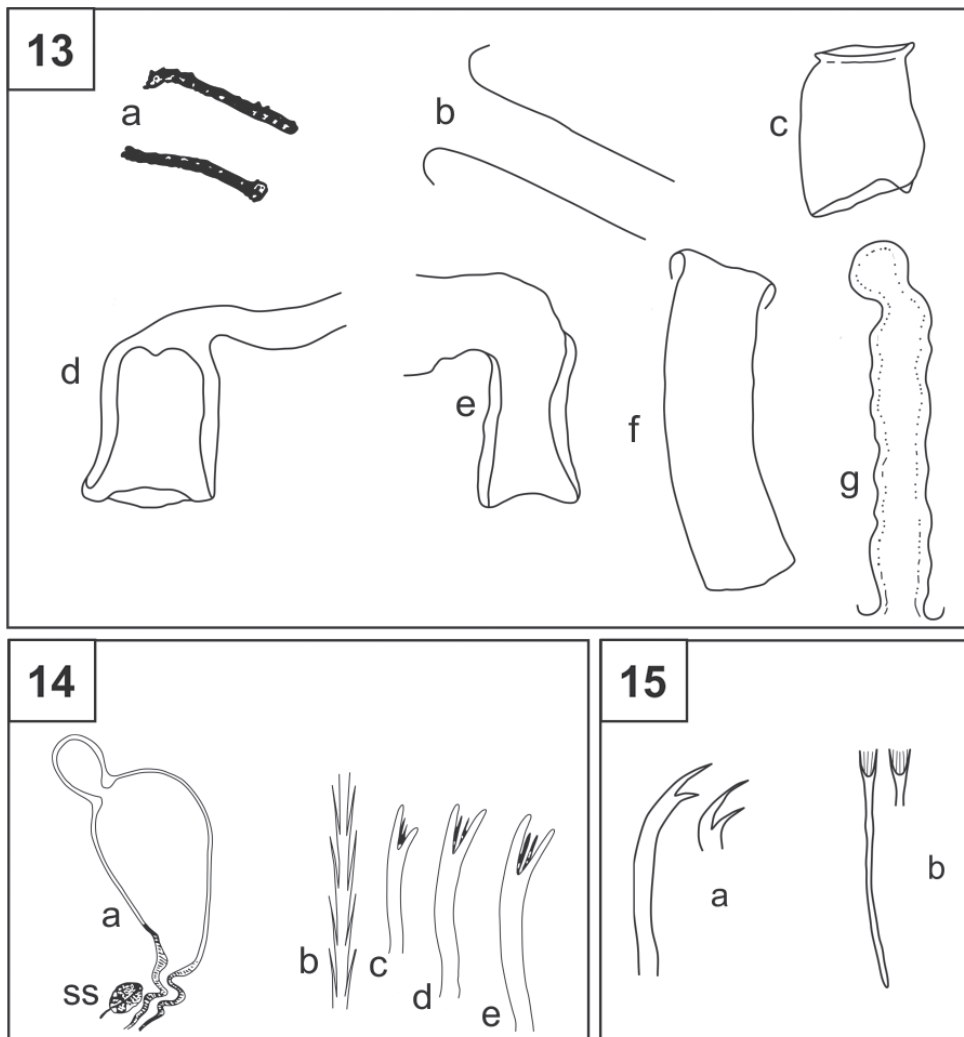


Figure 12. Reconstruction of the genital organs (from sagittal sections) **A** *Haber speciosus* (Hrabč, 1931) **B** *Haber monfalconensis* (Hrabč, 1966) **C** *Haber zavreli* (Hrabč, 1942). Abbreviations on the figure: at – atrium; de – ductus ejaculatorius; ff – femal funnel; mf – male funnel; o – ovary; pa – penial apparatus; pr – prostate gland; pss – penial setal sac; ss – sperm sac; st – spermatheca; sts – spermathecal seta; t – testis; vd – vas deferens. In original paper figure **C** without scale bar. (**A** after Holmquist 1978 **B, C** after Holmquist 1979).



Figures 13–15. **13** Shape of thickened basal membrane **a** *H. speciosus* (after Hrabě 1931) **b** *H. speciosus speciosus* (after Hrabě 1966) **c** *H. speciosus* sensu Brinkhurst (1966) **d** *H. speciosus fluminalis* from USA (after Milligan 1986) **e** *H. speciosus simsi* (after Milligan 1986) **f** *H. zavreli* (after Hrabě 1942) **g** *H. monfalconensis* (after Hrabě 1966) **14** *Haber vetus* (Semernoy, 1982) **a** spermatheca **b** serrated hair seta **c–e** anterior dorsal setae **c** in segment II **d** in segment III **e** in segment V. Abbreviation on figure: ss – spermathecal seta (after Semernoy 1982, modified) **15** *Haber turquinae* (Juguet & Lafont, 1979) shape of setae **a** anterior ventral setae **b** anterior dorsal setae (after Juguet and Lafont 1979).

(Fig. 13f) and 6 : 1 for *H. monfalconensis* (Fig. 13g). On Holmquist’s figures showing reconstructions of genital organs of species representing *H. speciosus* group the shape of the thickened basal membrane is not visible for nominative species (Fig. 12A) whereas their shapes and dimensions are very similar for *H. monfalconensis* and *H. zavreli* (Fig. 12B, C). All mature specimens collected by the authors have almost identical

shape and length of the basal membrane (see Fig. 6) as in the original figure (Fig. 13f) drawn by Hrabě (1942). It is possible that some differences of shape and length of thickened basal membrane depend on the method of material's preservation, which results in various degrees of its shrinking.

In accordance with Martin et al. (2017) and WoRMS the genus *Haber* comprises nine species. The majority of them could be easily distinguished from *H. zavreli* even by the shape of their setae, as illustrated by Milligan (1986) (table 2 in Milligan's paper). It seems that *Haber vetus* (Semernoy, 1982) – described as *Tubifex speciosus vetus* from Lake Baikal (Semernoy 1982) shares some morphological and anatomical features with *H. zavreli*. Both these species have ventral setae with longer upper tooth, the same localisation of spermathecal pores and irregular shape of spermathecal ampullae (Fig. 14a). In addition, both species have the ectal part of vas deferens narrower than atrium. Nevertheless, other features such as: (1) – serrated hair setae (Fig. 14b), (2) – dorsal setae with distinctly longer upper tooth in segment II (Fig. 14c) and with only two intermediate teeth (Fig. 14c–e), (3) – comparatively long ejaculatory duct and ectal duct of spermatheca (both set off gradually from atrium and ampulla, respectively) and (4) – long vas deferens having the same width along its whole length allow distinguishing sexually mature specimens of *H. vetus* from those of *H. zavreli*.

The morphology of anterior setae of the stygobiotic species *H. turquinae* (Fig. 15a, b) resembles that of *H. zavreli*. Although the genital organs of *H. turquinae* were not fully described, different shape of spermatheca, as well as different localisation of spermathecal openings, allow to distinguish these species. Moreover *H. turquinae* is significantly smaller (length 1.3–2.6 mm) than *H. zavreli* (10–12 mm) (Hrabě 1942 and our measurements).

A great part of species belonging to the genus *Haber* is known from restricted areas: *H. amurensis* (Sokolskaya & Hrabě, 1969) – from Far East (Hrabě 1969), *H. dojranensis* (Hrabě, 1958) – Greece and Macedonia, *H. hubsugulensis* (Semernoy, 1972) – Lake Hubsugul (Khuvsgul) in Mongolia (Semernoy and Tomilov 1972) and Lake Baikal (Snmščíkova 1985), *H. pyrenaicus* (Juguet & Giani, 1974) – France/Spain border, *H. svirenkoi* (Lastočkin, 1937) (or *H. swirenkoi* in WoRMS) – lower course of the Dnieper River (Ukraine), including its mouth (Finogenova 1972) and Black Sea (Hrabě 1973), *H. turquinae* (Juguet & Lafont, 1979) – cave waters in the department Ain (France) and *H. vetus* (Semernoy, 1982) – Lake Baikal. All these species were rarely caught.

According to the literature, *H. speciosus* seems to be the only species with a wide distribution. In Europe, this species is mainly known from oligotrophic or mesotrophic water bodies of many countries, from Scandinavian Peninsula (Sloreid 1995; Erséus et al. 2005) to Turkey (Balik et al. 2004; Arslan et al. 2007). It was also found in running waters and tidal freshwater marsh in the eastern part of North America (Milligan 1986). Some data concerning the occurrence of *H. speciosus*, for example in Czech Republic (Schenkova et al. 2010) deal with *H. zavreli* (according to an earlier paper by Hrabě (1981)). Furthermore, up to now, specimens identified as *H. zavreli* have been found only in subterranean waters, either in Slovakia (Hrabě 1942; Šporka 2003), Italy (Dumnicka 1990) or in the Dinaric region (Giani et al. 2011; Martinez-Ansemil et al.

2016), which suggests that it is a stygobiotic species. The species was also mentioned in the checklist of Italian oligochaetes (beside *H. speciosus* and *H. monfalconensis*) (Paoletti and Sambugar 1996) and in the list of subterranean aquatic oligochaetes (des Châtelliers et al. 2009).

Two specimens, probably representing *H. zavreli* were previously found in Poland by Kasprzak (1973) in wells, but these specimens seem to be not fully mature – instead of typical modified penial seta, they had “in XI segment the seta similar to normal bifid somatic seta placed in big glandular sac”. Moreover, the main features of genital organs were not observed, except for the “penial sheath”.

On the basis of all the elements discussed above (including the detailed description of the setal formula and genital organs), *Haber zavreli* can be clearly distinguished from related species. We, therefore, feel justified to revalidate the species.

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